RESEARCH ARTICLE

On the importance of non-linear relationships between landscape patterns and the sustainable provision of ecosystem services

Adrienne Grêt-Regamey · Sven-Erik Rabe · Ricardo Crespo · Sven Lautenbach · Andrea Ryffel · Barbara Schlup

Received: 17 April 2013/Accepted: 21 October 2013/Published online: 10 November 2013 © Springer Science+Business Media Dordrecht 2013

Abstract Marginal land use changes can abruptly result in non-marginal and irreversible changes in ecosystem functioning and the economic values that the ecosystem generates. This challenges the traditional ecosystem services (ESS) mapping approach, which has often made the assumption that ESS can be mapped uniquely to land use and land cover data. Using a functional fragmentation measure, we show how landscape pattern changes might lead to changes in the delivery of ESS. We map changes in ESS of dry calcareous grasslands under different land use change scenarios in a case study region in Switzerland. We selected three ESS known to be related to species diversity including *carbon sequestration* and *pollination* as regulating values and *recreational experience*

Electronic supplementary material The online version of this article (doi:10.1007/s10980-013-9957-y) contains supplementary material, which is available to authorized users.

A. Grêt-Regamey (⋈) · S.-E. Rabe ·

R. Crespo · A. Ryffel Planning of Landscape and Urban Systems (PLUS), Institute for Spatial and Landscape Planning, ETH Zürich, Wolfgang-Pauli-Strasse 15, 8093 Zurich, Switzerland e-mail: gret@ethz.ch

S. Lautenbach

Institute for Geodesy and Geoinformation, University of Bonn, Nußallee 1, 53115 Bonn, Germany

B. Schlup Hintermann & Weber AG, Aarbergergasse 61, 3011 Bern, Switzerland as cultural value, and compared them to the value of two production services including *food* and *timber production*. Results show that the current unceasing fragmentation is particularly critical for the value of ESS provided by species-rich habitats. The article concludes that assessing landscape patterns is key for maintaining valuable ESS in the face of human use and fluctuating environment.

Keywords Ecosystem services · Functional fragmentation · Landscape metrics · Food and timber production · Pollination · Recreational experience

Introduction

Growing need for food, housing and transportation is associated with increasing land conversion (Lambin et al. 2001). These land use changes are among the worst threats to biodiversity (Sala et al. 2000; Pereira et al. 2010). They result in widespread changes in the spatial structure of native habitats, markedly influencing ecological functioning (Collinge 1996) and the capacity of the ecosystems to provide services critical to human survival (Palmer et al. 2004). Despite the increasing recognition of the economic value of these services (TEEB 2010), management of ecosystem services (ESS) is often not related to the planning of landscape patterns. ESS assessments are mostly done on an ecosystem- or habitat-based approach, obscuring



the known influence of spatial land use patterns on ecological processes. But, while the additional benefit of understanding the spatial pattern of various ecosystems on the provision of ESS has not yet been a central concern of ecologists nor landscape planners, it could support achieving many conservation goals where congruence exist between areas of high biodiversity value and areas important for multiple ESS delivery (Naidoo et al. 2006) and thus foster recognition of landscape's economic value (Polasky et al. 2005).

Most of the ESS mapping studies assume that ESS provision responds to gradual land use changes in a smooth way and that ESS change linearly with critical habitat variables such as size (e.g. Chan et al. 2006; Naidoo and Ricketts 2006; Grêt-Regamey et al. 2008; Naidoo et al. 2008; Egoh et al. 2009; Nelson et al. 2009; Maes et al. 2012). Such approaches can however introduce errors because they do not account for spatial variability in biophysical variables or processes (Eigenbrod et al. 2010). Dale and Polasky (2007) give examples highlighting the importance of the spatial dimension, and in recent years several authors have demonstrated that not considering ecological processes such as species-area relationships can dramatically change the ESS values. Dobson et al. (2006) for example investigated the implications of habitat loss for ESS provision showing that management should focus on securing ecosystems viable for species with larger area requirements. Aburto-Oropeza et al. (2008) and Barbier et al. (2008) investigated the effect of mangrove areas and fringes on ESS values, and concluded that temporal and spatial non-linearities had to be taken into account for, if we are to accurately estimate the value of ESS. Finally, Koch et al. (2009) expanded on the paper by Barbier et al. (2008) by incorporating the effect of both plant species and tidal level on wave attenuation and emphasized the nonlinear properties of ESS in mangrove areas. If thus we recognize these non-linear relationships as ecological theory suggests (MacArthur and Wilson 1967; Levins 1969), we need to take them into account in ESS mapping for providing robust assessments for landscape planning and support management decisions.

Landscape ecology studies have provided a broad knowledge on the relationships between spatial patterns and ecological processes on a range of scales (Wu 2013), and conservation plans are since more than a decade including information on size, shape and configuration for maintaining ecological and

evolutionary processes (Cowling et al. 1999; Rouget et al. 2003). But studies investigating links between spatial patterns and ESS delivery are rare and have especially been focusing on regulating services (e.g. Bianchi et al. 2006; Ricketts et al. 2008). In recent years however, the spatial perspective of the ESS concept has become increasingly important, and has even led to a new concept of landscape services (Termorshuizen and Opdam 2009). Several authors have investigated spatial discounting into the economic analysis of ESS (e.g. Georgiou et al. 2000; Bateman et al. 2006; Kozak et al. 2013) or have investigated changes in values depending on the spatial scales at which ESS are supplied (e.g. Hein et al. 2006). The effect of spatial heterogeneity of ESS and the consequences of this heterogeneity for the value of these services has however only recently received attention. Syrbe and Walz (2012) reviewed the literature on the spatial characteristics of ESS and how they relate to quantified measures of landscape structure methods. Frank et al. (2012) investigated the use of landscape metrics for appraising the potential of landscape to deliver ESS, showing that if landscape metrics are not considered, the potential of a landscape to provide ESS can be overestimated. Fürst et al. (2013) used a set of landscape metrics to assess the impact of land use patterns on the potential of a region to provide ESS, and Frank et al. (2013) presented an approach on assessing landscape aesthetics with landscape metrics. But while spatial patterns and their thresholds related to ecological processes have been identified as crucial for sustainable ESS provision (Carpenter et al. 2009), ways to integrate them into ESS mapping are missing.

