Protecting multiple dimensions of biodiversity to achieve conservation targets

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To my parents, for their unconditional support

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Summary

Biodiversity is the repository of Earth's evolutionary history and the source of irreplaceable benefits for humans, both material and spiritual. Changes driven by human development and population growth threaten different dimensions of biodiversity at multiple scales. Despite increased efforts and advancements in conservation science, pressure continues to increase on global ecosystems. This thesis is organized in four studies addressing three research areas that are critical for answering the current biodiversity challenges. I will systematize the contributions of my thesis by describing how they address the Aichi Biodiversity Targets, agreed in 2010 in Nagoya as global priority areas for the decade 2011 - 2020.

Research area 1. In the first study, I answer the research question: is one approach to area prioritization sufficient to protect multidimensional biodiversity targets? I test two species-based approaches: hotspots, which prioritize areas of highest species richness, vulnerability and rarity; and complementarity, which gradually adds new areas based on the presence of unrepresented species. Additionally, I test wilderness mapping as an ecosystem-based approach based on conserving the areas that have suffered the least human impact. I assess the results of the prioritization approaches based on several biodiversity targets: species coverage, wilderness, coverage of important areas for megafauna, and three regulating ecosystem services. The species and ecosystem-based approaches select different areas as important for conservation. Species-based approaches maximize species coverage while the ecosystem-based approach maximizes wilderness, coverage of important areas for megafauna and ecosystem services.

The results of this study are relevant especially for ***Target 11*** which recommends the expansion of terrestrial and marine protected areas to 17% and 11% respectively, of the global area while also ensuring effective management of these areas. This study also contributes to ***Target 14*** which envisions the restoration and safeguarding of essential services.

Research area 2. In the second study of this thesis I map four wilderness metrics at European level. I consider two metrics that measure mainly the perception of wilderness but have also ecological relevance: remoteness from roads and human settlements, and impact of artificial night light. I also consider two metrics that quantify mainly the ecological dimension of wilderness: deviation from potential natural vegetation and proportion of harvested primary productivity. The four wilderness metrics show a common pattern of high wilderness values in mountainous areas and in northern Europe. However, the differences between metrics uncover also the different human factors that shape landscapes. For instance, drier southern areas with a long history of farming have a high

deviation from potential natural vegetation but a relatively low percentage of harvested primary productivity. Meanwhile, the forested areas of Scandinavia have a low deviation from potential natural vegetation but relatively high percentage of harvested primary productivity as a result of forestry.

Due to changes in agricultural markets and increased labor costs, farmland abandonment is taking place in Europe, leading to ecological changes in rural landscapes. Appropriate restoration strategies can increase the resilience of the resulting ecosystems and provide habitats for diverse communities. Building on wilderness mapping, the third study explores the opportunities and challenges of ecological rewilding as a management and restoration option for abandoned farmland in Europe. I extract the wilderness metrics mapped in the previous chapter to the areas projected to be abandoned by 2040 according to the Dyna-CLUE model. This analysis shows regional differences in the dimensions of wilderness which are lacking in areas of abandonment. However, in most cases, the impact of infrastructures is low while the deviation from potential natural vegetation is high which suggest low human densities and large changes in the structure of ecosystems due to agriculture. Management should be directed at improving the wilderness dimensions most affected by human pressures in each area.

The second and third studies of this thesis are relevant for achieving ***Target 15*** which proposes the restoration of at least 15% of degraded areas. Thus, these results also contribute insights for the effective management of protected areas in Europe (***Target 11)***.

Research area 3. Ecosystem services have a multilayered relationship with biodiversity. Some services depend on multiple ecosystem functions driven by whole ecological communities. These services are usually estimated based on ecosystem-level metrics of biodiversity such as vegetation cover. I call them here biophysical-based services. Other services depend directly on service-providing species. I refer to them as biodiversity-based services. Spurred by the growth of remote-sensing products, most large-scale assessments include only biophysical-based services. Thus, policy and management decisions aimed at improving the supply of ecosystem services are based on incomplete assessments.

In the fourth study, I address this gap at European level by estimating nine biodiversity-based services. These results complement current assessments that include only biophysical-based services. The analysis shows that areas providing high levels of biophysical-based services do not necessarily provide also high levels of biodiversity-based services. Regardless of the type of services, the relationship with biodiversity is stronger the more services are considered. Thus, incomplete

assessment of services can lead to the underestimation of the importance of biodiversity for service supply.

These results are particularly important for ***Target 14***, which provides for the restoration and safeguarding the ecosystems that provide essential services. However, there are important implications also for prioritizing areas for biodiversity and ecosystem services (***Target 11***).

Chapter 1

Introduction

1.1 Biodiversity dimensions

Biodiversity has gradually become an integrator of all conservation targets (Mace 2014). With growing understanding of social-ecological dynamics, new dimensions have been added to the concept of biodiversity. First, wilderness conservation as expression of freedom and beauty became prominent in the nineteenth century in North America (Nash 2001). Then, awareness of the negative effects of human activities (Carson 1962) brought a preoccupation for species preservation and extinction risk (Rodrigues *et al.* 2006). The concept of ecosystem services was integrated after researchers described the important benefits that humans derive from ecosystems (Ehrlich and Mooney 1983; Daily 1997). More recently, ecosystem functions and processes have been recognized as the mechanisms driving both services (Isbell *et al.* 2011) and the structure and composition of ecosystems (Mazancourt *et al.* 2013). These different approaches to biodiversity have complemented each other rather than replaced each other (Mace 2014), leading to the development of new research areas.

The different biodiversity dimensions are difficult to capture by one metric (Pereira *et al.* 2012; Schippers *et al.* 2014; Santini *et al.* 2016). However, multiple measures of biodiversity show consistently a decline caused by human impact (Butchart *et al.* 2010). For instance, wilderness areas have decreased by one tenth in the last two decades, especially in the areas of high species richness (Watson *et al.* 2016). Species extinctions have increased by several orders of magnitude compared to background rates (Pimm *et al.* 2014). Land-use and related pressures lead to significant declines in local biodiversity, both in terms of species and abundances (Newbold *et al.* 2015). Research suggests that species loss can lead to loss of ecosystem functions (Cardinale *et al.* 2006) which cascades into service decline (Balvanera *et al.* 2006; Isbell *et al.* 2015).

While all these biodiversity dimensions are strongly connected and have similar drivers of decline, they are also very difficult to address together in management and policy decisions (Adams 2014; Kleijn *et al.* 2015). In order to deal with biodiversity loss, the Aichi Biodiversity Targets were agreed by world leaders in Nagoya in 2009 as a new strategy for biodiversity conservation for the decade between 2011-2020 (Secretariat of CBD 2010). Mirroring the complexity of biodiversity science and the challenges ahead, the Aichi Biodiversity Targets suggest multiple paths for addressing biodiversity loss but the interconnections are strong between the different elements of the biodiversity strategy (Marques *et al.* 2014). Recent assessments indicate that substantial efforts are still necessary to reach the targets for 2020 (Tittensor *et al.* 2014).

This thesis provides contributions applicable in achieving three of the 20 Aichi Biodiversity Targets by integrating several dimensions of biodiversity: species richness, vulnerability and rarity, wilderness, megafauna and ecosystem services.

1.2 Expansion of protected areas

Target 11 of the Aichi Targets envisions 17% of the terrestrial areas and 10% of the coastal and marine areas being conserved and effectively managed through the expansion of protected areas and other conservation measures (Secretariat of CBD 2010). Moreover, the expansion of the protected areas should particularly target areas important for biodiversity and ecosystem services. The challenges related to this target are multiple. One of the most difficult to overcome is the limited resources available for effectively expanding protected areas (Halpern *et al.* 2006). Thus, appropriate metrics and methodologies are needed to identify the area that would provide the highest benefits for biodiversity and ecosystem services (Margules and Pressey 2000). Another important challenge is designing and implementing effective management for conserving biodiversity and ecosystem services (Leverington *et al.* 2010).

Competing with multiple land-uses, conservation needs to focus on areas that would deliver the highest biodiversity benefits through conservation. While in the past the criteria for the location of natural parks were scenic beauty and availability of hunting game (Nash 2001), researchers have more recently proposed a range of biodiversity surrogates and methodologies. These approaches use different metrics to assess potential conservation areas based on two criteria: irreplaceability and vulnerability (Margules and Pressey 2000; Brooks *et al.* 2006). Most approaches prioritize areas of high irreplaceability measured based on species endemism, taxonomic uniqueness or expert opinion (Brooks *et al.* 2006). In terms of vulnerability, some methodologies prioritize highly vulnerable areas and Brooks *et al.* (2006) define them as reactive approaches. Other methodologies, prioritize areas of low vulnerability, thus being proactive in preventing biodiversity loss and taking advantage of low protection costs (Brooks *et al.* 2006). Measures of vulnerability usually include amount of habitat loss (Myers *et al.* 2000) and other measures of human pressures (Sanderson *et al.* 2002).

One of the best known reactive approaches for designating conservation priorities is biodiversity hotspots. This approach was initially applied at global scale (Myers 1988) but it was used subsequently for prioritization at smaller extents (Williams *et al.* 1996; Kati *et al.* 2004). As a measure of irreplaceability, the downscaled approaches use species richness or rarity while vulnerability is often assessed in terms of species vulnerability.

Systematic conservation planning aims to further improve the efficacy of priority setting through establishing conservation targets and selecting areas based on their contribution to the unrepresented conservation targets (Margules and Pressey 2000; Ardron *et al.* 2008). This approach emphasizes the complementarity between areas and removes redundancy in the representation of conservation features in order to increase the effectiveness of limited resources. Several algorithms have been created in order to increase the efficiency of the selection of conservation areas such as Marxan (Ball *et al.* 2009) and Zonation (Moilanen *et al.* 2009). These algorithms have been applied to networks of protected areas (Day 2002) but they have also been used to address more conceptual questions on how to reconcile different conservation goals (Chan *et al.* 2006).

Proactive approaches usually emphasize the intactness of ecosystems and use metrics of human presence or ecological intactness as measures of vulnerability (Carver 1996; Aplet *et al.* 2000; Selva *et al.* 2011). The aim is to protected areas that are closest to their natural state and present the most complete trophic networks and ecosystem processes (Watson *et al.* 2009; Carver 2010).

Reactive and proactive approaches are difficult to reconcile at large scales, proposing different areas for conservation (Brooks *et al.* 2006; Klein *et al.* 2009). However, assessments at finer scales are lacking. Most comparisons between prioritization approaches have involved only reactive approaches such as hotspots and complementarity (Williams *et al.* 1996; Kati *et al.* 2004). Moreover, considering the multiple biodiversity goals of conservation, these different prioritization approaches have not been assessed in terms of representing simultaneously several biodiversity metrics.

An underrepresented topic in conservation prioritization is also the use of prioritization approaches in zoning of protected areas for effective management (but see del Carmen Sabatini *et al.* 2007; Geneletti and van Duren 2008). Marine areas have benefited more from research on this approach, especially to reconcile conservation with fishing activities (Villa *et al.* 2002). But despite the IUCN guidelines that suggest zoning as a management tool for achieving protection goals (Dudley 2008), few studies address this aspect in terrestrial protected areas. As their metrics are intuitive and well-studied in the literature, prioritization approaches could provide valuable insights for the implementation of zoning to achieve multiple conservation goals.

1.3 Restoration of degraded ecosystems

Target 15 envisions the restoration of at least 15 per cent of degraded ecosystems in order to contribute to ecosystem resilience and to combat climate change and desertification (Secretariat of CBD 2010). One of the fundamental issues for restoration is the definition of degraded areas (Balaguer *et al.* 2014). The perception of degradation differs depending on the context and history of human occupation. Thus, addressing restoration requires an assessment of the context of degradation and the opportunities for implementation (Suding 2011).

Some forms of land degradation are uncontroversial. For instance, soil degradation with loss of fertility is recognized as one of the major problems for agricultural production and the prevention of desertification (Liu *et al.* 2008). Similarly, damages produced by mining activities are salient through their high level of toxicity and immediate effects (Deikumah *et al.* 2014). However, in cases where human societies have gradually modified the landscape during long time periods, people come to see the modified landscape as the natural state of ecosystems (Navarro and Pereira 2012). This phenomenon is called shifting baseline syndrome (Papworth *et al.* 2009) and it is strongly evident in some European reactions to farmland abandonment (Halada *et al.* 2011; Prach *et al.* 2013).

In reality, millennia of agriculture in Europe have led to a reduction of fauna, particularly at the top of the trophic chains (Barnosky 2008), and to a complete change of vegetation cover (Kaplan *et al.* 2009). Moreover, large herbivores were removed from the landscape in order to make space for domestic herbivores (Navarro *et al.* 2015). This has resulted in ecological communities lacking resilience to disturbances (Proença *et al.* 2010) and becoming dependent on human presence (Sirami *et al.* 2008). These changes also affect ecosystem services (Cerqueira *et al.* 2015). For instance, carbon stocks were reduced and soil protection decreased, amplifying the potential for desertification in the drier areas of the continent (Maestre *et al.* 2009).

In the past decades, due to socio-economic changes, rural areas of low agricultural productivity became depopulated and abandoned (Rey Benayas *et al.* 2007). Ecological communities are also changing as a result of decreased human presence. Several species of megafauna are taking advantage of the new resources and are reclaiming the lost territory (Enserink and Vogel 2006). While some researchers advocate for continuous management interventions in order to maintain the current ecological communities (Prach *et al.* 2013), others propose an approach based on naturally evolving systems (Pereira and Navarro 2015) or subtle interventions that can rebuild resilience (Rey Benayas *et al.* 2008).

Ecological rewilding is the largely passive management of ecological succession after farmland abandonment with the goal of restoring natural processes and reducing human influence on the landscape (Navarro and Pereira 2012). Rewilding aims to rebuild aspects of wilderness that were lost through human occupation but a large-scale approach to managing rewilding is lacking. Wilderness mapping at European level shows that much of the remaining wilderness in Europe can be found in mountainous areas (Carver 2010). As many abandoned areas are found around mountainous areas, there is a huge potential for building on current wilderness areas for a successful rewilding, especially in terms of benefiting from seed banks and residual wildlife populations.

1.4 Restoration and safeguarding of essential ecosystem services

Target 14 envisions that ecosystems providing essential services are safeguarded and restored, taking into account especially the needs of the most vulnerable groups (Secretariat of CBD 2010). One of the thorniest issue in biodiversity science has been until now the relationship between ecosystem services and biodiversity (Adams 2014). The effective preservation of both ecosystem services and biodiversity rests on coordinating the conservation and restoration of these two biodiversity dimensions.

The relationship between biodiversity and ecosystem services has benefitted from a long and fruitful debate in the literature. For instance, conservation prioritization studies at regional and local scales have pointed out that biodiversity and ecosystem services do not always coincide spatially (Chan *et al.* 2006; Schröter *et al.* 2014). Studies at field level have also pointed out that species richness does not drive pollination services, thus these services are not a sufficient argument for the conservation of wild pollinators (Kleijn *et al.* 2015). This has led many to the conclusion that biodiversity and ecosystem services should be kept as two separate goals in conservation (Adams 2014). On the other hand, Isbell *et al.* (2011) show that considering an increasing number of environmental conditions, locations and services, leads to an increasing number of species being needed for supplying adequate levels of ecosystem functions and services.

The reason for these apparently contradictory results might stem from the fact that not all services have the same causal relationships and, implicitly, the same connection to biodiversity (Mace *et al.* 2012). Some services are dependent on several ecosystem processes, which, in turn, depend on multiple species and interactions between biotic and abiotic components. For instance, climate control depends on productivity and carbon sequestration, which depend on whole ecological communities and their interactions with their physical environment (Ruesch and Gibbs 2008). The estimation of these services is usually based on biodiversity data at ecosystem-level such as land cover (Maes *et al.* 2012). Other services, such as pest control, are directly dependent on certain species and functional groups, without direct influences from other ecological processes (Karp *et al.* 2013). However, most service assessments have equated all services with those relying on nonlinear and complex biotic and abiotic interactions, without accounting for services supplied directly by biodiversity (Chan *et al.* 2006; Naidoo *et al.* 2008; Maes *et al.* 2012). This results in management and policy decisions based on incomplete assessments of ecosystem services.

1.5 Objectives of the thesis

The overall objective of this thesis is to contribute to research areas crucial to addressing the current biodiversity challenges. The contribution of each of the chapters inteded for publication can be mapped to at least one of the Aichi Biodiversity Targets.

Chapter 2 contributes to the issue of prioritizing areas for conservation and zoning of protected areas. In this chapter I answer the question: is one type of prioritization sufficient to reach multidimensional biodiversity targets? The results of my analysis are relevant for ***Target 11*** that recommends the expansion of terrestrial protected areas to 17% of the globe. In order to achieve the maximum biodiversity benefits, the areas for expansion need to be chosen based on clear methodologies that maximize multiple biodiversity targets. The work in **Chapter 2** is also relevant for ***Target 14*** which provides for the restoration and safeguarding of ecosystems supplying essential services (Figure 1.1).

The work of **Chapter 2** was published as: Ceauşu, Silvia, Inês Gomes, and Henrique Miguel Pereira. "Conservation Planning for Biodiversity and Wilderness: A Real-World Example." *Environmental Management* 55, no. 5 (May 2015): 1168–80.

Chapters 3 and 4 address rewilding as a restoration approach for abandoned farmland. First, **Chapter 3** maps several dimensions of wilderness which have been modified by different human drivers. These changes have led to ecological and subjective impacts that influence ecological communities and the human perception of wilderness. Based on these metrics, **Chapter 4** assesses the opportunities and challenges for implementing and managing rewilding. The wilderness metrics mapped in **Chapter 3** are extracted at areas of projected abandonment by 2040. This highlights which wilderness dimensions are lacking in target areas and allows for a discussion on strategies to address these gaps. Moreover, this assessment of rewilding opportunities emphasizes the different time scales necessary for changes in the effects of human impact. The results of **chapters 3 and 4** are particularly relevant for ***Target 15*** which envisions the restoration of 15% of degraded areas. However, the results have also important implications for the management of protected areas, especially in Europe where many sites of the Natura 2000 network are close to areas of projected abandonment. Thus, **chapters 3 and 4** contribute also to ***Target 11*** (Figure 1.1).

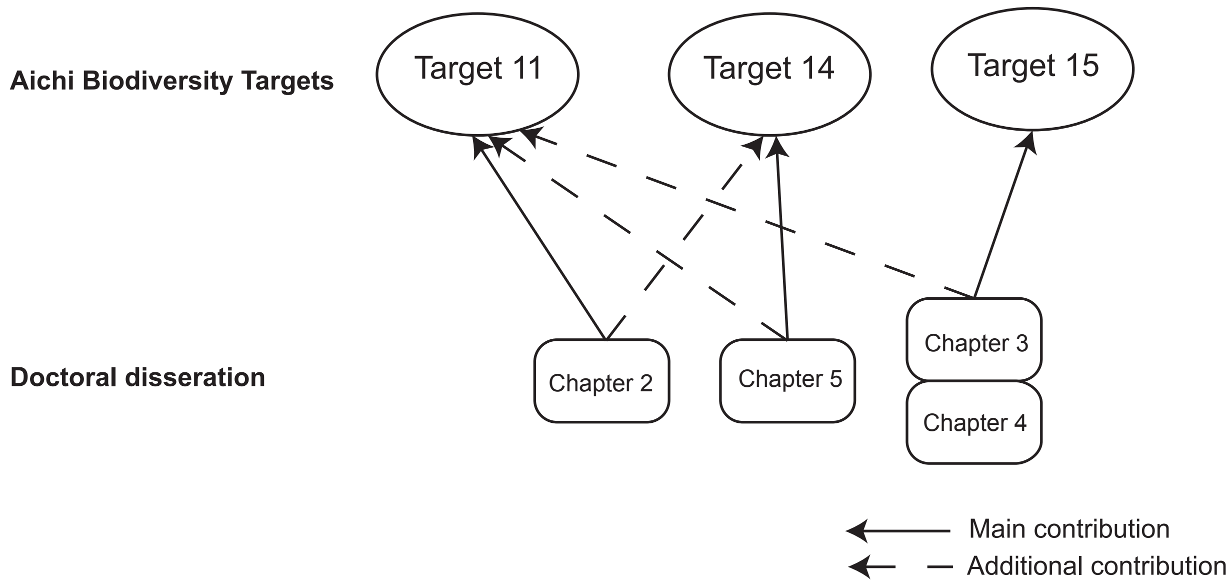

Figure 1.1. The contributions of the chapters of this thesis to the three Aichi Biodiversity Targets. This figure highlights both main and additional contributions. ***Target 11*** recommends the expansion of terrestrial and marine protected areas to 17% and 11% respectively, of the global area while also ensuring effective management. ***Target 14*** envisions the restoration and safeguarding of essential services. ***Target 15*** proposes the restoration of at least 15% of degraded areas

Chapter 3 was published as: Ceaușu, Silvia, Steve Carver, Peter H. Verburg, Helga U. Kuechly, Franz Holker, Lluís Brotons, and Henrique M. Pereira. "European Wilderness in a Time of Farmland Abandonment." In *Rewilding European Landscapes*, Pereira H.M. and Navarro L.M., 25–46. Springer Netherlands, 2015.

