DISSERTATION / DOCTORAL THESIS

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Biodiversity and Landscapes: Where is the missing link?

verfasst von / submitted by

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"A real environment has a hierarchical structure.
That is to say, it is like a checkerboard of habitats,
each square of which has, on closer examination,
its own checkerboard structure of component subhabitats.
And even the tiny squares of these component checkerboards
are revealed as themselves checkerboards, and so on. All
environments have this kind of complexity, but not all have
equal amounts of it."

Robert MacArthur (1972)

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Declaration

I certify that this work contains no material which has been accepted for the award of any other degree or diploma in my name, in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text. In addition, I certify that no part of this work will, in the future, be used in a submission in my name, for any other degree or diploma in any university or other tertiary institution without the prior approval of the University of Vienna. I give consent to this copy of my thesis when deposited in the University Library, being made available for loan and photocopying, in total or in part, on request of other institutions or individuals for the purpose of research. I acknowledge that copyright of published works contained within this thesis resides with the copyright holder(s) of those works. I also give permission for the digital version of my thesis to be made available on the web, via the University's digital research repository.

Abstract

Around 15 years ago, the term ´Anthropocene´ was popularized by Nobel Prize-winning meteorologist Paul J. Crutzen, who described a new era of human induced global environmental change that put an end to the Holocene epoch with beginning of the industrial revolution in the late 18th century. Hence, the adverse consequences of this development regarding global biodiversity pools are manifold either being caused by direct actions such as urbanisation, land transformation and associated land use change among others or insidiously affecting our biosphere by ever-increasing CO_2 emissions.

Accordingly, as a landscape ecologist and conservation biologist my doctoral thesis is dealing with various human induced impacts that affect ecosystem functioning and biodiversity patterns on different spatial scales.

In the first section of this thesis I refer to the ´pattern and process paradigm´ which basically states that landscape structure is always reflecting its underlying processes. As the structural attributes of basic spatial units that constitute a landscape, i.e. landscape elements can be quantified by certain indices, they may in turn being used as a toolset to quantify certain ecological key functions a landscape is able to provide to both, local biodiversity as well as human society. The four associated research articles presented within this first section are addressing i) the development of a rule set to quantify ecological key functions based on landscape structural parameters; ii) major services landscapes are able to provide for human well-being; iii) a comparison if landscape structure is able to landscape service provision throughout protected and unprotected areas and iv) a spatially explicit assessment to estimate landscape service potential. The scientific works listed above have been conducted in a trans-boundary study region around Lake Neusiedl.

In the scientific fields of ecology and nature conservation, one major restraining factor that limits spatially explicit research assessments on broader scales is the availability of comprehensive and recent base datasets. Although advances in remote sensing techniques, data processing and storage capacities have facilitated the emergence of new environmental raw data, the issues of data validation and subsequent post-processing still remain. In the second section of the thesis I present v) the results of a combined approach including spatial data aggregation and harmonization from various sources complemented by additional modelling steps to establish a new habitat distribution map which covers the eastern alps and adjacent regions. This spatially and thematically fine scaled map facilitates application within a broad range of research fields such as ecological modelling and network planning, landscape/ecosystem service provision or invasion biology to name a few.

In the third and final section of my thesis I present four articles in the frame of spatio-temporal assessments in nature conservation. Article vi) presents a spatially explicit study

targeting Emerald Ash Borer invasion risk in Central Europe in the course of changing climate while article vii) outlines climate change impacts within a typical Austrian cultural landscape towards farm profits, landscape appearance and biodiversity. Article viii) focusses on phylogeography and range dynamics of a high mountain Cerastium species endemic to the western Balkan Peninsula and article ix) compares predicted distribution patterns of various plant and insect species between Central European lowlands and the alpine region in view of the disproportional availability of suitable target habitats.

Zusammenfassung

Vor etwa 15 Jahren wurde der Begriff des “Anthropozäns“ immer mehr ins Licht der öffentlichen Wahrnehmung gerückt, allem voran durch den Nobelpreisgewinner Paul J. Crutzen. Hierbei beschreibt das Anthropozän ein neues, das Holozän ablösendes Zeitalter, welches sich grob mit Beginn der industriellen Revolution und den damit beginnenden, und von der Menschheit selbst induzierten Umweltveränderungen globalen Maßstabs datieren lässt. Die negativen Auswirkungen dieser Entwicklung auf unsere Umwelt, und insbesondere wie in dieser Arbeit behandelt, auf die weltweite Artenvielfalt gehen mit dem immer stärker werdenden Grad an Urbanisierung, Industrialisierung, sowie der von der Agrarwirtschaft forcierten Landschaftsumwandlung und Intensivierung von Landnutzung einher. Zudem führen vor allem die im letzten Jahrhundert immer unkontrollierter von Statten gegangenen Treibhausgasemissionen zu einer anthropogen provozierten Klimaveränderung, die bereits jetzt deutliche Auswirkungen zeigt.

Im Rahmen dieser Dissertation beschäftige ich mich aus landschaftsökologischer und naturschutzfachlicher Sicht mit verschiedenen menschlichen Einflussfaktoren die auf ökosystemarer Ebene einwirken und sich folglich in sich verändernden Verteilungsmustern an pflanzlicher und tierischer Artenvielfalt manifestieren.

Im ersten Abschnitt meiner Doktorarbeit beziehe ich mich auf das sogenannte “Muster-Prozess-Paradigma“, worin ausgegangen wird, dass landschaftsstrukturelle Muster immer die vor Ort einwirkenden Prozesse reflektieren. Da sich die Geometrie einzelner Landschaftselemente durch verschiedene mathematische Maße quantifizieren und vergleichen lässt, können diese Indikatoren wiederum dazu verwendet werden um den Grad an ökosystemaren Prozessen, die die Elemente im Stande sind zu erfüllen, abzuleiten. Die vier, in diesem Themenkreis durchgeführten Arbeiten beschäftigen sich im Detail mit i) der Entwicklung eines methodischen Ansatzes um den Grad verschiedener ökosystemarer Kernfunktionen die für den Erhalt von in-situ Biodiversität immanent sind von landschaftsstrukturellen Parametern ableiten zu können; ii) der Entwicklung eines Bezugssystems, das anhand eines kombinierten Ansatzes aus Experteneinschätzung und durch Kartierungen erlangten Parametern eine räumlich extrapolierbare Erfassung von Ökosystemdienstleistungen die eine Landschaft erbringen kann, ermöglicht; iii) eine vergleichende Arbeit der zuvor angeführten Studien; und iv) der Entwicklung einer Methode um auch das Potential von Landschaften in Bezug auf Ökosystemdienstleistungen quantifizieren zu können. Alle, in diesem Abschnitt beschriebenen Studien wurden in einem grenzüberschreitenden Arbeitsgebiet rund um den Neusiedler See durchgeführt.

In den wissenschaftlichen Disziplinen der Ökologie und des Naturschutzes schränken der Mangel an Datenverfügbarkeit bzw. deren Uneinheitlichkeit durch unterschiedliche

Erhebungsmethoden auf unterschiedlichen räumlichen und/oder thematischen Ebenen überregionale Studien oftmals ein. Obwohl durch moderne Fernerkundungstechniken und der Weiterentwicklung an Datenverarbeitungskapazität immer mehr Rohdaten erzeugt werden, bleiben dennoch einige Hürden wie die Datenharmonisierung bestehen. Im zweiten Abschnitt meiner Dissertation präsentiere ich v) eine Studie, in deren Rahmen eine neue, thematisch und räumlich hochauflösende Habitatkarte für die Länder Österreich, Liechtenstein, Schweiz, sowie Südtirol, Bayern und Baden-Württemberg generiert wurde.

Der letzte Abschnitt der Dissertation umfasst vier angewandte Arbeiten die sich mit den Themen der invasionsbiologischen Risikoabschätzung, dem zukünftigen Landnutzungswandel, sowie der räumlich-zeitlichen Modellierung von Artverbreitungsmustern auseinandersetzen. In Artikel vi) findet die in Artikel v) vorgestellte Habitatkarte ihre erste Anwendung, um eine Invasionsrisikoabschätzung des Asiatischen Eschenprachtkäfers für Mitteleuropa durchführen zu können. Artikel vii) beschäftigt sich mit Anpassungsstrategien von Landwirten auf den prognostizierten Klimawandel und deren unterschiedliche Auswirkung auf Landschaftsbild, ökosystemare Funktionen und pflanzliche Biodiversität. Im Zentrum der Artikel viii) und ix) stehen Artverbreitungsmuster, wobei viii) sich im Detail mit der Phylogeographie eines Westbalkanendemiten (*Cerastium dinaricum*) auseinandersetzt und ix) das Gefährdungspotential verschiedener alpiner und nichtalpiner Pflanzen- und Insektenarten in Hinblick auf zukünftige Artverbreitungsmodelle in Kombination mit Habitatverfügbarkeit vergleicht.

Synopsis

This dissertation evolved during my employment at the former Department (now Division) of Conservation Biology, Vegetation Ecology & Landscape Ecology at the University of Vienna.
As the first section of this thesis includes articles resulting from scientific projects in the frame of the Landscape Ecology workgroup, sections two and three include various studies also targeting the fields of Vegetation Ecology and Conservation Biology.
The respective study areas encompass a transboundary Austrian-Hungarian region around Lake Neusiedl; a substantial part of Central Europe including Austria, Switzerland, Liechtenstein, South Tyrol and the German federal states of Bavaria and Baden-Württemberg; the Dinaric mountain region located in the Western Balkans; and a Lower Austrian cultural landscape located between the Danube basin and the Alpine foothills.

Short introduction to the underlying scientific projects

Within the scope of my dissertation I address several aspects in the frame of environmental and human related drivers that affect biodiversity patterns. Thus, assemblage of the various research works was only made possible through participation within several national and international research projects during the years of 2010 – 2015.
The articles summarized in the first section were derived from the projects ´ Biodiversity and Ecosystem Services as scientific foundation for the sustainable implementation of the Redesigned Biosphere Reserve “Neusiedler See”´ (BIOSERV), financed by the Austrian Academy of Sciences and ´TransEcoNet –Landscapes without borders´, financed by the EU´s Central Europe programme.
Within the frame of BIOSERV different possibilities of re-defining and re-designing the first generation Biosphere Reserve Neusiedler See were developed by applying the concept of Ecosystem (i.e. Landscape) Service provision in order to achieve compatibility with the Sevilla Strategy guidelines.
TransEcoNet aimed at investigating transnational ecological networks across Central Europe by following an interdisciplinary approach which integrated research from Landscape Ecology, Nature Conservation, Regional Development, Cultural Sciences and History. The project focussed on the analysis and comparison of protected and unprotected landscapes regarding ecological connectivity, landscape history and Landscape Service provision on different spatial scales, ranging from local case studies towards supra-regional assessments.
Articles v) and ix) resulted from research activities within the frame of the project ´Climate change driven species migration, conservation networks, and possible adaptation strategies´ (SPEC-ADAPT). This still running research project is dealing with species´ range dynamics

caused by changing climate and the role of nature conservation networks to mitigate potential range losses. It received funding from the Austrian Climate Research Program.

Article vii) was prepared in the frame of ´Analysing climate change mitigation and adaptation strategies for sustainable rural land use and landscape developments in Austria´ (CC-ILA) and has been financed by the Austrian Academy of Sciences. There, a data-model-policy concept was elaborated to test cost-effective mitigation and adaptation strategies for farmers and sustainable landscape development in the context of climate, market, and policy instrument changes.

Last, article viii) resulted from the project ´Evolution, biodiversity and conservation of indigenous plant species of the Balkan Peninsula´ (BALKBIODIV) which received funding by the SEE-ERA.NET PLUS scheme. This project focussed on molecular analysis on ploidy-levels among several endangered plant species native to the Western Balkan region in order to gain knowledge on intraspecific diversity and sympatric speciation which are at least with-causing the high levels of biodiversity in the area.

– Introduction to Section A –

Assessment of Ecological Key Functions affecting Biodiversity and Human Well-Being

In this first section of my doctoral thesis I present four thematically linked articles that are dealing with the overall topic of service provision and functional capacity that landscapes are able to provide for both, the natural environment as well as for mankind. At this, the first article (i) introduces the readership to a concept that relates geometrical aspects of landscape elements (i.e. landscape structure) to their inherent capacity for the fulfilment of ecological key functions such as habitat provision, connectivity or permeability to foster species migration and dispersal among the landscape. The assessment is loosely based on the matrix-patch-corridor model (Forman, 1995) and can be adapted for various species groups or guilds, provided that respective trait information is available. As numerous research studies focussed to unravel the underlying drivers and processes behind species´ demography patterns such as e.g. population dynamics, there is a broad consensus that habitat loss and fragmentation are critically contributing to local extinctions, as habitat loss reduces the carrying capacity and fragmentation additionally aggravates dispersal and gene flow within landscapes of interest. Such developments are thus leading to a decrease in species numbers and genetic variability within local populations (Baguette et al., 2013). As the composition of various land use/cover (LUC) classes throughout a certain target landscape in conjunction with their structural attributes (i.e. configuration) are affecting population dynamics (Noss, 1990) and latter are in turn influencing biodiversity patterns (Walz & Syrbe, 2013), a close relationship between different levels of species and structural diversity exists. Thereby, human induced impacts on the landscape do not equally affect all organismic groups. For example, alteration of the landscape configuration (e.g. by land use intensification) which is causing a decrease in geometrical complexity across agricultural landscapes (Wrbka et al., 2004) has been identified even more detrimental for plant biodiversity while changes in landscape composition (e.g. by land transformation) are particularly detrimental for mammal and bird diversity (Uuema et al., 2013). In this regard, we aimed to consider both aspects of composition and configuration within article (i) by assigning single LUC classes to functional groups first and then quantifying group-related ecological key functions by structural indices. In order to comprehensively measure the ecological state of our target landscape, we tested our study design for a pre-defined virtual umbrella species, serving as a surrogate for disturbance sensitivity. The outcomes of this study can be explicitly visualized on the level of single landscape elements within tested target sites but were also extrapolated to compare the functional state of larger geomorphological entities. Further, the assessment is easily repeatable in condition on the availability of recent base data and thus it would serve suitable for monitoring purposes. In this relation, the indicator of structural based landscape functionality fulfils three main functions of indicators as mentioned by Walz 2015: (a) illustrating the status quo and thus serving as a communication tool for stakeholders; (b) being applicable as a monitoring tool; and (c) identifying areas where action is needed to set appropriate planning measures.

Although Lausch et al. 2015 state that extrapolation of results stemming from spatially explicit analyses of landscape sections only are limited in terms of general relevance, we tried to overcome this issue by the use of a random stratified sampling design within a well-elaborated spatial reference framework in order to select a statistically robust number of most representative sites across our study region. Other concerns listed by Lausch et al. 2015 according scale and thematically and/or spatially insufficient delineation of landscape elements and their borders can be ruled out in case of this study, as we applied a rather extensive list, consisting of 52 different LUC classes and a horizontal resolution of 1m for landscape metric evaluation. As the investigated study region consists of both, areas of agricultural use sharing distinct boundaries that are partly intermingled by remnants of (semi)natural habitats on the one side and larger near-natural dry and wet steppic grasslands, wetlands and forests on the other side, the meaningfulness of a gradient analysis of the latter mentioned habitats cannot be denied (cf. Lausch et al., 2015). However, we chose the landscape-element based approach for the sake of flexibility in analysis of landscape patterns and the ability for clear assignment of ecological key functions to certain LUC classes after literature review. At this, we developed a general and applicable assessment to quantify landscape functionality that is adaptable for various European cultural landscapes. If a more refined delineation is demanded in order to account for the particular fulfilment of certain ecological processes across larger patches or matrix elements, plant community analysis within the target patch may be one option, as plants serve well as ecological indicators (Niemi & McDonald, 2004; Sauberer et al., 2004). Additionally, upcoming research potential definitely lies in the development of combined assessments of gradient and element-specific landscape analysis.

Land use regimes and associated processes of intensification and transformation throughout cultural landscapes are not only altering ecological state and affecting biodiversity pools on various spatial levels but also impacting ecosystem service provision for the society (Haines-Young, 2009). Additionally, underlying feedback mechanisms that have been triggered by human induced global change processes which in turn affect biodiversity and thus also ecosystem services, indirectly fall back to society as well (Chapin et al., 2000). For example, the processes of habitat fragmentation in conjunction with ongoing climate change are causing a so called “deadly anthropogenic cocktail” for biodiversity as outlined by Travis

2003. On the other hand, as biodiversity loss leads to enhanced vulnerability within the remaining species pool (Duffy, 2003) it concurrently facilitates the invasion of non-native taxa (e.g. Hermoso et al., 2011; Alofs & Fowler, 2013). This, in turn, has a negative impact on both, in-situ biodiversity and society in terms of diminished capacity in ecosystem service provision (Vilá et al. 2011). Hence, there is a growing need for spatially explicit assessments and monitoring schemes to quantify a possibly broad range of ecosystem services. Article (ii) presented within this doctoral thesis is tackling this subject by introducing a refined approach of ecosystem service mapping on local (i.e. landscape element) level and corresponding upscaling towards a regional assessment of service supply. The survey aims at quantifying 25 different services which are sectioned by the main groups of “habitat”, “regulation”, “information”, “provision” and “carrier”. As it would not be reasonable to measure all single services at local level (full list of services included in Table 1 within article (ii)), some have been quantified on higher spatial level and subsequently combined with the remaining set by the use of an integrative framework. It is also important to mention that we used the term “landscape services” instead of “ecosystem services” under reference to Termorshuizen & Opdam, (2009). The underlying classification scheme of services applied within this current study is based on de Groot (2006) while the capacity matrix which indicates for the degree of service provision of certain habitat types (classified from “0” [no relevant capacity] to “5” [very high relevant capacity]) is adapted from Burkhard et al. (2009). Additionally we introduced a set of qualifiers for the refinement of capacity values that have been mapped throughout a field campaign on landscape-element basis. The major criticism on such expert-knowledge driven assessments centres on the fact that assignment of capacity values are always somehow with-depending on the expert´s personal thoughts and opinions. Therefore, we tried counteract this issue by introducing additional field qualifiers within the landscape-element specific service evaluation and further used demographic and spatial (remote sensing) data for the evaluation of services at the regional level. In order to quantify multifunctional aspects provided by the investigated landscape, different approaches and data sources are required (Gulickx et al., 2013). However, some open issues still remain unsolved such as the fact that provision of certain services simultaneously acts on various spatial scales. The same is true for temporal and spatial influence on service provision. Hence, our study rather tackles the status quo within the landscape of interest than being able to identify the spatiotemporal drivers which are responsible for the dynamics within service provision. Nonetheless, our assessment facilitated the comparison and visualization of service provision throughout various landscapes. At this, aggregation of single service values towards the aforementioned main service groups and according visualization by the use of spider-web diagrams helped to transport the outcomes of our assessment more concisely and further illustrated trade-offs between the sections of the study region as well as between the single service groups (cf. Querioz et al., 2015). Moreover we could identify hot and cold spots of service provision which might serve as a useful basis for upcoming planning decisions. The establishment of a capacity matrix by expert knowledge is still one of the most popular tools for ecosystem service assessments, mainly due to its adaptability in different study regions, technical simplicity, and descriptiveness in terms of spatial explicit visualization of outcomes (Jacobs et al., 2015). Although this technique has recently attracted criticism in terms of being thematically too vague and relying on subjective perspectives of so called “experts” only, these issues can be resolved by either applying fine scaled base-data which is complemented by qualifiers and other empiric data sources as already conducted within the presented study, plus additional tests on model confidence, reliability and validation as suggested by Jacobs et al., (2015).

Although ecosystem services are usually emphasizing on human well-being, they may also act as indirect measure of biodiversity as Cardinale et al. (2012) revealed a strong interconnectedness between the magnitude of “provision” and “regulation” services and biodiversity. In this concern landscape connectivity appears to be a key point interlinking these aspects, as for many ecosystem services the degree of connectivity across the landscape of interest is directly or at least indirectly affecting the magnitude of service provision, e.g. the effectiveness of pollination and pest regulation as well as water regulation and the flow of nutrients amongst others (Mitchell et al., 2013). As the state of connectivity has also been considered as a decisive factor influencing the state of landscape functionality (see also article (i)) we evaluated the relationship between structure based landscape functionality and ecosystem service assessment. Here, the underlying hypothesis that structural landscape patterns, which are recapitulating “frozen” ecosystem processes (Wrbka et al. 2004) and thus serving as basic variables for the evaluation on landscape functionality, are concurrently determinants of various ecosystem services (Syrbe & Walz, 2012).

In article (iii) we examined this relationship by regressing outcomes of the landscape service mapping campaign (please refer to article (ii)) with the results obtained from the assessment of structural functionality. This study was made possible as both assessments had been conducted within the same field sampling sites and were both based on the spatial unit of landscape elements. However, we could not include the landscape main service groups “carrier” and “information” within this study as the service providing units were defined on a broader (i.e. regional) spatial scale. In particular, we found strong links between levels of metric driven landscape functionality and the “habitat”, “provision” and “regulation” main landscape service outcomes. The results within article (iii) are thus underpinning the findings of Frank et al. (2012) who argue that the use of landscape metrics would considerably help to further improve actual ecosystem service assessment frameworks.

As already stated, the multi-functionality of landscapes has been measured in view of different aspects, either intrinsically towards the natural environment with special reference towards biodiversity and on the other hand towards society. Recent studies even went one step further by accounting for supply as well as demand of particular ecosystem services and thus enabling the development of so called ecosystem service footprints which are aiming to identify mismatches in the course of unsustainable exploitation of ecosystem services (Burkhard et al., 2012). The underlying drivers causing such imbalances in service provision are particularly associated with societal needs and expectations, regardless of whether the sustainable supply of certain services is provided or not (Paetzold et al., 2010).
On the contrary, the ecosystem service potential a pristine landscape could possibly provide has remained recently underresearched, although the basic concept of “landscape potential” already originated in the beginning second half of the 20th century (cf. Bobek & Schmithüsen, 1949). In this regard, article (iv) presented in this frame deals with the issue of how to deduce the potential service supply a landscape would possibly able to contribute. Thereof we are able to compare actual service supply rates (please refer to article (ii)) with the landscape´s potential in order to estimate if e.g. particular services are already overexploited.
The main challenge of how to grasp knowledge on landscape service potential is owed to the fact that pristine landscapes more or less entirely vanished throughout the whole of Europe, apart from small remnants of natural forest stands (Schnitzler, 2014) and some upper alpine and nival ecosystems. Especially within our study region we were lacking on reference information as almost no fractions that would represent the environment´s natural state have been left, apart from the reed bed surrounding Lake Neusiedl. To overcome this issue we first had to model so called ´constructed vegetation types´ (CVT) on a spatial explicit basis across the study area. Basic information on the CVTs was derived from rather coarse maps illustrating potential natural vegetation in the broader region which have subsequently been refined by geomorphological attributes specifically representing suitable site conditions for the according vegetation types. Thus, we could apply capacity matrix values for the designated CVTs and extrapolate potential landscape service values which consequently enabled us for a comparison with former results gained from the assessment of actual landscape service provision.

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Section A - *Assessment of Ecological Key Functions affecting Biodiversity and Human Well-Being*

Article 1 (i)

Kuttner, M., Hainz-Renetzeder, C., Hermann, A., Wrbka, T. 2013. *Borders without barriers – Structural functionality and green infrastructure in the Austrian-Hungarian transboundary region of Lake Neusiedl*. Ecological Indicators, 31, 59-72.

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Borders without barriers – Structural functionality and green infrastructure in the Austrian–Hungarian transboundary region of Lake Neusiedl

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Ecoprofile

ABSTRACT

Many ongoing processes in today's landscapes impact our environment considerably. Thus, it is enormously important to gather information on qualitative characteristics of our landscapes in order to effectively counteract the negative developments. Structural functionality as proxy for the assessment of habitat quality and species patterns has already proven potential to successfully describe ecological values. Completed by the measurement of green infrastructure information for a defined profile of a functional trait, a rapid and rough assessment of the qualitative state of habitats seems feasible. We therefore present in this study (i) an assessment of structural functionality based on the statistical analysis of landscape metrics, (ii) the measurement of green infrastructure and travelling costs for the ecoprofile of a Disturbance Sensitive Species Group (DSG) and (iii) an investigation if functionality and green infrastructure change between different types of landscapes and protection status. In the Lake Neusiedl region we selected 41 landscape samples based on a stratified random process. Based on orthophoto interpretation, we calculated landscape metrics with FRAGSTATS and reduced them to a core set of 13 indices by combining statistical results with literature review. Their relation to main ecological processes determined if the individual metric related positively or negatively with the land cover category and structural functionality was given by the average value of the landscape metrics. Green infrastructure elements were allocated with GUIDOS, whereas the travelling costs to move between them was also considered. Landscape elements of valuable matrix and connecting corridors ranked highest in structural functionality based on the calculated landscape indices but showed large differences between different land use regimes. Correlation and regression analysis confirmed the dependence of green infrastructure elements (corr. $r^2 = 0.877$) as well as travelling costs (corr. $r^2 = 0.669$) to functionality values. Protection status of the landscape samples proved to be a determining factor because functionality values as well as green infrastructure differed significantly (both with a p-value < 0.05) with the exception of dissecting corridors, stepping stones and travelling costs. We conclude that one simple guideline for a holistic assessment of structural functionality is hardly reachable but we did set up a comprehensive rule set. Based on a transparent sampling procedure, a qualitative assessment of habitats and landscapes can easily be conducted. The complementary use of an ecoprofile enables the valuation of green infrastructure elements and the identification of major driving forces along with scenario development for sustainable landscape planning.

1. Introduction

Processes like urbanisation, industrialisation, large-scale land transformation, and climate change put our landscapes at risk (Millennium Ecosystem Assessment, 2003). These dangers have induced a notable loss of habitats and therewith biodiversity. But the functioning of landscapes is essential for the provision of ecosystem services and affects human well-being enormously (Hermann et al., 2011; Millennium Ecosystem Assessment, 2003). Science, society and politics have realised the need to assess the impact of broad-scale changes in our environment and reacted with efforts in research and political will to counteract these developments with the implementation of a European-wide network on protected areas (Council of the European Union, 1992), agreements on halting the loss of biodiversity (European Commission, 2011) or the European Landscape Convention (Council of Europe, 2000) amongst others. All these conventions and strategies aim at

Abbreviations: LFT, landform type; GI, green infrastructure; DSG, Disturbance Sensitive Species Group; MSPA, Morphological Spatial Pattern Analysis.

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preserving the values of the landscapes and the habitats and species they are including.

The central role of structural characteristics for the assessment of ecological quality per se and in particular the viability of site-based biodiversity was demonstrated in a series of studies (a.o. Bierwagen, 2007; Moser et al., 2002; Pascual-Hortal and Saura, 2008; Torras et al., 2009; Vos et al., 2001). Especially in cultural landscapes it is essential to evaluate the qualitative state of remnant (semi)-natural areas along with the prevailing agrarian matrix in order to outline the major structural driving forces behind eco-functional issues like the support of local/regional biodiversity (Walz, 2011). Turner et al. (2001) stressed the importance of the spatial configuration of landscape elements, and thus landscape functionality. This can be exemplified with intensive farming activities leading to geometrisation (Forman, 1995; Turner et al., 2001) which severely decreases the complexity of boundaries within landscapes, resulting in increased compactness of the affected landscape elements (Forman, 1995). As these processes are altering structural landscape complexity as such, often resulting in simplified landscape patterns, highly structured natural and semi-natural remnant areas are more and more facing decline (Mander et al., 1999; Wrbka et al., 2008) which in turn determines species diversity patterns (Eriksson et al., 2002; Moser et al., 2002). In the last decades, landscape structure has been very often topic of scientific literature and yielded in a high amount of papers. The use of landscape metrics computed with software packages like Fragstats 3.3 (McGarigal et al., 2002) aims at the analysis of landscape patterns, ideally in relation to their function (Forman and Godron, 1986). Many studies stress the importance of the statistical analysis of these landscape metrics in order to avoid correlations and redundancies and to distill the most meaningful indices (Bender et al., 2003; Bennett, 1998; Cushman et al., 2008; Fahrig, 2003; Richards et al., 2002; Tischendorf, 2001; van Lier, 1998; With et al., 1997). The main determining fundamentals in view of landscape composition and configuration, hence strongly influencing functional integrity as such (Botequilha Leitão and Ahern, 2002), need to be comprehensively examined and base the final selection of the metrics for further analysis of landscape functionality.

Opdam et al. (2008) stressed the point, that ecosystem type, quality area and connectivity are the main determinants for the distribution of species on the landscape level. They therefore suggested designing an “ecoprofile” for a certain target species group in order to allow for a measurement and planning tool for the spatial configuration of the landscape in question. Such a design is based on generalised ecological traits of species demanding for an ecosystem network which persists on the regional scale. With this concept, it is possible to measure the green infrastructures (Benedict and McMahon, 2002) and count the costs and effort to move between these structures as it targets the most important spatial characteristics of ecosystems. Functionally, such a network should serve as physical linkage between habitat patches within a landscape (Freemark et al., 2002) which is structurally specified by quality-determining factors like width and connectivity (Forman, 1995). This research topic also includes further investigating the role of protected areas in regards to landscape functionality and green infrastructure. Landscapes are generally protected because they exhibit a higher biodiversity or better ecosystem functioning. As such, one would assume that also functionality ranges higher and more networks are provided.

In this study we therefore tested (i) how landscape functionality can be analysed with landscape metrics, which allows to differentiate between Land Use/Cover Classes (LUCC) of different ecological functions. Additionally, we (ii) quantified green infrastructure (GI) for a predefined ecoprofile of Disturbance Sensitive Species Group (DSG) and their efforts crossing landscapes based on a cost surface model. At last, we (iii) tested the hypothesis if values of (i) and (ii) differed significantly between protected and unprotected landscape samples.

2. Materials and methods

2.1. Study area and sampling design

The trans-frontier region of Lake Neusiedl is part of the Small Hungarian Plain in Central Europe, representing the westernmost extension of the Pannonian Basin. Although its origin can be traced to tectonic movements in the mid-Tertiary, the final shape of the landscape relates to the late Quaternary, when Tertiary sediments were partly covered by clay, sand and loess deposits during the glacial periods. The region is characterised by a hot, dry Pannonian climate with an annual precipitation of 600–700 mm and annual mean temperature of >9 °C (ZAMG, 2002). It is dominated by the Lake Neusiedl itself which lies in a flat basin bordered by uplands to the west and a series of small satellite waters on the eastern part called ‘Seewinkel’ which together constitute the westernmost alkali lakes in Europe. The southern Hungarian part (Fertö) mainly consists of lowlands with gentle hills on the western side. The northern Austrian part shares contrasting western and eastern sides: the former is formed by the pronounced slope zone of a low mountain ridge, whereas the latter represents the lowest region in Austria with an altitude of about 115–125 m a.s.l. Adjacent to the lake, a semi-natural zone still forms Europe’s second largest reed–wetland complex (Schmidt and Csaplovics, 2010), serving as internationally important sanctuary for migrating, wintering and breeding waterbird species (Steiner and Parz-Gollner, 2003). Beyond the wetlands the area is still extremely rich in habitats, from the unique dry alkaline steppe up to closed deciduous forests a series of different vegetation types with plants and animals of Alpine, Asiatic and Mediterranean biogeographic region, as well as northern species are present are leading to high overall biodiversity in the study region. Due to its bio-cultural richness parts of the study area are labelled by various nationally and internationally protected areas, including the national parks in Austria and Hungary, Ramsar sites, Biosphere reserves and NATURA 2000 sites. Additionally in 2001, the whole region of Lake Neusiedl/Fertö was designated as an UNESCO World Heritage Site.

The study region incorporates seven landform types (LFT; Konkoly-Gyuró et al., 2010) stretching over an area of >2000 km^2 (Fig. 1). These LFTs represent the main geomorphological features of the study area: ‘Lake Basin’ (LFT 1), ‘Marshlands’ (LFT 2), ‘River Floodplains’ (LFT 3), ‘Low lying terrace’ (LFT 4), ‘Elevated terrace’ (LFT 5), ‘Hilly area and hill range’ (LFT 7) and ‘Low and middle range mountains’ (LFT 8). In a stratified selection process (Appendix A), we randomly selected three protected and three unprotected 2 km × 2 km samples in each LFT based on the regular raster of the European Grid system (INSPIRE, 2009). In all, the region was covered by 41 landscape samples thereof 15 were located in Hungary and 26 in Austria. This distribution pattern of sample sites resulted from single LFT proportions over the entire transnational investigation area, without considering a country-wise designation of sites.

2.2. Methods

The methodological implementation involved a series of sequential steps (Fig. 2). In principle, the main steps are (i) segmentation and interpretation of land cover, (ii) calculation of landscape functionality through statistical analysis of landscape metrics, (iii) defining an ecological profile for a DSG and (iv) allocating GI on basis of Morphological Spatial Pattern Analysis (MSPA) and cost surface analysis.

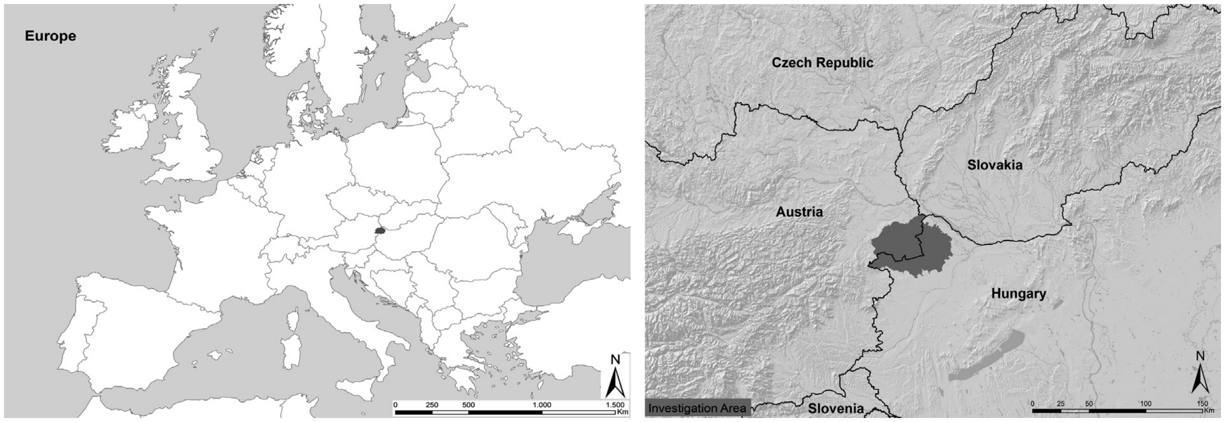

Fig. 1. Overview of the study area, located in a transboundary region in the east of Austria and western Hungary.

2.2.1. Segmentation and interpretation of land cover

The first step was to delineate landscape elements within the samples by an Object-Based Image Analysis (OBIA). This step was carried out in eCognition Developer 8 (Definiens AG, 2009a,b) by taking orthophotos as the operational base data. The OBIA resulted in quite properly segmented layers and hence quickened further interpretation work as it already delivered distinct segments. Still, especially in the agricultural landscapes, additional correction of the segments had to be done manually in ArcGIS 9.3 (ESRI, 2008), whereas in more forested landscapes OBIA provided rather good results. Land Use/Cover Classes (LUCC) were based on the hierarchy of CORINE (Co-Ordination of Information on the Environment) land cover 2000 (CLC 2000) with a few adaptions to local conditions made on the fourth and fifth level, all in all resulting in 52 different categories (Table 1). A minimum mappable unit (MMU) of 100 m^2 was set for all single landscape elements, except for hedgerows, tree-dominated fallow lands and woods where a MMU of 250 m^2 seemed more appropriate. In case of hedgerows, an additional maximum width, not exceeding 15 m was further applied. Important artificial centres of reference like small huts, wells or other control points superficially not exceeding 100 m^2 were also mapped as discrete entities.

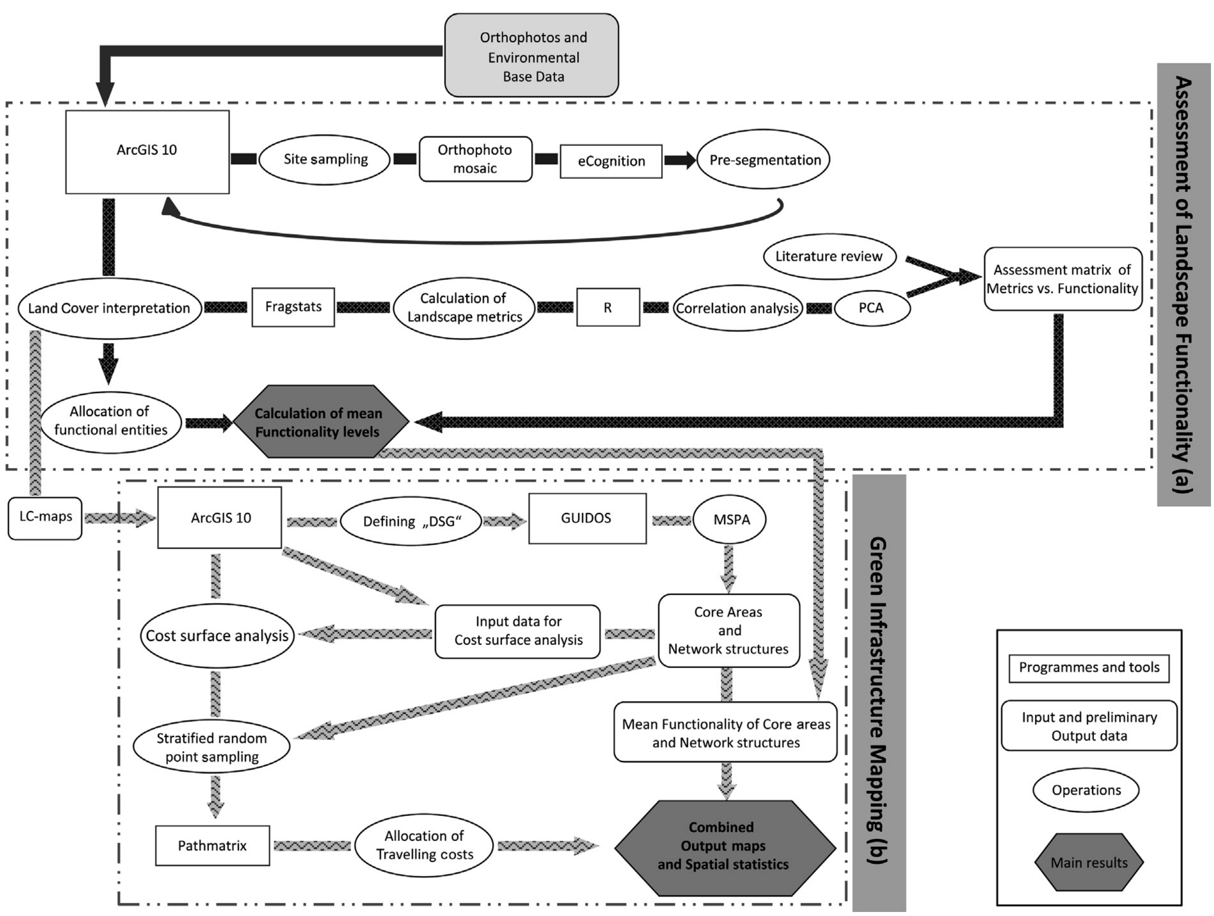

Fig. 2. Flow chart providing an overview of the methodological steps implemented in the framework of this study. The chart consists of two interrelated sections, pointing out for (a) assessment of landscape functionality and (b) green infrastructure mapping.

Table 1
Definition table including all identified LUCC classes, their relation to a Functional group; Habitat suitability status for the DSG and defined Dispersal costs.

LUCC classes based on CORINE Land Cover (CLC) categories	CLC code	Functional group	DSG suitability	Dispersal costs
Residential discontinuous urban fabric	1.1.2.1.	Artificial matrix	Non-habitat	10
Residential discontinuous sparse urban fabric	1.1.2.2.	Artificial matrix	Non-habitat	9
Single building	1.1.2.3.	Artificial matrix	Non-habitat	10
Industrial, commercial, public units, mainly sealed	1.2.1.1.	Artificial matrix	Non-habitat	10
Industrial, commercial, public units, partly sealed	1.2.1.2.	Artificial matrix	Non-habitat	9
Fast transit roads	1.2.2.1.	Dissecting corridor	Non-habitat	10
Main roads	1.2.2.2.1.	Dissecting corridor	Non-habitat	9
Side road, tarmaced	1.2.2.2.2.	Dissecting corridor	Non-habitat	8
Waterbound driveway	1.2.2.2.3.	Dissecting corridor	Non-habitat	7
Non-waterbound driveway	1.2.2.2.4.	Dissecting corridor	Non-habitat	6
Railways	1.2.2.3.	Dissecting corridor	Non-habitat	7
Mineral extraction sites	1.3.1.	Stepping stone	Non-habitat	3
Dump sites	1.3.2.	Artificial matrix	Non-habitat	7
Construction sites	1.3.3.	Artificial matrix	Non-habitat	7
Other green, man-made areas	1.4.1.3.	Disturbed matrix	Non-habitat	5
Other sport- and leisure facilities, sealed	1.4.2.1.2.	Artificial matrix	Non-habitat	9
Other sport- and leisure facilities, not sealed	1.4.2.1.3.	Artificial matrix	Non-habitat	8
Garden Plot	1.4.2.2.1.	Disturbed matrix	Non-habitat	8
Parks outside of town	1.4.2.2.2.	Stepping stone	Non-habitat	1
Arable land	2.1.1.1.	Disturbed matrix	Non-habitat	7
Garden and market gardening	2.1.1.2.	Disturbed matrix	Non-habitat	7
Foil tunnel- and greenhouse gardening	2.1.1.3.	Artificial matrix	Non-habitat	9
Vineyards	2.2.1.	Disturbed matrix	Non-habitat	6
Fruit tree meadows	2.2.2.1.	Valuable matrix	Habitat	3
Orchard	2.2.2.2.	Disturbed matrix	Non-habitat	5
Other fruit trees and berry plantations	2.2.2.3.	Disturbed matrix	Non-habitat	6
Meadows	2.3.1.1.	Valuable matrix	Non-habitat	5
Permanent pastures	2.3.1.2.	Valuable matrix	Habitat	4
Heterogeneous agricultural areas	2.4.	Disturbed matrix	Non-habitat	6
Bosk, grove	2.4.3.1.	Stepping stone	Habitat	1
Treerow	2.4.3.2.	Connecting Corridor	Non-habitat	3
Hedge with distinct proportion of trees	2.4.3.3.	Connecting Corridor	Habitat	1
Hedge	2.4.3.4.	Connecting Corridor	Habitat	1
Agro-forestry areas	2.4.4.	Disturbed matrix	Non-habitat	2
Baulks	2.4.5.1.	Connecting Corridor	Habitat	5
Broad-leaved forests	3.1.1.	Valuable matrix	Habitat	1
Black Locust forest	3.1.1.1.	Disturbed matrix	Non-habitat	2
Coniferous forests	3.1.2.	Valuable matrix	Habitat	2
Mixed forests	3.1.3.	Valuable matrix	Habitat	1
Natural grassland	3.2.1.	Valuable matrix	Habitat	4
Transitional woodland shrub	3.2.4.	Valuable matrix	Habitat	1
Beaches, dunes and sand plains	3.3.1.	Valuable matrix	Habitat	4
Bare rock	3.3.2.	Valuable matrix	Non-habitat	5
Sparely vegetated areas	3.3.3.	Stepping stone	Habitat	5
Burnt areas	3.3.4.	Disturbed matrix	Non-habitat	6
Fallow land	3.4.1.	Disturbed matrix	Non-habitat	5
Fallow land, high share of shrubs	3.4.2.	Stepping stone	Habitat	4
Fallow land, high share of wooden plants	3.4.3.	Stepping stone	Habitat	3
Inland marshes	4.1.1.1.	Stepping stone	Habitat	5
Artificial water courses (canals/ditches)	5.1.1.2.	Connecting Corridor	Non-habitat	6
Natural standing waterbodies	5.1.2.1.	Valuable matrix	Habitat	3
Artificial reservoirs	5.1.2.2.	Stepping stone	Habitat	6

2.2.2. Landscape functionality

For the resulting LUCC maps, landscape indices on patch and class level were calculated in Fragstats 3.3. (McGarigal et al., 2002). Starting with 46 different class metrics (Appendix B), a correlation analysis in R 2.7.1. (R Development Core Team, 2008) with the function "cor" and Kendall–Tau method was performed to sort out all highly correlated indices (correlation coefficients of ± 0.8) leading to a remaining set of 21 metrics (see also Tischendorf, 2001). These were log- or squareroot-transformed except from Aggregation Index (AI) and *Contiguity Index* (CONTIG), where an arcsine squareroot transformation was applied (McCune and Grace, 2002) in order to approximate Gaussian distribution.

The landscape metrics of the different LUCC were pooled into six functionality groups (Table 1): [1] *connecting corridors* including water courses, hedgerows, line of trees and baulks; [2] *dissecting corridors* such as roads and railways; [3] *valuable matrix* consisting of categories considered to be of a certain conservation value like extensively managed grasslands, forests, bogs or other semi-natural habitats; [4] *disturbed matrix* including elements which are highly anthropogenic influenced, e.g. arable land, orchards, vineyards or planted black locust forests; [5] *artificial matrix* dominated by sealed surfaces like urban areas and associated classes and [6] *stepping stones* where categories are included which can serve as proxy- or transitional habitats like partly abandoned extraction sites, fallow land, vegetated cemeteries or parks.

For each of the functionality groups, a principal component analysis (PCA) was performed on the 21 remaining indices using the function "principal" taken from the library "psych" (Revelle, 2011) with Varimax rotation.

Based on the statistical results and supported by literature review (Fahrig, 2003; Tischendorf, 2001; Bennett, 1998; van Lier, 1998; Richards et al., 2002; With et al., 1997; Bender et al., 2003), an assessment matrix with the final selection of 13 landscape metrics was set up (Table 2). The main determining fundamentals in view of landscape composition and configuration, hence strongly influencing functional integrity as such, are comprehensively examined by

Table 2
Assessment matrix indicating the relationship of the functionality groups to selected landscape metrics. A positive relation (+) indicates increasing metric values lead to increasing functionality while a negative relation (−) increasing metric values induce decreasing functionality.

Landscape metrics	Connecting corridors	Dissecting corridors	Valuable matrix	Disturbed matrix	Artificial matrix	Stepping stones
Aggregation index (AI)			+	−		
Mean patch area (AREA_MN)	+	−	+	−		+
Total (Class) area (CA)	+	−	+	−	−	+
Connectance index (CONNECT)	+	−				+
Mean contiguity index (CONTIG_MN)			+	−	−	+
Mean core area (CORE_MN)			+	−	−	
Area weighted mean Euclidean nearest-neighbour distance (ENN_AM)	−	+	−	+	+	−
Mean fractal dimension index (FRAC_MN)	+	−		+	−	
Largest patch index (LPI)		−	+			
Landscape shape index (LSI)	+	−			−	+
Patch density (PD)	+	−			−	+
Mean proximity index (PROX_MN)	+	−	+	−	−	+
Area weighted mean shape index (SHAPE_AM)	+		+	+	−	+

this classification system. The final selection of the metrics is supported by the findings of Cushman et al. (2008) who investigated strength, universality and consistency of diverse class-level metrics. 9 out of 13 metrics selected in the framework of our study were already tested highly significant regarding expressiveness and universal applicability. Additionally for metric *Mean Proximity* (PROX_MN) Schindler et al. (2008) revealed a high amount of expressiveness according to interpatch-distance/fragmentation measurement. The assessment matrix related the influence of landscape metrics on each functionality group as positive, negative or non-existent. All transformed values of the indices were normalised to the range of 0–100 for positive related indices and 100–0 for negative related ones. The functionality of the landscape elements were finally calculated as the mean of all normalised indices of the respective functionality group to which the element belonged to. For areal statistics, we classified the mean functionality values into five functionality classes based on an equal interval classification of 20% break-values for each functionality group in SPSS 16 (SPSS Inc., 2007). For overall functionality per landscape sample, the mean was calculated of all landscape functionality values per km^2.

2.2.3. Disturbance Sensitive Species Group (DSG)

The concept of ecoprofile was based on Opdam et al. (2008). We wanted to design the profile for a species group subtle to the general qualitative state of agricultural landscapes, therefore sensitive to regular disturbance. This Disturbance sensitive Group (DSG) was supposed to be sensitive to transformed and degraded agricultural LUCC and artificial areas. Hence, only remnants of natural and semi-natural areas would serve as viable habitat (Ferrier, 2002) irrespective of open- or woodland-dominated categories. Our method loosely followed the concept of 'ecologically scaled landscape indices' presented in Vos et al. (2001) but focused more on the general qualitative state of entire landscapes than predicting the viability of distinct (meta)populations. The different LUCC were classified as *Habitat* and *Non-Habitat* according to the DSG (Table 1). The selection criteria for habitat suitability of the single land cover types were again based on expert judgement and literature (Ferrier, 2002; Koellner and Scholz, 2008). Altogether 18 out of 52 land cover classes seemed suitable for the DSG, specifically including e.g. natural forests and grasslands, hedges, orchards, fallow lands and areas influenced by (ground)water. Additional information on the permeability of the landscape regarding to the DSG was needed, ranging from easily crossable (semi)natural LUCC to man-made infrastructures like heavily frequented roads or buildings which hinder movement almost completely (Adriaensen et al., 2003). It was also assumed that the DSG would incur higher risks by moving through open landscapes than woodland-dominated ones. Practically, a classification system ranging from 0 (easy to cross) to 10 (barrier) was applied to the LUCC (Table 1).

2.2.4. Green infrastructure

The habitat/non-habitat layers were rastered to 1.5 m pixel size binary input grids for further processing in the GUIDOS (**G**raphical **U**ser **I**nterface for the **D**escription of image **O**bjects and their **S**hapes) software environment (Vogt et al., 2007; Vogt, 2010). This raster size has been chosen under the consideration of not losing any thematical information, respectively of not producing spatial inconsistencies on site level after the shape-file conversion process. GUIDOS allowed us to quantify the degree of habitat provision and interconnectedness of suitable core habitats by performing a Morphological Spatial Pattern Analysis (MSPA). Three sub-scenarios with different viable minimum core habitat sizes (0.1 ha, 1 ha, and 10 ha) were defined, depending on varying spatial requirements for DSG. An edge width of 9 m (6 pixels) was set, as a transitional zone between different habitat/non-habitat patches. However, 9 m edge width seemed appropriate to reveal the structural transitions between different LUCC (Gates and Mosher, 1981). Additional program settings in GUIDOS such as "Eight neighbour rule", "No Transitions" and "No Intext" were applied for the MSPA.

After the MSPA, the output classes BRANCH, BRIDGE, EDGE, ISLET, LOOP, PATCH and PERFORATION were combined to one metaclass of possible network structures in ArcGIS highlighting connections between single CORE areas, which represent large, compact patches of habitats. Together, detected possible network structures and core areas were summarised under the heading green infrastructure-network (GI-network).

The GI-network was taken as source location data for the cost distance modelling. Two cost distance layers, separately targeting core areas and network structures, were created and combined afterwards, using "Mean" aggregation technique in ArcGIS to reach one final cost surface layer. In order to allocate average travelling costs from one designated source location to single destination points within each sample site and to compare different outcomes between the sites, a standardised set of rules was applied. Initially, the centroid points of the largest core area within the GI-network were located in every site. Then a buffer zone, encompassing a 1 km radius was set starting from the centroids. The radius of 1 km has been chosen in subject to the 2 km × 2 km size of the sample sites – even if the centroid of the largest core area would be located in the centre of one designated site, the buffer circle would not exceed the site boundary. At the circular line of the buffer, points were set in 15°-intervals. To guarantee autonomy of the sampled points, subsets of seven points per site were randomly chosen (Fig. 3).

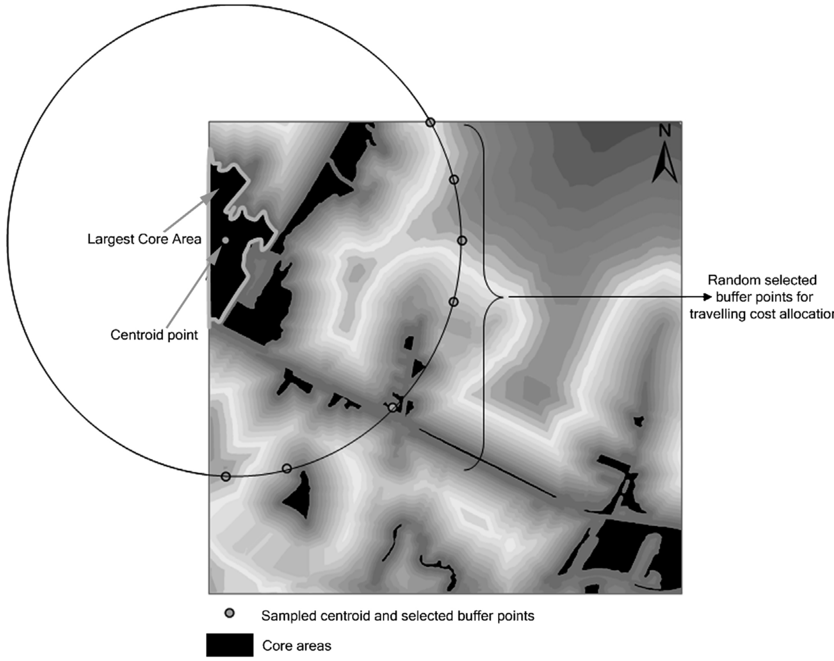

Fig. 3. Schematic overview of the travelling cost allocation process. Random stratified point sampling was followed by effective cost distance calculation and averaging of the resulting values to obtain one single value in each sample site.

To allocate cumulative travelling costs from the core area centroids to the endpoints the tool PATHMATRIX (Ray, 2005), operating in ArcView 3 (ESRI, 1995–2011) was chosen. It effectively computed geographic distances among samples based on least cost path algorithms, in fact resulting in seven different travelling cost values per sample site. The outcomes were first transformed via square-root transformation as a necessity to create a comparable range-level of least cost values between the sites. After that, one final travelling cost value per site was generated by calculating the mean of the seven single values. Since nearly the entire investigation area is located in a very flat basin, relief-caused obstructions were not included in the cost surface analysis but only information on basis of the LUCC classification.

In order to measure qualitative distinctions between structurally based landscape functionality levels of GI-networks, the landscape functionality values of the single landscape elements were referred to all detected possible core areas and network structures. To overcome the problem of spatial incoherence an area-weighted re-calculation was essential to assign proper functionality values for the GI-elements. In several cases the GI-elements covered more than one neighbouring landscape element, unless that they were previously classified as suitable habitat for the DSG. Oppositely, network structures often covered just the inner parts of existing elements because of considered edge effects. Therefore area weighted proportions of element-based landscape functionality values were joined and averaged to gain one final output value per core area or network structure.

An Oneway Analysis of Variance [ANOVA] was performed in order to test for significant differences among the GI-elements concerning their functionality. On basis of a Pearson's correlation analysis, the relation between the area and number of GI-elements, travelling costs and overall functionality in the landscape samples were tested. Subsequently, quadratic regression analysis was calculated to stress the dependence of overall functionality with the area of GI-elements whereas logarithmic regression analysis confirmed their relation to the travelling costs.

Finally, we considered dissimilarities between protected and unprotected sites. Our hypothesis was that landscape functionality is higher in protected landscape samples than in unprotected ones independent from the functionality group and for each group separately. Additionally, we looked at the functional disparities of the GI-networks dependent on their protection status. This was tested with a Welch Two Sample *t*-test.

3. Results

3.1. Landscape functionality

The differences in functionality values among the six different groups were clearly visible (Fig. 4). As expected, connecting corridors (median = 53.10 ± 0.59) and valuable matrix (median = 65.13 ± 0.45) showed the highest values while dissecting corridors (median = 42.97 ± 0.37) turned out to be lower but still

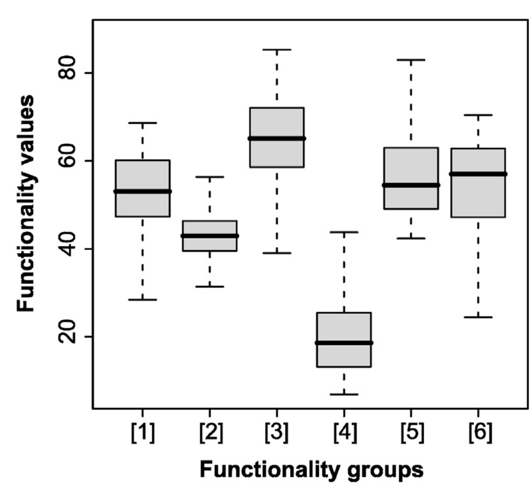

Fig. 4. Boxplots showing the mean functionality of the different functionality groups, derived by transforming, normalising and averaging landscape metrics on class level; [1] connecting corridors, [2] dissecting corridors, [3] valuable matrix, [4] disturbed matrix, [5] artificial matrix and [6] stepping stones.

Table 3
Areal percentages of functionality classes ('very low' to 'very high') in the individual landform types.

	Very low	Low	Moderate	High	Very high
Lake basin (LFT 1)	57.8	2.8	2.8	9.2	27.4
Marshland (LFT 2)	40.8	3.5	3.9	11.5	40.4
River floodplain (LFT 3)	70.9	4.0	2.7	5.4	17.1
Low lying terrace (LFT 4)	78.8	3.8	3.9	2.6	10.9
Elevated terrace (LFT 5)	76.3	3.6	2.6	5.8	11.7
Hilly area and hill range (LFT 7)	29.6	3.4	3.5	12.8	50.6
Low and middle range mountains (LFT 8)	3.2	1.6	3.8	7.8	83.6

ranging higher than the disturbed matrix (median = 18.62 ± 0.27), which clearly differentiated from the other functionality groups.

The areal distribution of single functionality classes (ranging from very low to very high) showed large dissimilarities (Table 3). The share of functionality class 'very high' is highest in LFT 8 (83.6%), followed by LFT 7 (50.6%) and LFT 2 (40.4%). Vice versa functionality class 'very low' turned out to be negligible in LFT 8, but was prevailing in LFTs 3 (70.9%), 4 (78.8%) and 5 (76.3%). In LFT 2 low and high functionality classes appeared to be most balanced, but class 'moderate' was covering only a very small part of its total area (3.9%) which was also true for the other LFTs.

At the local scale, varying distribution patterns of landscape functionality were mainly due to significant differences in the major land use regimes of the samples. Fig. 5a exemplifies a landscape sample located in the low lying terrace of the study region (LFT 4), representative for intensive arable land of medium field size. Although field margins were loosely accompanied by tree rows and hedges, highly-functional nonlinear elements were very rare in this transformed agricultural landscape, resulting in rather low overall functionality of 16.86. The opposite was true for the sample landscape in Fig. 5b, located in the marshland landform (LFT 2). Extensive wetland meadows and (semi)natural forest remnants constituted its matrix, complemented by small arable fields and reed beds, thus resulting in a various but multifunctional landscape, quantified by overall functionality of 57.85.

Altogether 1,263 different habitat and network elements were detected within the 41 investigated sample sites, thereof 515 were identified as possible core areas and 748 as possible network structures. The area of designated GI-elements extended around 5800 ha, compared to the total investigation area of 16,400 ha the share of the GI-network is about 35%. However the distribution of these areas differed widely according to regional disparities between the single LFTs. More than 56% of GI-elements were located in LFT 7 and LFT 8, whereas LFTs 3, 4 and 5 together only covered 15.5%. Regarding the distribution of possible core area size classes, 229 elements extended over 1 ha, encompassing a total area of 4700 ha while 70 elements were ranging greater than 10 ha covering approx. 4200 ha. Most of the biggest core areas were located in the forest dominated regions within the investigation area. This trend was also replicated by the travelling cost distribution between the samples and consequently between the LFTs. Mean travelling costs turned out lowest in LFTs 8 (188.8), 7 (202.6) and 2 (257.5); ranging up to 745.2 in LFT 4. Plot related travelling costs ranged between 122.6 (located in LFT 8) and 1,417.9 (located in LFT 5).

The Oneway ANOVA revealed the dependencies of the different GI-elements to landscape functionality values (F = 169.226, p < 0.01). Possible network structures showed lowest functionality values (mean = 50.15, std. = 13.59) followed by 0.1 ha core areas (mean = 60.36, std. = 11.83) and 1 ha core areas (mean = 65.43, std. = 12.46), whereas core class >10 ha ranked highest (mean = 71.27, std. = 9.50). Pearson's correlation analysis confirmed the dependence of functionality of GI-elements. The relation between the area and number of GI-elements, travelling costs and overall functionality in the landscape samples were tested. Overall functionality of the landscape samples correlated significantly with functionality of GI-elements (cor = 0.921, p < 0.01) and area of GI-elements (cor = 0.934, p < 0.01) whereas the travelling costs correlated negatively with functionality of GI-elements (cor = −0.641, p < 0.01) and area of GI-elements (cor = −0.704, p < 0.01).

Quadratic regression analysis approved the strongly significant dependencies of functionality values per landscape sample with GI-area (corr. r^2 = 0.877, Fig. 6).

Further statistical testing revealed significant relationships between sample-based travelling cost allocation and areal proportion as well as functionality values of the GI-network structures. Two logarithmic regression models showed medium to strong interdependency of travelling costs from the areal proportion of GI elements (corr. r^2 = 0.723, Fig. 7a) and their functionality (corr. r^2 = 0.669, Fig. 7b). Interestingly, the dependency of travelling costs from overall functionality per se turns out to be rather loosely related.

3.2. Protection status

Welch Two Sample t-test proved that landscape functionality is higher in protected than in unprotected sample sites regardless of the single functionality groups a (t = 5.5741, df = 12,020.66, p-value < 0.01). Also all groups showed significant differences (p-value < 0.05) among protected and unprotected samples except for dissecting corridors and stepping stones.

According to functional disparities of GI-networks between protected and unprotected sites, functionality values ranged significantly higher (mean$_{(\text{prot})}$ = 59.9, std. = 1.422/mean$_{(\text{unprot})}$ = 52.8, std. = 1.191) in protected sites among the pooled classes of GI-elements. Functionality levels of each GI core and network class were also tested significantly higher in protected than in unprotected sites (p-value > 0.05) (Fig. 8). While the ratio of network structures areal proportions was almost balanced, the core area cover turned out to be 1.5 times higher in protected areas (2940 ha/1866 ha). However, no apparent differences between the previously calculated site based travelling costs could be outlined between protected and unprotected sites.

4. Discussion

4.1. Landscape functionality

Landscape functionality outcomes strongly were depended on the relationship of the different functionality groups in respect to the sets of landscape metrics that have been assigned to the single groups. The according assessment matrix was the crucial driver for the resulting functionality values and therefore is discussed and argued for at this place in more detail.