In this contribution, we present an approach on how to integrate landscape spatial patterns into ESS mapping. We link a functional fragmentation measure to the provision of selected ESS of dry calcareous grasslands in the Swiss Canton Aargau—a region characterized by strong urban sprawl (Wissen et al. 2011). The nutrient poor and dry calcareous grasslands are amongst the most species-rich habitats of Central Europe, harboring a high diversity of characteristic plants of which roughly one-third is restricted to this type of habitat (Ellenberg 1988; Wallis De Vries et al. 2007; European Environment Agency 2013). The link between the ecological processes affected by a change in fragmentation and ESS delivery is established by selecting a set of ESS know to be positively related to species diversity. Based on the



results of a study of a grassland-dominated landscape from the central French Alps (Lavorel et al. 2011), we selected three ESS including carbon sequestration and pollination as regulating values and recreational experience as cultural value, and compared them to the value of two production services including food and timber production. As spatial and ecological characteristics of habit fragments are known to influence ecological processes with a threshold effect (e.g. see Collinge 1996 for a review), we incorporated a theoretical critical threshold level in ESS delivery linked to the fragmentation measure. We illustrate the sensitivity of the ESS delivery by modifying the ESS provision capacity when a critical level is passed, as suggested by Walker et al. (2010). We map the changes of the five selected ESS under different land use scenarios, and show that management that recognizes the influence of landscape patterns on ESS delivery can enhance the likelihood of a sustained provision of the services under land use and environmental changes. Finally, we discuss advantages and limitations of the suggested approach.

Materials and methods

Fragmentation index

For assessing functional connectivity, most studies have dealt with species or population level and measured gene flow in terms of the dispersal of plant seeds or the movement of pollen. For the conservation of plant communities, however, methods are required that measure functional connectivity at an entire community level rather than at population level. Landscape connectivity as the combination of functional and structural connectivity is both species- and landscape-specific (Tischendorf and Fahrig 2000; Brooks 2003; Taylor et al. 2006). In order to determine functional landscape connectivity, it is therefore essential to understand how the movement behavior of organisms interacts with landscape structure (Goodwin 2003). Theoretical and empirical work on metacommunities is based on a range of approaches to explain the diversity and relative abundance of species in ecological communities in space and time (Hubbell 2001; Leibold et al. 2004; Holyoak et al. 2005).

Schlup (2009) used spatial rank consistency (RC) for detecting fragmentation effects at the plant community level. Spatial RC is an aggregated

measure of the mean squared differences of species ranks. It can be interpreted as the variability of community composition, and can be calculated based on the abundances of plant species in a plot or study area. Based on field studies in the Swiss Canton Aargau, Schlup (2009) analyzed how species richness and species RC, thus the shifts in species ranks in space, differed along gradients of size and isolation of calcareous grassland communities. While no fragmentation effects could be detected for species richness, small and isolated grasslands had a significantly lower RC and an enhanced variation in βdiversity than large and connected ones. Patch area had a statistically significant effect on RC for habitat specialists of intact calcareous grasslands, where small patches showed higher variability in species ranks than large ones. Thus habitat specialist species were strongly affected by increased stochasticity in small patches. The effect of isolation was greatest for species with low capacity for wind-dispersal, but in isolated sites even highly dispersible species were affected. Hence the dispersal capacity of plants species was largely responsible for the isolation effects and was expressed in an increased spatial variability of calcareous grassland communities. The fact that wind dispersal capacity strongly modified the isolation effect supports the interpretation that the isolation effects found in RC are related to the process of dispersal, suggesting that they may provide an indirect measure of functional connectivity by seed flow at the community level.

On this basis Schlup and Nobis (2011) derived a fragmentation index establishing a link to a functional measure in terms of the variability of community composition for grasslands. The measure of the variability of community composition is sensitive to patch size and isolation of a grassland and was tested by real data of calcareous grassland communities in the case study region in the Canton Aargau (Switzerland). Unlike common fragmentation or connectivity measures, which are based on the spatial arrangement or the structural connectivity of habitat patches, the index thus allows for extending the somewhat arbitrary definition of area (small vs. large) and isolation (isolated vs. connected) to an assignment of critical thresholds. The index can be calculated on the basis of the patch size and isolation of a grassland in the case study region according to the following two relationships:



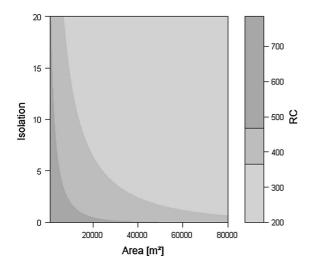


Fig. 1 Variability of species composition as a function of patch area and isolation classified by three levels of fragmentation (RC)

Isolation can be calculated for each grassland site as the sum of areas with suitable habitat, weighted by the distance from the target site using Hanski's (Hanski 1994) formula as recommended by Moilanen and Nieminen (2002):

$$I_i = \sum_{j \neq i} \exp(-\alpha d_{ij}) A_j \tag{1}$$

where I_i is the isolation of patch i, d_{ij} is the distance between the centroids of patches i and j, A_j is the area of patch j and α is the parameter of the exponential distribution describing the dispersal distance. Schlup and Nobis (2011) used centroid-to-centroid distance because of the compact and small extent of the grassland patches.

Based on statistical analyses described in Schlup and Nobis (2011), the fragmentation index can then be calculated as follows:

$$RC_i = 1254.87 - 68.04x_i^{(1)} - 135.22x_i^{(2)}$$
 (2)

where $x^{(1)}$ is the log(patch size[m²]); $x^{(2)}$ is the $\sqrt{\sqrt{\text{isolation}}} = I_i$.