Chapter 4 was published as: Ceaușu, Silvia, Max Hofmann, Laetitia M. Navarro, Steve Carver, Peter H. Verburg, and Henrique M. Pereira. "Mapping Opportunities and Challenges for Rewilding in Europe." *Conservation Biology* 29, no. 4 (2015): 1017–1027.

Chapter 5 addresses the relationship between biodiversity and ecosystem services. Specifically, it addresses the gap in the studies mapping and assessing ecosystem services at large scales as these studies address almost exclusively services provided indirectly by biodiversity and estimated based on biophysical data. We complement these assessments with a European assessment of services provided directly by biodiversity and estimated based on species presence data. This work is extremely relevant for ***Target 14*** which stipulates the restoration and safeguarding of essential services. However, the results of this work have important implications also for prioritizing and managing conservation areas (***Target 11***) (Figure 1.1). The manuscript of this chapter is currently in preparation for submission.

Chapter 6 synthesizes the contributions of the previous chapters by organizing them according to the relevant Aichi Biodiversity Target. It integrates the results into a discussion on how to address the growing challenges of global change and improve the efficacy of conservation actions.

Bibliography

Adams WM. 2014. The value of valuing nature. *Science* **346**: 549–551.

Aplet G, Thomson J, and Wilbert M. 2000. Indicators of wildness: Using attributes of the land to assess the context of wilderness. In: Proceedings: Wilderness Science in a Time of Change. Ogden (UT): USDA Forest Service, Rocky Mountain Research Station. Proc. RMRS-P-15.

Ardron JA, Possingham HP, and Klein CJ. 2008. Marxan Good Practices Handbook. External review version. *Pac Mar Anal Res Assoc Www Pacmara Org Vanc BC Can*: 155.

Balaguer L, Escudero A, Martín-Duque JF, *et al.* 2014. The historical reference in restoration ecology: Re-defining a cornerstone concept. *Biol Conserv* **176**: 12–20.

Ball IR, Possingham HP, and Watts M. 2009. Marxan and relatives: software for spatial conservation prioritisation. *Spat Conserv Prioritisation Quant Methods Comput Tools Oxf Univ Press Oxf U K*: 185–195.

Balvanera P, Pfisterer AB, Buchmann N, *et al.* 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecol Lett* **9**: 1146–56.

Barnosky AD. 2008. Megafauna biomass tradeoff as a driver of Quaternary and future extinctions. *Proc Natl Acad Sci* **105**: 11543–8.

Brooks TM, Mittermeier RA, Fonseca GA. da, *et al.* 2006. Global biodiversity conservation priorities. *Science* **313**: 58.

Butchart SH., Walpole M, Collen B, *et al.* 2010. Global biodiversity: indicators of recent declines. *Science* **328**: 1164.

Cardinale BJ, Srivastava DS, Duffy JE, *et al.* 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature* **443**: 989–992.

Carmen Sabatini M del, Verdiell A, Rodríguez Iglesias RM, and Vidal M. 2007. A quantitative method for zoning of protected areas and its spatial ecological implications. *J Environ Manage* **83**: 198–206.

Carson R. 1962. Silent Spring. *Honghton Mifflin Co Boston*.

Carver S. 1996. Mapping the wilderness continuum using raster GIS. *Raster Imag Geogr Inf Syst OnWord Press N M*: 283–288.

Carver S. 2010. Mountains and wilderness. *Eur Environ Agency 2010 Eur Ecol Backbone Recognising True Value Our Mt Eur Environ Agency Cph*: 192–201.

Cerqueira Y, Navarro LM, Maes J, *et al.* 2015. Ecosystem services: the opportunities of rewilding in Europe. In: Rewilding European landscapes. Springer.

Chan KM., Shaw MR, Cameron DR, *et al.* 2006. Conservation planning for ecosystem services. *PLoS Biol* **4**: e379.

Daily G. 1997. Nature's services: societal dependence on natural ecosystems. Island Press.

Day JC. 2002. Zoning—lessons from the Great Barrier Reef marine park. *Ocean Coast Manag* **45**: 139–156.

Deikumah JP, McAlpine CA, and Maron M. 2014. Mining matrix effects on West African rainforest birds. *Biol Conserv* **169**: 334–43.

Dudley N. 2008. Guidelines for applying protected area management categories. IUCN.

Ehrlich PR and Mooney HA. 1983. Extinction, substitution, and ecosystem services. *BioScience* **33**: 248–254.

Enserink M and Vogel G. 2006. Wildlife conservation: the carnivore comeback. *Science* **314**: 746.

Geneletti D and Duren I van. 2008. Protected area zoning for conservation and use: A combination of spatial multicriteria and multiobjective evaluation. *Landsc Urban Plan* **85**: 97–110.

Halada L, Evans D, Romão C, and Petersen JE. 2011. Which habitats of European importance depend on agricultural practices? *Biodivers Conserv* **20**: 2365–2378.

Halpern BS and others. 2006. Gaps and mismatches between global conservation priorities and spending. *Conserv Biol* **20**: 56–64.
Isbell F, Calcagno V, Hector A, *et al.* 2011. High plant diversity is needed to maintain ecosystem services. *Nature* **477**: 199–202.
Isbell F, Tilman D, Polasky S, and Loreau M. 2015. The biodiversity-dependent ecosystem service debt. *Ecol Lett* **18**: 119–134.
Kaplan JO, Krumhardt KM, and Zimmermann N. 2009. The prehistoric and preindustrial deforestation of Europe. *Quat Sci Rev* **28**: 3016–3034.
Karp DS, Mendenhall CD, Sandí RF, *et al.* 2013. Forest bolsters bird abundance, pest control and coffee yield. *Ecol Lett* **16**: 1339–1347.
Kati V, Devillers P, Dufrene M, *et al.* 2004. Hotspots, complementarity or representativeness? Designing optimal small-scale reserves for biodiversity conservation. *Biol Conserv* **120**: 471–480.
Kleijn D, Winfree R, Bartomeus I, *et al.* 2015. Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. *Nat Commun* **6**.
Klein CJ, Wilson KA, Watts M, *et al.* 2009. Spatial conservation prioritization inclusive of wilderness quality: A case study of Australia's biodiversity. *Biol Conserv* **142**: 1282–1290.
Leverington F, Costa KL, Pavese H, *et al.* 2010. A global analysis of protected area management effectiveness. *Environ Manage* **46**: 685–698.
Liu J, Li S, Ouyang Z, *et al.* 2008. Ecological and socioeconomic effects of China's policies for ecosystem services. *Proc Natl Acad Sci* **105**: 9477–9482.
Mace GM. 2014. Whose conservation? *Science* **345**: 1558–1560.
Mace GM, Norris K, and Fitter AH. 2012. Biodiversity and ecosystem services: a multilayered relationship. *Trends Ecol Evol* **27**: 19–26.
Maes J, Paracchini ML, Zulian G, *et al.* 2012. Synergies and trade-offs between ecosystem service supply, biodiversity, and habitat conservation status in Europe. *Biol Conserv* **155**: 1–12.
Maestre FT, Bowker MA, Puche MD, *et al.* 2009. Shrub encroachment can reverse desertification in semi-arid Mediterranean grasslands. *Ecol Lett* **12**: 930–941.
Margules CR and Pressey RL. 2000. Systematic conservation planning. *Nature* **405**: 243–253.
Marques A, Pereira HM, Krug C, *et al.* 2014. A framework to identify enabling and urgent actions for the 2020 Aichi Targets. *Basic Appl Ecol* **15**: 633–8.
Mazancourt C, Isbell F, Larocque A, *et al.* 2013. Predicting ecosystem stability from community composition and biodiversity. *Ecol Lett* **16**: 617–625.
Moilanen A, Kujala H, and Leathwick JR. 2009. The Zonation framework and software for conservation prioritization. *Spat Conserv Prioritization*: 196–210.
Myers N. 1988. Threatened biotas:" hot spots" in tropical forests. *The environmentalist* **8**: 187–208.
Myers N, Mittermeier RA, Mittermeier CG, *et al.* 2000. Biodiversity hotspots for conservation priorities. *Nature* **403**: 853–858.
Naidoo R, Balmford A, Costanza R, *et al.* 2008. Global mapping of ecosystem services and conservation priorities. *Proc Natl Acad Sci* **105**: 9495.
Nash R. 2001. Wilderness and the American mind. Yale Nota Bene.
Navarro L and Pereira H. 2012. Rewilding Abandoned Landscapes in Europe. *Ecosystems* **15**: 900–12.
Navarro LM, Proença V, Kaplan JO, and Pereira HM. 2015. Maintaining Disturbance-Dependent Habitats. In: Rewilding European landscapes. Springer Netherlands.
Newbold T, Hudson LN, Hill SL, *et al.* 2015. Global effects of land use on local terrestrial biodiversity. *Nature* **520**: 45–50.

Papworth SK, Rist J, Coad L, and Milner-Gulland EJ. 2009. Evidence for shifting baseline syndrome in conservation. *Conserv Lett* **2**: 93–100.

Pereira HM and Navarro LM. 2015. Rewilding European landscapes. Springer.

Pereira HM, Navarro LM, and Martins IS. 2012. Global Biodiversity Change: The Bad, the Good, and the Unknown. *Annu Rev Environ Resour* **37**: 25–50.

Pimm SL, Jenkins CN, Abell R, *et al.* 2014. The biodiversity of species and their rates of extinction, distribution, and protection. *Science* **344**: 1246752.

Prach K, Jongepierová I, and Řehounková K. 2013. Large-Scale Restoration of Dry Grasslands on Ex-Arable Land Using a Regional Seed Mixture: Establishment of Target Species. *Restor Ecol* **21**: 33–39.

Proença VM, Pereira HM, Guilherme J, and Vicente L. 2010. Plant and bird diversity in natural forests and in native and exotic plantations in NW Portugal. *Acta Oecologica* **36**: 219–226.

Rey Benayas JM, Bullock JM, and Newton AC. 2008. Creating woodland islets to reconcile ecological restoration, conservation, and agricultural land use. *Front Ecol Environ* **6**: 329–36.

Rey Benayas JM, Martins A, Nicolau JM, and Schulz JJ. 2007. Abandonment of agricultural land: an overview of drivers and consequences. *CAB Rev Perspect Agric Vet Sci Nutr Nat Resour* **2**: 1–14.

Rodrigues ASL, Pilgrim JD, Lamoreux JF, *et al.* 2006. The value of the IUCN Red List for conservation. *Trends Ecol Evol* **21**: 71–6.

Ruesch A and Gibbs HK. 2008. New IPCC Tier-1 Global Biomass Carbon Map for the Year 2000http://cdiac.ornl.gov/epubs/ndp/global_carbon/carbon_documentation.html#datafiles. Viewed 2 Jun 2016.

Sanderson EW, Jaiteh M, Levy MA, *et al.* 2002. The human footprint and the last of the wild. *BioScience* **52**: 891–904.

Santini L, Belmaker J, Costello MJ, *et al.* 2016. Assessing the suitability of diversity metrics to detect biodiversity change. *Biol Conserv*.

Schippers P, Teeffelen AJA van, Verboom J, *et al.* 2014. The impact of large herbivores on woodland–grassland dynamics in fragmented landscapes: The role of spatial configuration and disturbance. *Ecol Complex* **17**: 20–31.

Schröter M, Rusch GM, Barton DN, *et al.* 2014. Ecosystem services and opportunity costs shift spatial priorities for conserving forest biodiversity. *PloS One* **9**: e112557.

Secretariat of CBD. 2010. Strategic Plan for Biodiversity 2011-2020 - Tenth Conference of the Parties.

Selva N, Kreft S, Kati V, *et al.* 2011. Roadless and low-traffic areas as conservation targets in Europe. *Environ Manage* **48**: 865–877.

Sirami C, Brotons L, Burfield I, *et al.* 2008. Is land abandonment having an impact on biodiversity? A meta-analytical approach to bird distribution changes in the north-western Mediterranean. *Biol Conserv* **141**: 450–459.

Suding KN. 2011. Toward an era of restoration in ecology: successes, failures, and opportunities ahead. *Annu Rev Ecol Evol Syst* **42**: 465.

Tittensor DP, Walpole M, Hill SLL, *et al.* 2014. A mid-term analysis of progress toward international biodiversity targets. *Science* **346**: 241–4.

Villa F, Tunesi L, and Agardy T. 2002. Zoning Marine Protected Areas through Spatial Multiple-Criteria Analysis: the Case of the Asinara Island National Marine Reserve of Italy. *Conserv Biol* **16**: 515–526.

Watson JE., Fuller RA, Watson AW., *et al.* 2009. Wilderness and future conservation priorities in Australia. *Divers Distrib* **15**: 1028–1036.

Watson JE, Shanahan DF, Di Marco M, *et al.* 2016. Catastrophic Declines in Wilderness Areas Undermine Global Environment Targets. *Curr Biol*.

Williams P, Gibbons D, Margules C, *et al.* 1996. A comparison of richness hotspots, rarity hotspots, and complementary areas for conserving diversity of British birds. *Conserv Biol* **10**: 155–174.

Chapter 2

Conservation Planning for Biodiversity and Wilderness: A Real-World Example

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Conservation Planning for Biodiversity and Wilderness: A Real-World Example

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Abstract Several of the most important conservation prioritization approaches select markedly different areas at global and regional scales. They are designed to maximize a certain biodiversity dimension such as coverage of species in the case of hotspots and complementarity, or composite properties of ecosystems in the case of wilderness. Most comparisons between approaches have ignored the multidimensionality of biodiversity. We analyze here the results of two species-based methodologies—hotspots and complementarity—and an ecosystem-based methodology—wilderness—at local scale. As zoning of protected areas can increase the effectiveness of conservation, we use the data employed for the management plan of the Peneda-Gerês National Park in Portugal. We compare the approaches against four criteria: species representativeness, wilderness coverage, coverage of important areas for megafauna, and for regulating ecosystem services. Our results suggest that species- and ecosystem-based approaches select significantly different areas at local scale. Our results also show that no approach covers well all biodiversity dimensions. Species-based approaches cover species distribution better, while the ecosystem-based approach favors wilderness, areas important for megafauna, and for ecosystem services. Management actions addressing different dimensions of biodiversity have a potential for contradictory effects, social conflict, and ecosystem services trade-offs, especially in the context of current European biodiversity policies. However, biodiversity is multidimensional, and management and zoning at local level should reflect this aspect. The consideration of both species- and ecosystem-based approaches at local scale is necessary to achieve a wider range of conservation goals.

Keywords Area prioritization · Conservation management · Complementarity · Conservation planning · Protected areas · Wilderness · Zoning

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Introduction

Biodiversity is facing tremendous threats from human-induced causes all over the world (Butchart et al. 2010; Pereira et al. 2010). In this context, academia, international organizations, and donors work intensely toward setting priorities in order to maximize the impact of conservation efforts (Meir et al. 2004; Halpern et al. 2006; Wilson et al. 2006). But despite the increased complexity of area prioritization methodologies and their growing implementation (Pressey and Bottrill 2008), indicators suggest little success in limiting the loss of biodiversity and ecosystem services (Butchart et al. 2010).

Designating biodiversity hotspots is one of the best known approaches. It is based at global scale on measures of species endemism and habitat loss (Myers et al. 2000), and at smaller scales on species richness and species rarity metrics (Rey Benayas and de la Montana 2003; Kati et al. 2004). The systematic conservation planning approach added complementarity into the site selection process as a measure of the contribution of a particular area to the overall unrepresented conservation targets, thus increasing the area efficiency of conservation areas (Ferrier et al. 2000; Margules and Pressey 2000). Wilderness methodologies on the other hand use continuous measures of the intensity of human encroachment in order to select the areas that have experienced the lowest impact of human presence and modern technologies (Klein et al. 2009; Watson et al. 2009). The aim is to protect those ecosystems that are closest to their natural state, have the most complete trophic networks, and therefore are still supplying specific regulating, supporting, and cultural ecosystem services (Naidoo et al. 2008; Watson et al. 2009, 2011).

When compared at bigger scales, these approaches, hotspots and complementarity on one hand and wilderness on the other, lead to different conservation priorities (Mittermeier et al. 2003; Brooks et al. 2006; Klein et al. 2009). Brooks et al. (2006) explain these differences as opposing attitudes toward vulnerability, with approaches like hotspots prioritizing areas of high vulnerability and wilderness approaches prioritizing areas of low vulnerability. However, another important conceptual difference between these approaches is the type of biodiversity dimensions that they are maximizing. While hotspots and complementarity have been designed to maximize separate ecosystem features such as species and vegetation types (Margules and Pressey 2000; Myers et al. 2000), wilderness methodologies address a composite quality of ecosystems (Aplet et al. 2000). There are few attempts to evaluate prioritization methodologies together and the focus has been mainly on species-based approaches (Kati et al. 2004; Diniz-Filho et al. 2006). When the comparisons have been more inclusive, the assessment was done unidimensionally against only one biodiversity criterion such as species richness (Klein et al. 2009; Watson et al. 2009) or ecosystem services (Naidoo et al. 2008).

In protected areas, much of the biodiversity management is done through land planning and land zoning in order to reconcile conservation actions with human use (Watts et al. 2009). Although zoning methodologies have been increasingly applied across a wide range of ecosystems (Salm and Siirila 2000; Villa et al. 2002; Linnell et al. 2005; Del Carmen et al. 2007; Geneletti and van Duren 2008; Watts et al. 2009), we lack a robust multidimensional comparison at local scale of zoning methodologies inclusive of ecosystem-based approaches. This is an important gap as zoning of established protected areas can have significant impacts on the results of conservation actions through higher resource efficiency, simplified management procedures, and higher predictability for the plans of local communities (Linnell et al. 2005).

Our research addresses the following research question: is one type of prioritization approach sufficient to reach multidimensional biodiversity targets at local scale? In order to answer this question, we approach two related problems: how different are the areas prioritized by species- and ecosystem-based approaches; and which prioritization approach maximizes each of the biodiversity targets considered. For this purpose, we map and compare zoning methodologies across multiple dimensions of biodiversity at local level in the Peneda-Gerês National Park (PNPG) in Northern Portugal (Fig. 1). We analyze the prioritization methodologies according to four criteria: total bird, reptile and amphibian species representativeness; coverage of wilderness as an indicator of naturally evolving ecosystems; coverage of the important areas for megafauna; and three regulating ecosystem services. Finally, we discuss the management implications, the advantages and the drawbacks of each prioritization methodology. While there are studies using complementarity and prioritization algorithms for wilderness and ecosystem services at larger scales (Chan et al. 2006; Klein et al. 2009; Moilanen et al. 2011), we chose to use wilderness as a separate prioritizing score and ecosystem services only as a comparison criterion in order to emphasize how zoning for different biodiversity dimensions leads to different solutions.

Methodology

Study Area and Datasets

The area of this study is the Peneda-Gerês National Park (PNPG) in northern Portugal (longitude 8°25′W and latitude 41°41′N), the only protected area with national park status in the country (Fig. 1). PNPG was initially established as a protected area in 1971 and it is included also in the Natura 2000 network (European Council 1979, 1992).

PNPG occupies a territory of approximately 700 km^2. The present human population living within the PNPG is approximately 8800 inhabitants (Instituto Nacional de

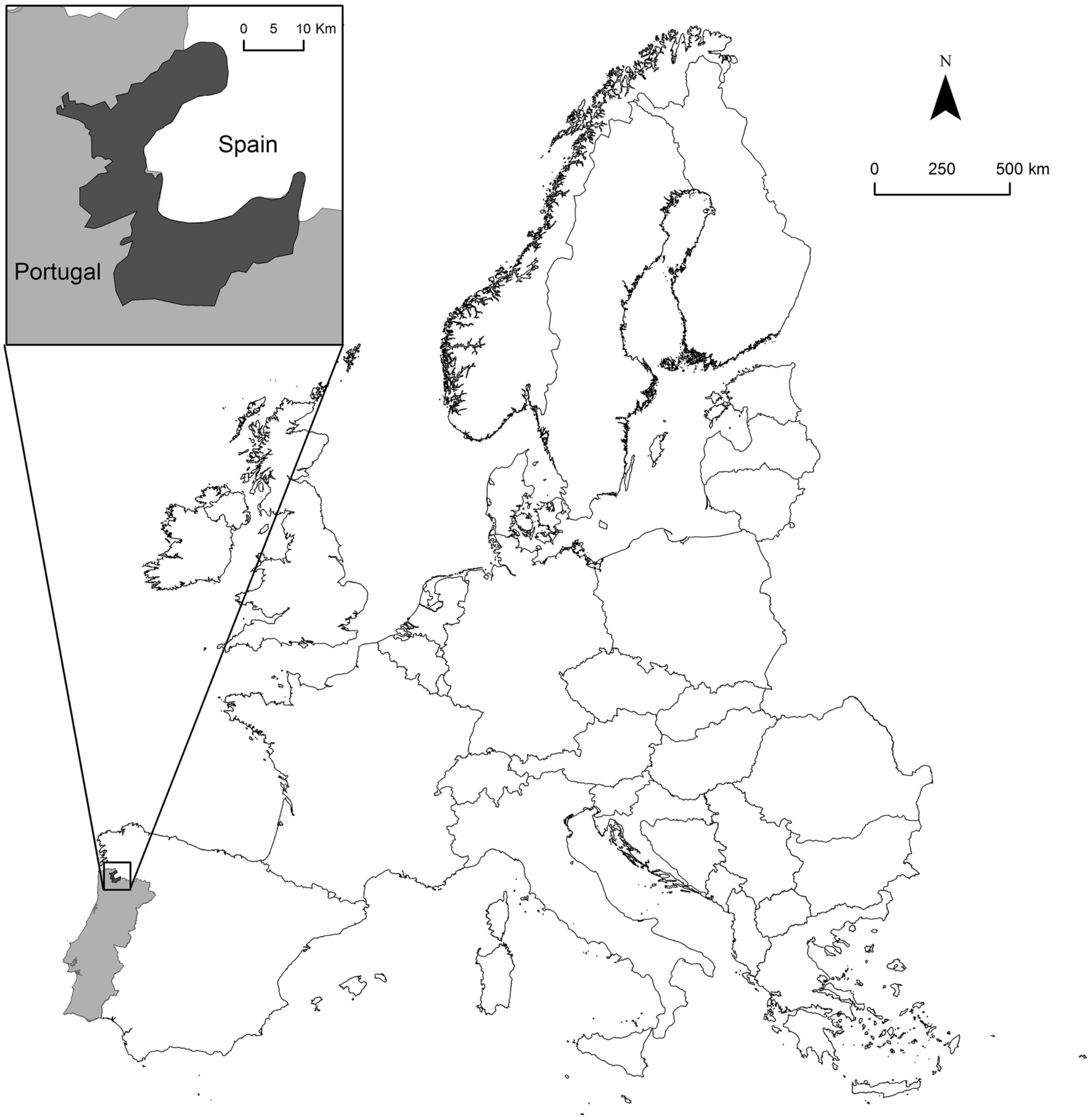

Fig. 1 The location of Peneda-Gerês National Park in the north of Portugal

Estatística 2011). Low-intensity agriculture and extensive grazing have been economically unproductive and the region is currently undergoing significant changes due to farmland abandonment. A significant area of the park has been classified as High Nature Value farmland by the European Union (European Environment Agency 2004). Habitat composition contains Atlantic and Mediterranean habitat types.