According to the *artificial matrix* group we anticipated that its arrangement least affecting landscape functionality is characterised by possibly small land consumption, low areal density, low contiguity, low proximity and compact shapes. Especially the latter

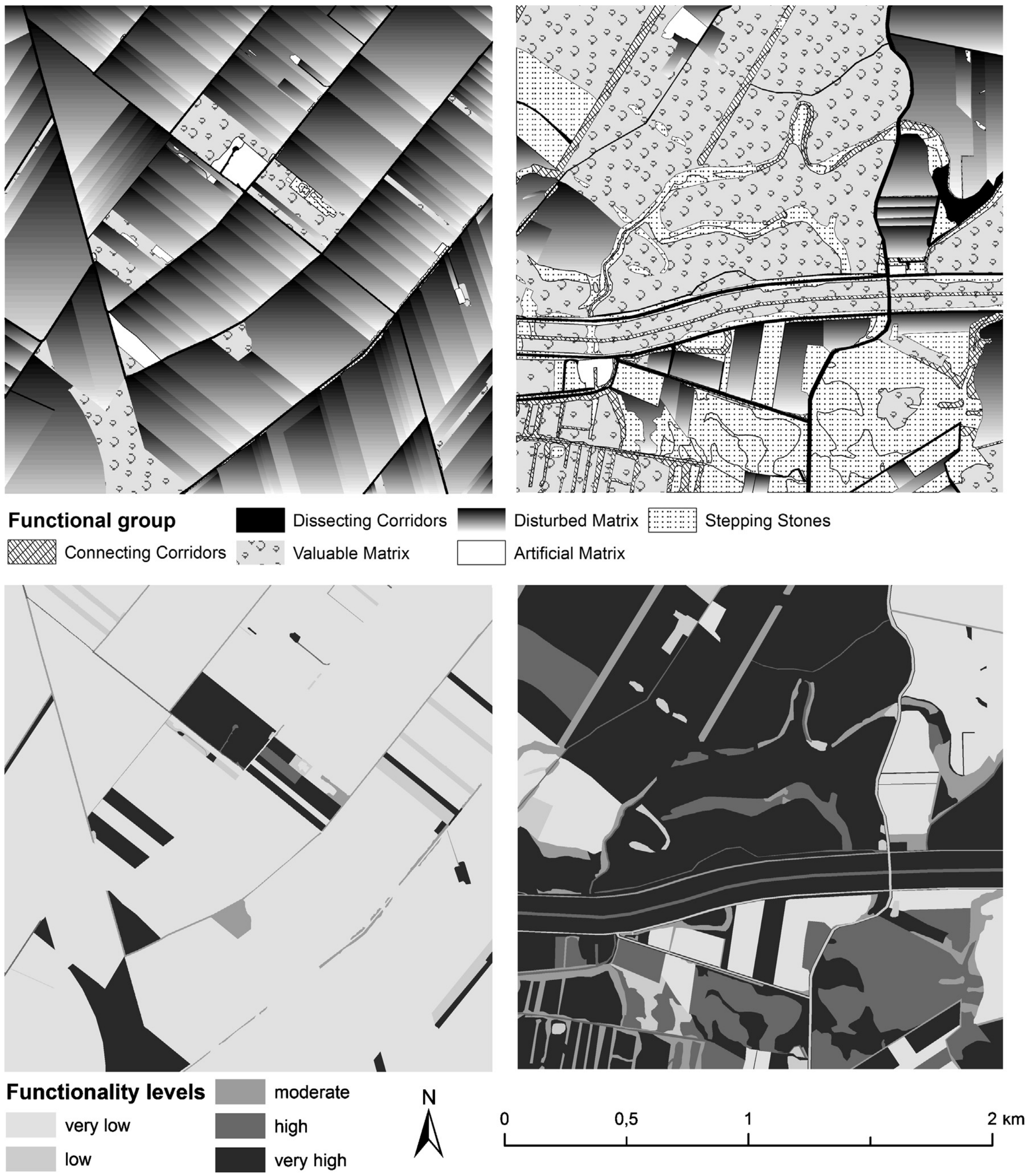

Fig. 5. Example landscape samples; (a) in intensive agricultural landscape disturbed matrix was prevailing resulting in low functionality values; (b) seminatural landscape sample constituted by valuable matrix showing high functionality values.

three factors are pointing out to be indicators for urban sprawl and hence strongly influencing landscape connectivity and dispersal success (Bierwagen, 2007). The *disturbed matrix* reaching for optimal functionality values follow similar outlines as the artificial matrix, except from ideally having irregular instead of compact patch shapes and a high fractal dimension. Smaller field sizes with raised shape complexity support higher structural and substrate diversity (Wrbka et al., 1999), allow for better sharing of resources (Haberl et al., 2004; Fahrig et al., 2011) and thus provide higher overall species diversity (Sauberer et al., 2004; Moser et al., 2002; Zechmeister and Moser, 2001). In case of the *Connecting Corridors* we assumed that a well-developed natural corridor network contribute with the most for a multifunctional landscape (Beier and Noss, 1998; Walz, 2011) but its efficiency is further depending on predominant land use regimes in the disturbed matrix (Dormann et al., 2007). Structural requirements for connecting corridors are expressed by a possibly high-density network of optimal width to guarantee dispersal and migration success for a wide range of species (Gustafsson and Hansson, 1997) and increased genetic variability of populations (Moonen and Bárberi, 2008). Moreover, increased shape complexity and linkage to remnant (semi)natural habitats and stepping stones are crucially contributing for the functional efficiency of connecting corridor networks (Metzger and Décamps, 1997). Stepping stones relate to the metrics similar than connecting corridors. They mainly fulfil the same ecological key processes of supporting species dispersal by decreasing inter-patch distances and providing habitat and shelter. However, especially high mobile species even prefer stepping stones than corridors for movement (Jepsen et al., 2005). Hence, stepping stones appear as inevitable parts in sustainably managed landscapes, mostly

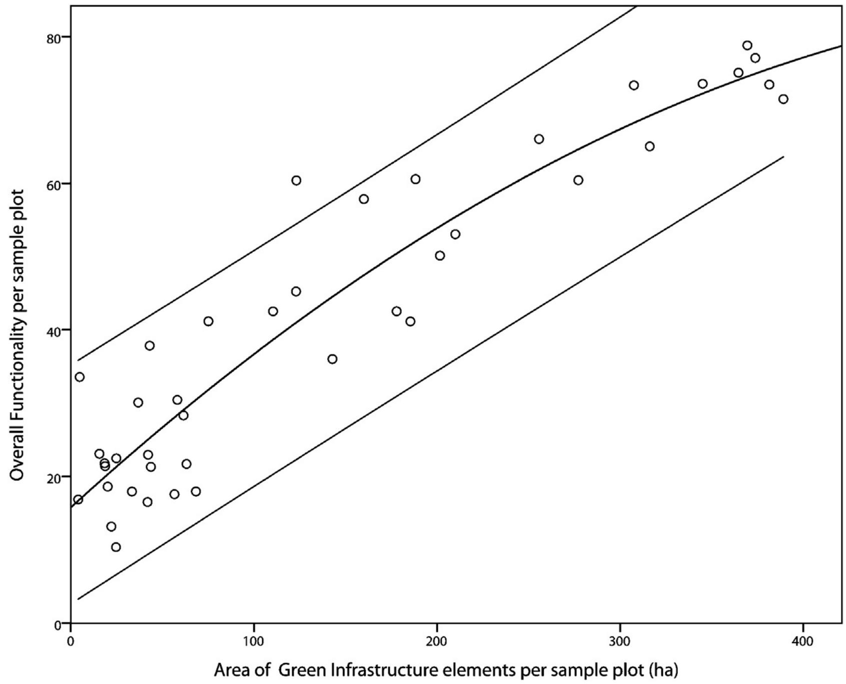

Fig. 6. Quadratic regression of overall functionality with the area of GI-elements. Lines indicate a confidence interval of 95%.

depending on patch location (isolation) and patch size/shape (Bender et al., 2003). Especially edge species would suffer most from a decline of stepping stones, while interior species would be more affected from habitat loss and fragmentation processes of larger habitat patches (Bender et al., 1998), subjected under the frame of the *valuable matrix*. It is in fact true, that the valuable matrix group pooled a variety of different LUCC and thus selective conservation measures for e.g. 'Open land categories' would not gain much direct benefit to forest-interior species (Holzkämper et al., 2006). But with regard to only structural attributes of the valuable matrix, similar major driving factors influencing landscape functionality and hence biodiversity as such can be specified over all incorporated LUCC (Schindler, 2010; Walz, 2011). They are characterised by large, complex shaped and well aggregated areas which allow for the maintenance of natural trophic chains, provide viable habitats for a possibly broad range of different organisms and buffer against human caused environmental influences (Fahrig, 2003; Heegaard et al., 2007; Saura and Carballal, 2004; Aune et al., 2005). Besides the artificial and highly disturbed matrix *dissecting corridors* are most problematic in diminishing the structural functionality of landscapes. In particular habitat fragmentation and impediment of species migration/dispersal patterns are the most severe negative driving factors caused by dissecting corridor networks, especially roads (Alexander and Waters, 2000). Though fragmentation processes are rather difficult to generalise and can also entail positive or neutral effects like enhancing immigration rates and habitat heterogeneity (Fahrig, 2003) or promoting edge effects, it must be considered that these drivers are strongly related to the (i) designated LUCC which would lead to fragmentation and (ii) the target categories suffering from dissection. E.g., a road corridor dissecting a large forest patch would just cause a migration barrier, despite of introducing further drawbacks like air and noise pollution or the risk of road kill (Forman and Alexander, 1998). Former habitat would be lost, the remaining patches would become more isolated and related ecological key processes would significantly deteriorate (Fischer and Lindenmayer, 2007). Consequently, only LUCC which tend to cause obvious negative effects within the target landscape were integrated in the dissecting corridor group. For generally maintaining a high level on landscape functionality of dissecting corridors we suggest a wisely connected but yet loose set which should require as little area as possible and thus resulting in low overall fractal dimension and variable mesh size (Forman and Alexander, 1998), similar to our suggestions for artificial matrix arrangements.

Due to the random stratified sampling process, we set the rule that artificial areas must not cover >10% to overcome the problem of an unbalanced share of artificial areas between the landscape samples. This resulted in rather high functionality values because of unbalanced values of the corresponding metrics. Especially for artificial areas, a structurally based functionality assessment needs to be further tested. Hence, the resulting functionality values for artificial areas cannot be interpreted consistently. The slightly high functionality values of the dissecting corridors can be explained by the fact that metrics react quite sensitive to long but narrow strips, consequently resulting in higher values than more compact elements would perform (Moser et al., 2002; Höbinger et al., in press). As such, only the two corridor functionality groups should be compared directly and here the better function of the connecting corridors was clearly visible.

4.2. Ecoprofile Disturbance Sensitive Species Group and green infrastructure

In the view of the landscape and regional perspective, we orientated ourselves on the ecoprofile approach (Opdam et al., 2008) as this concept allows for a flexible adaptation for the functional trait in question, especially considering the lack of comprehensive and reliable data on species distribution. It stresses also the argumentation that single-species approaches may also be inappropriate to evaluate functionality on the landscape level. Investigations on one target species however could only provide meaningful results for intrinsic functional requirements but would not admit for drawing general conclusions on the landscape scale. Additional scaling effects, particularly in combination with chosen landscape metrics and their ecological meaning for the designated group must be also taken under consideration (Schindler et al., 2008).

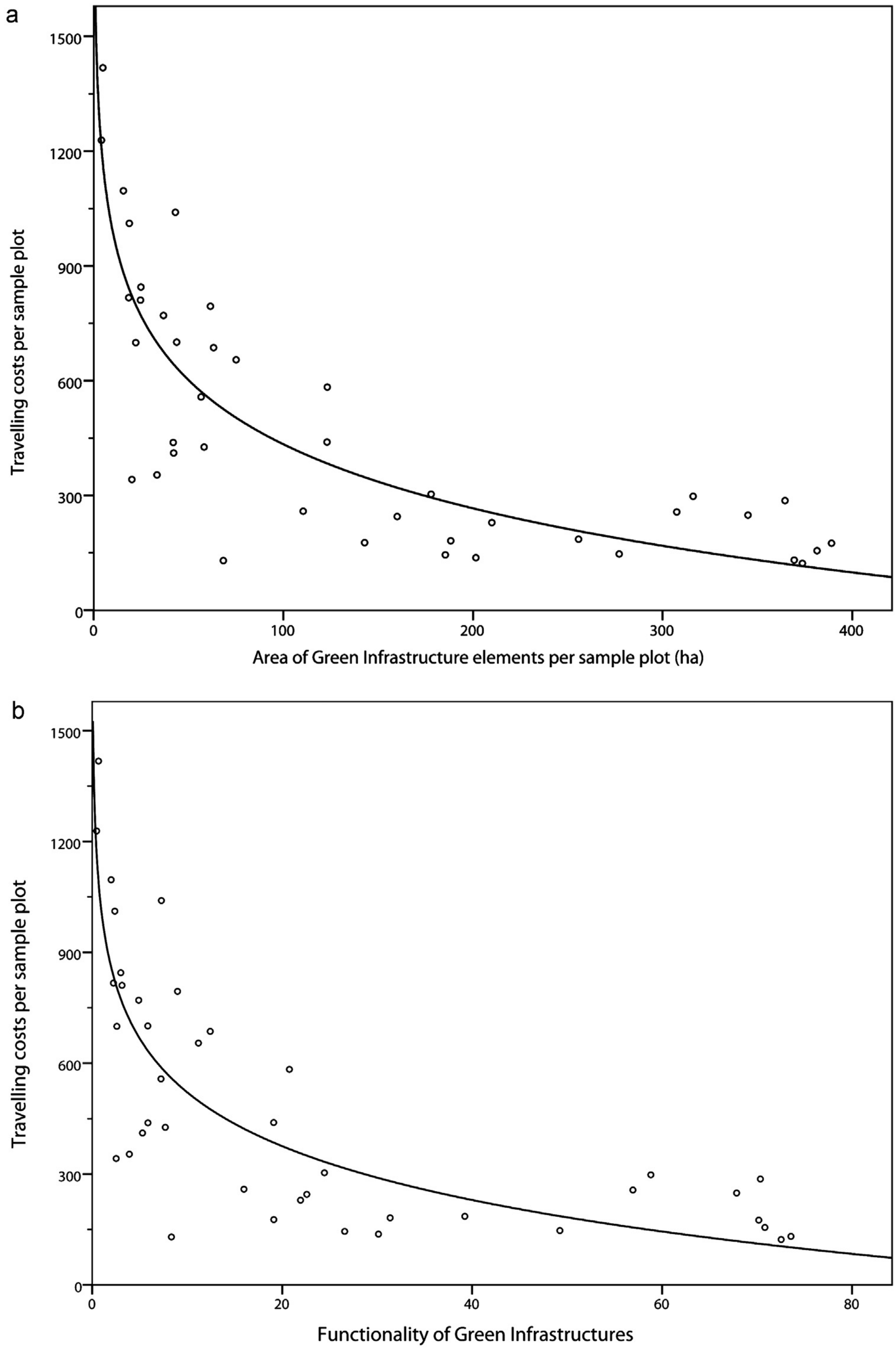

Fig. 7. Logarithmic regression of (a) travelling costs with the area of GI-elements and (b) travelling costs with the functionality of GI-elements. Lines indicate confidence interval of 95%.

In this context, we considered the combination of MSPA with cost surface modelling most valuable to overcome the dilemma of just displaying the landscape as habitat and non-habitat. Semi-natural areas and ecological barriers were also taken into account for estimating dispersal possibilities between different habitat sources (Watts et al., 2010). Again, this method allowed for generally comparing cost-efficiency of movement paths in variably managed landscapes rather than predicting the best ways to cross a certain area of interest. Moreover, concrete trails in comparison to predicted movement paths for a distinct target species are further determined by numerous co-factors such as feeding places or the opportunity to choose several ways of passing through a hostile matrix which cause non-directional movement patterns (Pullinger and Johnson, 2010) that are hardly predictable. Thus cost path allocations complement the landscape related connectivity approach as part of the functionality assessment by pointing out movement opportunities between ecologically valuable habitats of the former derived GI-elements.

Large GI-networks proved to be most important for DSG-viability, especially in agriculturally dominated landscapes. High

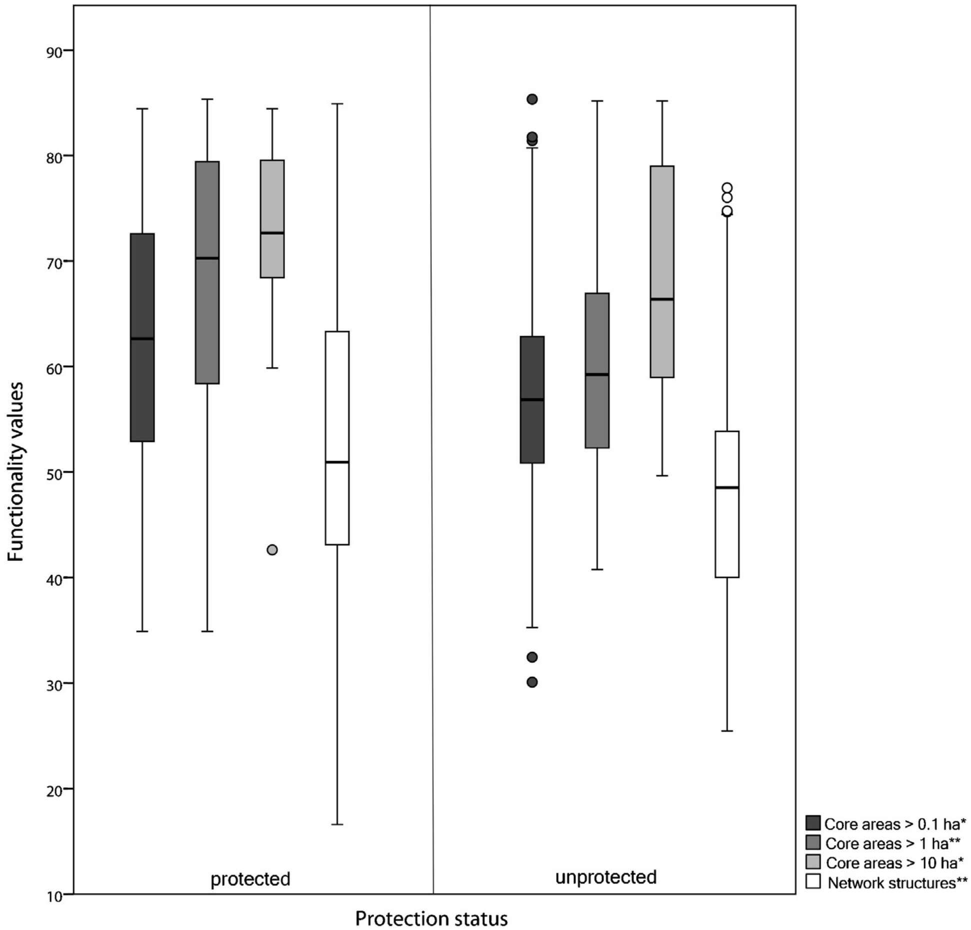

Fig. 8. Differences between functionality values of GI-classes between protected and unprotected landscape samples visualised as boxplots. The asterisks on the right side of the legend are pointing out for significant differences between protected and unprotected sites on the 95% (*) and 99% (**) level according to each investigated GI-class when a Welch Two Sample *t*-test was performed.

functionality values were closely tied to size and number of possible cores and network structures as validated by the regression analysis. Vice versa, these results confirmed the negative influence of the predominant land use systems agriculture and viticulture on landscape's overall functional capacity, most evidently in LFTs 3, 4 and 5.

4.3. Protection status

According to functional disparities between protected and unprotected sites dissecting corridors along with stepping stones did not show significant differences. Especially for the dissecting corridors, almost comprised of roads and other linear transport features, it was not very surprising because they more or less shared the same geometrical characteristics, unaffected by the state of protection. Regarding the stepping stones several explanations may be drawn: (i) Conservation measures may have been focused more on extensification and setting-aside of previously existing cultivated areas than on the implementation of new elements to enhance network connectivity up till now. (ii) Significant differences could not be detected due to our stratified sampling procedure where particularly high-natural but inaccessible areas were left out of the study region. (iii) Some of the protected sites were predominantly comprised by valuable matrix, e.g. dominated by forests and hence the share of stepping stones was inherently lower than in landscapes dominated by agriculture where stepping stones still exist as small remnants of a former matrix. The travelling cost allocation turned out insignificantly between protected and unprotected sites, what can however be also explained by sampling effects. Especially in LFTs 3 and 5 only marginal differences occurred in terms of structural characteristics between protected and unprotected sites, thus resulting in almost balanced travelling costs within the sample plots. The protected areas therein have been recently assessed by the Natural Habitats and Wild Birds Directive (NATURA 2000), mainly focusing on breeding areas of the Great Bustard (*Otis tarda*) which is listed in the Annex I of the EU Birds Directive. As land-use regimes have already been adapted to the demands for the protection of local Great Bustard populations, conservation measures are focused on use-extensification but also on the maintenance of the open cultural landscape. In reflection to an ideally well-connected landscape with appropriate share of (semi)natural residual areas following the demands of the DSG as previously outlined, functionality of the respective landscape samples turned out rather poor in combination of high travelling costs because of lacking in corridors and stepping stones. These limitations of the assessment must be considered but methodological adaptions towards one single target species like the Great Bustard could be flexibly reached.

5. Conclusions

To conclude, one simple guideline for a holistic assessment of structurally driven landscape functionality was hard to reach because individual ecosystematical and species demands often differ widely (Walz, 2011). However, we tried to set up a comprehensive rule set, respecting as many ecologically decisive driving factors as possible with respect to the designated target area. Processing single structurally based functions separately from the first seemed therefore most appropriate to reach more distinctive and unambiguous results. Combining the outcomes of the single groups afterwards crucially contributed to the assessment because lacking values in one group were consequently affecting landscape functionality en bloc.

Still, we consider the transparent sampling and selection procedure of the landscape metrics as an advantage of our method. It was easy to conduct and generally applicable. Same is true for the combined predictive modelling approach which was rather general in our study, but is flexibly adaptable for a various range of species profiles, target habitats and research questions in context. Classifying and comparing landscapes on the basis of functional disparities as well as the identification of the major driving forces behind, along with scenario development for sustainable landscape planning and nature conservation is facilitated.

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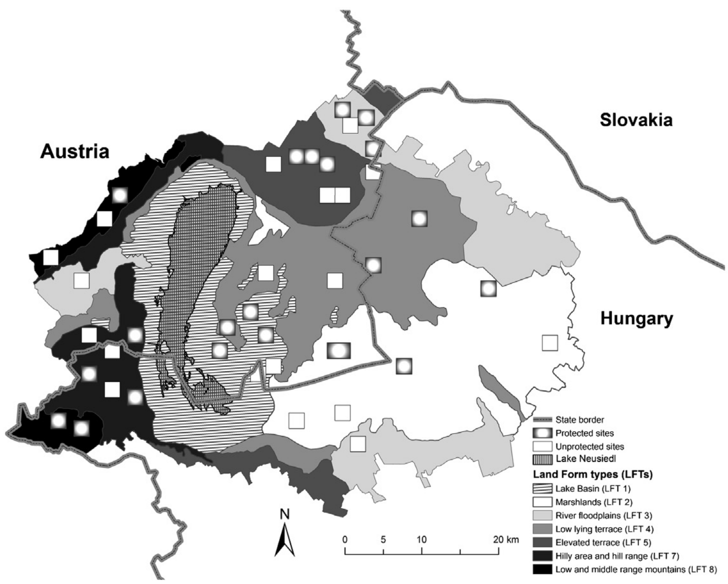
Appendix A.

Detailed overview of the study region, including information on the LFTs and sample sites. An additional table points out for the rules that have been applied during the random stratified site selection procedure.



Geodatasets used for the site selection process

*Location of Lake Neusiedl and not accessible areas such as the reed belt

*Extent and location of shallow lakes

*Location of artificial surfaces

*Location of other non-accessible protected areas

Rule-set for the selection process of the sampling plots (improper grid cells were sorted out in a stepwise approach)

*Rejection of grid-cells overlapping less than 99 % with the investigation area

*Rejection of grid-cells overlapping more than 1 % with inaccessible areas (Neusiedler See, large reed belts, other restricted conservation areas)

*Rejection of grid-cells dedicated to one single Landform type with less than 99 % of the cell-area

*Rejection of grid-cells with more than 30 % cover of shallow lakes

*Rejection of grid-cells sharing more than 10 % artificial surfaces (Basedata originating from: Corine Landcover 2006)

*Rejection of grid-cells distant less than 400 m to a LFT-border

*Rejection of grid-cells dedicated to either a protected or non-protected area sharing less than 75 % of its cell-area with the targeted class

Appendix B.

Based on correlation analysis and subsequent Principal Component Analysis, the initial 46 landscape metrics were gradually reduced to a final set of indices used for the calculation of landscape functionality.

Landscape metric full name	Landscape metric abbreviation	Metrics left after correlation analysis	Final set of metrics after PCA and literature review
Class area	CA	CA	CA
Percentage of Landscape	PLAND		
Patch density	PD	PD	PD
Largest patch index	LPI	LPI	LPI
Landscape shape index	LSI	LSI	LSI
Area	AREA_MN; _AM; _SD; _CV	AREA_MN; _CV	AREA_MN
Shape index	SHAPE_MN; _AM; _SD; _CV	SHAPE_AM; _CV	SHAPE_AM
Fractal dimension index	FRAC_MN; _AM; _SD_CV	FRAC_MN; _CV	FRAC_MN
Perimeter–area ratio	PARA_MN; _AM; _SD; _CV	PARA_CV	
Contiguity index	CONTIG_MN; _AM; _SD; _CV	CONTIG_MN; _CV	CONTIG_MN
Perimeter-area fractal dimension	PAFRAC	PAFRAC	
Total core area	TCA		
Core area percentage of landscape	CPLAND		

Landscape metric full name	Landscape metric abbreviation	Metrics left after correlation analysis	Final set of metrics after PCA and literature review
Number of disjunct core areas	NDCA		
Core area	CORE_MN; _AM; _SD; _CV	CORE_MN	CORE_MN
Disjunct core area distribution	DCORE_MN; _AM; _SD; _CV		
Proximity index	PROX_MN; _AM; _SD; _CV	PROX_MN; _CV	PROX_MN
Euclidean nearest-neighbour distance	ENN_AM	ENN_AM	ENN_AM
Interspersion and juxtaposition index	IJI	IJI	
Connectance index	CONNECT	CONNECT	CONNECT
Patch cohesion index	COHESION		
Landscape division index	DIVISION		
Aggregation index	AI	AI	AI

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Section A

Article 2 (ii)

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Assessment framework for landscape services in European cultural landscapes: An Austrian Hungarian case study

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ABSTRACT

European cultural landscapes are characterised by a high level of anthropogenic fragmentation which is known as a major reason for the loss of biodiversity in industrialised countries. To receive support for adequate choices in sustainable landscape planning, information on the spatial distributions of landscape functions and services is needed. Therefore, the objective of this study was to develop an integrative assessment framework to evaluate a wide range of landscape services at different spatial scales. The proposed methodology was applied within the cross-border region of Austria and Hungary. Embedded in a spatial reference framework we assessed and visualised five main landscape services within the investigation area: *regulation, habitat, provision, information and carrier*. Considering location and spatial extent three different levels of service assessment were distinguished: (1) the Landform Approach was based on seven different Landform Types within the study area. All services were directly observable either by the use of Corine land cover or by clearly identifiable spatial indicators. (2) The Broader Habitat Approach focused on the assessment of services at the landscape element scale within randomly selected landscape sample sites. It was based on the use of an expert driven capacity matrix, which values were revised by semi-quantitative data gained from field work. (3) The *information* services occurring at a broader scale were assessed at the Landscape Character Type scale within the Socio-cultural Approach. Additional indicators mainly based on geo-data were defined. Finally, all services were extrapolated to the Landform Types revealing the actual landscape service provision within the study area. The results presented hot and cold spots of service provision at different spatial scales as well as the trade-offs between the different services. The landscape service maps might provide regional stakeholders with valuable information on service supply and can therefore be used as knowledge basis in cross-border landscape planning decision processes. Making landscape services spatially explicit and combining empirical data with spatial information presents an innovative approach to landscape research in the field of assessing and visualising landscape services. This would enable the development of a decision support tool, which can be used for the systematic evaluation of goal attainments and conflict detection.

1. Introduction

European cultural landscapes are known to provide a wide range of functions and services that are useful for humans. However, the supply of ecosystem services and biodiversity is threatened, mainly caused by a high level of habitat loss and fragmentation (MEA, 2005). One reason for the loss of ecosystems in cultural landscapes is the lack of integrating ecosystem service values in regional spatial planning projects. The ecosystem service concept is therefore aiming at supporting the development of policies and instruments by integrating ecological, socio-cultural and economical perspectives to provide insights into human impacts on ecosystems and the welfare effects of management policies (TEEB, 2010). This scientific concept has experienced increasing attention in the last decades as it provides the means of documenting the importance and benefits of ecosystems and landscape for human society. One of the most relevant publications is the Millennium Ecosystem Assessment (MEA, 2005) which provides the basic framework for assessing the interactions between ecosystems and humans and

Abbreviations: LFT, Landform Type; LCT, Landscape Character Type; BHT, Broader Habitat Type; BHS, Broader Habitat(type) value; LESV, Landscape Element Service value.

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how these can be measured, evaluated and strengthened for future human well-being. After the release of the Millennium Assessment (MEA, 2005), which focused on the benefits people derive directly and indirectly from ecosystems, the literature concerning ecosystem services has increased exponentially all over the world (Fisher et al., 2009). Several authors have been dealing with classifying, quantifying, mapping and valuing of ecosystem services in order to integrate the concept into decision making processes (e.g. Costanza et al., 1997; Daily, 1997; de Groot et al., 2010; Fisher et al., 2009; Hermann et al., 2011). However, despite the enhancing interest in ecosystem service research, still many open questions remain to fully integrate the ecosystem service concept in landscape research and decision making.

Because landscape sciences focus on spatial pattern and scale, they can provide useful insights into how the spatial distribution of human activities influences important landscape processes and structures from which services are derived (Jones et al., 2008). The central notion in landscape development has always been that people are part of the landscape and that landscapes are changed for their benefit (Antrop, 2001; Linehan and Gross, 1998). Especially, in Central and Eastern Europe both the analysis of landscape pattern and processes and the assessment of landscape functionality as a basis for land use planning have a long tradition (Bastian and Schreiber, 1994; Buchwald and Engelhardt, 1968; Lee et al., 1999). In recent years, the terms 'landscape function and service' have become more important in literature (Bastian and Schreiber, 1999; de Groot et al., 2010; Willemen et al., 2010). To receive support for adequate choices in landscape planning, information on the spatial distributions of landscape functions and services is needed. Although in the last years considerable progress has been made in assessing, quantifying and mapping a multitude of landscape services, implementing the concept into sustainable landscape planning and management still remains a challenge (Hermann et al., 2011; Norgaard, 2010). Regarding the state-of-the-art, better insight into interactions between land cover, use and function and methods to assess and map land use and landscape function is still needed (e.g. Verburg et al., 2009). Visualisation should illustrate the spatial heterogeneity in quality and quantity of services provision, which is due to differences in biophysical and socioeconomic conditions at different scale levels (Meyer and Grabaum, 2008; Wiggering et al., 2006). Therefore, landscape services are to be addressed and assessed on various scales (Hein et al., 2006). Assessing and mapping the multitude of services provided by different landscapes at different scales is seen as prerequisite for sustainable landscape management (Verburg et al., 2009). This would enable the development of a decision support tool, which can be used for the systematic evaluation of goal attainments and conflict detection. As assessing and mapping of services is mainly dependent on data availability and finding the appropriate indicator, most publications focused either on selected landscape services and/or emphasised only on one assessment scale (e.g. Burkhard et al., 2009; Troy and Wilson, 2006; Willemen et al., 2008). An integrative framework that takes a wide range of ecosystem/landscape services into account is still under development. Such a framework should be comprehensible, feasible and able to be applied at wide range of scales to different ecosystems or landscapes (Hein et al., 2006). We want to meet these challenges by the development of a framework which will link the processes in the landscapes with the services provided at different scales.

The aim of this paper is therefore to present a spatially explicit methodology evaluating a broad set of landscape services by meeting the following research objectives: (i) mapping the hot and cold spots of service provision within different landscape types (ii) visualising the trade-offs between the services within the investigation area (iii) testing the concept of landscape services as an operational tool to evaluate ecologically sensitive regions.

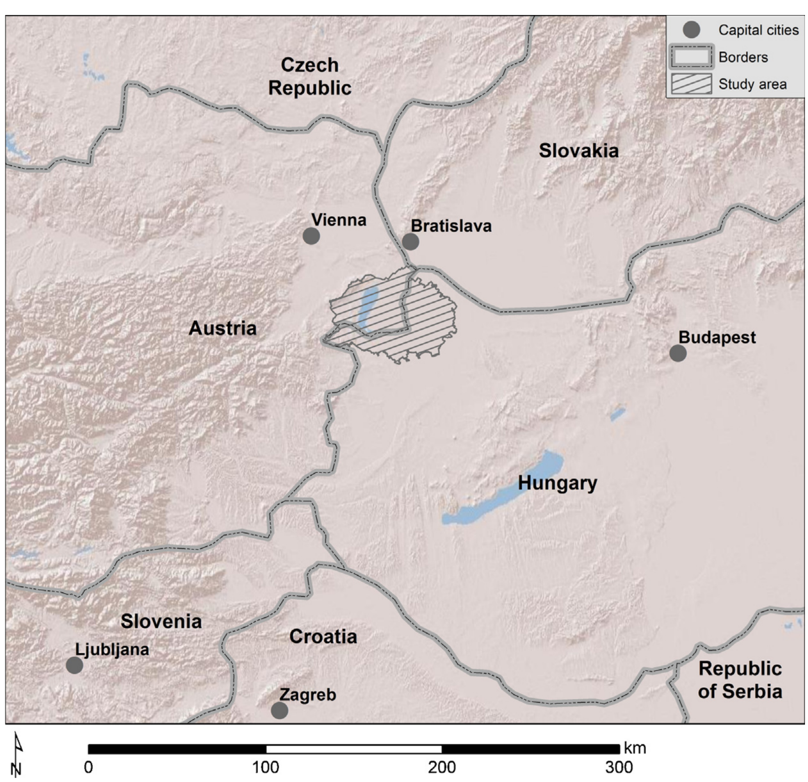

Fig. 1. Location of the study area in the transboundary region of Austria and Hungary in Central Europe. Topographical map is made with Natural Earth and www.ArcGIS.com.

2. Materials and methods

2.1. Study area

The project region covers the Austrian-Hungarian transboundary region of the Neusiedler See/Fertő (Fig. 1) extending over 2000 km^2. It is part of the Small Hungarian Plain in Central Europe representing the westernmost extension of the Pannonian Basin. The shallow lake Neusiedler See which lies in a flat basin is dominating the landscape view. The southern Hungarian part (Fertő) is mainly lowland with gentle hills on the western side. The northern part belonging to Austria has contrasting western and eastern sides: the former is formed by the pronounced slope zone of a low mountain ridge, whereas the latter, the Seewinkel, represents the lowest land in Austria. The region is characterised by a hot, dry Pannonian climate with an annual precipitation of 700–800 mm and annual mean temperature of >9 °C (ZAMG, 2002). In a relatively small area, plants and animals with Alpine, Asiatic and Mediterranean affinities, as well as northern species, are present, resulting in high species diversity. Thus, on both sides of the border, different protection categories were declared in the last decades: Nationalparks Neusiedler See-Seewinkel and Fertő-Hanság, Ramsar Sites, UNESCO World Heritage Site, Biosphere Reserves, various Natura2000-areas and different national conservation labels can be found throughout the region.

Today two main economy sectors dominate the area: intensive agriculture particularly crop-growing, wine growing and greenhouse-vegetable gardening and tourism, which is especially centred around the lake and focused on rather small areas. In the last decades the typical lake tourism changed to a more diversified tourism based on nature, the national park, cycling and other sports activities, cultural traditions and events. Nowadays severe problems arise from the growing conflict between these two demands caused by increasing requirement of land for their anthropogenic uses, additionally interfering with nature conservation issues. Because of the multifunctional landscape and the diverging claims on land utilisation we used that region to develop the proposed approach.

2.2. Landscape services

In our study we used the concept of landscape services (Termorshuizen and Opdam, 2009). As 'landscapes' may be more attractive to non-ecological scientific disciplines in contrary to the term 'ecosystem' and may be associated with people's local environment, we preferred the term 'landscape services' instead of 'ecosystem services'. In contrast, 'ecosystem' may be related with natural processes and conservation instead of with human habitat and cultural patterns. In our definition landscape services are therefore all goods and services that landscapes provide for well-being. They include potentials, materials and processes of nature (e.g. biomass, raw materials, primary productivity) and services of cultural elements and constructions that come into being through human creation (e.g. buildings, settlements, infrastructure) (Konkoly-Gyuró, 2011). Based on the list provided by de Groot (2006), a general set of landscape services was derived (Table 1). The individual sub-services are grouped into five main services (1) *regulation*, (2) *habitat*, (3) *provision*, (4) *information* and (5) *carrier*. Whereas the *regulation* services are related to the capacity of cultural landscapes to regulate essential ecological processes and life support systems through biogeochemical cycles, the *habitat* services describe the capacity to provide refuge and reproduction habitat to wild plants and animals. As the habitat requirements differ from species to species they are defined in terms of the carrying capacity and spatial needs (minimum critical biotope size) of the specific biotope type. The *provision* services are targeting the supply of natural resources concerning 'edible wild plants and animals', 'raw materials', 'genetic' and 'medicinal resources'. Whereas the *information* services include all services referring to spiritual enrichment, cognitive development, recreation and aesthetic experiences, the *carrier* services describe the capacity of landscapes to provide suitable substrate (soil) for 'cultivation', 'habitation', 'tourism facilities', 'energy conversion' and 'transportation'.

2.3. Overall methodology

The overall methodological framework (Fig. 2) is based on data availability and spatial scales of assessments. Individual sub-services were assessed at the specific service providing unit and were finally aggregated to the main services (Table 1). Driven by the link between landscape service and service providing unit, three different scales for landscape service assessment were distinguished and integrated into a spatial reference framework representing different homogenous assessment units (Renetzeder et al., 2008). Landform Types (LFT) by Konkoly-Gyuró et al. (2010) formed the common basis for our integrative assessment of Austrian and Hungarian landscapes. They represent the main geomorphological and hydrological features of the study area (Fig. 3): 'Lake Basin' (LFT 1), 'Marshlands' (LFT 2), 'River Floodplains' (LFT 3), 'Low lying terrace' (LFT 4), 'Elevated terrace' (LFT 5), 'Hilly area and hill range' (LFT 6) and 'Low and middle range mountains' (LFT 7). Because spatially explicit data was not available for all sub-services, we selected landscape sample sites within the different Landform Types. This was done by a stratified random sampling method. In each Landform Type, six sample sites of 1 km × 1 km size according to the European Grid System (INSPIRE, 2009) were randomly selected after applying a list of sampling rules resulting in 41 landscape sample sites (Fig. 3). These sampling rules included terms for the exclusion of grid cells with more than 1% not accessible areas, >30% water surfaces, or >10% artificial areas. The cells needed to be 99% within the same Landform Type and have at least 500 m distance to the border of the investigation area. The assessment of the *information* services that required another spatial scale was based on Landscape Character Types (LCT) representing a combination of relief, dominant land cover and land use intensity within the different Landform Types (Konkoly-Gyuró et al., 2010; after Swanwick, 2002).

This spatial reference framework served to link the individual landscape services and their assessment approaches on the different scales with each other in a hierarchical way. Dependent on the different service providing units at the different scales three assessment approaches, namely the (a) the Broader Habitat Approach based on the sample sites (b) Landform Approach based on the LFTs, and (c) the Socio-Cultural Approach based on the LCTs were distinguished (Fig. 2).

(a) Broader Habitat Approach: As the service providing units were located at the landscape element scale (Forman and Godron, 1986), this approach was carried out within the 41 landscape sample sites. The assessment was based on the use of a capacity matrix (Burkhard et al., 2009), which values were revised by qualifiers, that derived from field surveys.
(b) Landform Approach: Assessment of landscape services that were directly observable for the entire Landform Types either by the use of Corine land cover CLC 2006 (EEA, 2007), or by clearly identifiable spatial indicators.
(c) Socio-cultural Approach: For the assessment of the *information* services we used the 14 LCTs as spatial units. Landscape metrics, biophysical and socio-economic landscape components were used to describe the location and the capacity of LCTs to provide

Table 1
List of main landscape services and their related sub-services with examples and information about the applied assessment approach (adapted from de Groot, 2006). The three Approaches Broader Habitat, Socio-cultural and Landform Approach are dependent on the service providing unit and are explained in more detail within the section 'overall methodology'.

Services	Definition	Examples	Applied approach
Regulation services			
Local climate regulation	Influence of broader habitat type on local climate	Maintenance of a favourable local climate (e.g. temp., moisture) e.g. human habitation, health, cultivation	Broader habitat Approach
Disturbance prevention	Influence of broader habitat on environmental disturbances	Storm protection and/or flood prevention (e.g. flood detention basin, shelter belt)	Broader habitat Approach
Water regulation	Role of broader habitat type in regulating runoff and river discharge	Drainage and natural irrigation	Broader habitat Approach
Water supply	Filtering, retention and storage of fresh water	Provision of water for consumptive use (e.g. drinking, irrigation and industrial use)	Broader habitat Approach
Soil retention	Role of vegetation root matrix and soil biota in soil retention	Maintenance of arable land; prevention of damage from erosion/siltation	Broader habitat Approach
Soil formation	Weathering of rock, accumulation of organic matter	Maintenance of natural productive soils	Broader habitat Approach
Nutrient regulation	Role of biota in storage (buffer) and recycling of nutrients (e.g. N, P and S)	Maintenance of healthy and productive ecosystems	Broader habitat Approach
Pollination	Role of biota in movement of floral gametes (is there any suitable habitat available for pollinators?)	Pollination of wild plant species and crops	Broader habitat Approach
Habitat services			
Refugium	Suitable living space for wild plants and animals	Maintenance of biodiversity, in particular	Broader habitat Approach
Nursery	Suitable reproduction habitat	Maintenance of commercially harvested species	Broader habitat Approach
Provision services			
Food	Conversion of solar energy into wild edible plants and animals	Maintenance of edible wild plants and fungi (not cultivated), game and fish	Broader habitat Approach
Raw materials	Conversion of solar energy into biomass	Material for human constructions (building and manufacturing), like lumber, fuel and energy wood	Broader habitat Approach
Genetic resources	Genetic material and evolution in wild plants and animals	Improve crop resistance to pathogens and pests and maintenance of old cultivated plants	Broader habitat Approach
Medicinal resources	Variety in chemical substances in natural biota	Drugs and pharmaceuticals	Broader habitat Approach
Information services			
Aesthetic information	Attractive landscape features and views	Enjoyment of scenery (scenic roads, housing etc.	Socio-cultural Approach
Recreation	Variety in landscapes with (potential) recreational uses	Travel to natural ecosystems for eco-tourism and (recreational) nature study	Socio-cultural Approach
Cultural and artistic information	Variety in natural and cultural features with cultural and artistic value	Use of natural and cultural landscape elements as motive in books, film, painting, folklore, national symbols, architect, advertising, etc.	Socio-cultural Approach
Spiritual and historic information	Variety in natural and cultural features with spiritual and historic value	Use of natural and cultural landscape elements for religious or historic purposes (i.e. heritage value of natural ecosystems and features)	Socio-cultural Approach
Science and education	Variety in nature with scientific and educational value	Use of nature for scientific research	Socio-cultural Approach
Carrier services			
Habitation	Providing suitable space for human living	Living space (ranging from small settlements to urban areas)	Landform Approach
Cultivation	Providing suitable substrate for cultivation (actual available)	Cultivated food and fodder	Landform Approach
Energy conversion	Providing suitable substrate or medium for energy conversion	Energy facilities (only wind)	Landform Approach
Waste disposal	Providing suitable substrate for waste disposal	Space for solid waste disposal	Broader habitat Approach
Transportation	Providing suitable substrate or medium for transportation	Main and side roads as well as railroad tracks	Landform Approach
Tourism-facilities	Providing space and facilities for human activities related to tourism	Tourism and leisure activities (e.g. outdoor sports)	Socio-cultural Approach

services. These different landscape data were translated into spatial indicators and linked to the related services.

Finally, to compare the different landscape types regarding their provision of landscape services, all individual sub-services were extrapolated to the Landform Types and aggregated to the main services. The main services *regulation, habitat, provision, information* and *carrier* were plotted onto a 5 axes spider web diagram illustrating their trade-offs.

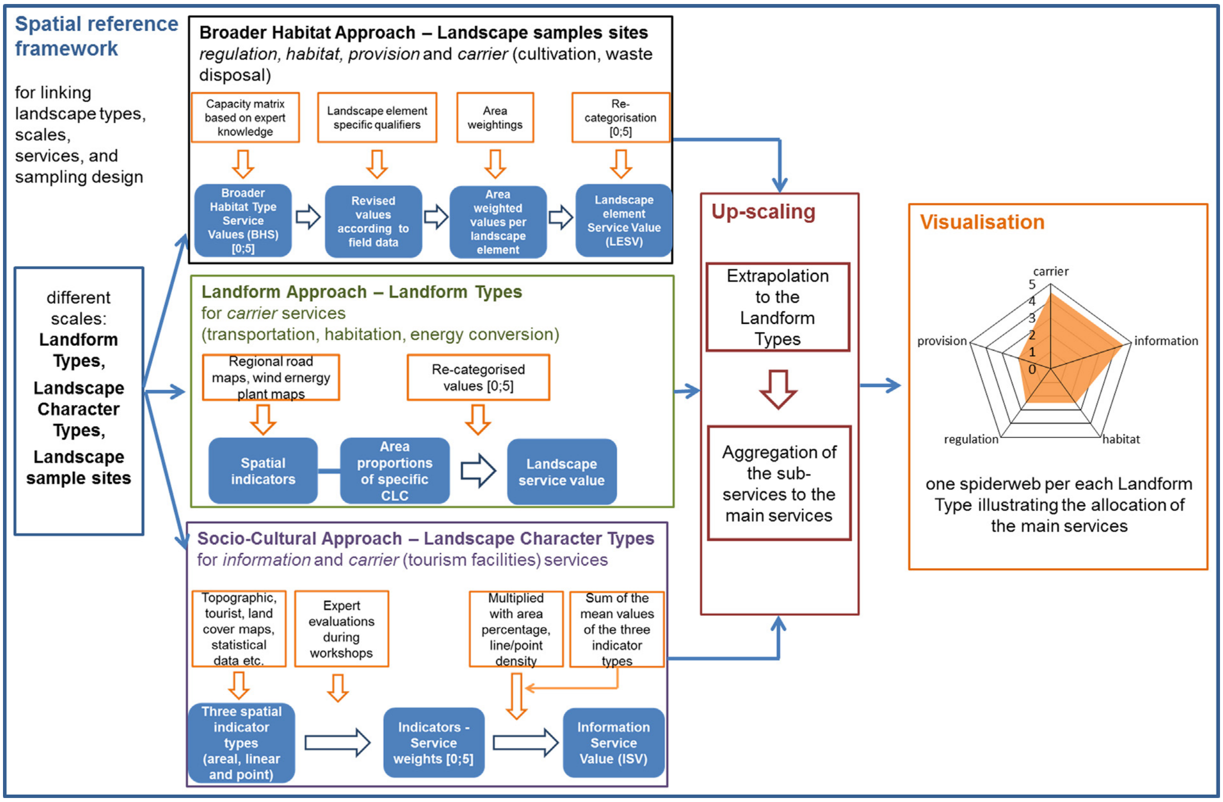

Fig. 2. Methodological assessment framework based on three scales: Landform Types, Landscape sample sites and Landscape Character Types. Dependent on the different service providing units at the different scales the Landform Approach, the Broader Habitat Approach and the Socio-cultural Approach can be distinguished. Finally, the aggregated service groups were visualised at the Landform Type scale; CLC = Corine land cover CLC 2006 (EEA, 2007).

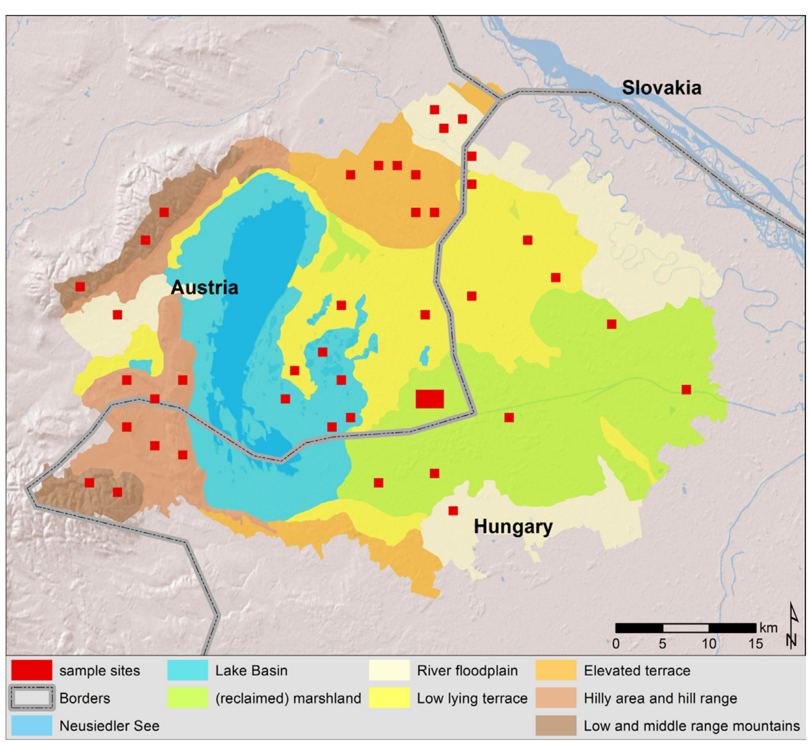

Fig. 3. Location of 41 sample sites within the seven Landform Types as defined by Konkoly-Gyuró et al. (2010). Topographical map is made with Natural Earth and www.ArcGIS.com.

In the next sections the three approaches as well as the extrapolation and the aggregation of data are presented in detail.

2.4. Assessing landscape services

2.4.1. Broader habitat approach

As data availability for specific service indicators (e.g. crops/ha; kJ/ha for cultivation service) was limited or often not comparable within our approach, *regulation*, *habitat*, *provision* and partly *carrier* (only 'cultivation' and 'waste disposal') services (Table 1) were consequently related to a specific Broader Habitat by the use of a capacity matrix (after Burkhard et al., 2009; Haines-Young and Potschin, 2008). The list of about 181 Austrian Broader Habitat types (BHT) was based on the definition lists of Essl et al. (2002). During field work (May to September 2010) each landscape element in the 41 landscape site samples was assigned a BHT. All field data were stored in a personal geodatabase in ArcGIS 10 (ESRI, 2011). In principle, the subsequent work flow (Fig. 2) consisted of four steps which were implemented within ArcGIS Modelbuilder in ArcGIS 10 (ESRI, 2011):

(i) As a first step towards creating the matrix, the capacities of all 181 BHTs regarding their provision of individual landscape services were set up by expert evaluations during several workshops on different disciplines of ecology (Vegetation Science, Zoology, Pedology and Climate Science). The so-called Broader Habitat (type) Service (BHS) values ranged from categories '0' (no relevant link) to '5' (very high relevant link). The resulting capacity matrix (Table A1) served as input table for subsequent analysis.

(ii) To enhance the expert based approach, further attributes gathered by field mapping were used for a closer look on the actual service provision of each landscape element. During field survey, additional qualifiers on 'broader habitat structure', 'management', 'pressure' and 'valuable attributes' within the 'landscape site samples' were separately collected for each investigated landscape element. These qualifiers exerted either a positive ('1'), negative ('−1') or no influence ('0') on the provision of a specific service (Table A2) and served as a further input table within the modelbuilder environment by calculating a specific 'landscape element service value' (LESV). Thus, the former values from the capacity matrix were revised by increasing, decreasing or remaining constant for each landscape element depending on qualifiers found in the field.

(iii) As the area of a landscape element has also an impact on the provision of a service (e.g. a large forested area has more impact on climate regulation than a small one), additional area-weighting was integrated into the assessment. Regarding waste disposal, area-weighting was not appropriate because direct relationships between area share and functional capacity could not be outlined.

(iv) The resulting values for each service were re-categorised ranging from '0' to '5' based on 20%-percentiles and then each service-specific layer, including the final 'landscape element service values' (LESV) was stored in the geodatabase.

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2013.01.019.

2.4.2. Landform approach

Location and extent of the *carrier* services 'transportation', 'habitation' and 'energy conversion' were clearly distinguishable.

Transportation service: To measure the actual state of 'transportation' within the investigation area, absolute running metres of transportation networks were calculated for each Landform Type. For this reason, main and side roads as well as railroad tracks that derived from regional road maps were integrated into the assessment. Due to traffic densities, the lengths of the main roads were double-weighted. Resulting track lengths were divided by the total area shares of the single LFTs, resulting in area density values of the transportation network.

Habitation service: To comprehensively include *settlement areas* and *other man-made facilities* such as *industrial* and *commercial sites* or *sport* and *leisure facilities* into the assessment, Corine land cover CLC 2006 (EEA, 2007) was taken as source layer. Area proportions of the aforementioned CLC classes of interest were again separately calculated for all LFTs by multiplying class areas with class specific BHS values.

Energy conversion service: The 'energy conversion' service considers facilities for the conversion of wind energy into electricity (see Table 1). On the basis of a map sheet 'Regionales Rahmenkonzept für Windenergieanlagen' ('regional framework for energy plants'), provided by the 'GIS Koordinationsstelle, Raumordnung Burgenland' all actual locations and suitable zones of wind power stations within the investigation area were detected and the area proportion was calculated and re-categorised. As this base layer was only available for Austria, wind power stations on the Hungarian side of the study region were mapped after visual interpretation of the latest aerial imagery available.

2.4.3. Socio-cultural approach

Information services and the sub-service 'tourism facilities' of the *carrier* services were assessed on the level of the LCTs as defined by the spatial reference framework (see Fig. 2). Indicators were developed for each sub-service and derived for the whole investigation area with the help of topographic-, tourist- and land cover maps, online Landmark Cadastral Register (Kollányi et al., 2012) database, as well as statistical data. The indicators for the 'tourism facilities' comprised *touristic nodes* (Ziener, 2003), *length of all touristic trails* and *water sport facilities* (the access of lake or pond and the existence of basic infrastructure like boat bridges). For the *information* services three main types of indicators have been developed: (1) areal landscape elements (e.g. water bodies, wetlands, forests), (2) linear landscape elements (e.g. forest edge, water edge, vineyard edge) and (3) point landscape elements (e.g. churches, chapels, look-out towers). All data were stored and processed in a personal geodatabase in ArcGIS 10 (ESRI, 2011). First, based on expert evaluations each of the indicators was assigned a service weight between '0' and '5' reflecting the relevance of the indicator for the sub-services (Table A3). In the next step, depending on the geometry of the data, the area percentage and the line/point density per LCT was multiplied with the service weight, then normalised between 0 and 5 and finally the mean of each indicator type was calculated. To reach one final *information* service value per LCT the sum of the mean values of the three indicator types were calculated. In the end the values were normalised again, in order to be comparable with the landscape service values assessed within the other approaches.

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2013.01.019.

2.4.4. Extrapolation and aggregation of the different landscape services to the main services

The services assessed by the Broader Habitat Approach had to be aggregated onto the Landform Type scale in a stepwise approach, for further comparison with the services assessed within the Landform and Socio-Cultural Approach.

To receive one single value for each sub-service per sample site, area-weighted mean values of all LESVs were separately calculated for the different sub services. The outcomes can be interpreted as

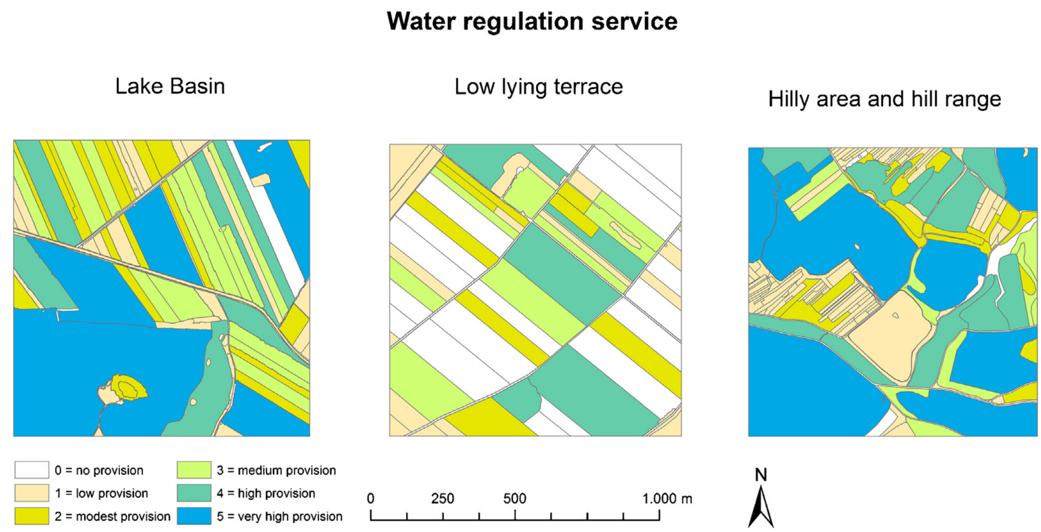

Fig. 4. 'Water regulation' service maps of the LFTs Lake basin, Low lying terrace and Hilly area and hill range (one sample site per LFT). 1 = low service provision, 2 = modest service provision, 3 = medium service provision, 4 = high service provision, 5 = very high service provision.

the actual state of each investigated sample site in the fulfilment of the individual services. These were extrapolated to LFT-level by calculating mean values for all six sample sites per LFT. Consequently, the main service values of *regulation*, *habitat* and *provision* were obtained by combining and calculating the mean values of the specific sub services on LFT level.

Hereby LFT 1, the 'Lake Basin', was regarded as special case, because representativeness of the sample sites for the up-scaling process was limited due to location of the 'Neusiedler See' itself plus its adjacent reed belt and satellite lakes within the LFT 1. However, these inaccessible areas make up more than 60% of LFT 1 and therefore must be taken into account for landscape service provision. To overcome these difficulties, LFT 1 was split up into 4 subparts such as the terrestrial region, characterised by the Broader Habitat outcomes, the lake itself, the reed belt and the satellite lakes. For the latter three, provision of landscape services was derived by calculating area-weighted values from the BHS table and afterwards combining them with sample site based results for the terrestrial area according to their area shares.

The services evaluated by the Socio-Cultural Approach also had to be scaled-up on LFT level. As the different LCTs were embedded within the LFTs (refer to spatial reference framework), area-weighted values of the LCT-based main services were calculated for each LFT. Finally, the area-weighted main service values within each LFT were summed up to reach one final value for the *carrier* and the *information* main services.

3. Results

3.1. Individual landscape service maps – hot and cold spots

3.1.1. Broader habitat approach

Resulting from the GIS model the individual LESVs can be mapped for each landscape sample site within the different LFTs, in order to explicitly visualise local differences in landscape service delivery. As an example we present the 'water regulation' service within one sample site of the LFT 'Lake basin', 'Low lying terrace' and 'Hilly area and hill range' (Fig. 4). Within the LFT 'Lake basin' the sample site shows grassland matrix interspersed by patches of arable land and vineyards providing medium to very high 'water regulation' values. Whereas the sample site of the 'Low lying terrace' represents an open and intensively used landscape supplying very low 'water regulation' service (cold spot), the sample site of the third LFT displays a heterogeneous land cover mosaic with very high landscape service values (hot spot) for the most part of the area.

3.1.2. Socio-cultural approach

The values of the individual landscape service 'tourism-facilities' were presented at the LCT level (Fig. 5). The very high value (hot spot) of the northern part of the lake basin which is dominated by open water (LCT 1b) resulted mainly from water sports. The big and middle divided touristic nodes (Ziener, 2003) on the lakeshore are only partly located in the lake basin (lake resorts), while the villages and towns are situated in the neighbouring LCTs. The hill areas on the western shore of the lake (LCT 3b) gained higher values than the flat areas on the eastern shore (LCT 1c and 2c), because of the diversified landscape pattern resulting in different structure of settlements and touristic nodes and a partly dense network of touristic trails. The marshland areas (LCT 1d and 2a) as well as the southern part of the lake basin which is dominated by the reed belt and wetlands (LCT 1a) showed the least 'tourism-facilities' values (cold spots). In former times the Hanság area was covered by extensive wetlands with the result that the settlements are very small. There, land use is dominated by agriculture and tourism is underdeveloped.

The distribution of the aggregated *information* services were visualised at the LCT level as well (Fig. 6). In general, these values ranged between 1.4 and 3.3 (low to medium service provision). The hot spots of *information* services were found in the LCTs 3a, 3b, and 1c, where hill ranges and foothills of low mountains with medium or intensive human use are dominated by a mosaic of forest, grasslands and water surfaces. Relatively high values also occurred in low intensity human use areas, which are remnants of marshlands. The lowest values were provided by LCT 2b, where the similar visual appearance is due to the equally flat surface and to the overwhelming intensive arable land parcels.

3.2. Trade-offs between the main landscape services within the investigation area

The resulting values ranging [0–5] showed the actual provision of the main services *carrier*, *information*, *habitat*, *regulation* and *provision* within the seven Landform Types (Table 2). They

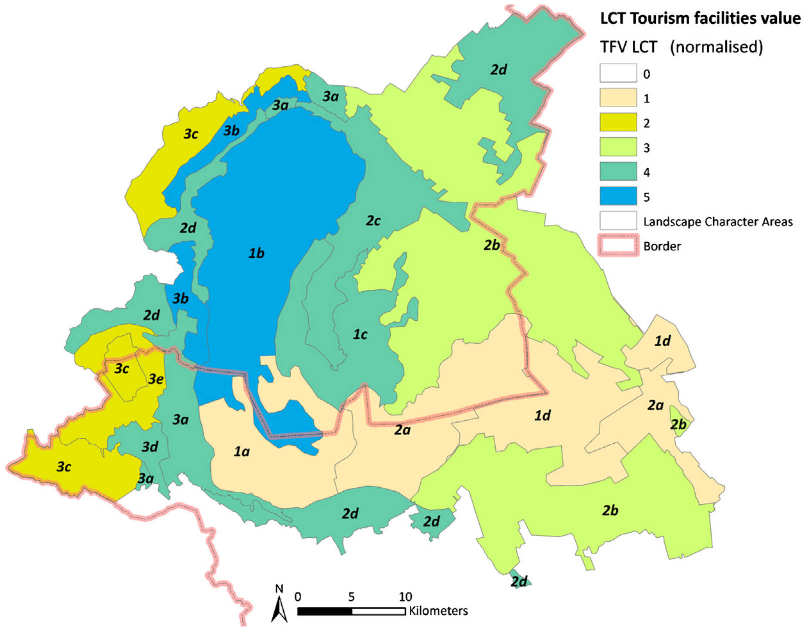

Fig. 5. 'Tourism facilities' service values for each LCT (1a, Lake basin dominated by reed and wetland; 1b, Lake basin dominated by open water; 1c, Satellite lake basin dominated by grassland and divers agriculture; 1d, Marshland dominated by a mosaic of forest, grassland and water; 2a, Reclaimed marshland and lake basin with arable- and grassland dominance; 2b, Flatland dominated by homogenous arable land cover; 2c, Slightly undulating flatland dominated by vineyards; 2d, Slightly undulating flatland with heterogeneous land cover; 3a, Hill range and foothills with heterogeneous land cover; 3b, Hill range and foothill with vineyard dominance; 3c, Low mountains and foothills covered by closed forests; 3d, Foothills and basins with historic towns and peri-urban areas; 3e, Foothills and basins, mainly arable and grassland dominance); 0 = no service provision, 1 = low service provision, 2 = modest service provision, 3 = medium service provision, 4 = high service provision, 5 = very high service provision.

represented the high diversity within the investigation area ranging from natural and semi natural areas such as the shallow lake and its immense reed belt, the remaining marshland and flood plains, the extensively used hilly area up to the intensive agricultural regions in the low lying terraces. Whereas most service values ranged between '0' and '3' the values calculated for the LFT 'Low and middle range mountains' mainly covered by forests resulted in very high *regulation*, *provision* and *habitat* service supply.

The diversifying LFTs 'Lake basin', 'Low lying terrace' and 'Hilly area and hill range' were selected to present the trade-offs between the main service categories (Fig. 7). The *regulation* and *carrier* services comprised the most different landscape services based on very diversifying individual sub-service values within the three selected LFTs (see Fig. 8, 9) The LFT 'Lake basin' presented a high provision of *habitat* and medium provision of *regulation* and *information* services, which was mainly due to the dominating shallow lake surrounded by the reed belt as well as on the natural and

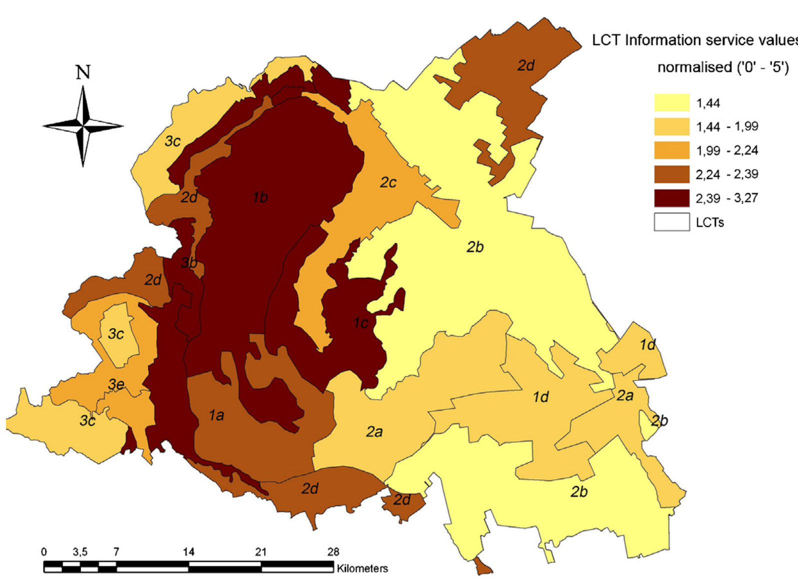

Fig. 6. *Information* service values for each LCT (1a, Lake basin dominated by reed and wetland; 1b, Lake basin dominated by open water; 1c, Satellite lake basin dominated by grassland and divers agriculture; 1d, Marshland dominated by a mosaic of forest, grassland and water; 2a, Reclaimed marshland and lake basin with arable- and grassland dominance; 2b, Flatland dominated by homogenous arable land cover; 2c, Slightly undulating flatland dominated by vineyards; 2d, Slightly undulating flatland with heterogeneous land cover; 3a, Hill range and foothills with heterogeneous land cover; 3b, Hill range and foothill with vineyard dominance; 3c, Low mountains and foothills covered by closed forests; 3d, Foothills and basins with historic towns and peri-urban areas; 3e, Foothills and basins, mainly arable and grassland dominance). The single values were pooled into five groups displaying the range between the lowest value (cold spots) and highest value (hot spots) reached within the investigation area.

Table 2
Aggregated service values of *carrier, information, habitat, regulation and provision* services for the seven Landform Types. The values can range between 0 (no service provision) and 5 (very high service provision).