For the grasslands investigated in this study, it can thus be assumed that the fragmentation parameters can be estimated from the variability measure by maximizing generalized likelihood of the RC. These relationships were used to create a general relationship between RC and the degree of fragmentation for the case study region: While values of $RC_i < 365$

correspond to small fragmentation, values >468 mean high fragmentation (Fig. 1).

Although this classification of Schlup and Nobis (2011) was not based on a biological threshold, analysis showed that it has strong biological relevance. Plant species with large seeds and the dispersal type gravity decreased significantly from the small to the large fragmentation class. Wind dispersed species showed no difference between the different classes of fragmentation. Moreover, habitat specialists of intact calcareous grasslands decreased from the small to the large fragmentation class, whereas plant species of more intensively managed grasslands increased. It can thus be assumed that the classification captures important ecological impacts of fragmentation at the level of plant communities.

Linking landscape patterns to ecosystem services delivery

Including critical threshold levels in ESS delivery linked to landscape patterns requires linking the quantification and monetization of ESS to critical measures in landscape patterns related to thresholds in ecological processes. Based on (1) the link between functional connectivity measure and species diversity as estimated with the RC measures, and (2) the link between species diversity and ESS given by Lavorel et al. (2011), we related the probability of getting a certain land use patch to the value of the services provided under this land use change analogously to Walker et al. (2010). As we did not have a clear threshold level between the degree of fragmentation and ESS provision, we assumed that only a RC value of >468 for a given patch has an impact on the ESS dependent on species diversity: when a dry grassland patch has an RC value larger than 468, we replaced the ESS values of the biodiversity rich dry grassland by the values of extensively managed grassland for carbon sequestration and recreational experience. For pollination, the ecosystem service value is set to zero as it is given by the difference between the pollination service of all land uses (particularly dry meadows, nearby forest edges and shrub land) and the service of all land uses but dry meadows. The threshold effect was considered only relevant for carbon sequestration, pollination, and recreational experience, which have been shown to be linked to species diversity (Lavorel et al. 2011). Food and



timber production were not influenced by patch size and connectivity. The ecosystem services value of dry grassland in the case study area was thus calculated as follows:

$$E[W] = \sum_{n=0}^{N} \sum_{i=0}^{I} (w_{CPR}p_i)_n + (w_{AT}p_i)_n$$
 (3)

where p_i is the probability of a change in land use i, w_{CPR} is the value of carbon sequestration (C), pollination (P), and recreational experience (R) for all RCi <468, wj is the value of food and timber production on all cells, and n is the total number of raster cells (hectare size) in the case study area. The sensitivity of ESS values to an RC_i >468 was investigated under different land use scenarios, which is described in the next paragraph.

Case study

Aargau

The study was carried out in the Swiss canton Aargau, which spreads from the Jura mountains in the north and west to the low Swiss midlands in the south and east and offers a diversely structured landscape with a wide variety of ecosystems. Located between three major urban agglomerations, Basel, Bern and Zürich, the 140,370 ha area is under strong settlement pressure with commuters to the nearby urban agglomerations and major transportation networks of national and international importance. Since the 1950s, changes in agricultural land use and reallocation of land for settlements or infrastructure have reduced the size of calcareous grassland significantly and split them into small and isolated fragments (Baur et al. 1996). From 1950 to 1985, 95 % of the total area of calcareous grasslands was reduced in the northeastern part of the canton (Möckli 1989) due to land use and agriculture intensification, afforestation, increasing shrub encroachment, and settlement expansion. Thanks to conservation efforts of the last 20 years, the rate of fragmentation has slowed down, but is still going on.

We therefore focused in this study on dry calcareous grassland prone to change to other extensively managed grassland, intensively managed grassland, arable land, scrub encroachment and forest. The land use data was obtained by aggregating the basic categories of the Swiss land use statistics (Bundesamt für Statistik (BFS) 2011), applying the categories in Bolliger et al. (2007). The Swiss land use statistics are based on aerial photo interpretation. The generated categories differ slightly from the categories in Bolliger et al. (2007) as we merged the categories forest and open forest and used the current nomenclature of the Swiss land use statistics, which we adjusted with additional geographical datasets for the actual land use such as the ecological compensation areas and the dataset of the dry grassland inventories (Bundesamt für Umwelt (BAFU) 2010). The resulting spatial distribution of the different land use types in the canton Aargau is shown in Fig. 1, and the current area of each land use type is provided in Appendix 1 (supplementary material).

Mapping ecosystem services

We selected five ESS including carbon sequestration, pollination, and recreational experience, which are known to be linked to species diversity, as well as food and timber production for which there are no clear links to species diversity. The selection of the speciesdiversity dependent ESS was based on three factors: (1) the ESS delivery is linked to species diversity (based on Lavorel et al. 2011), (2) the ESS are provided by dry grassland and sensitive to changes to extensively managed grassland, intensively managed grassland, arable land, scrub encroachment, and forest (the dry grassland is a sub-category of extensively managed grassland, which can be turned into intensively managed grassland or—in the case of abandonment—can change into scrub encroachment and later, managed or unmanaged, into forest), and/or (3) ESS are dependent on landscape structures such as pollination (e.g. Ricketts et al. 2008) and recreational experience (Boyd and Wainger 2002).

We quantified the changes in the selected ESS using state-of-the-art GIS-based models. We focused on studies in Switzerland and the close-by Alps for parameterizing the values, thus also incorporating gray literature such as diploma theses and reports from administrative offices. The data from the quantification step was converted into monetary units applying different valuation methods in accordance with the ESS to be valued. The services were calculated per hectare and year. All monetary values were converted into dollars with the average historical exchange rate



(OANDA Corporation 2013) of the year of investigation. Subsequently, a cost of living adjustment to the target year of 2010 was conducted (Bundesamt für Statistik 2012). Details about the procedures used for each ecosystem service are provided in Appendix 2 (supplementary material).