For the hotspots and the complementarity approaches, the territory of PNPG was divided in a grid of UTM quadrats of 2 km × 2 km, the highest resolution common to all species data. We used presence-absence data covering 13 species of amphibians, 20 species of reptiles, and 144 species of birds. Out of the total of 233 quadrats included in the analysis, information was missing for 13, 11, and 16 quadrats for birds, reptiles, and amphibians, respectively. The species data are atlas distribution data collected at the level of PNPG and published in Pimenta and Santarém (1996) for birds, and in Soares et al. (2005) for herpetofauna. The data represent recorded presences through multi-year monitoring of the territory of the park based on several methodologies (visual encounter surveys, calls surveys, search of potential shelters). The data also include ad hoc observations by the authors and the staff of PNPG. The data do not include abundance records.

For wilderness mapping, we rasterized the territory of the PNPG and the adjacent area in a grid with a pixel resolution of 10 m^2. We based the analysis (see below) on infrastructure data extracted from maps of the Portuguese Geographical Institute of the Army (Instituto Geográfico do Exército 1997).

We defined megafauna as the species in PNPG with the largest body mass for which we had data (PNPG-ICN 2008). As such, we used point data for locations of dens of wolf *Canis lupus* (Linnaeus, 1758), and past and present nesting sites for the eagle-owl *Bubo bubo* (Linnaeus, 1758), and golden eagle *Aquila chrysaetos* (Linnaeus, 1758). These data are based on annual monitoring of the wolf population and annual surveys of the nests of the birds of prey (PNPG-ICN 2008). We also used polygon data for important areas for wild goat *Capra pyrenaica* (Schinz, 1838), which were defined based on habitat characteristics (Moço et al. 2006). We created a buffer of 1 km around the point locations and we merged these buffer areas with those important for the wild goat. We chose this size of the buffer based on the literature on the effects of human disturbances on wolves and birds of prey (Thiel et al. 1998; Martínez et al. 2003; Penteriani et al. 2005; Ruddock and Whitfield 2007; Iliopoulos et al. 2014).

We used a digital elevation model (DEM) to define areas important for landslide protection (Earth Remote Sensing Data Analysis Center 2011) by prioritizing terrains with slopes steeper than 30°. We merged these areas with spring protection areas and groundwater recharge areas, which were calculated by the administration of PNPG based on the methodology described in Brilha (2005). The calculation was done based on land use, slope and elevation, hydrology of the area, and data collected from 130 locations across the park (PNPG-ICN 2008). These data refer to the supply of ecosystem services. The local population utilizes these ecosystem services through the use of local water and soil resources but the available data do not make it possible to estimate the spatial variation in the use of ecosystem services.

We used the ArcGIS 10 software package (Esri, CA, USA) for mapping and spatial analysis. We used MARXAN software (Ball et al. 2009) for applying the complementarity prioritization approach (Ardron et al. 2008). Statistical analyses were carried out in the R software package (R Development Core Team 2011).

Species-Based Approach: Hotspots

We calculated the number of species present and an average rarity and vulnerability for each grid cell. The rarity value of each species was the inverse of the number of cells in which the species was present. We assigned vulnerability scores to species on a scale from 0 to 10 according to the national red list (Cabral et al. 2005). We gave the least concern species the score 0 and to the critically endangered the maximum score of 10. We assigned scores to the next two threat categories at an equal distance of two units: 8—threatened, 6—vulnerable. Both near threatened and data-deficient categories contain species which cannot be assigned to a threatened category but which can also not be considered of least concern due to lack of data or due to impeding future threat. Thus, we combined these species into one mixed bag category, and we gave it the middle vulnerability score between least concern and vulnerable—3. We increased the difference in units compared to the threatened categories but, in the same time, we gave it a higher vulnerability score than the least concern category because it contains species that might be threatened presently or in the future. We assigned the value corresponding to the data-deficient class to the species for which information was not available. The choice of the scoring methodology does not have a strong impact on the ranking of the grid cells based on the hotspots methodology (Online resource 1).

We normalized the richness, average rarity, and average vulnerability into the [0,1] interval according to the formula:

$$x_{\mathrm{n}} = \frac{x - x_{\min}}{x_{\max} - x_{\min}}, \tag{1}$$

where x_{n} is the normalized value, x is the initial value, and $x_{\min}$ and $x_{\max}$ are the minimum and the maximum values across all species.

We prioritized the grid cells using $\mathrm{AI} = \mathrm{SR}_{\mathrm{n}} + R_{\mathrm{n}} + V_{\mathrm{n}}$, where AI is the aggregated index according to which we define biodiversity hotspots, and SR_n, R_n, and V_n are the normalized values for species richness, rarity, and vulnerability, respectively, for each grid cell. We decided to give them equal weight in our calculation because species richness, rarity, and vulnerability are all frequently used in conservation prioritization, many times jointly (Williams et al. 1996; Lawler et al. 2003; Brooks et al. 2006), but they often prioritize different areas without a consensus on which metric is better at capturing conservation value (Lennon et al. 2004; Orme et al. 2005).

Species-Based Approach: Complementarity

For the complementarity analysis, we simplified the vulnerability scoring used for the hotspots methodology. We classified as vulnerable all species which were not included in the least concern category of the national red list (56 out of 177 species). After several test runs, we considered a coverage of 50 % of the total number of occurrences of each vulnerable species and 10 % of the occurrences of each non-vulnerable species. We chose these percentages because they were the highest values for which all representation targets were fulfilled while allowing

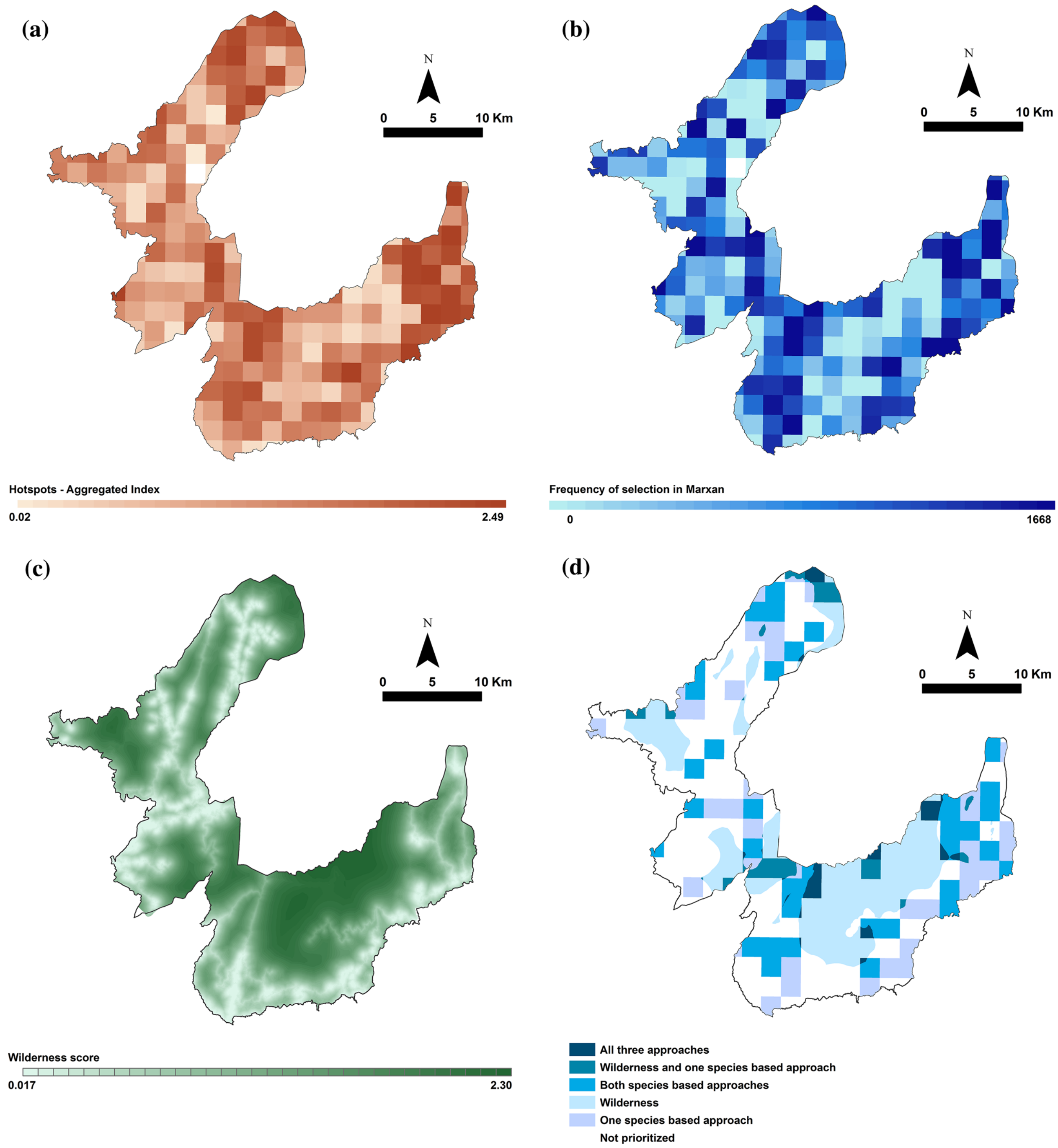

Fig. 2 The prioritization of the territory of Peneda-Gerês National Park (PNPG) according to **a** the hotspots approach; **b** the complementarity approach; **c** the wilderness approach. **d** The spatial congruence between the three approaches at 30 % prioritized area

enough variation in the different sets of selected areas (Ball et al. 2009). We set the target representation at 100 % for the species present in only one planning unit and we considered the costs of all planning units equal to unity. We performed 2000 runs of the MARXAN software and we used only the results meeting all the conservation targets. We then used the frequency of selection of each cell, also known as summed irreplaceability (Pryce et al. 2006; Ardron et al. 2008), as the prioritizing score.

Species-Based Approach: Wilderness

We used five infrastructure elements: the primary and secondary road networks, the human settlements, the power grid, and the hydroelectric dams. We chose these elements based on the local context of the park and on the literature (Fritz et al. 2000). Other elements used in the wilderness mapping literature, especially at larger scales, include railroads, human population density, biophysical naturalness based on expert opinions, and size of ecologically intact regions (Sanderson et al. 2002; Mittermeier et al. 2003; Woolmer et al. 2008). We expect such metrics to be highly correlated to the wilderness value calculated based on our selected infrastructures (e.g. human population density) or to be irrelevant for the scale of our study area (e.g. size of ecologically intact regions). We included in the analysis both the infrastructure inside the territory of the park, and the infrastructure found in the proximity of the park and which was likely to have an impact inside PNPG. As such, the external infrastructures were located in an air distance radius around the park of approximately 20 km in the case of the primary road network, and approximately 10 km in the case of the secondary road network, the power grid and the human settlements. We chose to consider infrastructures at these radiuses outside the park in order to account for both biodiversity effects and the human access and visual impact dimensions of wilderness (Fritz and Carver 1998; Cinzano et al. 2000; Carver et al. 2012).

We calculated the distance from each pixel to the nearest infrastructure of each type. We normalized the values into the interval [0,1] according to the formula:

$$d_n = 1 - \frac{1}{1 + \alpha * d}, \quad (2)$$

where d_n is the normalized value, d is the distance to the closest infrastructure element of the considered type, and α is a scaling constant equal to 0.001. We used this value of the scaling constant in order to describe the nonlinear relationship between human infrastructures and its impacts on biodiversity (Thiel et al. 1998; De Molenaar et al. 2006; Ruddock and Whitfield 2007) and on the perception of wilderness (Cinzano et al. 2000; Kuechly et al. 2012). These impacts are strong and rapidly decreasing in the first hundreds of meters or the first kilometers, depending on the type of infrastructure. Our formula leads to a rapid decrease of human impact in the 2 km adjacent to human infrastructures and the impact reaches an asymptote beyond this distance.

We calculated the wilderness index according to the formula:

$$W = \sum_i \beta_i d_i, \quad (3)$$

where W is the wilderness score in any pixel of the map, d is the distance from that pixel to the closest infrastructure element of type i, and β_i is the weight assigned to infrastructure of type i. We assigned the weights for each infrastructure based on the assessment of the technical staff of PNPG and the impacts documented in the literature (Fritz et al. 2000; Carver et al. 2002). Thus, primary roads and human settlements had $\beta_i = 1$, and secondary roads, power lines, and hydroelectric dams had $\beta_i = 0.25$.

Comparison of the Prioritization Approaches

The comparison of the three prioritization approaches includes the spatial congruence between the three approaches and the coverage of four biodiversity dimensions: species representativeness, wilderness coverage, coverage of important areas for megafauna, and ecosystem services. We calculated the spatial congruence between the three approaches for three levels of high-priority areas for conservation: 10, 20, and 30 % of the PNPG territory. Due to the lower resolution of the data used for the hotspots and complementarity approaches, the percentage cut-offs for the highest priority areas for these approaches have a variation from the high-priority targets of ±2 % of the total area.

We calculated Spearman's rank correlations between the prioritizing score of each approach, species richness, rarity, and vulnerability. We averaged the wilderness scores overlapping each of the 233 grid cells and used it to calculate the correlations.

We assessed the efficiency of species- and wilderness-based approaches by calculating the average percentage of each biodiversity dimension (BD) being protected per percentage unit of prioritized area. We calculated BD according to the formula:

$$\mathrm{BD}\,(\%) = \frac{1}{\Lambda}\frac{\mathrm{BD}_\Lambda}{\mathrm{BD}_{\max}}$$

where Λ is the percentage of area being prioritized; BD_Λ is the value of the biodiversity dimension covered by the prioritized area; and BD_{max} is the maximum value for the respective biodiversity dimension, either number of species, total wilderness value, or total important area for ecosystem services, and megafauna. We assigned Λ two percentage values: approximately 28 %—the minimum complementarity prioritized area that covers all the species in our list; and approximately 44 %—the minimum hotspots prioritized area that covers all the species. The percentages are approximations because of the different spatial units used for each approach but the difference between the sizes of the prioritized areas is never larger than 1 % of the total area of PNPG. Values are rounded up to two decimal places.

In order to calculate the cumulative representativeness of species, wilderness, and important areas for megafauna and ecosystem services, we converted the maps of the hotspots and complementarity approaches to rasters with a

Table 1 Spearman's rank correlation coefficients (ρ values) between the values of the prioritization parameters for the three approaches, species richness, species rarity, and species vulnerability

Parameter	Complementarity	Hotspots index	Wilderness score	Species richness	Species rarity	Species vulnerability
Complementarity		0.790***	−0.194**	0.643***	0.703***	0.415***
Hotspots index	–		−0.130*	0.628***	0.829***	0.685***
Wilderness score	–	–		−0.432***	−0.239***	0.299***
Species richness	–	–	–		0.492***	0.003
Species rarity	–	–	–	–		0.482***
Species vulnerability	–	–	–	–	–	

* $P < 0.05$; ** $P < 0.005$; *** $P < 0.0005$

pixel resolution equal to the resolution of the wilderness map. We ranked all the points of the three prioritization maps into a K number of ranks of equal area, from the highest to the lowest values of the respective prioritizing score, with rank 1 representing the highest values and rank K representing the lowest values. Due to the high clustering of summed irreplaceability values, the value of K was 19 for the complementarity approach, and 25 for the hotspots and wilderness approaches. We derived the set of points belonging to each rank K for each map as $\{(x_K^1, y_K^1), (x_K^2, y_K^2), \ldots, (x_K^n, y_K^n)\}$ where x, y were the spatial coordinates of each of the n points of rank K.

We classified as rare those species that were present in less than 25 % of the total number of cells. We calculated the cumulative number of total, rare, and vulnerable species by intersecting the ranks of each prioritization map with the species data. We then counted the number of unique species covered by each rank. In the case of the hotspots and complementarity maps, the points corresponding to different ranks overlapped with the grid cells of the species data. In the case of the wilderness map, we considered a species covered by a certain rank when the points of the respective rank intersected at any rate the grid cells in which that species was present.

We calculated the coverage of the areas important for megafauna and ecosystem services by intersecting the rank points of each prioritization map with the total amount of important areas for megafauna and ecosystem services, respectively. We calculated the coverage of megafauna and ecosystem services areas for each rank K, weighted by the number of megafauna species and ecosystem services, respectively, present in overlapping areas.

We measured the wilderness coverage of the three approaches by intersecting the rank points of the prioritization maps with the wilderness score map. We extracted the wilderness value for each point of each rank. We then calculated the total wilderness covered by each rank according to the formula:

$$W_K = \sum_{i=1}^{n_K} W(x_K^i, y_K^i), \tag{4}$$

where W_K is the total wilderness score covered by rank K and $W(x_K^i, y_K^i)$ is the wilderness value corresponding to the point i of the n_k number of points corresponding to rank K.

Results

The species richness for each 2 km × 2 km cell ranges between one and 107 with an average of 40.7 species (standard deviation = 18.52). The 177 species have between one and 212 occurrences with an average of 53.5 occurrences. The eastern and northern parts of PNPG have a bigger number of cells spatially clustered into hotspots of species richness, rarity, and vulnerability (Fig. 2a). Between the two larger areas there is a mosaic of cells with both high and low values.

For the complementarity approach, out of the 2000 runs of the MARXAN selection, 1668 runs achieved all the conservation targets. Of these, 20 planning units were always selected and 55 cells were never selected. The complementarity values are very similar to the hotspots but the highest values are limited to a lower number of cells (Fig. 2b). The central areas of PNPG seem to increase in importance in the complementarity approach compared with the hotspots.

Highest values of wilderness are recorded in a large patch in the central part of the park, at the border of the park (Fig. 2c). The northern and western areas also show high wilderness values but confined to smaller patches. Low wilderness areas border the southern and eastern edges of PNPG. The low wilderness values in the northern and central part of the park follow the road network and human settlements location. The wilderness variation across the map is smoother than in the case of hotspots and complementarity due to the continuous values of the wilderness range.

The prioritizing scores of the hotspots and complementarity approaches are highly positively correlated (Table 1). They both show a weak but significant negative correlation with the wilderness score. There is also a high correlation between the prioritizing scores of both the hotspots and complementarity approaches, and all species indices. Wilderness score shows a relatively weak positive correlation with species vulnerability and negative correlations with species richness and rarity (Table 1). There is no correlation between species richness and vulnerability on the territory of PNPG but there is a positive correlation between species richness and rarity.

Considering the three levels of high-priority areas, only the 20 % and the 30 % prioritization levels allow for an overlap between species-based and wilderness approaches (Table 2). Even in these cases, the overlap is limited to a few percentages of the area of the park (Fig. 2d). The area prioritized commonly by hotspots and complementarity is relatively high at all three percentage levels (Table 2).

We then assessed each approach against four criteria: species representativeness, wilderness coverage, important areas for megafauna, and ecosystem services. The species-based approaches cover all species in the smallest area (Fig. 3a, Online resource 2), while the wilderness approach covers wilderness, ecosystem services, and megafauna more efficiently (Fig. 3b–d). Complementarity is the most efficient for species protection, covering a higher number of species per percentage unit of prioritized area (Table 3). The best performance of the wilderness approach relative to the species-based approaches is the coverage of the important areas for megafauna (Table 3).