LFT	Carrier	Information	Habitat	Regulation	Provision
Lake basin	1.15	2.64	3.53	2.66	1.80
Marshland	0.88	1.74	2.80	3.06	1.73
River floodplain	1.51	1.90	1.62	1.77	0.89
Low lying terrace	1.77	1.73	1.67	1.78	0.55
Elevated terrace	1.97	1.87	1.75	1.78	0.58
Hilly area and hill range	1.65	2.59	2.93	2.99	2.45
Low and middle range mountain	0.81	1.90	4.45	4.45	4.12

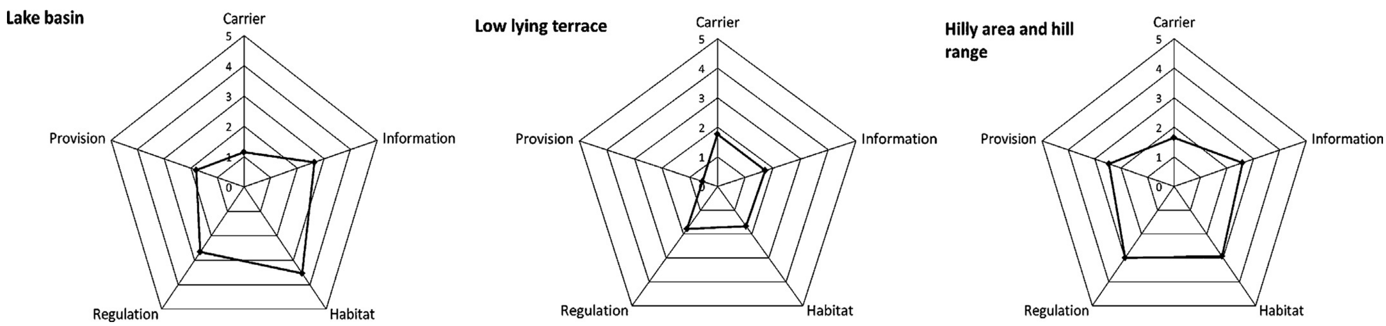

Fig. 7. Trade-offs between the main landscape services: *carrier, information, habitat, regulation and provision* for the LFTs 'Lake basin', 'Low lying terrace' and 'Hilly area and hill range'.

semi-natural area in the southern and eastern part of the Landform Type. These areas are intrinsically providing conservation functions, as they serve as nesting and feeding habitats for colonies of reed-nesting birds (e.g. egrets, spoonbills). Within the *regulation* services the 'water and nutrient regulation' as well as the 'disturbance prevention' services were dominating (see Fig. 8). Although 'tourism facilities' are very important in that area, the *carrier* services had only reached low values due to the low values of the other sub-services ('energy conversion' and 'habitation' services) in that category.

Compared to the other LFTs the 'Low lying terrace' at the same time presented the lowest values of the *provisioning* and *information* and high values of *carrier* services (Table 2). Predominant is the equally flat surface covered by intensive arable land parcels and peri-urban zones with growing horticultural establishments (see high values of 'habitation' and 'cultivation services' in Fig. 9). These areas are less attractive, sharing only little recreational nature conservation potential.

The service values of the LFT 'Hilly area and hill range' were well balanced (Fig. 7) reflecting a diversified landscape including both extensive and intensive rural areas accompanied by some semi-urban settlements. The higher values of *regulation* and *habitat* services were based on the semi open landscape on the western sandstone hill, mainly in Hungary. These landscapes are intensively used mainly covered by vineyards. Tourism is based on the wine culture and the dense cycling road network inserted into the landscape, which led to high *carrier* services.

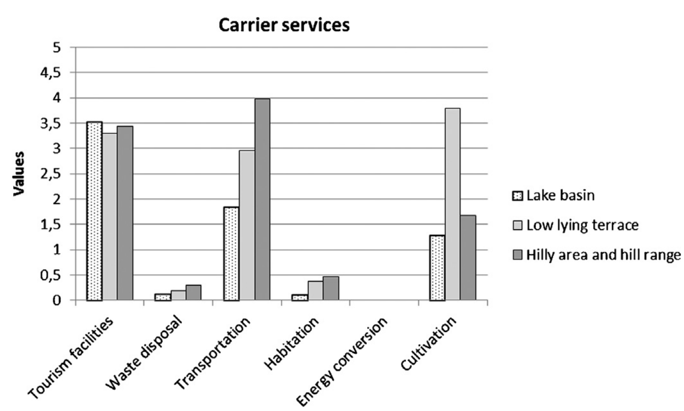

Fig. 9. Distribution of the *carrier* sub-services of the LFTs 'Lake basin', 'Low lying terrace' and 'Hilly area and hill range'.

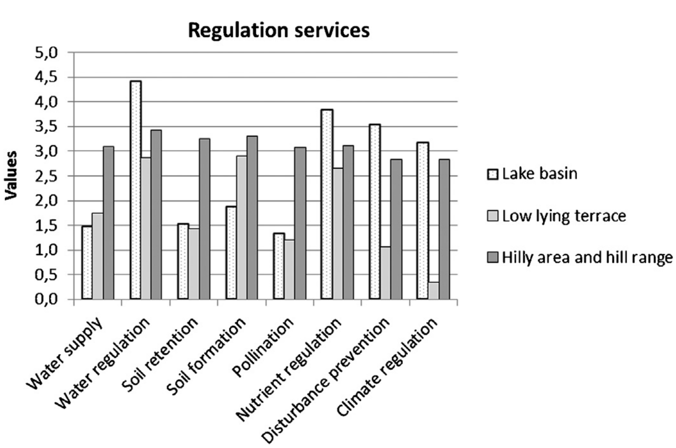

Fig. 8. Distribution of the *regulation* sub-services of the LFTs 'Lake basin', 'Low lying terrace' and 'Hilly area and hill range'.

4. Discussion

4.1. Evaluation of the methodology

Within our study we assessed a wide range of landscape services at different spatial scales to provide a good overview of the services people derive from the investigated landscapes. It has to be acknowledged that the proposed framework is a model of reality trying to reduce the complexity of human-environmental systems in an appropriate, logical and reproducible manner. Hence, generalizations and simplifications have to be tolerated in order to receive a holistic picture of complex systems. As different landscapes have different functions based on their structure and related processes the individual landscape service provision are strongly linked to natural conditions: e.g. water holding capacity, soil conditions, fauna and flora, elevation, slope and climate as well as anthropogenic influences, such as changing land use, greenhouse and aerosol effects. However, finding appropriate indicators related to the specific service providing unit and exploring how functions and services are correlated with different landscape scenarios are still unresolved questions (Seppelt et al., 2011; Wallace, 2007). Current landscape service indicators are still limited by insufficient data and an overall low ability to convey information (Layke, 2009). Therefore, we used an expert driven evaluation in assessing most of the landscape services, extended by empirical data and spatial indicators. Earlier studies have already applied assessment matrices (e.g. Haines-Young and Potschin, 2008; Burkhard et al., 2009, 2011; Koschke et al., 2012), where land cover types were linked by hypothetical values to selected ecosystem service supply capacities. This method enables a rapid service assessment and supplies a good overview to see first trends for landscape service provision (Burkhard et al., 2009). Applying a relative five step scale enables a comparison between the different landscapes providing landscape service by harmonisation of the different indicators, and offers the opportunity to avoid value-laden units, such as monetary terms. However, we are aware, that these expert based values are dependent on the observer's ability to make appropriate evaluations and often lack objectivity. By including additional data from a field survey (for the Broader Habitat Approach) and spatial data (for the Socio-Cultural Approach) into our assessment, we tried to reduce this expert bias. The way forward to explicitly address each subservice would be to develop indicator sets including data from monitoring, measurements, and computer based modelling targeted to each of these. But this would encompass the need of very detailed data and statistical relationships which are not available yet for the wide range of services.

Whereas most previous studies used CORINE data as service providing units (e.g. Burkhard et al., 2009, 2011, Naidoo and Ricketts, 2006; Koschke et al., 2012), we applied land cover data of higher spatial resolution within our Broader Habitat Approach, in order to be locally explicit and further to be able to integrate our approach in regional landscape planning projects. Using habitat specific qualifiers, such as 'habitat structure', 'management', 'pressure' and 'valuable attributes' gives researchers the possibility to identify and quantify site-specific relations between landscape services and the environment. However, to fully assess services, both temporal and spatial scale effects additionally have to be integrated into the assessment framework (Bastian et al., 2012). For instance, *regulation* services can occur both at landscape scale (e.g. water regulation of the whole marshland area) and landscape element-scale (e.g. water holding capacity of a single mire) (de Groot, 1992). Also pressures on ecosystem services can have effects at different scales. In general, physical processes on small scales are often driven by the impact of long term phenomena at larger scales (climate patterns, hurricanes, fires) (Limburg et al., 2002). Hence, for the analyses of the dynamics of service supply it is very important to consider the drivers and processes at scales relevant for service generation. To integrate effects at broader scales e.g. the landscape scale, both spatial configuration of the landscape elements (see Frank et al., 2012), effects of neighbouring features (e.g. power plant) and temporal dynamics have to be considered in future projects.

Embedded within a spatial reference framework the individual landscape services of all three approaches were extrapolated to the Landform Type scale, in order to grasp the main differences between different landscapes and land cover types. Such a spatial framework enabled us to map locally explicit service provision as well as to visualise different service supply at the landscape scale. However, it has to be taken into account that the aggregation of the sub-services to the main 5 services as well as the extrapolation to the Landform Type scale blurred to some extent the picture of the services' provision due to the averaging. Also the effects on the Landform Type scale might be different from that at the Landscape Character Type or landscape sample site scale. Investigations on the extent of service delivery as well as on interactions among multiple landscape services across different scales (Willemen et al., 2010) have to be undertaken by further investigations.

Our approach was based on the assessment of the single subservices that were finally aggregated to the main service groups, which resulted in a loss of information. A sort of weighting of the single sub-services within one main service group could partly solve the problem. Such a weighting might be carried out within a stakeholder workshop. In the present state our levelled [0–5] and aggregated service values only provided information on service provision with limited accuracy (Table 2). This may also be with the reason why the differences between the final main service values are not very big.

Another delicate issue is the proper assessment of socio-cultural (*information*) services. Although such cultural services play an essential part in the enhancement of human welfare, they are only marginally present in the current research activities due to yet unsolved assessment difficulties (Benayas et al., 2009; Vejre et al., 2007; Gee and Burkhard, 2010). Within our Socio-Cultural Approach, the indicator development for the *information* services was highly dependent on data availability. For linear elements, we currently used only the indicator of visually relevant edges in the landscapes. This set could be enlarged by integrating data on e.g. roads with panoramic view or tree rows. Areal indicators would profit from the inclusion of data on accessibility, visibility and diversity of land cover. Unfortunately the lack of data availability limited us to the actual set.

4.2. The concept of landscape services as an operational tool to evaluate ecologically sensitive regions

By applying the proposed methodological framework, users will be provided with information on the landscape without intensive new data gathering. Although the methodology has been specifically targeted to our investigation area, the framework should be applicable in other regions as well. Especially in regions, where data availability on specific landscape services is limited or incomplete (e.g. transboundary areas are often lacking homogeneous data) it would deliver a good overview of the service provision of the different landscapes. Certainly, other areas will require an adaptation of the spatial reference framework as well as of the service providing units and will be also dependent on a certain extent of available data (qualifiers for the Broader Habitat Approach and indicators for the Socio-Cultural and Landform Type Approach). However, there is the possibility to use only one of the proposed approaches to generate information of selected services, depending on the research question.

The service values resulting from the presented methodology may support spatial planners by providing information on service distribution within the target region. Whereas the aggregated results at the Landform Type supply an overview on total service provision, the distribution of the individual sub-services at lager scales (landscape sample sites and LCTs) can provide a detailed insight into the service provisions of landscapes. In this way, areas of high nature conservation value or potential for demographic development can be identified. Especially, for areas with high pressure on land resources, a visualisation of the actual service provision can help policy makers and spatial planners to make informed choices.

The implementation of our assessment framework into participating sustainable landscape planning has already started within our investigation area. We tried to integrate the landscape service concept into the establishment of the nature conservation and regional development project: 'Biosphere Reserve Neusiedler See'. According to the Statutory Framework of the World Network of Biosphere Reserves, the recognition of new and already existing Biosphere Reserves requires, among other things, 'the involvement and participation of a suitable range of inter alia public authorities, local communities and private interests . . .'(UNESCO, 1996: 17, Art.4, 6). Only the involvement and participation of the resident population and all stakeholders could increase the acceptance and traceability of decisions, strengthen the identification of citizens and stakeholders with decisions, as well as increase confidence in politics and public administration (Standards der Öffentlichkeitsbeteiligung, 2008). Therefore, to promote the expansion of the territory of the already existing Biosphere Reserve 'Neusiedler See' and the implementation of the Seville Strategy, representatives of important interest groups, landowners and NGOs were involved in an opinion-forming process. The stakeholders were asked to discuss and evaluate some of the related services of different types of landscapes within the region 'Neusiedler See', in order to identify sensitive areas, where land use pressure is very high. Preliminary results of discussions showed that the landscape service concept has potential to be the basis of a participatory approach, but still needed to be further developed to be used as a successful communication tool. In following projects an advanced version of the proposed framework is planned to be developed, in order to be applied for finding an overall concept for the Biosphere Reserve 'Neusiedler See'.

5. Conclusions

Embedded in a spatial reference framework a good overview of the distribution of the different landscape services within the transnational study area could be provided. Additionally Hot as well as Cold spots of the individual service provisions were identified. Thus, the concept of landscape services might be a useful tool to evaluate sensitive regions and provide a basis for cross border landscape planning decisions. Applying such a spatially explicit methodology provides useful information on how spatial patterns contribute to different service provision. Whereas in most cases homogenous landscapes only emphasise on one specific landscape service, complex landscapes reveal a more diversified picture. However, for more detailed analyses further investigations, especially on scaling effects and spatial characteristics as well as interactions between the different services have to be conducted. Making landscape services spatially explicit and combining empirical data with spatial information offers an innovative approach to landscape research in the field of visualising the provision of landscape services. While most other assessment methods only focus on selected services occurring at one scale, we present a first step in the methodological development to assess and map spatial variability of landscape services.

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Section A

Article 3 (iii)

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Do landscape patterns reflect ecosystem service provision? – A comparison between protected and unprotected areas throughout the Lake Neusiedl region

Michael Kuttner, Anna Schneidergruber & Thomas Wrbka

Keywords: ecosystem services, landscape indices, biodiversity, green infrastructures, sustainability

Abstract

Nowadays, anthropogenic landscape fragmentation and land-use change are recognized as major driving forces for the ongoing worldwide loss of biodiversity. Though nature conservation areas, such as Austria's national parks, serve as retreat habitats for a broad range of biota, they are embedded in a complex of landscapes where diverse conflicts of interests meet, for instance tourism, agriculture and nature conservation. As a first step to improving the multifunctional quality of landscapes in terms of connectivity and flows of energy, material and information across the boundaries of protected zones, the status quo of such landscape mosaics has to be evaluated. The main aim of this study was to test if protected areas generally supply a higher share of environment-related ecosystem services than the surrounding landscape. We also investigated to which extent the structural composition and configuration of landscape sections reflects their volume of ecosystem service provision. We selected our study sites within the Austrian-Hungarian transnational study region around Lake Neusiedl and developed a methodological framework for assessing and mapping ecosystem services based on expert knowledge, spatial information and field data. The crucial linkage between landscape structure and its contribution for sustaining distinct ecological key functions was investigated through comprehensive use of landscape metrics, habitat and connectivity mapping. We were able to verify that levels of ecosystem service provision as well as the share and function of ecologically viable landscape elements were higher within the national park and that a statistical correlation between the aforementioned assessments exists. The outcomes of this study may support local stakeholders with valuable information on the service provision capacity and functional state inside and outside protected landscapes and illustrate hot and cold spots of network patterns. This in turn will allow the development of well-focused and efficient planning measures to strengthen ecosystematic functioning in terms of sustainable landscape development vis-à-vis society.

Profile

Protected area

Lake Neusiedl / Fertö Hanság National Park

Country

Austria & Hungary

Introduction

In recent decades the demand for natural resources has grown considerably due to exponential economic growth, resulting in an enormous pressure on the earth's ecosystems. As a consequence, our society is faced with various negative impacts on the environment, such as habitat loss, fragmentation and degradation, climate change, biological invasions, overexploitation and pollution at global, national and regional level. European cultural landscapes in particular are characterized by a high level of anthropogenic fragmentation and habitat loss which are known major reasons for the decline of biodiversity in industrialized countries and also have a negative influence on ecosystem service provision (Walz & Syrbe 2013). Old cultural landscapes, on the other hand, which have been shaped and used for centuries, like the region around Lake Neusiedl, are composed of a mosaic of different habitat types reflected in a highly diverse landscape structure. Based on these geometrical aspects, which can also be regarded as *frozen processes* (Wrbka et al. 2004), the crucial relationship between structural patterns and functional indicators in landscapes has been stressed repeatedly (Forman 1995; Turner et al. 2001; Moser et al. 2002; Blaschke 2006; Walz 2011). Such multifunctional landscapes not only share a rather high potential for biodiversity and ecosystem functioning but are also beneficial for society (Otte et al. 2007).The concept of ecosystem services is said to have great potential for adding value to current conservation approaches, in particular for local and regional planning (Maes et al. 2012; Chan et al. 2006; Daily & Matson, 2008; Nelson et al. 2009; Egoh et al. 2009). However, this potential remains poorly explored across Europe (Haslett et al. 2010; Harrison et al. 2010). Therefore we have investigated the relation of two promising options to provide a knowledge basis to meet the needs of sustainable landscape development and conservation management inside and outside protected areas. While Kuttner et al. 2013 introduced an assessment of structural landscape functionality that has been devel-

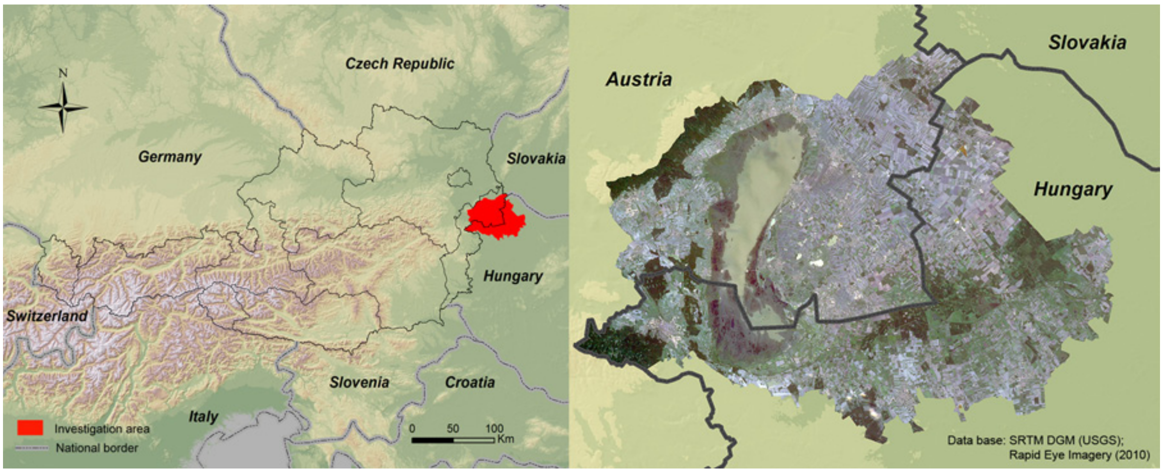

Figure 1 – Location of the study area within the cross-border region of Austria and Hungary.

oped to provide a comprehensive overview of location and quality of ecologically valuable landscape elements and networks, Hermann et al. (2014) created a flexible approach for mapping and spatio-thematic aggregation of various ecosystem services (ESS). Both assessments were conducted on the same sample plots throughout the transnational study region around Lake Neusiedl.

The main aim of our study was to find out if ecosystem service provision differs significantly, depending on status and category of protection, with a special focus on Lake Neusiedl / Fertö Hanság National Park (NP). As stated by Syrbe & Walz (2012), structural configuration and land-use regimes have a strong influence on several ecological key processes which have been quantified by ESS evaluation. We also tested if a statistical relation existed between the results of the former studies and identified hot and cold spots of ESS supply, which we subdivided into the main groups of *Provision*, *Habitat* and *Regulation* services. We tested the strength and quality of coherence between them and the outcomes of the structural assessment on landscape functionality. Innovative conservation assessment and planning may benefit from this approach because it allows for an integrative evaluation of conservation areas and their contribution to human wellbeing (Chan et al. 2006; Egoh et al. 2008).

Study region

The investigation area of approx. 2015 km² is located on both sides of the border between Hungary and Austria (see Figure 1). Therein the cross-border Lake Neusiedl / Fertö-Hanság NP, founded in 1993, covers an area of around 90 km² in Austria and 230 km² in Hungary. At 114 m, Austria's lowest elevation (47° 44.1' N, 16° 51.8' E) is situated in the centre of the study area near the village of Apetlon.

The predominant climate is Pannonian, with annual precipitation rates around 600 – 800 mm and an annual mean temperature of > 9 °C (ZAMG 2002). The continental lake basin between the Alps and the Carpathians is a north-western overhang of the Small Pannonian Plain at the foothills of the Leithagebirge and the Ruster Hügelland.

Lake Neusiedl and a series of small satellite lakes on the eastern part, the Seewinkel area, constitute the westernmost alkali lakes in Europe and the semi-natural zone around them still forms Europe's second largest reed wetland vegetation, which is one of the most important bird sanctuaries in Central Europe, both for breeding and migratory birds. Beyond the wetlands the area includes extremely rich habitats, presenting a transition zone between the mountain ranges and the lowlands of the Pannonian Basin. From the unique dry alkaline steppe up to the closed deciduous forests, a series of different vegetation types results in a high level of landscape diversity, also promoting biodiversity as such. Due to the biocultural richness of the region, a series of other nationally and internationally protected areas, such as species management areas (IUCN Cat. IV) and protected landscapes (IUCN Cat. V) (Dudley 2008), Natura 2000 sites and a transnational biosphere reserve that covers the entire surface area of the lake have been created here. While these sites largely overlap the outer zones of the NP, they add support to sustainable landscape management strategies inside the park. In contrast, the rather dispersed Natura 2000 network ensures target-oriented protection of single species, e. g. the Great Bustard (*Otis tarda*), and their required core habitats beyond the NP boundaries. Further, the entire Lake Neusiedl plus its adjacent reedbelt, covering a total area of over 440 km², have been added to the list of internationally important wetland ecosystems by the RAMSAR convention in 1983. Finally, the Fertö-Lake Neusiedl region was designated a UNESCO World Heritage Site in 2001 to foster the preservation of the traditional cultural landscape and to support sustainable regional development.

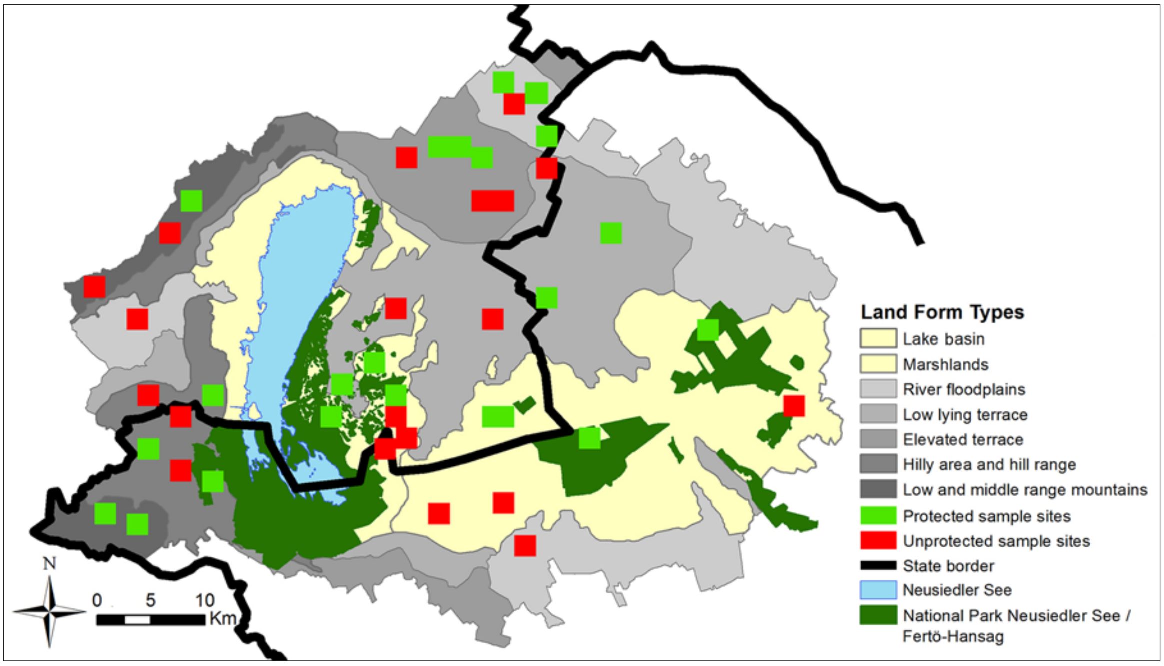

Figure 2 – Overview of the entire study region, including the division into LFTs and location of local sample sites. Lake basin and Marshlands are highlighted on the map and cover the area of the NP.

Methods

Landscape division and local site sampling procedure

In order to reach statistically neat results that could be scaled up and compared, we developed a common spatial reference framework, including a nested sampling design for the selection of test sites, which followed several stratifications. As a prerequisite, the region was subdivided into seven Land Form Types (LFTs) (Konkoly-Gyuró et al. 2010). These LFTs are expressed by geomorphological peculiarities that form the characteristic shapes of the target region and result in greatly varying land-use strategies: Lake basin, Marshlands, River floodplains, Low lying terrace, Elevated terrace, Hilly area and hill range, Low and middle-range mountains. Within each LFT, we randomly selected six 2 x 2 km^2 sample sites by applying a predefined set of exclusion criteria, including inaccessibility of NP core zones or minimum distance to adjacent villages. The final set consisted of a balanced proportion of sites located inside or outside protected areas (Figure 2).

Assessment of structural landscape functionality

We delineated single landscape elements across all sample sites through object-based image analysis of the latest available orthophotos and manually corrected spatial misclassifications afterwards by on-screen digitizing. Then we applied a key for visual land cover interpretation, where the CORINE land cover interpretation system served as thematic basis to identify 65 different land cover classes. The resulting land cover maps were used for landscape structure analysis, where we first calculated a comprehensive set of 46 landscape metrics at class level using Fragstats 3.3 (McGarigal et al. 2002) and computationally reduced them to 21 by sorting out all highly correlated metrics after conducting a rank-based correlation analysis in R 2.7.1 (R Development Core Team 2008). Then we performed a Principal Component Analysis to detect the metrics that emerged as most important in describing variance throughout the input dataset. We then compared these outcomes with other recent literature and reduced the final set of metrics to 13. This core set of indices is subdivided into AREA (mean patch area; largest patch; total class area), SHAPE (area-weighted mean shape; landscape shape index; mean fractality), CONNECTIVITY (mean proximity; connectance; contiguity), ISOLATION (patch density; Euclidean nearest neighbour; aggregation index) and CORE (mean core area). For a differentiated assessment of the landscape's ecological state based on its underlying structural features, we sectioned the different land cover classes into six discrete functional groups (connecting corridors, dissecting corridors, valuable matrix, disturbed matrix, artificial matrix, stepping stones) and set up a classification scheme where positive or negative relations between the selected metrics and each functional group were assigned in terms of quantifying structural landscape functionality. In case of ambiguous or negligible relations, we excluded the relevant metrics from subsequent group calculations. In order to reach one final functionality value per sample site, we transformed and rescaled metric values per group, with a range of 0 – 100 for positively correlated or 100 – 0 for negatively correlated metrics, and summarized their outcomes per site. Further, to detect most valuable Green Infrastructure (GI) elements and ecologically valuable network structures,

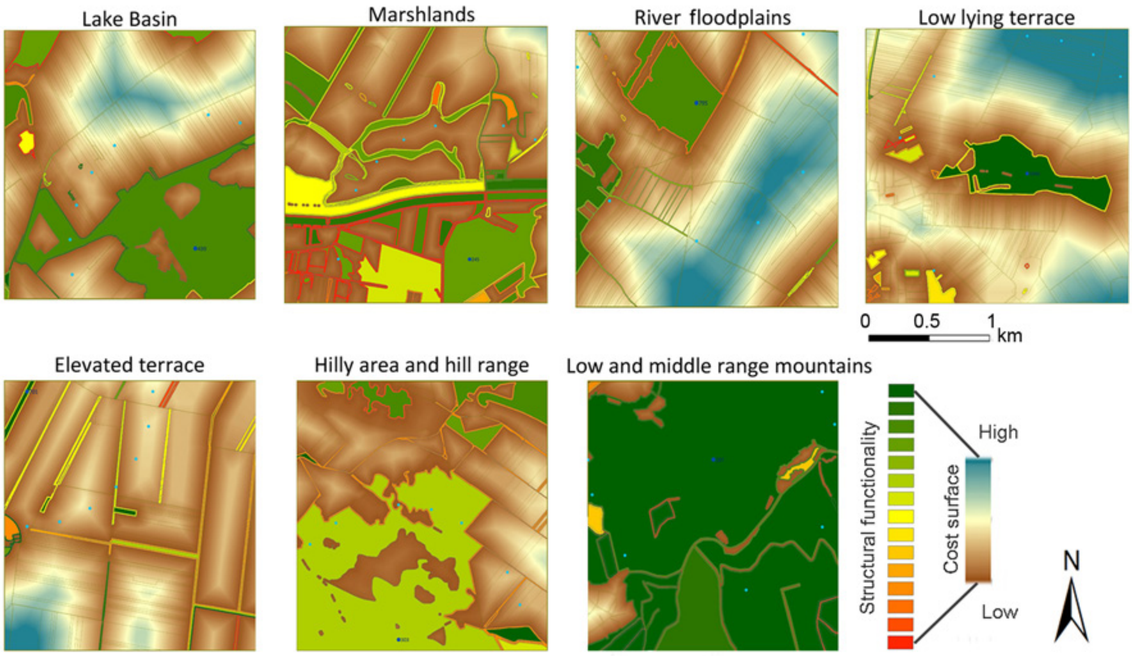

Figure 3 – Combined landscape functionality maps for each LFT, visualizing GI networks and results cost surface modeling approach.

we performed a morphological spatial pattern analysis plus additional cost surface mapping for a predefined virtual species group we called *specialists*, which would require less or non-disturbed parts of the landscape as their living space. At this, we set up a series of seven way points located at a standardized distance (=1 km) from the centroid point of the largest GI element per sample plot and simulated least cost path walks to each point. The parameterization quantifying accessibility of the various landuse types to cross have been specifically suited to our target species group and consequently one final least cost path value per plot has been generated by calculating the mean out of the seven single walks. For further details on the previously described technical part of this study, please also refer to Kuttner et al. (2013).

Evaluation of ecosystem services

We also assessed and mapped 14 ESS within the aforementioned spatial reference framework for each sample site of the single LFTs. The ESS were grouped into three main service categories: Regulation (local climate regulation, disturbance prevention, water regulation, water supply, soil retention, soil formation, nutrient regulation, pollination), Habitat (sanctuary, nursery) and Provision (wild plants and game, raw materials, genetic resources, medicinal resources) (mainly adapted from de Groot 2006). To distinguish different service providing units, we used the Broader Habitat Type (BHT) classification system (Bunce et al. 2008, 2011). BHTs were linked to their capacities for providing various ESS by an expert-based classification system, on a scale of 0 to 5, with the highest value denoting the closest general relation between the BHT and its related service. This so-called Broader Habitat Approach (Hermann et al. 2014) is based on a capacity matrix, with values altered by semi-quantitative field data (qualifiers). These qualifiers describe *in-situ* characteristics of single service providing units (landscape elements) with regard to their structural peculiarities, management practices and disturbance regimes. We then aggregated the service data into the main service categories and extrapolated them to gain statistically comparable results between the LFTs and protected and unprotected areas.

Interrelation of the assessments and comparison between areas of different protection status

In order to test if the outcomes of the two divergent assessments were pointing in the same direction, we conducted various univariate and multivariate linear regression analyses to identify both single and main ecosystem services that are correlated with structural landscape functionality and the share of green infrastructure networks.

In a separate step we tested if protected landscapes could be distinguished from non-protected areas in terms of service provision by applying a series of One-way Analysis of Variance (ANOVA) tests.

Results

Results of the structural functionality assessment

The combined outcomes of the structural landscape functionality assessment are represented in Figure 3, including sample GI maps for each LFT. Ecologically most valuable GI networks and corresponding functionality rating, which would serve as potential habitats and migration corridors for the virtual *specialist* species group, are marked. In the background, outcomes of the cost surface modelling approach are outlined, ranging from areas that are easy to cross (brown) to barriers (blue).

Results of the coparison of ESS provision in protected and unprotected areas

The resulting boxplots (Figure 4) represent LFT-based mean service values for the main categories of *Regulation, Habitat* and *Provision*.

The course of the lines is quite similar, reflecting that the three environment-related service categories are positively correlated to each other and that there are no specific trade-offs between them. However, the importance of the single main groups is different. Whereas the main services *Regulation* and *Habitat* ranked close to each other, the *Provision* services resulted in distinctly lower values. Considering the different LFTs, outcomes reflected the high diversity within the study area, from natural and semi-natural areas, such as the shallow lake and its reed beds, the remaining marshland and flood plains, to the extensively used hilly area and the intensive agricultural regions in the low-lying and elevated terraces. Results of ANOVA testing confirmed significant differences ($p \leq 0.05$) throughout main service values across the single LFTs.

When comparing main service values of protected and unprotected sites within each LFT, most of them differed significantly. However, of the protected sites only Marshlands and Lake basin resulted in clearly higher values ($F = 6.7902$; $p \leq 0.001$) for all ecosystem main services compared to the unprotected sites. These LFTs are particularly interesting with regard to their conservation value as large parts are covered by Lake Neusiedl / Fertö-Hanság NP (see also Figure 2). Another series of ANOVA testings also pointed to significantly increased levels of structural functionality ($p \leq 0.001$) and share of GI elements ($p \leq 0.05$) within the NP territory.

Comparison between ecosystem services and structural landscape functionality

The scatterplots displayed in Figure 5 represent results of three different regression analyses that tested the dependency of main ecosystem services from the outcomes of the survey on structural landscape functionality, which are based on mean values of the single sample sites ($n = 41$). Relations proved to be significant ($p \leq 0.001$) in all cases and the strength of the statistical models ranged from corr. $r^2 = 0.691$ for the main service Habitat to corr. $r^2 = 0.737$ for Regulation and corr. $r^2 = 0.802$ for Provision.

The performance of a stepwise multivariate regression analysis, where all subservice variables ($n = 14$) were chosen as predictors at once, resulted in corr. $r^2 = 0.875$ for the four service variables of Soil retention (Regulation), Sanctuary (Habitat), Food and Genetic resources (both Provision) for the final model. A second multivariate regression analysis that focused on the relation between subservice values and GI network area returned corr. $r^2 = 0.862$ using 8 out of 14 variables. The majority and most influential ones of those, when referring to the summary of the stepwise regression, belonged to the main group of Provision services.

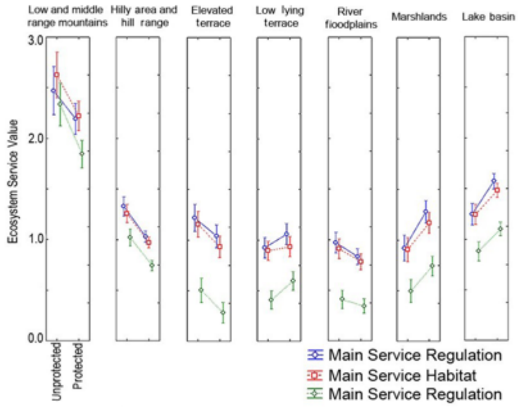

Figure 4 – Boxplots of ANOVAs targeting main service distribution between individual LFTs and subdivided into protected and unprotected areas. The NP is located in the LFTs Lake basin and Marshlands.

Discussion

The remarkable higher outcomes of both ESS and structural functionality assessments within the protected sites of the LFTs Marshlands and Lake basin (Figure 4) might be due to the fact that most of these subregions are covered by Lake Neusiedl-Seewinkel / Fertó-Hansàg NP and thus follow a broad conservation concept with core areas and buffer zones. Figure 6 exemplifies the outcomes of the structural functionality and ecosystem service assessments for the LFT Lake basin. However, non-protected areas within these LFTs also range above average in ESS supply, leading to the assumption that large and effectively managed nature reserves support ESS supply beyond its borders. Apart from those cases, the majority of LFTs showed a rather unclear and partly contrasting picture of ESS provision inside and outside local protected zones. There are several possible explanations for this:

- Some protected area categories, such as the protected landscapes (IUCN Cat. V) or biosphere reserve buffer zones, only prescribe minor conservation conditions for local land use and forestry.
- Other special protection areas, e.g. those under the EU Birds Directive, often follow specific management plans to foster local populations. In the Lake Neusiedl region, protected nesting areas of the Great Bustard (*Otis tarda*) located in LFT Elevated terrace demand an open and extensively utilized agricultural matrix without high proportions of corridor networks and stepping stone elements. In turn, this leads to comparatively low structural landscape functionality (Kuttner et al. 2013) and mediocre provision of Regulation, Habitat and Provision services in the protected parts of this LFT.

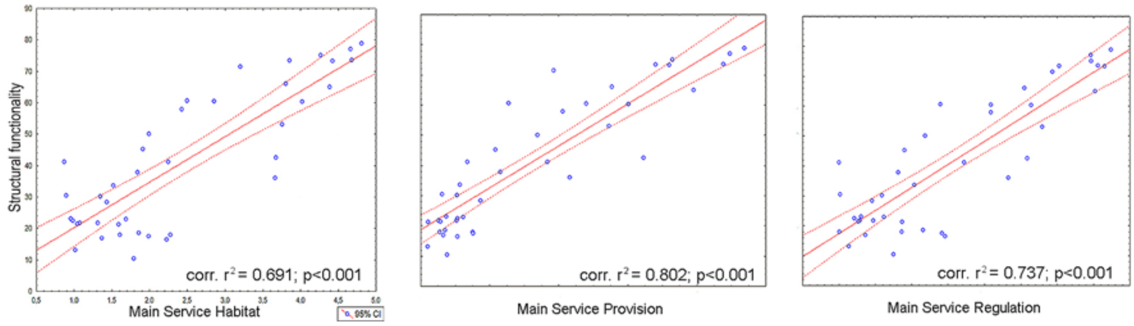

Figure 5 – Three scatterplots visualizing outcomes of linear regression analyses between structural functionality and ecosystem main services.

- Privately owned land like the extensive oak-hornbeam forests in the Leithagebirge region enjoy no protection status. Hence, within the LFT Low and Middle range mountains with its vast private forest stands, the protection status might not be a determining factor for ecological quality and ESS provision. The fact that some of the sample sites within the LFT Elevated terraces also include large privately owned forest areas explains the rather high values within the unprotected areas.

However, ESS provision did not turn out to be significantly higher in some of the protected areas within the single LFTs. Distribution of GI elements and structural functionality values consistently showed higher outcomes. While the investigated ESS main groups are rather highly correlated to the outcomes of the structural assessment, not all of the single subservices showed such strong interdependency and thus cannot be explained by structural proxies only, as Syrbe et al. had already found in 2012. For example, abiotic services such as climate-, nutrient regulation or soil formation shared a rather high service potential in non-protected but still sustainably managed areas as well. Nevertheless, both assessments are strongly correlated as most ecologically valuable elements share a rather high potential for providing the investigated ESS. As our results confirm, land management generally does not seem to be overexploitative in the region, especially in non-favourable sites (e.g. wooded slopes and wet or dry areas that have not been reclaimed / drained). On the other hand, areas that have been intensively used for decades, such as the LFTs Low terrace and Elevated terrace, performed least well, both in ecosystem service provision and structural functionality. Future management of ecosystems to enhance their functioning and service provision must consider the trade-offs between the different services. While we found positive correlations between ecologically valuable areas and the supply of the environment related services, traditional food production and services of crops and livestock are likely to be higher in intensively used areas (Hermann et al. 2014; Maes et al. 2012).

Our results are congruent with the outcomes of a global study carried out by Naidoo et al. (2006), in which they demonstrated that regions selected to maximize biodiversity do not provide as many ecosystem services as regions chosen randomly. However, it strongly depends on the target of the respective conservation area. Despite the lack of general concordance, win-win areas – regions important for both ecosystem services and biodiversity – could also be identified, especially on smaller scales. However, the results might be biased by the methods chosen to assess ecosystem services. As some services, such as providing a sanctuary, are locally explicit, while other services, such as climate regulation, occur on a regional scale (Hermann et al. 2011), it is difficult to assess a wide range of services within a specific service providing unit, e.g. a conservation area. Bridging the gap between different approaches to conservation and adaptive management of ecosystems to support service provision is part of new global and regional biodiversity policies. However, levels of congruence between biodiversity and ecosystem services are poorly understood, and the little quantitative evidence available so far has led to mixed conclusions (Chan et al. 2006; Metzger et al. 2006). According to the Convention on Biological Diversity's definition of biodiversity and the UK National Ecosystem Assessment report, biodiversity may act as a regulator of underpinning ecosystem processes as a final ecosystem service and as a good that is subjected to valuation, whether economic or otherwise (Mace et al. 2012). Thus, to really understand this complex relationship, we need to develop an interdisciplinary science of ecosystem management, bringing together ecologists, conservation biologists as well as resource economists. Despite these challenges, comparisons between biodiversity-related and ecosystem service assessments have the potential to viably support decision-making processes. More research on the quantification and mapping of ecosystem services would improve our understanding on synergies and trade-offs between services and biodiversity. Sustainable development should involve managing for both in order to enhance human welfare that is linked in diverse ways to biodiversity, conservation and ecosystem services (Naidoo et al. 2006).

Applicability and outlook

Although the methods of the ESS and structural landscape functionality assessments have been specifically targeted to our study region, their overall framework will be applicable in other areas as well. Particularly in protected mountain landscapes, various biotic and abiotic base datasets are often available even on a broader scale, but quantification of specific ESS is still limited or incomplete. There the use of regionally adapted capacity matrices, including appropriate land cover classes, would provide a good overview of trends in ESS provision along and between entire mountain regions. Similarly, the structural assessment of landscape functionality along with the identification of key landscape elements and GI networks for certain target species or guilds could be established. Together, these concepts allow a comprehensive insight into the mutual benefits that landscapes can provide for both society and nature if sustainable development and use of natural resources is guaranteed. As the proposed methods are comprehensible as well as easily applicable along a wide range of different landscapes, it seems that they are well suited for integration into existing ecosystem monitoring techniques.

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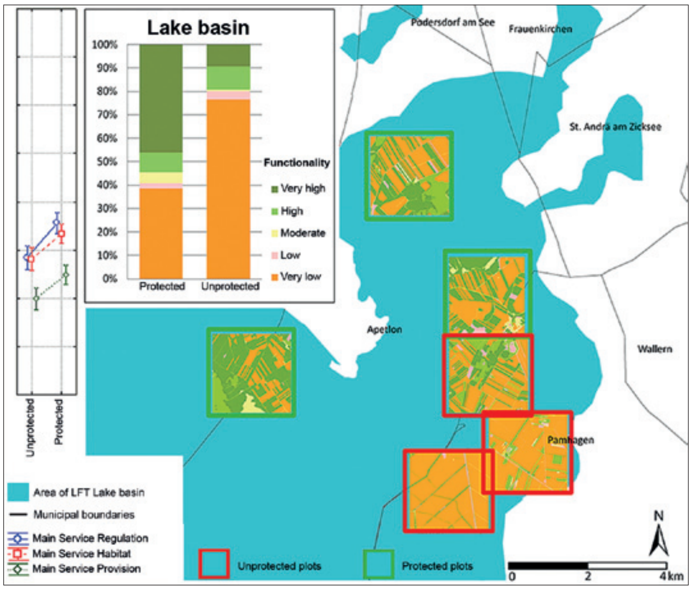

Figure 6 – Overview of the sample plots selected in LFT Lake basin and corresponding structural functionality (histogram) and main ecosystem service distribution charts (boxplot – see also Figure 4), distinguishing between protected and unprotected sites.

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Section A

Article 4 (iv)

Hainz-Renetzeder, C., Schneidergruber, A., **Kuttner, M.**, Wrbka, T. 2015. *Assessing the potential supply of landscape services to support ecological restoration of degraded landscapes: A case study in the Austrian-Hungarian trans-boundary region of Lake Neusiedl.* Ecological Modelling, 295, 196-206.

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Assessing the potential supply of landscape services to support ecological restoration of degraded landscapes: A case study in the Austrian-Hungarian trans-boundary region of Lake Neusiedl

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ABSTRACT

The concept of ecosystem functions and services has increasingly gained attention in the scientific and political community in the last decade. Lot of work has been performed to assess the actual delivery of different services for society. Still, the reference of the landscape's potential to supply these actual services has not been investigated satisfactory so far. We thus aimed at assess the potential supply of landscape services in the study area of Lake Neusiedl in Austria – a region of acknowledged diversity and environmental quality – and compared these to the actual ones. We did this by setting up a map of constructed vegetation type where physiographic site conditions were used to calculate potential land cover in the area in GIS. These constructed vegetation types were linked to landscape services within a capacity matrix giving a weight between 0 (no supply) and 5 (high supply) to which amount one type can provide each single service. The resulting map showed large differences in areal extent of the different vegetation types reflecting the different landscapes in the region such as the dominance of forest steppe in the terraced landscapes or the occurrence of halophytic vegetation only in the lake basin. The same is true for the different landscape services. Some services like 'nursery' and 'raw materials' were quite highly provided throughout the area with values between 2.12 and 4.84, whereas 'genetic resources' and 'pollination' were only little provided (all values <2). On the other hand, functions like 'nutrient regulation' or 'refugium' exhibited their large potential with values >4 in the study area. The aggregation of the services by averaging values to finally derive three main service groups gave the highest values always to *habitat* (values between 3.1 and 4.8), followed by *regulation* (2.5–4.2) and then *provision* (1.9–3.2). Comparing the potential with the actual service supply, nearly all landscapes in the study area resulted in higher potential than the actual service supply. We further discuss possibilities to use the potential supply as a leitbild where restoration projects might be settled in the study area even though more detailed local data will be needed to set these projects up.

1. Introduction

The concept of ecosystem functions, goods and services (MA, 2005) is an approach widely debated at the moment to quantify and to value the benefits ecosystems and landscapes provide to society. As such it is also highly dynamic with many publications and insights in a rather short period (e.g. Boyd and Banzhaf, 2007; Burkhard et al., 2013; Costanza et al., 1997; Daily and Matson, 2008; De Groot et al., 2002; Hermann et al., 2014; Willemen et al., 2012). In particular, since the release of the Millennium Ecosystem Assessment report (MA) in 2005 it has gained increasing attention and importance in science and policy in respect of natural resource management decision making. On a global scale one of the most recognized publications is The Economics of Ecosystems and Biodiversity TEEB (Kumar, 2010), while at national scale it is the United Kingdom National Ecosystem Assessment (Bateman et al., 2011).

However, despite all such efforts in making the performance of ecosystems and landscapes popular, we are still far from a sustainable use of our natural capital. Instead we notice an increasing degradation of ecosystems and its natural assets worldwide (Heinberg, 2010). One most likely reason for this is the absence of ecosystem service values in environmental planning processes. Current approaches to integrate the concept into environmental planning seem to be insufficient in supporting decision processes

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about changing the landscape to improve ecosystem service supply.

From a European perspective, the biodiversity strategy of the European Union (EU) to 2020 demands improving the knowledge of ecosystem services and obliges its member states to map and assess the state of ecosystems and their services in their national territories by 2014. Following the EU biodiversity target 2 the member states have to preserve and enhance the supply of ecosystem services and are required to restore at least 15% of degraded ecosystems. According to the Society for Ecological Restoration (SER) both the protection of biodiversity and the sustainable provision of the necessary functions and services for human survival can be achieved by restoring ecosystems (Benayas et al., 2009; Palmer and Filoso, 2009). Ecological restoration means either removing the original cause of damage and let the system to recover on its own (passive recovery) or actively supporting the system to recover (active restoration) (SER, 2004). In particular, restoration projects with special focus on the enhancement of ecosystem services are seen as a major opportunity to reconnect people with nature and to simultaneously justify the need for restoring the damage humans have caused. As underlying ecosystem processes and consequently ecosystem services change with different restoration options, specific restoration goals have to be defined (Jones, 2013). In the quest for the optimum restoration target different environments however require different solutions. One possibility is to follow a 'landscape potential' oriented restoration process (White and Walker, 1997). This is also the reason why we chose the term 'landscape services' instead of 'ecosystem services'.

According to Bastian et al. (2012) the 'landscape potential concept' developed by landscape ecologists in the 1970s might offer such an alternative to set sustainable use levels. As Bastian et al. (2012) explained, the origin of this concept can be traced back to Bobek and Schmithüsen (1949), but Lüttig and Pfeiffer (1974) have first published 'maps of natural landscape potentials' (cp. Durwen, 1995; Leser, 1997). Focusing more on social and economic processes Neef (1966) defined a '(regional) economic potential of a landscape' which was further developed by Haase (1978). When addressing the issue on landscape's potential, it is very much driven by the reference scale which needs to be set. One way would be to look at former time points and compare land use systems and related land consumption (Biró et al., 2013; Frondoni et al., 2011; Prinz et al., 2010). This implies that former land use was oriented at the potential of the landscapes (Biró et al., 2013; Frondoni et al., 2011). As natural systems, whose components are the result of natural selection, are supposed to be ecologically sustainable (Ewel, 1999), we choose another way by excluding land use at all and try to derive the potential of the landscape regardless of any human activity.

Zampieri and Lionello (2010) stressed the fact that land cover types are closely connected to vegetation types, as vegetation together with urban areas, lakes, glaciers and ice caps are the characterizing key elements of the land surface. This concept very much refers to the concept of Potential Natural Vegetation (PNV), originally described by Tüxen (1956) and further developed by several authors, as described in detail by Chiarucci et al. (2010). The PNV concept is very much disputed in literature and its applicability is questioned by several authors (Chiarucci et al., 2010; Zerbe, 1998) whereas other authors strongly support the concept (Loidi et al., 2010). Despite the criticism mainly due to the hypothetical nature of the concept and its related methodological problems, Somodi et al. (2012) stressed the usefulness of PNV as a null model. Many studies documented the applicability of the concept, mostly to obtain the reference of potential distribution pattern of vegetation communities with the objective to develop reference lines for climate change studies (e.g. Franke and Köstner, 2007; Zampieri and Lionello, 2010), to provide a biogeographic classification (Vuerich et al., 2001) or to support decision processes in landscape planning (Brzeziecki et al., 1993; Liu et al., 2009, amongst others).

In principle, there are two ways of approaching the potential distribution of vegetation communities: either by setting up (i) equilibrium vegetation or biome models (e.g. Haxeltine and Prentice, 1996) where ecological and physiological processes are simulated until an equilibrium with climate variables are reached; or (ii) statistical models which apply relationships between site variables and observational data (Brzeziecki et al., 1993; Franke and Köstner, 2007; Liu et al., 2009; Miller and Franklin, 2002; Vuerich et al., 2001, amongst others).

In this context, we want to follow a more straight-forward, pragmatic approach where on the one hand statistical relationships of existing vegetation data cannot be used because of too little field data on natural vegetation in the area. But on the other hand, geographical and GIS-compatible data (geodata) on ecologically relevant site conditions can be applied to develop vegetation-site relationships and thus potential land cover. These relationships between community types and their environment are often presented as graphical ecological schemes which are called 'ecograms' (Brzeziecki et al., 1993; Ellenberg, 1988). We want to avoid using the term Potential Natural Vegetation because (i) of the outlined conceptual problems and (ii) of insufficient reference data on climax vegetation in the area. Thus PNV might be misleading and we introduce here the term "constructed vegetation types". We use geodata on current site factors to construct vegetation-site relationships for broadly defined vegetation types. In these terms we follow Somodi et al. (2012) who suggested a transparent and formalized estimation of potential vegetation by clearly defining the natural site factors which act as predictors. A similar approach was also proposed by Chytrý (1998) with the concept of Potential Replacement Vegetation.

In this article, we aim at mapping ecologically homogeneous units, each of them populated by a specific vegetation type and presenting a map of constructed vegetation types that are based on geodata on current site factors in the region of Lake Neusiedl. Most literature is targeting at the actual supply of services which can be yielded at the moment (Alkemade et al., 2014; Kroll et al., 2012; Nedkov and Burkhard, 2012; Seppelt et al., 2012). But this may not be in line with the potential supply of services which can be provided based on differences in site conditions.

Therefore, based on this map, we are further aiming to assess the potential supply of landscape services. We will test if the potential supply of services based on land cover regardless of any human activity is different from the actual supply of services based on current land use data. We also want discuss if the potential landscape can be used as a 'Leitbild' (Gerhards, 1997) for ecological restoration in the region Lake Neusiedl.

2. Materials and methods

2.1. Study area

The project region covers the Austrian-Hungarian transboundary region of the Lake Neusiedl/Fertő extending over 2000 km^2. It is part of the Small Hungarian Plain in Central Europe representing the westernmost extension of the Pannonian Basin. Konkoly-Gyuró et al. (2010) defined seven so-called landform types, describing the main geomorphological relief features in the area (Fig. 1). The "Lake basin" embedding the shallow Lake Neusiedl in its centre is dominating the landscape view. Geological, climatic and geomorphological conditions have led to soda accumulation in the soil and to the existence of salt pans (alkaline waters). East of the lake, the landscape mainly consists of flat landform types "Marshland" and "Low terrace" representing the lowest places in Austria,

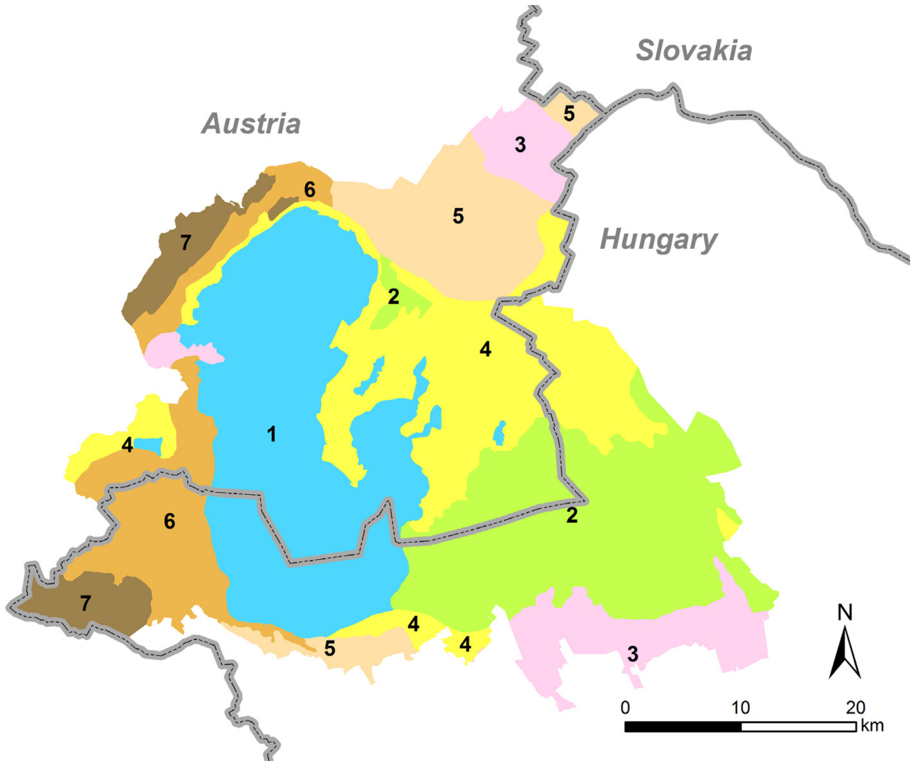

Fig. 1. Cross-border study area is divided into seven landforms: (1) Lake basin, (2) Marshland, (3) River floodplains, (4) Low terrace, (5) Elevated terrace, (6) Hilly area and hill range, and (7) Low and middle range mountains.

whereas west of the lake, gentle hills with a pronounced slope zone form the landforms "Hilly area and hill range" and "Low and middle range mountains". "River floodplains" are only marginally present at the borders of the project region as well as the "Elevated terrace". Within this relatively small area, plants and animals sharing various biogeographic origins are present, hence resulting in high α-diversity. In favour to conserve these unique landscapes, protection areas of different labels were assigned in the last decades throughout the whole region, in turn (actively) involving the local population into the regional development. Growing conflicts between agricultural production incorporating water drainage and lowering of the groundwater level as well as fertilization and nature conservation activities to maintain and restore wetland ecosystems provided the background for the development of the project.

2.2. Constructed vegetation types

In principle, we took existing vegetation maps of the region for gathering information on potential vegetation communities of the area in question. Niklfeld (1970/1989) described eight types of natural vegetation, which would evolve under current climate and soil conditions irrespective if these have undergone human-induced changes. He explicitly stresses the point not to provide PNV, since Tüxen's definition would include all irreversible anthropogenic influences even though Niklfeld's vegetation types might include types of PNV. Bohn et al. (2000/2003) aimed at "*presenting natural site potential in the form of the current natural vegetation, which corresponds to the actual climatic conditions, soil properties (nutrient and water budget as well as soil depth) and the native flora in the various landscapes*". Both maps work on a large scale: 1:2 000 000 and 1:2 500 000, respectively. Thus, the spatial resolution is poor and not applicable for our objectives, we want to provide a better resolution on a smaller scale. Still, both maps gave us valuable information of the vegetation communities which are most likely to occur in the project region.

Based on Bohn et al. (2000/2003) and Willner and Grabherr (2007), specific site conditions for each vegetation type were extracted (Table 1). In principle, the region is characterized by a strong control of standing and ground water leading to the development of azonal communities like halophytic vegetation, reed belt, fens, alder swamp forests and alluvial forests. Only where the influence of water is of minor importance, zonal communities can grow. They follow a height gradient from the lowland steppe-forests, followed by communities with different oak species at higher elevations. We modified the list of vegetation types by also introducing the vegetation type of beech forest, as submontane conditions exist in the Sopron Mountains (Table 1).

We translated the site conditions into selection criteria of geodata where we used data on soil (source: Bodenkarte von Österreich, Bundesforschungs- und Ausbildungszentrum für Wald, Naturgefahren und Landschaft; Agrotopographic Map of Hungary), geology (source: Geologische Bundesanstalt; Geological Institute of Hungary (MÁFI)) and a digital elevation model (source: SRTM).

Climate variation is strongly correlated to topography (Körner, 2003) and thus not directly implemented into the niche descriptions. This construction of relationships between geodata-driven site conditions and broadly defined vegetation types allow for variation within one type (e.g. proportion of grassland in forest steppe might vary within the area due to little variations in site conditions). This construction of niche descriptions is no common PNV assessment method and therefore we call the vegetation types "constructed vegetation types".

By using ArcGIS 10.0 (ESRI, Redlands), we processed all geodata sets with the tool "identity" and cleaned the resulting shape. Additionally, we included the information on streams and rivers into the map by buffering running waterbodies by 10 m. The minimum mapping unit (MMU) for all spatial analyses has been set to 400 m^2. The different attributes of the geodata were assigned

Table 1
Vegetation types according to Bohn et al. (2000/2003) and Niklfeld (1970/1989) with respective site conditions used for defining the distribution pattern of the types.

	Bohn et al. (2000/2003)	Niklfeld (1970/1989)	site conditions
	water body	water body	
azonal	inland halophytic vegetation	halophytic vegetation	salty and alkaline soils, annual precipitation <450 mm; Solonchak- or Solonetz-soils
azonal	freshwater tall reed swamps	reed bed	(nearly) permanent water cover, water saturated soils, meso- to eutrophic standing water bodies on diverse subhydric to semiterrestric soils
azonal	Alder carrs and swamp forests	fens and alder swamp forests	high standing ground water in silted up water bodies, valleys, depressions; soils: different kinds of peat and gley
azonal	Hardwood alluvial forests in combination with softwood alluvial forests and wet lowland forests	Alluvial forests	coarse grained sediments with sandy-silty cover layer, periodically to episodic flooded
zonal	Beech forest[a]	Beech forest[a]	submontane forests preferring carbonate but also existing on more humid, only slightly carbonate influenced sites
zonal	colline-submontane sessile oak-hornbeam forest	oak-hornbeam forest of central European hills	flat to slightly inclined warm sites mostly on loess, but also on brown chernozem and cambisols, rather distant groundwater
zonal	Italian-Pannonian-central Balkan colline-submontane (to montane) sessile oak-(pedunculate oak-) bitter oak forests	Pannonian bitter oak-sessile oak forests	flat to slightly inclined, preferably S-,W-aspect on lime-free sediments, shallow loamy-sandy cambisols to deep stagnosols
zonal	Pannonian lowland mixed pedunculate oak forests	Submediterranean and Pannonian forests and copsewood with downy oak	dry, shallow soils (often Rendzina), substrate carbonate or lime on strongly inclined S- and W- slopes
		submediterranean influenced loess forest steppe with mixed oak forests	slightly to strongly inclined S- and W- slopes; loess, limestone, marl
	Anthropogenic deposits[b]		

[a] List of vegetation types is modified by adding Beech forest not identified by the authors in that region.
[b] Classification label originating from the geological basemap kept in the list.

in a hierarchical way (first azonal, then zonal communities) to the individual vegetation types via attribute selection, eventually ending up with a map of constructed vegetation types. For example, the vegetation type of halophytic plants is characterized by salty and alkaline soils, low annual precipitation and Solonchak or Solonetz soils. No other vegetation type can be established under these conditions. So we selected all polygons which are labelled with the correct soil types and are no permanent waterbody and assigned it with the constructed vegetation type of "halophytic vegetation".

Only the vegetation type "alluvial forest" was also treated by a spatial selection of all alluvial soil polygons within a given search radius of 250 m around running waterbodies. Additionally, polygons of the geological basemap labelled with "anthropogenic deposits" were not assigned a vegetation type but we kept the label. Doing this, we followed the recommendation of Kowarik (1987) to avoid construction of vegetation types on artificial man-made habitats.

2.3. Assessment of the potential supply of landscape services

In our study we followed the concept of landscape services, which are defined as all goods and services that landscapes provide for well-being. They include materials and processes of nature (e.g. biomass, raw materials, primary productivity) and services of cultural elements and constructions that come into being through human creation (e.g. buildings, settlements, infrastructure) (Konkoly-Gyuró, 2011). Whereas the actual supply is based on the capacity of the current land use/cover types to provide landscape services, the potential supply of landscape services in particular is defined as *the ability of natural landscapes to achieve the sustainable provision of goods and services that satisfy human needs, directly and indirectly* (modified after De Groot, 2006). We concentrated on those services that can be derived from the potential land cover, i.e. the constructed vegetation types. Thus, based on the list provided by De Groot (2006) and modified by Hermann et al. (2014) we assessed the actual as well as the potential supply of three main service groups (1) *regulation*, (2) *habitat* and (3) *provision*. The *regulation* group incorporates all services that regulate essential ecological processes through biogeochemical cycles, namely 'local climate regulation', 'disturbance prevention', 'water regulation', 'water supply' (including ground and surface water for industrial as well as private use), 'soil retention', 'soil formation', 'nutrient regulation' and 'pollination' of wild pant species and crops by bees and butterflies. Whereas the *habitat* services provide suitable living space ('refugium') and reproduction habitat ('nursery') for wild plants and animals, the *provision* services promote the supply of natural resources concerning 'food' (edible wild plants and animals), 'raw materials' (mainly timber and reed), 'genetic resources' (genetic material and evolution in wild plants and animals) and 'medicinal resources' (e.g. drugs and pharmaceuticals).

By means of an assessment matrix (after Hermann et al., 2014) these landscape services were linked to the constructed vegetation types by expert evaluations set up during several workshops on different disciplines of ecology (Vegetation Science, Zoology, Pedology and Climate Science). Whereas in the columns the selected landscape services were placed, in the rows the 12 constructed vegetation types were located marking the capacity for providing the services at the intersections (Table 2). The so-called 'Vegetation Type Value' (VET) ranged from categories 0 (no relevant link between the vegetation type and the specific service) and 5 (very high relevant link). The higher the category value, the higher is the capacity of a specific vegetation type to provide a service. For example, the vegetation type 'reedbed', which is very common in the study area, has a high capacity (category 5) to provide suitable habitat (refugium service) for wild animals, in particular for wading bird species. In contrast, the services 'genetic resources' and 'medicinal resources' are less provided (category 1) by this mono-dominant vegetation type (see Table 2).

For receiving the final Potential Landscape Service values, we calculated the area-weighted mean of the VET-values within each landform type. Finally, we took the mean value of the services within each main service group in order to plot the potential supply of the three main services *provision*, *regulation* and *habitat* onto a 3-axes spider web diagram per landform type together with the resulting values of the actual supply of landscape services which were assessed within a previous study provided by Hermann et al. (2014). The actual supply of landscape services was also assessed with the use of an expert-based assessment matrix. There, field-based land use maps with a MMU of 10 m^2 were used as service providing units whereby the expert evaluation values has been further revised by qualifiers originating also from field surveys. For detailed information on the calculation of the actual supply of services please refer to Hermann et al. (2014).

3. Results and discussion

3.1. Constructed vegetation types

In general, the different vegetation communities did separate very well. Comparing the map of constructed vegetation types (Fig. 2) with the large-scaled maps of Bohn et al. (2000/2003) and Niklfeld (1970/1989), the distribution of vegetation types give the same picture, even though our map showed more detail in resolution.

Table 2
Assessment matrix of different vegetation types for providing individual landscape services. 0 = No relevant link between vegetation type and specific function, 1 = low relevant link, 2 = relevant link, 3 = medium relevant link, 4 = high relevant link, 5 = very high relevant link.