Land use scenarios

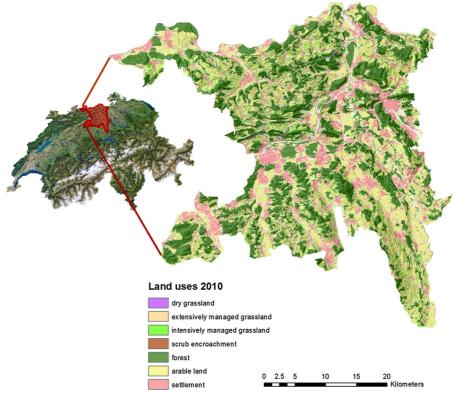
We estimated the probabilities of land use changes [p_{i,n} in Eq. (3)] using a multi-logistic regression. The land use changes were regressed on a set of external explanatory variables including climate data—considered thermic (frost frequency, degree day sum) and hygric variables (mean monthly precipitation sum, water budget in July, and indicators for continentality [MeteoSchweiz (Bundesamt für Meteorologie und Klimatologie) 2011]—slope [Swisstopo (Bundesamt für Landestopografie) 2010b], and the subsidies for each land use type. Further, we calculated the distances to the different land use types, to settlements, roads and train stations (as binary values taking 1 if there is a main road, highway or a train station within

multinom() function in the net package (Venables and Ripley 2003) based on the land use changes between 1992, 2000 and 2010 on a ha raster cell. Based on the regression, we calculated probabilities of land use changes for 2030 (business-as-usual-scenario). By adjusting the probabilities following the basic assumption of the scenarios in Bolliger et al. (2007), we calculated a liberalization and a moderately reduced agricultural production scenario for 2030. The liberalization scenario suggests liberalized agricultural markets as a result of WTO requirements with no state support of agriculture or conservation and agrienvironmental regulations. The lowered agricultural production scenario relies on a strong conservation policy under a liberalized agricultural market as a result of WTO requirements and general globalization. Society subsidizes conservation and agro-biodiversity stronger that today. Figure 2 shows the resulting land use changes under the different scenarios. Details about the transition matrices used for generating the scenarios are provided in Appendix 3 (supplementary material).

1 km, 0 otherwise [Swisstopo (Bundesamt für Lan-

destopografie) 2010a]. We fitted the model using the

Fig. 2 Case study area with land uses in 2010. The *small inset* shows the location of the Canton Aargau in Switzerland





Results

Results show that current unceasing fragmentation is critical for the ESS provided by dry grassland (Fig. 3). The difference between the aggregated ESS values considering fragmentation effects and the values calculated only based on a traditional mapping approach are more than 50 % in all scenarios. Acknowledging that we only valued five ESS including timber and food production, carbon sequestration, pollination, and recreational experience, the estimated yearly ESS value of 1,735 USD/ha in 2010 (not considering the running costs) compared to an average of agro-ecological subsidies provided to Swiss farmers in 2010 of around 500 USD/ha (Bundesamt für Landwirtschaft 2010) seems reasonable. The observed changes in ecosystem service values considering fragmentation effects are driven by changes (1) in land use types, (2) in patch size and isolation of the ecosystems, (3) in environmental conditions including

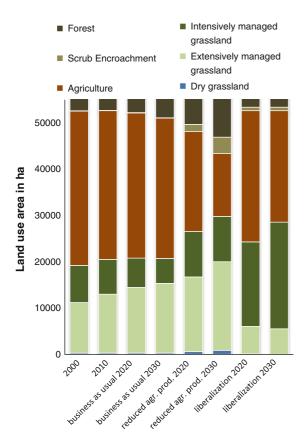


Fig. 3 Land use changes under the different scenarios for the Swiss Canton Aargau 0

temperature and precipitation over the case study area, and (4) in land use maintenance costs. Even if the total area of dry grassland stays nearly the same such under the business-as-usual scenario, the decrease in patch sizes leads to an increase in the fragmentation index. The liberalization scenario particularly leads to large fragmentation as both the total area of the dry grassland decreases and the isolation of the patches increases. The fragmentation is so high, that the costs of maintenance of the isolated and small patches exceed the value of the ESS. Even under a scenario of reduced agricultural production, the fragmentation index decreases as the planning of the new dry grasslands was not coordinated and spatial isolation of the dry grassland parcels was not considered. Details about changes in the fragmentation index are provided in the Appendix 5 (supplementary material) (Fig. 4).

The increase in fragmentation has particularly an impact on recreational experience and pollination. Table 1 shows the estimated ESS values and the ratio of the estimated ESS value and the related maintenance costs for each scenario. The timber and food production capacities of the dry meadows, which are rather low compared to other land uses, will not be impaired by the fragmentation. Small differences are

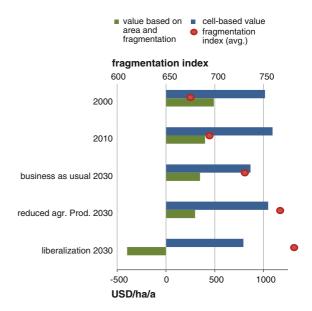


Fig. 4 Changes in fragmentation index (*bullets*) and associated influence on ESS under different land use change scenarios in the Canton Aargau, Switzerland. The values in the *blue columns* are based on a cell-based ESS calculation. The *green columns* include the effect of fragmentation on ESS values



172

Maintenance costs to ESS ratio

(indexed to the year 2000)

different scenarios in the Swiss Canton Aargau; based on the fragmentation approach					
	2000	2010	Business as usual 2030	Reduced agr. prod. 2030	Liberalization 2030
Food production	694	694	694	697	703
Carbon sequestration	134	134	133	131	128
Recreational experience	871	865	874	840	823
Pollination	44	35	0.2	0.25	0
Ratio maintenance costs to ESS	0.72	0.77	0.79	0.82	1.23

111

107

Table 1 Average ecosystem service values (in USD/ha/year) and ratio of maintenance costs to ESS values of dry meadows for the different scenarios in the Swiss Canton Aargau; based on the fragmentation approach

due to the spatial reallocation of patches and therefore changed environmental factors. The carbon sequestration varies only slightly, as the decreasing species diversity of fragmented dry meadows causes only a minor change in carbon storage in roots and soil. While the values of agricultural production and carbon sequestration remain almost at the same level and are hardly affected by the fragmentation, fragmentation has a significant effect on the other two ESS. Recreational experience and pollination are significantly dependent on species diversity, on the one hand due to the aesthetic perception, on the other hand, for reasons of habitat suitability for pollinating insects. Therefore considerably reduced values are found in the scenarios with high fragmentation.