Discussion

Our research compares species-based and ecosystem-based prioritization approaches used in zoning the Peneda-Gerês National Park in Northern Portugal. PNPG was initially established for the protection of wilderness (Pinto and Partidário 2012). Now it is also a Natura 2000 site, listed under both the Habitats and the Birds Directive (European Council 1979, 1992). As the national and European trend turned from wilderness to a more species-oriented approach, the subsequent management plans favored species richness and cultural landscapes (Pinto and Partidário 2012). The area selection of the European network of protected areas is debated but it has been shown to cover a significant number of threatened taxa (Araújo 1999; Araújo et al. 2007; Donald et al. 2007), while low human impact areas are inconsistently represented (Martin et al. 2008; Selva et al. 2011).

Our zoning results show the two species-based approaches prioritizing similar areas, while the ecosystem-based approach offers significantly different results. The patterns in our study area of 700 km^2 concur with the results at global level described by Brooks et al. (2006). Moreover, the negative correlation between wilderness and species richness suggests a positive correlation between human density and species richness at the scale of our study. Other studies also find a spatial concurrence between high species richness and high human densities. In sub-Saharan Africa, species richness of mammals, birds, snakes, and amphibians is positively correlated with human population density (Balmford et al. 2001). The same is true in Europe for plant, mammal, reptile, and amphibian species richness (Araújo 2003), and for bird species richness in South Africa (Chown et al. 2003). Although there are wilderness areas which exhibit high species richness (Mittermeier et al. 2003), these do not represent most cases.

Although in some cases human management can lead to an increase of species richness (Rey Benayas et al. 2007), the generality of this pattern rather suggests that the drivers of high species richness, such as the level of primary productivity, are the same as the drivers of high human densities (Chown et al. 2003). However, the dominant view of current biodiversity policies is that European species richness is dependent on traditional agriculture (Halada et al. 2011). Therefore low-intensity agricultural practices are currently supported at European level through subsidy schemes aimed at High Nature Value farmland (European Commission 2005). But the current management actions

Table 2 Overlap between the prioritization approaches at three levels of designated high-priority areas: 10, 20, and 30 % of the total area of Peneda-Gerês National Park (PNPG)

Approaches	10 % prioritized area (%)	20 % prioritized area (%)	30 % prioritized area (%)
Wilderness + hotspots + complementarity	0	0.7	2.31
Wilderness + hotspots	0	1.52	2.42
Wilderness + complementarity	0	0	1.09
Hotspots + complementarity	6.1	12.94	17.89
Covered by at least one approach	25.17	46.04	63.29

The results are given as percentage of the total area of the park

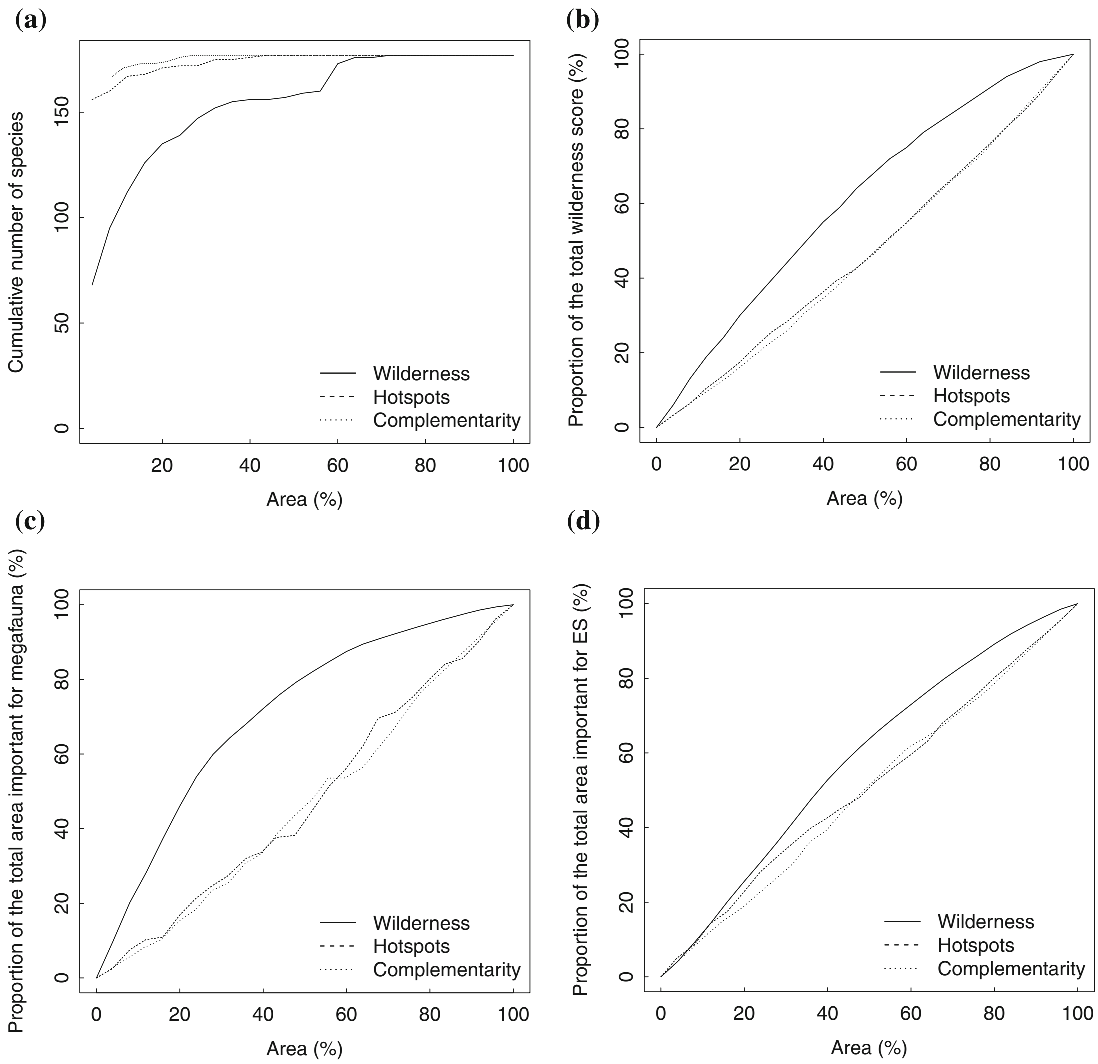

Fig. 3 Cumulative representativeness of biodiversity criteria plotted against the percentage of prioritized PNPG area according to the species-based and wilderness approaches for **a** all species considered; **b** wilderness; **c** areas important for megafauna; **d** areas important for ecosystem services (ES)

Table 3 Average percentages of biodiversity criteria (BD) being protected per percentage unit of prioritized area through the three approaches

Approaches	Total species (%)		Vulnerable species (%)		Rare species (%)		Wilderness (%)		Ecosystem services (%)		Megafauna (%)	
Size of prioritized area:	I	II	I	II	I	II	I	II	I	II	I	II
Complementarity	3.70	–	3.70	–	3.70	–	0.82	0.88	0.93	1.02	0.82	0.88
Hotspots	3.46	2.27	3.43	2.27	3.43	2.27	0.93	0.91	1.14	1.05	0.89	0.88
Wilderness	2.96	2	2.86	2.02	2.65	1.86	1.43	1.34	1.29	1.30	2.14	1.73

Values are calculated for two percentages of prioritized area: I—28 % and II—44 %

for the maintenance of species diversity offer no guarantees as species occurrences are the complex result of a multitude of factors (Chown et al. 2003; Guisan and Thuiller 2005).

Large body mass species in particular face strong competition from humans in terms of resources (Barnosky 2008) and space (Ceballos and Ehrlich 2002) which suggests that megafauna has often better chances of survival away from human presence. For example, in a recent study, Schuette et al. (2013) find that apex predators avoid human presence through spatial and temporal niche partitioning in an area occupied by semi-nomadic human populations, while in Greece, Iliopoulos et al. (2014) showed wolves consistently avoid roads and human presence. In PNPG, wilderness areas are the preferred territory of several megafauna populations (Fig. 3c). These species play important roles in modulating trophic networks, community composition, and ecosystem properties (Duffy 2003; Schmitz 2006; Ritchie and Johnson 2009); therefore, their conservation is particularly important for ecologic processes.

The relation between species diversity and ecosystem services is complex. In the Californian Central Coast ecoregion, there are few and weak positive correlations between ecosystem services and high species diversity areas (Chan et al. 2006). At the global scale, wilderness coincides with areas important for carbon storage and sequestration, whereas hotspots better support water provision and the grassland production of livestock (Naidoo et al. 2008). At the scale of our study, the wilderness conservation approach selects a larger area important for the three regulating ecosystem services than species-based approaches (Fig. 3d), while species-directed conservation actions currently support the maintenance of low-intensity farmland (European Environment Agency 2004). Wilderness-favoring management could allow self-sustaining ecosystems and complex food webs to expand and increase resilience of ecosystems (Walker 2002) but it would lead to a decrease in provisioning ecosystem services by limiting human farming activities in the area. Such trade-offs between provisioning and regulating services have also been pointed out in the literature (Naidoo et al. 2008; Maes et al. 2012).

The drawbacks of species-based approaches are mainly related to the data used for prioritization, while the drawbacks of ecosystem-based approaches are related to their potential for social conflict. For example in our case, although the species data are the highest quality available for the zoning of PNPG, there are indications of undersampling as we have grid cells listing only one species occurrence in an area of 2 km × 2 km. In species-based approaches, there is also a strong bias toward more speciose or more charismatic taxonomic groups (Andelman 2000; Rodrigues and Brooks 2007). Such biases are common in the data available at the scale of conservation actions and the topic is hotly debated in the literature because it impacts decision making (Andelman 2000; Hess et al. 2006; Cabeza et al. 2007; Rodrigues and Brooks 2007; Roth and Weber 2008) and the consequences are still poorly understood (Gaston and Rodrigues 2003). Moreover, there are few cases in which species data were used for real-world zoning or designating of protected areas (but see Howard et al. 1997), area zoning being often done opportunistically (Hull et al. 2011). Wilderness on the other hand has the lowest requirements and uncertainty in terms of data among the tested approaches in our study. We used spatial data on infrastructures and human settlements, which are usually readily available from government agencies or geographical institutes. From an implementation point of view, ecosystem-based approaches are clearer than species-based approaches in prescribing measures for the protection of wilderness such as reducing human activities and infrastructure development in priority areas (Fritz et al. 2000). However, wilderness management actions have a high potential for social conflict, even in areas with dwindling farming populations (Navarro and Pereira 2012).

Our research shows that species- and ecosystem-based approaches prioritize different areas that maximize different biodiversity targets. However, we do not consider them as competing in conservation. As biodiversity encompasses all levels of complexity (Secretariat of the Convention on Biological Diversity 2001), conservation should address all biodiversity dimensions (Kareiva and Marvier 2003; Lee and Jetz 2008). Serious consideration must be given to the effects of possibly conflicting management actions at local scale but we consider that in areas of both high wilderness and high species richness, differentiated conservation targeting and zoning is necessary for addressing all dimensions of biodiversity.

Conservation is context dependent (Gillson et al. 2011) and contexts are extremely different across the globe. However, we are confident that prioritizing for species or ecosystem properties targets will yield similar results across the world as many mechanisms driving biodiversity and ecosystem services are common. We disagree that the goals of species conservation and wilderness should be kept distinct (but see Sarkar 1999). Wilderness areas show consistently to be important for several ecosystem services (Naidoo et al. 2008) and they contain the biological communities closest to their unaltered pre-human state (Bryant et al. 1997). Although many times these approaches are presented as mutually exclusive, we consider that they target different dimensions of biodiversity conservation. A serious consideration of species-based alongside ecosystem-based approaches in conservation management would achieve more goals than a single-minded direction, and can have important benefits for the long-term preservation of biodiversity and ecosystem services.

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References

Andelman SJ (2000) Umbrellas and flagships: efficient conservation surrogates or expensive mistakes? Proc Natl Acad Sci 97:5954–5959. doi:10.1073/pnas.100126797

Aplet G, Thomson J, Wilbert M (2000) Indicators of wildness: using attributes of the land to assess the context of wilderness. In: Wilderness science in a time change. Proceedings RMRS-P-51. USDA Forest Service, Rocky Mountain Research Station, Ogden, UT

Araújo MB (1999) Distribution patterns of biodiversity and the design of a representative reserve network in Portugal. Divers Distrib 5:151–163

Araújo MB (2003) The coincidence of people and biodiversity in Europe. Glob Ecol Biogeogr 12:5–12

Araújo MB, Lobo JM, Moreno JC (2007) The effectiveness of Iberian protected areas in conserving terrestrial biodiversity. Conserv Biol 21:1423–1432

Ardron JA, Possingham HP, Klein CJ (2008) Marxan good practices handbook. External review version, vol 155. Pacific Marine Analysis and Research Association, Vancouver. www.pacmara.org

Ball IR, Possingham HP, Watts M (2009) Marxan and relatives: software for spatial conservation prioritisation. In: Moilanen A, Wilson KA, Possingham H (eds) Spatial conservation prioritisation: quantitative methods and computational tools. Oxford University Press, Oxford, pp 180–210

Balmford A, Moore JL, Brooks T et al (2001) Conservation conflicts across Africa. Science 291:2616

Barnosky AD (2008) Megafauna biomass tradeoff as a driver of Quaternary and future extinctions. Proc Natl Acad Sci 105:11543–11548. doi:10.1073/pnas.0801918105

Brilha JB (2005) Património Geológico e Geoconservação: a conservação da natureza na sua vertente geológica. Palimage, São Paulo

Brooks TM, Mittermeier RA, da Fonseca GA et al (2006) Global biodiversity conservation priorities. Science 313:58

Bryant D, Nielsen D, Tangley L (1997) Last frontier forests: ecosystems and economies on the edge. World Resources Institute, Forest Frontiers Initiative, Washington, DC

Butchart SH, Walpole M, Collen B et al (2010) Global biodiversity: indicators of recent declines. Science 328:1164

Cabeza M, Arponen A, Van Teeffelen A (2007) Top predators: hot or not? A call for systematic assessment of biodiversity surrogates. J Appl Ecol 45:976–980

Cabral M, Almeida J, Almeida P et al (2005) Livro vermelho dos vertebrados de Portugal. Peixes dulciaquícolas e migradores, anfíbios, répteis, aves e mamíferos. Instituto da Conservação da Natureza, Lisboa

Carver S, Evans AJ, Fritz S (2002) Wilderness attribute mapping in the United Kingdom. Int J Wilderness 8:24–29

Carver S, Comber A, McMorran R, Nutter S (2012) A GIS model for mapping spatial patterns and distribution of wild land in Scotland. Landsc Urban Plan 104:395–409

Ceballos G, Ehrlich PR (2002) Mammal population losses and the extinction crisis. Science 296:904

Chan KM, Shaw MR, Cameron DR et al (2006) Conservation planning for ecosystem services. PLoS Biol 4:e379

Chown SL, van Rensburg BJ, Gaston KJ et al (2003) Energy, species richness, and human population size: conservation implications at a national scale. Ecol Appl 13:1233–1241

Cinzano P, Falchi F, Elvidge CD, Baugh KE (2000) The artificial night sky brightness mapped from DMSP satellite Operational Linescan System measurements. Mon Not R Astron Soc 318:641–657

De Molenaar JG, Sanders ME, Jonkers DA (2006) Road lighting and grassland birds: local influence of road lighting on a black-tailed godwit population. Ecol Consequences Artif Night Light 169:114–136

Del Carmen SM, Verdiell A, Rodríguez Iglesias RM, Vidal M (2007) A quantitative method for zoning of protected areas and its spatial ecological implications. J Environ Manag 83:198–206

Diniz-Filho JAF, Bini LM, Pinto MP et al (2006) Anuran species richness, complementarity and conservation conflicts in Brazilian Cerrado. Acta Oecol 29:9–15

Donald PF, Sanderson FJ, Burfield IJ et al (2007) International conservation policy delivers benefits for birds in Europe. Science 317:810–813

Duffy JE (2003) Biodiversity loss, trophic skew and ecosystem functioning. Ecol Lett 6:680–687

Earth Remote Sensing Data Analysis Center (2011) ASTER Global Digital Elevation Model Version 2

European Commission (2005) Agri-environment measures. Overview on general principles, types of measures, and application. European Commission, Brussels

European Council (1979) Council Directive 79/409/EEC on the conservation of wild birds. European Council, Brussels

European Council (1992) EU Habitats Directive (92/43/EEC). Consol. Text Off. Off. Publ. Eur. Union CONSLEG 1992LOO43-0105-2004. European Council, Brussels

European Environment Agency (2004) High nature value farmland. Characteristics, trends and policy challenges. European Communities, Luxembourg

Ferrier S, Pressey RL, Barrett TW (2000) A new predictor of the irreplaceability of areas for achieving a conservation goal, its application to real-world planning, and a research agenda for further refinement. Biol Conserv 93:303–325

Fritz S, Carver S (1998) Accessibility as an important wilderness indicator: modelling Naismith's rule. In: GISRUK'98, Edinburgh

Fritz S, Carver S, See L (2000) New GIS approaches to wild land mapping in Europe. In: McCool SF, Cole DN, Borrie WT, O'Loughlin J (eds) Comps 2000 Wilderness Science in a Time Change Conference, vol 2

Gaston KJ, Rodrigues AS (2003) Reserve selection in regions with poor biological data. Conserv Biol 17:188–195

Geneletti D, van Duren I (2008) Protected area zoning for conservation and use: a combination of spatial multicriteria and multiobjective evaluation. Landsc Urban Plan 85:97–110

Gillson L, Ladle RJ, Araújo MB (2011) Baselines, Patterns and Process. In: Ladle RJ, Whittaker RJ (eds) Conservation Biogeography, John Wiley & Sons, Ltd, Chichester, UK

Guisan A, Thuiller W (2005) Predicting species distribution: offering more than simple habitat models. Ecol Lett 8:993–1009

Halada L, Evans D, Romão C, Petersen JE (2011) Which habitats of European importance depend on agricultural practices? Biodivers Conserv 20:2365–2378

Halpern BS, Pyke CR, Fox HE et al (2006) Gaps and mismatches between global conservation priorities and spending. Conserv Biol 20:56–64

Hess GR, Bartel RA, Leidner AK et al (2006) Effectiveness of biodiversity indicators varies with extent, grain, and region. Biol Conserv 132:448–457

Howard P, Davenport T, Kigenyi F (1997) Planning conservation areas in Uganda's natural forests. Oryx 31:253–264. doi:10.1046/j.1365-3008.1997.d01-124.x

Hull V, Xu W, Liu W et al (2011) Evaluating the efficacy of zoning designations for protected area management. Biol Conserv 144:3028–3037. doi:10.1016/j.biocon.2011.09.007

Iliopoulos Y, Youlatos D, Sgardelis S (2014) Wolf pack rendezvous site selection in Greece is mainly affected by anthropogenic landscape features. Eur J Wildl Res 60:23–34

Instituto Geográfico do Exército (1997) Carta Militar de Portugal. Instituto Geográfico do Exército, Lisbon

Instituto Nacional de Estatística (2011) Censos 2011—Resultados Provisórios. Instituto Nacional de Estatística, Lisbon

Kareiva P, Marvier M (2003) Conserving Biodiversity Coldspots Recent calls to direct conservation funding to the world's biodiversity hotspots may be bad investment advice. Am Sci 91:344–351

Kati V, Devillers P, Dufrene M et al (2004) Hotspots, complementarity or representativeness? Designing optimal small-scale reserves for biodiversity conservation. Biol Conserv 120:471–480

Klein CJ, Wilson KA, Watts M et al (2009) Spatial conservation prioritization inclusive of wilderness quality: a case study of Australia's biodiversity. Biol Conserv 142:1282–1290

Kuechly HU, Kyba C, Ruhtz T et al (2012) Aerial survey and spatial analysis of sources of light pollution in Berlin, Germany. Remote Sens Environ 126:39–50

Lawler JJ, White D, Master LL (2003) Integrating representation and vulnerability: two approaches for prioritizing areas for conservation. Ecol Appl 13:1762–1772

Lee TM, Jetz W (2008) Future battlegrounds for conservation under global change. Proc R Soc B 275:1261–1270

Lennon JJ, Koleff P, Greenwood JJD, Gaston KJ (2004) Contribution of rarity and commonness to patterns of species richness. Ecol Lett 7:81–87. doi:10.1046/j.1461-0248.2004.00548.x

Linnell JDC, Nilsen EB, Lande US et al (2005) Zoning as a means of mitigating conflicts with large carnivores: principles and reality. Conserv Biol 9:162

Maes J, Paracchini ML, Zulian G et al (2012) Synergies and trade-offs between ecosystem service supply, biodiversity, and habitat conservation status in Europe. Biol Conserv 155:1–12

Margules CR, Pressey RL (2000) Systematic conservation planning. Nature 405:243–253

Martin VG, Kormos CF, Zunino F et al (2008) Wilderness momentum in Europe. Int J Wilderness 14:34–38

Martínez JA, Serrano D, Zuberogoitia I (2003) Predictive models of habitat preferences for the Eurasian eagle owl *Bubo bubo*: a multiscale approach. Ecography 26:21–28

Meir E, Andelman S, Possingham HP (2004) Does conservation planning matter in a dynamic and uncertain world? Ecol Lett 7:615–622

Mittermeier RA, Mittermeier CG, Brooks TM et al (2003) Wilderness and biodiversity conservation. Proc Natl Acad Sci 100:10309