Constructed vegetation type	Local climate regulation	Disturbance prevention	Water regulation	Water supply	Soil retention	Soil formation	Nutrient regulation	Pollination	Refugium function	Nursery function	Food	Raw materials	Genetic resources	Medicinal resources
Alluvial	5	5	5	4	5	5	5	3	5	4	2	4	2	3
Anthropogen	2	2	1	0	1	0	1	1	1	0	0	0	0	0
Beech	5	5	5	3	5	5	5	2	5	5	3	5	2	3
Bitter + sessile oak	5	5	5	3	5	5	5	2	5	5	3	4	2	3
Downy oak	3	3	4	2	4	4	5	2	4	3	3	3	2	3
Fens	3	4	5	4	3	5	5	2	5	3	1	3	0	2
Forest steppe	1	2	3	1	3	3	4	2	4	2	3	2	2	3
Halophytic	0	2	3	0	3	3	3	2	5	2	1	0	0	0
Oak-hornbeam	5	4	5	3	5	5	5	2	5	5	3	5	2	3
Reedbed	5	5	5	1	2	2	5	1	5	5	5	4	1	1
Rivers	4	4	4	5	0	0	4	1	4	4	3	0	0	0
Waterbodies	5	4	5	1	0	0	4	1	4	3	4	0	1	0

Adapted from Hermann et al. (2014).

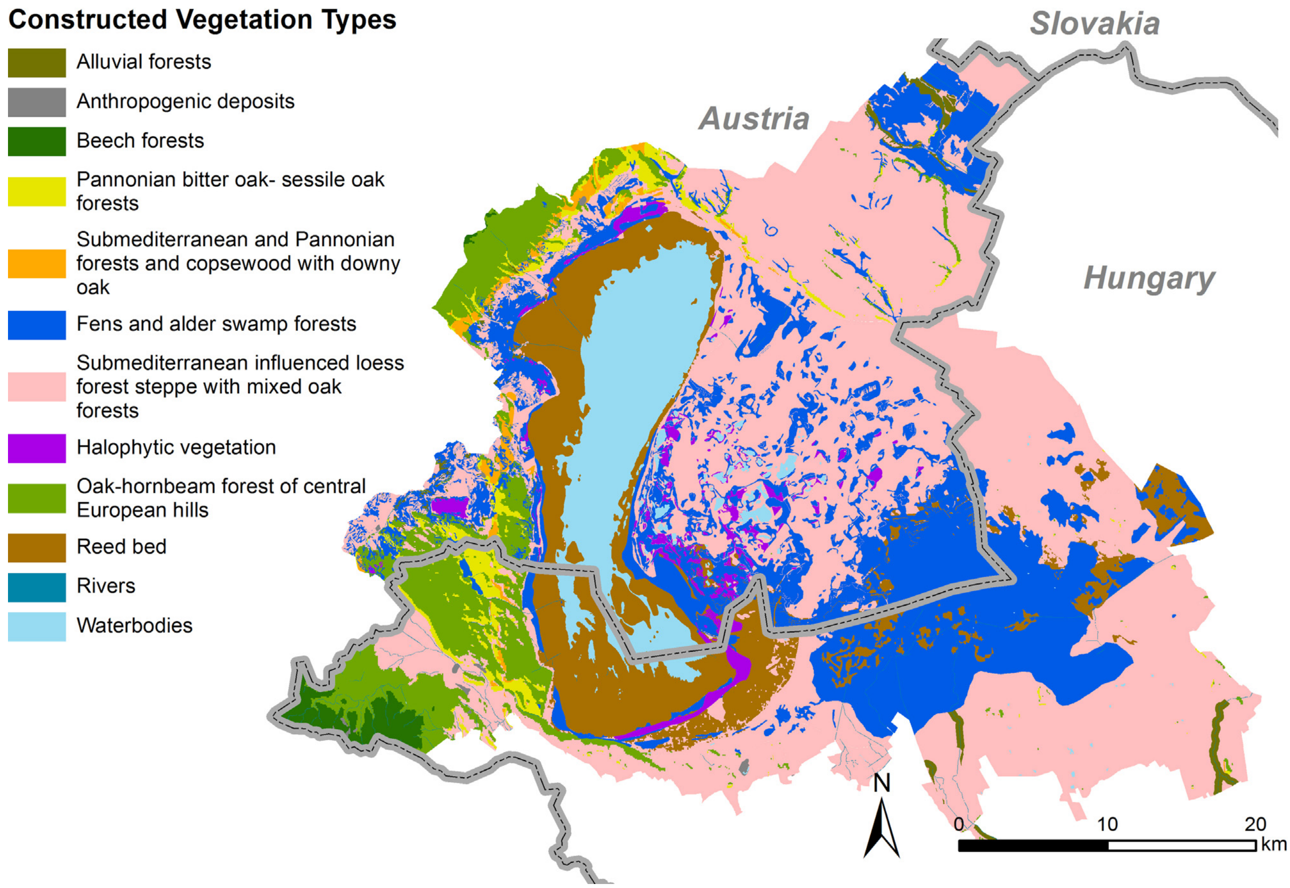

Fig. 2. Constructed vegetation types in the cross-border study area. Types 'anthropogenic deposits' and 'Rivers' are not presented in this generalized map since their extent is too small to show.

Going more into detail, alluvial forests seem underrepresented along the rivers Leitha and Kleine Leitha in the North of the project region. Also along the Wulka flowing into Lake Neusiedl on the eastern shore, different forest types occur but alluvial forests are only present in relatively small patches. Patches of halophytic vegetation are also underrepresented or missing along the lake shore according to personal field observations. Constructed vegetation types which are mainly described by their soil properties are likely to be underrepresented in this map. In general, these problems are associated to the fact, that the dataset on soils does not cover the entire area, as information on soils of artificial areas and forests is generally excluded from the soil base map used in the frame of this study. Also additional data on hydrological levels could improve especially the spatial distribution of reed versus alder swamps stands. The information on dry grasslands is missing and must be discussed as a mosaic with forest steppe.

The distribution of the different constructed vegetation types among the landforms did to some extent follow the intrinsic definition of the landforms (Table 3). Reedbed (18 961 ha) and waterbodies (15 588 ha) were mainly located in "Lake Basin", as well as the halophytic vegetation type encompassing 2827 ha. Landform "Marshland" was dominated by fens (22 799 ha) and forest steppe (14 989 ha). Alluvial forests were mostly prominent in the "River floodplains" accounting for 1093 ha. The oak-hornbeam forests (8463 ha) and mixed oak forests (3069 ha) followed the elevation gradient in "Hilly area and hill range" as well as the even higher elevated beech forests (2516 ha) in "Low and middle range mountains". The vegetation type Forest steppe predominantly occurred in landforms "River floodplain", "Low terrace" and "Elevated terrace".

We want to stress the point that the construction solely based on geodata is reproducible and transparent despite the shortcomings of the geodata that can be attributed to (i) differences in resolution and scale and (ii) incomplete coverage. When necessary the definition of the selection criteria and the hierarchical sequence can be adapted and refined. Also validation of the resulting map showed some pitfalls: usually, validation of the models can either be achieved by dividing the original dataset into training data and test data or by taking external independent validation data, and thus getting an accuracy measure. The latter are often existing (field-based) PNV maps which are compared with the model outcome (Lapola et al., 2008; Liu et al., 2009; Tichy, 1999). This might be problematic, as existing PNV maps usually were drawn on a different scale and generalisations had been conducted or these maps were developed solely by expert-knowledge and not data-driven. We therefore forwent this step, as the only validation data would be the large-scale maps of Bohn et al. (2000/2003) and Niklfeld (1970/1989).

3.2. Potential supply of landscape services

Based on the assessment matrix and the location of the constructed vegetation types, a picture of the potential supply of the individual services can also be drawn. As an example we present the potential supply of the service 'local climate regulation' (Fig. 3). 'Local climate regulation' depending on the presence of water and forests was therefore mostly located in the landforms lake basin, the wetlands and the forests along the hillsides. The potential supply of the services 'nursery', 'raw materials' and 'water supply' was also rather equally distributed in its values throughout the area (all

Table 3
Area [%] of constructed vegetation types per landform.

	Lake basin	Marshland	River floodplain	Low lying terrace	Elevated terrace	Hilly area and range	Low and middle range mountain
Alluvial	0.1	0.1	6.6	0.3	0.1	0.3	0.1
Anthropogenic	0.0	0.0	0.0	0.0	0.2	0.5	0.5
Beech	0.0	0.0	0.0	0.0	0.0	0.0	27.7
Bitter + sessile oak	0.0	0.1	0.1	0.2	1.8	15.2	3.2
Downy oak	0.0	0.0	0.0	0.1	0.3	4.6	5.1
Fens	16.0	54.7	22.0	14.3	3.1	8.9	0.3
Forest steppe	10.9	35.9	69.8	83.4	92.6	27.5	0.7
Halophytic	5.5	0.0	0.0	0.8	0.0	0.2	0.0
Oak-hornbeam	0.1	0.1	0.6	0.1	1.8	41.9	61.4
Reedbed	37.0	8.8	0.0	0.6	0.0	0.2	0.0
Rivers	0.1	0.3	0.6	0.1	0.0	0.6	1.1
Waterbodies	30.4	0.0	0.2	0.1	0.0	0.1	0.0

values are presented in Appendix A). ‘Genetic resources’ and ‘pollination’ were only little provided reflecting the low values in the capacity matrix. On the other hand, the services such as ‘nutrient regulation’ or ‘refugium’ exhibited the large potential in the study area.

Looking more closely to the potential supply of the landscape services per landform, the values varied from each other (see Appendix A). In Fig. 4, the example of the service group *provision* reflects the general findings also valid for the other two service groups. The majority of services with values >4 occurred in the “Low and middle range mountains”. The lowest values could be determined in the landform “Elevated Terrace”. “Lake Basin” showed contrasting potential in the services – within the group of *regulation* services, both, values >4 and <2 can be found. In all landforms, ‘nutrient regulation’ resulted in values >4, whereas ‘genetic resources’ was displayed nowhere >2.

The aggregation of the services by averaging values along the landform strata to finally derive three main potential service groups blurred the picture of the potential supply of the services to some extent. Therefore, the general picture of the service groups looks more or less similar in all landforms, giving the highest values always to *habitat*, followed by *regulation* and then *provision*. Depending on the area-weighting of the VET-values, the mean potential landscape service looked more differentiated among the landforms when looking at the detailed values (Table 4).

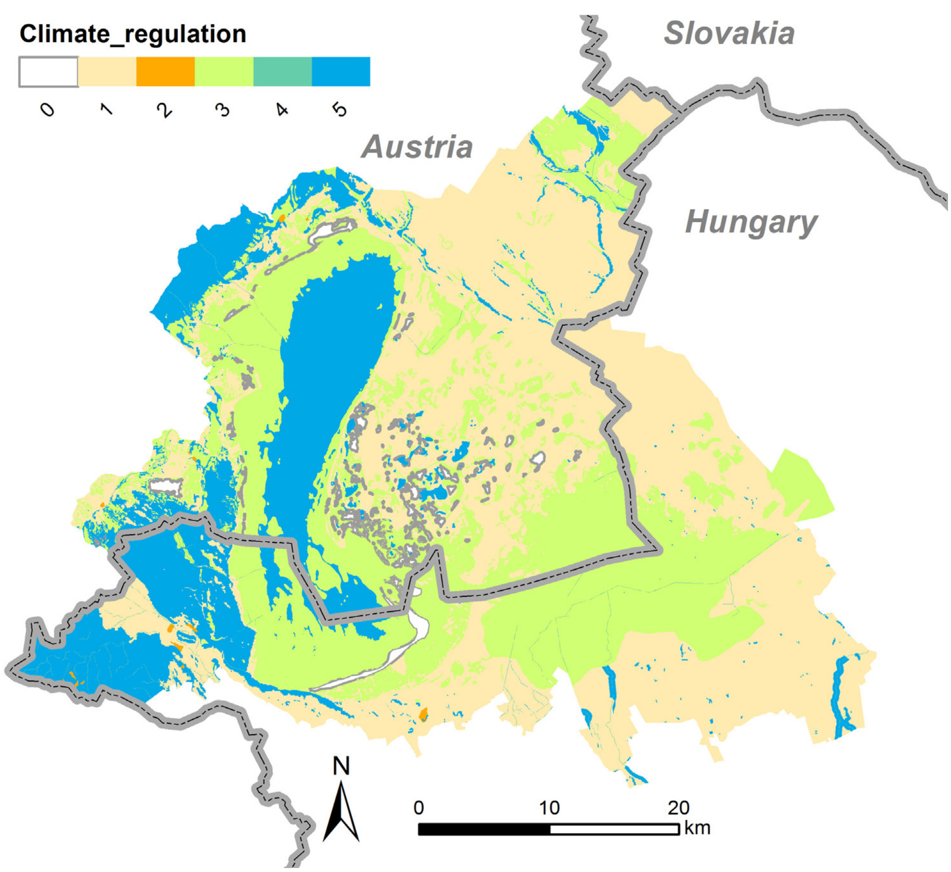

Fig. 3. Potential supply of service ‘local climate regulation’ throughout the study area. 0 = No provision, 1 = low provision, 2 = modest provision, 3 = medium provision, 4 = high provision, 5 = very high provision.

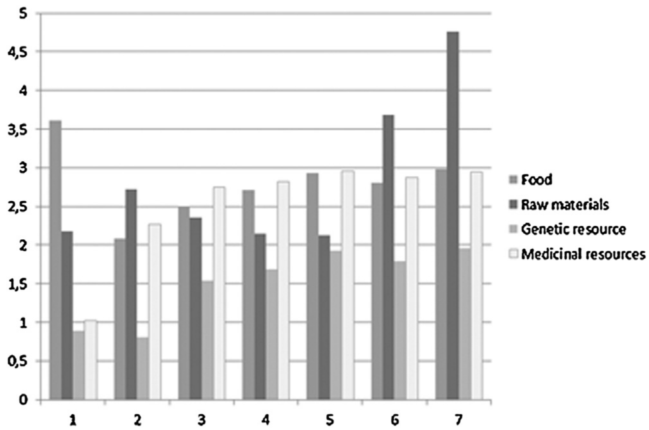

Fig. 4. Potential supply of service group *provision* in the seven landforms: (1) Lake basin, (2) Marshland, (3) River floodplains, (4) Low-lying terrace, (5) Elevated terrace, (6) Hilly area and hill range, and (7) Low and middle range mountains.

Table 4
Potential supply of landscape service groups in each landform. The higher the value on the scale of 0–5, the higher the potential supply.

	Regulation	Habitat	Provision
Lake basin	2.959	4.082	1.928
Marshland	3.279	3.731	1.971
River floodplains	2.870	3.341	2.287
Low-lying terrace	2.606	3.171	2.340
Elevated terrace	2.493	3.101	2.486
Hilly area and hill range	3.648	4.256	2.785
Low and middle range mountains	4.200	4.875	3.164

3.3. Comparison with actual supply of landscape services

Comparing the potential with the actual supply of landscape services revealed differences between the constructed vegetation types' and the current land use types' capacities to provide services (Fig. 5). In principle, nearly all landforms resulted in higher potential than the actual service provision. Within the present landforms "Lake Basin", "Marshland" and "Hilly area and hill range", the potential supply was nearly reached, except for the *habitat* axis which showed the least actual supply and thus the highest possibilities for further development. The relatively high service values within these landforms are based on the high ecological quality of the investigated landscapes. Whereas nowadays "Lake Basin" and "Marshland" are dominated by protected areas and remaining wetland and forest patches, "Hilly area and hill range" is characterized by a diversified landscape including both extensive and intensive rural areas, accompanied by some semi-urban settlements. In contrast, the actual service supply of the landforms "River floodplain", "Low lying terrace" and "Elevated terrace" was far lower than the potential suggests, mainly due to intensive anthropogenic land use over the last decades. Whereas small river corridors with flood plain forests are still present in the land form "River floodplain", within the other two former mentioned landforms the predominantly flat surface is mainly covered by intensive arable land parcels, peri-urban zones and growing horticultural establishments. One big exception is constituted by landform "Low and middle range mountains" which exhibited higher actual *regulation* and *provision* services compared to the potential service supply.

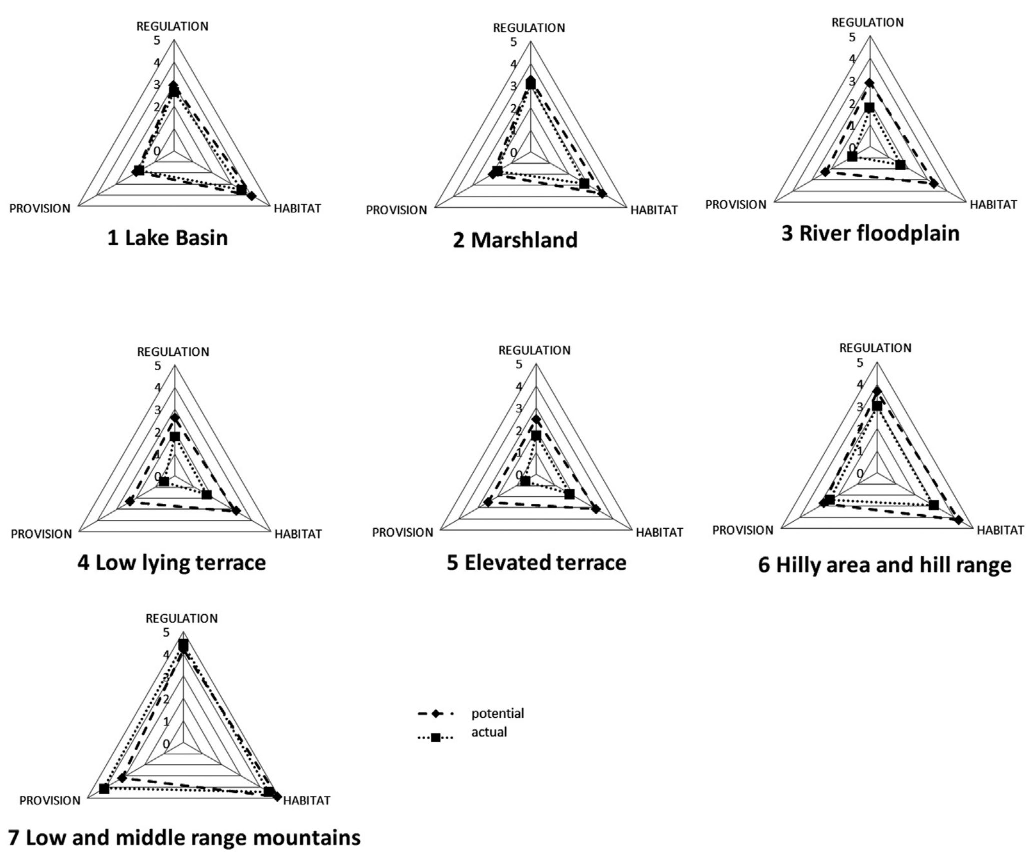

Fig. 5. Comparison of potential supply of services vs. actual supply of services in each landform. Dotted line shows actual and dashed line shows potential supply.

This landform is presently dominated by sustainably managed forests with few grassland patches and arable fields in between.

In order to locate restoration potential within the study area, we can see that in all landforms except “low and middle range mountains”, the potential supply of services is higher than the actual one which would mean that renaturation would lead to an enhancement of the regulation services. These landforms showed spatially diversified vegetation communities in the map of constructed vegetation types. As land management has concentrated the last decades on arable farming, uniformisation of land use and landscape has led to change of water level, salt content and other environmental site factors. For example, the landform “Marshland” is potentially driven by the strong control of ground water. Due to land use activities in the last decades, the ground water level has decreased enormously in order to provide suitable arable land therefore replacing reed and alder swamp communities and has led to a degradation of valuable wetland areas. Thus, many regulation services showed now lower supply which could be originally provided. Many nature conservation activities in the last years concentrated on the renaturation and restoration of the Hanság within the landform “Marshland” to establish again a higher ground water level. This would lead to a better performance of services like water regulation, soil formation, and refugium for wetland species. Other landforms like “Low terraces” showed a large spatial variation in the distribution of potential as well as the actual supply. Here, a more detailed examination of the local conditions needs to exhibit the potential for restoration projects following the landscape’s leitbild where our results can only show on the regional level possibilities for the improvement of regulation services. The objective pursued is not to reconstruct landscapes of the past, but to study ways how valuable elements and areas can be preserved or restored and become functionally embedded in the modern urbanized and globalized society. The definition of reference systems at the landscape level could be a starting point to re-establish basic landscape functions by integrating the concept of landscape functions and services into restoration ecology which is a step in the right direction (Jones, 2013). For the establishment of a detailed restoration plan, not only the very local conditions but also stakeholder involvement and feasibility studies are indispensable.

The big exception in the comparison of potential with actual supply is the landform “Low and middle range mountains”. The map of constructed vegetation types showed for this landform only forest communities. But nowadays, large forest patches coexist with land use types of cultural landscapes like vineyards and meadows resulting in a highly diverse and only extensively used landscape. This enhanced habitat diversity resulted in the provision of high levels of supply of their services beyond the potential supply.

Based on our results we hence conclude that landscapes shaped by humans do have the ability to provide high service values in respect to the landscape properties if they were managed in a sustainable way. According to Austad (2000) and Jones (2013) a diversified landscape managed upon knowledge of its historical development and past functioning can indeed be very valuable for humans by providing a wide range of life sustaining services.

However, we have to be aware that the potential supply of services is based on constructed vegetation types whereas the actual one derived from land use and land cover types. The fact that the actual service assessment was based on higher resolution data might explain some differences between the results. The minimal mapping unit was quite different between both methods: whereas the MMU was 400 m^2 for the constructed vegetation types, the MMU for the field-based land use maps was 10 m^2. However the results where generalized on the same level as the potential supply.

One key challenge is to explore the trade-offs and synergies between different services that specific restoration actions would entail. For example, reforesting a cultivated area will take away the service ‘crop production’ but reinstate ‘soil retention’, ‘water regulation’ and ‘disturbance prevention’. Within the present study we have assessed the regulation services so far. In order to reach an even more detailed trade-off analysis, the study has to be extended to *production* and socio-*cultural* services as well.

4. Conclusions

In general, the direct link between the constructed vegetation types and the potential supply of regulation landscape services showed a high value for all services. Only in the details, some services would be better supported and provided by other vegetation types than the ones potentially occurring in the region of Lake Neusiedl. Looking at the different landforms within the study area, we can conclude that considering at the potential supply in order to develop a leitbild for restoration activities is worthwhile in landscapes dominated by arable farming whereas landscapes with a diverse land use system already exhibit large service supply.

The focus on these three service groups was set deliberately as we wanted to fathom the use of physiographic conditions for the assessment. Still this method cannot be applied for all services. To estimate of landscape’s potential to deliver the services e.g. aesthetic values, other approaches need to be sought covering a wide array of research topics and a large community. The way forward to explicitly address each service is to develop indicator sets targeted to each of these (Crossman et al., 2013; Gulickx et al., 2013; Haines-Young et al., 2012, amongst others). But this would encompass the need of very detailed data and statistical relationships which are not available yet for the study area.

Nevertheless, our study showed the possibilities of an overview assessment appropriate to grasp the main differences between different landscapes and different vegetation and land cover types.

Acknowledgements

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Appendix A.

Table A1.

Table A1
Potential supply of the landscape services per landform; landforms are described in Section 2.1.

Landform	Lake basin	Marshland	River floodplain	Low terrace	Elevated terrace	Hilly area and hill range	Low and middle range mountains
Local climate regulation	3.97	2.47	1.76	1.34	1.22	3.60	4.84
Disturbance prevention	4.04	3.37	2.67	2.33	2.16	3.55	4.24
Water regulation	4.67	4.28	3.60	3.31	3.14	4.37	4.91
Water supply	1.43	2.66	1.90	1.44	1.17	2.48	2.95
Soil retention	1.72	2.91	3.12	3.00	3.07	4.16	4.86
Soil formation	2.04	4.00	3.56	3.29	3.13	4.34	4.86
Nutrient regulation	4.48	4.64	4.29	4.15	4.06	4.69	4.96
Pollination	1.33	1.91	2.06	1.99	2.00	1.99	1.99
Refugium	4.59	4.64	4.29	4.16	4.06	4.65	4.91
Nursery	3.58	2.82	2.39	2.18	2.14	3.86	4.84
Food	3.61	2.08	2.50	2.71	2.93	2.80	2.98
Raw materials	2.18	2.72	2.35	2.15	2.12	3.68	4.76
Genetic resource	0.89	0.81	1.54	1.69	1.93	1.79	1.96
Medicinal resources	1.02	2.27	2.75	2.82	2.96	2.87	2.95

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– Introduction to Section B –

Establishing a new spatial data source for applying various ecological implications on supra-regional level

In the second and rather short section of my thesis I present one research article (v) that addresses the generation of a new high-resolution habitat map which may serve as a basic dataset for a broad range of applications in the fields of ecological modelling, nature conservation practise and landscape planning.

Up to now, the latest version of CORINE land cover (CLC) which has been established 2006 (EEA, 2007) still serves as the most popular data source in various scientific disciplines when spatially explicit information on land cover is demanded on a mid to large scale across Europe. The advantages when applying CLC are obvious and can be grouped by four main statements: (a) CLC is freely available; (b) it covers almost all of Europe; (c) it follows a standardized mapping scheme; and (d) for major parts, short and mid-term time series are available which facilitate the quantification on land use change for roughly the last 25 years (e.g. Verburg et al., 2006). Despite these advantages, CLC faces limitations for local assessments of e.g. land cover (change) (Pachecoa & Gutiérreza, 2014) because of its relatively coarse minimum mapping unit of 25ha and, moreover, CLC categories proved to be too crude in sufficiently describing habitat heterogeneity for in-depth assessments on biodiversity-environment relationships (Keil et al., 2012).

As recently as ten to fifteen years ago, a first wave of new remote sensing based data sources derived from e.g. Advanced Very High Resolution Radiometer (AVHRR) or Moderate Resolution Imaging Spectroradiometer (MODIS) sensors, have been introduced to improve large scale land cover mapping. However, the rather coarse horizontal resolution of their outcomes (up to 1km) and consequently their insufficient accuracy in mapping heterogeneous land cover types such as forests, sparsely vegetated areas or wetlands (Waser & Schwarz, 2006) hampered their application in the past. During the last years, newly introduced sensors and continued growth of computational power (referred to as "Moore´s law"; Moore 1965) facilitated a rapid development in remote sensing based data collection, post-processing, storage, and finally, accessibility for the scientific community. For example, pan-european, yet monothematic maps of forest distribution as provided by the Joint Research Centre (Kempeneers et al., 2011) or by the GIO land monitoring service (Langanke, 2013) represent a giant leap forward by improving the spatial resolution of the according datasets to 25m. In parallel, the coverage and quality of detailed and freely available land cover data, provided by the Open Street Map community has constantly risen over the past decade. Additionally, more and more biotope inventory datasets on rare and/or threatened habitats which have been gathered and maintained on behalf of public authorities are becoming available.

Altogether, these recently emerged data sources facilitated the generation of a new, thematically as well as spatially high resolution habitat map as presented in article (v). The map consists of 19 different habitat classes at a horizontal resolution of 25m by covering the countries of Austria, Switzerland, Liechtenstein, the region of South Tyrol as well as the German federal states of Bavaria and Baden-Wurttemberg. Our habitat categorization follows the CLC and EUNIS (European Nature Information System) (Davies et al., 2004) classification systems, however, we tried to overcome some issues of CLC by unravelling the mixed classes of *Land principally occupied by agriculture* (4.1.2) or *Complex cultivation patterns* (2.4.2). All source data we applied, especially the supra-national remote-sensing data on forest cover was checked and corrected beforehand by the use of e.g. exclusion layers and geospatial correction tools, followed by posterior checks on mapping accuracy with independent reference data. In order to guarantee constant quality and consistency of our map throughout all encompassing countries we carefully selected the underlying base data to ensure conformity within our designated habitat classes. However, for this reason we could not refine our classification scheme, even if thematically more fine-scaled data was available for only some parts of our mapping region. For example, we did not differentiate our grassland typology by main type of use, i.e. being utilized either as pasture or meadow but only by land use intensity. In case of artificial surfaces, a delineation of distinct sub-classes such as industrial/commercial sites or residential areas would have been possible but has not been in our focus when establishing the habitat map. Other supra-national base datasets, e.g. on mixed forests are currently being developed. As the map has been set up in a modular way, refinements, data updates and introduction of new classes can be performed either by the individual user and is also foreseen to be done by the map authors at regular intervals.

As already mentioned, the applications of this new so called Central European Habitat Map (CEH-Map) are manifold. For instance, many of the studies mentioned or referred to in the first section of my thesis that are dealing with the topics of landscape functionality or landscape/ecosystem service provision are at least partly relying on land cover data. In this context, finer resolution input data could yield more distinct results in e.g. ecosystem service assessments as Koschke et al. (2012) already stated that, despite better knowledge, they had to assume land use does not vary within each of the 100m CORINE raster cells they used in that specific study. Another current hot topic regarding ´Mapping and Assessment of Ecosystems and their Services´ (MAES) which is defined as target 2 of the EU Biodiversity Strategy requires the quantification of ecosystem services in order to fulfil its goal of restoring at least 15% of threatened and degraded ecosystems throughout each member state. At this,

Albert et al. (2015) propose a national assessment of ecosystem services which may serve as a superstructure not only for implementing MAES but also to better coordinate upcoming planning and decision making processes on lower administrative levels. In case of Austria, the CEH-map could be applied as one major base data set to meet these requirements.
Other fields of map application are outlined within article (v), and additionally the map has already been used within recent scientific studies as described in the associated articles (vi) and (ix).

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Section B - *Establishing a new spatial data source for applying various ecological implications on supra-regional level*

Article 5 (v)

Kuttner, M., Essl, F., Peterseil, J., Dullinger, S., Rabitsch, W., Schindler, S., Hülber, K., Gattringer, A., Moser, D. 2015. *A new high-resolution habitat distribution map for Austria, Liechtenstein, southern Germany, South Tyrol and Switzerland*. eco.mont, 7/2, 18-29.
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A new high-resolution habitat distribution map for Austria, Liechtenstein, southern Germany, South Tyrol and Switzerland

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Keywords: biosphere reserves; Central Europe; Eastern Alps; EUNIS habitats; habitat distribution; land cover; mapping; national parks; nature conservation areas

Abstract

There is a growing need for fine-scale data on habitat distribution for large areas to comprehensively detect changes in biodiversity patterns, ecosystem service provision and sustainable landscape development against global change. We present a map of 19 habitat classes at a resolution of 25 m for Austria, Germany (Baden-Wurttemberg, Bavaria), Liechtenstein, Italy (South Tyrol) and Switzerland. Fine-scale data from various sources in the public domain (e.g. habitat mapping campaigns, Open Street Map, CORINE land cover 2006 (CLC2006), Joint Research Centre forest mapping, GIO-Land high resolution layers) were harmonized and supplemented by remote mapping and modelling techniques. Spatio-thematic accuracy checks with independent data sources have been conducted and the habitat classes further compared to the CLC2006 classification scheme. As a first map application we provide habitat class-specific proportions for national parks and biosphere reserves located within the mapping area in relation to their surroundings and further discuss additional fields of applications. The map will be freely available for non-commercial scientific use.

Introduction

The most widely used dataset to derive land-cover patterns in Europe is CORINE land cover 2006 (CLC2006) (EEA 2007). Its wide coverage, largely homogeneous methodology, the data quality and a resolution of 100 m are attractive for many applications. However, its limited thematic accuracy, particularly the poor differentiation of (semi)natural ecosystems, and the coarse minimum mapping area of 25 ha, make it insufficient for many ecological questions, which focus on small remnants of particularly interesting habitats like dry grasslands or wetlands. In contrast, datasets of high spatial and thematic resolution, such as national inventories of ecosystems of high conservation value (e.g. floodplains, dry grasslands, mires; Holzner 1986; Steiner 1992), biotope mapping campaigns (e.g. LfU 2012; LUBW 2014), Natura 2000 mapping (European Commission 2006), forest inventory databases (Bauerhansl et al. 2008) or agricultural databases (e.g. the land parcel information system LPI), are mainly gathered at a (sub)national level in Central Europe and therefore have a restricted spatial range. Although high-resolution layers on a larger spatial scale have become recently available for specific habitat and land cover classes, such as forests (Joint Research Centre; JRC (Kempeneers et al. 2011) and GIO land monitoring service (Langanke 2013)), built-up areas and transport networks (Open Street Map; OSM), or grasslands and waterbodies (GIO land (Langanke 2013)), substantial methodological differences (e.g. different classification schemes) have hampered their integration at a supra-national level.

Here we present the first high-resolution Central European Habitat map (CEH) (freely available at: ftp://131.130.33.15) that is focusing on semi-natural habitat classes of high conservation value. It covers approx. 240 000 km² across Austria, Liechtenstein, southern Germany (Bavaria, Baden-Wurttemberg), Italy (South Tyrol) and Switzerland. Standardized procedures of resampling, harmonizing and merging of available high-resolution mapping and remote sensing data ensure a ready-to-use dataset consisting of 19 habitat classes.

We also provide a comparison with the most commonly used land-cover dataset of CLC2006.

Methods

Data preparation and map generation

Datasets from various sources (Table 1) were projected to the ETRS 1989 LAEA spatial reference system. Vector data were converted into native ESRI GRID raster format with a spatial resolution of 25 m × 25 m. To be consistent with other European datasets, the grid origin was defined by CORINE. Original data were reclassified according to our habitat specifications and separate grid layers for each class were generated. As a general purpose we applied fine-scale data wherever available to improve the spatial and thematic accuracy of CORINE, but used CLC2006 data to fill the remaining gaps.

Roads, railways, watercourses and lakes

Data on *Roads*, *Railways* and *Watercourses* were extracted from OSM line vector datasets. For the sake of consistency with the grid cell size (25 m) only motorways, main railway lines and large rivers (i.e. wider than 30 m) were considered. Data on *Lakes* originating from the ECRINS database and provided in vector format were converted to raster format.

Built-up areas

We merged several built-up land-cover classes from OSM (*village green*; *residential*; *industrial*; *commercial*) and CLC2006 (*Continuous urban fabric* (1.1.1); *Discontinuous urban fabric* (1.1.2); *Industrial and commercial units* (1.2.1); *Dump sites* (1.3.2); *Construction sites* (1.3.3)) and additionally integrated high-resolution data on *imperviousness* from GIO-Land to capture even single farmsteads and hamlets.

Forests

Obviously misclassified forest pixels from JRC source data, located in the nival and upper alpine altitudinal belt, were deleted using exclusion masks derived from CLC2006 layers *Glaciers and perpetual snow* (3.3.5) and *Bare rock* (3.3.2).

Shrub lands

For this ecosystem class we extracted habitat-specific data from mapping campaigns (Bavaria, Baden-Wurttemberg) and a WebGIS service (*Geobrowser*) for South Tyrol. For Austria we extracted data from national biotope mapping (*2656 – F2 Arctic, alpine and subalpine scrub, 2784 – F3 Temperate and mediterranean-montane scrub, 2889 – F4 Temperate shrub heathland, 3355 – F8 Thermo-Atlantic xerophytic scrub*). For Switzerland and Liechtenstein we used the CLC2006 class *Transitional woodland scrub* (3.2.4).

Extensive grasslands and alpine grasslands

These habitat classes comprise mesic low-impact pastures and meadows below the tree line as well as alpine grasslands. For Bavaria and Baden-Wurttemberg we compiled data from the latest available biotope and FFH mapping campaigns, particularly the *Bayrisches Ökoflächenkataster* and *Biotopverbund Baden-Württemberg* (LfU 2012; LUBW 2014). For Switzerland we used data from *Réseau écologique national* (Berthoud et al. 2004). For Liechtenstein extensively used grasslands were identified by a supervised image classification which was conducted using ArcGIS 10.1 and later corrected by cross-checking with data on low-nutrient grassland habitats from the geodata portal of Liechtenstein. South Tyrolean data originated from a remote sensing campaign which has been conducted by the Italian Department of Agriculture (AGEA) in 2008 and were accessed via Geobrowser. Finally, Austrian data were again taken from IACS by integrating a selection of EUNIS Level III classes which indicate low-impact management (summarized under EUNIS Level II class *2182 – E2 Mesic grasslands*). We additionally used EUNIS class *2302 – E4 Alpine and subalpine grasslands*, derived from Dirnböck & Peterseil 2014, for completion. Remaining gaps were filled by CLC2006 class *Natural grassland* (3.2.1). To differentiate extensively managed lowland from alpine grasslands across all countries we modelled the actual forest lines. Forest data from JRC and GIO-Land were cleaned from misclassified pixels using CLC2006 exclusion layers and restricted to areas with a minimum mean temperature of 6.4 °C during the growth period and a minimum length of the growth period of 90 days, beyond which climate conditions are unsuitable for tree growth (Körner 2012). Altitude was derived from the latest pan-European digital elevation data (EU-DEM) with a common spatial resolution of 25 m (EEA 2013). By applying focal statistics and kriging interpolation techniques we obtained a final dataset on the actual distribution of the upper tree limit across the Alps.

Dry grasslands

This ecosystem class includes various types of dry and semi-dry meadows and pastoral lands. We used several data sources: biotope mapping campaigns (Bavaria, Baden-Wurttemberg, Liechtenstein), *Bundesamt für Umwelt* (BAFU, Switzerland) and an updated version of the Austrian inventory of dry grasslands (Holzner 1986 – updated 2013). For South Tyrol we again used data provided by the WEBGIS source Geobrowser. Gaps in the South Tyrolean dataset were filled by a niche modelling approach. We defined the thresholds for the potential occurrence of dry grasslands with respect to annual precipitation (< 832 mm), slope (> 10° and < 48°), aspect (south 155°–205°) and elevation (< 1 680 m) as the mean plus the twofold standard deviation of already outlined dry grassland sites across South Tyrol. Those reference values were then compared with the Swiss dataset in order to check if dimensions of the ecological space of dry grasslands appear reasonable. Topographic parameters and precipitation were derived from EU-DEM and from WorldClim (Hijmans et al. 2005; spatial resolution: 30 arc s; i. e. approx. 1 km × 1 km), respectively. Additionally, dry grassland patches complying with these rules had to be previously identified as *Extensive grasslands*.

Mires and wet grasslands

For the compilation of this class, which includes wet grasslands, sedge stands, reed beds, fens and mires, we compiled data from the same sources as for *Dry grasslands*. For Austria, in addition, data from the Austrian mire inventory (Steiner 1992) were used, together with several classes from Dirnböck & Peterseil 2014 (*5257 – X04 Raised bog complexes*; *1724 – D4 Base-rich fens and calcareous spring mires*; *1589 – D2 Valley mires, poor fens and transition mires*, *1515 – D1 Raised and blanket bogs*, *1404 – C3 Littoral zone of inland water bodies*, *1797 – D5 Sedge and reed beds without free standing water*, *2238 – E3 Seasonally wet and wet grasslands*) who compiled additional data sources from national habitat monitoring efforts.

Vineyards and orchards

Similar to *Built up areas*, OSM data were used to enhance the spatial coverage for vineyards and orchards which were based on CLC2006 data. For South Tyrol we integrated information on vineyards and orchards, identified by the AGEA remote sensing campaign

Table 1 – Summary of the major data sources used to compile the CEH. Geographic code: AT = Austria; BA = Bavaria; BW = Baden-Wurttemberg; CH = Switzerland; LI = Liechtenstein; ST = South Tyrol

Habitat Class	Data source	Geographic coverage
Coniferous forest [CFO] Broad leaved forest [BLFO]	JRC-forest mapping campaign	whole area
Shrub lands [SHRUB]	CLC2006; Geobrowser; Biotope mapping data	CLC2006 = CH, LI (partly in AT, ST, BA, BW for completion); Geobrowser = ST; Biotope mapping data = AT, BA, BW
Arable land [ARAB]	CLC2006; IACS data	CLC2006 = CH, LI, ST, BA, BW; IACS = AT
Intensively used grasslands [IGR]	CLC2006; GIO-LAND	CL2006 = whole area; GIO-LAND = whole area
Vineyards [VIN]	CLC2006; OSM; Geobrowser; IACS data	CLC2006 = BA, BW, CH; OSM = whole area; Geobrowser = ST; IACS = AT
Orchards [ORC]	CLC2006; OSM; Geobrowser	CLC2006 = BA, BW, CH, AT; OSM = whole area; Geobrowser = ST
Lakes [LAKE]	EEA data (ECRINS database)	whole area
Major rivers [RIV] Major railways [RAIL] Major roads [ROAD]	OSM	whole area
Built up areas [BUA]	CLC2006; OSM; GIO-LAND	whole area
Extensive grasslands [EXTGR] Alpine grasslands [ALPGR]	Biotope mapping data; REN; Supervised Image Classification; Geobrowser	Biotope mapping data = BA, BW, AT; REN = CH; SIC = LI; Geobrowser = ST
Mires and wet grasslands [WET]	Biotope mapping data; Geobrowser; Austrian mire inventory	Biotope mapping data = BA, BW, CH, LI; Geobrowser = ST; Ami = AT
Dry grasslands [DRY]	Biotope mapping data; Geobrowser; Austrian Inventory of dry grasslands (updated 2013)	Biotope mapping data = BA, BW, CH, LI; Geobrowser = ST; Adg = AT
Gravel banks [GRAVEL]	Visual classification campaign	whole area
Rocks [ROCK] Glaciers [GLAC]	CLC2006	whole area

Source of freely available data, their original spatial resolution and date of origin	
JRC forest mapping Resolution: 25 m / 2006	http://forest.jrc.ec.europa.eu/activities/forest-mapping/forest-cover-map-2006/
ECRINS database Vector data* / 2011	http://projects.eionet.europa.eu/ecrins/library/hydrography/v1/ecrlakmdb
OSM Vector data / **	http://download.geofabrik.de/europe.html
CLC2006 Resolution: 100 m / 2006	http://www.eea.europa.eu/data-and-maps/data/corine-land-cover-2006-raster
GIO-LAND Resolution: 10 m / 2012	http://land.copernicus.eu/pan-european/high-resolution-layers/view/
Biotope mapping BA Vector Data / 2012	http://www.lfu.bayern.de/gdi/dls/biotopkartierung.xml
Biotope mapping BW Vector data / 2012	http://www.lubw.baden-wuerttemberg.de/servlet/is/61722/
Biotope mapping CH Vector data / 2007–2013	http://www.bafu.admin.ch/gis/02911/07403/index.html?lang=de
WebGIS Liechtenstein Vector data / NA	http://geodaten.llv.li/geoshop/naturlandschaft.html/
Geobrowser South Tyrol Vector data / 2008–	http://gis2.provinz.bz.it/geobrowser/?project=geobrowser_pro&view=geobrowser_pro_atlas-b&locale=de

** Not all acquired vector datasets share a specific resolution or minimum mapping unit*

*** OSM-datasets are continuously updated by the user community (date of download: April 2013)*

and accessed by using the Geobrowser. Vineyards in Austria were updated by data from the IACS database (reference year 2012) of the Austrian Federal Ministry of Agriculture, Forestry, Environment and Water Management.

Arable land

To define *Arable land* we used IACS data for Austria, supplemented by the CLC2006 classes of *Non-irrigated arable land* (2.1.1) and *Complex cultivation patterns* (2.4.2) in the other countries.

Intensively used grasslands

We used the CLC2006 classes *Pastures* (2.3.1) and *Land principally occupied by agriculture, with significant areas of natural vegetation* (2.4.3) which had not yet been classified as another class (e.g. *Extensive grassland*, *Mires and wet grasslands*, etc.) in any of the fine-scale datasets. Additionally we used the *Permanent grasslands* layer from GIO-Land for areas that were already covered by the *Arable land* class.

Table 2 – Nineteen habitat classes of the CEH and their corresponding CLC2006 and EUNIS habitats. Habitat class abbreviations correspond to Table 1.

Habitat Class	Corresponding EUNIS Level 1/2/3 habitat	Remarks – EUNIS	Corresponding CLC2006 habitat (Level 3/4)	Remarks – CLC
CFO	G3	Transition to class G4 (mixed forests) occurs	3.1.2	Transitions to 3.1.3 (Mixed forests) may occur
BLFO	G1	Transition to class G4 (mixed forests) may occur	3.1.1	Minor transitions to 3.1.3 (Mixed forests) may occur
SHRUB	F2/F3/F4/F9/E5.2	E5.2 indicates shrub dominated woodland fringes	3.2.2.2/3.2.4	3.2.2.2 indicates *Pinus mugo* stands
ARAB	I1/(I2)	Some parts of *Arable land* may also be covered by class I2	2.1.1/2.4.2	–
IGR	E2.1/E2.2/E2.6	–	2.3.1/2.4.3.2	–
VIN	FB.4	–	2.2.1	–
ORC	FB.3	–	2.2.2	–-
LAKE	C1	–	5.1.1.1	–
RIV	C2	–	5.1.2.1	–
RAIL	J4.3	–	1.2.2.2	–
ROAD	J4.2	–	1.2.2.1	–
BUA	J1/J2	Coverage of class J2 is limited by the minimum area corresponding J2-elements are comprising	1.1.1/1.1.2/1.2.1	–
EXTGR	E2.1/E2.2/E2.7	Classes are partly overlapping with IGR, but include areas at the extensive end of the land use gradient	3.2.1	–
ALPGR	E2.3/E4	Some low-lying parts of class E2.3 may fall into EXTGR	3.2.1	–
WET	D/E3.4/E3.5	–	4.1.1/4.1.2	–
DRY	E1/H2.5/H2.6	Semi-open thermophilous sites are covered by classes H2.5/6	3.2.1	Dry grasslands s.str. are not distinguished in CLC, thus they are covered by class 3.2.1
GRAVEL	C3.6/C3.7	–	3.3.1.3	–
ROCK	H2/H3/H5	–	3.3.2	–
GLAC	H4	–	3.3.5	–

EUNIS-levels are indicated by letter only (=Level 1); letter+number (=Level 2); letter+point-separated number (=Level 3). The CLC2006 classification scheme follows point-separated number codes, the number of digits corresponding to the hierarchical level (e.g. 3-digit code=Level 3)

Gravel banks

The *Gravel banks* class was established by an on-screen visual interpretation based on Google Earth satellite imagery. Gravel banks along river systems across the entire study region with an approximate width > 25 m were digitized as vector polygons and then converted to raster format.

Glaciers, rocks

The habitat classes *Glaciers* and *Rocks* are based on the CLC2006 classes of *Glaciers and perpetual snow* (3.3.5) and *Bare rock* (3.3.2), respectively.

For setting up the final map we mosaicked the thematic layers by following the general rule that classes of high nature conservation value, which are often restricted to rather small areas, must not be overlain by more widespread classes like *Arable land*. In detail, the order for mosaicking the single class layers from top to bottom is: GRAVEL, GLAC, DRY, WET, EXTGR/ALPGR, SHRUB, ROCK, BUA, ROAD, RAIL, RIV, LAKE, ORC, VIN, IGR, ARAB, CFO/BLFO. This leads to a refinement of the coarse CLC2006 boundaries. For map harmonization and edge clearance purposes we finally applied minor boundary cleaning and majority filtering techniques.

Habitat classification

The CEH habitat classes are tied to the European classification systems of CORINE and EUNIS. Class specific assignments and additional remarks are listed in Table 2.

Data accuracy

To assess the degree of spatio-thematic precision between several datasets used for map generation, which is particularly important for remote-sensing-based datasets, we calculated a series of Kappa statistics using the Kappa statistics add-on tool in ArcGIS 10.1 by comparing the JRC forest layers (BLFO and CFO) and the layer on *Intensive used grasslands* (IGR) with reference datasets from the IACS database not used for map creation. The forest evaluation data are spatially based on Austrian map ÖK 50 forest margins and thematically originate from GSE Forest Monitoring, while data on intensive grasslands were derived by filtering corresponding EUNIS classes. For the calculation of Kappa statistics we resampled IACS grassland data first to correspond with the final resolution of the CEH (i.e. 25 m). We applied the same procedure with forest data after integrating the class *mixed forest* of the evaluation data into the class *coniferous forest* to comply with the CEH mapping scheme. For testing

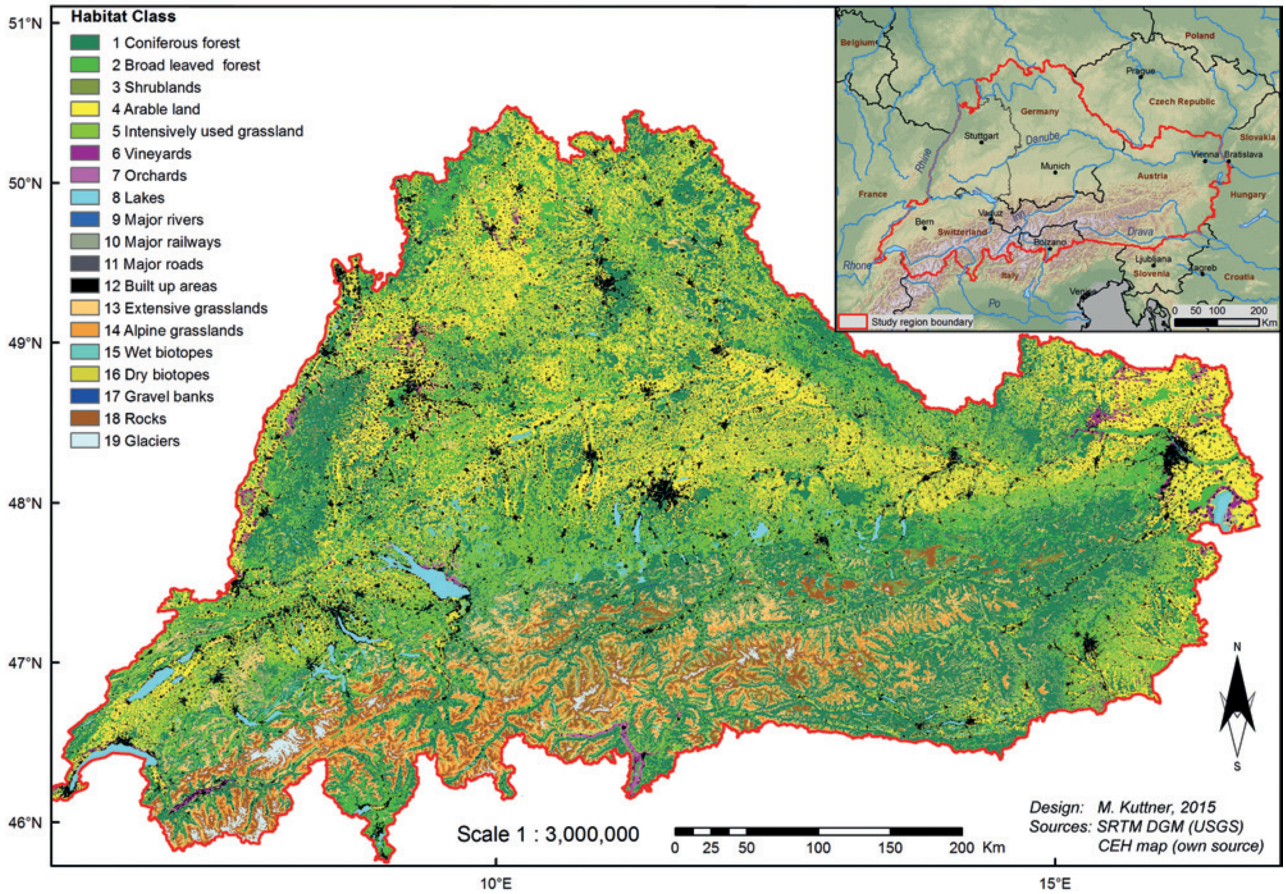

Figure 1 – The CEH (covering Austria, Baden-Wurttemberg, Bavaria, Liechtenstein, South Tyrol, Switzerland) represents 19 habitat classes

each dataset we randomly selected 250 000 data points across Austria.

In addition we calculated Kappa statistics on a larger spatial scale by applying GMES Urban Atlas datasets for all available (peri-)urban areas within our mapping region. The area covered by these data corresponds to approx. 17% of the CEH. Urban Atlas classes with artificial areas of various densities were pooled to comply with CEH habitat class *Built up areas*, while *Fast transit roads*, *Railways* and *Water* could be easily related to corresponding CEH habitat classes. In order to gain a thematically comparable class that could be related to *Agricultural, Semi-natural and wetland areas*, we pooled the CEH classes *Arable land, Intensive used grasslands*, *Vineyards*, *Orchard*s, *Extensive grasslands* and *Mires and wet grasslands*. We also pooled the CEH classes *Coniferous forest* and *Broad leaved forest* to comply with *Forest* as defined in the Urban Atlas. Again we selected a set of 250 000 random points for computing Kappa statistics.

As independent reference data for South Tyrol and Switzerland are lacking, we extracted nationwide shares in major land-use / land-cover classes that could be related to our classification scheme from federal statistical databases. In the case of South Tyrol, forest classification also included (sub-)alpine dwarf pine stands, which have been classified as SHRUB within the CEH. The fuzzy distinction between those classes is indicated by the dot-dashed line in Table 5. Similarly, the South Tyrolean proportion of *Arable land* should be treated as land used for intensive agriculture and therefore CEH class IGR must be also considered when comparing area proportions of this class as indicated by dashed lines in Table 5.

Mapping CEH class proportions of important protected areas

As a first application of the CEH we calculated proportional shares of habitat classes for all national parks (NPs) and biosphere reserves (BRs) and their environs within the CEH region. To do so, we calculated minimum bounding geometries of each conservation area in ArcGIS 10.1. To allow for a comparison of reserve areas with their surroundings, we extended the bounding envelopes to include at least 1.5 times the conservation area and calculated the proportional shares of habitat classes also for the surrounding areas.

Results

The CEH consists of more than 383 million grid cells, covering an area of approximately 240 000 km², and consists of 19 habitat classes (Figure 1). The four most abundant habitat classes are *Coniferous forests* (28.8%), *Arable land* (21.4%), *Intensively used grassland* (11.6%) and *Broad leaved forests* (9.6%), which jointly cover approx. 71% of the study region. Proportional shares of all habitat classes for individual countries and federal states are given in Table 3.

The proportional shares of habitat classes differ markedly across the study region depending on altitude, geomorphology, land-cover proportions, land-cover diversity, and land-use intensity as exemplified for selected landscapes in Figure 2.

Table 2 shows a crosslink between the habitat classification of the CEH and higher hierarchical levels of the most widely used European classification schemes, i.e. the EU Nature Information System (EUNIS) and CORINE (CLC2006). Clearly characterized CLC2006 classes, such as urban areas, arable lands or rock outcrops, are well represented by corresponding CEH classes, while complex CLC2006 categories, such as *Complex cultivation patterns* (2.4.2) or *Transitional woodland-shrub* (3.2.4), were split up and are represented by various CEH classes (Figure 3). The class *Natural grasslands* (3.2.1) (Figure 3 (b)) in particular was subdivided into EXTGR and ALPGR and the mixed class of *Moors and heathland* (3.2.2) was split up into classes CFO, SHRUB and EXTGR. Moreover, *Complex cultivation patterns* (2.4.2) as well as *Land principally occupied by agriculture* (4.1.2) (Figure 3 (c)) were divided into an agricultural matrix mainly consisting of ARAB, IGR, EXTR and BUA.

Table 3 – Habitat class composition across the study region and for Austria (AT), Switzerland (CH), Liechtenstein (LI), South Tyrol (ST), Bavaria (BAV), Baden-Wurttemberg (BW).

Habitat Class	Mean overall share (%)	% AT	% BAV	% BW	% LI	% CH	% ST
CFO	28.8	35.1	27.3	23.1	34.7	22.5	33.3
BLFO	9.6	9.7	8.1	14.5	4.9	9.2	3.1
SHRUB	2.4	4.8	0.7	0.6	1	1.3	5.4
ARAB	21.4	16.7	32.3	27.1	9.4	10.7	1.4
IGR	11.6	7.3	17.1	12.5	7.7	11.2	6.7
VIN	0.6	1	0.1	0.9	0.03	0.3	1
ORC	0.2	0.02	0.03	0.5		0.1	2.9
LAKE	1.2	0.6	0.8	1		2.2	0.2
RIV	0.4	0.4	0.4	0.4	0.7	0.4	0.2
RAIL	0.3	0.3	0.3	0.4	0.2	0.4	0.1
ROAD	0.5	0.5	0.5	0.5	0.5	0.5	0.3
BUA	6.8	5.2	7.8	9.8	11.9	6.9	1.4
EXTGR	7.7	10.3	3	5.2	21.8	10.7	17.3
ALPGR	3.3	3.6	0.1		4.9	9.1	12.2
WET	1	0.5	1.1	2.2	1.7	0.8	0.2
DRY	0.6	0.4	0.3	1.3	0.7	0.8	1.1
GRAVEL	0.04	0.04	0.02		0.00	0.1	0.04
ROCK	3	3	0.2		0.1	8.9	11.1
GLAC	0.7	0.7				2.9	1.6
Total Shares (km^2)	239 005	83 855	70 553	35 752	160	41 285	7 400

Map validation

A verification of the modelled forest limit was conducted by comparison with an available dataset on Swiss tree lines commissioned by the AGROSCOPE Institute (Szerencsits 2012). The mean deviation of our dataset from the Swiss treeline data equals at 128.5 m, which corresponds well with the findings of Szerencsits (2012) who calculated mean deviations between forest lines and tree lines for major climatic regions of Switzerland between 81 m and 213 m.

The results of the Kappa statistics revealed an observed agreement rate among GIO-LAND *Intensive used grassland* and IACS grassland data of 90.7% and a corresponding Kappa coefficient of 45.6%. In case of the compared forest datasets, the observed agreement rate was 86.3% and the Kappa coefficient 75.5%. Evaluation statistics of classes extracted from Urban Atlas data resulted in an overall observed agreement rate of 87.8% and a Kappa coefficient of 79.7%.

The comparison between land cover derived from federal area statistic databases and proportional shares of CEH habitat classes is summarized in Table 5. Forests, arable land, grasslands and urban areas correspond well.

Habitat distribution within major conservation areas and their environs

To provide a first application of CEH, we calculated the proportion of the habitat classes within NPs and BRs and their environs (Table 6). We found substantial differences in habitat proportions between protected areas and their environs. In particular, there often is a higher proportion of habitat classes of high nature conservation value, such as extensive grasslands, forests, dry and wetlands, in protected areas. Conversely, the proportions of heavily modified habitats, such as arable land, intensive grassland or built up areas, are higher outside nature reserves in most cases.

Discussion

Advances over previous ecosystem distribution maps

The CEH combines high spatial resolution with a thematic resolution that is suitable for an advanced and standardized representation of Central European habitats, allowing for analyses beyond that are supported by previous trans-national or national sources. For instance, the widely used European CLC2006 has a minimum mapping unit of 25 ha and a thematic resolution of 44 land-cover classes for the whole of Europe (EEA 2007). However, about 20% are complex land-cover classes containing fundamentally different habitats (e.g. mixed arable land). This is a great obstacle for many ecological studies that depend on clearly delineated and fine-scale land-cover data (Schmit et al. 2006). In contrast, the CEH avoids mixed classification and aims at a spatially and thematically explicit distinction of individual habitats. For instance, we differentiate areas of intensively managed grassland from arable lands, whereas CLC2006 partly merges these classes into *Land principally occupied by agriculture* (4.1.2) or *Complex cultivation patterns* (2.4.2), together

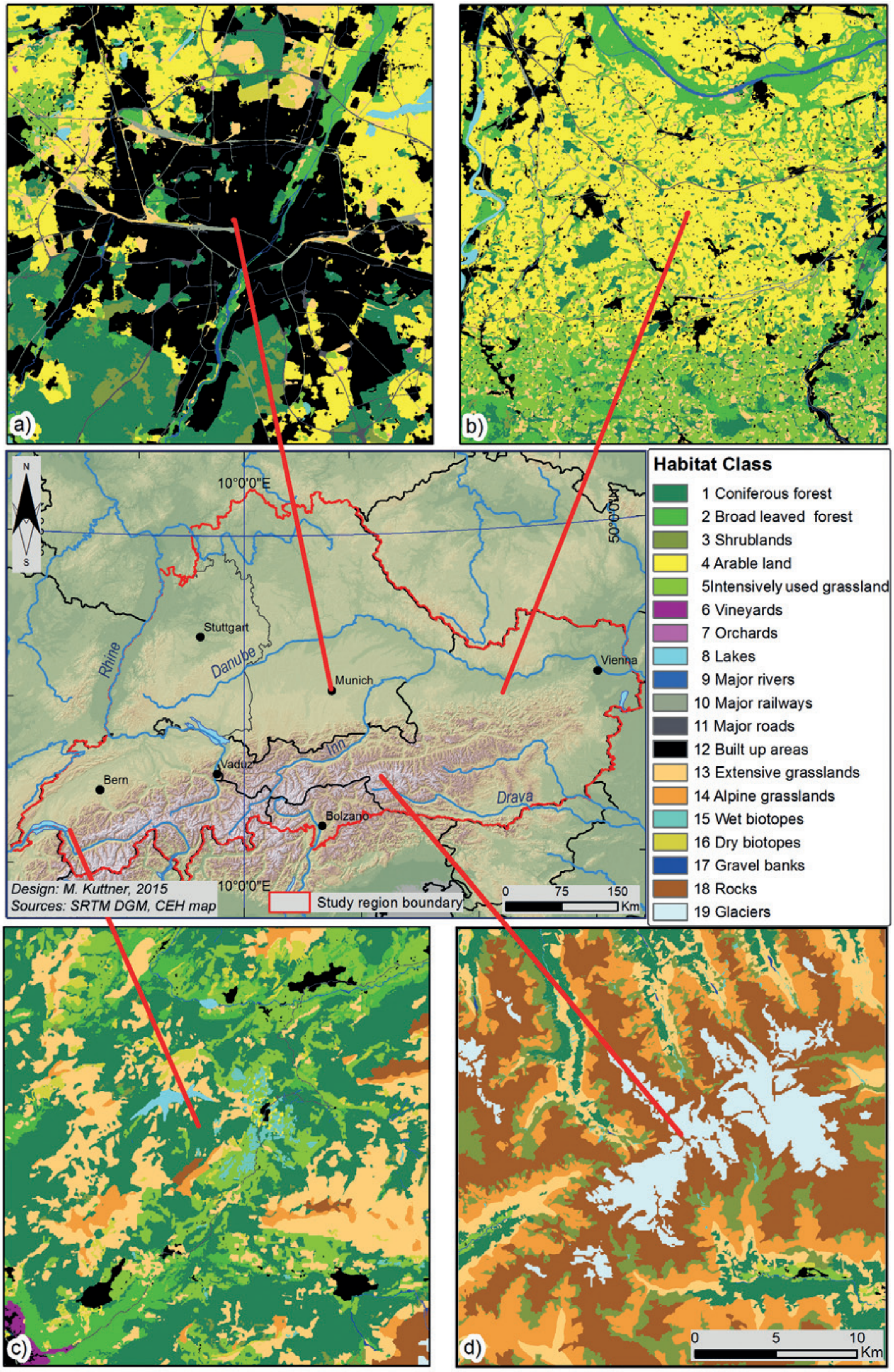

Figure 2 – Habitat classes of the CEH for sample landscapes: (a) a (peri)urban landscape (Munich, Germany); (b) an intensively used agricultural landscape (south-east of Linz, Austria); (c) an extensively used agricultural landscape (east of Lake Geneva, Switzerland); and (d) a high-altitude landscape with low land-use intensity in the Alps (Mount Großvenediger in the Hohe Tauern, Austria)

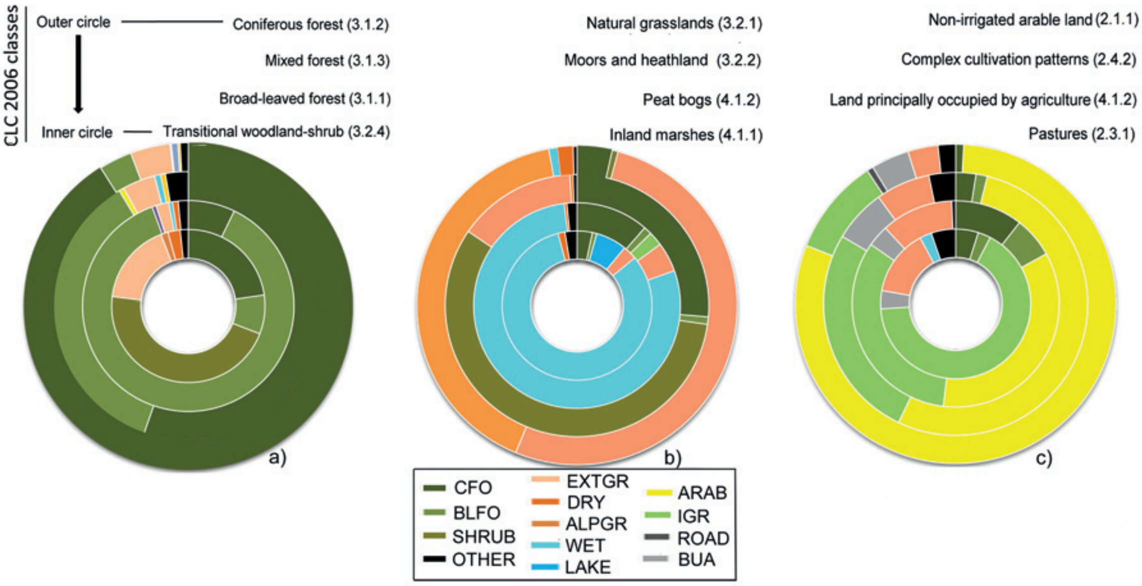

Figure 3 – CEH proportions compared to the most widely distributed CLC2006 classes, sectioned by (a) forest and shrub land classes, (b) grasslands and heath classes and (c) agriculturally dominated classes across the study region. Each circle represents one CLC2006 class.

with other minor land-use classes (cf. Figure 3). Further, we differentiate various types of (semi-)natural grasslands, such as *Extensive grasslands*, *Alpine grasslands*, *Dry grasslands* and *Wet grasslands*, which are of particular high value for nature conservation and serve as a reference point to analyse changes in habitat area and connectivity for rare and / or endangered species on large spatial scales (e.g. Hooftman & Bullock 2012). In sum, the CEH substantially advances existing data sources on ecosystem distribution for the study region.