100

The ratio of estimated ESS values and related maintenances costs shows that management costs increase with increasing fragmentation: the smaller the patches and the more scattered they are, the more expensive is the management. Under a reduced agricultural production scenario characterized by an increase in ecological direct payments tied to agrienvironmental regulations and contributions for individual conservation contracts, the number of dry meadow patches increases considerably, and the forest and scrub encroachment expands over agriculture areas. The unmanaged distribution of the parcels results in a high fragmentation, so that the ESS are reduced. If subsidies are abolished and prices for agriculture goods are decreasing as under a liberalization scenario, we see an increase of intensive agriculture and forest areas at the cost of dry grasslands and extensively managed parcels, and consequently a strong decrease in services of extensive grassland which are accompanied by increased maintaining costs. As the maintenance costs of dry meadows exceed the value of the ESS they provide, the total value of a dry meadow parcel becomes negative. An uncoordinated increase in dry grassland areas does thus not necessarily lead to an increase in ESS provision. A strategy directed at connecting them, which can be developed and monitored using land-scape metrics (Frank et al. 2012, 2013; Fürst et al. 2013), is therefore essential if ESS are to be provided in the long-term.

114

Discussion

The study demonstrates that managing for ESS needs a deep understanding of the influence of the spatial distribution of ecosystems on ecological processes and thus ESS delivery. Increasing patch sizes of speciesrich ecosystems will not guarantee sustainable ESS delivery. In other words, if ESS are to be mapped under different stressors, we need to understand the spatial pattern of ecosystems and their ecological consequences. While our analysis only showed how a fragmentation measure can be integrated into ESS mapping, it supports work done by Koch et al. (2009) showing the relevance of addressing non-linearity for ESS assessments, but further research is needed to elucidate the value of the spatial threshold levels relevant for the shifts in the provision of ESS bundles in case studies.

Recent progresses in ecology have shown how functional trait-based approaches could improve on the pure land-use approaches and support the assessment of trade-offs and synergies at the landscape level. While ESS delivery has been related to ecosystem



biological characteristics (Kremen 2005), and more specifically to functional traits (e.g. Chazal de et al. 2008; de Bello et al. 2010), there is growing evidence for the effects of community-level functional traits on ecosystem process that underlie important ESS (Suding and Goldstein 2008). Lavorel et al. (2011) mapped hot and cold spots of ES delivery using abiotic variables and plant traits rather than land use showing that using plant functional variation across landscapes is a powerful approach to understanding the fundamental ecological mechanisms underlying ES provision. Furthermore, consequences on associations and trade-offs among different plant traits for ecosystem functioning and the resulting ability for ecosystem to provide multiple services has only started to be explored (Lavorel and Grigulis 2012). While the isolation pattern as expressed in the RC in our study is related to the process of dispersal limitation and is thus a measure of functional connectivity, there is missing knowledge of a direct link between dispersal capacity of plants and the ESS provided. How responses of seed dispersal traits to key environmental and landscape structural changes are expected to scale-up to ecosystem properties and ESS need to be investigated.

Furthermore, if a threshold concept is applied for ESS mapping, not only thresholds in the functioning of ecosystems should be considered as done in this study, but the dynamic changes of human demands for ESS needs also to be addressed (Plummer and Armitage 2007). Human perception, behavior and decisionmaking are prone to drastic changes, surprise, unpredictability and complexity. Folke et al. (2002) describes management that also sustains the demand for ESS as "resilience-building management, which attends to slowly-changing, fundamental variables that create memory, legacy, diversity, and the capacity to innovate in both social and ecological components of the system." Mapping ESS for decision-making thus not only requires understanding the importance of spatial patterns for maintaining ecological processes, but understanding how local users perceive the value of ESS and how they control and transform their delivery under different stressors. A threshold concept for ecosystem service mapping should therefore also consider thresholds in socio-ecological systems.

While the total sum of the ESS values we have considered in this contribution is important, we are still only considering a small set of ESS. Cultural ESS for example are one of the ESS highly dependent on spatial patterns (Daniel 2001; Daniel et al. 2012; Frank et al. 2013). Many have investigated the relationships between objective landscape descriptors and scenic beauty (e.g. Bishop and Hulse 1994; Hunziker and Kienast 1999). Studies on land use pattern in a catchment area and their effects on hydrological ESS also show the importance of the spatial distribution of ecosystems for ESS provision (e.g. Le Maitre et al. 2009), and the relationships between urban patterns on ESS provision have been investigated, for example for planning zero-energy cities (e.g. Grêt-Regamey et al. 2013). But even if one understands the interaction between spatial patterns and ecosystem functioning, we still fail in linking it to the value of humans, which depends on social/cultural construction models. Here a close cooperation between landscape planners, landscape architects and landscape ecologists is needed for creative design of the spatial configuration of landscapes sustaining the integrity of ecological systems and the long term provision of ESS.