Moço G, Guerreiro M, Ferreira AF et al (2006) The ibex *Capra pyrenaica* returns to its former Portuguese range. Oryx 40:351–354

Moilanen A, Anderson BJ, Eigenbrod F et al (2011) Balancing alternative land uses in conservation prioritization. Ecol Appl 21:1419–1426

Myers N, Mittermeier RA, Mittermeier CG et al (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858

Naidoo R, Balmford A, Costanza R et al (2008) Global mapping of ecosystem services and conservation priorities. Proc Natl Acad Sci 105:9495

Navarro L, Pereira H (2012) Rewilding abandoned landscapes in Europe. Ecosystems 15:900–912. doi:10.1007/s10021-012-9558-7

Orme CDL, Davies RG, Burgman MA et al (2005) Global hotspots of species richness are not congruent with endemism or threat. Nature 436:1016–1019. doi:10.1038/nature03850

Penteriani V, Delgado MDM, Maggio C et al (2005) Development of chicks and predispersal behaviour of young in the Eagle Owl *Bubo bubo*. IBIS 147:155–168

Pereira HM, Leadley PW, Proença V et al (2010) Scenarios for global biodiversity in the 21st century. Science 330:1496

Pimenta M, Santarém ML (1996) Atlas das Aves do Parque Nacional da Peneda-Gerês. ICN, PNPG, Lisboa

Pinto B, Partidário M (2012) The history of the establishment and management philosophies of the Portuguese protected areas: combining written records and oral history. Environ Manag 49:788–801

PNPG-ICN (2008) Revisão do Plano de Ordenamento—Parque Nacional da Peneda-Gerês. Relatório de Síntese 1ª Fase. Parque Nacional da Peneda-Gerês—Instituto da Conservação da Natureza e Biodiversidade, Braga

Pressey RL, Bottrill MC (2008) Opportunism, threats, and the evolution of systematic conservation planning. Conserv Biol 22:1340–1345

Pryce B, Iachetti P, Wilhere G et al (2006) Okanagan Ecoregional Assessment, The Nature Conservancy of Canada, Victoria, Canada

R Development Core Team (2011) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Rey Benayas JM, de la Montana E (2003) Identifying areas of high-value vertebrate diversity for strengthening conservation. Biol Conserv 114:357–370

Rey Benayas JM, Martins A, Nicolau JM, Schulz JJ (2007) Abandonment of agricultural land: an overview of drivers and consequences. CAB Rev Perspect Agric Vet Sci Nutr Nat Resour 2:1–14

Ritchie EG, Johnson CN (2009) Predator interactions, mesopredator release and biodiversity conservation. Ecol Lett 12:982–998

Rodrigues ASL, Brooks TM (2007) Shortcuts for biodiversity conservation planning: the effectiveness of surrogates. Annu Rev Ecol Evol Syst 38:713–737. doi:10.1146/annurev.ecolsys.38.091206.095737

Roth T, Weber D (2008) Top predators as indicators for species richness? Prey species are just as useful. J Appl Ecol 45:987–991

Ruddock M, Whitfield DP (2007) A review of disturbance distances in selected bird species. Natural Research Ltd., Inverness

Salm RV, Siirila E (2000) Marine and coastal protected areas: a guide for planners and managers. IUCN, Gland

Sanderson EW, Jaiteh M, Levy MA et al (2002) The Human Footprint and the Last of the Wild: the human footprint is a global map of human influence on the land surface, which suggests that human beings are stewards of nature, whether we like it or not. Bioscience 52:891–904

Sarkar S (1999) Wilderness preservation and biodiversity conservation—keeping divergent goals distinct. Bioscience 49:405–412

Schmitz OJ (2006) Predators have large effects on ecosystem properties by changing plant diversity, not plant biomass. Ecology 87:1432–1437

Schuette P, Wagner AP, Wagner ME, Creel S (2013) Occupancy patterns and niche partitioning within a diverse carnivore community exposed to anthropogenic pressures. Biol Conserv 158:301–312

Secretariat of the Convention on Biological Diversity (2001) Handbook of the convention on biological diversity. Earthscan, London

Selva N, Kreft S, Kati V et al (2011) Roadless and low-traffic areas as conservation targets in Europe. Environ Manag 48:865–877

Soares C, Alvares F, Loureiro A et al (2005) Atlas of the amphibians and reptiles of Peneda-Gerês National Park, Portugal. Herpetozoa 18:155–170

Thiel RP, Merrill S, Mech LD (1998) Tolerance by denning wolves, *Canis lupus*, to human disturbance. Can Field Nat 112:340–342

Villa F, Tunesi L, Agardy T (2002) Zoning marine protected areas through spatial multiple-criteria analysis: the case of the Asinara Island National Marine Reserve of Italy. Conserv Biol 16:515–526

Walker B (2002) Conserving biological diversity through ecosystem resilience. Conserv Biol 9:747–752

Watson JEM, Fuller RA, Watson AWT et al (2009) Wilderness and future conservation priorities in Australia. Divers Distrib 15:1028–1036

Watson A, Matt R, Knotek K et al (2011) Traditional wisdom: protecting relationships with wilderness as a cultural landscape. Ecol Soc 16:36

Watts ME, Ball IR, Stewart RS et al (2009) Marxan with Zones: software for optimal conservation based land-and sea-use zoning. Environ Model Softw 24:1513–1521

Williams P, Gibbons D, Margules C et al (1996) A comparison of richness hotspots, rarity hotspots, and complementary areas for conserving diversity of British birds. Conserv Biol 10:155–174

Wilson KA, McBride MF, Bode M, Possingham HP (2006) Prioritizing global conservation efforts. Nature 440:337–340

Woolmer G, Trombulak SC, Ray JC et al (2008) Rescaling the human footprint: a tool for conservation planning at an ecoregional scale. Landsc Urban Plan 87:42–53

Supplementary material 1

Our assigned vulnerability score is the following: 10 – critically endangered, 8 – threatened, 6 – vulnerable, 3 – data deficient and near threatened, and 0 – least concern. We assessed the sensitivity of our results to our choice of the vulnerability scoring system by defining 4 alternative scorings:

1) – no vulnerability score;
2) – all species, except the least concern ones, receive a vulnerability score equal to 1;
3) – the vulnerability scale goes from 0 to 4 with an increment of 1 for each threat level: 4 – critically endangered, 3 – threatened, 2 – vulnerable, 1 – data deficient and near threatened, and 0 – least concern;
4) – the vulnerability scale goes from 0 to 8 with an increment of 2 for each threat level: 8 – critically endangered, 6 – threatened, 4 – vulnerable, 2 – data deficient and near threatened, and 0 – least concern;

We then calculated the Spearman rank correlation coefficient between each alternative scoring and the one used in our analysis in order to assess how the alternative scoring systems change the ranking of the grid cells based on the hotspots aggregated index (AI).

Alternative scoring	ρ values (relative to the scoring used for the hotspots prioritization)
1	0.812***
2	0.981***
3	0.999***
4	0.999***

***$p<0.0005$

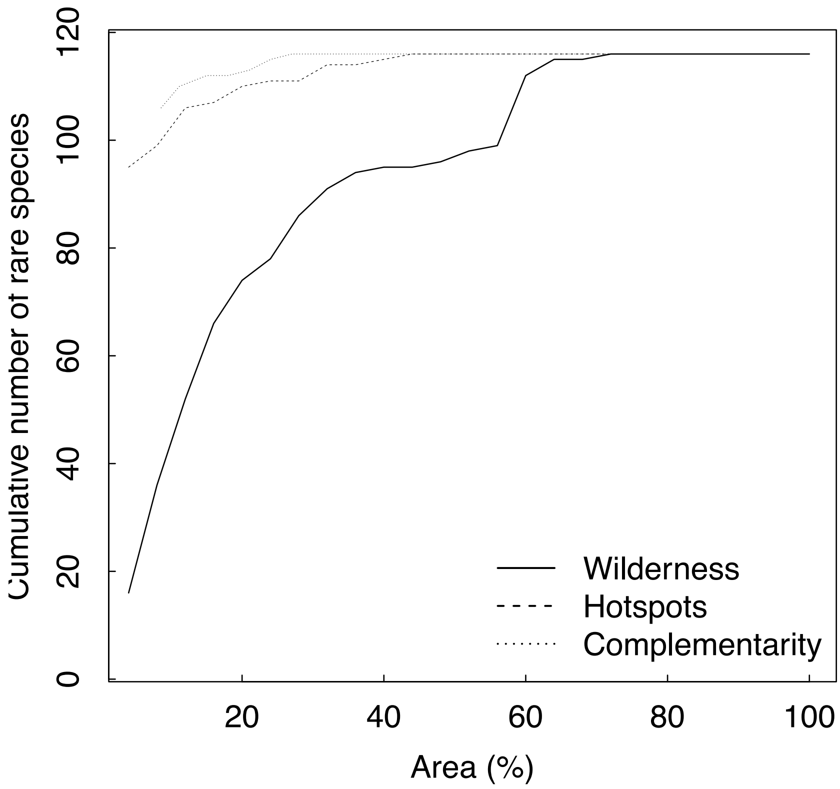

Fig. S1. Cumulative rare species representativeness plotted against the percentage of prioritized PNPG area according to the species-based and ecosystem-based approaches.

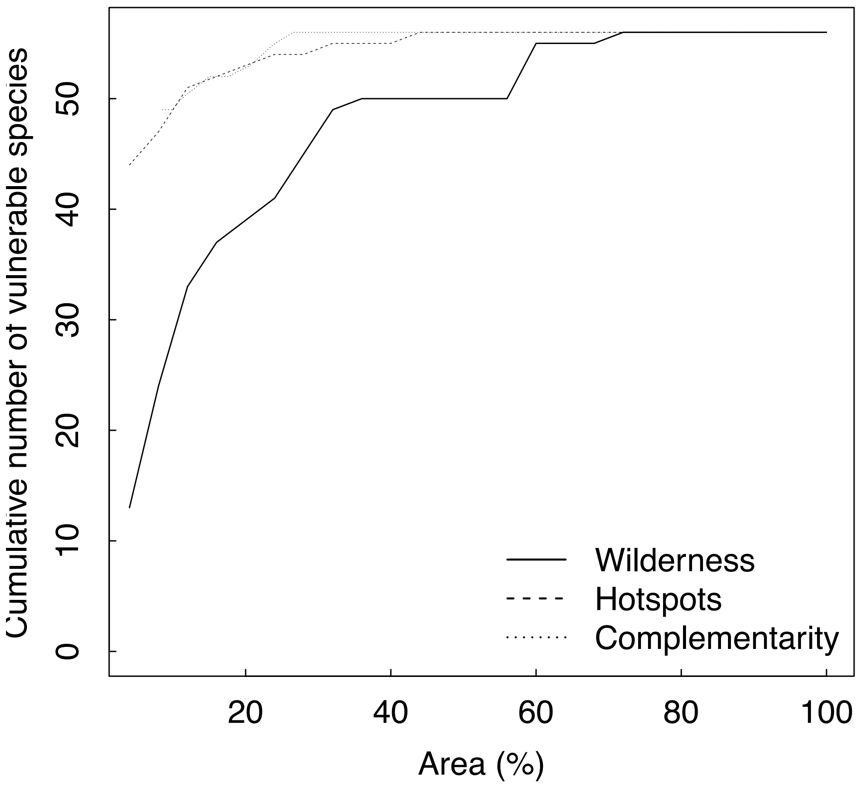

Fig. S2. Cumulative vulnerable species representativeness plotted against the percentage of prioritized PNPG area according to the species-based and ecosystem-based approaches.

Chapter 3

European Wilderness in a Time of Farmland Abandonment

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Chapter 2
European Wilderness in a Time of Farmland Abandonment

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Abstract Wilderness is a multidimensional concept that has evolved from an aesthetic idea to a science-based conservation approach. We analyze here several subjective and ecological dimensions of wilderness in Europe: human access from roads and settlements, impact of artificial night light, deviation from potential

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natural vegetation and proportion of harvested primary productivity. As expected, high wilderness in Europe is concentrated mainly in low primary productivity areas at high latitudes and in mountainous regions. The use of various wilderness metrics also reveals additional aspects, allowing the identification of regional differences in the types of human impact and a better understanding of future modifications of wilderness values in the context of land-use change. This is because farmland abandonment in the next decades is projected to occur especially at intermediate wilderness values in marginal agricultural landscapes, and thus can release additional areas for wild ecosystems. Although the subjective wilderness experience will likely improve at a slower pace due to the long-term persistence of infrastructures, the ecological effects of higher resource availability and landscape connectivity will have direct positive impacts on wildlife. Positive correlation between megafauna species richness and wilderness indicate that they spatially coincide and for abandoned areas close to high wilderness areas, these species can provide source populations for the recovery of the European biota. Challenges remain in bringing together different views on rewilding and in deciding the best management approach for expanding wilderness on the continent. However the prospects are positive for the growth of self-regulating ecosystems, natural ecological processes and the wilderness experience in Europe.

Keywords Wilderness · Human footprint · Artificial light · Potential natural vegetation · Harvested primary productivity · Megafauna · Farmland abandonment

2.1 The History and Value of Wilderness

Wilderness is a comprehensive measure of conservation value capturing both the subjective human experience, and the ecological dimension of minimally impacted ecosystems (Cole and Landres 1996; Hochtl et al. 2005). But the concept of wilderness has gone through dramatic historical changes in terms of both the context and connotation in which the term was used. During the centuries of exploration and colonization of new territories, wilderness was perceived negatively as a land that is unfavourable for human habitation and should be altered and tamed (Nash 2001).

"Wilderness" gradually entered the North American language of conservation in the nineteenth century after the end of the frontier exploration, especially promoted by the hunting community. It developed as an aesthetic and ethical concept related to the protection of pristine nature in the face of galloping technological progress and rapid disappearance of natural environments. Thus wilderness became synonymous with freedom, natural beauty, sanctuary and retreat from everything that was perceived as overwhelming in the modern lifestyle (Nash 2001).

Some have argued that past landscape modifications by human populations and pervasive human impacts across scales make the idea of wilderness inconsequential (Heckenberger et al. 2003). Wilderness also attracted considerable controversy in North America, particularly raising questions relating to equity and the rights of humans living in, or next to, areas allocated to wilderness protection (Nash 2001). The same issues were raised on all other continents that were colonized by European settlers. The establishment of protected parks and hunting reserves in South Africa was accompanied by the relocation of native populations and social strife (Carruthers 1995). Australia has also experienced some controversy surrounding the definition of wilderness and its disconnection from the culture and lifestyle of aboriginal populations (Mackey et al. 1998).

Such developments gave "wilderness" the impetus to evolve towards a more relevant concept for the twenty-first century, incorporating both human dimensions and needs as well as new research results from areas such as paleoecology or climate science (Gillson and Willis 2004). A science-based understanding of the human influence on ecosystems informs presently one of the main current conservation approaches (Brooks et al. 2006; Kalamandeen and Gillson 2007). In this context, wilderness represents one extreme of the gradient of human presence and impact across the landscape. While still retaining an aesthetical element and an existence value among growing numbers of enthusiasts in the Western industrialized countries, wilderness also refers to the biophysical reality of natural processes, ecological communities, and the resulting ecosystems that develop in the absence of human management. Therefore, wilderness is of major importance both for research and management in the areas of ecosystem services (ES) (Naidoo et al. 2008, see Chap. 3), biodiversity conservation (Watson et al. 2009), and the establishment of ecosystem baselines (Vitousek et al. 2000).

Appreciation of European wilderness has had a different path from that on other continents due to the long history of human occupation, agriculture and landscape management. Many of the species that used to dominate the landscape in the distant past have been hunted to extinction or have been driven away from the most favourable habitats (Barnosky 2008, see Chaps. 4, 8) and natural vegetation cover has been cut or burnt down to make space for farmland. Thus both laymen and naturalists have come to regard and appreciate this new state as the natural biodiversity of the continent. As a result of a shifting baseline syndrome, traditional agricultural landscapes have become the benchmark against which biodiversity change was measured (Papworth et al. 2009). However, a growing movement in Europe advocates now for wilderness protection and recognition, and policy steps have been taken in this direction, including a resolution of the European Parliament on wilderness in Europe (Martin et al. 2008; European Parliament 2009). Research has also been undertaken in order to identify and map wilderness on the continent (Fritz et al. 2000; Carver 2010). In this favourable context, rewilding of abandoned farmland can gain momentum as a way of expanding the areas that provide both increased opportunities for wilderness experience and more extensive self-regulating and self-sustaining ecosystems (Rey Benayas et al. 2007; Munroe et al. 2013, see Chaps. 1, 11).

Considering the diversity of possible definitions, we approach wilderness in this chapter from several points of view. In the next section we review the literature on wilderness mapping and to identify some of the most important ecological and aesthetical aspects of wilderness in Europe. We then map and discuss the spatial agreement between wilderness based on (a) human access from roads and settlements, (b) impact of artificial light, (c) deviation from potential natural vegetation, and (d) proportion of primary productivity harvested by humans, as metrics of wilderness value over space. We further explore the health of trophic chains by looking at megafauna species and their spatial concurrence with wilderness. Megafauna such as the large herbivores, apex predators and birds of prey have an important role in maintaining and returning ecosystems to a higher naturalness state through establishment of natural trophic cascades (see Chaps. 4, 5, and 8). As such we also map the distribution of high body mass species across Europe and discuss the overlaps with high-wilderness quality and farmland abandonment areas. We then explore the possible spatial and temporal dynamics of wilderness in Europe over the next few decades in the context of farmland abandonment and rewilding. We examine how aspects of wilderness could increase due to agricultural abandonment and we suggest means to maximize the potential success of rewilding efforts.

2.2 Measuring and Mapping Wilderness—A Brief Review of Metrics and Methods

Wilderness has been mapped and analysed across scales, from global to local level. The methodologies generally make use of available spatial data on human infrastructures, land cover, area size of ecologically intact regions, etc. as proxies for wilderness quality, but also employ expert knowledge on degree of naturalness and ecosystem modification. Despite the obvious challenges of mapping a multidimensional concept such as wilderness, studies using relevant indicators at a similar extent and resolution offer highly congruent results, likely because they share a common perception of the attributes and values of wilderness.

At the global level, Mittermeier et al. (2003) used a combination of human population density, intactness, and area size of the intact areas to define wilderness areas. Much of their assessment was based on literature and expert opinions. The wilderness areas identified coincided with the areas of the lowest human footprint identified by Sanderson et al. (2002) although the two studies used largely different metrics. The map of the human footprint at the global level used human population density, the transformation of land through the building of settlements, roads and railroads, and measures of human access. Power infrastructures were also quantified, using satellite night maps (Sanderson et al. 2002). Despite data limitations, these global studies reveal a fairly consistent big picture of the overall pattern and magnitude of human impact on the biosphere, both for terrestrial and marine ecosystems (Halpern et al. 2008).

In Australia, the Heritage Commission's National Wilderness Inventory used four metrics for defining wilderness: remoteness from settlements, remoteness from access, biophysical naturalness and apparent naturalness (Lesslie et al. 1995). In this case, thresholds were defined for minimum levels of these metrics that would characterize wilderness. Other approaches emphasize a wilderness continuum across the landscape (Fritz et al. 2000). Building on the Heritage Commission's National Wilderness Inventory research, Carver et al. (2002) added remoteness from national population centres and altitude in order to map wilderness in the United Kingdom.

Remoteness from national population centres was a measure of the accessibility to the whole British population in addition to the accessibility to the local population in the calculation of wilderness. The authors used multicriteria evaluation (MCE) and explored public perceptions of wilderness through the use of interactive tools by allowing the user to change the weights of the wilderness metrics. As expected, resulting wilderness maps were not radically different, but allowed for insights on what affects the perceptions of wilderness (Carver et al. 2002). This approach was further detailed at the level of the Cairngorms National Park, and the Loch Lomond and The Trossachs National Park in Scotland (Carver et al. 2012) at a resolution of 20 m and later expanded to cover the whole of Scotland in a study by the Scottish Natural Heritage (Scottish Natural Heritage 2012).

At lower spatial extents the indicators of wilderness and human footprint remain the same but higher quality data are usually available making the mapping and modelling process more reliable and accurate. For example, Woolmer et al. (2008) rescaled the human footprint methodology of the Sanderson et al (2002) for the area of approximately 300,000 km^2 of the Northern Appalachian ecoregion. They used ten datasets compiled from several sources: population density, dwelling density, urban areas, roads, rail, land cover, large dams, watersheds, mine sites, utility corridors for the electrical power infrastructure. The general patterns of human footprint were maintained when comparing the map based on 90 m^2 resolution data at ecoregional scale with the map derived from the global analysis of Sanderson et al (2002) conducted with 1 km^2 resolution data. However, the Spearman rank correlation coefficients between the two sets of human footprint data steadily decreased with the scale, reaching 0.41 ($p < 0.001$) at 0.1 % of the Northern Appalachian ecoregion. The difference in the human footprint scores is that the ecoregion calculation compared with the global calculation leads to a reduction in the area with low levels of human footprint (46 % ecoregion extent vs. 59 % global extent) and an increasing of the area with moderate or high levels of human footprint (34 % ecoregion extent vs. 21 % global extent), evening out more the distribution of human footprint scores. A key finding was also that three parameters models add the most information to the calculation of human footprint while the model incorporating human settlements, roads and land-use was the best approximating model from all combinations of the ten datasets considered.