Map validation

We used Kappa statistics to test if transnational data sources, derived from remote sensing campaigns represent certain habitat classes adequately in terms of spatial and thematic accuracy. We found that this condition was met with some variability between different classes, documented by a range of Kappa coefficients from 45% for a subset of the *Intensively used grassland* habitat class (indicating a *moderate strength* of agreement according to Landis & Koch 1977) to 75% for the forest classes, which corresponds to *substantial strength* of agreement. Good results were also achieved by the statistical validation using Urban Atlas Data (observed agreement rate: 87.8%; Kappa coefficient: 79.7%), see Table 4.

Those results should be interpreted in the context of observed agreement rates, which turned out even higher (> 90%) in cases of grasslands, even though Kappa coefficients only indicated *moderate strength*. The likely main reason for these somewhat divergent results is a high prevalence of negative cases (approx. 88% of *No-Data* points) in our grassland data, as already explained by Kundel & Polansky (2003). Vice versa, agreement rates and Kappa coefficients for Urban Atlas Data are rather close to each other because of almost full coverage of the respective point dataset within the test areas, which in turn means only few negative cases.

Spatial and thematic accuracy and their limitations

We aimed at using only current data sources (2006 or younger) for creating the CEH to account for rapid changes in landscape structure and ecosystem distribution in Central Europe (Falcucci et al. 2007). However, we occasionally had to resort to older datasets (e.g. Steiner 1992) to fill gaps in the distribution of high nature value habitat classes. We are aware that this approach might bias the maps towards greater spatial extension and lower fragmentation of habitat classes on high conservation value, particularly for the classes *Mires and wet grasslands* and *Dry grasslands*, because these ecosystems have continuously declined in recent decades (Klötzli & Grootjans 2001; Cremene et al. 2005).

Table 4 – Confusion matrix obtained from Kappa statistic evaluation between Urban Atlas and CEH-map classes. AGRI = [ARAB, IGR, VIN, ORC]; FOREST = [CFO, BLFO]; ARTIFICIAL = [BUA]; WATER = [LAKE, RIV]; RAIL = [RAIL]; ROAD = [ROAD]

	AGRI	FOREST	ARTIFICIAL	WATER	RAIL	ROAD
AGRI	**99789**	6746	2820	550	147	62
FOREST	4874	**66178**	699	565	27	51
ARTIFICIAL	4008	1491	**19253**	161	124	41
WATER	368	248	90	**1200**	5	1
RAIL	341	121	282	20	**362**	11
ROAD	454	201	288	10	11	**403**
Counts	109834	74985	23432	2506	676	569
	Observed Agreement: 87.88 %		Chance Agreement: 40.1%		Kappa Coefficient: 79.76%	

Table 5 – Area statistics (%) of major land cover classes, derived from federal statistical databases within the mapping region, compared to CEH-class-specific shares (CEH-[country name]). Dotted line: indicating a fuzzy distinction between the classes; dashed lines: intenivly used arable land.

<table>
<tr><th>Habitat class</th><th>AT %</th><th>CEH-AT%</th><th>CH %</th><th>CEH-CH %</th><th>BW %</th><th>CEH-BW %</th><th>BA %</th><th>CEH-BA %</th><th>ST %</th><th>CEH-ST %</th><th>LI %</th><th>CEH-LI %</th></tr>
<tr><td>CFO</td><td rowspan="2">44.2</td><td rowspan="2">44.8</td><td rowspan="2">32.8</td><td rowspan="2">31.7</td><td rowspan="2">38</td><td rowspan="2">37.6</td><td rowspan="2">35.1</td><td rowspan="2">35.4</td><td rowspan="2">46.7</td><td rowspan="2">36.3</td><td rowspan="2">41</td><td rowspan="2">39.6</td></tr>
<tr><td>BLFO</td></tr>
<tr><td>SHRUB</td><td></td><td></td><td>2.1</td><td>1.3</td><td></td><td></td><td></td><td></td><td></td><td>5.4</td><td></td><td></td></tr>
<tr><td>ARAB</td><td>16.2</td><td>16.7</td><td>9.9</td><td>10.7</td><td>26.6</td><td>27.1</td><td>29.6</td><td>32.2</td><td rowspan="2">8.4</td><td>1.4</td><td>8.8</td><td>9.4</td></tr>
<tr><td>IGR</td><td>6.7</td><td>7.3</td><td rowspan="2">24.8</td><td rowspan="2">21.9</td><td rowspan="2">17.6</td><td rowspan="2">17.7</td><td rowspan="2">19.5</td><td rowspan="2">20.1</td><td>6.7</td><td rowspan="2">25.3</td><td rowspan="2">29.5</td></tr>
<tr><td>EXTGR</td><td>8.7</td><td>10.3</td><td>17.5</td><td>17.3</td></tr>
<tr><td>VIN</td><td>0.6</td><td>0.9</td><td>3.7</td><td>0.3</td><td>0.8</td><td>0.9</td><td></td><td></td><td rowspan="2">4</td><td rowspan="2">3.9</td><td></td><td></td></tr>
<tr><td>ORC</td><td>0.1</td><td>0.01</td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td>BUA</td><td>3.6</td><td>5.1</td><td>5.1</td><td>6.9</td><td>8.5</td><td>9.8</td><td>6.7</td><td>7.8</td><td>1.6</td><td>1.4</td><td>10</td><td>11.9</td></tr>
<tr><td>WET</td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td>0.2</td><td>0.2</td><td></td><td></td></tr>
<tr><td>ROCK</td><td></td><td></td><td>8.7</td><td>8.9</td><td></td><td></td><td></td><td></td><td>8</td><td>11.1</td><td></td><td></td></tr>
<tr><td>GLAC</td><td></td><td></td><td>2.8</td><td>2.9</td><td></td><td></td><td></td><td></td><td>1.6</td><td>1.6</td><td></td><td></td></tr>
</table>

<table>
<tr><th>Country</th><th>Source</th><th>Links</th></tr>
<tr><td rowspan="2">AT</td><td>Statistik Austria</td><td>http://www.statistik.at/web_de/statistiken/land_und_forstwirtschaft/index.html</td></tr>
<tr><td>Waldinventur 2007 / 2009</td><td>http://bfw.ac.at/030/pdf/1818_pi24.pdf</td></tr>
<tr><td>CH</td><td>Bundesamt für Statistik</td><td>http://www.bfs.admin.ch/bfs/portal/de/index/themen/02/03/blank/data/01.html</td></tr>
<tr><td rowspan="2">D</td><td>Statistisches Landesamt Baden-Württemberg</td><td>http://www.statistik-bw.de/BevoelkGebiet/Landesdaten/geb_Flaechennutzung.asp</td></tr>
<tr><td>Bayrisches Landesamt für Statistik</td><td>https://www.statistik.bayern.de/statistik/landwirtschaft/</td></tr>
<tr><td rowspan="2">IT</td><td>Abtlg. Natur, Landschaft und Raumentwicklung</td><td rowspan="2">http://www.provincia.bz.it/natur-raum/themen/landeskartografie-realnutzungskarte.asp</td></tr>
<tr><td>Flächenstatistik der Realnutzungskarte</td></tr>
<tr><td>LI</td><td>Agrarbericht 2009</td><td>http://www.llv.li/files/au/pdf-llv-au-agrarbericht_2009.pdf</td></tr>
</table>

Furthermore, variation in data quality, spatial resolution and coverage between data sources might have caused differences in map quality across geographic regions (countries and federal states). For example, gaps in datasets of *Dry grasslands* in South Tyrol were filled by modelling approaches which potentially introduce errors. However, such effects on model quality should be low, because i) only very small parts of the CEH were complemented by modelling and ii) we carefully checked the additionally delineated cells by visual comparison with orthophoto imagery. Nevertheless, it is still possible that a few of the designated patches of *Dry grasslands* are irrigated and, thus, should be classified as extensive grasslands.

Applicability and outlook

A first application of the CEH has already been presented by calculating habitat distribution inside and outside the NPs and BRs covered by the map. However, those proportions must be considered case by case, as the location of the investigated conservation areas ranges from rather intensively used low-altitude landscapes to marginally utilized high-alpine space.

Other fields of application of habitat maps are manifold and relevant in various scientific disciplines, such as ecology, geography or nature conservation and landscape planning at different spatial scales, ranging from local case studies to trans-national analyses. For instance, the spatial extension and distribution of ecosystems are key indicators for the status of biodiversity, species extinction risks (IUCN 2010) and, by definition, of ecosystem status (Keith et al. 2013). Further, the quantitative and qualitative potential in provision of most ecosystem services is intimately linked to the composition and spatial configuration of the underlying habitat classes within the landscape of interest (Burkhard et al. 2012; Helfenstein & Kienast 2014). The distribution of habitats may form the basis for relating structural and functional landscape heterogeneity to analyse biodiversity patterns in landscapes (Fahrig et al. 2011; Schindler et al. 2013) and may be useful to identify high nature value farmlands (Paracchini et al. 2008). The explanatory power of species distribution models can also be improved by using more accurate spatial information on ecosystems (Thuiller et al. 2004). Data on habitat distribution may also serve as a basis for quantifying the impact of invasive biota (Chytry et al. 2012). Finally, ecological network analysis, especially on broader scales, and associated conservation and planning actions (Groves et al. 2002; Watts et al. 2010) also need high-resolution ecosystem distribution data, e. g. to measure degrees of habitat fragmentation (Ostapowicz et al. 2006). In conclusion, we think that the CEH map represents a valuable tool for advancing both ecological research and spatial management planning in Central Europe.

Data status and accessibility

Latest update

15.02.2015

Proprietary restrictions

This dataset is freely available for non-commercial scientific use.

Table 6 – Proportional shares (%) of habitat classes in conservation areas and their surroundings (columns marked with asterisks) within the CEH mapping region. National parks and biosphere reserves are given in the upper and lower section, respectively. Highlighted fields either indicate greater (green) or reduced (red) shares of the corresponding habitat classes within protected areas.

CEH class	National Parks																					
	Austria												Germany						Italy		Switzer-land	
	DON*	DON	GES*	GES	HOT*	HOT	KAL*	KAL	NEU*	NEU	THA*	THA	BRW*	BRW	BER*	BER	SCH*	SCH	STJ*	STJ	GRB*	GRB
CFO	0.3	1.4	67.5	49.6	35.2	8.4	44.0	46.2	0	0	6.4	1.1	55.9	58.4	44.4	39.4	76.2	79.5	20.6	25.3	34.9	25.8
BLFO	11.5	72.3	11.4	9.5	1.5	0.2	33.7	34.4	1.1	0.4	58.6	91.7	4.0	24.9	5.6	1.7	1.0	0.7	0.9	0.4	0.0	0.0
SHRUB	0	0	4.3	14.7	12.1	16.7	0.5	11.1	0	0	0	0	0.1	14.8	11.0	11.2	6.1	13.0	6.0	9.0	1.5	1.7
ARAB	65.3	4.4	0.0	0.0	0.4	0.0	0.0	0.0	43.9	1.7	32.1	0.4	0.5	0.0	0.1	0.0	1.6	0.0	2.7	1.0	0	0
IGR	1.0	1.8	2.0	0.1	4.0	0.1	10.1	0.0	2.8	3.1	0.3	0.0	28.1	0.3	5.2	0.1	1.6	0.1	6.1	2.0	5.4	0.0
VIN	0.2	0.0	0	0	0	0	0	0	21.2	1.7	0	0	0	0	0	0	0.1	0.0	0.1	0.0	0	0
ORC	0	0	0	0	0	0	0	0	0.0	0.0	0	0	0	0	0	0	0	0	6.2	0.2	0	0
LAKE	0.7	1.1	0.2	0.1	0.3	0.0	0.1	0.0	19.4	30.1	0	0	0.2	0.0	0.1	2.8	0.1	0.0	0.2	0.3	0.0	0.1
RIV	0.8	6.9	0.4	0.4	0.3	0.0	0.5	0.5	0	0	0.0	1.9	0.2	0.0	0.4	0.1	0.6	0.1	0.3	0.2	0.6	0.2
RAIL	1.4	0.2	0.5	0.2	0.1	0.0	0.2	0.0	0.1	0.0	0	0	0.4	0.1	0.1	0.0	0.2	0.0	0.1	0.0	0	0
ROAD	1.8	0.1	0.4	0.2	0.2	0.0	0.5	0.0	0.1	0.0	0.1	0.0	0.3	0.0	0.6	0.0	0.5	0.4	0.2	0.1	0.5	0.2
BUA	14.4	0.3	0.8	0.0	1.6	0.0	1.5	0.0	4.6	0.1	2.1	0.4	6.4	0.1	2.2	0.0	3.0	0.0	1.5	0.2	0.5	0.0
EXTGR	0.9	3.1	8.7	4.4	21.2	10.9	7.3	7.5	2.2	9.7	0.2	1.4	2.1	0.5	8.0	8.3	6.5	0.2	20.3	16.4	12.9	14.2
ALPGR	0	0	0.4	0.5	14.8	21.3	0.0	0.1	0	0	0	0	0	0	1.6	6.3	0.0	0.0	17.2	14.3	23.2	21.7
WET	0.1	1.2	0.2	0.0	0.4	0.3	0.2	0.0	2.8	43.6	0	0	1.7	0.7	0.7	0.2	1.4	4.5	0.1	0.1	0.0	0.0
DRY	1.7	7.2	0.0	0.0	0.2	0.0	1.4	0.0	1.7	9.7	0	3	0.2	0.1	0.5	0.7	1.2	1.4	4.0	0.2	1.5	0.0
GRAVEL	0	0	0.0	0.2	0.1	0.0	0.1	0.1	0	0	0	0	0	0	0.0	0.5	0	0	0.0	0.1	0.0	0.0
ROCK	0	0	3.1	20.1	7.3	34.3	0	0	0	0	0	0	0	0	19.6	28.7	0	0	11.6	23.2	18.7	36.0
GLAC	0	0	0	0	0.4	7.7	0	0	0	0	0	0	0	0	0	0	0	0	1.9	6.9	0.2	0.0

DON = Donauauen; GES = Gesäuse; HOT = Hohe Tauern; KAL = Kalkalpen; NEU = Neusiedler See; THA = Thayatal; BRW = Bayrischer Wald; BER = Berchtesgaden; SCH = Schwarzwald; STJ = Stilfser Joch; GRB = Graubünden

CEH class	Biosphere reserves																			
	Austria										Germany						Switzerland			
	NEU*	NEU	NOC*	NOC	ULB*	ULB	WAL*	WAL	WIW*	WIW	SCA*	SCA	BGL*	BGL	RHÖ*	RHÖ	ENT*	ENT	VAM*	VAM
CFO	0.1	0.0	53.0	49.5	0.0	0.2	28.4	25.4	11.1	3.9	12.4	4.2	33.0	43.8	17.1	25.5	49.3	48.2	24.2	23.4
BLFO	12.4	0.0	0.9	1.3	36.1	65.5	3.6	5.4	24.3	60.3	24.9	36.4	9.8	8.6	24.2	25.2	5.4	3.2	0.1	0.0
SHRUB	0.1	0.0	9.5	9.2	0	0	9.9	12.0	0	0	0.1	0.0	5.3	5.0	0.1	0.3	1.0	0.1	2.2	1.4
ARAB	18.4	0.1	1.1	0.1	31.8	3.8	0.7	0.0	31.6	7.7	31.8	19.8	1.3	2.0	38.3	16.3	0.8	0.4	0.9	0.0
IGR	2.7	0.1	3.9	2.2	1.9	0.3	3.1	3.8	3.9	3.9	13.7	15.3	21.1	17.1	8.0	11.7	14.6	30.4	5.9	3.0
VIN	40.5	0	0	0	0	0	0	0	2.0	2.0	0	0	0	0	0	0	0	0	0	0
ORC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0.0
LAKE	3.5	55.2	1.6	0.2	2.5	5.1	0	0	0.3	0.0	0.1	0.0	1.2	0.9	0	0	0.7	0.0	0.6	0.1
RIV	0	0	0.3	0.2	4.7	0.0	0.4	0.7	1.2	0.3	0.2	0.1	0.5	0.7	0.4	0.2	0.4	0.5	0.3	0.2
RAIL	0.2	0	0	0	0.1	0.0	0.1	0.0	1.1	0.3	0.3	0.2	0.4	0.3	0.2	0.1	0	0	0	0
ROAD	0.2	0	0.4	0.4	0.2	0.0	0.5	0.3	1.3	0.8	0.5	0.3	0.8	0.7	0.6	0.4	0.2	0.2	0.3	0.3
BUA	6.0	0.1	2.5	1.5	7.7	0.0	3.4	0.8	18.1	11.6	8.9	6.1	8.0	4.7	7.4	4.8	1.4	1.6	0.8	0.3
EXTGR	5.4	0.1	18.0	22.9	4.0	1.4	34.2	39.6	3.3	6.1	5.1	13.4	7.2	5.5	2.3	12.7	18.0	6.9	13.7	16.9
ALPGR	0	0	8.4	12.1	0	0	10.7	8.4	0	0	0	0	0.6	1.6	0	0	1.3	0.5	28.7	26.3
WET	4.5	44.4	0.2	0.5	0.1	0.0	3.2	1.2	0.0	0.1	0.4	0.2	1.4	1.0	0.4	1.7	5.3	5.9	0.2	0.1
DRY	6.1	0	0	0	10.8	23.7	0.4	0.2	1.9	2.9	1.6	3.8	0.2	0.6	0.9	1.0	0.3	0.3	1.6	0.4
GRAVEL	0	0	0	0	0	0	0.2	0.1	0	0	0	0	0.0	0.1	0	0	0.2	0.1	0.1	0.0
ROCK	0	0	0	0	0	0	1.2	2.1	0	0	0	0	9.1	7.3	0	0	0.9	1.3	18.3	27.7
GLAC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1.8	0.0

NOC = Nockberge; ULB = Untere Lobau; WAL = Großes Walsertal; WIW = Wienerwald; SCA = Schwäbische Alp; BGL = Berchtesgadener Land; RHÖ = Rhön; ENT = Entlebuch; VAM = Val Muestair

Citation

Data users must cite this Data Paper properly in any publication that results from an analysis using the provided data as a whole or in parts as: Kuttner, M., F. Essl, J. Peterseil, S. Dullinger, W. Rabitsch, S. Schindler, K. Hülber, A. Gattringer & D. Moser 2015. A new high-resolution habitat distribution map for Austria, Liechtenstein, southern Germany, South Tyrol and Switzerland. eco.mont 7(2): 18–29.

Collaboration

Data users might consider collaboration and/or co-authorship with the data owners.

Storage location

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– Introduction to Section C –

Spatio-temporal assessments in nature conservation: Quantification of biodiversity patterns and identification of species´ vulnerabilities due to environmental change

In the last section my thesis I included four recent research articles originating from different scientific projects I have been involved in during the last years, but altogether they are dealing with the overarching topic of how biodiversity patterns have evolved over time and will sustain already ongoing global change. The underlying processes of change are affecting our environment on almost all spatial scales, from entire ecosystems down to intraspecific patterns, but they have one thing in common: Human-caused environmental change has rapidly sped up since beginning of the ´Anthropocene´ (Steffen et al., 2011; Ellis, 2015).
At this, in particular climate change is directly affecting both ecosystem equilibria and consequently also biodiversity patterns, which adversely affect ecosystem service provision, and on the other hand climate change influences socio-economic decisions that, in turn, are altering ecosystem service provision as well (Schröter et al., 2005).
All of the articles presented in this section are focusing on (potential) climate change impacts on biodiversity, though article (vi) investigates on the invasion risk by the non-native Emerald Ash Borer (*Agrilus planipennis*) who appears as the major threat to Common Ash (*Fraxinus excelsior*) populations across (Central) Europe in the upcoming decades under climate warming. Common Ash trees are among the most widespread and important key tree species among Europe´s temperate forests and already being endangered due to another invasion by the so called ash dieback (*Hymenoscyphus pseudalbidus*). This pathogen fungi started to infest European Ash populations back in the 1990ies and has been first observed in North-Eastern Poland (Pautasso et al., 2013). Furthermore, current climate warming facilitates the spread of the neobiotic Emerald Ash Borer from Russia towards Central Europe in the upcoming decades. On the basis of the previously introduced CEH-map (see also Section B) we established a distribution map of the Common Ash throughout the mapping region and consequently deduced a risk assessment of Emerald Ash Borer invasion for the area.

Article (viii) also deals with the distribution of a single plant species, namely the endangered *Cerastium dinaricum*, a member of the Caryophyllaceae family which is endemic to only some mountainous screes and rock outcrops in the Western Balkan Peninsula. Here, the central questions were to examine its phylogeographic structure, which turned out to significantly differ between north-western and south-eastern populations and to set up correlative species distribution models in order to predict the potential impact of climate change on the species´ current range size for the second half of the 21st century. Long-time isolation on several non-glaciated mountain top refugia during glacial periods of the Pleistocene which were followed by yet rather limited upward migration capabilities due to warming by beginning of the Holocence have shown primarily responsible for the highly fragmented current distribution pattern of the investigated species. In general, high mountain endemic species are seemingly most affected by changing climates due to their restricted ranges and their limited possibility in in shifting their current ranges further upward to track climate change (Dirnböck et al., 2011). Though static modelling approaches, as used in this current study, tend to overestimate range decline it is most likely that most mountain species will be able to bear unsuitable climatic conditions for a few decades before either going extinct or managing to adapt to the altered environmental conditions (Dullinger et al., 2012). Hence, in case of *Cerastium dinaricum* (which is most likely true for other high mountain endemic plants as well), immediate implementation of nature conservation actions is required, for example by translocation of single specimen to adjacent mountains where environmental conditions remain suitable, as proposed by Thomas (2011).

The remaining articles are not solely focusing on one single species of interest but are either directly (article ix) or indirectly (article vii) dealing with human-caused effects on biodiversity patterns at higher functional levels. At this, within the study presented by article (vii) we applied a so-called integrated modelling framework in order to outline different storylines of farm production under a changing environment and their impact towards farm incomes and the environment. In detail, single scenarios were drawn under the assumptions of graduated mitigation, adaptation or combined strategies in response to climate change till 2040 by integrating several kinds of economic data on e.g. average crop yields, gross margins and subsidies as well as environmental indicators on landscape appearance, habitat quality in terms of landscape functionality (also refer to article (i)), farmland plant species richness and hemeroby. Overall, there is no doubt that climate change will affect agricultural ecosystem service provision in the future (e.g. Kirchner et al., 2015, Fezzi et al., 2015). Within this study we quantified its effect on farmland productivity which in turn directly affects the ecological state across our target landscape by applying various climate and policy scenarios. Although we did not aim to directly address the provision of certain ecosystem services, our outcomes can nevertheless be related to certain service groups such as food production, habitat quality or landscape aesthetics. It turned out that the rather moderately accounted climate change impact (+1.5K mean warming by 2040) will likely have no detrimental effects on species richness and landscape functionality at all in the investigated case study area where altered precipitation and warming patterns are seemingly still within a range to be able to deal with, provided that mitigation policies and actions are conducted. Accordingly, related ecosystem service groups such as ´habitat´, ´provision´ or ´regulation´ are neither likely to be affected. On the other hand, economic outcomes might even improve as also revealed by a nation-wide study by Bateman et al., 2013.

The last article (ix) I present within the frame of my dissertation introduces a current study targeting on varying patterns of species distribution between the Alpine region and adjacent lowlands. Basically, future projections on species distributions conducted by the use of correlative species distribution models (SDMs) generally tend to either over- or underestimate predicted ranges due to the basic assumptions of "unlimited" or "no" species dispersal (Guisan & Thuiller, 2005). While on a larger scale, climatic variables are foremost determining species distribution patterns (Thuiller et al., 2004), land cover data may serve as an with-determining co-variable on finer-scaled modelling approaches to predict future species distributions (Luoto et al., 2007; Randin et al., 2009). At this, we conducted a multi-species modelling approach by investigating 58 target species of butterflies, grasshoppers and vascular plants at a rather fine resolution of 100m. The study encompassed the same countries as already outlined in section B (see also article (v)), thus including substantial parts of the (eastern) Alps. We projected potential current and future distributions (for the second half of the 21st century) and according changes in range size by applying three different scenarios of climate change and further corrected those outcomes by species-specific demands on certain habitats. This enabled us to gain new insights on the (mis)match of climatically suitable space and the distribution of suitable habitats for the present situation as well as compared to the future predictions. Moreover, we detected significant differences of outcomes within our pool of target species, namely between the two main groups of lowland and alpine species.

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Section C

Article 6 (vi)

Valenta, V., Moser, D., **Kuttner, M.**, Peterseil, J., Essl, F. 2015. *A High-Resolution Map of Emerald Ash Borer Invasion Risk for Southern Central Europe.* Forests, 6/9, 3075-3086.

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Article

A High-Resolution Map of Emerald Ash Borer Invasion Risk for Southern Central Europe

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Abstract: Ash species (*Fraxinus* spp.) in Europe are threatened by the Emerald Ash Borer (*Agrilus planipennis*, EAB), an invasive wood boring beetle native to East Asia and currently spreading from European Russia westwards. Based on a high-resolution habitat distribution map (grid cell size: 25 × 25 m) and data on distribution and abundance of Common Ash (*Fraxinus excelsior*), the most widespread and highly susceptive host species of EAB in Europe, we assess the spatial distribution of EAB invasion risks for southern Central Europe (Austria, Switzerland, Liechtenstein, southern Germany, South Tyrol). We found highest *F. excelsior* abundance and thus invasion risks in extensive lowland floodplain forests, medium risks in zonal lowland forests and low risks in upper montane and subalpine forests. Based on average velocities of spread in Russia (13–31 km/year) and North America (2.5–80 km/year) from flight and human-assisted transport, EAB is likely to cover the distance (1500 km) between its current range edge in western Russia and the eastern border of the study region within few decades. However, secondary spread by infested wood products make earlier introductions likely. The high susceptibility and mortality of *F. excelsior* leave no doubt that this beetle will become a major forest pest once it reaches Central Europe. Therefore, developing and testing management approaches with the aim to halt or at least slow down the invasion of EAB in Europe have to be pursued with great urgency.

Keywords: *Agrilus planipennis*; alien species; EAB; forests; *Fraxinus*; impact; management

1. Introduction

Ash species (*Fraxinus* spp.) are widespread in temperate and subtropical zones of the northern hemisphere. Three of the 43 species of this genus are native in Europe and also occur in Central Europe: the Common Ash (*F. excelsior*), the Narrow-leaved Ash (*F. angustifolia*) and the Manna Ash (*F. ornus*) [1]. Those ash species are widespread components of mixed deciduous forests—*F. excelsior* throughout Europe, *F. angustifolia* in the South and Southeast, and *F. ornus* in South and South-East Europe [2]. Another ash species occurring in Europe is the American species *F. pennsylvanica*, which has been planted across Europe for timber or as ornamental tree [2,3]. This species has become a fast-spreading alien species in parts of Central Europe, in particular in floodplain forests [4].

European ash species are at risk of getting- or already are -attacked by the Emerald Ash Borer (EAB) (*Agrilus planipennis* Fairmaire, Coleoptera: Buprestidae) (Figure 1). This wood-boring beetle native to Asia has been introduced to North America probably in the 1990s and has had substantial impact on ecosystems and economy since then [3,5]. EAB has also been found in European Russia in 2003 (Figure 2) and is making its way westwards towards Central Europe [6] putting European forestry and environment in danger [7].

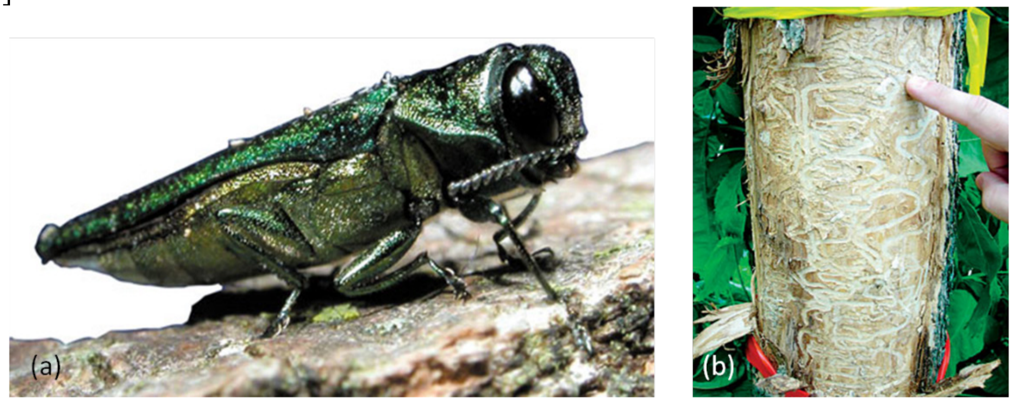

Figure 1. Pictures of adults (**a**) and galleries (**b**) of *Agrilus planipennis*. (Sources: Wikimedia Commons)

Therefore, here we assess the risk of EAB invasion for the by far most widespread ash species (*F. excelsior*) in southern Central Europe, *i.e.*, Austria, Switzerland, Liechtenstein, southern Germany, and South Tyrol. We use a recently compiled high-resolution habitat distribution map [8], data on ash distribution and abundance, and on the impact caused by EAB on *F. excelsior* in Russia, to assess the spatial distribution and scale of impacts by future EAB invasion.

2. Material and Methods

2.1. Forest Distribution Map

We used a recently compiled high-resolution habitat distribution map with a spatial resolution of 25 × 25 m [8]. This map is based on fine-scaled data from a range of data sources (e.g., habitat mapping campaigns, biotope inventories), which were harmonized and supplemented by remote mapping and modeling techniques (see [8] for details). This habitat distribution map contains two forest land cover classes (Broad Leaved Forests; Conifer Forests), which were refined by additional data from various sources in the public domain (e.g., forest inventory databases; [9,10]) to assess the distribution and abundance of *F. excelsior*. These data were harmonized and supplemented by remote mapping and modeling techniques (see [8] for details).

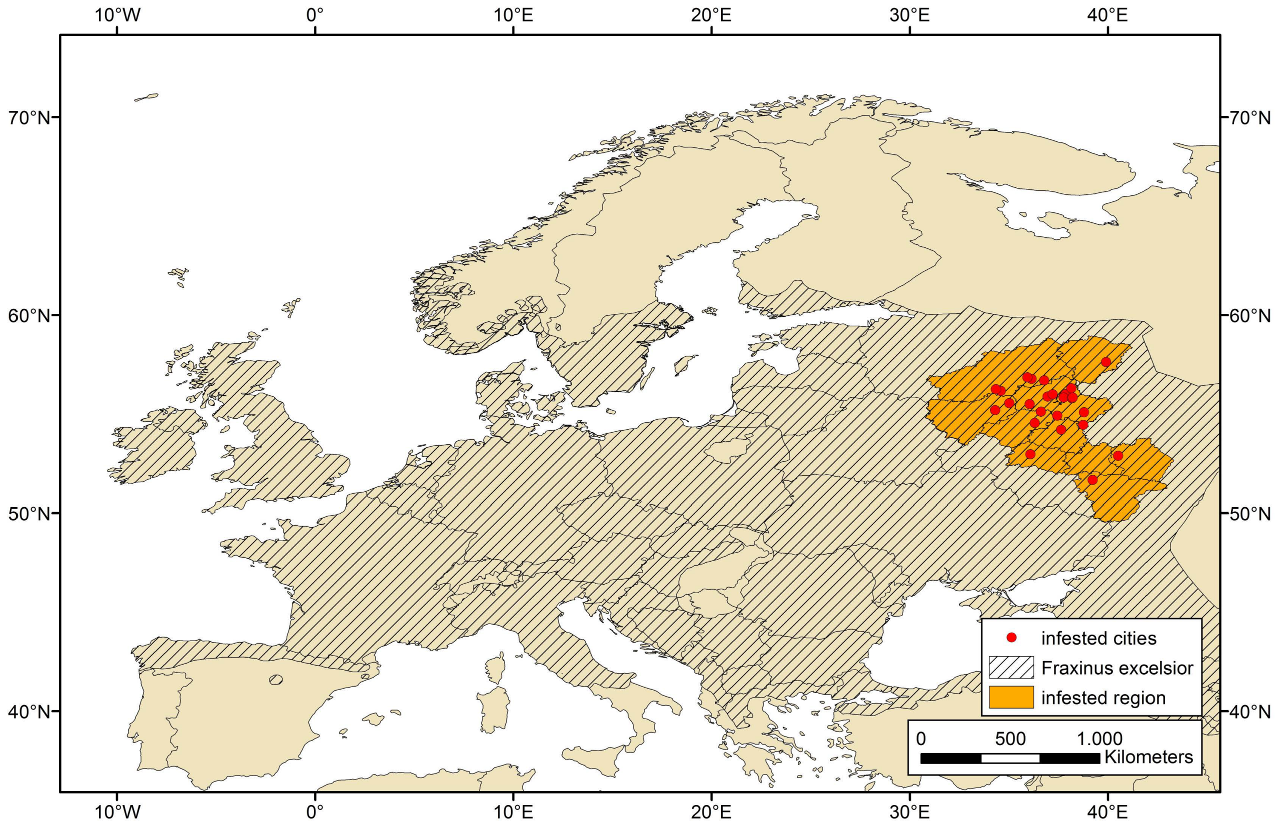

Figure 2. European range of *Agrilus planipennis*, showing infested regions of Russia (orange) and cities (red) where the beetle has been detected together with the distribution of *Fraxinus excelsior* [11]. Based on [6,12].

We note that *F. excelsior* also occurs as an important species in small landscape elements (e.g., hedgerows) in cultural landscapes and public urban spaces, which—due to their small spatial extent—are not shown in the habitat distribution map and hence excluded here.

2.2. Regionalizing Common Ash Distribution and Abundance

Fraxinus excelsior is a widespread species in Central Europe which is a constant and sometimes (sub) dominant component in a range of different forest types (Supplementary Table S1). Highest constancies of occurrence are documented for floodplain forests (Alnenion glutinoso-incanae, Ulmenion, Tillio-Acerion), but also in some zonal (Fagion sylvaticae) and sub-mediterranean extrazonal forests (Quercion pubescenti-petraeae) [13]. In the Austrian Alps, forest inventory data and relevé data from the Austrian Phytosociological Database ([14], Starlinger pers. comm.) show that the species only exceptionally occurs above 1200 m above sea level (a.s.l.) This altitudinal distribution limit holds true across all of Austria, without any conspicuous regional differences.

Below this altitude, Austrian Forest Inventory data [15] show that *F. excelsior* abundance increases towards lower altitudes as the share of ash in deciduous forests is ~2% (900–1200 m a.s.l.) and is ~6% (<900 m a.s.l.). Hence, we applied these altitudinal thresholds by intersecting the distribution of broad leaved forests with a Digital Elevation Model (DEM) to identify forests with different abundance of *F. excelsior* (Table 1). In addition, as *F. excelsior* is a particularly abundant in floodplain forests (>8%), we integrated the data of the Austrian [16], German [17] and Swiss [18] floodplain inventories to delineate the distribution of floodplain forests.

Table 1. Criteria used for mapping the regional distribution of *Fraxinus excelsior* in the study region (Austria, Germany—Baden-Wurttemberg (BW) and Bavaria (BAV)—Switzerland, South Tyrol).

Criteria	Austria	Germany (BW/BAV)	Switzerland	South Tyrol	References
Proportion of *Fraxinus excelsior* in forests	2.7%	4.9%/1.1%	3.4%	<2%	[19–22], Buechsenmeister pers. comm.
Altitudinal distribution	<900: ~6%	<900: ~6%	<900: ~6%	<900: ~6%	[15]
	900–1200: ~2%	900–1200: ~2%	900–1200: ~2%	900–1200: ~2%	
	>1200: 0%	>1200: 0%	>1200: 0%	>1200: 0%	
Distribution of floodplain forests	Floodplain Inventory	Floodplain Inventory	Floodplain Inventory	Not available	[16–18]

3. Results

The distribution of broad leaved forests of different *F. excelsior* abundance is highly heterogenous on the landscape scale (Figure 3, Table 2). Highest abundances are found in extensive lowland floodplain forests along major rivers (e.g., Danube, Inn, Isar, Rhine), medium abundances are found in forests of the lowlands outside the Alps, whereas abundance in forests in the Alps is low.

The total area of broad leaved forest with *F. excelsior* occurrence in the study region—based on the second-level NUTS regions of the European Union (= sub-national socio-economic regions within Europe, [23])—varies notably (Table 2). Forests of medium *F. excelsior* abundance are most wide-spread, whereas forests of high and low abundance are more restricted.

Based on the NUTS2 regions we found that *F. excelsior* amounts to 2% of the total forest area in Austria, 1.9% in Switzerland and 1.8% in Southern Germany (Table 2). The proportions are considerably lower in Liechtenstein (0.7%) and South Tyrol (0.4%).

The digital high-resolution map of EAB invasion risk is available on request from the authors.

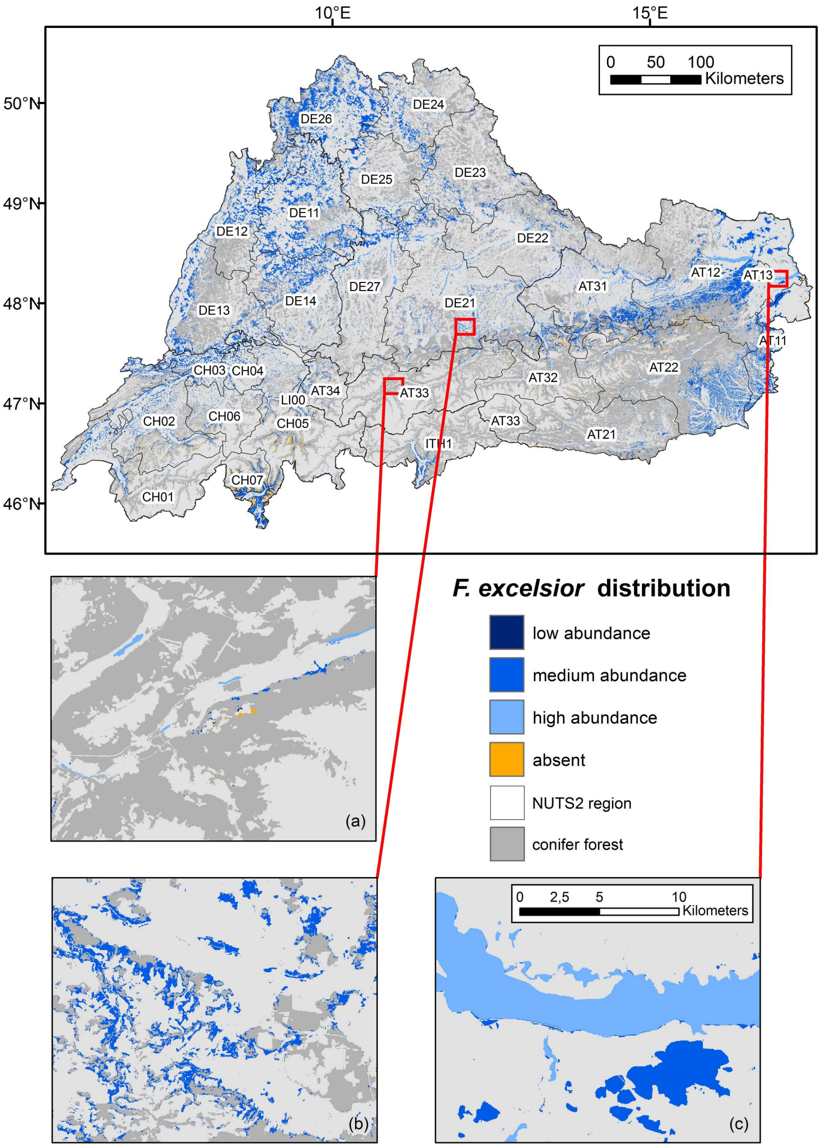

Figure 3. Risk map of future infestation by *Agrilus planipennis* based on *F. excelsior*-distribution for Austria, Bavaria, Baden-Wurttemberg, Liechtenstein, Switzerland and South Tyrol; with examples of landscapes differing in abundance of *F. excelsior* in the study region (see Table 2 for definitions): (**a**) mountainous landscape of the upper Inn Valley in Tyrol (near Innsbruck); (**b**) an agricultural landscape in the Bavarian Alpine Foothills (near Miesbach); (**c**) lowland floodplain forests along the Danube (east of Vienna) and adjacent remnant forests in a intensively used agricultural landscape. The acronyms and location of the NUTS2 (second-level Nomenclature of Units for Territorial Statistics) regions used in Table 2 are given. Study region: Austria (AT), Switzerland (CH), South Germany (DE), South Tyrol (ITH), and Liechtenstein (LI).

Table 2. Forest extent and distribution of *Fraxinus excelsior* in the NUTS2 (second-level Nomenclature of Units for Territorial Statistics) regions in the entire study region: Austria (AT), Switzerland (CH), South Germany (DE), South Tyrol (ITH), and Liechtenstein (LI). The total area of forest, broad leaved forests (BL) and the percentage of forested area of *F. excelsior* with different levels of abundance—low (~2%), medium (~6%) and high (~10%) are given. The total extent of *Fraxinus* forests and the proportions of different classes of *Fraxinus* forests on broad-leaved forest extent are also given. See Figure 3 for location of NUTS2 regions.

NUTS ID	NUTS Name	Nuts Region Area (km^2)	Forest Area (km^2)	BL Forest Area (km^2)	Low *Fraxinus* Abundance, Forest (~2%) (km^2)	Medium *Fraxinus* Abundance, Forest (~6%) (km^2)	High *Fraxinus* Abundance, Forest (~10%) (km^2)	Total *Fraxinus* Forests (km^2)	Proportion Low Abundance, *Fraxinus* Forest on BL Forest Area	Proportion Medium Abundance, *Fraxinus* Forest on BL forest Area	Proportion High Abundance *Fraxinus* Forest on BL Forest Area	Percentage Fraxinus Forests in %
AT11	Burgenland	3944.1	1272.1	918.7	0.0	846.5	65.2	911.7	0	66.6	5.1	71.7
AT12	Lower Austria	19,184.7	7971.3	3143.0	80.4	2544.3	468.5	3093.2	1.0	31.9	5.9	38.8
AT13	Vienna	413.4	90.7	84.6	0.0	60.3	24.3	84.6	-	66.5	26.8	93.2
AT21	Carinthia	9525.7	5363.5	309.2	56.4	156.5	63.5	276.4	1.1	2.9	1.2	5.2
AT22	Styria	16,436.0	9748.8	1948.0	141.8	1627.6	71.7	1841.1	1.5	16.7	0.7	18.9
AT31	Upper Austria	11,966.4	5081.6	1408.7	171.3	1030.3	133.9	1335.5	3.4	20.3	2.6	26.3
AT32	Salzburg	7155.5	3168.6	416.1	87.8	232.9	28.4	349.0	2.8	7.4	0.9	11.0
AT33	Tyrol	12,644.2	4327.5	149.6	30.0	57.0	39.3	126.2	0.7	1.3	0.9	2.9
AT34	Vorarlberg	2591.7	860.8	152.3	30.1	89.3	23.4	142.8	3.5	10.4	2.7	16.6
AT total	**Austria**	**83,861.6**	**37,884.9**	**8530.3**	**597.7**	**6644.7**	**918.1**	**8160.6**	**1.5**	**24.9**	**5.2**	**31.6**
CH01	Lake Geneva region	8737.7	2327.5	481.7	57.9	323.0	58.0	438.8	2.5	13.9	2.5	18.9
CH02	Espace Mittelland	10,016.4	3454.3	1034.3	127.1	767.1	65.2	959.3	3.7	22.2	1.9	27.8
CH03	Northwestern Switzerland	1969.2	692.9	481.3	2.9	469.2	9.2	481.3	0.4	67.7	1.3	69.5
CH04	Zurich	1734.1	484.9	199.2	1.6	191.8	5.6	199.1	0.3	39.6	1.2	41.1
CH05	Eastern Switzerland	11,524.4	3483.0	715.4	124.4	395.1	70.3	589.8	3.6	11.3	2.0	16.9
CH06	Central Switzerland	4483.3	1324.1	199.4	26.8	140.7	17.9	185.4	2.0	10.6	1.4	14.0
CH07	Ticino	2831.6	1434.5	864.9	170.2	435.6	19.7	625.4	11.9	30.4	1.4	43.6

Table 2. *Cont.*

NUTS ID	NUTS Name	Nuts Region Area (km^2)	Forest Area (km^2)	BL Forest Area (km^2)	Low *Fraxinus* Abundance Forest (~2%) (km^2)	Medium *Fraxinus* Abundance Forest (~6%) (km^2)	High *Fraxinus* Abundance Forest (~10%) (km^2)	Total *Fraxinus* Forests (km^2)	Proportion Low Abundance *Fraxinus* Forest on BL Forest Area	Proportion Medium Abundance *Fraxinus* Forest on BL forest Area	Proportion High Abundance *Fraxinus* Forest on BL Forest Area	Percentage Fraxinus Forests in %
CH total	**Switzerland**	**41,296.7**	**13,201.1**	**3976.3**	**510.9**	**2722.4**	**245.9**	**3479.2**	**3.5**	**28.0**	**1.7**	**33.1**
DE11	Stuttgart	10,568.2	3402.8	2127.0	0.0	2126.2	0.8	2127.0	-	62.5	0.0	62.5
DE12	Karlsruhe	6909.7	2948.4	1088.0	0.0	1004.2	83.8	1088.0	-	34.1	2.8	36.9
DE13	Freiburg	9493.2	4343.8	995.5	9.2	897.3	88.6	995.1	0.2	20.7	2.0	22.9
DE14	Tübingen	9093.9	2897.0	1088.8	16.8	1059.1	13.0	1088.8	0.6	36.6	0.5	37.6
DE21	Oberbayern	17538.4	6076.4	1090.8	45.7	824.0	209.9	1079.6	0.8	13.6	3.5	17.8
DE22	Niederbayern	10,332.3	3551.0	510.2	44.5	394.5	65.0	503.9	1.3	11.1	1.8	14.2
DE23	Oberpfalz	9663.3	3952.5	384.4	0.6	382.0	1.7	384.4	0.0	9.7	0.0	9.7
DE24	Oberfranken	7224.3	2744.3	570.6	0.0	565.8	4.9	570.6	-	20.6	0.2	20.8
DE25	Mittelfranken	7286.6	2439.6	543.6	0.0	542.7	1.0	543.6	-	22.3	0.0	22.3
DE26	Unterfranken	8542.5	3392.0	2161.8	0.2	2157.6	4.0	2161.8	0.0	63.6	0.1	63.7
DE27	Schwaben	10,030.2	2794.6	577.6	9.1	423.3	143.0	575.5	0.3	15.2	5.1	20.6
DE total	**Germany**	**106,682.6**	**38,542.2**	**11,138.3**	**126.1**	**10,376.6**	**615.5**	**11,118.2**	**0.3**	**28.2**	**1.5**	**29.9**
ITH1	**Bolzano**	**7425.0**	**2680.5**	**225.2**	**35.8**	**178.4**	**0.0**	**214.2**	**1.3**	**6.7**	**0.0**	**8.0**
LI00	**Liechten-stein**	**163.7**	**66.9**	**8.2**	**0.5**	**7.4**	**0.1**	**7.9**	**0.7**	**11.0**	**0.1**	**11.8**

4. Discussion

4.1. Distribution and Abundance of F. excelsior

Fraxinus excelsior is able to grow under highly different environmental conditions, from riparian zones to mountains forests and on nutrient-rich and poor soil [24]. In addition, *F. excelsior* has been widely planted in cities, parks and along roads as shade or ornamental trees. Its native range in Europe is limited by cold winter temperatures, late spring frosts and dry, hot summers [1,3]. Common Ash has an intermediate status between pioneer species and old-growth forest components. It usually occurs in groups within broad leaved forests, is often a dominant species in juvenile forest stands, but rarely attains dominance in older forest stages [1,24].

In southern Central Europe, *F. excelsior* occurs in a range of habitats and thus it is the 4th most common broadleaved tree species ([25], Büchsenmeister pers. comm.). We found that *F. excelsior* amounts to 1.8%–2.0% of the total forest area in Austria, Switzerland and Southern Germany, while proportions are considerably lower in the smaller regions Liechtenstein (0.7%) and South Tyrol (0.4%). However, recent forest inventory data report somewhat higher proportions of *F. excelsior*, maybe due to differing inventory methods: It is assumed that the proportion of *F. excelsior* in Austria is ca. 2.7% of all forest trees, 3.4% in Switzerland, 4.9% in Baden-Wurttemberg and 1.1% in Bavaria [19–21]. No data are available for South Tyrol and Liechtenstein.

4.2. EAB Invasion Risks into Central Europe

The spread of *A. planipennis* is facilitated by two spread mechanisms—*i.e.*, endogenous spread (by flight) and human-assisted transportation [7]. Whereas the first mechanism is most relevant for short-range dispersal and range-infilling, the second one is particularly so for long-distance dispersal. Given observed average velocities of spread in Russia (13–31 km year^{-1}) and North America (2.5–80 km year^{-1}) [7], it is likely that EAB will cover the distance (1500 km) between its current range edge in western Russia and the eastern border of the study region within a few decades. In addition, spread of EAB in the study region will be facilitated by the rather continuous distribution of *F. excelsior*. In the study region, potential corridors for spread can be found particularly along rivers and more generally in the lowlands (Figure 2), while the higher elevations of the Alps may serve as a barrier slowing or halting regional spread. Given the high connectivity of occurrences of *F. excelsior* in low and medium altitudes, it seems unlikely that the availability of host trees will be a major factor for limiting spread outside the Alps.

Human-assisted secondary long-range dispersal is most likely with infested wood and wood products. Although import restrictions of ash wood products from infested regions into the European Union have been introduced (e.g., [26,27]), secondary spread (e.g., by infested wood products) into Central Europe is increasingly likely to occur, the larger the infested area in Eastern Europe becomes. Thus, introduction into Central Europe may occur at any time. Invasion history shows that ports and trade centers are main gateways for such accidental introductions of alien species through international trade [28]. As EAB is able to cope with wide range of climatic condition [29,30], it is likely that it will be able to colonize the full range of *F. excelsior*-habitats in Central Europe.

We note that although the results of this study are not based on modeling the spread of EAB using habitat characteristics and the species' ecological needs as has been done for North America [31,32], our study is the first one which provides a spatially explicit analyses of the invasion risks posed by EAB into a European region. Due to the high-resolution habitat distribution map [8] as the foundation of our analyses, we were able to regionalize invasion risks to a high extent. This information provides a basis for quantifying the scale of the likely impacts caused by EAB, and it identifies likely corridors of spread once EAB spreads into the study region

5. Conclusions

The high susceptibility and mortality of *F. excelsior* to infestations of EAB in Russia [7] leave no doubt that this beetle will become a major forest pest once it reaches Central Europe. This will put additional pressure on *F. excelsior*, which is also suffering from a fungal disease for several years, leading to wide spread ash dieback [24].

Although experience from the spread of EAB in North America has shown that halting its spread is difficult (reviewed by [7]), developing and testing management approaches with the aim to halt or at least slow down the invasion of EAB in Europe must be pursued with great urgency. Therefore, Central European countries not yet infested should develop dedicated precautionary measures to prevent inadvertent import of EAB into their territory. Additional education campaigns will help to raise awareness of the potential risk of *A. planipennis* invasions with the wider public, forest managers, and also in the scientific community.

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Author Contributions

V.V., F.E. and D.M. led the analyses and writing. M.K. and J.P. contributed land cover data, discussed the results and commented on the manuscript.

Conflicts of Interest

The authors declare no conflict of interest.

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Section C

Article 7 (vii)

Schönhart, M., Schauppenlehner, T., **Kuttner, M.**, Kirchner, E., Schmid, E. 2015. *Climate change impacts on farm profits, landscape appearance, and the environment: policy scenario results from integrated field-farm-landscape modelling in Austria.*

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Climate change impacts on farm profits, landscape appearance, and the environment: policy scenario results from integrated field-farm-landscape modeling in Austria

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Abstract

Climate change is among the major drivers of agricultural land use change and demands autonomous farm adaptation as well as public mitigation and adaptation policies. In this article, we present an integrated modeling framework (IMF) combining bio-physical models and a bio-economic farm model at field, farm and landscape level. The IMF is applied on a cropland dominated landscape in Austria to analyze impacts of climate change and mitigation and adaptation policy scenarios on farm production as well as on the abiotic and biotic environment. Changes in aggregated total farm gross margins from three climate change scenarios for 2040 range between +1% and +5% without policy intervention and compared to a reference situation under the current climate. Changes in aggregated gross margins are even higher if adaptation policies are in place. However, increasing productivity from climate change leads to deteriorating environmental conditions such as declining plant species richness and landscape appearance. It has to be balanced by mitigation and adaptation policies taking into account the considerable spatial heterogeneity revealed by the IMF.

Keywords

integrated land use modeling, climate change impacts, mitigation, adaptation, landscape, environment

1 Introduction

Climate change will cause major changes in agricultural land use systems in the upcoming decades (Howden et al., 2007). While mitigation of climate change is a global concern demanding immediate and concerted global efforts, adaptation is required at different spatial and temporal scales, i.e. from field and farm to global levels and from immediate to postponed action. Such heterogeneity results from spatially and temporally diverse climate change impacts, which are mediated by location, farming systems, and farm resource constraints (c.f. Niles et al., 2015). Farmers autonomously adapt to direct climate change impacts, such as local changes in temperature and precipitation patterns, in order to alleviate losses, exploit gains, and protect their production resources (for recent and ancient examples see Niles et al., 2015; Chen et al., 2015). More indirectly, agricultural land use decisions are driven by climate change affected market impacts and incentivized by adaptation and mitigation policies. Knowledge on farm level vulnerability, mitigation potentials, and adaptation options is crucial to understand climate change impacts and adaptation responses even at larger scales of spatial aggregation beyond the farm level (Reidsma et al., 2010). It can help to design efficient adaptation policies that alleviate negative and utilize positive climate change effects. Environmentally adverse autonomous adaptation by farmers, such as increasing land use intensity, can be detected early enough to counteract if demanded by the society. Knowledge on the mitigation potential of agricultural land use at the farm scale and its trade-offs to other environmental and socio-economic objectives supports the design of efficient mitigation policies at the national to EU level.

Research approaches that combine multiple scales are required to manage such policy issues. They should be interdisciplinary, quantitative, and should cover multiple scales. Integrated land use modeling (ILM) has emerged in agricultural sciences to fulfill such demands. ILM on climate change impacts and adaptation frequently consist of economic land use optimization models and bio-physical process models on plant and livestock production. Consequently, ILM usually rely on interdisciplinary knowledge about systems behavior, which is often analyzed by integrating disciplinary concepts, data, models, and scenarios. Such demanding prerequisites enable ex-ante analyses of systems with high complexity and uncertainty.

Climate change impact and adaptation studies based on ILM are available at different spatial scales ranging from field (e.g. Lehmann et al., 2013) to regional (e.g. Henseler et al., 2009; Leclère et al., 2013; Schönhart et al., 2014; Kirchner et al., 2015) and global levels (e.g. Nelson et al., 2014). Global as well as large-scale regional studies usually model price effects from climate change endogenously. Such representation of market effects is accompanied by coarse spatial resolution of bio-physical impact characteristics and superficial representation of farm management and endowments. Consequently, large scale studies hardly take farm level adaptation into account so far. On the contrary, field level studies can consider high resolution bio-physical impact data to evaluate the effectiveness of farm adaptation measures. As in the case of large scale models, lacking interactions at the farm level, such as competition for land, labor and capital resources aggravate conclusions on the economic efficiency of adaptation from a farm perspective (Gibbons and Ramsden, 2008).

Consequently, farm scale analysis are required to represent land use choices in ILM studies on climate change adaptation and complement global, regional, and field level studies. ILM at the farm level is synonymous to bio-economic farm modeling (Janssen and van Ittersum, 2007). A number of different studies on climate change impacts and farm adaptation are available at this scale. They analyze responses of different farming systems to mainly external changes (e.g. Dono et al., 2013; Kanellopoulos et al., 2014), which shall support farm and policy decision making. Other applications focus on inter-annual farm processes and decision making such as scheduling of field work (e.g. Aurbacher et al., 2013). Land use decisions are taken at the farm scale but many land use impacts on environmental quality and social welfare – e.g. soil sediment loads, ecological functionality, or landscape appearance – are effective at the landscape scale. Hence, another group of studies apply bio-economic farm models to analyze climate change effects on land use and the environment at the landscape to small regional level (e.g. Briner et al., 2012). These studies aggregate farm level model output, either from all individual or selected farms in a small region. A high spatial resolution provides interfaces for landscape level analysis such as on landscape appearance and issues related to nature conservation (Boyle et al., 2015).

Climate change impact analyses for Austria indicate moderate increases of average producer rents up to 2040 due to more favorable production conditions and autonomous adaptation in agriculture

(Schönhart et al., 2014). However, the impacts are expected to be i) heterogeneous with winners and losers among regions and farm types, ii) uncertain concerning changes in precipitation patterns and extreme events, and iii) unclear with respect to environmental consequences such as on biodiversity and landscape appearance. We present an integrated modeling framework (IMF) at the field, farm, and landscape level. It builds on former studies on the effectiveness of agri-environmental programs in an Austrian case study landscape (Schönhart et al., 2011a; b). In this article, the IMF is extended to analyze impacts from climate change as well as mitigation and adaptation measures on farm profitability, landscape appearance, and the abiotic and biotic environment. It is applied on a cropland dominated landscape in Austria and addresses the research demands i-iii raised above. Results should serve both scientific and policy objectives by developing a novel research method and by providing guidance for farm management and in developing mitigation and adaptation policies. Section 2 describes the method and data, the case study landscape as well as the applied climate and policy scenarios. Section 3 presents results, which are discussed in section 4. Section 5 concludes on the modeling results and raises emerging research questions.

2 Methods and data

2.1 Integrated modeling framework (IMF)

2.1.1 IMF overview and crop rotation modeling

The IMF combines the crop rotation model CropRota (Schönhart et al., 2011d), the bio-physical process model EPIC (Williams, 1995) and the bio-economic farm model FAMOS[space] (Schönhart et al., 2011c). The latter provides optimal choices on livestock and plant production, which are drivers of abiotic and biotic environmental as well as landscape outcomes (see Figure 1).

The choice on crop rotations is fundamental to the economic and environmental outcomes of agricultural systems. Nevertheless, knowledge on applied crop rotations at farm scale is usually limited. In the IMF, the crop rotation optimization model CropRota shall fill this knowledge gap. It generates typical crop rotations at farm and regional level based on observed land use and agronomic judgments on the value of crop sequences. CropRota also provides a relative share for each generated crop rotation such that the observed land use is reproduced at the highest attainable agronomic value of the crop rotations. In this article, we run CropRota for each individual farm and select up to four crop rotations ranked by their relative share. To increase the adaptive capacity of a farm towards impacts from markets, policies, and climate, we add three crop rotations to each farm, which have the highest shares at the landscape level according to CropRota.

2.1.2 Bio-physical process modeling of crop yields and environmental outcomes

Crop rotations are input to EPIC complementing a portfolio of crop management measures (i.e. tillage, intensity, irrigation, mowing frequency), geo-referenced field data (i.e. soil, slope, elevation) and climate data (i.e. temperature, precipitation, humidity, wind speed and solar radiation as well as assumptions on CO_2 concentrations) to simulate crop yields and environmental outcomes such as soil sediment losses and soil organic carbon stocks (see Appendix A). EPIC has already been applied several times at 1km² resolution to support climate change impact and adaptation studies for Austria (e.g. Mitter et al., 2014; Schönhart et al., 2014; Kirchner et al., 2015). In this study, the individual fields of a case study landscape are the simulation units. EPIC simulates at daily resolution and output is available for each simulated year. To account for variability in weather conditions, we average EPIC outputs to a 15-year time period in the reference period and the future (Appendix A). Consequently, the crop yield and environmental outcomes transferred to FAMOS[space] are unique for each crop on a particular field under a specific management and climate. CropRota and EPIC outputs are sequentially linked to FAMOS[space].

2.1.3 Farm optimization

FAMOS[space] is a static spatially explicit generic mixed-integer mathematical programming model at farm level. The model – typical to bio-economic farm models (cf. Janssen and van Ittersum, 2007) – seeks for gross margin maximizing production choices subject to field and farm resource endowments. Production choices are taken under perfect information about bio-physical, market, and policy conditions and the resulting land use and livestock activities are typical to a defined period. Interactions among farms are not considered yet but sales and purchases of livestock, feed, and fertilizer are management variants. The farm specific resource endowments include on-farm family labor, livestock housing capacity, as well as land represented by field size and soil quality. Resource endowments are transformed by Leontief-type production technologies to economic outputs and environmental outcomes. The latter include crop rotation choices, establishment or removal of landscape elements (i.e. orchard trees), soil management (e.g. cover crops and minimum tillage), land use intensity levels (i.e. fertilizer application rates, mowing frequency on meadows), and irrigation. Besides production and management alternatives within a particular land cover category, transitions between four different land covers, i.e. cropland, grassland, forestry, and abandoned land are possible subject to the policy scenario. If not stated otherwise, grassland is synonymous to different permanent grassland categories such as meadows and pastures in this article. With respect to forests, only afforestation and reforestation on former agricultural land are considered. Existing forests are neither represented in FAMOS[space] nor in the output indicators.

Model validation is crucial to any integrated modeling study but frequently difficult due to lacking observations at high spatial resolution and uncertain future developments. We tackle model uncertainty by a four step approach at the level of model development and output validation. With respect to model development (i), we build upon validated, documented, and reviewed single model components. The experience of the involved scientists from applications in similar regions, spatial scales, or research topics reduces the risks of unrecognized misbehavior of models. Furthermore, the rich detail in economic and bio-physical processes within the models and data reduces the risks of biases from poor systems representation. Model results are face-validated by the scientists based on (ii) plausibility checks and descriptive statistics such as on extreme values. Major model assumptions and model results are discussed using the scientific literature (iii) (see section 4.1 and 4.3) to allow for judgements on the robustness of the results. Finally, face validation included a one-time focus group discussion of results with local stakeholders, i.e. farmers and farm advisors, in the project region (iv) (see section 4.1).

2.1.4 Indicator calculation

All output indicators are calculated ex-post to the optimization. Maximized gross margins at farm and landscape level indicate the profitability of production. Total farm gross margins are the sum of market revenues, subsidies, and annuities for forestry and short rotation forestry (SRF) minus variable costs. Market revenues are obtained from crop and livestock product sales and subsidies are granted for certain crop and livestock production measures. Variable costs result from crop and livestock production and off-farm labor demand. FAMOS[space] also provides data on on-farm labor demand and nutrient balances. The indicators provided by EPIC, such as soil sediment load and soil organic carbon content, were weighted by the resulting area of a particular management. Greenhouse gas (GHG) emissions are calculated according to IPCC guidelines (IPCC, 2006) and Austrian specific data (Anderl et al., 2014). GHG relevant activities in FAMOS[space] such as livestock production (enteric fermentation) and fertilization (soil emissions) represent ca. 84% of all GHG emissions from agriculture in Austria (for further details see Kirchner et al., 2015). Biodiversity indicators on vascular plant species richness, shannon index on the vegetation ($Shannon_{veg}$), hemeroby index, and landscape functionality are based on field observations in the case study landscape (see chapter 2.2.3). Local plant species diversity was assessed following a standardized method for surveying vegetation and phytosociological analysis (Braun-Blanquet, 1964) within pre-selected land use categories. It was accompanied by a multiparametric classification of site-specific hemeroby levels (Pollheimer et al., unpublished report). The indicator value on landscape functionality (cf. Kuttner et al., 2013) quantifies the contribution of distinct landscape elements to various ecological key functions such as ecosystem functioning and safeguarding of local biodiversity based on their spatial composition and configuration.

Similar to biodiversity, impacts of changes in agricultural land use on landscape appearance is assessed using diverse indicators to cover the multiple dimensions of this topic. Landscape metrics provide well-known spatially explicit indicators to assess biodiversity effects as well as impacts on landscape aesthetics and structural richness, such as patch density (PD), mean patch size (MPS), edge density (ED), and Shannon diversity index (SDI) (McGarigal and Marks, 1995; Uuemaa et al., 2009). Patch density represents the number of different patches (i.e. land uses) per 100 ha and can be used to compare decreases or increases of different land use classes among the scenarios. Together with MPS it indicates the fragmentation of a certain landscape. ED is defined as edges (in meters) per ha. An increasing edge density indicates an increase in the complexity of a landscape (Palmer, 2004). The Shannon diversity index (SDI) is a wide spread indicator in ecology and landscape aesthetics (Franco et al., 2003; Dramstad et al., 2006) as it measures the diversity of species or land use patterns in a community or landscape. It is applied on both the vegetation ($Shannon_{veg}$) to indicate biodiversity and on land use classes to indicate landscape appearance (SDI). We assume that visual quality increases with increasing landscape complexity because small structured landscapes are rated higher by citizens regarding scenic beauty (e.g. Schüpbach et al., 2009). A major disadvantage of these metrics-based indicators is that visual qualities of specific landscape elements are undervalued. Therefore, we complement the analysis by calculating an agricultural crops and vegetables value (ACVV). This indicator is based on Schüpbach et al. (2009), who surveyed citizens on their value judgements about individual crops and landscape elements in Swiss landscapes. We present many indicators at landscape level as well as on smaller sub divisions, i.e. hexagons with 50 ha each (diameter approx. 900m). Results in this article are processed with the R software package (R Core Team, 2014). Indicators based on landscape metrics are calculated using the PatchAnalyst software package (Rempel et al., 2012).