In conclusion, while this contribution only shows a first approach on how to consider relationships between landscape patterns and ESS delivery for ESS mapping, it demonstrates the importance of integrating spatial measures such as fragmentation into ESS assessments. How size, shape and configuration of ecosystems support ESS provision under different stressors needs to be investigated in multiple approaches such as surveys, experimental manipulations, and models. But mapping ESS without consideration of thresholds over space and time can lead to strong overestimations of ESS. Collaboration between landscape and conservation planners is thus essential in this process if we want to accurately assess ESS changes in the face of increasing land use changes and demand for their services.

Acknowledgments This research was funded by the Federal Office for the Environment (FOEN) in Switzerland. The project was developed in close collaboration with the members of the section "Species, Habitats, and Ecological Networks". This work was supported by the canton Aargau, especially by providing the geodata.

References

Aburto-Oropeza O, Ezcurra E, Danemann G, Valdez V, Murray J, Sala E (2008) Mangroves in the Gulf of California increase fishery yields. Proc Natl Acad Sci 105(30): 10456–10459



- Barbier EB, Koch EW, Silliman BR, Hacker SD, Wolanski E, Primavera J, Granek EF, Polasky S, Aswani S, Cramer LA, Stoms DM, Kennedy CJ, Bael D, Kappel CV, Perillo GME, Reed DJ (2008) Coastal ecosystem-based management with nonlinear ecological functions and values. Science 319(5861):321–323
- Bateman IJ, Cole MA, Georgiou S, Hadley DJ (2006) Comparing contingent valuation and contingent ranking: a case study considering the benefits of urban river water quality improvements. J Environ Manag 79:221–231
- Baur B, Joschi J, Schmid B, Hänggi A, Borcard D, Stary J, Pedroli-Christen A, Thommen GH, Luka H, Rusterholz H (1996) Variation in species richness of plants and diverse groups of invertebrates in three calcareous grasslands of the Swiss Jura Mountains. Rev Suisse Zool 103(4):801–833
- Bianchi FJ, Booij CJ, Tscharntke T (2006) Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. Biol Sci 273(1595):1715–1727
- Bishop ID, Hulse DW (1994) Prediction of scenic beauty using mapped data and geographic information systems. Special Issue Landscape Plan 30(1–2):59–70
- Bolliger J, Kienast F, Soliva R, Rutherford G (2007) Spatial sensitivity of species habitat patterns to scenarios of land use change (Switzerland). Landscape Ecol 22(5):773–789
- Boyd J, Wainger L (2002) Landscape indicators of ecosystem service benefits. Am J Agr Econ 84:1371–1378
- Brooks CP (2003) A scalar analysis of landscape connectivity. Oikos 102(2):433–439
- Bundesamt für Landwirtschaft (2010) Agrarbericht 2001. http:// www.blw.admin.ch/old/agrarbericht1/d/direktzahlung/ oekodirekt.htm. Accessed 12 April 2013
- Bundesamt für Statistik (2012) LIK-Teuerungsrechner. http://www.portal-stat.admin.ch/lik_rechner/d/lik_rechner.htm. Accessed 15 April 2013
- Bundesamt für Statistik (BFS) (2011) Arealstatistik 2004/09. NOA S04. Neuchatel
- Bundesamt für Umwelt (BAFU) (2010) Bundesinventar der Trockenwiesen und -weiden von nationaler Bedeutung. Bern
- Carpenter SR, Mooney HA, Agard J, Capistrano D, DeFries RS, Diaz S, Dietz T, Duraiappah AK, Oteng-Yeboah A, Pereira HM, Perrings C, Reid WV, Sarukhan J, Scholes RJ, Whyte A (2009) From the cover: science for managing ecosystem services: beyond the millennium ecosystem assessment. Proc Natl Acad Sci 106(5):1305–1312
- Chan KMA, Shaw MR, Cameron DR, Underwood EC, Daily GC (2006) Conservation planning for ecosystem services. PLoS Biol 4(11):2138–2152
- Collinge SK (1996) Ecological consequences of habitat fragmentation: implications for landscape architecture and planning. Landsc Urban Plan 36(1):59–77
- Cowling RM, Pressey RL, Lombard AT, Desmet PG, Ellis AG (1999) From representation to persistence: requirements for a sustainable system of conservation areas in the species-rich mediterranean-climate desert of southern Africa. Divers Distrib 5(1–2):51–71
- Dale VH, Polasky S (2007) Measures of the effects of agricultural practices on ecosystem services. Ecol Econ 64(2):286–296
- Daniel TC (2001) Whither scenic beauty? Visual landscape quality assessment in the 21st century. Our Visual Landscape 54(1–4):267–281