In Europe, an increased wilderness momentum has led to efforts by different actors to protect wilderness and advance a progressive wilderness research agenda (Jones-Walters and Čivić 2010). A continental level map of wilderness continuum has been produced using population density, road and rail density, linear distance from the nearest road and railway line, naturalness of land cover and terrain ruggedness (Carver 2010). This analysis identified wilderness areas concentrated in the Scandinavian Peninsula and the mountainous regions of Europe, revealing a strong positive altitudinal and latitudinal relationship. The same pattern was maintained even if terrain ruggedness was eliminated from the calculation. Beside the Scandinavian mountains and arctic areas, the Pyrenees, The Eastern Mediterranean islands, the Alps, the British Isles, the south-eastern Europe and the Carpathians also had significant areas of wilderness (Carver 2010) but one has to temper this with the knowledge that the current spatial data often misses historical information on local land use management such as past deforestation, drainage and grazing by domestic livestock. Currently, the wilderness mapping is being updated through the project of the European Wilderness Registry, which will record the most important wild sites, thus facilitating priority setting for protection.

2.3 Wilderness Metrics

The set of metrics used in the wilderness mapping literature can be divided into two major dimensions of defining wilderness: the subjective or perceived wilderness experience and ecological intactness. Most wilderness metrics attempt to describe both aspects. For example, the presence of roads and human settlements indicate both easiness of access, visual impact, and the ecological impact of these infrastructures. Yet some indicators address the two dimensions separately as it is the case with apparent naturalness and biophysical naturalness (Lesslie et al. 1988). For the purposes of this chapter, we chose a series of four metrics: two that describe both the subjective human experience of wilderness and the ecological impact, and two that have mainly an ecological dimension. The metrics used here quantify human impact thus wilderness increases with the decrease of the metrics.

Remoteness from roads and human settlements is an important dimension in the feeling of solitude intrinsic to the wilderness experience. However, roads and other human access infrastructure have also a strong impact on wild populations and ecosystems. The most obvious impact is road mortality, shown to affect mammals (Philcox et al. 1999; Seiler 2005; Grilo et al. 2009), birds (Orlowski 2005), reptiles (Iosif et al. 2013) and amphibians (Patrick et al. 2012). But impacts of roads, traffic and human access can be much more profound, affecting population and community structure (Habib et al. 2007), trophic interactions (Kristan III and Boarman 2003; Whittington et al. 2011), ecosystem functioning and structure (Christensen et al. 1996; Hansen et al. 2005; Rentch et al. 2005), and environmental conditions through high pollution levels (Hatt et al. 2004). Roads can favour the expansion of invasive species (Jodoin et al. 2008; Vicente et al. 2010), and of exotic and human-favoured predators (Alterio et al. 1998). They also expose forest habitats to edge effects (Tabarelli et al. 2004). These ecological impacts of roads and human settlements alter a range of ecological conditions compared with the context that would exist without these human infrastructures. Here we evaluate human access from roads and settlements by calculating the cost distance to paved roads and settlements according to the Naismith's rule which assumes differentiated relative traveling times depending on terrain, land cover, and river networks (Carver and Fritz 1999). We extracted the data on paved roads from the Eurogeographics Road database and the Open Street Map database, land use data from Corine Land Cover 2000 and 2006, and terrain ruggedness data from the Shuttle Radar Topography Mission (SRTM) at 1 km resolution. The range of the human access score values is expressed from 0 to 1. In Europe, the mountainous areas, the Iberian Peninsula, the Balkans, Scotland, and Scandinavia are the least accessible regions and the least impacted by roads and settlements (Fig. 2.1a).

Artificial night light has a similar dimension in the definition of wilderness. Light pollution has been decried for its impact on the visibility of the natural night sky (Cinzano et al. 2000), diminishing the night wilderness experience. But artificial light has also strong ecological impacts (Longcore and Rich 2004; Navara and Nelson 2007; Hölker et al. 2010b; Gaston et al. 2013), affecting invertebrates (Davies et al. 2012, see Chap. 6), fish (Becker et al. 2013), mammals (Boldogh et al. 2007) and bird populations (Montevecchi et al. 2006). Direct mortality (Hölker et al. 2010b), impacts on trophic relations and community structure (Perkin et al. 2011), disruption of migratory routes (Gauthreaux Jr et al. 2006) by night light lead to profound modifications of ecosystems functions (Hölker et al. 2010a). Nocturnal species such as bats and moths (see also Chap. 6) receive the brunt of the impact. We assess the impact of artificial light on ecosystems and wilderness experience by using the satellite data of the upwards emitted and reflected artificial light with a spectral range of 0.5–0.9 μm in Europe from the Visible Infrared Imaging Radiometer Suite (VIIRS) of the Soumi National Polar-orbiting Partnership (SNPP) for the year 2012 (NOAA National Geophysical Data Center 2012) with a resolution of 15 arc sec (approximately 450 m). We apply a kernel function to distribute the impact over a radius of approximately 10 km (Fig. 2.1b) as a conservative approximation meant to cover the night glow effects reported in the literature (Kyba et al. 2011) along with the direct ecological impacts (Longcore and Rich 2004). In each pixel, the light impact score is the sum of all the impact scores from the surrounding light sources and it represents a relative measure aimed at encompassing both the ecological aspect and the impact on the subjective wilderness experience (Fig. 2.1b).

The last two metrics that we consider here are qualitative and quantitative measures of the human modification of ecosystems and thus they convey mainly, although not exclusively, an ecological significance. Anthropogenic change of natural habitat is one of the major drivers of biodiversity loss (Pereira et al. 2010) and it has been studied extensively for a large range of taxa (Bolliger et al. 2007). The most conspicuous element of habitat loss is the change in vegetation, and intact vegetation cover has been used before as a wilderness indicator (Bryant et al. 1997). Human changes in vegetation tips the balance in favour of species benefiting from human presence and impacts habitat-sensitive ones (Leu et al. 2008). Therefore we use here the deviation from potential natural vegetation (dPNV) as a qualitative measure of the human impact on the landscape. We used the potential natural vegetation (PNV) classes of the map developed by Bohn et al. (2000). We calculate the similarity of current land cover to PNV by estimating the probability that the CORINE 2000 land cover class in any one location in Europe belongs to the local PNV type (Bohn et al. 2000). The probability of agreement was classified in four classes with different scores: assumed = 1, most probable = 0.75, probable = 0.5 and possible = 0.1. The resulting map was combined with the grazing density data from Food and Agriculture Organization, which was previously linear transformed to a scale from 0 to 1, where 1 represents a density of 20 heads/km^2 or more. We used

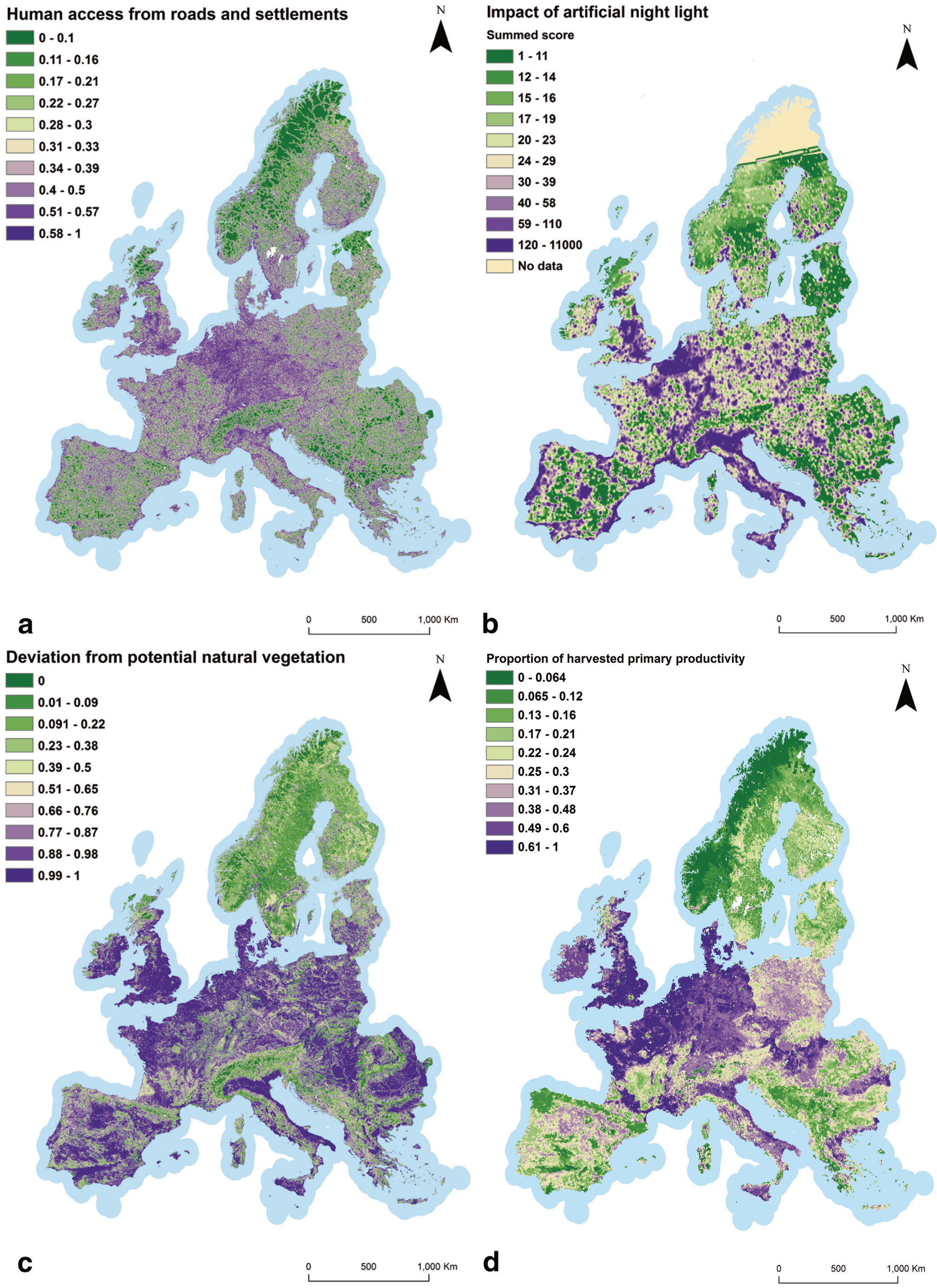

Fig. 2.1 Wilderness areas according to four metrics. **a** Access from roads and human settlements. **b** Artificial night light. **c** Deviation from potential natural vegetation. **d** Proportion of harvested primary productivity out of the potential primary productivity. Wilderness value increases with the decrease of the metrics

grazing density to account for human transformations in semi-natural grasslands. We expressed the dPNV value by subtracting from 1 the score calculated according to the described methodology. (Fig. 2.1c).

Through agriculture, hunting, fishing and forestry, humans are removing significant quantities of biomass from the ecosystems. Primary productivity (PP) is the foundation of trophic networks and it influences the structure and functions of ecosystems in a domino effect across trophic levels (Haberl et al. 2004). Humans have reduced drastically the PP available to other species and this has changed the composition of the ecological communities (Barnosky 2008; Pereira et al. 2012). We map the proportion of human harvested PP out of the total potential PP in Europe as another indicator of wilderness and using the data analysed in Haberl et al. (2007). We calculated the harvested PP by extracting net PP remaining in ecosystems after harvest from the net PP of the actual vegetation. We then calculated the proportion of harvested PP by dividing net harvested PP by net PP of the potential vegetation. The data are calculated based on country-level statistics of the Food and Agriculture Organization (Haberl et al. 2007) while potential PP is estimated using the Lund-Potsdam-Jena dynamic global vegetation model (Sitch et al. 2003). Some abnormalities can be noticed in the harvested PP map which are due to the assumptions of the model and the FAO national level data. The map has to be interpreted with this limitation in mind (Fig. 2.1d).

The four resulting maps based on the selected metrics show a common pattern of high human footprint in the lowlands of central Europe (Fig. 2.1). The most unaltered values of all metrics occur in high mountainous areas and Scandinavia. But the differences at intermediate values of wilderness provide a key signal to what are the strongest determinants of human footprint at regional level in Europe. For example, although the dPNV is very low in almost all of Scandinavia (Fig. 2.1c), the proportion of harvested PP is comparatively higher, consistent with high forestry harvest in the Nordic countries (Fig. 2.1d). The reverse pattern is noticeable in the Iberian Peninsula where although the drier climate restricts high harvesting of PP, the current vegetation is quite far from PNV as measured in our map and consistent with the degradation of the Mediterranean habitats (Myers et al. 2000). In the same region, the significant differences between the inland and coastal values of the night light impact and human access (Fig. 2.1a and b) indicates the high difference between the human population densities inland compared with the coastal regions. These differences in the distribution of human populations are masked in the PNV score and harvested PP maps (Fig. 2.1c and d). The map of artificial light (Fig. 2.1b) also points out to a discrepancy in the relative wilderness values in East and South-East Europe compared with the dPNV score map for example (Fig. 2.1c). The lower economic activity in this area results in lower light impact although the level of vegetation change is very high (Doll et al. 2006).

The lowest wilderness areas in Europe have usually low scores for all the wilderness dimensions considered, and they represent mainly areas of high human densities and intense economic activity. Conversely, high wilderness areas are the wildest from all the points of view taken here. But the areas of intermediate wilderness values are strongly impacted by only one or two metrics with very low wilderness values. Especially dPNV and harvested PP have a farther reach, affecting even ecosystems where infrastructure and artificial light impacts are reduced. These indicators are connected with more extensive land-uses such as agriculture and forestry, and less with high human population densities and infrastructure.

The synergies and interactions between the different elements of our wilderness mapping emphasize even further their ecological significance. In areas of high habitat quality the road mortality can be higher in absolute terms because it affects more abundant populations (Patrick et al. 2012) while road lighting can increase the impact of the road itself on the local ecological communities by favouring certain types of predation (Rich and Longcore 2005) or providing additional perches for improved hunting efficiency of raptors such as kestrels (Sheffield et al. 2001).

2.4 Wilderness Conservation

The designation, coverage and implementation of protected areas and Natura 2000 sites vary widely across European countries. However, looking at the continental map, we discern some regional patterns in wilderness protection. Many mountainous areas in the Pyrenees, the Apennines, the Massif Central and the Carpathians are covered by Natura 2000 sites and, to a lesser extent, by nationally designated protected areas (Fig. 2.2) (European Environment Agency 2012a, b). Large protected areas included both in the Natura 2000 network and in the national networks protect the Scandinavian mountains. As already pointed out in the literature (Gaston et al. 2008), many of the designated areas overlap because countries have co-designated under Natura 2000 and their own national systems. However, important differences between the two protected areas systems can also be noticed (Fig. 2.2). For example, the Iberian Peninsula and South-Eastern Europe seem to have a much larger area under protection by the Natura 2000 network than from nationally designated protected areas. Conservation seems to have benefitted in these areas from a push from the European conservation policies (European Council 1979, 1992). Meanwhile, Germany and France have smaller and fewer terrestrial protected areas under the Natura 2000 network than under the national network.

It has been suggested in the literature that the designation of protected areas has been done opportunistically and thus that they are more likely to cover low productivity, high altitude, wilderness areas (Pressey et al. 1993; Margules and Pressey 2000). Although largely lacking continental coordination, Natura 2000 network has some features common with systematic conservation planning and aims to protect species and habitats threatened at continental level (Gaston et al. 2008). Surprisingly however, the terrestrial Natura 2000 sites have a lower continental average proportion of harvested PP than nationally designated protected areas: 26.7 % for Natura 2000 sites against 34.3 % for the nationally designated protected areas. The continental average values for the impact of artificial night light in Natura 2000 sites is 38 while in nationally designated protected areas network is 31, showing the same pattern as in the case of harvested PP. However, we have to keep in mind that

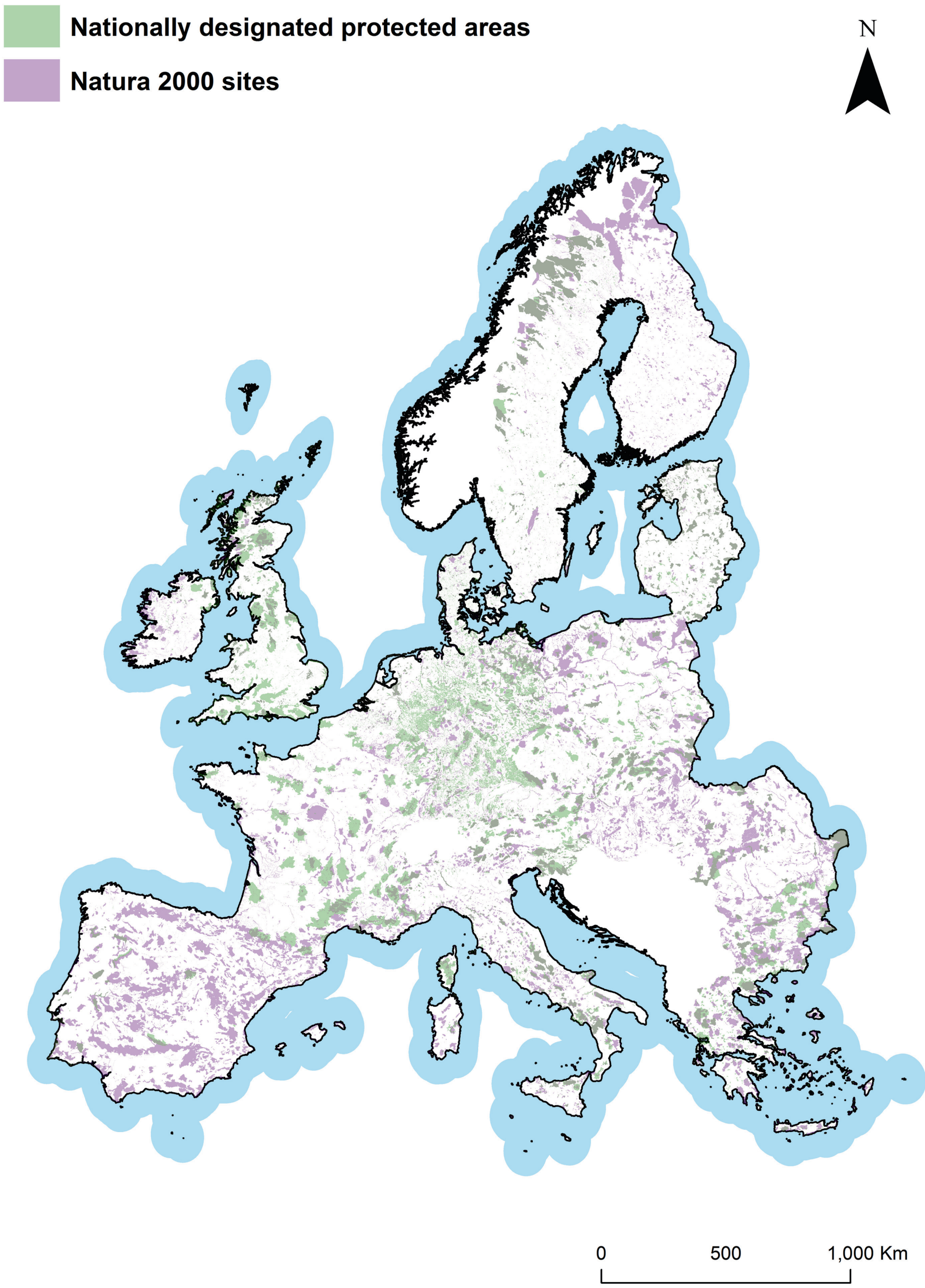

Fig. 2.2 Protected territory in Europe under the Natura 2000 network and nationally designated protected areas

there are big regional differences between the patterns of wilderness in protected areas in Europe. For instance, analysis concentrating on Germany as a case study demonstrated that the Natura 2000 areas in Western Germany largely fail to protect the roadless and the low-traffic areas, whereas in former East Germany a better congruence was achieved (Selva et al. 2011).

Indicative of higher resource availability, we verified that higher species richness of megafauna species coincides with high wilderness. We selected the mammals with an adult bodyweight of an average of 10 kg or more (Jones et al. 2009) from the data of the Atlas of European Mammals (Mitchell-Jones et al. 1999). These include species of large herbivores and apex predators such as the wolf (*Canis lupus*) and the lynx (*Lynx lynx*). We also selected the bird species with an adult bodyweight of an average of 5 kg or more (Myers et al. 2013; Tacutu et al. 2013) using data from the atlas of the European Bird Census Council (Hagemeijer and Blair 1997). These species include several birds of prey as well as other species such as the great white pelican (*Pelecanus onocrotalus*) or the great bustard (*Ardeotis nigriceps*). In the end, we obtained a megafauna list of 30 mammal species and 13 bird species distributed in a grid of 50×50 km^2 covering the European territory. At a visual examination, the highest species richness areas in terms of megafauna coincide with high wilderness areas in Europe such as the Carpathians, the Apennines and the Pyrenees (Fig. 2.3). We calculated rank correlations between the megafauna species richness and average values per grid cell of the four wilderness metrics. The results suggest that wilderness and megfauna populations spatially coincide in Europe ($\rho=0.18$, $p<0.0001$ for access from roads and settlements, $\rho=-0.28$, $p<0.0001$ for light impact, $\rho=0.34$, $p<0.0001$ for dPNV score, $\rho=-0.26$, $p<0.0001$ for harvested PP). There are several mechanisms that could underlie this pattern such as the direct persecution of carnivores and birds of prey countered by conservation programs in areas of lowest social conflict (Valkama et al. 2005; Enserink and Vogel 2006). This pattern could also be related to a phylogenetic bias determined by the strong predominance of a few bird and mammal orders in our selection which could be limited to certain habitats only based on their common evolutionary history. We also did not consider the possible spatial autocorrelation in our datasets. However, from the perspective of abandonment, the spatial concurrence between megafauna species richness and high wilderness is important because it means that abandoned farmland closer to high wilderness areas will have a better chance of being repopulated by these species. This will lead to a quicker recovery of trophic networks and natural ecological processes.