2.2 Data

2.2.1 Data on socio-economic development, farms, and field characteristics

The IMF consists of data on farm resource endowments, markets, bio-physical site characteristics, land use and management as well as landscape structure. IACS data from several years (2000-2008) serve as central data source. It describes fields and farms in detail with respect to crop and livestock production, agri-environmental management measures, and subsidies from the 1st and 2nd pillar of the Common Agricultural Policy (CAP). Gross margins on annual farm production activities are calculated from the standard gross margins catalogue (BMLFUW, 2008) and literature surveys. Annuities for production activities with investment character are calculated for permanent crops such as SRF (maintained on land cover class cropland) or permanent forestry (individual land cover class). Annuity calculations for SRF are based on data from the Austrian advisory board for agricultural engineering and development (ÖKL) as well as expert interviews. Economic data on forestry are based on the standard gross margins catalogue (BMLFUW, 2008). Region specific forestry yield data is derived from Kirchner et al. (2015) based on results from the forest growth model Caldis vâtis (Kindermann, 2010). Farm labor demand is based on a detailed set of standard working units (Handler et al., 2006) and literature reviews. Family farm labor endowments result from farm survey data from the year 1999. A digital soil map (Bundesforschungs- und Ausbildungszentrum für Wald, Naturgefahren und Landschaft, BFW), and a digital elevation map (Bundesamt für Eich- und Vermessungswesen, BEV) complement the field characteristics of the case study landscape. Future market price developments are based on OECD-FAO (2013) and adapted to national circumstances.

2.2.2 Landscape element data

Spatial information on landscape elements like hedgerows, small forest patches and orchard meadows are derived from ortho-rectified aerial images applying automatic pixel segmentation and semi-automatic classification (for a description of this method, see Schauppenlehner et al., 2010). We process 3-band color aerial images from 2008 to digitalize recent landscape elements. The historic patterns of landscape elements are derived from grey-scale aerial images from the first Austrian forest inventory in the 1960s. These images show the distribution of landscape elements slightly after a peak of orchard cultivation for juice and cider production in the Mostviertel region. Since the 1960s, orchard meadows have decreased rapidly due to changing consumer preferences and increasing opportunity costs from mechanization in agriculture. Consequently, we consider the historic and recent distribution of orchard meadows as potential sites in the policy scenarios.

2.2.3 Biodiversity indicator data

Data on local plant species richness was collected by local field surveys during May 2011 and 2012. In order to obtain a statistically representative set of relevés we pre-stratified observed land use data for cropland, grassland, and landscape elements (see also 2.2.2) and randomly sampled subsets within derived categories of land use intensity. We conducted 121 vegetation surveys that have been complemented by a comprehensive grading scheme to assess site specific hemeroby levels (Pollheimer et al., unpublished report). It consists of 12 single parameters: frequency of use, biomass extraction, damage on plants, accumulation of matter, soil compaction, ploughing, water balance, fertilizer input, biocide input, replanting, potential of plant regeneration and state of succession. By aggregating and rescaling those parameters we gain final values on hemeroby for each vegetation plot. Shannon_{veg} (Shannon and Weaver, 1949) is directly derived from respective relevés by using the software package JUICE (Tichý, 2002). Apart from vegetation sampling we also mapped landscape structure across four randomly selected quadrants (500m × 500m) that were equally distributed in the case study landscape. The dataset was further complemented by mapping data from 2007 and 2008 where the same classification system has been applied as in our study. The procedure used for the calculation of landscape functionality is adapted from Kuttner et al. (2013) by quantifying land use class specific capabilities to support ecological key processes based on structural parameters. Thus, this index also acts as a proxy to quantify levels of farmland biodiversity. Table 1 presents indicator values, which are linked to land use results from FAMOS[space]. Changes in vascular plant species richness, Shannon_{veg}, and hemeroby index are estimated for agricultural areas only, but afforested areas are taken into account by the landscape functionality indicator.

2.3 Case study landscape

We apply the IMF on a landscape in the Lower Austrian Mostviertel region. This region has been chosen due to its variety in land uses, the importance of landscape elements such as orchard meadows, and its pronounced land use intensity and climate gradients. The core of the case study landscape is a rectangle covering ~2,000 ha. It includes all agricultural fields which are represented by the IACS system, i.e. nearly all agricultural areas excluding forest patches, infrastructure and open water. We model those 113 farms that manage at least one field within the core of the case study landscape. Furthermore, we model all fields belonging to an individual farm. Consequently, the case study consists also of farms and fields situated outside the core of the case study landscape. These fields and farms are represented in most results except for spatial indicators and maps.

The case study landscape is intensively managed, rather homogeneous with respect to landscape elements and dominated by cropland (84% cropland, 16% grassland). It is likely prone to further intensification in the future. Observed average annual precipitation is about 1.000 mm and the average annual temperature ranges between 8 to 9°C (unpublished data from Strauss et al., 2013). Predominant arable crops in the period 2005 to 2009 have been corn (31%), winter wheat (23%), winter barley (12%) and silage maize (7%). Red clover – grass mixtures and rapeseed account for 3% each and thus are the most important non-grain crops.

2.4 Climate and policy scenarios

Simulations in the IMF are based on scenarios to anticipate plausible future changes in climate and policies (see Table 2 and Table 3). Market prices and other socio-economic parameters are kept invariant among the scenarios. With respect to policies, three mitigation and adaptation scenarios have been developed and combined with three climate scenarios until 2040. In the IMF, the climate signal drives the bio-physical output of EPIC and is subsequently transmitted to FAMOS[space], while the mitigation and adaptation policies directly impact land use and livestock choices in FAMOS[space].

The climate and policy scenario impacts are compared to a reference scenario *REF_2040*. *REF_2040* is presented in Table 2 and includes major changes of the CAP reform 2014-2020 and market policies such as the abolition of the dairy quotas and suckler cow premiums, the introduction of regional single farm payments and greening. A major difference to the current situation is the absence of any agri-environmental program (AEP). AEPs are not represented in *REF_2040* because they are similar to many mitigation and adaptation policies and therefore covered in the policy scenarios. The scenario analysis aims at assessing the effectiveness of mitigation and adaptation policies, which is achieved by comparing scenario results to a counterfactual reference. Furthermore, *REF_2040* is defined by the current climate situation.

To analyze climate change impacts, we apply three contrasting climate change scenarios (Table 2). The climate change scenarios cover six climate parameters at daily resolution and are based on a statistical climate model and historic trend observations (Strauss et al., 2013). A significant temperature trend has been observed in the past for Austria, which is linearly extrapolated to +1.5°C in 2040. Scenarios on precipitation have been developed to capture the inherent uncertainties of precipitation changes in the future (Gobiet et al., 2014). Scenario *CS01* imitates past precipitation patterns. Total daily precipitation increases by 20% in *CS05* and decreases by 20% in *CS09*, i.e. patterns of daily precipitation events are similar to past observations but different with respect to rainfall volumes.

We define four policy scenarios to model i) climate change impacts including autonomous adaptation (*CSXX_i*, were *CSXX* is synonymous to all the three climate change scenarios *CS01*, *CS05*, and *CS09*), ii) mitigation policies (*CSXX_m*), iii) planned adaptation policies (*CSXX_a*) and iv) a combination of mitigation and adaptation policies (*CSXX_m&a*). All policy scenarios as well as *REF_2040* have in common identical market conditions and most elements of the CAP reform but are different with respect to their specific policies (Table 3). The CAP reform is implemented differently only with respect to the greening measures, i.e. relaxed in *CSXX_m* and abolished in *CSXX_a* and *CSXX_m&a*.

In the impact scenario *CSXX_i* no additional policies beyond *REF_2040* are introduced. Compared to *REF_2040* this scenario presents climate change impacts based on autonomous adaptation such as crop and crop rotation choices, dietary choices for livestock, irrigation, fertilization and land cover change. The portfolio of policies in *CSXX_m* supports soil carbon sequestration and the production of agro-fuels. Establishment of SRF and cultivation of energy crops (i.e. corn, rye, soybean, sunflower, winter wheat, winter barley, rapeseed) is allowed on fallow land in the greening measure. Premiums for orchard meadows and SRF (120€/ha per year (p.a.)) as well as afforestation (one-time payment of 3850€/ha) should enhance soil carbon and agro-fuels supply in the future. Reduced tillage (40€/ha p.a.) and reduced tillage including sowing of cover crops (150€/ha p.a.) enhance soil carbon sequestration. Measures on reduced fertilization intensity aim on N_2O emission reductions and biodiversity enhancement. Participation in the latter is possible only for the whole farmland and additionally requires extensification of grassland (5% of total grassland area on a farm) and establishment of fallow land on cropland (2% of total cropland area on a farm). All premium levels in *CSXX_m* imitate the Austrian AEP ÖPUL in the rural development programming period 2007-2013. Apart from the expected positive climate impacts, the measures in *CSXX_m* should be favorable to other environmental concerns, such as biodiversity enhancement, landscape protection, reduced nutrient leakage, and erosion control. The overarching strategy of *CSXX_a* is to maintain the adaptive capacity of farmers towards climate change and agricultural production. Consequently, the greening measures (see Table 3) are abolished. Annual premiums for maintenance of steep meadows (slope ≥ 25% and < 35%: 105 €/ha, ≥ 35% and < 50%: 235 €/ha, > 50%: 370 €/ha) and an irrigation premium of 40€/ha p.a. are introduced in *CSXX_a*. Scenario *CSXX_m&a* combines the policy portfolios of *CSXX_m* and *CSXX_a*. It offers most freedom to the modelled farms with respect to land use choices and consequently will show equal or higher total farm gross margins than either *CSXX_m* or *CSXX_a*.

3 Results

3.1 Climate change impacts on crop yields

Climate change impacts are simulated in EPIC for each individual field and management variant. Figure 2 presents changes on modelled crop yields under the current climate for the five most dominant arable crops. Each data point represents an individual field for standard ploughing averaged over all crop rotations and intensity levels in the case study landscape. Impacts on 1-cut and 3-cut grasslands are presented in Appendix B. Climate change increases average yield potentials for most crops according to EPIC. This tendency is mainly independent from the climate scenarios and is particularly true for winter wheat and grassland categories. Differences among the climate scenarios appear moderate but follow a unique pattern: CS09 achieves the largest yield increases followed by CS01 and CS05. Maize crop variants such as corn and silage maize behave differently in EPIC and result in yield losses on average in all three climate scenarios compared to the current climate. In EPIC, corn cannot benefit from temperature increases such as wheat does due to an already low number of low temperature stress days under current climate conditions. Water stress is low for both arable crops even under diminishing precipitation in CS09. Under humid conditions, such as for the case study landscape, additional rainfall can even reduce yields, e.g. by increasing nutrient leaching. Nitrogen appears to be the most limiting growth factor because nitrogen stress increases in all three climate scenarios for winter wheat and corn. Results for disaggregated yield changes under different fertilization levels in EPIC support such conclusion as well: the lower the fertilization level, the lower are the yield gains for wheat and the larger become the losses for corn and silage maize.

3.2 Land use and livestock effects

Land use and land cover changes in the reference scenario *REF_2040* in FAMOS[space] result from climate change impacts on crop yields and mitigation and adaptation policies. Figure 3 presents fallow land on cropland and orchard meadows because both are important drivers of biodiversity enhancement and landscape appearance. Results for further land use categories, i.e. cropland, intensive and extensive grassland, forests, and SRF, are presented in Appendix C.

Apparently, neither climate change nor the policy scenarios lead to substantial land abandonment in the model. Only a few hectares become idle at all and are neither under forest nor agricultural land use. However, there are some shifts among land use and land cover categories such as a transition from agricultural to forest land use in *REF_2040* compared to the observed endowment. Afforestation premiums stimulate forest growth by additional 3ha to 12ha in both *CSXX_m* and *CSXX_m&a*. It shows a considerable relative change in forest conversion although still minor in absolute levels.

Grassland consists of the following categories: extensive grassland, intensive grassland, and orchard meadows. Impacts are considerable especially for extensively managed grassland such as 1-cut meadows and extensively managed pastures. Premiums for orchard meadows maintain 56 ha in the *CSXX_m* scenarios – i.e. the observed endowment of orchard meadows – compared to hardly any orchard meadows in *REF_2040*. The abolishment of greening in *CSXX_a*, which prevented conversion of grassland to cropland before, reduces grassland by 27% on average among all climate change scenarios. No orchard meadows and hardly any extensively managed grassland remain in this scenario. The pressure from *CSXX_m&a* on total grassland is moderate compared to *CSXX_a* with losses of 8%. However, the area of orchard meadows is also only about 89% its value in *CSXX_m*. Furthermore, the model results in land use change towards SRF. It is the consequence of both climate change impacts that increase cropland productivity, and both mitigation and adaptation policies favoring cropland management and permitting conversion of grassland to cropland.

Variation among arable crops is modest among the scenarios (Appendix D). Climate change increases the profitability of SRF in *CSXX_i* but a major increase in SRF is modelled for *CSXX_m* due to supporting policies. On average across all climate change scenarios (*CSXX_m*), SRF is cultivated on 4% of total cropland, i.e. the sum of the categories cropland and SRF in Appendix C, compared to hardly any SRF in *REF_2040*. Increasing SRF areas come at the cost of fallow land, which is reduced by 61% in *CSXX_m* compared to *REF_2040* (see Figure 3) and more or less disappears in *CSXX_a*. The combined mitigation and adaptation policies in *CSXX_m&a* lead to fallow land between the levels in *REF_2040* and *CSXX_a*. This is due to a mitigation measure coupled to both the provision of fallow land and extensive grassland management.

Figure 4 presents the aggregated area (ha) devoted to a particular soil management on cropland. Autonomous adaptation in *CSXX_i* increases the area under reduced tillage. Reduced tillage combined with cover crops (see category cover crops in Figure 4) is hardly observed. Policies targeted towards soil conservation in *CSXX_m* strongly increase the area under reduced tillage combined with cover crops indicating sufficient incentives from premiums. However, incentives and climate change impacts do not attract irrigation. It is chosen in the model only for a few hectares and crops. Livestock is hardly impacted by both climate change and policies in the model. Farms produce livestock more or less at their assumed housing capacities in all scenarios (Table 4).

3.3 Effects on abiotic agri-environmental indicators

From an economic point of view, choices on fertilization intensity are a function of natural production potentials and market and policy opportunities, i.e. driven by the marginal value product of fertilization and the marginal fertilization costs. The marginal value product is impacted by climate change and mitigation and adaptation policies (Table 4). In *REF_2040*, FAMOS[space] results in average nitrogen application rates of 141 kg/ha. Climate change increases average fertilization levels (*CSXX_i*) by 1% to 2% at the landscape level, but fertilization intensities are strongly reduced on cropland and grassland in the mitigation scenario (*CSXX_m*). It is triggered by effective policies reducing land use intensity. In total, nitrogen amounts decrease by 6% to 9% compared to *CSXX_i*. Changes in phosphorus fertilization are similar to those of nitrogen in general. Policy driven enhanced adaptive capacity in the adaptation scenario (*CSXX_a*) increases fertilization rates on cropland due to the loss of fallow land and the conversion from grasslands to croplands. Fertilization intensity in *CSXX_m&a* ranges between *CSXX_i* and *CSXX_a* results.

GHG emissions are mainly impacted by changes in livestock numbers and land use management in the IMF (Figure 5). Climate change leads to increasing emissions in the case study landscape. The effective mitigation policies in *CSXX_m* as well as *CSXX_m&a* reduce emissions by 2% – 6% compared to *REF_2040*. However, autonomous (*CSXX_i*) and planned adaptation (*CSXX_a*) both increase emissions compared to *REF_2040* triggered mainly by changing fertilization levels.

The development of soil organic carbon (SOC) content represents another component of the global carbon cycle in agriculture (Figure 6). SOC is impacted by both climate change and policies. Precipitation patterns determine the direction of change with increasing precipitation (*CS05*) leading to SOC losses and vice versa. Changes are between -12% and +1% on cropland and -2% to +3% on grassland. Obviously, the variability of relative changes is much larger on cropland than grassland. Absolute changes are smaller between both due to higher SOC contents on grassland.

Soil sediment load from water erosion impacts both soil fertility and nutrient losses and, consequently, determines farm incomes and environmental impacts of land use in the long run. Soil sediment load on cropland in the IMF is sensitive to both precipitation patterns and policies (Figure 7). Relative changes range from -43% to +59%. Soil protection policies turn out to be particularly effective in *CS05_m* but less so in *CS09_m*, which indicates potential public benefits from targeting agri-environmental policies towards climate change.

3.4 Effects on biodiversity and landscape

In the IMF, biodiversity is influenced by changes in land use, i.e. choices of land use categories, crops or land use intensity (see Table 1 and Figure 8). Impacts from climate change (*CSXX_i*) are moderate due to moderate land use changes. However, policies strongly impact biodiversity indicators in the IMF. Mitigation policies foster biodiversity due to less intensive land use on both cropland and grassland and the establishment of orchard meadows. For example, average vascular plant species richness increases between 3% and 5% in *CSXX_m*. On the contrary, more flexibility in land use gained from adaptation policies (*CSXX_a*) reduces habitat quality and species richness. Similar to other indicators, the combined mitigation and adaptation policies (*CSXX_m&a*) result in values between *CSXX_m* and *CSXX_a*, whereby indicators tend towards *CSXX_m*.

Figure 9 presents the results from *CS09* and all four policy scenarios on landscape appearance. Values are aggregated at the landscape level. PD, SDI, and ACVV perform in a comparable way but with varying intensity. ACVV reacts strongly on the reduction of landscape elements with a high visual value such as orchard meadows or extensive grasslands. This explains the strong decrease of ACVV in *CS09_i* and *CS09_a* while SDI shifts more slightly in these scenarios. ED does not vary substantially among the different scenarios as there are little changes in field sizes and subdivisions of fields. An increasing MPS indicates larger homogenous agricultural production units and therefore a decreasing scenic beauty in *CS09_a*.

Besides aggregated landscape-based indicators, we estimate the indicator values also for regularly distributed hexagonal subdivisions (50 ha; see Figure 10 and Figure 11 for *REF_2040* and *CS09_m*) in order to identify local differences among the scenarios. The maps show considerable differences between the two scenarios depending on the local position. Again, ACVV reacts stronger than the SDI. It results from orchard meadows established in scenario *CS09_m*. They strongly influence the visual quality and scenic beauty but have little impact on the performance of structural indicators, which do not differentiate among land uses as long as the field patterns remain unchanged.

3.5 Farm economic effects

Land use change, climate change, and policies affect farm profitability. Figure 12 presents changes in total farm gross margins from the reference scenario *REF_2040* aggregated at the landscape level. The distribution of changes for the individually modelled farms is presented in Appendix E. In the absence of mitigation and adaptation policies (*CSXX_i*), climate change and corresponding autonomous adaptation increase total farm gross margins on average. Aggregated at the landscape level (i.e. sum over all total farm gross margins in the landscape), it increases by 1% to 5% depending on the three climate change scenarios (Figure 12). At farm level and for different climate change scenarios, gross margins range between the first and third quartile by -2% and +8% (Appendix E). Therefore, climate change impacts lead to higher farm profitability, but the effects are heterogeneous among the different assumptions on precipitation patterns.

The introduction of mitigation policies (*CSXX_m*) increases aggregated total farm gross margins by 6% to 9% (Figure 12). Among individual farms, ranges between the first and third quartile are between +3% and +14% (Appendix E). Average changes in total farm gross margins aggregated at the landscape level (see Figure 12) are lower than average values over all individual farms (Appendix E) due to larger relative impacts for smaller farms. Total farm gross margins increase if constraints are relaxed (e.g. enhanced production of energy crops and SRF on fallow land) and agri-environmental measures are in place that foster climate change mitigation in *CSXX_m*. In *CSXX_a*, the greening requirement is abolished and irrigation subsidized. While the latter hardly shows any impact – irrigation is introduced on only 1ha in *CS09_i* and *CS09_a*, respectively – ceasing the greening requirement enhances flexibility in the model. Consequently, aggregated total farm gross margins increase by 3% to 7% compared to *REF_2040*. At the individual farm level, changes from adaptation policies (*CSXX_a*) are between +3% and +9% on average among the three climate change scenarios. The combined mitigation and adaptation scenario (*CSXX_m&a*) further enhances production flexibility and leads to the highest farm gross margins among all scenarios. Total farm gross margin at landscape level increases by 6% to 10% (Figure 12). For individual farms, ranges between the first and third quartile are between -1% and +11% (Appendix E). Apparently, climate change effects are robust among all policy scenarios, i.e. *CS09* leads to the largest increases in total farm gross margins followed by *CS01* and *CS05*. The results are also robust with respect to the mitigation and adaptation policies. Climate change scenarios induce larger variability but the impacts from the policy scenarios on farm gross margins are still in clear order for a particular climate scenario with *CSXX_m&a* > *CSXX_m* > *CSXX_a* > *CSXX_i*. Nevertheless, the combination of climate change scenarios and policies increase uncertainty about the ranking of policies. For example, gains from beneficial adaptation policies under increasing temperature, CO_2-levels and precipitation (*CS05_a*) are lower than benefits from increasing temperature, but decreasing precipitation even in the absence of any beneficial policy (*CS09_i*) in the IMF.

From the perspective of public budget spending, there is a clear order among the policy scenarios with little variation among the climate change scenarios (Figure 13). Mitigation policies in *CSXX_m* considerably increase spending by 27% to 28% compared to *REF_2040*. On the contrary, adaptation policies hardly impact public budgets because changes in greening requirements are budget neutral and the uptake of other measures in *CSXX_a* is minor. In *CSXX_m&a* the combination of mitigation and adaptation policies increases spending to more or less *CSXX_m* levels. Figure 13 (left) splits farm revenues and costs into single components. In *REF_2040*, subsidies account for 13% to the total revenues from market sales and subsidies. In *CSXX_m* it increases by 16% to 17% compared to *REF_2040* due to increasing subsidy levels and decreasing market income. Nevertheless, higher total gross margins in *CSXX_m* compared to *REF_2040* indicate economic benefits to farmers from the proposed mitigation management measures and therefore provide economic incentives for a management transition.

Labor demand is a socio-economic indicator at farm level determining quality of life to farmers and, consequently, land use choices. In FAMOS[space], autonomous climate change adaptation (*CSXX_i*) slightly reduces labor demand by 1% to 2% (Table 5). Further reductions are the result of mitigation policies (*CSXX_m*). Adaptation triggered by policies in *CSXX_a* increase demand even above *REF_2040* levels.

4 Discussion

4.1 Climate change impacts on farm production

We present an integrated modeling framework (IMF) combining the bio-physical process model EPIC and forest growth data from the Caldis vâtis model with the bio-economic farm model FAMOS[space]. The IMF has been applied to analyze climate change impacts and the effectiveness of mitigation and planned adaptation policies in an Austrian case study landscape. The reference situation in 2040 (*REF_2040*) assumes a liberalized agricultural sector lacking any agri-environmental program. Climate change scenarios include a single temperature trend of +1.5°C up to 2040 but different precipitation patterns with no changes in annual precipitation sums (*CS01*) compared to the current climate as well as -20% (*CS09*) and +20% (*CS05*) in annual precipitation. The modelled climate change and CO_2 fertilization impacts are beneficial on average to most farms within the IMF independent from the particular climate scenarios. Yields of most crops and grassland forage are increasing, despite minor yield losses for maize. Contrary to our initial expectations, reduced precipitation (*CS09*) turns out to be more beneficial on average than increasing precipitation (*CS05*) according to the results from EPIC. This may be explained by currently sufficient average annual precipitation levels of 1.000 mm. In *CS09*, average annual precipitation decreases to 800 mm, which is still sufficient for cropland and grassland production in the bio-physical model EPIC to sustain or even increase yields. Such result is also driven by enhanced CO_2 levels that can decrease water stress for grasslands (Soussana and Lüscher, 2007). Furthermore, reduced precipitation in humid regions can decrease soil sediment loads and nutrient leakage, which both are beneficial to crop yields and environmental outcomes.

Discussions with regional experts confirmed some but not all of our results. In general, our results appeared plausible to the experts especially concerning the variation of impacts among farms such as depicted in Figure 2 and Appendix E. It is justified by the considerable regional heterogeneity in slope and soil conditions ranging from wet heavy clay rich soils to light sandy soils with low water retention capacity. According to the stakeholders, precipitation levels are sufficient in the region. They even face wet periods and extreme rain events, which can challenge the timing of harvest and can lead to soil erosion. Increasing intensification is considered plausible, but irrigation will hardly play a major role in the future, which is confirmed by our model results. Nevertheless, stakeholders also challenged some of the bio-physical results and thereby revealed future research demand. It includes the losses in corn and silage maize yields despite the future warming trend or the modelled increases in winter wheat yields. The latter appear implausible to the stakeholders due to elevated temperatures, which likely shorten the grain filling period in the future.

The validation of our results with the scientific literature is ambiguous. Kirchner et al. (2015) and Schönhart et al. (2014) provide spatial analysis on climate change impacts for all over Austria based on methods similar to our study. Their results show similar impacts concerning productivity gains on grassland and cropland for the wider case study region. Ciscar et al. (2011) modeled crop yield increases of 5% on average under more pronounced temperature increases of 2.5°C for Austria. In the case of +4.1°C and -4% in precipitation levels, yields are still positive on average with +3% but become moderately negative (-3%) in case of severe temperature changes of +5.4°C and precipitation reductions of 16%. Finger et al. (2010) modeled grassland yield increases for Switzerland of up to 40% considering a CO_2 fertilization effect and substantial decreases of precipitation during the vegetation period and Fuhrer et al. (2013) confirm productivity increases on grassland in the Swiss Rhone catchment subject to sufficient irrigation water availability. However, Mitter et al. (2014) provided estimates for a larger case study region including our case study landscape. They applied the same climate change scenarios and bio-physical process model, but derived decreasing average dry matter yields of typical arable crops for scenario *CS09* in contrast to *CS05*, which may result from heterogeneous local soil and climate conditions. Schaumberger (2011) applied a statistical grassland model to estimate yield impacts from drought all over Austria. A simulation of the drought year 2003 implying reductions in precipitation of about 30% leads to forage yield losses for large parts of Austria. Such results indicate the sensitivity of bio-physical production on climate change and the interplay with crops and crop management, soil conditions and slope. The inherent uncertainty within climate change impact studies due to location and applied models proves the need for multiple impact studies even for similar locations. Additional research should examine these uncertainties, such as by applying ensembles of bio-physical models (for an example on the AgMIP model intercomparison project see Rosenzweig et al., 2013). Another uncertainty comes from livestock production. We considered only one indirect climate change impact, i.e. availability of forage. Model results for heat stress based on temperature humidity indices do not indicate significant challenges to Austrian cattle production on average (Schönhart and Nadeem, 2015). It is unclear so far whether these results hold at regional level – impacts may be significant for particular locations even within alpine regions (Fuhrer et al., 2013) – and whether new pests and diseases will harm livestock under climate change in the future.

4.2. Effects, trade-offs and synergies between mitigation and adaptation policies

Climate change mitigation and adaptation measures likely occur simultaneously with mutual impacts and trade-offs among different environmental objectives (Smith et al., 2007). Our study shows that the effects from mitigation and adaptation policies are mediated by location. Location factors such as soil type and slope determine the endowment of cropland and grassland on a farm and its production potential under alternative managements and thereby impact land use choices in the model. Total farm gross margins, aggregated at the landscape level, increase by about 5%-points to 6%-points if mitigation policies are introduced. Mitigation measures considered in our study include premiums for maintenance of orchard meadows and reduction of fertilization intensity on grasslands, soil protection measures on croplands, as well as relaxed management constraints on mandatory fallow land. Mitigation policies increase extensively managed grassland, orchard meadows and SRF areas and stimulate afforestation. Soil protection is facilitated by supporting minimum tillage and planting of cover crops although the effectiveness of minimum tillage on SOC is unclear in general (Powlson et al., 2014) and thus should be subject to further analysis. As a result of mitigation policies, environmental quality improves according to the IMF. For example, plant species richness increases in *CSXX_m* compared to *REF_2040*, while in *CSXX_i* vascular plant biodiversity levels remain stable or even decline. Gains in *CSXX_m* occur despite allocations of more than half of the fallow land in *CSXX_i* towards the production of agro-fuels in *CSXX_m*. Soil sediment loads are reduced in all three climate scenarios, although with low effectiveness for *CS09_m* due to reduced precipitation levels. It indicates potentials to increase cost-effectiveness of the applied soil protection measures to local precipitation patterns and field slope and to consider long-term climate change impacts. SOC is increasing in *CSXX_m* compared to *CSXX_i* in most cases and greenhouse gas emissions are decreasing by 2% to 6% mainly due to reduced fertilization levels of 6% to 9%. These directions of changes are expected results of mitigation policies. However, the magnitude of change is smaller compared to other studies. The IMF takes account of the economic mitigation potential, which can be up to 80% below the technical mitigation potential in agriculture (Smith et al., 2007). Blandford et al. (2014) modelled mitigation policies in the Norwegian farm sector. They constrained GHG emissions to 70% compared to the baseline via a Pigouvian tax. It results in N fertilizer reductions of only 5%, but substantial increases in milk yields of 19% and shifts from beef cattle to dairy and poultry production. Such results indicate the large mitigation potential in livestock management, which has not been considered in *CSXX_m*. Consequently, mitigation policies that are oriented towards particular management alternatives likely do not capture the full mitigation potential of the agricultural sector.

Adaptation policies (*CSXX_a*) increase gross margins with levels of about 2%-points to 3%-points above *CSXX_i* values. Relaxing the management constraints via abolished greening requirements mainly impacts cropland production and to a lesser degree grassland management. The irrigation premium, which is part of the policy portfolio in *CSXX_a*, is ineffective in the IMF due to sufficient precipitation levels in the case study landscape. However, there is a trade-off between relaxing policy constraints to increase adaptive capacity of farmers on the one hand and decreasing environmental quality on the other. Despite moderate impacts on farm gross margins, considerable land use changes from *CSXX_a* occur in the model. From an environmental perspective, the most important impacts are the loss of fallow land and the increase in cropland at the cost of extensive and intensive grasslands. Fallow land and orchard meadows diminish nearly completely in *CSXX_a*, hence leading to a homogenization of habitats within the landscape. Cropland increases at the cost of extensive and intensive grasslands due to relaxing constraints on grasslands maintenance. Such results indicate the effectiveness of current CAP policies that restrict management options based on environmental concerns. The costs of such constraints, mainly opportunity costs, increase with increasing land productivity, which – according to the model results – appears likely for the case study region in the coming decades under climate change. Environmental and landscape quality decreases with the adaptation policies proposed in *CSXX_a*. Biodiversity indicators decline compared to *REF_2040* meaning a loss in habitat functionality and in plant species richness of about -5% to -7%. Conversely, hemeroby levels increase under this scenario compared to *REF_2040*. This development suggests that the measures applied in *CSXX_a* are detrimental in terms of preserving ecosystem functioning and safeguarding local species pools (Peterseil et al., 2004; Walz, 2015). Soil sediment losses are at higher levels approaching those under autonomous adaptation by farmers (*CSXX_i*). Changes in SOC are heterogeneous between land use types and climate scenarios but less so among the policy scenarios, which indicates limited effectiveness of short term policies. Greenhouse gas emissions in *CSXX_a* increase and reveal a trade-off between mitigation of climate change and farm adaptation in this particular landscape. It is driven by increasing production potentials and cropland intensification but further studies are required to assess a more elaborated set of adaptation policies and management measures.

Scenario *CSXX_m&a* combines mitigation and adaptation scenarios. It imitates a policy of flexible land management to adapt to climate change while at the same time offering financial incentives to mitigate climate change. There are several likely conflicts of public interests such as with the maintenance of grasslands to sequester carbon (mitigation) and the conversion of grasslands to cultivate arable crops under a warming climate. Total farm gross margins in *CSXX_m&a* are about 1%-point above *CSXX_m* levels. Clearly both policy portfolios, i.e. mitigation and adaptation policies, do not simply add up due to conflicting objectives, and farms in the IMF cannot benefit from both simultaneously. The most obvious example is the requirement of mitigation policies to fulfill minimum ecological standards on fallow land and crop rotations. This outweighs adaptation policies such as the abolishment of greening. Premiums are obviously large enough in the model to trigger adoption of minimum ecological standards by the modeled farms. Land use change in *CSXX_m&a* ranges between *CSXX_m* and *CSXX_a* results tending towards the former especially for fallow land and orchard meadows. Expansion of croplands take place at a lower rate than in *CSXX_a*. Land use changes determine the environmental outcomes of *CSXX_m&a*. Changes in habitat quality and species richness as well as soil sediment losses are close to results from *CSXX_m*. Changes in SOC tend towards larger *CSXX_a* levels, but greenhouse gas emissions are close to *CSXX_m*. To sum up, scenario *CSXX_m&a* is clearly beneficial to farmers as it offers most freedom in land use choices among all four policy scenarios. Similar to *CSXX_m*, *CSXX_m&a* is beneficial to the environment compared to *CSXX_i* and *CSXX_a* but both, *CSXX_m* and *CSXX_m&a*, show a clear trade-off between environmental impacts and public budget spending.

4.3 Model assumptions and uncertainty

Rosenzweig et al. (2013) elaborated a cascade of uncertainties in global crop modeling including the development of greenhouse gas emissions, related climate simulation results, the choice on crop models, and represented management. For integrated land use modeling as applied in this study, further sources of uncertainty include the full range of climate change impacts, farm level behavior towards climate change, the relationship between environmental indicators and environmental quality, the choice of land use model, and assumptions on market conditions. By choosing three contrasting climate scenarios with one significant temperature trend and varying precipitation patterns, we intended to depict a reasonable range of future climate conditions although we cannot quantify the likelihood of each of these scenarios to become reality. We applied one bio-physical process model to transfer climate change signals into crop yield impacts. Model inter-comparison projects such as AgMIP (e.g. Rosenzweig et al., 2013) show a plausible range of uncertainty from crop model choices and future research should build on such results to reduce uncertainty from the application of a single crop model. In the IMF farm management is chosen according to its contribution to gross margins subject to farm specific constraints. We provide a broad range of farm management options that are essential in order to gain meaningful optimal management choices on livestock production and land use. These choices imitate rational farming behavior under perfect information. Uncertainty emerges from unknown behavior of land users in reality, who likely consider objectives for their land use decisions besides maximization of farm gross margins. They may also face other personal constraints beyond on-farm labor supply. Empirical studies on farm level adaptation reveal such constraints and determining factors of adaptation and complement quantitative model applications (Niles et al., 2015). Furthermore, the full range of future adaptation options is unknown today. It is subject to the particular farm (e.g. the management skills of a farmer), future technological developments, or legal constraints. We have chosen a bio-economic farm model that maximizes gross margins, which is common to climate change impact assessments in agriculture. A major advantage compared to economic models considering both variable and fixed costs is the lower demand on model parameters and simpler model structure. However, a crucial aspect in our IMF is the rigid behavior towards investment decisions particularly in livestock production. We constrained maximum values in the model to observed livestock numbers, which can moderate adaptations in grassland intensity despite increasing yield potentials. A model version based on full-cost accounting may be beneficial particularly for adaptation decisions in livestock production. Crop prices have to be assumed due to a lacking representation of demand in the IMF. Our price coefficients are derived from OECD-FAO (2013), but are not specific to the climate scenarios due to a lack of data. Productivity increases on larger scales in the agricultural sector likely reduce market prices and vice versa, which can buffer climate change impacts or can even lead to losses in competitiveness (cf. Hermans et al., 2010). Leackage effects from regional mitigation policies can trigger GHG emissions globally (Pelikan et al., 2015). Consequently, further research should also include sensitivity analysis on the mutual impacts of climate, policy, and price developments at the international level despite the considerable challenges with respect to data and model development.

5 Conclusions

Quantitative analyses of complex systems require integrated modeling tools. If spatially explicit at high spatial resolution such as the field scale, they offer multiple opportunities to pursue inter-disciplinary research questions. In this article, we applied an IMF to analyze climate change impacts, mitigation, and adaptation for an Austrian case study landscape. Its spatially explicit representation of fields belonging to an individual farm improves the representation of mechanization costs (e.g. distances of fields to the farm, size of fields), yield impacts, and environmental outcomes from field to landscape level. Vector-based landscape data within the IMF enables analysis of landscape structure and land use intensity at field scale and serve as proxies of landscape appearance and biodiversity under a changing climate. However, the assessment of impacts on the scenic beauty requires a set of indicators. An approach driven only by landscape metrics neglects the overarching importance of certain landscape elements such as orchard meadows, tree rows or extensively managed fields. Therefore, a weighted approach concerning the visual importance of specific landscape structures supplements the pure structural approach in assessing the scenic beauty.

Case study results frequently have limited significance beyond its boundaries. However, we may still be able to derive some general policy conclusions. Our study indicates that farm incomes may increase from climate change in those parts of Austria that are currently limited by temperature in plant production but less so with respect to precipitation levels. While there is much debate in the scientific literature on possible productivity gains from climate change in northern latitudes, equal arguments should be valid for regions with large diversity in altitudes such as in alpine areas. Potential benefits from climate change require farm level adaptation efforts. Autonomous adaptation by farmers as well as mitigation and planned adaptation policies turn out to be effective in maintaining or even increasing farm profitability but face several trade-offs between farm profits, public budget spending, and environmental outcomes. However, such model results are based on important assumptions including sufficient autonomous adaptation by farmers, limited impacts from extreme weather events, infestation from pests and diseases, or the effectiveness of CO_2-fertilization.

While climate change mitigation may not be a main interest of farmers, farm level adaptation will become increasingly important in the future. It is subject to the awareness of farmers on climate change, the availability of adaptation options and adaptation costs. All of those are affected by policies and policy adaptation to climate change may be required to maintain the productive potential of agriculture in the future. For example, it may include a revision of management guidelines and legislation such as for fertilization governed by the EU nitrate directive. With respect to rural development programs, increasing productivity from climate change increases the opportunity costs of AEP participation on croplands. Impacts on grasslands are driven by the utilization options of forage crops. The effects are similar to increasing market prices and likely challenge the design and affordability of AEPs in the future. AEP programs will therefore have to capture changing market and productivity conditions to maintain participation rates.

Appendices

[Appendix A-E]

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Table 1: Biodiversity indicator values

Crop and grassland activity	Intensity	Landscape functionality	Plant species richness	$Shannon_{veg}$	Hemeroby index
Root crops and maize	high	25	7.7	1.8	81.7
Root crops and maize	medium	28	9.5	2.0	73.1
Root crops and maize	low	31	10.3	2.0	69.3
Other arable crops	high	33	7.7	1.8	81.7
Other arable crops	medium	35	9.5	2.0	73.1
Other arable crops	low	38	10.3	2.0	69.3
Fallow land	low	45	10.3	2.0	69.3
Orchard meadows	high, medium, low	58	28.9	2.6	2.8
Short rotation forestry	high, medium, low	39	13.5	2.1	36.2
Extensive pastures	low	56	24.2	2.5	37.7
Pastures	high	36	20.0	2.4	40.9
Pastures	medium	38	25.5	2.6	28.9
Pastures	low	41	24.2	2.6	38.0
Meadows, 1-cut	low	40	24.3	2.5	19.7
Meadows, >1-cut	high	47	22.6	2.5	52.8
Meadows, >1-cut	medium	45	23.7	2.5	46.5
Meadows, >1-cut	low	40	24.0	2.5	33.1
Forestry	high	60	-	-	-
Forestry	medium	62	-	-	-
Forestry	low	65	-	-	-

Source: own data

Table 2: Agricultural policy assumptions and climate change scenarios

Scenario name	Agricultural policies	Climate change
REF_2040	• no dairy quota • no livestock premiums • regional farm payment • greening: max 75% of single crop, min 5% fallow land, no permanent grassland conversion • 2008 levels of less favored area payments • no agri-environmental program	no
CS01_i/m/a/m&a	like REF_2040 if not stated otherwise (see Tab. 2)	+1.5°C / ±0% precipitation
CS05_i/m/a/m&a	like REF_2040 if not stated otherwise (see Tab. 2)	+1.5°C / +20% precipitation
CS09_i/m/a/m&a	like REF_2040 if not stated otherwise (see Tab. 2)	+1.5°C / -20% precipitation

Note: i: impact, m: mitigation, a: adaptation
Source: own illustration

Table 3: Mitigation and adaptation policy scenarios

Scenario	Mitigation policies	Adaptation policies
REF_2040	no	no
CS01_i CS05_i CS09_i	no	no
CS01_m CS05_m CS09_m	• energy crops and SRF on fallow land • premium for orchard meadows and SRF • premium for afforestation • premium for reduced tillage & cover crops • premium for reduced fertilization intensity	no
CS01_a CS05_a CS09_a	no	• irrigation premium • abolishment of greening (see Tab. 2) • premium for maintenance of steep grassland
CS01_m&a CS05_m&a CS09_m&a	• premium for orchard meadows and SRF • premium for afforestation • premium for reduced tillage (& cover crops) • premium for reduced fertilization intensity	like CS01_a – CS09_a

Note: i: impact, m: mitigation, a: adaptation, SRF: short rotation forestry, min.: minimum
Source: own illustration

Table 4: Changes in fertilization intensity (average nitrogen N and phosphorus P per ha) on cropland and grassland and livestock numbers (all in % from REF_2040) for four policy (i, m, a, m&a) and three climate (CS01, CS05, CS09) scenarios

Scenario	cropland		grassland		cattle	pig	pou ltry	small rumi-nants
	N	P	N	P				
CS01_i	1	3	1	0	0	0	0	1
CS05_i	1	2	1	-2	0	1	0	1
CS09_i	2	3	1	-3	0	1	0	0
CS01_m	-6	-5	-3	8	0	0	0	2
CS05_m	-9	-7		9	0	0	0	2
CS09_m	-4	-4	-4	8	0	0	0	1
CS01_a	6	6	-1	-3	0	0	-2	1
CS05_a	4	4	-2	3	0	0	-2	1
CS09_a	7	6	-2	-5	0	0	-2	0
CS01_m&a	-4	-4	-3	8	0	0	0	2
CS05_m&a	-8	-6	-4	10	0	0	0	2
CS09_m&a	-2	-3	-4	9	0	0	0	1

Source: own data

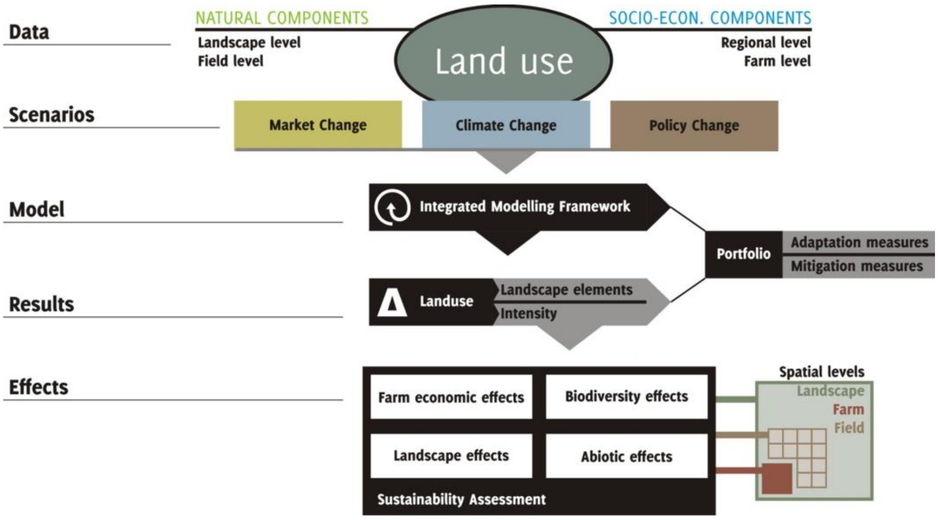

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Figure 1: The integrated modeling framework (IMF)

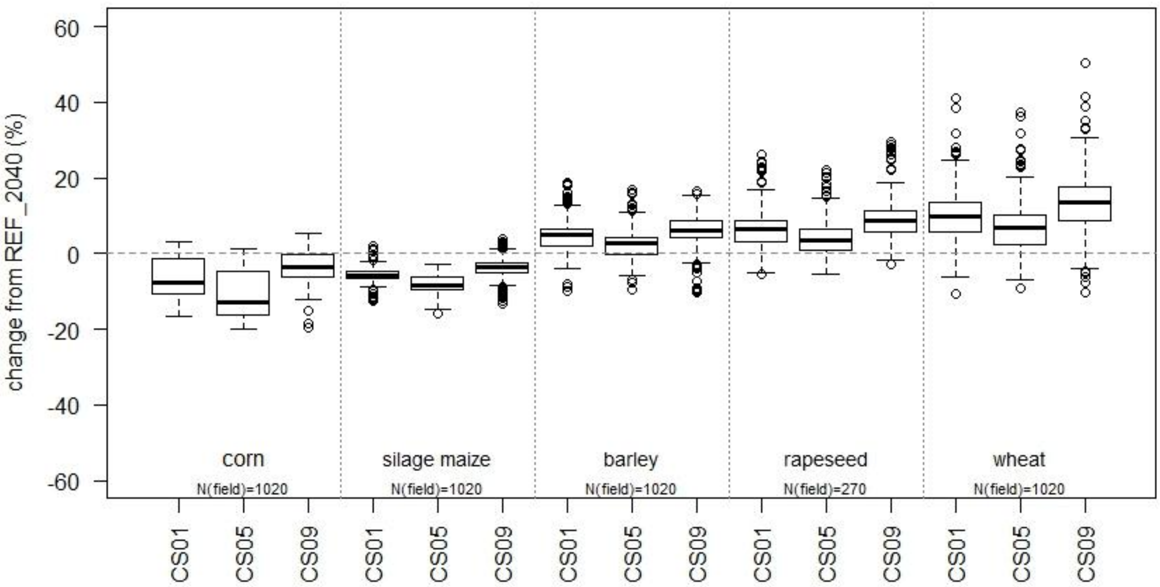

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Figure 2: Crop yield changes from climate change scenarios at field level by EPIC for the five most dominant arable crops with standard ploughing (average over all intensity levels and crop rotations; REF_2040: current observed climate)

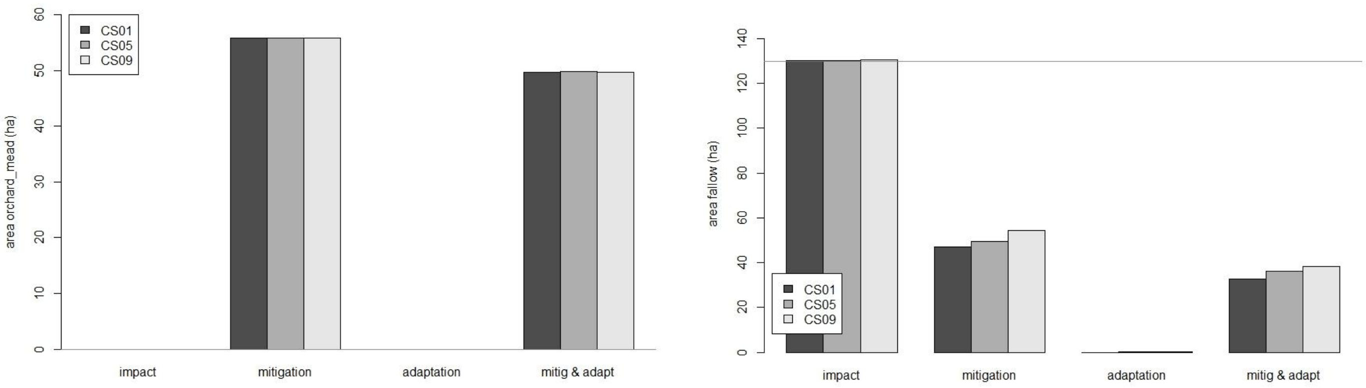

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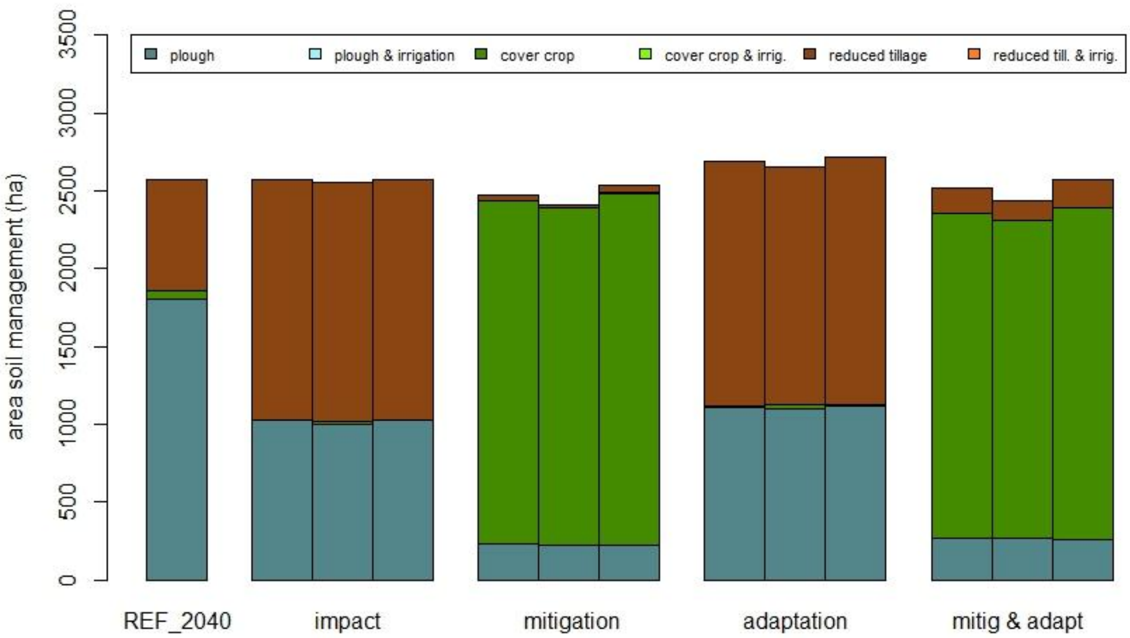
Figure 3: Total fallow land (ha) and total orchard meadows area (ha) at landscape level for four policy and three climate scenarios (grey line = result from REF_2040)



Note: plough: standard soil management with mould board plough, irrig.: irrigation, cover crop: reduced tillage with cover crops were appropriate in the crop rotation, reduced till.: reduced tillage.

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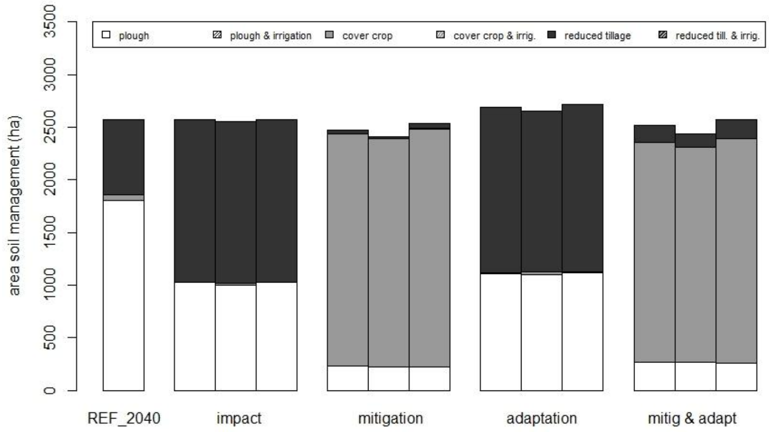
Figure 4: Soil management on cropland (ha) for the reference without climate change (REF_2040) and four policy and three climate scenarios (order of climate change scenarios in each block: CS01, CS05, CS09)



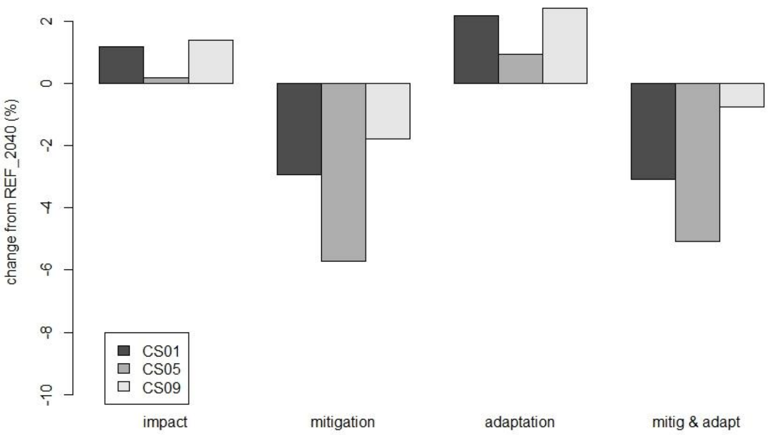


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Figure 5: Changes of agricultural greenhouse gas emissions from REF_2040 for four policy and three climate scenarios

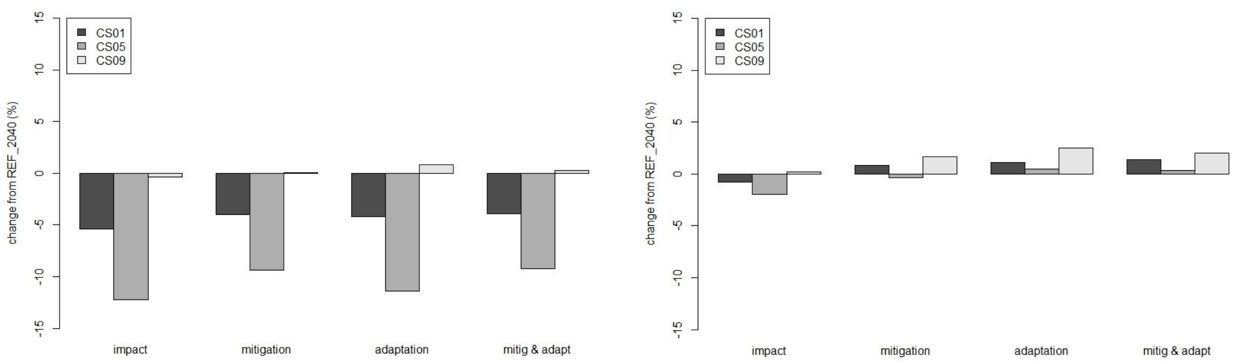

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Figure 6: Changes of soil organic carbon (SOC) from REF_2040 on cropland (left and grassland (right) for four policy and three climate scenarios

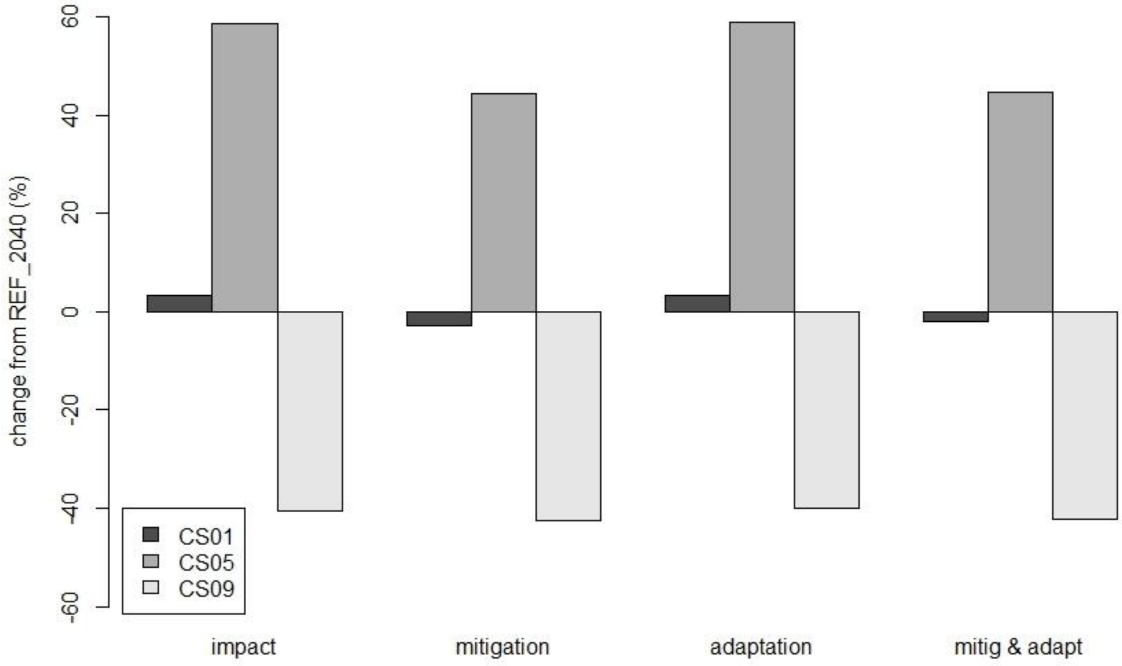

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Figure 7: Changes in soil sediment load from REF_2040 on cropland for four policy and three climate scenarios

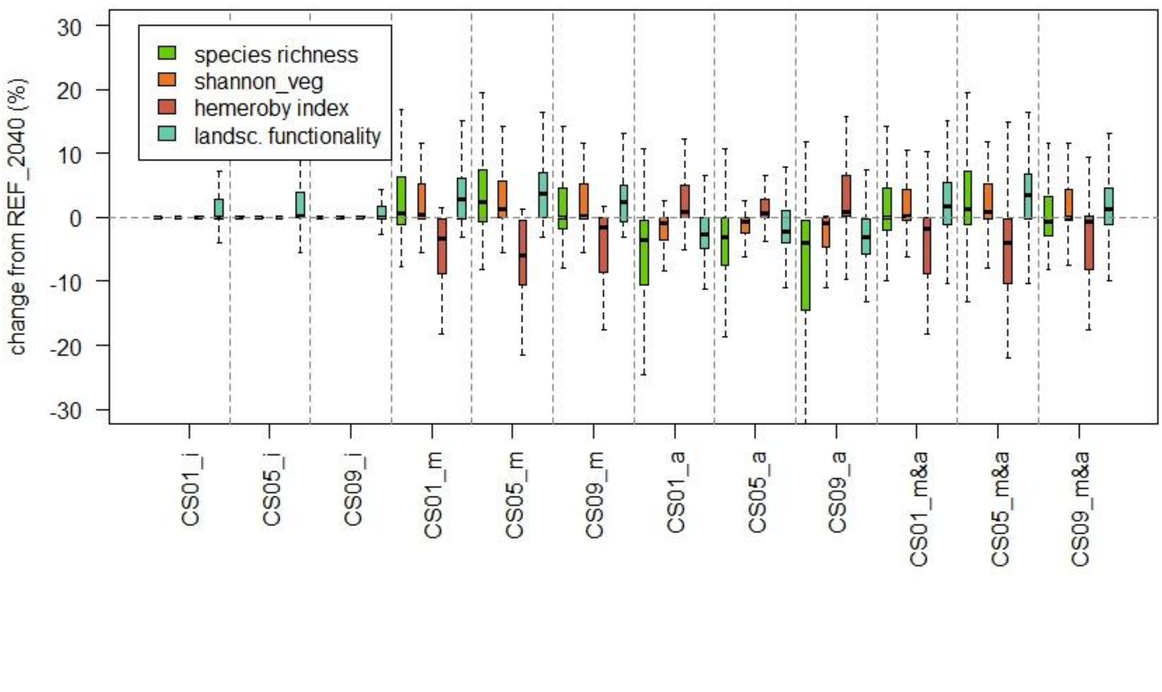

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Figure 8: Changes of vascular plant species richness, Shannon$_{veg}$, hemeroby index, and landscape functionality from REF_2040 for four policy and three climate scenarios

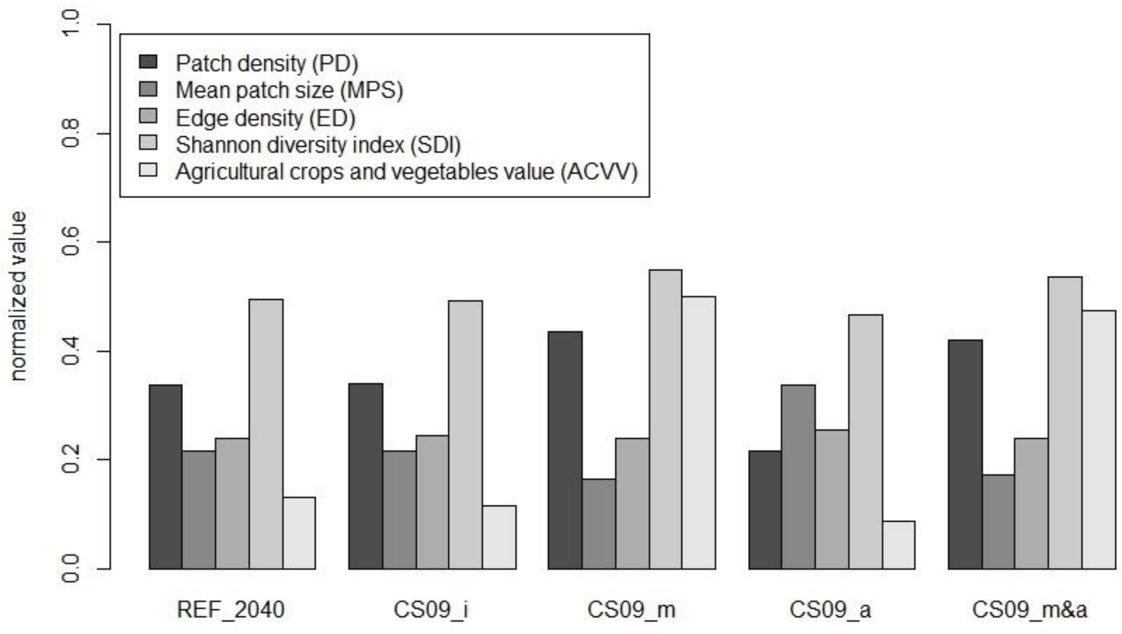

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Figure 9: Landscape indicators (all indicator values are normalized) for REF_2040 and four policy scenarios under climate scenario CS09

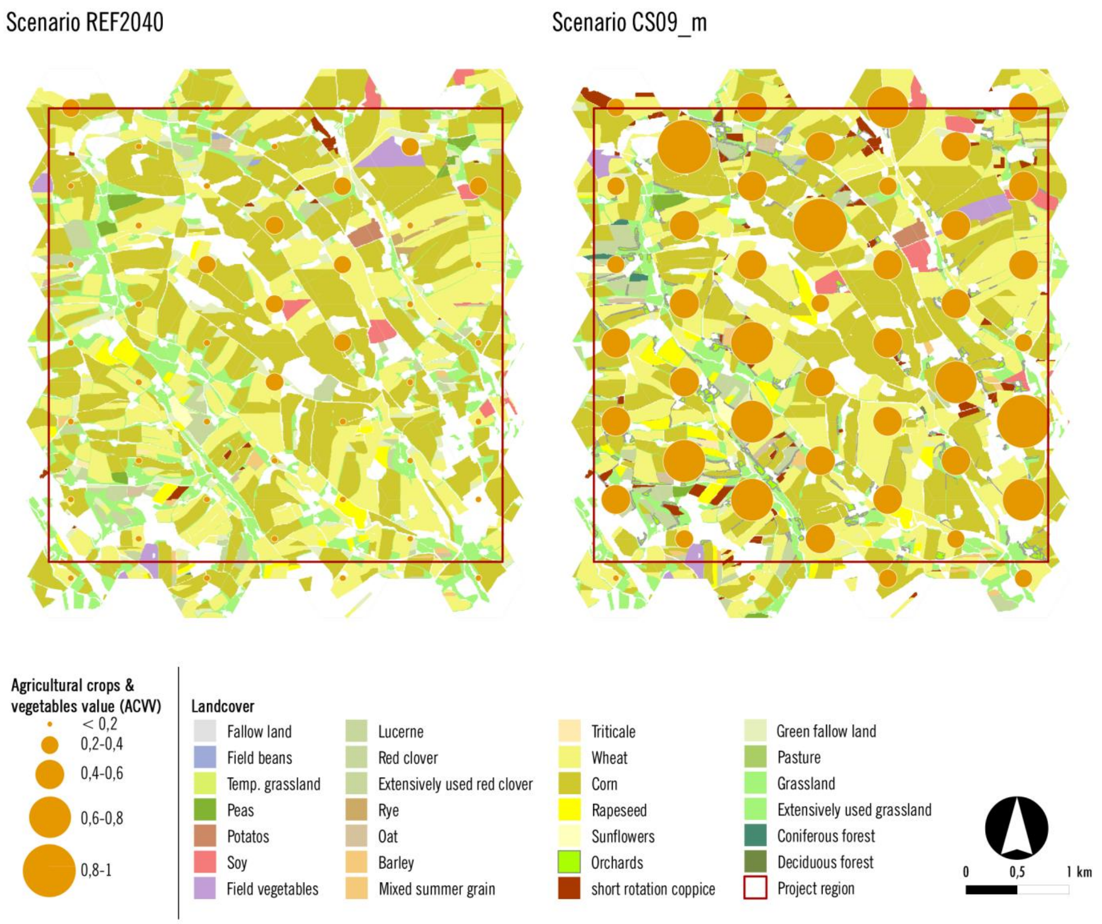

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Figure 10: Local differentiation of the ACVV indicator for the scenarios REF_2040 and CS09_m