- Daniel TC, Muhar A, Arnberger A, Aznar O, Boyd JW, Chan KMA, Costanza R, Elmqvist T, Flint CG, Gobster PH, Gret-Regamey A, Lave R, Muhar S, Penker M, Ribe RG, Schauppenlehner T, Sikor T, Soloviy I, Spierenburg M, Taczanowska K, Tam J, von der Dunk A (2012) Contributions of cultural services to the ecosystem services agenda. Proc Natl Acad Sci 109(23):8812–8819
- de Bello F, Lavorel S, Díaz S, Harrington R, Cornelissen J, Bardgett R (2010) Towards an assessment of multiple ecosystem processes and services via functional traits. Biodivers Conserv 19(10):2873–2893
- de Chazal J, Quétier F, Lavorel S, van Doorn A (2008) Including multiple differing stakeholder values into vulnerability assessments of socio-ecological systems. Glob Environ Gov 18(3):508–520
- Dobson A, Lodge D, Alder J, Cumming G, Keymer J, McGlade J (2006) Habitat loss, trophic collapse, and the decline of ecosystem services. Ecology 87(8):1915–1924
- Egoh B, Reyers B, Rouget M, Bode M, Richardson DM (2009) Spatial congruence between biodiversity and ecosystem services in South Africa. Biol Conserv 142(3):553–562
- Eigenbrod F, Armsworth PR, Anderson BJ, Heinemeyer A, Gillings S, Roy DB (2010) The impact of proxy-based methods on mapping the distribution of ecosystem services. J Appl Ecol 47(2):377–385
- Ellenberg H (1988) Vegetation ecology of Central Europe, 4th edn. Cambridge University Press, Cambridge
- European Environment Agency (2013) european nature information system: Eunis. http://eunis.eea.europa.eu/. Accessed 15 April 2013
- Folke C, Carpenter S, Elmqvist T, Gunderson L, Holling CS, Walker B (2002) Resilience and sustainable development: building adaptive capacity in a world of transformations. J Hum Environ 31(5):437–440
- Frank S, Fürst C, Koschke L, Makeschin F (2012) A contribution towards a transfer of the ecosystem service concept to landscape planning using landscape metrics. Challenges of sustaining natural capital and ecosystem services. Quant Model Valuat Acc 21:30–38
- Frank S, Fürst C, Koschke L, Witt A, Makeschin F (2013)
 Assessment of landscape aesthetics—validation of a
 landscape metrics-based assessment by visual estimation
 of the scenic beauty. Ecol Ind 32:222–231
- Fürst C, Frank S, Witt A, Koschke L, Makeschin F (2013) Assessment of the effects of forest land use strategies on the provision of ecosystem services at regional scale. J Environ Manag 127:96–116
- Georgiou S, Bateman I, Cole M, Hadley D (2000) Contingent ranking and valuation of river water quality improvements: Testing for scope sensitivity, ordering and distance decay effects. CSERGE working paper GEC 2000–2018. Norwich, UK: Centre for Social and Economic Research on the Global Environment, University of East Anglia and University College London
- Goodwin BJ (2003) Is landscape connectivity a dependent or independent variable? Landscape Ecol 18:687–699
- Grêt-Regamey A, Bebi P, Bishop ID, Schmid W (2008) Linking GIS-based models to value ecosystem services in an Alpine region. J Environ Manag 89:197–208
- Grêt-Regamey A, Celio E, Klein TM, Wissen HU (2013) Understanding ecosystem services trade-offs with



- interactive procedural modeling for sustainable urban planning. Special Issue 109(1):107–116
- Hanski I (1994) A practical model of metapopulation dynamics. J Anim Ecol 63(1):151–162
- Hein L, van Koppen K, de Groot R, van Ierland E (2006) Spatial scales, stakeholders and the valuation of ecosystem services. Ecol Econ 57(2):209–228
- Holyoak M, Leibold MA, Mouquet N, Holt RD, Hoopes MF (2005) Mata communities: a framework for large-scale community ecology. In: Holyoak M, Leibold MA, Holt RD (eds) Metacommunities: spatial dynamics and ecological communities. Chicago University Press, Chicago, pp 1–32
- Hubbell SP (2001) The unified neutral theory of biodiversity and biogeography. Monographs in population biology 32.
 Princeton University Press, Princeton
- Hunziker M, Kienast F (1999) Potential impacts of changing agricultural activities on scenic beauty—a prototypical technique for automated rapid assessment. Landscape Ecol 14(2):161–176
- Koch EW, Barbier EB, Silliman BR, Reed DJ, Perillo GME, Hacker SD, Granek EF, Primavera JH, Muthiga N, Polasky S, Halpern BS, Kennedy CJ, Kappel CV, Wolanski E (2009) Non-linearity in ecosystem services: temporal and spatial variability in coastal protection. Front Ecol Environ 7(1):29–37
- Kozak J, Lant C, Shaikh S, Wang G (2013) The geography of ecosystem service value: the case of the Des Plaines and Cache River wetlands, Illinois. Appl Geogr 31(1):303–311
- Kremen C (2005) Managing ecosystem services: what do we need to know about their ecology? Ecol Lett 8(5):468–479
- Lambin EF, Turner B, Geist HJ, Agbola SB, Angelsen A, Bruce JW, Coomes OT, Dirzo R, Fischer G, Folke C, George P, Homewood K, Imbernon J, Leemans R, Li X, Moran EF, Mortimore M, Ramakrishnan P, Richards JF, Skånes H, Steffen W, Stone GD, Svedin U, Veldkamp TA, Vogel C, Xu J (2001) The causes of land-use and land-cover change: moving beyond the myths. Global Environ Change 11(4):261–269
- Lavorel S, Grigulis K (2012) How fundamental plant functional trait relationships scale-up to trade-offs and synergies in ecosystem services. J Ecol 100(1):128–140
- Lavorel S, Grigulis K, Lamarque P, Colace MP, Garden D, Girel J (2011) Using plant functional traits to understand the landscape distribution of multiple ecosystem services. J Ecol 99(1):135–147
- Le Maitre DC, Milton SJ, Jarmain C, Colvin CA, Saayman I, Vlok JHJ (2009) Linking ecosystem services and water resources: landscape-scale hydrology of the Little Karoo. Front Ecol Environ 5(5):261–270
- Leibold MA, Holyoak M, Mouquet N, Amarasekare P, Chase JM, Hoopes MF, Holt RD, Shurin JB, Law R, Tilman D, Loreau M, Gonzalez A (2004) The metacom-munity concept: a framework for multi-scale community ecology. Ecol Lett 7:601–613
- Levins R (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. Bull ESA 15(3):237–240
- MacArthur RH, Wilson EO (1967) The theory of island biogeography. Princeton University Press, New Jersey
- Maes J, Hauck J, Paracchini ML et al (2012) A spatial assessment of ecosystem services in Europe: methods, case