2.5 Farmland Abandonment as Opportunity for Wilderness Expansion

Farmland abandonment in Europe is a result of the economic and social changes at national, continental and global levels. Abandonment happens especially in areas where land productivity is not sufficiently high to sustain an adequate income for

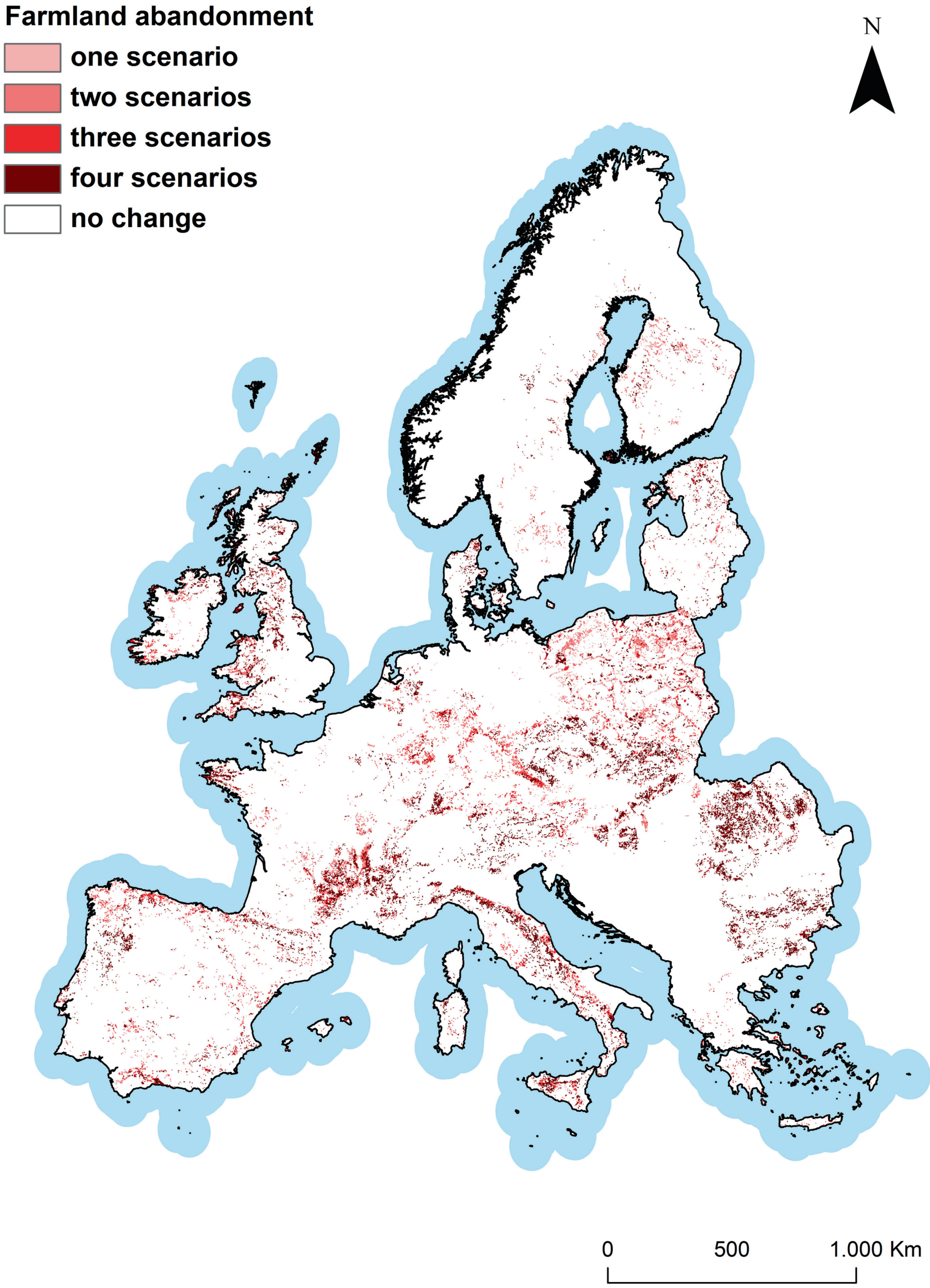

Fig. 2.3 Farmland abandonment in Europe projected for the year 2040 by the Dyna-CLUE model based on four VOLANTE scenarios. We indicate in how many of the four scenarios land abandonment is found significant across the continent

farmers, even with the support of subsidies (Rey Benayas et al. 2007, see Chap. 1). These land-use changes raise challenges in terms of lifestyles, social structure and biodiversity (Munroe et al. 2013). Thus, predicting these changes has received considerable importance in recent research. We map the areas in Europe where farmland abandonment is projected to take place based on the Dyna-CLUE model (Verburg and Overmars 2009) (Fig. 2.3). For the projections of the social and economic drivers driving farmland abandonment, we used four VOLANTE scenarios describing different development paths towards the year 2040 (Paterson et al. 2012). These scenarios are loosely based on the Special Report on Emission Scenarios (SRES) of the Inter-governmental Panel on Climate Change (Nakicenovic et al. 2000) and they cover the range of socio-economic conditions across the axes of regionalization versus globalization, and willingness versus reluctance against sustainable lifestyle changes at the societal level. We indicate here in how many of the four scenarios land abandonment is found significant across Europe (Fig. 2.3).

How will farmland abandonment affect wilderness value? The answer to this question depends on where farmland abandonment takes place. Many areas of abandonment can be found around mountainous regions such as the Apennines, the Massif Central, the Carpathians, the Balkans, areas of higher altitude and lower productivity that have already experienced abandonment in the past decades (Fig. 2.3). These areas have a low density of human population and a low level of infrastructure development. As the human density will decrease even more, the use of artificial light will decrease as well, but the physical infrastructures will withstand for longer than the outmigration of people albeit with lower intensity of use. Spurred by the already existing infrastructure, many abandonment areas might also see a surge in tourism, biofuels cultivation and renewable energy industries, replacing the agricultural activities (Laiolo and Tella 2006).

From an ecological point of view, farmland abandonment will directly lead to a decrease in harvested PP as grazing and cultivation are projected to drop. This will increase the resources available to wild populations and ecosystems, and vegetation cover will evolve towards a more natural state (Rey Benayas et al. 2007). Previous studies have showed that increased availability of biomass and reduced presence of humans lead to growing numbers of wild herbivores in south Asia (Madhusudan 2004). The recovery of ecosystems to a wilderness state depends on rebuilding natural trophic cascades and networks that are both resilient to natural disturbances and able to sustain key ecosystem functions. In these networks, megafauna and apex predators have a fundamental role, especially in the depleted conditions of the current European biota (Schmitz 2006; Sekercioglu 2006; Johnson 2009; Ritchie and Johnson 2009). For the natural recovery of ecosystems and the return of these species, the presence of source populations is paramount and adjacency to existing core wilderness areas will be a key driver (see Chaps. 4, 8).

We explore the chances for a natural recovery of European fauna by mapping the distribution of megafauna (Fig. 2.4). The results are encouraging for many areas of future agricultural abandonment: megafauna richness is high in the adjacent areas and many wild populations have already begun to recover, especially in the case of mammals (Enserink and Vogel 2006). In the case of birds, the literature reports significant changes in the community patterns due to abandonment, especially negative effects on populations of farmland birds with narrow habitat preferences (Sirami et al. 2008). The correlation between the number of mammal species and the percentage of projected abandoned area in a grid cell is $\rho = 0.14$ ($p < 0.001$) whereas for bird species it is negative at $\rho = -0.15$ ($p < 0.001$). Thus megafauna mammal species might be in a better position to take advantage of the new resources and space made available by farmland abandonment. We did not consider here the possible spatial autocorrelation of the data because we were interested only in the spatial coincidence between abandonment and megafauna.

However, some of the future abandoned areas have been affected by invasive species, fire suppression practices, and missing trophic links during thousands of years of human use (Proença et al. 2010; Wehn et al. 2011). Thus abandonment may not be sufficient to return these areas to a vegetation close to PNV in a short term without management actions (see Chap. 8). But even in these areas the abandonment will have immediate positive effects on wildlife by reducing human disturbance, increasing landscape connectivity, and releasing ecological processes from human control and thus increasing the wilderness value of the land (see Chap. 1).

Aplet et al. (2000) describe the two dimensional space defined by the axes of freedom and naturalness as a framework for wilderness management. Freedom is understood as the absence of human control over ecological processes (i.e self-willed) while naturalness is the degree to which ecosystems are close to an accepted ecological benchmark. Such a framework is readily usable for mapping the trade-offs related to human management in areas affected by invasive and exotic species, thus increasing naturalness but decreasing freedom (Landres et al. 2000; Sydoriak et al. 2000), but also the current views on rewilding as some advocate for serious management commitments in order to achieve a certain perception of wilderness (Donlan et al. 2006). However, we consider that the ultimate aim of rewilding is not to recreate some image of pre-human ecosystems, but to facilitate new, self-regulating systems that appear naturally out of the current conditions. A realistic expectation is that in the absence of human management, the new rewilded areas will form novel ecosystems that share elements with the pre-human past but also integrate current factors. Minimum human management and this new wilderness of natural and self-sustaining ecosystems should be the goal of rewilding.

2.6 Conclusions

Wilderness in Europe has been pushed into the high altitude areas of the mountain ranges and into the high latitude areas of Scandinavia. The metrics we use here agree on the general patterns of European wilderness but regional differences between our metrics emphasize the different factors that affect wilderness values regionally and locally (Fig. 2.1). New opportunities for wilderness expansion have appeared in Europe

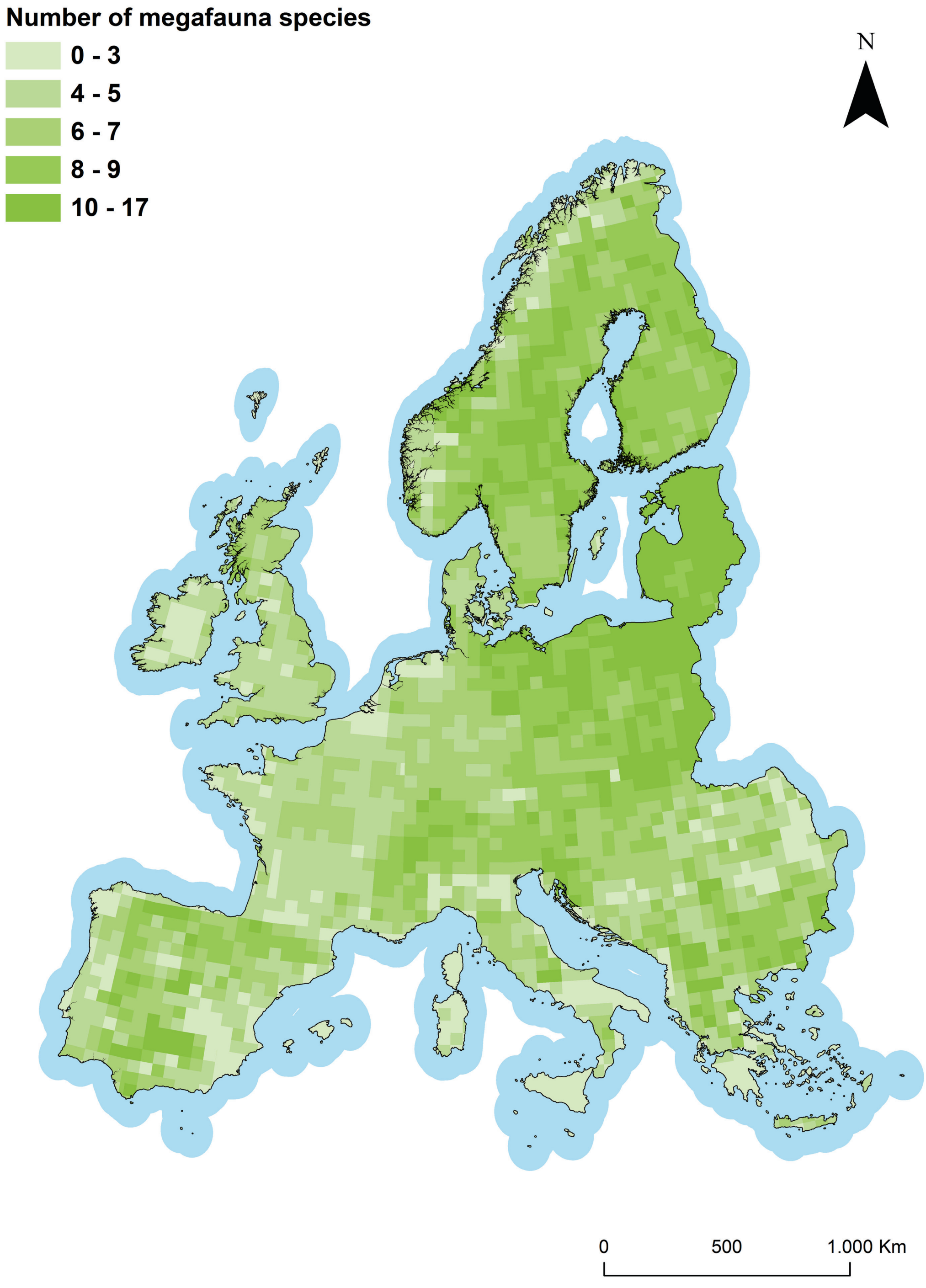

Fig. 2.4 Species richness of European megafauna. We calculate it as the number of species of mammals with adult body mass equal or higher than 10 kg and birds with adult body mass equal or higher than 5 kg in each grid cell

due to farmland abandonment and a decrease of human presence can lead to a drop in several human footprint indicators and a recovery of natural trophic networks. Although management trade-offs have to be made in some places between intervening for a faster recovery and stepping back for an unrestrained adaptation of ecosystems, we favour an approach of minimum intervention and self-regulating ecosystems.

The next few decades are crucial for how wilderness will evolve in Europe. New research is necessary on how different dimensions of wilderness will change as a result of land use changes and what will be the effects on ecosystems and wildlife. Moreover, research is need on how to restore not only ecosystems but also the collective memory to encompass what wilderness may have been like, what it is and what it may or should be. This would help consolidate the crucial link between research on one hand, and management and policy on the other, an area that still requires substantial work (see Chap. 11). Challenges remain in bringing together rewilding views, and negotiating diverging social and economic interests. A focus on the benefits of natural ecosystem for the society at large can ease the tensions between different stakeholders in continental policy-making. From a global perspective, Europe will continue to be at the lower end of the wilderness continuum (Mittermeier et al. 2003) but favourable opportunities are arising at continental level to improve ecosystem functions and we should seize them wisely.

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References

Alterio, N., Moller, H., & Ratz, H. (1998). Movements and habitat use of feral house cats Felis catus, stoats Mustela erminea and ferrets Mustela furo, in grassland surrounding Yellow-eyed penguin Megadyptes antipodes breeding areas in spring. *Biological Conservation, 83,* 187–194.

Aplet, G., Thomson, J., & Wilbert, M. (2000). Indicators of wildness: Using attributes of the land to assess the context of wilderness. Proceedings: Wilderness Science in a Time of Change. Ogden (UT): USDA Forest Service, Rocky Mountain Research Station. Proc. RMRS-P-15

Barnosky, A. D. (2008). Megafauna biomass tradeoff as a driver of quaternary and future extinctions. *Proceedings of the National Academy of Sciences, 105,* 11543–11548. doi:10.1073/pnas.0801918105.

Becker, A., Whitfield, A. K., Cowley, P. D., et al. (2013). Potential effects of artificial light associated with anthropogenic infrastructure on the abundance and foraging behaviour of estuary-associated fishes. *Journal of Applied Ecology, 50,* 43–50.

Bohn, U., Gollub, G., Hettwer, C., et al. (2000). *Karte der natürlichen Vegetation Europas, Maßstab 1: 2,500,000.[Map of the Natural vegetation of Europe. Scale 1: 2,500,000]*. Bonn: Bundesamt für Naturschutz.

Boldogh, S., Dobrosi, D., & Samu, P. (2007). The effects of the illumination of buildings on house-dwelling bats and its conservation consequences. *Acta Chiropterologica, 9,* 527–534.

Bolliger, J., Kienast, F., Soliva, R., & Rutherford, G. (2007). Spatial sensitivity of species habitat patterns to scenarios of land use change (Switzerland). *Landscape Ecology, 22,* 773–789.

Brooks, T. M., Mittermeier, R. A., da Fonseca G. A., et al. (2006). Global biodiversity conservation priorities. *Science, 313,* 58.

Bryant, D., Nielsen, D., & Tangley, L. (1997). *Last frontier forests: Ecosystems and economies on the edge*. Washington, D. C.: World Resources Institute, Forest Frontiers Initiative.

Carruthers, J. (1995) *The Kruger National Park: A social and political history*. Pietermaritzburg: University of Natal Press.

Carver, S. (2010). Mountains and wilderness. European Environment Agency (2010) Europe's ecological backbone: Recognising the true value of our mountains. European Environment Agency, Copenhagen, pp. 192–201.

Carver S., Evans AJ., Fritz S. (2002). Wilderness attribute mapping in the United Kingdom. *International Journal of Wilderness 8,* 24–29.

Carver, S., & Fritz, S. (1999). Mapping remote areas using GIS. Landscape character: Perspectives on management and change Natural Heritage of Scotland Series, HMSO, pp. 112–126.

Carver, S., Comber, A., McMorran, R., & Nutter, S. (2012). A GIS model for mapping spatial patterns and distribution of wild land in Scotland. *Landscape and Urban Planning, 104,* 395–409.

Christensen, D. L., Herwig, B. R., Schindler, D. E., & Carpenter, S. R. (1996). Impacts of lakeshore residential development on coarse woody debris in north temperate lakes. *Ecological Applications, 6,* 1143–1149.

Cinzano, P., Falchi, F., Elvidge, C. D., & Baugh, K. E. (2000). The artificial night sky brightness mapped from DMSP satellite Operational Linescan System measurements. *Monthly Notices of the Royal Astronomical Society, 318,* 641–657.

Cole, D. N., & Landres, P. B. (1996). Threats to wilderness ecosystems: Impacts and research needs. *Ecological Applications, 6,* 168–184.

Davies, T. W., Bennie, J., & Gaston, K. J. (2012). Street lighting changes the composition of invertebrate communities. *Biology Letters, 8,* 764–767.

Doll, C. N., Muller, J.-P., & Morley, J. G. (2006). Mapping regional economic activity from night-time light satellite imagery. *Ecological Economics, 57,* 75–92.

Donlan, C. J., Berger, J., Bock, C. E., et al. (2006). Pleistocene rewilding: An optimistic agenda for twenty-first century conservation. *The American Naturalist, 168,* 660–681.

Enserink, M., & Vogel, G. (2006) The carnivore comeback. *Science, 314,* 7476–7749.

European Council. (1979). Council Directive 79/409/EEC on the conservation of wild birds.

European Council. (1992). EU Habitats Directive (92/43/EEC). Consolidated Text. Office for Official Publication of The European Union. CONSLEG: 1992LOO43-01.05-2004.

European Environment Agency. (2012a). Natura 2000 data-the European network of protected sites. http://www.eea.europa.eu/data-and-maps/data/natura-3. Accessed 5 July 2013.

European Environment Agency. (2012b). Nationally designated areas (CDDA). http://www.eea.europa.eu/data-and-maps/data/nationally-designated-areas-national-cdda-7. Accessed 5 July 2013.

European Parliament. (2009). Resolution on Wilderness in Europe.

Fritz, S., Carver, S., & See, L. (2000). New GIS approaches to wild land mapping in Europe. Proceedings of the Wilderness science in a time of change conference. USDA Forest Service, Missoula, Montana, pp. 120–127

Gaston, K. J., Jackson, S. F., Nagy, A., et al. (2008). Protected areas in Europe. *Annals of the New York Academy of Sciences, 1134,* 97–119.

Gaston, K. J., Bennie, J., Davies, T. W., & Hopkins, J. (2013). The ecological impacts of nighttime light pollution: A mechanistic appraisal. *Biological Reviews, 88,* 912–927.

Gauthreaux, S. A., Jr., Belser, C., Rich, C., & Longcore, T. (2006). Effects of artificial night lighting on migrating birds. In C. Rich & T. Longcore (Eds.) Ecological Consequences of Artificial Night Lighting (pp.67–93). Washington D.C.: Island Press.

Gillson, L., & Willis, K. J. (2004). As earth's testimonies tell: Wilderness conservation in a changing world. *Ecology Letters, 7,* 990–998.