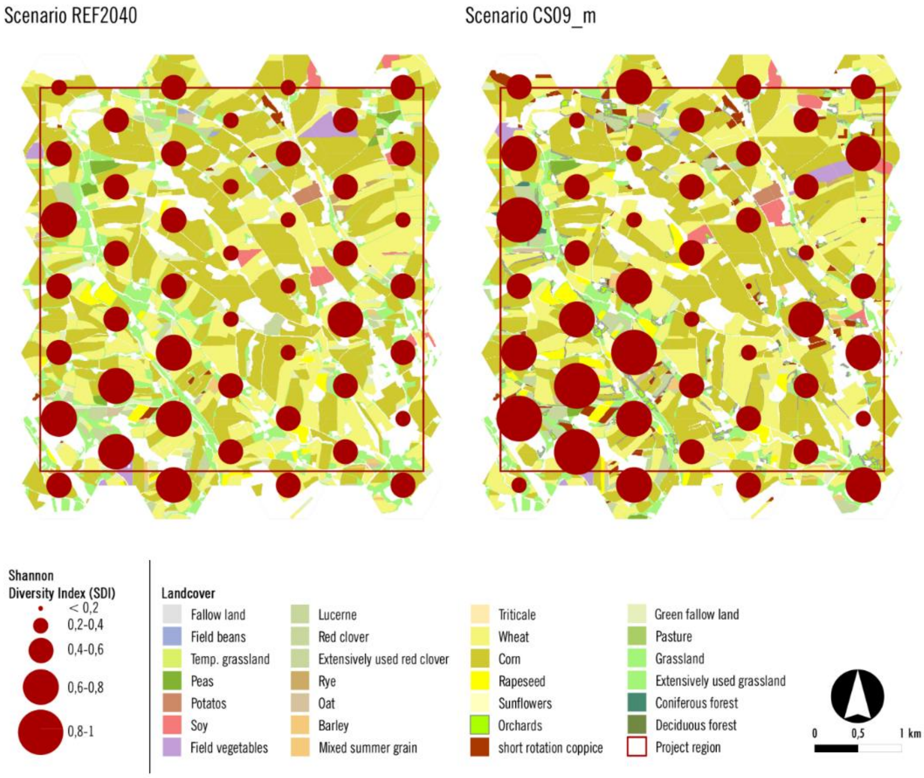

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Figure 11: Local differentiation of the SID indicator for the scenarios REF_2040 and CS09_m

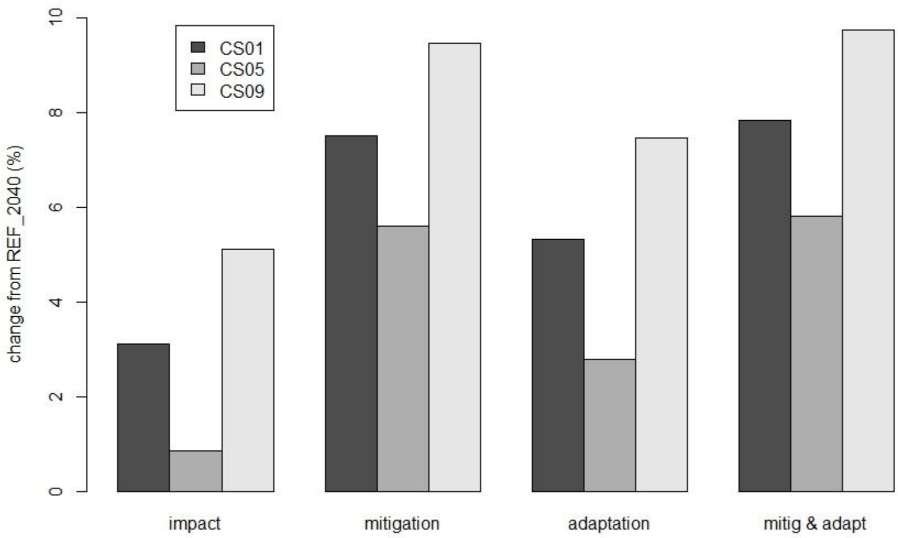

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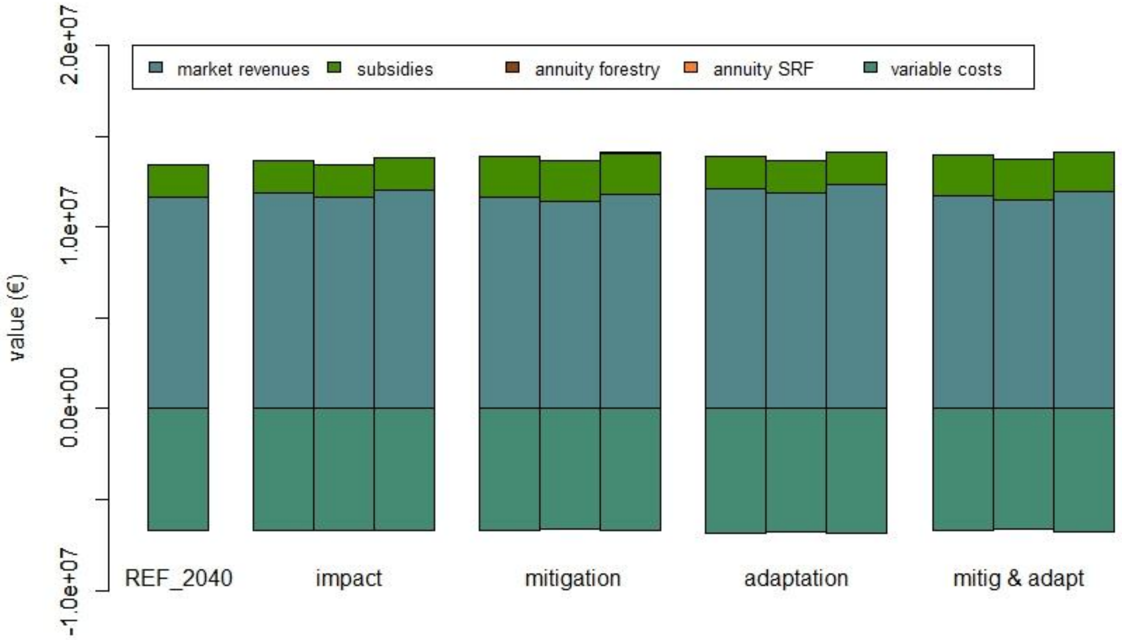
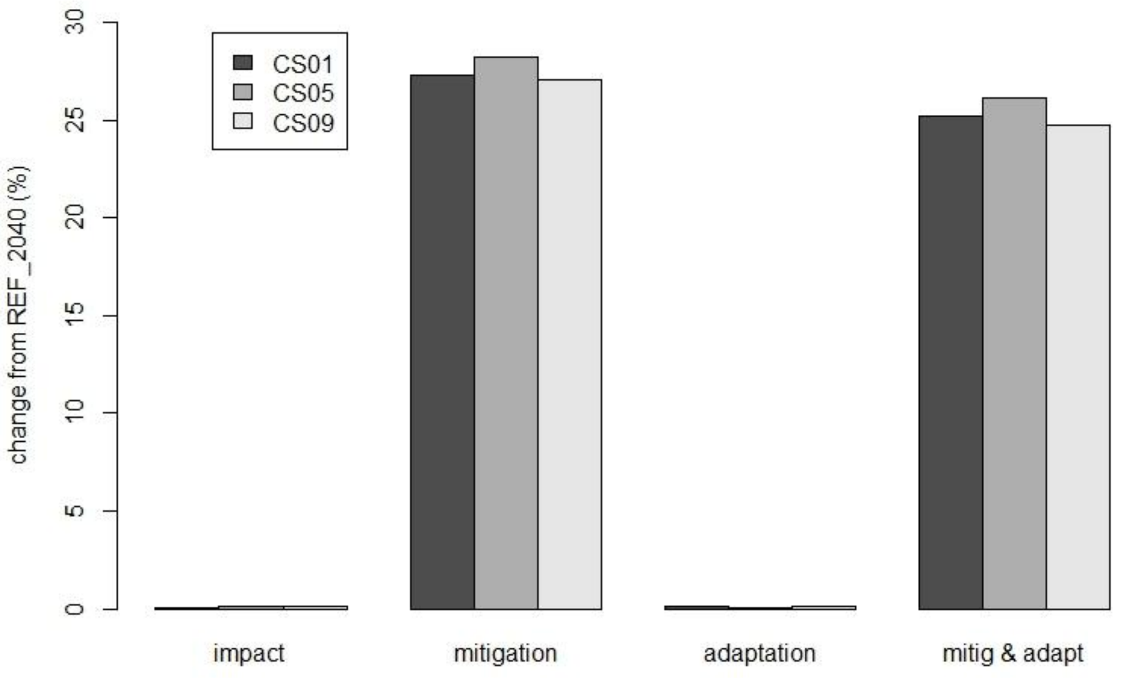
Figure 12: Changes in total farm gross margin from REF_2040 aggregated at the landscape level for four policy and three climate scenarios

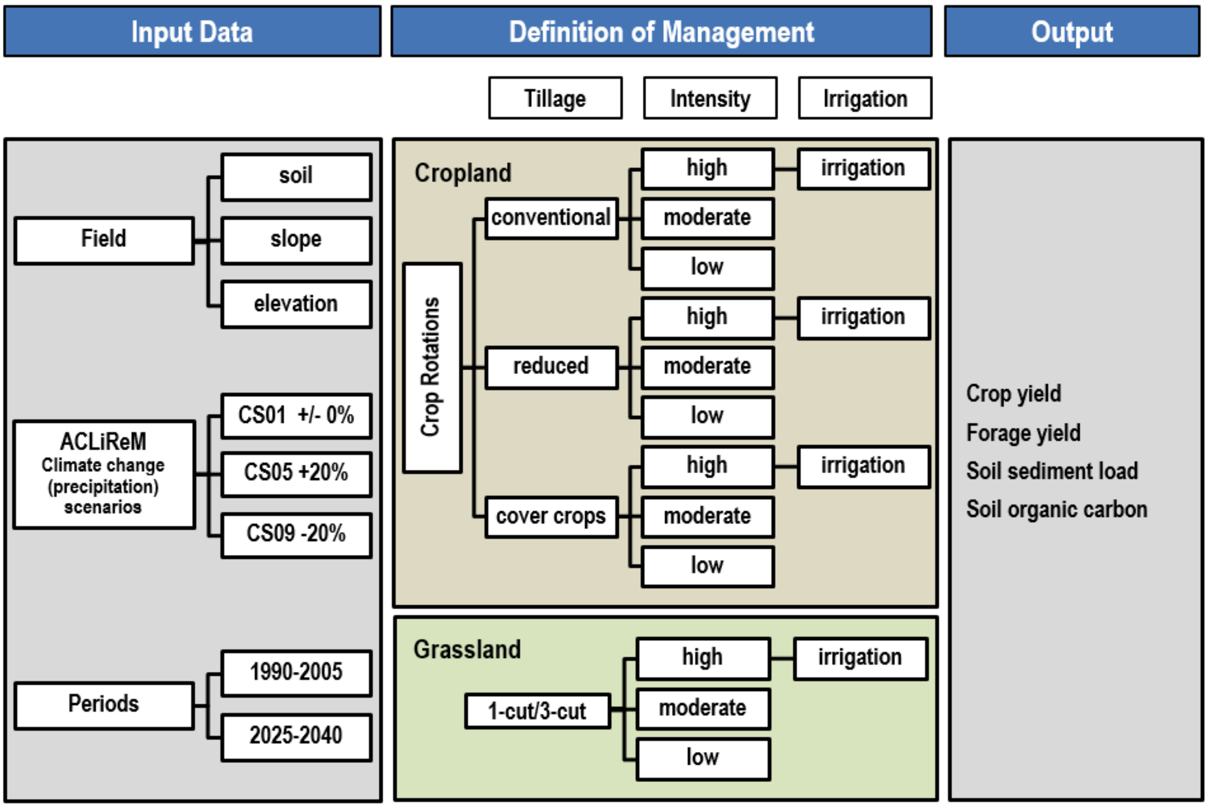




Note (upper figure): Black bars indicate total farm gross margins aggregated at landscape level, i.e. revenues + subsidies + annuity forestry + annuity SRF – variable costs; SRF: short rotation forestry.
Source: own illustration

Figure 13: Public budget spending: aggregated farm revenues, subsidies, and costs (€) at landscape level for the reference without climate change (REF_2040) and four policy and three climate scenarios (above; order of climate change scenarios in each block: CS01, CS05, CS09) and changes in total aggregated subsidies from REF_2040 at landscape level for four policy and three climate scenarios (below)

Appendix A: Overview on the management options considered in EPIC



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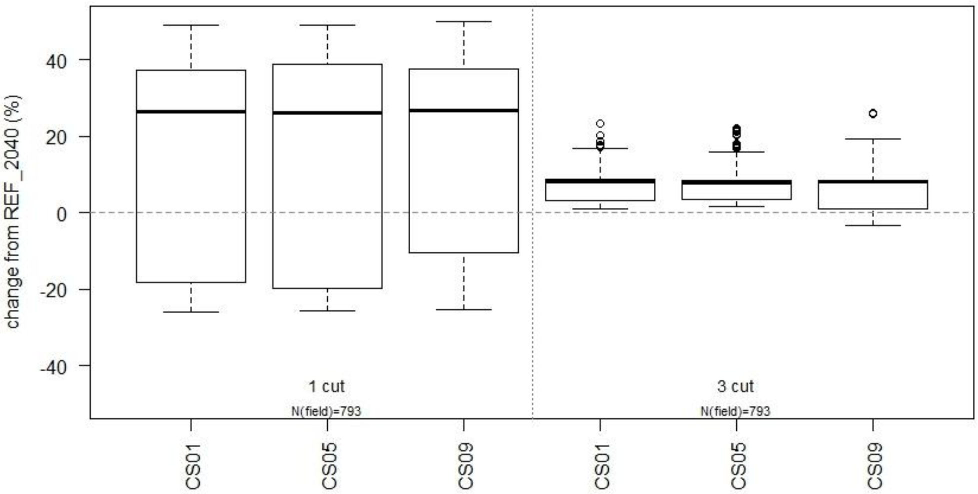
Appendix B: Average grassland yield changes from climate change scenarios at field level by EPIC for one-cut and 3-cut regimes (average over all intensity levels; REF_2040: current observed climate)



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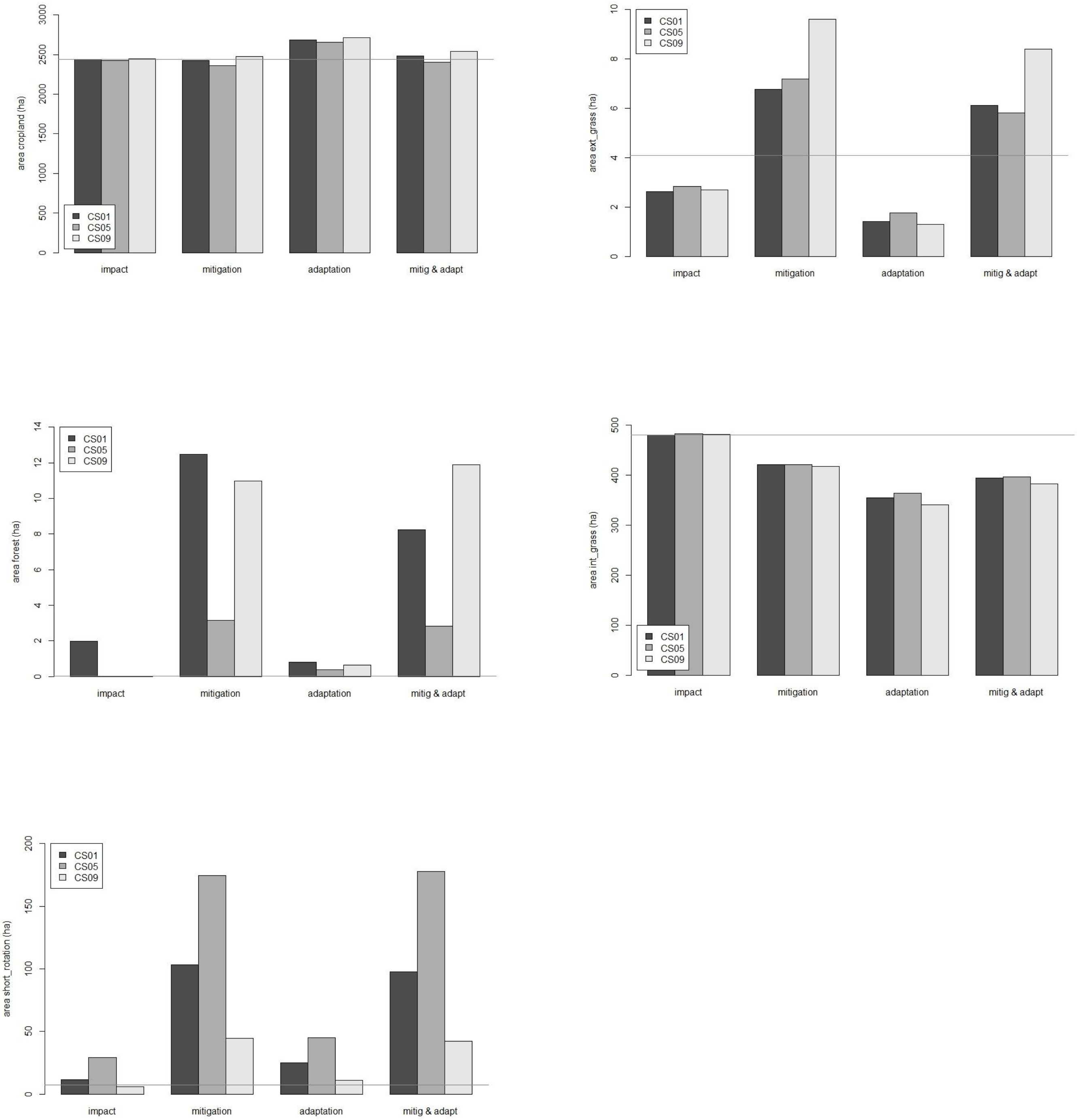
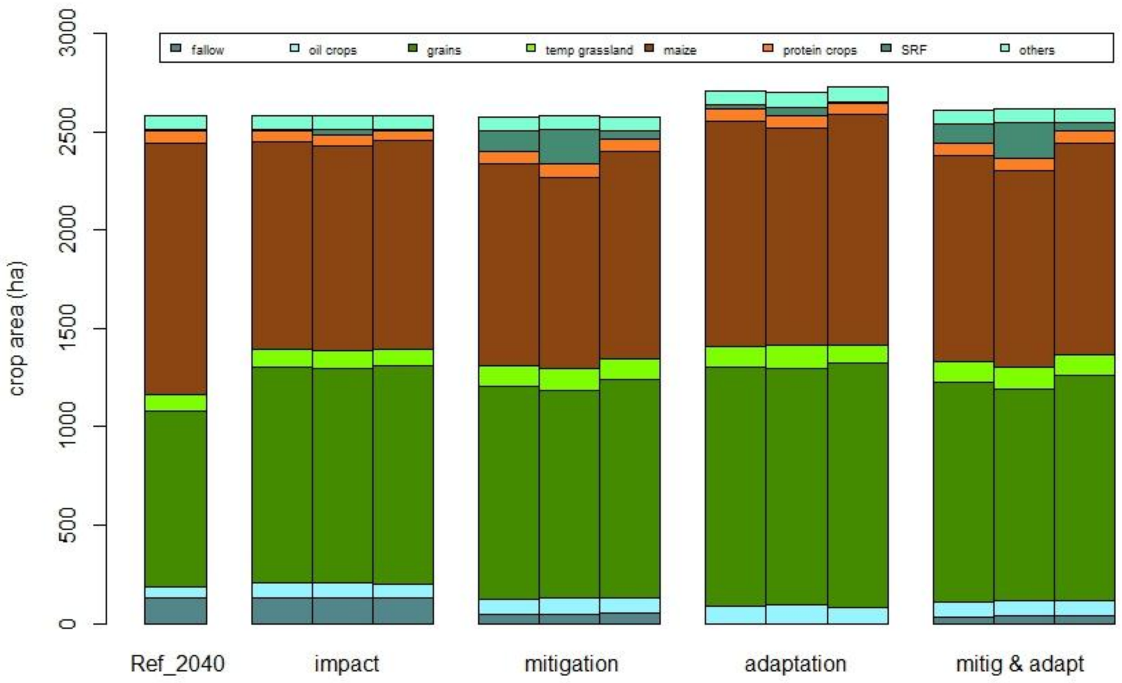
Appendix C: Total cropland, intensive and extensive grassland, SRF, and forest area at landscape level (in ha) for four policy and three climate scenarios (grey line = reference scenario REF_2040)



Note: SRF can be established on cropland only in the model but is presented as individual land use category. The category “forest” only indicates afforestation and reforestation but does not take existing forests into account.
Source: own illustration

Appendix D: Total area of arable crops at landscape level (crop categories, ha) for the reference without climate change (REF_2040) and four policy and three climate scenarios (order of climate change scenarios in each block: CS01, CS05, CS09)



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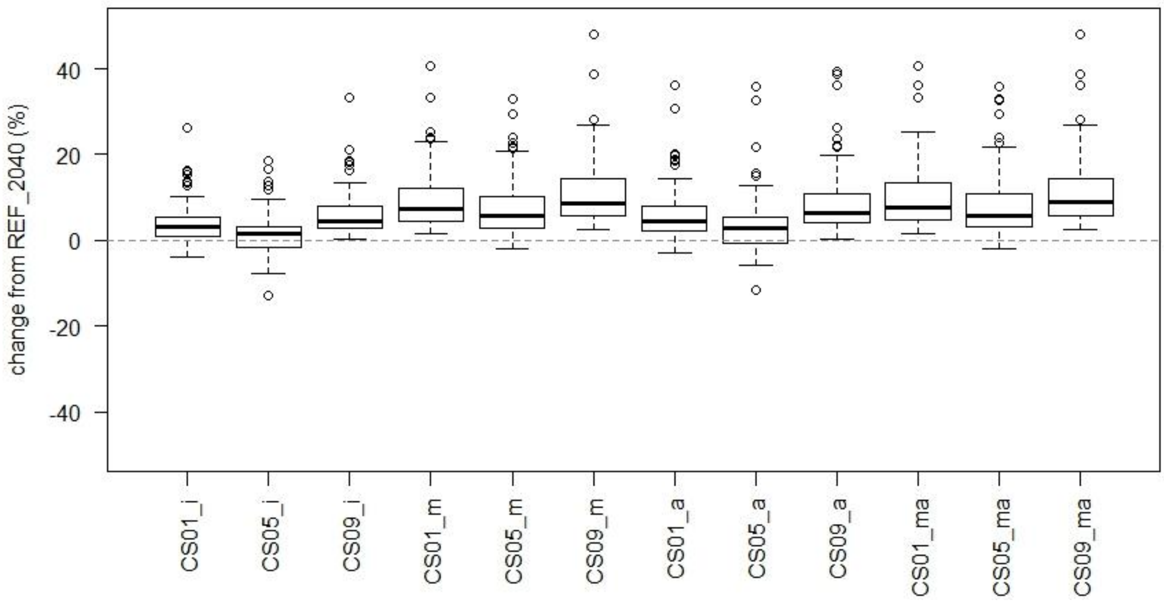
Appendix E: Distributions of changes in total farm gross margin from REF_2040 for four policy and three climate scenarios at farm level (N=113)



Source: own illustration.

Section C

Article 8 (viii)

Kutnjak, D., **Kuttner, M.**, Niketić, M., Dullinger, S., Schönswetter, P., Frajman, B. 2014. *Escaping to the summits: Phylogeography and predicted range dynamics of Cerastium dinaricum, an endangered high mountain plant endemic to the western Balkan Peninsula.* Molecular Phylogenetics and Evolution, 78, 365-374.

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Escaping to the summits: Phylogeography and predicted range dynamics of *Cerastium dinaricum*, an endangered high mountain plant endemic to the western Balkan Peninsula

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A B S T R A C T

The Balkans are a major European biodiversity hotspot, however, almost nothing is known about processes of intraspecific diversification of the region's high-altitude biota and their reaction to the predicted global warming. To fill this gap, genome size measurements, AFLP fingerprints, plastid and nuclear sequences were employed to explore the phylogeography of *Cerastium dinaricum*. Range size changes under future climatic conditions were predicted by niche-based modeling. Likely the most cold-adapted plant endemic to the Dinaric Mountains in the western Balkan Peninsula, the species has conservation priority in the European Union as its highly fragmented distribution range includes only few small populations. A deep phylogeographic split paralleled by divergent genome size separates the populations into two vicariant groups. Substructure is pronounced within the southeastern group, corresponding to the area's higher geographic complexity. *Cerastium dinaricum* likely responded to past climatic oscillations with altitudinal range shifts, which, coupled with high topographic complexity of the region and warmer climate in the Holocene, sculptured its present fragmented distribution. Field observations revealed that the species is rarer than previously assumed and, as shown by modeling, severely endangered by global warming as viable habitat was predicted to be reduced by more than 70% by the year 2080.

1. Introduction

The Balkan Peninsula is a hot spot of European biodiversity and endemism (Kryštufek and Reed, 2004; Kier et al., 2009). The underlying processes are complex, with environmental stability through geologic history (Hewitt, 2004; Tzedakis, 2004; Médail and Diadema, 2008) and topographic as well as climatic diversity likely acting as key factors (Kryštufek and Reed, 2004). The mountain range shaping the western Balkan Peninsula are the mostly calcareous Dinaric Mountains (Dinaric Alps, Dinarides). Their topography is highly complex, with summits reaching far up into the alpine zone and deeply incised valleys with thermophilous submediterranean vegetation (Surina et al., 2011).

The Dinaric Mountains have been less affected by Pleistocene glaciations than other southern European mountain systems such as the Alps and the Pyrenees (Bognar et al., 1991; Milivojević et al., 2008). The combination of incomplete glaciation and topographical complexity generated multiple glacial refugia which were facilitating strong genetic differentiation on a small geographical scale (Kryštufek et al., 2007; Médail and Diadema, 2008). Divergence in multiple Pleistocene microrefugia has already been highlighted as a key factor for the evolution of intraspecific diversity within the Iberian macrorefugium ('refugia-within-refugia hypothesis'; Gómez and Lunt, 2007). The few available studies of animal (Podnar et al., 2004; Kryštufek et al., 2007; Ursenbacher et al., 2008; Previšić et al., 2009) and plant species (Frajman and Oxelman, 2007; Surina et al., 2011) suggest that this pattern also applies to biota of the Balkan Peninsula. So far, no general patterns have emerged, and the area remains largely neglected despite of its

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1055-7903/

importance for understanding and conserving European biodiversity on a broader scale (Hewitt, 2004).

Pleistocene climatic fluctuations and gradual warming after the Last Glacial Maximum have likely shaped both phylogeographic structure and today's highly fragmented distribution of the Dinaric endemic *Cerastium dinaricum* Beck & Szyszył. (Caryophyllaceae). This (paleo)tetraploid (Niketić et al., 2013) species shows a highly disjunct distribution in the (sub)alpine zone from Mt. Snežnik in Slovenia in the northwest to the Prokletije Mts. in Montenegro in the southeast (Wraber, 1995; Niketić, 2007; Fig. 1). It inhabits north-facing limestone screes, rocky grounds and rock crevices with cold microclimate in the altitudinal range of 1430–2200(2370) m a.s.l. (Niketić, 2007). Cold-adapted species like *C. dinaricum* likely had larger, more connected distribution ranges during cold stages and were restricted to small, isolated high-altitude habitats during periods of warmer climate (Stewart et al., 2010). The two disjunct partial distribution areas of *C. dinaricum* differ in topographical complexity – whereas the southeastern part is highly structured with mountain ranges separated by deep valleys, the northwestern part is more homogeneous and lacks obvious barriers. Partly based on the results derived from *Edraianthus serpyllifolius*, another endemic high-alpine mountain plant of the southern Dinaric Mountains (Surina et al., 2011), we hypothesize that in the south of its range *C. dinaricum* most likely responded to Quaternary climatic oscillations with altitudinal range shifts on a small geographical scale, whereas in the North horizontal range expansions during cold periods may also have occurred. This scenario results in stronger genetic differentiation among southern populations as compared to northern ones.

Recent continent-wide plant diversity studies on multiple European mountain summits (Gottfried et al., 2012; Pauli et al., 2012) showed increasing impact of global warming in such environments. The underlying process was termed 'thermophilization' and results in a progressive decline of more cold-adapted species and an increase of more warm-adapted species (Gottfried et al., 2012). The effects of the current climate warming are anticipated to have strong deleterious effects for cold-adapted, high-alpine biota of the Dinaric Mountains, as their elevation is substantially lower compared to, e.g., the Alps. Consequently, the possibilities for upward altitudinal migrations of alpine biota are very limited. This seems especially relevant for rare endemics such as *C. dinaricum*, whose populations only comprise a few individuals at some sites (Wraber, 1995; B. Frajman, D. Kutnjak, personal field observations). Accordingly, the risk of habitat loss by upward displacement is considerable (Rull and Vegas-Vilarrúbia, 2006; Gottfried et al., 2012). Further, *C. dinaricum* is also a species of high conservation priority in Europe, listed in the Annex II of the EU Habitats directive, and therefore a qualification species for the NATURA 2000 network of protected areas.

Here, we examine the phylogeographic structure of *C. dinaricum* using amplified fragment length polymorphisms (AFLPs), nuclear ribosomal ITS and plastid *trnT–ndhJ* sequences as well as relative genome size data obtained from almost all known extant populations. Our specific aims were (i) to unravel the species' response to Quaternary climatic oscillations and to test the refugia-within-refugia hypothesis; as well as (ii) to compare the genetic structure between the topographically less structured northwestern and the more complex southeastern part of the occurrence. Finally, (iii) we search for evolutionary significant units (ESUs) within the species and (iv) model the contraction of its distribution area under increasing global warming. The results will provide a better understanding of the processes, which have shaped the spatial distribution of biodiversity on the western Balkans and will also be relevant for designing specific conservation strategies for this highly threatened species. The gained insights into the range dynamics of this cold-adapted southern European species will additionally contribute to our understanding of influences and risks of global warming in the near future.

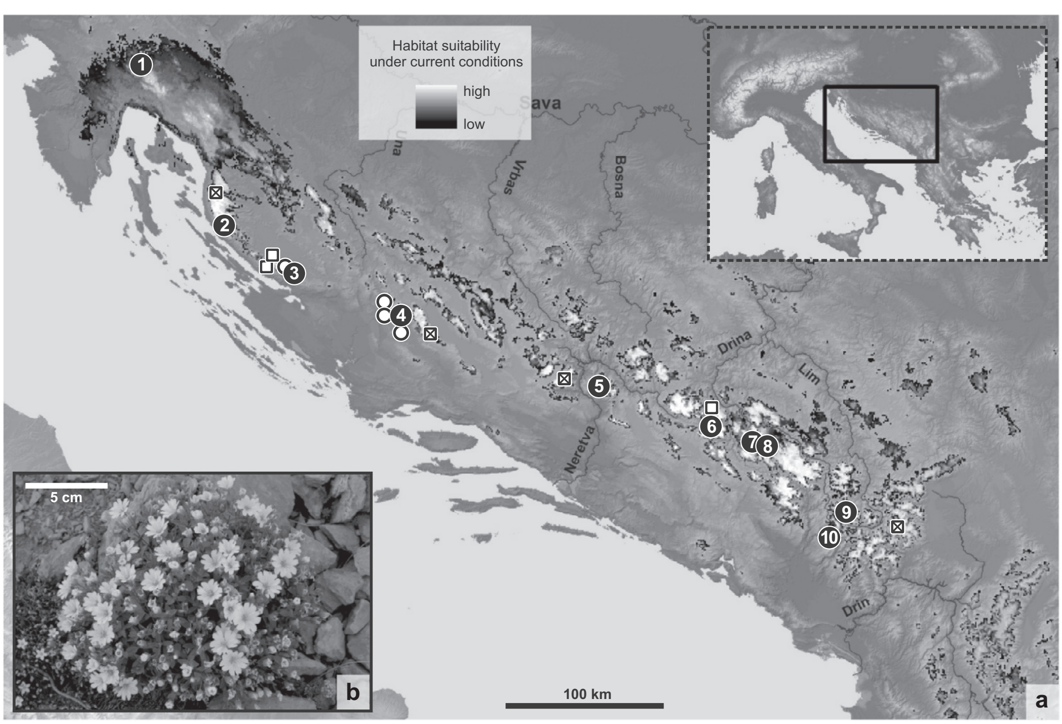

Fig. 1. Distribution, sampled populations, modeled habitat suitability and habit of *Cerastium dinaricum*. (a) Black dots numbered 1–10, sampled populations; empty circles, not sampled populations documented with herbarium specimens; squares, not sampled populations indicated in the literature for which we could not trace herbarium specimens; crosses, populations, where *C. dinaricum* could not be found in spite of considerable efforts. (b) *C. dinaricum* on its locus classicus, Kom Kučki in the Komovi mountain range, Montenegro (photo: P. Schönswetter).

2. Materials and methods

2.1. Study species and sampling

We visited 14 localities of *C. dinaricum* known from literature and/or herbaria along its entire distribution range. Presence of the species was confirmed in 10 localities (for details see Table 1 and Fig. 1) and leaf material from four to thirty individuals per population was sampled in silica gel. *Cerastium dinaricum* was also reported from two localities positioned within the distribution gap between populations 4 and 5 (Fig. 1, see Niketić, 2007, for details), but we were not able to find it there in spite of considerable efforts. The indications are likely erroneous as no herbarium material exists; alternatively the current absence could be the result of recent extirpations. Voucher specimens are deposited in the herbaria of the Universities of Innsbruck (IB) and Zagreb (ZA), and in the Natural History Museum Belgrade (BEO).

2.2. Genome size measurements using flow cytometry

Flow cytometry (FCM) of 40,6-diamidino-2-phenylindole (DAPI)-stained nuclei was used to estimate relative genome size and DNA ploidy level of silica gel-dried *C. dinaricum* samples. *Pisum sativum* cv. Kleine Rheinländerin (2C = 8.84 pg) was selected as a reference standard (Greilhuber and Ebert, 1994). Desiccated green leaf tissue (c. 0.5 cm^2) of two individuals from the same population was co-chopped with an appropriate amount of fresh reference standard and processed as described by Suda and Trávnícek (2006). The relative fluorescence intensity of 3000 particles was recorded using a Partec (Münster, Germany) CyFlow Space flow cytometer. Generally, only histograms with both peaks (sample and standard) of approximately the same height were considered. If the coefficient of variation (CV) of the G_0/G_1 peak of the sample exceeded the 5% threshold, the analysis was discarded and the sample re-measured. The number of measurements per population yielding high quality FCM histograms is given in Table 1.

Relative genome size was calculated as a ratio between the relative fluorescence of sample and standard. Statistical analyses were performed using R 2.13.1 (R Development Core Team, 2011). The data were visualized using the 'R ggplot2' package (Wickham, 2009). After testing for normal distribution, the difference between two observed subgroups was tested using Student's *t*-test. The genome size difference between two groups of populations was also tested experimentally with simultaneous isolation, staining and measurement of nuclei of two individuals from populations 1 and 9.

2.3. DNA isolation and AFLP fingerprinting

Total genomic DNA was extracted from silica gel-dried tissue (c. 10 mg) with DNeasy 96 Plant Kit (QIAGEN, Hilden, Germany) following the manufacturer's protocol.

The AFLP procedure followed Vos et al. (1995) with the modifications described in Schönswetter et al. (2009). In addition, 0.25 U of polymerase were used in the preselective and selective amplifications (0.4 U for the NED-labeled primer combination). The two final primer combinations for the selective PCR (fluorescent dye in brackets) were *Eco*RI (6-Fam)-ATC/*Mse*I-CTG and *Eco*RI (VIC)-AAG/ *Mse*I CTG. Purification and visualization of PCR products were done as described in Rebernig et al. (2010). Two blanks were included to test for contamination and seven individuals were replicated to test the reproducibility (Bonin et al., 2004).

Raw data were collected and aligned with the internal size standard using ABI Prism GENESCAN software 3.7.1 (Applied Biosystems). Subsequently, the GeneScan files were imported into GENOGRAPHER 1.6.0 (Montana State University) for scoring of the fragments. Each AFLP fragment was scored using the 'thumbnail' option. The results of the scoring were exported as a presence/absence matrix. The error rate (Bonin et al., 2004) was calculated as the ratio of mismatches (scoring 0 vs. 1) over matches (1 vs. 1) in AFLP profiles of replicated individuals. Fragments present in only one individual and low quality fragments (for which presence/absence was inconsistent in at least two pairs of replicates) were excluded from further analyses.

2.4. Analysis of AFLP data

Nei's (1987) gene diversity index and frequency down-weighted marker values (DW; Schönswetter and Tribsch, 2005; Winkler et al., 2010) were calculated for each population using

Table 1
Locality details, herbarium voucher, number of individuals included in AFLP analyses (N_{AFLP}), genetic diversity (Nei's GD) and rarity (DW), number of genome size measurements with two pooled individuals each (N_{GS}), relative genome size with standard deviation (SD), number of individuals for which the plastid *trnT–ndhJ* region was sequenced (N_{cpDNA}), corresponding haplotypes (H_{cp}), and GenBank accession numbers of all investigated populations of *Cerastium dinaricum.* SLO, Slovenia; CRO, Croatia; BiH, Bosnia and Herzegovina; MNE, Montenegro. For population 6 only ploidy level could be determined (the same as for other populations) owing to the low quality of the genome size measurements.

Pop. number	Sampling locality	Latitutde/ longitude	Elevation (m)	Herbarium voucher	N_{AFLP}	Nei's GD	DW	N_{GS}	Genome size ± SD	N_{cpDNA}	H_{cp}	GenBank accession numbers (*trnT–ndhJ*; ITS)
1	SLO: Notranjska, Snežnik	45.5953 N 14.4539 E	1431	IB-12813	15	0.0535	1.387	7	0.3011 ± 0.0029	4	I	KJ716517; KJ716507
2	CRO: Velebit, Malovan	44.6502 N 15.0313 E	1579	ZA-H-011	4	–	–	2	0.3066 ± 0.0017	4	III	KJ716518; KJ716508
3	CRO: Velebit, Vaganski vrh	44.3655 N 15.5042 E	1690	ZA-H-010	11	0.0519	1.217	6	0.3060 ± 0.0016	5	II	KJ716519; KJ716509
4	CRO: Dinara, Dinara	44.0626 N 16.3833 E	1831	ZA-H-023	15	0.1204	2.035	10	0.3081 ± 0.0031	3	II	KJ716520; KJ716510
5	BiH: Hercegovina, Prenj	43.5486 N 17.8817 E	1864	IB-12864	18	0.0910	1.528	10	0.3202 ± 0.0051	5	VI	KJ716521; KJ716511
6	BiH: Bosna, Volujak	43.2535 N 18.6934 E	2100	BEO-016	16	0.1129	1.682	–	–	4	V	KJ716522; KJ716512
7	MNE: Durmitor, near Škrčko jezero, Ćuskija	43.1283 N 19.0300 E	1883	IB-12909	17	0.0384	0.999	12	0.3226 ± 0.0035	5	V	KJ716523; KJ716513
8	MNE: Durmitor, Velika Kalica	43.1189 N 19.0719 E	1977	IB-12902	17	0.0714	1.332	11	0.3265 ± 0.002	5	V	KJ716524; KJ716514
9	MNE: Komovi, Kom Kučki	42.6775 N 19.6458 E	2259	IB-12930	18	0.0915	1.423	19	0.3228 ± 0.0038	6	V	KJ716525; KJ716515
10	MNE: Žijevo, Žijevo	42.5539 N 19.5064 E	2140	IB-13017	17	0.0858	1.215	10	0.3249 ± 0.0033	4	V	KJ716526; KJ716516

the R script AFLPdat (Ehrich, 2006). To balance the unequal sample sizes, both indices were calculated with eleven (randomly chosen) individuals per population, excluding population 2 from which only four individuals were found. Analyses of molecular variance (AMOVAs) were calculated with ARLEQUIN 3.11 (Excoffier et al., 2005).

Using SplitsTree 4.12.3 (Huson and Bryant, 2006), a Neighbour-Net diagram was produced from Nei–Li distances (Nei and Li, 1979) calculated with TreeCon 1.3b (Van de Peer and De Wachter, 1997). A neighbor-joining analysis was conducted based on the same distance matrix and bootstrapped (2000 pseudoreplicates) with the same program.

Structure 2.2 with a Bayesian clustering approach developed for dominant markers (Falush et al., 2007) was used with an admixture model with uncorrelated allele frequencies and recessive alleles. Ten replicate runs for each *K* (number of groups) ranging from 1 to 10 were carried out, using a burn-in of 10^5 iterations followed by 10^6 additional Markov chain Monte Carlo (MCMC) iterations. Similarity among results of different runs for the same *K* was calculated according to Nordborg et al. (2005) using the R-script Structure-sum-2009 (Ehrich, 2006). We identified the number of groups as the value of *K* where the increase in likelihood started to flatten out, the results of replicate runs were identical (similarity coefficients 1; for an exception see below; Rosenberg et al., 2002) and the clusters were non-empty. For each group identified at the optimal *K*, a separate STRUCTURE analysis was carried out.

The genetic covariance structure among sampled populations was modeled within a graph theoretic framework (Population Graphs: Dyer and Nason, 2004) using POPGRAPHS (available from http://dyerlab.bio.vcu.edu/software/). Populations, which constitute the nodes, were connected into a population network only if significant genetic covariance existed between the populations after removing the covariance each population had with the remaining populations (see Dyer and Nason, 2004 for a more detailed description of the method). If genetic covariance was spatially structured, the physical distances should be proportional to the genetic distances; otherwise the populations were either closer (compressed edges) or further apart (extended edges) than expected given the genetic distances. Isolation by Graph Distance analysis defining normal, extended and compressed edge sets was conducted with Graph from the GENETIC STUDIO program suite (Dyer, 2009). Stability of edges among geographic groups was assessed using a bootstrap approach with 200 bootstrap pseudoreplicates, which were generated using seqboot from the PHYLIP package (Felsenstein, 1989) and analysed as the original data set. The proportion of replicates where a certain edge is found constitutes its bootstrap support. Edges with bootstrap support of 50% or more were considered stable (Escobar García et al., 2012).

In order to reconstruct the potential extant source populations of the genetically depauperate and divergent population 7, which is located in close proximity of the large and genetically more diverse population 8, assignment tests were performed using AFLPOP 1.1 (Duchesne and Bernatchez, 2002) with the default settings. All other populations were considered as potential source populations, and allocation was tested using three levels (0, 1 and 2) of minimal log-likelihood differences with frequency values of zero replaced by 1/(sample size +1).

2.5. Sequencing of plastid trnT–ndhJ and nuclear ribosomal ITS

The *trnT–ndhJ* region was sequenced for three to six individuals per population. Amplification was done in reaction volumes of 30 μL, comprising 12 μL REDTaqReadyMix (Sigma–Aldrich, Vienna, Austria), 0.3 μL BSA (10 mg/mL, New England Biolabs), 1 μL template DNA of unknown concentration, and the primers TabA (Taberlet et al., 1991) and ndhJ (Shaw et al., 2007) at a final concentration of 0.2 μM. PCR conditions were 5 min at 95 °C, 35 cycles of 30 s at 95 °C, 30 s at 60 °C and 4 min at 65 °C, followed by 10 min at 65 °C.

The ITS region was sequenced for one to two individuals per population. Sequences were amplified using primers 17SE/26SE (Sun et al., 1994) or P17/26S-82R (Popp and Oxelman, 2001). Reaction volumes were 16.5 μL, comprising 6 μL REDTaqReadyMix, 0.7 μL BSA (10 mg/ml), 1 μL template DNA of unknown concentration and primers at final concentration of 0.24 μM. PCR conditions were 4 min at 94 °C, 35 cycles of 1 min at 95 °C, 1 min at 56 °C and 70 s at 72 °C, followed by 10 min at 72 °C.

PCR products were purified using Exonuclease I and Calf Intestine Alkaline Phosphatase (CIAP; MBI-Fermentas, St Leon-Rot, Germany) according to the manufacturer's instructions. Cycle sequencing was performed using BigDye Terminator chemistry (Applied Biosystems) according to the manufacturer's instructions. The *trnT–ndhJ* was sequenced using the primers TabA, TabD, TabE (Taberlet et al., 1991) and ndhJ (Shaw et al., 2007), whereas ITS was sequenced using both PCR primers. Electrophoresis was performed on ABI 3130xl sequencer (Applied Biosystems).

Contigs were assembled and aligned using Geneious 5.5.6 (Biomatters Ltd., 2010). A statistical parsimony network was constructed from the plastid sequences using TCS 1.21 (Clement et al., 2000), coding indels longer than 1 bp as single characters and treating sequence gaps as fifth character state. *Cerastium subtriflorum* (Rchb.) Pacher, which is – to the best of our knowledge – the closest relative of *C. dinaricum* (B. Frajman, unpublished data), was used as outgroup (GI accession number: KJ716527). A NeighbourNet diagram of ITS sequences was constructed using SplitsTree 4.12.3 (Huson and Bryant, 2006).

2.6. Species distribution modeling

Spatially explicit modeling of viable habitat for *C. dinaricum* under current and changing environmental conditions was conducted using the R-package 'biomod2' (Thuiller et al., 2012). We used all available occurrence data of *C. dinaricum* (17 data points, details given in Appendix A1 in Supplementary material). Bioclimatic variables for present conditions were obtained from the WORLDCLIM database (Hijmans et al., 2005, spatial resolution: 30″, i.e. c. 1 × 1 km). For the climate of the two future target years 2050 and 2080 we selected emission scenario 'mpi_echam5_A1B' (IPCC, 2007), assuming an average global temperature rise of 2.8 K (1.7–4.4) until 2100. In addition, we used the digital elevation model 'srtm90_100m' (Jarvis et al., 2008) and spatially extrapolated it to align with the grain size of the other environmental variables.

In order to reduce collinearity, we only included variables with Kendall's Tau (τ) rank correlation ($\leqslant |0.7|$) in the predictor set. Hence, the number of bioclimatic variables could be reduced from 19 to eight. The variable 'elevation' was added to the set of predictors as it is a useful compound proxy for the physical environment in high mountain habitats (Körner, 2007).

As true absence data for *C. dinaricum* was not available, 3 × 500 pseudo absence (PA) points were randomly selected with 'biomod2'. For modeling purposes we selected the default set of parametric and non-parametric regression techniques and machine-learning algorithms in the ensemble modeling and forecast routines (generalized linear models, GLM; generalized additive models, GAM; artificial neural networks, ANN; surface range envelops, SRE; classification trees, CTA; random forests, RF; multivariate adaptive regression splines, MARS and flexible discriminant analysis, FDA). Further, we conducted a fivefold cross validation of the input data as suggested by Araújo et al. (2005) and Guisan & Thullier (2005). We used True skill statistics (TSS) and Receiver Operating Characteristics (ROC) to evaluate the performance of each of the 120 single models (3 PA datasets × 8 algorithms × 5 repetitions) and defined a threshold of TSS > 0.7 for the respective models to be considered in the subsequent ensemble modeling procedure. The final ensemble forecast was based on 'committee averaging' across single projections. Consensus model predictions for current and future climatic conditions were finally compared in terms of potential range size changes to quantify the potential habitat loss of *C. dinaricum* in the future. All outcomes of the 'biomod2'-projections and range size change evaluations were saved as multilayer raster data in IMAGINE file format (.img) with a spatial resolution of 1 × 1 km and post-processed for map creation in ArcGIS 10.1. (ESRI 2013).

3. Results

3.1. Genome size variation

The estimated DNA ploidy level was the same for all measured samples (the FCM histograms of population 6 were discarded from further analyses due to the high CV of the measurements, but evidently suggested the same ploidy level as measured for the other populations). Average relative genome size ranged from 0.301 in population 1 to 0.327 in population 8 (Table 1), with evident bimodal distribution. One mode corresponds to the northwestern populations (populations 1–4) and the other to the southeastern ones (populations 5, 7–10; Fig. 2a). The difference between the means of the groups' relative fluorescence was highly significant (*t*-test, $p < 0.001$). Differences in DNA content between the two groups were confirmed by the presence of double peaks of simultaneously measured samples (Fig. 2b): the genome size of the sample from population 1 was 8.3% smaller than the genome size of the sample from population 9. The mean relative genome size of the NW group was 5.8% smaller than that of the SE group.

3.2. AFLPs

After the removal of fragments present in only one individual and after discarding low quality fragments the two AFLP primer combinations yielded 170 fragments in 148 individuals from ten populations, out of which 88.8% were polymorphic. The error rate (Bonin et al., 2004) was 2.2% before and 0.85% after the exclusion of low quality fragments. The values of both, Nei's gene diversity and frequency down-weighted marker values (DW) were highest in population 4 and lowest in population 7 (Table 1, Figs. 3c and d). Non-hierarchical AMOVA attributed 61.94% of the overall genetic variation to the among-population component. In the hierarchical AMOVA (NW group, SE group; see below) 42.41% of variation was attributed to the between-group component (details in Appendix A2).

Analyses of the AFLP data set strongly support separation of the northwestern populations 1–4 from the southeastern populations 5–10 with 100% bootstrap support (BS) from the neighbor-joining analysis (Fig. 3b). Within both groups the northernmost population is separated from the other populations. Bayesian clustering (Fig. 3e) revealed the same overall genetic structure. Separate analysis of the SE group supported two possible substructures. In the first case (lower likelihood, $\ln(P) = -5777.83$, but identical solutions among replicates) two genetic clusters were identified, corresponding to the NeighbourNet diagram. The second solution (with higher likelihood, $\ln(P) = -5070.87$, but a similarity coefficient of 0.82 among replicated runs) suggested five genetic clusters: populations 6 and 8 clustered together, whereas each of the other four populations formed its own genetic cluster. There was no or little admixture between clusters. Population membership coefficients for different values of *K* are presented in Fig. 3e.

Populations were connected in two separate graphs in the Population Graphs analysis (Fig. 3a), which are congruent with the two groups identified with the other methods. Most of the edges had a bootstrap support of ⩾50%. In the NW group each population was connected with all other populations of the group and the covariance structure within this group was characterized by extended edges. In the SE group the connectivity of populations was lower and some compressed edges were present.

The assignment test, using a cut-off level of 0, suggested populations 8 (in 70.6% of cases) and 9 (in 29.4% of cases) as most likely source populations for population 7. Using a cut-off level of 1, nine of 17 individuals were allocated, eight of them to population 8 and one to population 9. With a cut-off level of 2 only one individual was allocated to population 8.

3.3. Nuclear ribosomal ITS and cpDNA haplotypes

The alignment of 45 plastid *trnT–ndhJ* sequences was 2273 bp long and included six variable characters (all indels). There was no intrapopulational variability in sequence data. Using statistical parsimony analysis five closely related haplotypes were identified (Table 1, Fig. 3f).

The alignment of ITS sequences of 11 individuals was 819 bp long and sequences showed very little variability. The test analysis (NeighbourNet, not shown) failed to provide any informative genetic structure.

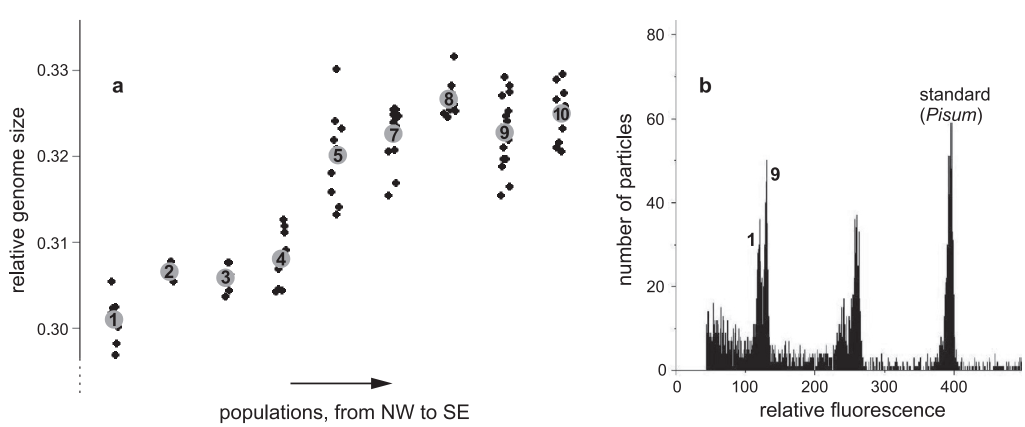

Fig. 2. Genome size variation within *Cerastium dinaricum*. (a) Relative genome size values for all measurements (black dots) with population means (bigger grey circles with population numbers), measurements for individuals from the same population are arranged vertically; (b) FCM histogram of simultaneous measurement of relative genome size of pooled samples from populations 1 and 9, measured together with *Pisum* as an internal standard; the peaks between 200 and 300 correspond to nuclei in the G2/M phase of the cell cycle.

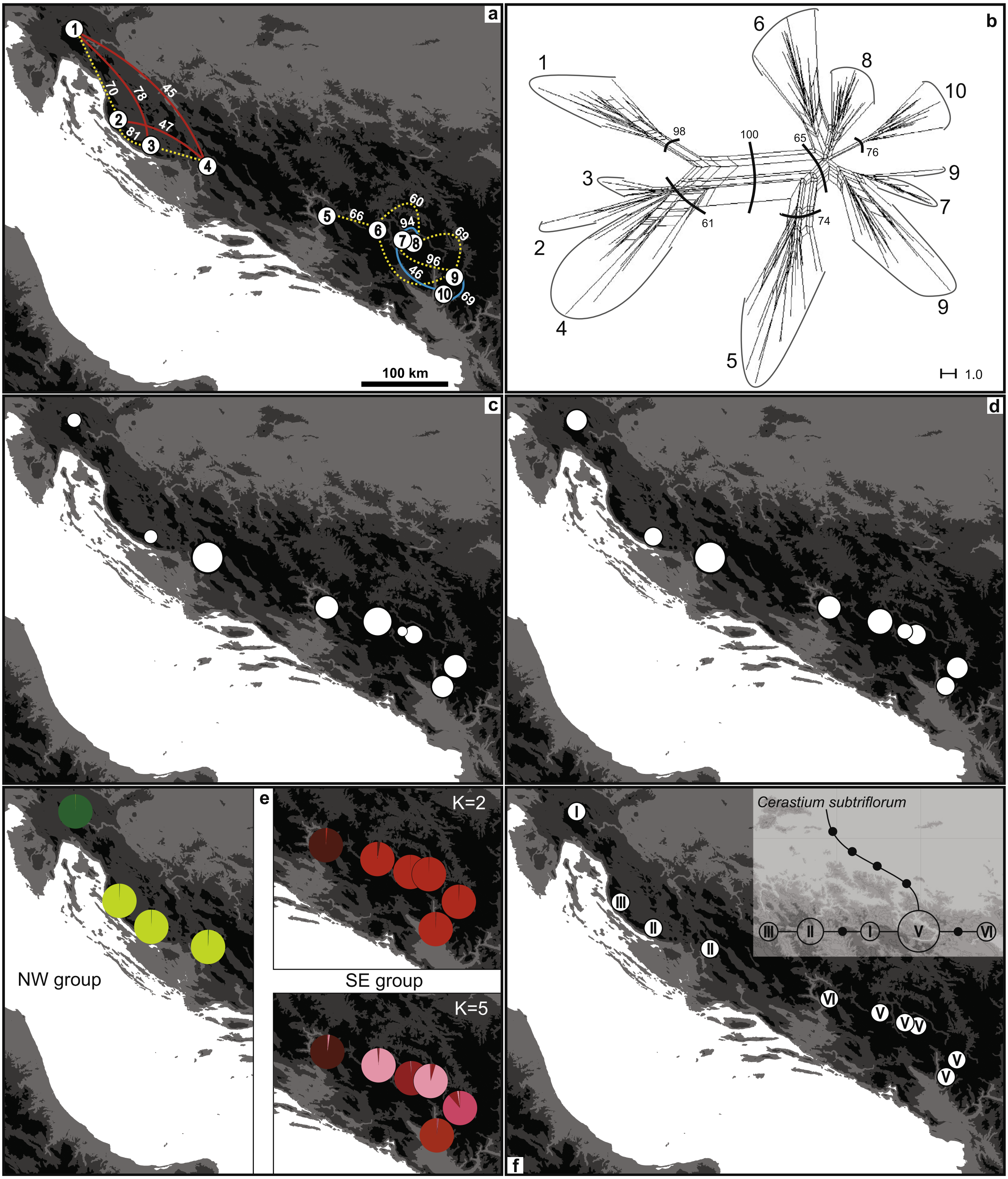

Fig. 3. Phylogeographic structure of *Cerastium dinaricum*. (a) Population graphs based on AFLP profiles; dashed yellow lines represent normal edges, red lines extended and blue lines compressed edges; numbers next to the edges represent their bootstrap support; (b) NeighbourNet diagram based on AFLPs, numbers from 1 to 10 are population numbers (see Table 1 and Fig. 1), numbers next to the bold lines are bootstrap support values for splits derived from a neighbor-joining analysis; (c) Nei's gene diversity; (d) frequency down-weighted marker values (DW); (e) STRUCTURE clustering of the AFLP data from separate analyses of the NW and the SE groups: for the SE group two solutions ($K = 2$, $K = 5$) were resolved; (f) geographic distribution and statistical parsimony network of plastid DNA haplotypes of *C. dinaricum* and the closely related *C. subtriflorum* as outgroup (the size of a circle in the network is proportional to a haplotype's frequency).

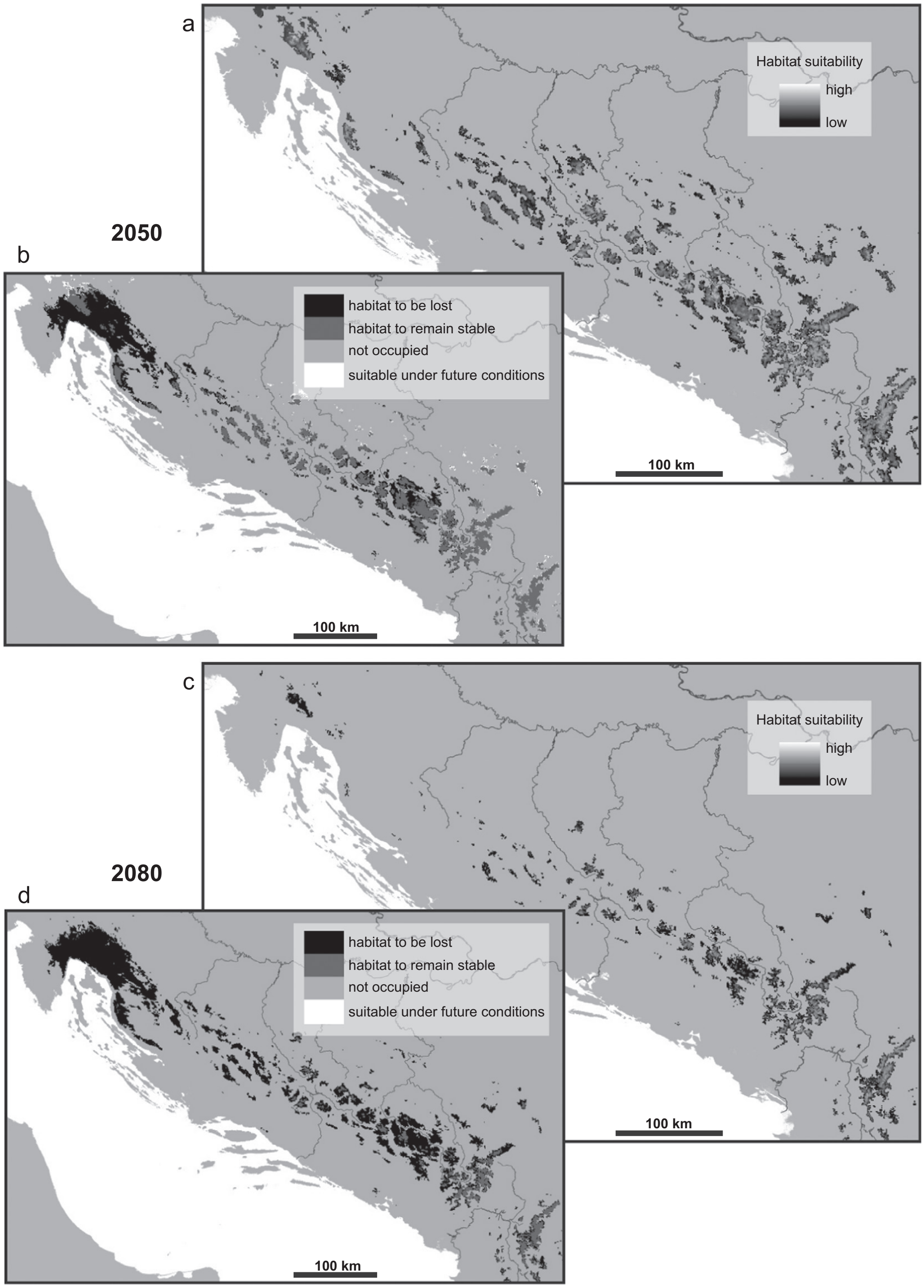

Fig. 4. Outcomes of niche based modeling of *Cerastium dinaricum* under future climatic conditions (2050; 2080) and corresponding range size change plots. Plots a and c illustrate the degree of habitat suitability for *C. dinaricum* over time, while plots b and d provide further details on changing spatial distribution patterns due to altered climatic conditions. Habitat suitability under current conditions is shown in Fig. 1.

3.4. Evaluation of 'biomod2' modeling

TSS and ROC evaluation scores revealed 'good' to 'excellent' (cf. Swets, 1988; Coetzee et al., 2009) overall performances for most statistical models. Overall mean values across the three PA datasets and associated repetition runs suggested highest scoring of the GAM model, followed by RF, MARS, FDA and CTA, all scoring at TSS values >0.9. GLM and ANN models still reached TSS scores greater than 0.85 and ROC scores greater than 0.9, respectively. Only SRE showed rather poor scores (TSS = 0.41; ROC = 0.7) and was not further considered for ensemble modeling. Evaluation scores for the computed ensemble models suggested high discrimination ability and predictive accuracy with TSS > 0.95 and ROC c. 0.99.

3.5. Predicted distribution and range size changes of C. dinaricum

Modeled current and future potential distributions of *C. dinaricum* are plotted in Fig. 4. *Cerastium dinaricum* is modeled to lose about 37% of its current potential range under a climate as forecasted for the year 2050. Under a 'full dispersal' assumption, i.e. if the species could in exchange colonize all sites that become suitable to it under this new climate, habitat loss would reduce to approximately 24%. Under the climatic conditions predicted for 2080, *C. dinaricum* is modeled to lose nearly 73% of its current potential range and only an area of 4% of this current range will become newly suitable for it.

4. Discussion

The rare and disjunctly distributed cold-adapted mountain plant *Cerastium dinaricum*, which is endemic to the Dinaric Mountains, the backbone of the western Balkan Peninsula, exhibits a deep phylogeographic split strongly supported by nuclear data (AFLPs and relative genome size; Figs. 2 and 3) splitting the northwestern populations 1–4 (NW group) from the southeastern populations 5–10 (SE group). The groups are separated by a distribution gap of about 100 km (Fig. 1). The northern border of the SE group is formed by the Neretva river valley (Bosnia and Herzegovina), a region coinciding with strong intraspecific breaks in animal (rodent *Dinaromys bogdanovi*: Kryštufek et al., 2007; lizard *Podarcis melisellensis*: Podnar et al., 2004) and plant species (*Edraianthus tenuifolius*: Surina et al., 2011). In groups that underwent speciation the Neretva valley functions as a contact zone of vicariant species pairs (*Campanula portenschlagiana* and *C. poscharskyana*: Park et al., 2006; Frajman and Schneeweiss, 2009; *Campanula pyramidalis* group: Lakušić et al., 2013; *Cardamine maritima* group: Kučera et al., 2010). However, the aforementioned plants are thermophilous and such pattern was not observed in cold-adapted species (e.g., *Edraianthus serpyllifolius*: Surina et al., 2011). At present, the Neretva valley is characterized by submediterranean vegetation very different from the mountain biomes on the upper slopes of the valley. Similar differences in vegetation might have been present also in the Pleistocene and possibly acted as barrier to dispersal, triggering allopatric divergence. In addition to the Neretva valley, the vast lower-altitude Livno karst field separating the Čvrsnica and Dinara mountain ranges may have acted as barrier for *C. dinaricum*. Alternatively, Lakušić et al. (2013) suggested that the genetic break in the *Campanula pyramidalis* complex along the lower Neretva valley was caused by divergent environmental conditions north and south of that valley during the Last Glacial Maximum, when the northern coast of the Adriatic was shifted southward to the Neretva estuary (Correggiari et al., 1996). The proximity of the sea has a detrimental influence on the distribution of extent vegetation types on the western Balkans (Horvat et al., 1974), and has likely played a similar role in the Pleistocene. In any event, further studies of Dinaric mountain biota and dating of divergence events based on external calibrations will be necessary to search for pervasive patterns and to identify the underlying processes.

The strongly disjunct distribution of *C. dinaricum* coinciding with patterns of genetic divergence supports the hypothesis of multiple refugia on the western Balkan Peninsula (Surina et al., 2011). Within both major population groups, the geographically isolated northernmost populations 1 and 5 are also genetically most divergent. This is supported both by AFLPs (Fig. 3b and e) and plastid DNA (Fig. 3f), suggesting relatively long isolation (Schönswetter and Tribsch, 2005). Both populations are small; the genetically impoverished (Fig. 3c) population 1, restricted to the lowermost point of a karst sinkhole characterized by temperature and vegetation inversion (Wraber, 1995) comprised only 15 individuals in July 2010 (B. Frajman, D. Kutnjak, personal field observations). Their genetic divergence might thus be a result of stochastic allelic drift due to severe population contractions (Freeland et al., 2011; Masel, 2011).