- studies and policy analysis-phase 2. PEER Report No 4. Partnership for European Environmental Research, Ispra
- MeteoSchweiz (Bundesamt für Meteorologie und Klimatologie) (2011): Klimadaten. Bundesamt für Meteorologie und Klimatologie, Zürich
- Möckli R (1989) Nutzungsbedingte Veränderungen auf Mesobromion—(Trespen-Halbtrockenrasen-) Standorten im östlichen Aargauer Jura. Mitteilungen der Aargauischen Naturforschenden Gesellschaft 32:141–165
- Moilanen A, Nieminen M (2002) Simple connectivity measures in spatial ecology. Ecology 83(4):1131–1145
- Naidoo R, Ricketts T (2006) Mapping the economic costs and benefits of conservation. PLoS Biol 4(11):2153–2164
- Naidoo R, Balmford A, Ferraro PJ, Polasky S, Ricketts TH, Rouget M (2006) Integrating economic costs into conservation planning. Trends Ecol Evol 21(12):681–687
- Naidoo R, Balmford A, Costanza R, Fisher B, Green RE, Lehner B (2008) Global mapping of ecosystem services and conservation priorities. Proc Natl Acad Sci 105(28): 9495–9500
- Nelson E, Mendoza G, Regetz J, Polasky S, Tallis H, Cameron DR (2009) Modeling multiple ecosystem services, biodiversity conservation, commodity production, and tradeoffs at landscape scales. Frontiers in ecology and the environment. Front Ecol Environ 7(1):4–11
- OANDA Corporation (2013) Historische Wechselkurse. OANDA Europe Limited. http://www.oanda.com/lang/de/ currency/historical-rates/. Accessed 15 April 2013
- Palmer M, Bernhardt E, Chornesky E, Collins S, Dobson A, Duke C, Gold B, Jacobson R, Kingsland S, Kranz R, Mappin M, Martinez LM, Micheli F, Morse J, Pace M, Pascual M, Stephen P, Reichman OJ, Simons A, Townsend A, Turner M (2004) Ecology for a crowded planet. Science 304(5675):1251–1252
- Pereira HM, Leadley PW, Proenca V, Alkemade R, Scharlemann JPW, Fernandez-Manjarres JF, Araujo MB, Balvanera P, Biggs R, Cheung WWL, Chini L, Cooper HD, Gilman EL, Guenette S, Hurtt GC, Huntington HP, Mace GM, Oberdorff T, Revenga C, Rodrigues P, Scholes RJ, Sumaila UR, Walpole M (2010) Scenarios for global biodiversity in the 21st century. Science 330(6010): 1496–1501
- Plummer R, Armitage D (2007) A resilience-based framework for evaluating adaptive co-management: linking ecology, economics and society in a complex world. Ecol Econ 61:62–74
- Polasky S, Nelson E, Lonsdorf E, Fackler P, Starfield A (2005) Conserving species in a working landscape: land use with biological and economic objectives. Ecol Appl 15(4): 1387–1401
- Ricketts TH, Regetz J, Steffan-Dewenter I, Cunningham SA, Kremen C, Bogdanski A (2008) Landscape effects on crop pollination services: are there general patterns? Ecol Lett 11(5):499–515
- Rouget M, Cowling RM, Pressey RL, Richardson DM (2003) Identifying spatial components of ecological and evolutionary processes for regional conservation planning in the Cape Floristic Region, South Africa. Divers Distrib 9(3): 191–210
- Sala OE, Chapin SF, Armesto III JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB,



- Kinzig A, Leemans R, Lodge DM, Mooney HA, Oesterheld M, Poff LN, Sykes MT, Walker BH, Walker M, Wall DH (2000) Global biodiversity scenarios for the year 2100. Science 287(5459):1770–1774
- Schlup B (2009) Assessing the connectivity of calcareous grassland plant communities. Dissertation, Eidgenössische Technische Hochschule (ETH), Zürich
- Schlup B, Nobis M (2011) Berechnung der Fragmentierung von Halbtrockenrasen. In: Hintermann, Weber AG (eds), Reinach
- Suding KN, Goldstein LJ (2008) Testing the Holy Grail framework: using functional traits to predict ecosystem change. New Phytol 180(3):559–562
- swisstopo (Bundesamt für Landestopografie) (2010a) VEC-TOR25 digitales landschaftsmodell der Schweiz. Bundesamt für Landestopografie, Wabern
- Swisstopo (Bundesamt für Landestopografie) (2010b) VEC-TOR25. Das digitale Höhenmodell der Schweiz. Bundesamt für Landestopografie, Wabern
- Syrbe RU, Walz U (2012) Spatial indicators for the assessment of ecosystem services: providing, benefiting and connecting areas and landscape metrics. Ecol Ind 21:80–88
- Taylor PD, Fahrig L, With KA (2006) Landscape connectivity: back to the basics. In: Crooks KR, Sanjayan M (eds) Connectivity conservation. Cambridge University Press, Cambridge

- TEEB (2010) The economics of ecosystems and biodiversity. In: Pushpam K (ed) Ecological and economic foundations. Island Press, Washington DC
- Termorshuizen J, Opdam P (2009) Landscape services as a bridge between landscape ecology and sustainable development. Landscape Ecol 24:1037–1052
- Tischendorf L, Fahrig L (2000) On the usage and measurement of landscape connectivity. Oikos 90(1):7–19
- Venables WN, Ripley BD (2003) Modern applied statistics with statistics and computing, 4th edn. Springer, New York
- Walker B, Pearson L, Harris M, Maler K, Li C, Biggs R, Baynes T (2010) Incorporating resilience in the assessment of inclusive Wealth: an example from South East Australia. Environ Resour Econ 45(2):183–202
- Wallis De Vries MF, Parkinson AE, Dulphy JP, Sayer M, Diana E (2007) Effects of livestock breed and grazing intensity on biodiversity and production in grazing systems. Effects on animal diversity. Grass Forage Sci 62(2):185–197
- Wissen HU, Jaeger JAG, Schwick C, Jarne A, Schuler M (2011) Measuring and assessing Urban Sprawl: what are the remaining options for future settlement development in Switzerland for 2030? Appl Spatial Anal 4(4):249–279
- Wu J (2013) Landscape ecology. In: Leemans R (ed) Ecological systems. Springer, New York