Except for the separation of populations 1 and 5 the patterns of plastid and nuclear AFLP divergence within both major groups are not congruent. Small isolated populations are more susceptible to stochastic events (faster spread and fixation, but also faster elimination of new mutations) as compared to larger populations interconnected by gene flow (Freeland et al., 2011; Masel, 2011). This might, in combination with the uniparental mode of plastid inheritance, explain the observed incongruences. In the NW group three plastid haplotypes were found whereas AFLPs revealed a fairly uniform gene pool (Fig. 3), suggesting a continuous distribution in lower elevations of the geographically close Velebit and Dinara mountain ranges during cold stages of the Pleistocene. This is also supported by high genetic diversity observed in population 4 from Mt. Dinara (Fig. 3c) and by extended edges in the Population Graphs analysis (Fig. 3a). On the other hand, populations 6–10 from the SE group share the same plastid DNA haplotypes, but AFLPs (STRUCTURE analysis at $K = 5$ as well as the NeighbourNet; Fig. 3) revealed several genetic groups roughly corresponding to major mountain ranges (Volujak plus Durmitor, Komovi, Žijevo). Some compressed edges in the Population Graph analysis of the SE group indicated low connectivity among populations suggesting vicariance (Fig. 3a). Phylogeographic patterns observed within this group thus likely reflect upslope migration of increasingly fragmented populations in the Holocene, followed by shallow genetic divergence. Especially within the topographically complex landscapes of Montenegro and southern Bosnia and Herzegovina mountain ranges are separated by deep valleys with heat-tolerant, submediterranean vegetation. These valleys are restricting migration and gene flow among populations at present, and will do so even more in the future due to global warming.

Whereas our data suggest a scenario of prevalent range stasis, they also provide evidence for a recent limited range expansion accompanied by a strong founder effect within the Durmitor mountain range in Montenegro. Population 7, separated from population 8 by only 3 km but positioned on the other side of the main ridge, represents a unique AFLP (sub)cluster, even though it is geographically positioned between populations 6 and 8, which in turn have been assigned to the same (sub)cluster. From all investigated populations, population 7 exhibited the lowest value of both genetic diversity and rarity (Fig. 3c and d). Assignment tests suggested population 8 as the most likely source. Therefore, the divergence of this population observed with STRUCTURE is likely the consequence of shifts of allele frequencies accompanying a recent founder effect (Templeton, 1980).

The strong AFLP and genome size divergence between NW and SE groups (Figs. 2 and 3) suggests presence of cryptic biological species. If the difference in genome size confers a crossing barrier or not (Roux et al., 2010) is biologically meaningless because of the entities' allopatric distribution that precludes gene flow. We suggest that the two divergent groups within *C. dinaricum* should be treated as Evolutionary Significant Units (ESUs) and future conservation strategies should focus on both entities, even if no consistent morphological differences between the two groups could be observed (M. Niketić, personal observations).

Areas identified as refugia likely have special properties important for the long-term persistence of species (Médail and Diadema, 2008). Therefore, special effort should be taken for their conservation. The genetic structure of *C. dinaricum* illustrates that the topographic complexity of the western Balkan Peninsula was crucial for long-term persistence of isolated populations of high mountain species. The increasingly evident global warming, however, might endanger the existence of such populations – or even of entire species – in the future (Gottfried et al., 2012; Pauli et al., 2012). This is even more threatening due to the relatively low altitudes of the Dinaric Mountains as compared to, e.g., the Alps and thus strongly reduced possibilities for upslope migration. Spatially explicit modeling of viable habitat for *C. dinaricum* suggested a decrease of up to 70% by the year 2080 (Fig. 4). We concede that the relatively coarse scale of our models might have drawn a slightly too pessimistic picture (Randin et al., 2009; Scherrer and Körner, 2011). However, as populations of *C. dinaricum* are usually small, environmental and demographic stochasticity will likely play an important role and even reaching nearby climatic microrefugia might be highly problematic for the species. At the coarser scale, *C. dinaricum* presently only inhabits a very small fraction of its potentially suitable habitat and the predicted habitat loss could actually result in range-wide extinction of the species in the very near future.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ympev.2014.05.015.

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Section C

Article 9 (ix)

Kuttner, M., Hülber, K., Moser, D., Rabitsch, W., Schindler, S., Wessely, J., Gattringer, A., *Essl, F.,*Dullinger, S. 2015. *Habitat availability disproportionally amplifies climate change risks for lowland compared to alpine species.*

*joint last authorship

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Abstract

At present, numerous studies have focussed on the issue of climate change impact on species distributions by the use of correlative distribution models (SDMs) which, in turn, have served as the most widely acknowledged tool for quantifying current and upcoming climate induced species´ range shifts. However, one major caveat that restricts the interpretability of such modelling outcomes is owed to the fact that they are not considering any other environmental constraints which will hinder species forthcoming persistence, first and foremost the distribution of suitable habitats. Although several studies have already evaluated the importance to integrate land cover within SDM environments, the mostly coarse spatial resolution of such data has been a limiting factor towards applicability. This is particularly the case in regions that have either been shaped by fine-scaled agricultural use over centuries or characterized by steep environmental gradients that are naturally determining a succession of various habitat types on a narrow geographical extent, such as the European Alps. In this study, we compared potential range shifts of 58 species originating from three different taxonomic groups (butterflies, grasshoppers, vascular plants) until the second half of the 21st century to their current distributions under the use of SDMs within a Central European case study region, thus covering major parts of the Eastern Alps and adjacent areas. We subsequently intersected individual SDM outcomes with a lately established high resolution habitat map to refine potential species´ ranges. We discovered that also accounting for the availability of appropriate habitat types can alter purely climate-driven risk assessments for species significantly. In this context, we revealed different patterns for alpine vs. lowland species, where for the latter human-caused habitat fragmentation may increase climate induced risk of persistence. In comparison, alpine species will likely be less affected due to the enhanced distribution of required (semi-)natural habitat types.

Key-words: Alpine species; Butterflies; Conservation; Ecological niches; Grasshoppers; Habitats; Land use; Lowland species; Plants; Species distribution modelling

Introduction

Climate warming and land use change are supposed to be the two most important drivers of expected 21st century biodiversity loss worldwide (Pereira et al. 2010). Indeed, many studies have already documented how species' populations have declined and/or shifted their geographical distributions in response to one of these two drivers (e.g. Tilman et al. 1994, Walther et al. 2002, Parmesan and Yohe 2003, Thuiller et al. 2005, Pauli et al. 2012, Jantz et al. 2015). In addition, their interactions are expected to create a "deadly anthropogenic cocktail" (Travis 2003) inasmuch as human destruction and fragmentation of (semi-)natural habitats may impede species migration. However, migration processes allow for an adaptation of geographical ranges to changing climatic conditions (e.g. Ellis and Ramankutty 2008, Klein Goldewijk et al. 2011, Dullinger et al. 2015).

The interplay of land use and climate change may affect species' ranges and biodiversity patterns. In particular, climate change may shift the climatically suitable ranges of species to regions where land use has already reduced or fragmented appropriate habitat types to a large extent; or, vice versa, where larger and less fragmented areas of such habitat types are still available. For example, a warmer climate might drive central European forest understorey species farther to the north-west of the continent, where land use intensification has greatly reduced the natural forest cover, or more to the north-east (Scandinavia), where forest cover is largely intact (Dullinger et al. 2015). As a consequence, purely climate based risk assessments will either under- or overestimate the actual threat to such species.

The extent to which the geographically varied availability of suitable habitat types will alter climate driven risks to species has been little explored so far (but see e.g. Oliver et al. 2015). Idiosyncratic land use histories will certainly play an important role in this context, but some general trends might nevertheless be expected because land use patterns often follow climatic gradients (Thuiller et al. 2004). In Europe, for example, land use intensity is highest in lowland areas, but much lower in the subalpine and alpine belts of mountain systems (Kampmann et al. 2012). It appears hence likely that shifts of potentially suitable climates that are confined within lower altitudes could drive species into areas where suitable habitat types have been drastically reduced and fragmented. By contrast, if climate warming shifts a species range towards higher altitudes, human fragmentation of suitable habitat types will rarely be an issue. As a corollary, the interplay with land use patterns could even buffer mountain species against climate threats to a certain degree and hence compensate for the formers' expected (e.g. Dirnböck et al. 2011, Engler et al. 2011) higher vulnerability to climate change.

Correlative species distribution models (SDMs) are the most frequently used tool to evaluate climate threats to biodiversity so far (e.g. Thuiller et al. 2005, Elith et al. 2010, Araújo et al. 2011, Engler et al. 2011). These models statistically relate occurrence data of species to environmental variables and are used to project altered (potential) species distributions in response to shifting climatic conditions (e.g. Guisan and Thuiller 2005). Interactive effects of land use can, in theory, be easily integrated into such models by using land use types as additional predictor variables in the models (e.g. Dirnböck et al. 2003, Luoto et al. 2007, Stanton et al. 2012.). In practice, however, this approach may face severe data limitations. Whereas climatic conditions are a more or less continuously varying feature of landscapes, and can thus be interpolated from point measurements with reasonable accuracy at a broad range of different spatial grains (e.g. Zimmermann et al. 2009, Pradervand et al. 2014), land use patterns represent a complex mosaic of possibly small units with sharp and often unpredictable boundaries which defies common downscaling procedures. Model accuracy is thus limited by the spatial resolution of both, mapping products and species occurrence data. These limitations are particularly relevant when modelling species in regions which are strongly modified by long-lasting human land use like the many cultural landscapes of Europe. Here, particularly the rare and endangered species are usually restricted to scattered remnants of natural and semi-natural habitats which often are (much) smaller than the grain size of species atlas or other occurrence datasets (e.g. Kurtto et al. 2013).

A way to circumvent this problem is overlaying the projections of coarser-grain species distribution models, which predict the response of species to climatic gradients, with finer-scale land use/cover maps that represent the template of habitat types suitable to a particular species (e.g. Broennimann et al. 2006). This approach is particularly applicable where regional floras and faunas are well known and individual species can hence be assigned to particular habitat types based on additional information on the species´ autecology as provided in distribution atlases (e.g. Baur et al. 2006, Kudrna et al. 2015), by expert knowledge or monographs (SBN 1987, Ebert and Rennwald 1993, Bühler-Cortesi 2009, Zuna-Kratky et al. 2009).

In this paper, we apply this approach to evaluate whether potential ranges derived from climate-driven projections are altered when also considering the availability of suitable habitat types. Our study has been conducted for 58 species stemming from three taxonomic groups (grasshoppers, butterflies, vascular plants) in a central European study region covering (parts of) five countries under three different climatic scenarios. We thereby particularly address the following hypotheses: 1) Geographically varied availability of appropriate habitat types can alter purely climate-driven risk assessments for species significantly. 2) Habitat fragmentation may increase climate induced risk for species persistence in lowland regions whereas for alpine species this risk may be attenuated due to lower land use intensity.

Methods

Study area

The study area encompasses the countries of Austria, Switzerland, Liechtenstein, the Federal States of Bavaria and Baden-Wurttemberg (Germany) and South Tyrol (Italy), i.e. approximately 240,000 km². Climate is mostly temperate humid with mean annual temperatures of ~7.5-10.0°C and annual precipitation sums of 600-1300 mm in the lowlands, whereas in alpine regions, annual mean temperatures decrease to < 0°C and precipitation sums may reach > 2000 mm. A long history of human land use has transformed the natural vegetation cover of this landscape considerably (e.g. Ellenberg 2009). Today, the lowlands are dominated by arable land and intensively used grasslands, with often only small remnants of (semi-)natural vegetation types like deciduous forests, wetlands or dry grasslands. By contrast, in mountain regions natural or near-natural forests still cover considerable parts of the landscape (Kuttner et al. 2015). Above the treeline, natural alpine grasslands predominate, together with rock and scree vegetation.

Species distribution and habitat data

Across the entire study region we collected 16,328, 16,510 and 50,050 occurrence records for 19 butterfly, 18 grasshopper and 21 plant species, respectively (see Appendix Table A1). Species were selected such that they represent a variety of ecological profiles, e.g. various range sizes, habitat affiliations and nature conservation status. They were mainly sampled from habitats of cultural landscapes such as of all sorts of grasslands (dry to wet, low to high intensity usage, lowland to alpine), and some other non-forest vegetation types (e.g. mires, river alluvions), as well as from deciduous and coniferous forests. Moreover, we took care to only include species with ranges that are largely restricted to the study area, or to areas with similar climates, to avoid truncated response curves in SDMs. In particular, we did not consider southern European species with northern range margins in the study area. Different spatial resolution in occurrence data of different origin needed to be harmonized to a combined dataset (see Appendix A1 for details). Information regarding habitat affiliation of the species was extracted from distribution databases and atlases, from a literature review and by expert knowledge. For vascular plant species, we used the information provided in the

Austrian Vegetation Database (Willner et al. 2012), for grasshoppers, we used information on habitat affiliation in Baur et al. (2006), Zuna-Kratky et al. (2009) and supplemented it by information from the Austrian Orthoptera Database (Zuna-Kratky et al. unpubl.). In case of butterflies, we used information provided in SBN (1987), Ebert and Rennwald (1993), Settele et al. (2000), Huemer (2004), Bühler-Cortesi (2009), Stettmer et al. (2011), and Bräu et al. (2013). This information on habitat affiliation combined with a recently published fine-scaled habitat distribution map of the area (Kuttner et al. 2015) – individual habitats are listed in Appendix Table A2 – was used to generate a binary map of the distribution of suitable habitat types for each species (called habitat map henceforth). Using the same data sources, species were moreover categorized according to their altitudinal centre of distribution into alpine, i.e. species mainly occurring above the treeline, and lowland species (see Appendix Table A2).

<u>*Climate data*</u>

Current climatic conditions

Maps of current climatic conditions were taken from WorldClim climate grids available online (www.worldclim.org). The WorldClim database provides monthly climate averages for the period of 1950-2000 for precipitation and temperature (minimum, average, maximum) (Hijmans et al. 2005). We scaled precipitation and temperature data down to 100 m horizontal resolution by applying a statistical downscaling procedure (Zimmermann et al. 2009, Tabor and Williams 2010; see Appendix A2 for further details). Subsequently, we used these spatially refined temperature and precipitation grids to derive maps of six bioclimatic variables. To reduce collinearity among these variables we only selected those that showed some independent variation across the study region (Pearson $r < |0.75|$, cf. Dormann et al. 2013): the maximum temperature of the warmest month (bio5), the minimum temperature of the coldest month (bio6), the temperature annual range (bio7), as well as the precipitation seasonality (bio15), the precipitation sum of the wettest quarter (bio16) and the precipitation sum of the driest quarter (bio17).

Future climatic conditions

Projections of monthly temperature and precipitation series until the end of the 21st century were taken from simulations of the regional climate downscaling experiment ENSEMBLE (http://ensembles-eu.metoffice.com/papers.html), which provides regional circulation models for Europe for the IPCC4 SRES scenario family (IPCC 2007). In detail, we applied: (i) The Hadley Centre Regional Climate Model (HadRM3.0) model runs (Collins et al. 2006), which are based on the Hadley Centre Coupled Model (hadcm3) general circulation model (GCM) for the A1B scenario with an original resolution of 25km; (ii) The climate limited-area modelling community (CLM) model runs (Hollweg et al. 2008), based on the ECHAM5 GCM for the A1B scenario that have been generated by the Max Planck Institute at a resolution of ca. 35km; and (iii) The Rossby Centre regional atmospheric climate model (RCA3) model runs (Kjellström et al. 2005), estimating from the Community Climate System Model (CCSM3) GCM for the B2 scenario and generated by the Swedish Meteorological and Hydrological Institute at a resolution of 50km. For the sake of simplicity, the presented climate forecast scenarios are henceforth called ´ccsm3/B2´, ´echam5/A1B´ and ´hadcm3/A1B´. Downscaling and derivation of bioclimatic variables was conducted similarly as for the current climatic dataset (see also Appendix A2).

SDM parameterization

SDMs were calibrated by linking species distribution data with the current climate conditions (named ´base´ from here on) at the central 100 × 100 m raster cell of each angular minute field across the study region. Based on these parameterized models, we subsequently generated ensemble projections of potential species distribution under current climate (mean of period 1950 – 1999) and under climatic conditions corresponding to the aforementioned climate forecast scenarios for the period 2050 – 2090. Species distribution modelling was conducted within the *biomod2* modelling framework (Thuiller et al. 2009), run under R 3.0.2 (*R* Development Core Team 2013). For modelling purposes we selected the default set of parametric and non-parametric regression techniques and machine-learning algorithms in the ensemble modelling and forecast routines (generalized linear models, GLM; generalized additive models, GAM; boosted Regression trees, GBM; artificial neural networks, ANN; random forests, RF; multivariate adaptive regression splines, MARS; maximum entropy, MAXENT and flexible discriminant analysis, FDA). To evaluate model quality for each species and modelling technique, we conducted data partitioning by randomly splitting it into two sub-sets, one for calibrating the models (80%) and one for evaluating them (remaining 20%) using the True Skill Statistic score (TSS, Allouche et al. 2006). Further, we applied a threefold cross validation of the input data. We gave equal weights to presence and absence records and determined the lower TSS threshold for using a particular model in the final ensemble projections at a value of 0.5. These ensemble projections were defined as mean consensus models where contributions of selected single models to the projected occurrence probability were applied according to their respective TSS scores.

Analyses

Probability-scaled ensemble forecasts were translated into binary projections (suitable vs. unsuitable) using the threshold that maximizes the TSS score (Liu et al. 2005). These maps (further referred to as climate-only projections) were then overlaid with the corresponding habitat maps in ArcGIS 10.1 (ESRI 2011) to identify all cells that are both climatically suitable to a species and belonging to a suitable habitat type (referred to as habitat-filtered projections). Current and potential future range sizes were defined as the number of cells suitable to the species in either the climate-only or the habitat filtered projections and were computed separately for each species and each climate scenario. Two ratios were derived from range sizes to be used as responses in linear mixed-effects models (LMMs): i) Temporal changes in range size were computed as the range size under each of the three climate forecast scenarios (ccsm3/B2, echam5/A1B, hadcm3/A1B) divided by the range size under current climatic conditions (base), separately for climate-only and habitat-filtered projections. We regressed the temporal change in range sizes against the type of projection (climate-only vs. habitat-filtered), Altitudinal Centre of Distribution (ACD; alpine/lowland), and their interaction. To test if additionally accounting for land use alters purely climate-based risk assessments differently for lowland and alpine species; ii) Habitat-induced effects in range size were defined as the range size of a species derived from habitat-filtered projections divided by those derived from climate-only projections and regressed against climate scenario, ACD, and their interaction. We used LMMs instead of (simple) linear regressions to account for potential clusters of data derived from the same species (both LMMs) and the same climate forecast scenario (only the second LMM) by including a random effect intercept term for the variable(s). Coefficients were estimated by optimizing the Restricted Maximum Likelihood criterion. As the contribution of each data point to the degrees of freedom (d.f.) is still under discussion in LMMs we used a conservative approach and calculated d.f. for t-tests as number of observations - number of fixed effects - number of random effects + number of random terms.

All statistical analyses were performed in R 3.0.2 (*R* Development Core Team 2013) using the package *lme4* (Bates et al. 2011) to fit LMM-models and *ggplot2* (Wickham and Chang 2015), *coefplot* (Lander 2013) as well as *lattice* (Sarkar 2015) for illustration purposes.

Results

Climate-only projections

Temporal changes in range size indicate an average loss of suitable ranges under future climates for both lowland and even more pronounced for alpine species (Figs. 1a, 2b; one-sided Wilcoxon signed ranks for climate only projections all $p < 0.001$), under each climate scenario (Fig. 2a). However, there are considerable differences among the taxonomic groups and their altitudinal centre of distribution (ACD). While alpine plants may lose up to ~70% of their currently suitable climatic range under the more severe climatic scenarios (Fig. 1c), lowland butterflies may rather profit from a warmer climate with predicted climatic range size gains of up to ~50% (Figs. 1b, c). In general, alpine butterfly and plant species show a more pronounced decrease than the respective lowland species. In contrast, for grasshoppers an idiosyncratic pattern is predicted: in particular, alpine grasshoppers are projected to lose a considerable proportion of their climatically suitable area (~ 60%) under ccsm3/B2, but even to gain (10 – 20%) climatically suitable area under the more pronounced scenarios (Fig. 1c). Lowland grasshoppers, by contrast, are predicted to face an approximately even and rather small reduction of their average climatically suitable range size (~ 10%) under all climatic scenarios (Figs. 1b, 1c). Overall, these differences among the investigated taxonomic groups make the effect of current altitudinal distribution on predicted future range size change statistically insignificant (Fig. A1).

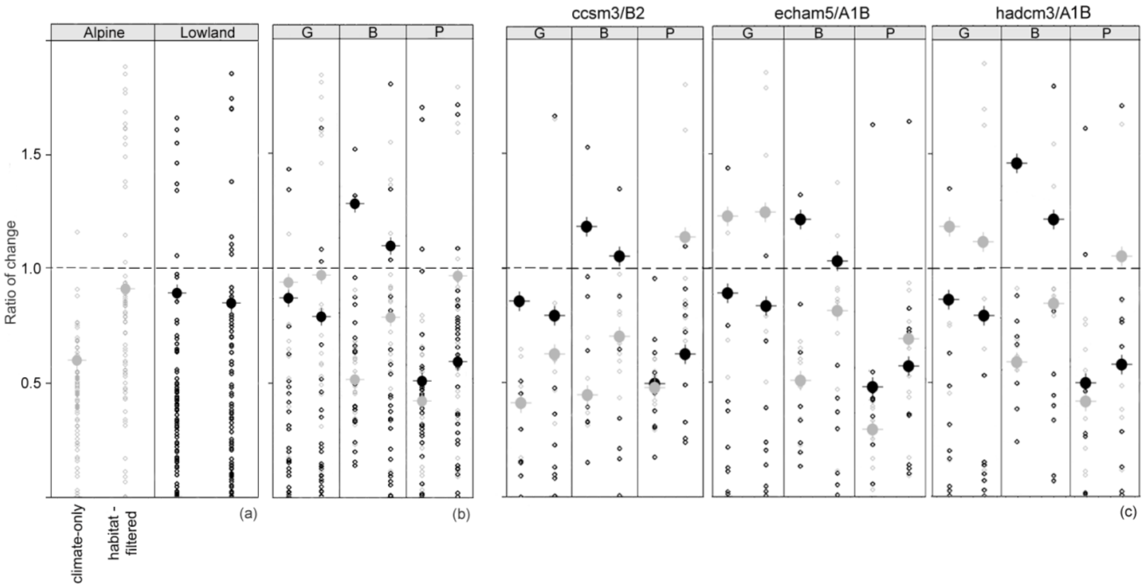

Fig. 1: Temporal changes in range size between the current and predicted future climate conditions for 2050-2090 based on climate-only (left column of each panel) and habitat-filtered projections (right columns). The panels illustrate projections grouped by (a) altitudinal centres of distribution (grey - alpine species; black – lowland species), (b) taxonomic groups (G – grasshoppers, B – butterflies, P – vascular plants), and (c) additionally separated for each climate forecast scenario. The dashed line highlights no projected change in range size.

Habitat-filtered projections

In general, predicted range sizes are much smaller (one-sided Wilcoxon signed ranks, $p < 0.001$) in habitat-filtered than in climate-only projections (Figs. 2a, A1). This difference is more pronounced under current climatic conditions (ratio ~ 1:5) than under the future climate scenarios (ratio ~ 1:3) (see also Fig. A2). However, temporal changes in range size are, on average, lower in habitat-filtered than in climate-only projections only for alpine species. Their predicted range sizes have been reduced to ca. 58% and 91% under climate-only, compared to habitat-filtered projections, respectively (Fig. 1a). Put it another way, for alpine species a warmer climate improves the match between the remaining climatically suitable areas and the distribution of appropriate habitat types: the habitat-induced effect on range size increases from ~30% under current climatic conditions, to 45 - 55% under future climates (Fig. 3a). By contrast, for lowland species, differences in the average temporal change in range size between climate-only (89%) and habitat-filtered projections (82%) are marginal, except for plants which follow the general pattern as revealed for alpine species (Fig. 1c).

The interaction between the altitudinal distribution of species and the effect of the habitat filter has been consistent across all climatic scenarios (Fig. 3b). It has been, however, not uniform across taxonomic groups but mainly driven by plants and, to a lesser extent, by butterfly species (Fig A3). By contrast, for alpine grasshopper species it has only been observed under the least pronounced climatic scenario (Fig. A3).

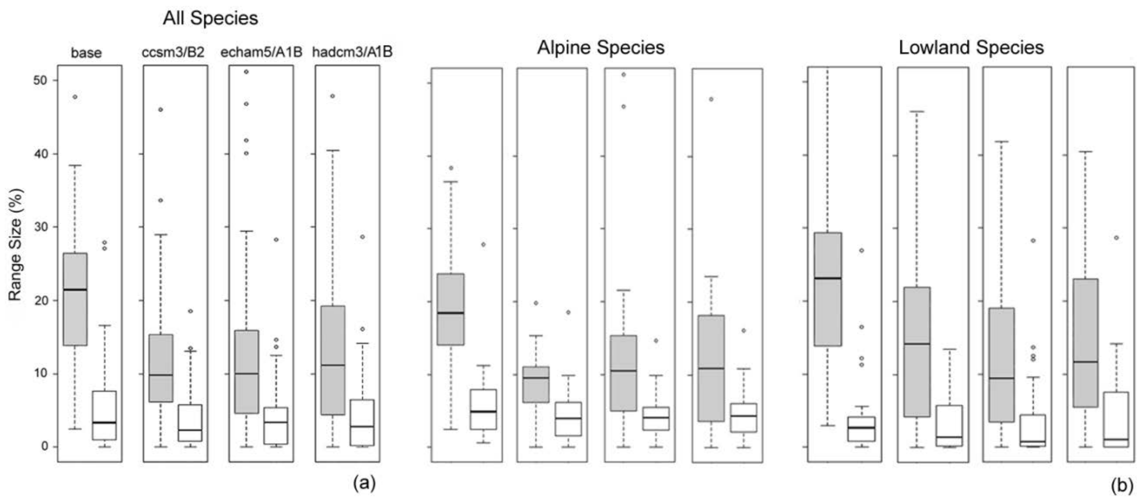

Fig. 2: Area predicted to be suitable to 58 study species from three taxonomic groups (butterflies, grasshoppers, vascular plants) with respect to climate (grey; climate-only projections) or with respect to climate and habitat affiliation (white; habitat-filtered projections) as a proportion of the overall study area. Species were (a) either pooled, or (b) separated by their altitudinal centre of distribution. Outlier values > 50% were omitted to enhance clarity of illustration.

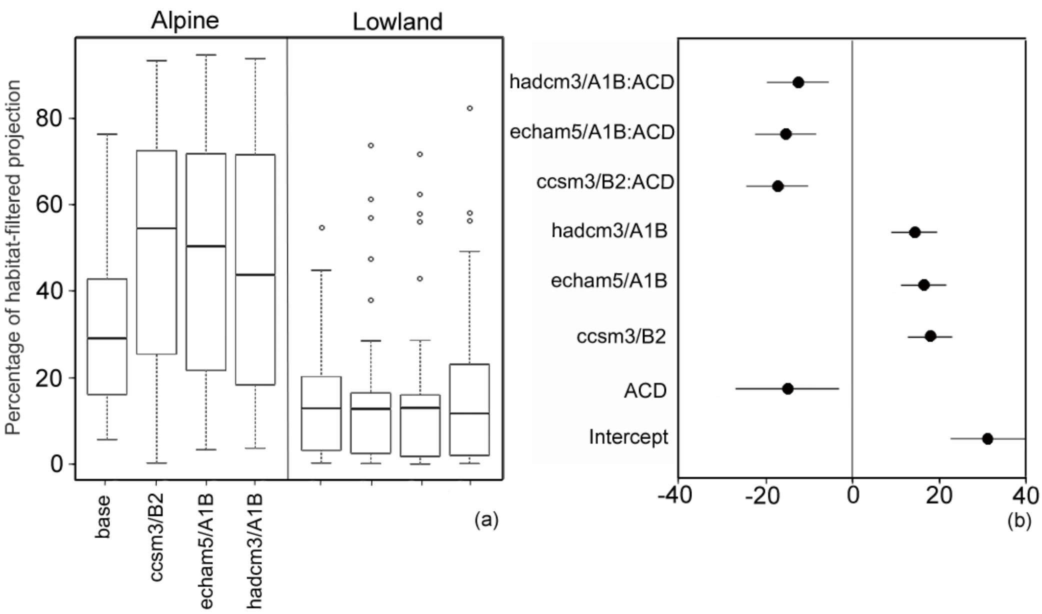

Fig. 3: Panel (a) illustrates habitat-induced effects in range size (i.e. range sizes derived from habitat-filtered projections as a proportion of those from climate-only projections) predicted under current climate (base) and three climate forecast scenarios for 28 alpine and 30 lowland species from three taxonomic groups (grasshoppers, butterflies, vascular plants). Panel (b) shows fixed-effect coefficients (lines indicating for the twofold standard deviation of the 95%-confidence intervals) of a Linear Mixed-effects Model relating these ranges to the species´ altitudinal centre of distribution (alpine versus lowland, ACD), the climate forecast scenarios (ccsm3/B2, echam5/A1B, hadcm3/A1B) and their interactions. (ACD: $p=0.015$, $t=-2.467$; ccsm3/B2 / echam5/A1B / hadcm3/A1B: $p < 0.0001$, $t=6.924$ / 6.344 / 5.553; ccsm3/B2:ACD / echam5/A1B:ACD / hadcm3/A1B:ACD: $p<0.001$, $t=-4.833$ / -4.290 / -3.522).

Discussion

As hypothesized, our results demonstrate that accounting for habitat suitability considerably alters SDM-based climate risk assessments for plant and insect species. However, the effect of updating climate-based projections by a habitat filter differs markedly for lowland and alpine species as well as among the investigated taxonomic groups. Although absolute range sizes are generally predicted to decrease, alpine species appear buffered against climate induced range losses by habitat availability to a certain extent, because a warmer climate increases the spatial match between climatically suitable ranges and the distribution of appropriate habitat types. Vice versa, in case of lowland species this mitigating effect was much weaker (for plants) or did not occur at all. Despite all this, lowland butterflies were projected to even expand their current distribution ranges in both cases, either when considering climate-only or habitat-filtered projections.

Uncertainties and stochastic variation within and across correlative species distribution models

Although we did not account for the factors of population dynamics or species interaction, the direction of species range changes that is triggered by environmental predictors and thereof predominantly by (bio)climatic variables can nevertheless be revealed by the use of SDMs (Araújo et al. 2011, Bucklin et al. 2015). Within the *biomod2* framework we used the mean ensemble modelling and forecasting approach in order to achieve most accurate and robust predictions on future distribution ranges of our target species (cf. Araújo and New 2007, Marmion et al. 2009). However, we have to acknowledge that correlative SDM outcomes always involve a number of uncertainties, either based on incompleteness of species distribution records, mismatches in scale of utilized data sources, or disregard of species-specific dispersal traits (Wiens et al. 2009) and are thus leading to predictions reflecting an approximation between fundamental and realized species niches (Beale and Lennon 2012). However, we tried to reduce model inherent uncertainties by carefully selecting only recent (> 1990) and reliable species distribution data and accounting for the suggestions already outlined by Araújo and Guisan (2006) during the modelling phase of this study.

Further, calculating mean species distributions from five consecutive decades (2050-2090) shares the decisive advantage to cover a broader array of variation within climate forecasts than merely relying to only one specific point in time. Although not only climatic envelopes but also soil properties such as preference to a certain substrate are often with-determining plant species´ distribution ranges (Dubuis et al. 2013) we did not consider this variable in order to keep model parametrization constant also for the investigated insect taxa over which soil acidity has no decisive influence.

Range size effects of climate change

Previous assessments of climate-induced risk to biodiversity have mostly suggested that range loss is increasing along an elevation gradient from colline through montane to alpine species (e.g. Engler et al. 2011). This pattern is strongly driven by the distribution of land area among elevational belts and is usually pronounced where mountains are shaped like pyramids as in case of the European Alps (Elsen and Tingley 2015). In our study, climate-only predictions for vascular plants and in particular for butterflies corroborate these earlier results. Surprisingly, the common patterns appear even reversed, however, in the case of grasshoppers, at least under the more severe climate scenarios (Fig. 1c). As we basically assigned emission scenarios that are representing a step from moderate up to a more pronounced rise of greenhouse gases (B2 vs. A1B) to three general circulation models (ccsm3 / echam5 / hadcm3), the resulting scenarios of climate change impact are thus graduated in terms of rising temperature. However, the bandwidth of simulated environmental vectors of precipitation and temperature varied considerably, both within and between the single GCMs. According to a hindcast simulation study that compared GCM outcomes to observational datasets, results showed that e.g. the ccsm3 model generally underestimated summer precipitation rates and in turn overestimated summer temperature, whereas echam5 tended to overestimate precipitation and hadcm3 appeared mostly balanced according precipitation but slightly underestimated temperature in the transitional seasons of spring and autumn (Bozkurt et al. 2011). We hypothesize that the inter-model variabilities somewhat co-influenced SDM outcomes as well, which rather applies for alpine grasshopper species that seemingly responded to underestimated precipitation patterns within the ccsm3 model. Conversely, precipitation sums that are predicted to generally increase within the echam5 and hadcm3 models across the Eastern Alpine region in the forthcoming decades, may thus contribute to the potential increase of climatically suitable space as noticed for this taxonomic group. On the other hand, the presumed effects of intra– and inter-GCM variability were not apparent in case of the lowland species group.

Interacting effects of climate change and habitat patterns on range size

Our results clearly underpin that current land use in Central Europe represents a highly selective filter that allows the studied species to only occupy roughly 20% of their (macro)climatically suitable ranges, on average, under current climatic conditions. As expected, lowland and high mountain regions differ widely in this respect, with percentages of ~ 10% and ~ 30%, respectively. Many (semi-)natural lowland habitats have become severely degraded, especially after World War II, by an array of measures like intensified application of fertilizers, herbicides and insecticides, multiple mowing of grasslands, land consolidation or amelioration techniques, or abandonment and afforestation of economically marginal sites (Poschlod et al. 2005, Graf et al. 2014). On the other hand, extensively managed habitat types characterized by low or moderate human usage, such as moderately fertilized grasslands that are mown once or twice a year, and/or by non-standard site conditions, such as dry and wet grasslands or other wetland ecosystems, have become increasingly rare throughout the study region (Jentsch and Beyschlag 2003, Henle et al. 2008, Čop et al. 2009, Janišová et al. 2011). Our selection of study species contains many taxa that are affiliated to such low-impact land use types as they represent a characteristic part of the non-forest central European flora and fauna that has been shaped over centuries (Tscharntke et al. 2005, van Swaay et al. 2006, Marini et al. 2008, Ellenberg 2009). It is hence not surprising that the current land use pattern imposes strong restrictions on the geographical distribution of many of them even where climatic conditions would be highly suitable. At higher elevations, by contrast, land cover becomes increasingly dominated by (semi-)natural and natural vegetation types which finally predominate above the alpine treeline. While some of these vegetation types, and hence the species affiliated to them, are naturally rare in the study area (e.g. snowbeds), others like forests (in the montane and subalpine belts) and grasslands (in the alpine belt), cover most of the terrain and the match between climatically suitable areas and appropriate habitat types is hence predicted to strongly increase for species of these habitats until the end of the century.

Although under a warming climate the majority of our study species are predicted to face decline of their climatically suitable ranges in absolute terms, we found that within the remaining areas, those parts that are also suitable in view of habitat lead to a slightly further decrease for lowland species ranges in general. Equally the reverse effect has been observed for the group of alpine species, where the higher abundance of suitable habitats mitigates the detrimental effect of range decline caused by climate change, so that overall loss rates in species´ ranges may be less severe than expected from climate-only projections under almost all scenarios. This general finding is in line with the results presented by Thuiller et al. (2014) who state that montane species are projected to face more severe decline in suitable areas by environmental change than alpine species till 2080. As already discussed, climate warming generally shifts the species' potential climatic ranges upward in elevation. Thus, new habitats will become potentially reachable by alpine species, provided that they are capable to keep track with the changing conditions (Thuiller at al. 2014). Oppositely, the decreasing share of appropriate habitat types in case of lowland species, of which many are adapted to open habitats (Table A2), mainly results from this upward shift into montane elevations where forests successively replace grasslands and arable land as the predominant vegetation type. Species that occur in extensively used grasslands and other low-intensity non-forest land use types might hence be driven from climatic ranges where land use intensity is too high towards climatic ranges where former agricultural land of marginal use has been afforested, which in turn mainly has happened in the montane altitudinal zone.

Many of our investigated alpine species have climatic requirements that would allow them to thrive at lower elevations. In fact, they are mainly excluded from such lower elevations by biotic interactions, in particular by competition (e.g. Alexander et al. 2015), but can occasionally be found there if competitive intensity is reduced e.g. by natural or human disturbance like in avalanche paths or on subalpine summer pastures cleared from forests. As a consequence, their current climatically suitable range actually includes at least parts of the subalpine belt where they are relatively rare, however, because the predominant forest cover constricts their distribution. Under a warming climate these ranges will shift upwards, mainly above the current treeline. As a consequence, the total size of the climatically suitable range decreases but the match with appropriate habitat types increases.

While these results suggest a certain buffer effect of habitat patterns on climatic threats to alpine species there is, however, an important caveat: our models assume that the current distribution of land use and vegetation types will remain constant over time. This assumption is unlikely to hold, at least in the long run. First, the future socio-economic development will alter economic interests in particular land use types (e.g. Spangenberg et al. 2012); and second, climate warming itself will change both the ecological suitability of landscapes and regions towards certain types of land use and the distribution of natural vegetation types. In particular, an upward shift of the alpine treeline under a warmer climate might reduce the detected buffer effect of land use for alpine species. Even if this upward shift will probably take a long time (Dullinger et al. 2004, Harsch et al. 2009, Rabasa et al. 2013) it will eventually make climatic threats to the distribution of alpine species even more severe than predicted from SDMs (Dirnböck et al. 2011). Under this perspective, the maintenance, or even the intensification of traditional high-mountain summer pasturing appears as an important land-use strategy to mitigate the negative long-term effects of climate warming on alpine species (cf. Dirnböck et al. 2003, Dullinger et al. 2003). Moreover, maintenance or re-vitalization of the currently declining traditional land use practises in montane areas, particular the usage of pastures and meadows (Chemini and Rizzoli 2003), may also help species from current low-intensity land use types of the lowlands to find appropriate habitats when their climatic ranges are shifted upward in elevation. Taken together, a re-adjustment of land use intensity gradients appears as a sensible strategy to help a considerable part of the species of Central European landscapes to cope with forthcoming climate warming to a certain extent: while decreasing land use intensity, combined with habitat restoration (Török et al. 2011, Prach et al. 2013, Joyce 2014) will reduce the combined pressure from climate and land use in lowland areas, (re-)establishing current low land use levels at higher elevations may conserve the necessary areas of retreat that species can colonize when climate warms. Such a mitigating strategy would, however, require that agricultural policies try to reverse current trends towards increasing disparities among regions of high rent and high intensity and those of low rent where rural activities decline or vanish altogether.

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Supplementary Figures

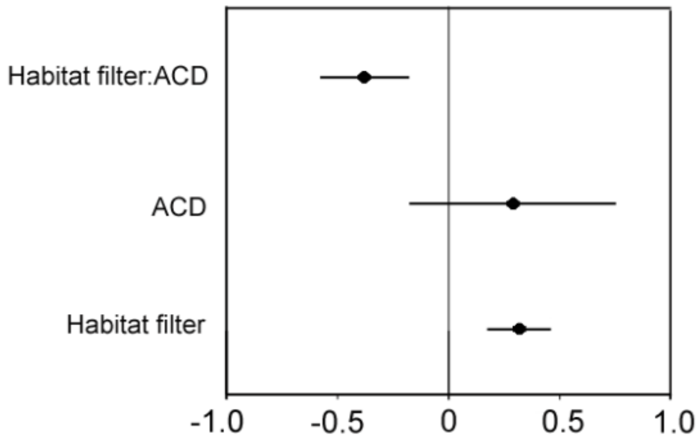

Fig. A1: Fixed-effect coefficients (lines indicating the twofold standard deviation of the 95%-confidence intervals) of a Linear Mixed-effects Model comparing the change of suitable range size under future climates from climate-only and habitat-filtered projections (Habitat filter) and for alpine and lowland species (ACD). (p-Habitat filter: p<0.0001, t=-4.464; p-ACD: p=0.214, t=1.243; Habitat filter:ACD: p<0.0002, t=-3.755).

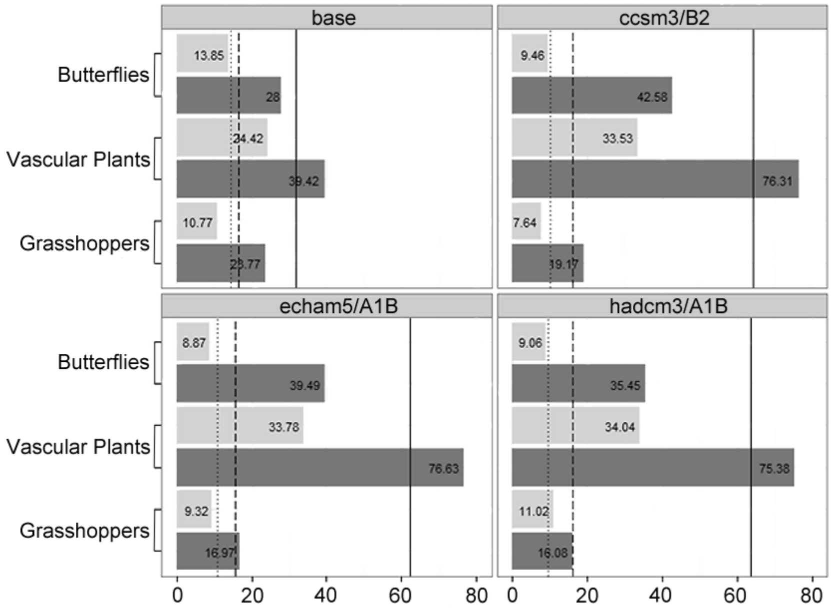

Figure A2: Habitat-induced effects on range size averaged for alpine (dark grey) and lowland species (light grey). Values refer to projections under current climate (base) and three climate forecast scenarios for the period 2050-90 (ccsm3/B2; echam5/A1B; hadcm3/A1B). Vertical lines indicate medians of taxonomic groups (solid: vascular plants; dashed: butterflies; dot-dashed: grasshoppers).

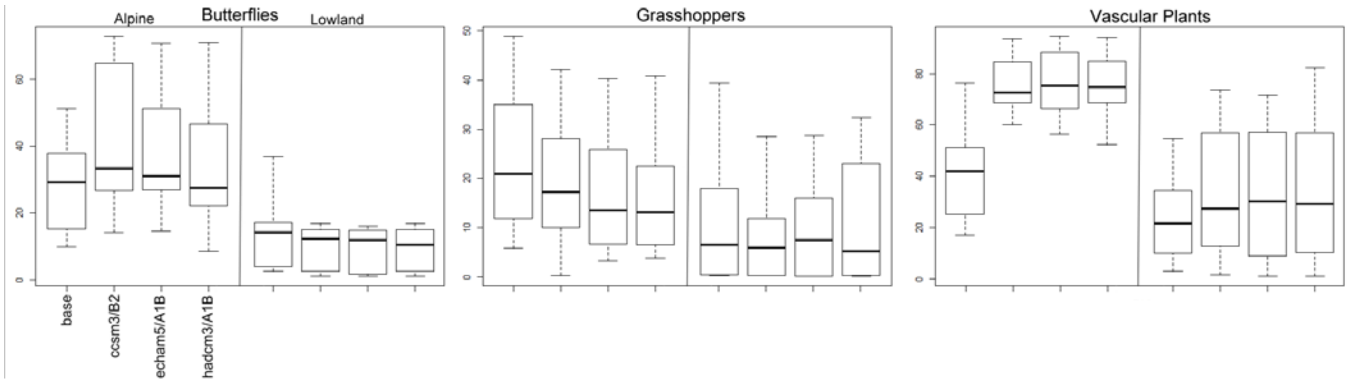

Figure A3: Habitat-induced effects on range size under current climate (base) and three climate forecast scenarios, separately plotted for investigated taxonomic groups of butterflies, grasshoppers and plants. Species were classified according their altitudinal centre of distribution as alpine or lowland.

Supplementary information (Appendix)

Appendix A1

Harmonization of Species Record Data

As we obtained species distribution data from various federal institutions, research groups and databases, spatial reference systems partly differed and resolution of the data was ranging from precise point data up to grid mapping specifications on angular minute or quadrant (i.e. 3 x 5 angular minutes) level. We consequently chose the minute field grid for data harmonization purposes: Fine-scaled point data was assigned to the centroid of the underlying minute field. We applied the same procedure for the minute-field data while in case of the coarser quadrant data we randomly selected one minute field within the target quadrant for the assignment. In case of overlapping data provision we always selected the finer-scaled and more recent data source. We set a threshold year for the occurrence data applied within this study by 1990; older records have not been considered. Further details on the accessed species distribution data, summarizing the number occurrence points per country and taxon is given in Table A1. Within every quadrant where a target species was not recorded we randomly set one minute-field as ´absent´ and assigned all remaining fields as ´NULL´ (i.e. NoData). Further, to avoid double counting we cleared the database and only kept the most recent entries. This procedure was iteratively conducted for all individual target species datasets to establish a standardized input table, consisting of 105,428 rows that regularly covered the entire study region of approx. 240,000 km².

Appendix A2

Statistical downscaling of current and future climate data

We downscaled the climate projections to a horizontal resolution of 100 m by using a statistical downscaling procedure that operates on the basis of spatially interpolated differences (i. e. the delta) between predicted historic and future climate conditions derived from low resolution data sets which are added to the observed historic climate data with higher resolution (WorldClim; http://www.worldclim.org/, Hijmans et al. 2005). The delta method had already been applied in studies of climate change effects (Zimmermann et al. 2009; Ramirez-Villegas & Jarvis 2010; Tabor & Williams 2010; Dullinger et al. 2012).

In detail, downscaling of the climate data was achieved by: (i) Calculation of long year mean values from hindcast projections of the same climate model, e.g. 1950-2000 corresponding to the reference period of WorldClim; (ii) Calculation of differences between future climate projections and the reference period (deltas); (iii) Spatial interpolation of the anomalies to the high resolution surface of the baseline observed climate date using thin plate spline methods;

and (iv) the interpolated anomalies were added to the high resolution observed climate data. Consequently, we were able to create monthly temperature and precipitation series for the time period from 2010 to 2090. In order to cope with particularly long computation times of the subsequent SDMs, we calculated averages of the climate parameters at 9-year mean intervals (2016-2024… 2086-2094). Based on these means, six bioclimatic variables following the WorldClim definition for bio5, bio6, bio7, bio15, bio16 and bio17 were computed.

	Species Name	AT[1,2]	BW[3]	BAV[4]	CH[5]	ST[6]	Total (species)
Grasshoppers	*Aeropedellus variegatus*	2	-	-	18	19	39
	Arcyptera fusca	106	19	45	172	77	419
	Bohemanella frigida	56	-	-	133	120	309
	Bryodemella tuberculatum	19	-	264	-	-	283
	Chorthippus pullus	50	-	191	12	3	256
	Conocephalus dorsalis	171	124	741	27	20	1083
	Isophya brevicauda	106	-	-	-	-	106
	Metrioptera saussuriana	35	-	-	235	-	270
	Miramella alpina	571	603	410	502	64	2150
	Nemobius sylvestris	450	1270	3216	679	157	5772
	Oedipoda germanica	23	370	220	188	33	834
	Pholidoptera fallax	210	-	-	21	-	231
	Polysarcus denticauda	174	264	207	93	-	738
	Stauroderus scalaris	190	794	1	502	266	1753
	Stenobothrus nigromaculatus	136	147	248	32	8	571
	Stenobothrus rubicundulus	89	-	-	51	106	246
	Stenobothrus stigmaticus	280	472	551	5	-	1308
	Tetrix tuerki	27	-	88	21	6	142
	Subtotal (Taxon/country)	2695	4063	6182	2691	879	16510

Data Sources

Datenbank AG Heuschrecken Österreichs, c/o Thomas Zuna-Kratky, Vienna, Austria [1]

Geffährdungsanalyse der Heuschrecken Deutschlands: Verbreitungsatlas, Gefährdungseinstufung und Schutzkonzepte, Germany [2]

Distribution database of Orthoptera in Germany, c/o Peter Detzel, Stephen Maas, Aloysius Staudt, Germany [3]

Artenschutzkartierung Bayern - Bayer. Landesamt für Umwelt, Bayern [4]

Centre Suisse de Cartographie de la Faune, Neuchâtel, Switzerland [5]

Distribution database of Orthoptera in South Tyrol, Naturmuseum Südtirol, Italy [6]

	Species Name	AT[1,2]	BW[3]	BAV[4,5,6]	CH[7]	ST[8]	Total
Vascular Plants	*Alchemilla anisiaca*	131	-	-	-	-	131
	Aster bellidiastrum	684	85	638	1330	296	3033
	Bistorta officinalis	412	822	1227	1074	99	3634
	Cerastium uniflorum	296	-	16	158	263	733
	Dianthus alpinus	275	-	-	-	-	275
	Drosera rotundifolia	436	140	1146	188	134	2044
	Gentiana clusii	280	-	798	437	120	1635
	Gentianella bohemica	36	-	146	-	-	182
	Gymnadenia conopsea	941	971	2076	5804	1487	11279
	Jasione montana	124	137	660	110	34	1065
	Leontopodium alpinum	130	-	55	286	238	709
	Nardus stricta	1096	283	1494	1917	404	5194
	Phyteuma spicatum	645	1501	1650	1699	12	5507
	Polygala chamaebuxus	552	18	817	1458	257	3102
	Primula auricula	252	-	297	378	24	951
	Rhinanthus glacialis	620	235	224	418	243	1740
	Saxifraga aizoides	608	-	131	548	307	1594
	Selinum carvifolia	213	187	997	83	19	1499
	Sibbaldia procumbens	305	-	29	235	267	836
	Trollius europaeus	707	300	695	1790	374	3866
	Veronica fruticans	308	6	52	413	262	1041
	Subtotal (Taxon/country)	9051	4685	13148	18326	4840	50050

Database of Austrian Endemic Species, Environment Agency, Austria [1]

Floristic Mapping Project of Austria, University Vienna, Austria [2]

Staatliches Museum für Naturkunde Stuttgart, c/o Arno Wörz, Germany [3]

Artenschutzkartierung Bayern - Bayerisches Landesamt für Umwelt, Germany [4]

Floristic Mapping Project of Bavaria, Germany [5]

Bayerisches Landesamt für Umwelt, Augsburg, Germany [6]

Info Flora, c/o Botanischer Garten, Altenbergrain 21, 3013 Bern, Switzerland [7]

Naturmuseum Südtirol, c/o Thomas Wilhalm, Italy [8]

	Species Name	AT[1-5]	BW[6]	BAV[7]	CH[8]	ST[5]	Total
Butterflies	*Boloria eunomia*	32	94	1484	-	4	1614
	Boloria thore	32	1	297	105	7	442
	Boloria titania	81	38	1269	521	1	1910
	Brenthis daphne	84	197		279	10	570
	Colias palaeno	31	54	1628	279	20	2012
	Colias phicomone	68	-	462	428	77	1035
	Erebia nivalis	72	-	-	8	5	85
	Euphydryas maturna	870	4	122	-	-	996
	Lopinga achine	298	174	547	95	1	1115
	Lycaena helle	53	8	281	76	-	418
	Maculinea teleius	745	165	979	81	-	1970
	Melitaea asteria	41	-	-	21	5	67
	Oeneis glacialis	21	-	77	191	18	307
	Parnassius apollo	411	27	515	479	122	1554
	Parnassius mnemosyne	538	33	166	148	-	885
	Parnassius phoebus	34	-	6	219	57	316

Article 17 report of the EU Habitats Directive [1]

Database Heinz Habeler, Graz, Austria [2]

Database Josef Pennerstorfer & Helmut Höttinger, Austria [3]

Database Endemic species of Austria, Environment Agency Austria [4]

Database Tiroler Landesmuseen Betriebsges. mbH, Innsbruck, Austria [5]

Staatliches Museum für Naturkunde Karlsruhe, Germany [6]

Bayerisches Landesamt für Umwelt, Augsburg, Germany [7]

Centre Suisse de Cartographie de la Faune, Neuchâtel, Switzerland [8]

	Plebeius optilete	42	28	263	176	19	528
	Pontia callidice	17	-	22	185	21	245
	Pyrgus armoricanus	15	13	127	103	1	259
	Subtotal (Taxon/country)	3485	836	8245	3394	368	16328
	Total (country)	15231	9584	27575	24411	6087	82888

Appendix Table A1: Complete list of the species distribution data used in this study. (Sub)total sums are separately given for each taxon and country. We included only records collected 1990 or later in the analyses. Abbreviations: AT = Austria, BAV=Bavaria, BW= Baden-Wurttemberg, CH=Switzerland, ST=South Tyrol.

Species Name	Taxon	Trait	ALLUV	ALPGR	BLFO	CFO	DRY	EXTGR	ROCK	SHRUB	WET
Aeropedellus variegatus	G	a		X							
Alchemilla anisiaca	P	a		X					X	X	
Arcyptera fusca	G	a					X	X			
Aster bellidiastrum	P	a	X	X					X	X	
Bistorta officinalis	P	n						X			X
Bohemanella frigida	G	a		X					X		
Boloria eunomia	B	n									X
Boloria thore	B	n			X	X					
Boloria titania	B	a		X							X
Brenthis daphne	B	n			X						
Bryodemella tuberculatum	G	n	X								
Cerastium uniflorum	P	a		X					X		
Chorthippus pullus	G	n	X								
Colias palaeno	B	a								X	X
Colias phicomone	B	a		X							
Conocephalus dorsalis	G	n									X
Dianthus alpinus	P	a		X					X	X	
Drosera rotundifolia	P	n									X
Erebia nivalis	B	a		X					X		
Euphydryas maturna	B	n			X						
Gentiana clusii	P	a		X					X	X	
Gentianella bohemica	P	n						X			
Gymnadenia conopsea	P	n		X			X	X	X	X	X
Isophya brevicauda	G	n					X	X			
Jasione montana	P	n					X	X			
Leontopodium alpinum	P	a		X					X	X	
Lopinga achine	B	n			X						
Lycaena helle	B	n									X
Maculinea teleius	B	n									X
Melitaea asteria	B	a		X							
Metrioptera saussuriana	G	a		X							
Miramella alpina	G	a		X				X			
Nardus stricta	P	n		X				X	X	X	X
Nemobius sylvestris	G	n			X	X				X	
Oedipoda germanica	G	a					X		X		
Oeneis glacialis	B	a		X					X		
Parnassius apollo	B	a					X		X		
Parnassius mnemosyne	B	n						X			
Parnassius phoebus	B	a		X						X	X
Pholidoptera fallax	G	n					X	X			
Phyteuma spicatum	P	n			X	X					
Plebeius optilete	B	n								X	X
Polygala chamaebuxus	P	n	X			X	X		X	X	
Polysarcus denticauda	G	n					X	X			
Pontia callidice	B	a		X					X		
Primula auricula	P	a		X					X		
Pyrgus armoricanus	B	n					X	X			
Rhinanthus glacialis	P	a	X	X		X		X	X	X	
Saxifraga aizoides	P	a	X	X					X	X	X
Selinum carvifolia	P	n						X			X
Sibbaldia procumbens	P	a		X					X		
Stauroderus scalaris	G	a					X	X			
Stenobothrus nigromaculatus	G	n					X				
Stenobothrus rubicundulus	G	a		X			X				
Stenobothrus stigmaticus	G	n					X	X			
Tetrix tuerki	G	n	X								
Trollius europaeus	P	n		X				X		X	X
Veronica fruticans	P	a		X					X	X	

Appendix Table A2: Complete Species list. Taxon abbreviations (B=Butterflies; G=Grasshoppers; P=Plants). Trait abbreviations (a=alpine; l=lowland). Habitat *abbreviations (ALLUV=Alluvions; ALPGR=Alpine Grasslands; BLFO=Broad-leaved Forest; CFO=Coniferous Forest; DRY=Dry Grasslands; EXTGR=Extensive Grasslands; ROCK=Rocklands /Scree; SHRUB=Shrublands /Dwarf Tree Stands; WET=Wet Grasslands)*

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Nationality	Austria
Date of Birth	28.09.1982
Gender	Male

Education	
11 / 15	Submission of my doctoral thesis for external evaluation
06 / 15	Beginning of the course of forest-related education
03 / 09	Start of my doctoral thesis "Biodiversity and Landscapes – where is the missing link?"
03 / 09	Graduation with honors from diploma studies of Ecology Title of my Master Thesis: „Die Abhängigkeit der lokalen pflanzlichen Biodiversität von den großen Landnutzungssystemen in der Region Mostviertel - Eisenwurzen"
10 / 01 – 03 / 09	Diploma Studies of Biology with focus on Ecology at the University of Vienna
10 / 00 – 10 / 01	Civilian Service as paramedic (Samariterbund Pöchlarn)
05 / 00	Graduation from highschool (BRG Waidhofen an der Ybbs)

Working Experience	
01 /15 – 11 / 15	Employment at the Department of Botany & Biodiversity Research at the University of Vienna – Division of Conservation Biology, Vegetation- and Landscape Ecology
01 / 13 – 12 / 14	Employment at the Vienna Institute For Nature Conservation & Analyses (VINCA)
01 / 10 – 06 / 13	Employment at the Department of Botany & Biodiversity Research at the University of Vienna – Division of Conservation Biology, Vegetation- and Landscape Ecology
11 / 09 – 12 / 09	Feasibility study for the implementation of Important Plant Areas in Austria in the frame of the GSPC project
08 / 09 – 10 / 09	Establishment of a Metadata-catalogue and geodata management for the *Central Europe project* "TransEcoNet"
03 / 09 – 07 / 09	Project assistance, photo editor and authorship in the frame of the exhibition "Grünes Band Europas – Grenze, Wildnis, Zukunft"
09 / 08	Biotope and vegetation mapping in the frame of the Fugnitz river monitoring project (at the National Park Thayatal)

Teaching Experience at the University of Vienna	
10 / 09 – 02 / 10 *10 / 08 – 02 / 09*	Tutor in the frame of the course "UE: Anwendung geographischer Informationssysteme, Geostatistik und Raumanalyse in den Biowissenschaften"
07 / 09	Tutor in the frame of the course "UE: Kenntnis mitteleuropäischer Lebensräume"
03 /09 – 07 / 09	Tutor in the frame of the course "UE: Vegetations- und Landschaftsökologie- Monitoring in Großschutzgebieten"

My scope of activities covered: active participation during project application; field work; data analyses; reporting; communication with stakeholders (e.g. in workshops); conference participation; scientific dissemination.	
Working experience in scientific projects (overview)	
AGRALE	Comparative analysis on change of landscape structure caused by agricultural abandonment and its impact on local biodiversity patterns throughout four Balkan countries. Geodata preparation; coordination.
BIOSERV	Modelling, calculation,and illustration of ecosystem services in the project region Neusiedler See. Scenario develpoment of potential ecosystem service provision with respect to reorientation of the biosphere reserve Neusiedler See.
CCILA	Establishment of a random stratified sampling design and field survey (vegetation and biotope mapping) in the project region Mostviertel. in der Region Mostviertel; generation of sets of indicators for predictive economic farmland modelling; map creation.
HABITCHANGE	Classification and quantification of Lake Neusiedl reed beds in order to detect changes in the open lake area for the time frame of 1985 to 2008.
TRANSECONET	Spatial analyses on green infrastructure and assessment on landscape structure-based functionality in the project region Neusiedler See. Comparison of landscpape structural patterns along the green belt of Europe. Comparative study on historical ecological network structures.
SPEC-ADAPT	Establishment of a high-resolution habitat map for selected countries (AT, CH, Bavaria, Baden-Wurttemberg; South Tyrol). Supra-national network analysis on the distribution of protected areas. Scenario-building for optimized conservation planning. Climate data processing. Modelling of future species distribution patterns (till 2100)

Participation at conferences, workshops and other courses	
04 / 15	16. Österreichischen Klimatag, Wien (Presentation)
06 / 13	5. Symposium zur Forschung in Schutzgebieten, Mittersill (Presentation)
10 / 12	Jahreskonferenz der deutschen Gesellschaft für Landschaftökologie “Klimawandel: Was tun!“, Eberswalde (DE) (Presentation)
03 / 12	Final Symposium “Transnational Ecological Networks in Central Europe – History, Status Quo and Potentials“, Dresden (DE) (Presentation)
11 / 11	Expert Workshop „Sevillakonforme Neuzonierungsoptionen des Biosphärenparks Neusiedler See anhand potentieller Ökosystemdienstleistungsszenarien“ (Co-organization, participation)
11 / 11	Symposiun “Landschaftsleistungen und ökologische Netzwerke”, Illmitz
10 / 11	Jahreskonferenz der deutschen Gesellschaft für Landschaftökologie “MMM – Modelle, Monitoring und andere quantitative Methoden in der Landschaftsökologie“, Berlin (DE) (Presentation)
11 / 10	ALTER-Net conference “Ecosystem Services and Biodiversity – What is the link between the two?“, Vienna (Poster presentation)
09 / 10	European Conference on Landscape Ecology (IALE Europe) “Landscape structures, functions and management: response to global ecological change”, Brünn (CZ) (Presentation)
04 / 10	“Workshop on Landscape History“, Sopron (HU) (Participation)
02 / 10	2. Jahrestagung der Plattform Biodiversität Forschung Austria (BDFA)”, Gumpenstein (Co-organization, participation)
11 / 09	Extended workshop „GIS & Remote Sensing Applications for Environmental Sciences“, Coimbra (PRT) (Participation)
07 / 09	European Conference on Landscape Ecology (IALE Europe) “European Landscapes in Transformation: Challenges for Landscape Ecology and Management”, Salzburg (Participation)

Selected publications in scientific journals
Kuttner, M., Hainz-Renetzeder, C., Hermann, A., Wrbka, T. Borders without barriers – Structural functionality and green infrastructure in the Austrian - Hungarian transboundary border region of Lake Neusiedl. *Ecological Indicators* 31: 59-72.(2013)
Hermann, A., **Kuttner, M.**, Hainz-Renetzeder, C., Konkoly-Gyuró, E., Tirászi, A., Brandenburg, C., Allex, B., Ziener, K., Wrbka, T.: Assessment framework for landscape services in European cultural landscapes – an Austrian Hungarian case study. *Ecological Indicators* 37: 229-240. (2014)
Kutnjak, D., **Kuttner, M.**, Niketic, M., Dullinger, S., Schönswetter, P., Frajman, B. Escaping to the summits: Phylogeography and predicted range dynamics of *Cerastium dinaricum,* an endangered high mountain plant endemic to the western Balkan Peninsula. *Molecular Phylogenetics and Evolution* 78: 365-374. (2014)
Kuttner, M., Schneidergruber, A., Wrbka, T. Do landscape patterns reflect ecosystem service provision? – A comparison between protected and unprotected areas throughout the Lake Neusiedl region. *EcoMont* 6/2: 13-20. (2014)
Hainz-Renetzeder, C., Schneidergruber, A., **Kuttner, M.**, Wrbka, T. Assessing the potential supply of landscape services to support ecological restoration of degraded landscapes: A case study in the Austrian-Hungarian trans-boundary region of Lake Neusiedl. *Ecological Modelling* 295: 196-206 (2015)
Kuttner, M., Essl, F., Peterseil, J., Dullinger, S., Rabitsch, W., Schindler, S., Hülber, K., Gattringer, A., Moser, D. A new high-resolution habitat distribution map for Austria, Liechtenstein, southern Germany, South Tyrol and Switzerland. *EcoMont* 7/2: 18-29. (2015)
Valenta, V., Moser, D., **Kuttner, M.**, Peterseil, J., Essl, F. A High-Resolution Map of Emerald Ash Borer Invasion Risk for Southern Central Europe. *Forests* 6: 3075-3086. (2015)
Schönhart, M., Schauppenlehner, T., **Kuttner, M.**, Kirchner, M., Schmid, E. Climate change impacts on farm profits, landscape appearance, and the environment: policy scenario results from integrated field-farm-landscape modeling in Austria. Submitted to *Agricultural Systems,* currently under review (July, 2015)
Dullinger, I., Wessely, J., Bossdorf, O., Dawson, W., Essl, F., Gattringer, A., Klonner, G., Kreft, H., **Kuttner, M**., Moder, D., Pergl, J., Pyšek, P., Thuiller, W., van Kleunen, M., Weigelt, P., Winter, M., Dullinger, S. 2015. Ornamental plants as a pool of future invaders in Europe under climate change. Submitted to *Global Change Biology,* currently under review (September, 2015)
Kuttner, M., Hülber, K., Dullinger, S., Moser, D., Rabitsch, W., Schindler, S., Wessely, J., Gattringer, A., Essl, F. Habitat availability disproportionally amplifies climate change risks for lowland compared to alpine species. In preparation to be submitted to *Ecography* in November 2015