Grilo, C., Bissonette, J. A., & Santos-Reis, M. (2009). Spatial-temporal patterns in Mediterranean carnivore road casualties: Consequences for mitigation. *Biological Conservation, 142,* 301–313.

Haberl, H., Schulz, N. B., Plutzar, C., et al. (2004). Human appropriation of net primary production and species diversity in agricultural landscapes. *Agriculture, Ecosystems & Environment, 102,* 213–218.

Haberl, H., Erb, K. H., Krausmann, F., et al. (2007). Quantifying and mapping the human appropriation of net primary production in earth's terrestrial ecosystems. *Proceedings of the National Academy of Sciences, 104,* 12942.

Habib, L., Bayne, E. M., & Boutin, S. (2007). Chronic industrial noise affects pairing success and age structure of ovenbirds Seiurus aurocapilla. *Journal of Applied Ecology, 44,* 176–184.

Hagemeijer, W. J., & Blair, M. J. (1997). *The EBCC atlas of European breeding birds: Their distribution and abundance*. London: T. & AD Poyser.

Halpern, B. S., Walbridge, S., Selkoe, K. A., et al. (2008). A global map of human impact on marine ecosystems. *Science, 319,* 948–952.

Hansen, A. J., Knight, R. L., Marzluff, J. M., et al. (2005). Effects of exurban development on biodiversity: Patterns, mechanisms, and research needs. *Ecological Applications, 15,* 1893–1905.

Hatt, B. E., Fletcher, T. D., Walsh, C. J., & Taylor, S. L. (2004). The influence of urban density and drainage infrastructure on the concentrations and loads of pollutants in small streams. *Environmental Management, 34,* 112–124.

Heckenberger, M. J., Kuikuro, A., Kuikuro, U. T., et al. (2003). Amazonia 1492: Pristine forest or cultural parkland? *Science, 301,* 1710–1714.

Hochtl, F., Lehringer, S., & Konold, W. (2005). "Wilderness": What it means when it becomes a reality-a case study from the southwestern Alps. *Landscape and Urban Planning, 70,* 85–95.

Hölker, F., Moss, T., Griefahn, B., et al. (2010a). The dark side of light: A transdisciplinary research agenda for light pollution policy. *Ecology and Society, 15*(4): 13.

Hölker, F., Wolter, C., Perkin, E. K., & Tockner, K. (2010b). Light pollution as a biodiversity threat. *Trends in ecology & evolution, 25,* 681–682.

Iosif, R., Rozylowicz, L., & Popescu, V. D. (2013). Modeling road mortality hotspots of Eastern Hermann's tortoise in Romania. *Amphibia-Reptilia, 34,* 163–172.

Jodoin, Y., Lavoie, C., Villeneuve, P., et al. (2008). Highways as corridors and habitats for the invasive common reed Phragmites australis in Quebec, Canada. *Journal of Applied Ecology, 45,* 459–466.

Johnson, C. N. (2009). Ecological consequences of Late Quaternary extinctions of megafauna. *Proceedings of the Royal Society B: Biological Sciences, 276,* 2509–2519.

Jones, K. E., Bielby, J., Cardillo, M., et al. (2009). PanTHERIA: A species-level database of life history, ecology, and geography of extant and recently extinct mammals: Ecological Archives E090-184. *Ecology, 90,* 2648–2648.

Jones-Walters, L., & Čivić, K. (2010). Wilderness and biodiversity. *Journal for Nature Conservation, 18,* 338–339.

Kalamandeen, M., & Gillson, L. (2007). Demything "wilderness": Implications for protected area designation and management. *Biodiversity and Conservation, 16,* 165–182.

Kristan, W. B. III, & Boarman, W. I. (2003). Spatial pattern of risk of common raven predation on desert tortoises. *Ecology, 84,* 2432–2443.

Kyba, C. C., Ruhtz, T., Fischer, J., & Hölker, F. (2011). Cloud coverage acts as an amplifier for ecological light pollution in urban ecosystems. *PLoS ONE, 6,* e17307.

Laiolo, P., & Tella, J. L. (2006). Fate of unproductive and unattractive habitats: Recent changes in Iberian steppes and their effects on endangered avifauna. *Environmental Conservation, 33,* 223–232.

Landres, P. B., Brunson, M. W., Merigliano, L., et al. (2000). Naturalness and wildness: The dilemma and irony of managing wilderness. *Proceedings RMRS-P-15Proceedings RMRSP-15, 5,* 377–381.
Lesslie, R. G., Mackey, B. G., & Preece, K. M. (1988). A computer-based method of wilderness evaluation. *Environmental Conservation, 15,* 225–232.
Lesslie, R. G., Maslen, A., Commission AH. (1995). National Wilderness Inventory Australia: Handbook of Procedures, Content, and Usage. Australian Government Pub. Service
Leu, M., Hanser, S. E., & Knick, S. T. (2008). The human footprint in the west: A large-scale analysis of anthropogenic impacts. *Ecological Applications, 18,* 1119–1139.
Longcore, T., & Rich, C. (2004). Ecological light pollution. *Frontiers in Ecology and the Environment, 2,* 191–198.
Mackey, B. G., Lesslie, R. G., Lindenmayer, D. B., et al. (1998). *The role of wilderness in nature conservation*. Australia: Canberra.
Madhusudan, M. D. (2004). Recovery of wild large herbivores following livestock decline in a tropical Indian wildlife reserve. *Journal of Applied Ecology, 41,* 858–869.
Margules, C. R., & Pressey, R. L. (2000). Systematic conservation planning. *Nature, 405,* 243–253.
Martin, V. G., Kormos, C. F., Zunino, F., et al. (2008). Wilderness Momentum in. Europe. *International Journal of Wilderness, 14,* 34–38.
Mitchell-Jones, A. J., Amori, G., Bogdanowicz, W., et al. (1999). *The atlas of European mammals*. London: Academic.
Mittermeier, R. A., Mittermeier, C. G., Brooks, T. M., et al. (2003). Wilderness and biodiversity conservation. *Proceedings of the National Academy of Sciences, 100,* 10309.
Montevecchi, W. A., Rich, C., & Longcore, T. (2006). Influences of artificial light on marine birds. In C. Rich & T. Longcore (Eds.) Ecological Consequences of Artificial Night Lighting (pp.94–113). Washington D.C.: Island Press
Munroe, D. K., van Berkel D. B., Verburg, P. H., & Olson, J. L. (2013). Alternative trajectories of land abandonment: Causes, consequences and research challenges. *Current Opinion in Environmental Sustainability, 5,* 471–476.
Myers, N., Mittermeier, R. A., Mittermeier, C. G., et al. (2000). Biodiversity hotspots for conservation priorities. *Nature, 403,* 853–858.
Myers, P., Espinosa, R., Parr, C. S., et al. (2013). The Animal Diversity Web (online). http://animaldiversity.org. Accesssed 10 July 2013.
Naidoo, R., Balmford, A., Costanza, R., et al. (2008). Global mapping of ecosystem services and conservation priorities. *Proceedings of the National Academy of Sciences, 105,* 9495.
Nakicenovic, N., Alcamo, J., Davis, G., et al. (2000). Special report on emissions scenarios: A special report of Working Group III of the Intergovernmental Panel on Climate Change. Pacific Northwest National Laboratory, Richland, WA (US), Environmental Molecular Sciences Laboratory (US).
Nash, R. (2001) *Wilderness and the American mind*. London: Yale Nota Bene.
Navara, K. J., & Nelson, R. J. (2007). The dark side of light at night: Physiological, epidemiological, and ecological consequences. *Journal of pineal research, 43,* 215–224.
NOAA National Geophysical Data Center EOG. (2012). VIIRS Nighttime Lights—2012.
Orlowski, G. (2005). Factors affecting road mortality of the Barn Swallows Hirundo rustica in farmland. *Acta Ornithologica, 40,* 117–125.
Papworth, S. K., Rist, J., Coad, L., & Milner-Gulland, E. J. (2009). Evidence for shifting baseline syndrome in conservation. *Conservation Letters, 2,* 93–100.
Paterson, J., Metzger, M., & Walz, A. (2012). Deliverable No: 9.1—The VOLANTE scenarios: Framework, storyline and drivers.
Patrick, D. A., Gibbs, J. P., Popescu, V. D., & Nelson, D. A. (2012). Multi-scale habitat-resistance models for predicting road mortality "hotspots" for turtles and amphibians. *Herpetological Conservation and Biology, 7,* 407–426.
Pereira, H. M., Leadley, P. W., Proença, V., et al. (2010). Scenarios for global biodiversity in the 21st century. *Science, 330,* 1496.

Pereira, H. M., Navarro, L. M., & Martins, I. S. (2012). Global biodiversity change: The bad, the good, and the unknown. *Annual Review of Environment and Resources, 37,* 25–50. doi:10.1146/annurev-environ-042911-093511.

Perkin, E. K., Hölker, F., Richardson, J. S., et al. (2011). The influence of artificial light on stream and riparian ecosystems: Questions, challenges, and perspectives. *Ecosphere, 2,* art122.

Philcox, C. K., Grogan, A. L., & Macdonald, D. W. (1999). Patterns of otter Lutra lutra road mortality in Britain. *Journal of Applied Ecology, 36,* 748–761.

Pressey, R. L., Humphries, C. J., Margules, C. R., et al. (1993). Beyond opportunism: Key principles for systematic reserve selection. *Trends in ecology & evolution, 8,* 124–128.

Proença, V., Pereira, H. M., & Vicente, L. (2010). Resistance to wildfire and early regeneration in natural broadleaved forest and pine plantation. *Acta Oecologica, 36,* 626–633.

Rentch, J. S., Fortney, R. H., Stephenson, S. L., et al. (2005). Vegetation–site relationships of roadside plant communities in West Virginia, USA. *Journal of Applied Ecology, 42,* 129–138.

Rey Benayas, J. M., Martins, A., Nicolau, J. M., & Schulz, J. J. (2007). Abandonment of agricultural land: An overview of drivers and consequences. *CAB reviews: Perspectives in agriculture, veterinary science, nutrition and natural resources, 2,* 1–14.

Rich, C., & Longcore, T. (2005). *Ecological consequences of artificial night lighting*. Washington, D.C.: Island Press

Ritchie, E. G., & Johnson, C. N. (2009). Predator interactions, mesopredator release and biodiversity conservation. *Ecology letters, 12,* 982–998.

Sanderson, E. W., Jaiteh, M., Levy, M. A., et al. (2002). The human footprint and the last of the wild. *BioScience, 52,* 891–904.

Schmitz, O. J. (2006). Predators have large effects on ecosystem properties by changing plant diversity, not plant biomass. *Ecology, 87,* 1432–1437.

Scottish, N. H. (2012). Wild land policy—Scottish Natural Heritage. http://www.snh.gov.uk/protecting-scotlands-nature/looking-after-landscapes/landscape-policy-and-guidance/wild-land/wild-land-policy/. Accessed 23 Aug 2013.

Seiler, A. (2005). Predicting locations of moose—Vehicle collisions in Sweden. *Journal of Applied Ecology, 42,* 371–382.

Sekercioglu, C. H. (2006). Increasing awareness of avian ecological function. *Trends in Ecology & Evolution, 21,* 464–471.

Selva, N., Kreft, S., Kati, V., et al. (2011). Roadless and low-traffic areas as conservation targets in Europe. *Environmental management, 48,* 865–877.

Sheffield, L. M., Crait, J. R., Edge, W. D., & Wang, G. (2001). Response of American kestrels and gray-tailed voles to vegetation height and supplemental perches. *Canadian Journal of Zoology, 79,* 380–385.

Sirami, C., Brotons, L., Burfield, I., et al. (2008). Is land abandonment having an impact on biodiversity? A meta-analytical approach to bird distribution changes in the north-western Mediterranean. *Biological Conservation, 141,* 450–459.

Sitch, S., Smith, B., Prentice, I. C., et al. (2003). Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Global Change Biology, 9,* 161–185.

Sydoriak, C. A., Allen, C. D., & Jacobs, B. F. (2000). Would ecological landscape restoration make the Bandelier Wilderness more or less of a wilderness. Proceedings: Wilderness science in a time of change conference, pp. 209–215.

Tabarelli, M., da Silva J. M. C., & Gascon, C. (2004). Forest fragmentation, synergisms and the impoverishment of neotropical forests. *Biodiversity & Conservation, 13,* 1419–1425.

Tacutu, R., Craig, T., Budovsky, A., et al. (2013). Human ageing genomic resources: Integrated databases and tools for the biology and genetics of ageing. *Nucleic acids research, 41,* D1027–D1033.

Valkama, J., Korpimäki, E., Arroyo, B., et al. (2005). Birds of prey as limiting factors of gamebird populations in Europe: A review. *Biological Reviews, 80,* 171–203.

Verburg, P. H., & Overmars, K. P. (2009). Combining top-down and bottom-up dynamics in land use modeling: Exploring the future of abandoned farmlands in Europe with the Dyna-CLUE model. *Landscape ecology, 24,* 1167–1181.

Vicente, J., Alves, P., Randin, C., et al. (2010). What drives invasibility? A multi-model inference test and spatial modelling of alien plant species richness patterns in northern Portugal. *Ecography, 33,* 1081–1092.

Vitousek, P. M., Aber, J. D., Goodale, C. L., & Aplet, G. H. (2000). Global change and wilderness science. Wilderness science in a time of change conference. RMRS-P-15-VOL-1, pp. 5–9.

Watson, J. E., Fuller, R. A., Watson, A. W., et al. (2009). Wilderness and future conservation priorities in Australia. *Diversity and Distributions, 15,* 1028–1036.

Wehn, S., Pedersen, B., & Hanssen, S. K. (2011). A comparison of influences of cattle, goat, sheep and reindeer on vegetation changes in mountain cultural landscapes in Norway. *Landscape and Urban Planning, 102,* 177–187.

Whittington, J., Hebblewhite, M., DeCesare, N. J., et al. (2011). Caribou encounters with wolves increase near roads and trails: A time-to-event approach. *Journal of Applied Ecology, 48,* 1535–1542.

Woolmer, G., Trombulak, S. C., Ray, J. C., et al. (2008). Rescaling the human footprint: A tool for conservation planning at an ecoregional scale. *Landscape and Urban Planning, 87*, 42–53.

Chapter 4

Mapping opportunities and challenges for rewilding in Europe

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Conservation Biology

Special Section

Mapping opportunities and challenges for rewilding in Europe

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Abstract: *Farmland abandonment takes place across the world due to socio-economic and ecological drivers. In Europe agricultural and environmental policies aim to prevent abandonment and halt ecological succession. Ecological rewilding has been recently proposed as an alternative strategy. We developed a framework to assess opportunities for rewilding across different dimensions of wilderness in Europe. We mapped artificial light, human accessibility based on transport infrastructure, proportion of harvested primary productivity (i.e., ecosystem productivity appropriated by humans through agriculture or forestry), and deviation from potential natural vegetation in areas projected to be abandoned by 2040. At the continental level, the levels of artificial light were low and the deviation from potential natural vegetation was high in areas of abandonment. The relative importance of wilderness metrics differed regionally and was strongly connected to local environmental and socio-economic contexts. Large areas of projected abandonment were often located in or around Natura 2000 sites. Based on these results, we argue that management should be tailored to restore the aspects of wilderness that are lacking in each region. There are many remaining challenges regarding biodiversity in Europe, but megafauna species are already recovering. To further potentiate large-scale rewilding, Natura 2000 management would need to incorporate rewilding approaches. Our framework can be applied to assessing rewilding opportunities and challenges in other world regions, and our results could guide redirection of subsidies to manage social-ecological systems.*

Keywords: biodiversity policy, conservation management, farmland abandonment, land-use change, Natura 2000, rewilding, wilderness

Mapeo de Oportunidades y Retos para el Retorno de la Vida Silvestre

Resumen: *El abandono de tierras agrícolas ocurre en todo el mundo debido a factores socio-económicos y ecológicos. En Europa, las políticas ambientales y agrícolas tienen el objetivo de prevenir el abandono y frenar la sucesión ecológica. La reintroducción o el retorno de la vida silvestre ("rewilding") representa una estrategia alternativa a esto. Desarrollamos un marco de trabajo para evaluar las oportunidades de reintroducción en diferentes dimensiones de naturaleza a lo largo de Europa. Mapeamos la luz artificial, la accesibilidad para humanos con base en la infraestructura de transporte, la proporción de productividad primaria (es decir, la productividad del ecosistema incautado por los humanos por medio de la agricultura o la silvicultura) y la divergencia de vegetación natural potencial en áreas que se proyecta estarán abandonadas para el 2040. A nivel continental, los niveles de luz artificial fueron bajos y la divergencia de vegetación natural potencial fue alta en las áreas de abandono. La importancia relativa de las medidas de naturaleza difirió regionalmente y estuvieron conectadas fuertemente a los contextos ambientales y socio-económicos locales. Las grandes áreas de abandono proyectado estuvieron localizadas frecuentemente en o alrededor de sitios Natura 2000. Con*

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base en estos resultados, argumentamos que el manejo debería ser fabricado para restaurar los aspectos de la naturaleza que son carentes en cada región. Todavía quedan muchos obstáculos con respecto a la biodiversidad en Europa, pero las especies de megafauna ya se están recuperando. Para potenciar aún más la reintroducción a gran escala, el manejo de Natura 2000 necesitaría incorporar estrategias de reintroducción. Nuestro marco de trabajo puede aplicarse a la evaluación de las oportunidades de reintroducción y a los obstáculos en otras regiones del mundo, y nuestros resultados pueden guiar la redirección de los subsidios para manejar los sistemas socio-ecológicos.

Palabras Clave: abandono de tierras agrícolas, cambio en el uso de suelo, manejo de la conservación, Natura 2000, naturaleza, políticas de biodiversidad

Introduction

Since the development of agriculture, large areas have been converted into farmland across the world (Ramankutty et al. 2002). Changes in technology, productivity, and markets have also led to abandonment of farmland in several instances (Fig. 1). In North America, immigration, population growth, and frontier exploration resulted in the cultivation of huge areas of the continent (Nash 2001). However, due to strong competition from agriculture in the Midwest and the Great Planes, farmland started to be abandoned in the northeastern United States from the middle of the 19th century onward (McGrory Klyza 2001). In tropical regions, many agricultural systems are still based on slash-and-burn techniques, which can be viewed as short-term abandonment (Namgyel et al. 2008; Siebert & Belsky 2014). In Europe, a modeled reconstruction of the land-use changes between 1950 and 2010 suggests that cropland has decreased by almost 19%, whereas pastures and semi-natural grasslands have decreased by almost 6% (Fuchs et al. 2012). Similarly, there has been a decrease in rural population of 17% since the beginning of the 1960s (Navarro & Pereira 2012).

In mountain areas and other marginal lands in Europe, cultivation has provided subsistence to local communities for many years. Upon globalization of agricultural markets and increased labor costs, agriculture in many of these areas is no longer profitable and abandonment occurs (Rey Benayas et al. 2007). However, extensive agriculture has supported high biodiversity of several taxa (Fischer et al. 2012), and there is a strong cultural attachment to these landscapes (Navarro & Pereira 2012). Although there are both species that benefit and species that are negatively affected by farmland abandonment (Sirami et al. 2008; Navarro & Pereira 2012), its impact on biodiversity is often perceived of as solely negative (Queiroz et al. 2014). Much of current European policy and legislation on biodiversity focuses on the protection of habitats and species characteristic of extensive farmland, including through mowing, subsidized grazing, and sowing of grasslands (EC 1979, 1992). Moreover, agri-environmental schemes included in the Common Agricultural Policy of the European Union provide subsidies for the maintenance of traditional agricultural practices (EEA 2004). Despite these policies, farmland abandonment and ecosystem changes are projected to continue in Europe (Verburg & Overmars 2009).

Rewilding has been proposed as an alternative approach to manage farmland abandonment in Europe. There are several approaches to rewilding, from the restoration of Pleistocene ecosystems (Donlan et al. 2006), with an emphasis on reintroduction of extinct species, to the passive management of ecological succession after abandonment, with an emphasis on restoring natural ecosystem processes and reducing the human influence on landscapes (Pereira & Navarro 2015). The latter approach has been called ecological rewilding (Pereira & Navarro 2015).

We developed a framework to explore the opportunities and challenges for ecological rewilding in Europe. We mapped wilderness quality in areas projected to be abandoned by 2040. We define *wilderness* as area of minimum human influence (Carver et al. 2012) as measured here by 4 metrics: artificial light at night (night light) (Sanderson et al. 2002), human accessibility (Carver et al. 2012), proportion of harvested primary productivity (pHPP) (Haberl et al. 2007), and deviation from potential natural vegetation (dPNV) (Rosati et al. 2008). These metrics indicate important human modifications that affect multiple taxa and ecosystem structure (Forman 2003; Haberl et al. 2005; Rich & Longcore 2005; Timmermann et al. 2015). Our hypothesis is that different wilderness metrics lead to the identification of different opportunities and management options for rewilding. We also investigated how current protected area systems support rewilding in and near areas of projected abandonment. We hypothesize that many areas undergoing abandonment are located around Natura 2000 sites, which are often managed for the maintenance of farmland habitats, which poses challenges for rewilding.

Methods

We used the land-use change projections of the Dyna-CLUE model at a resolution of 1 km^2 (Verburg & Overmars 2009) to identify areas undergoing farmland abandonment in Europe. Available Dyna-CLUE projections are restricted to the European Union before 2013, the EU27

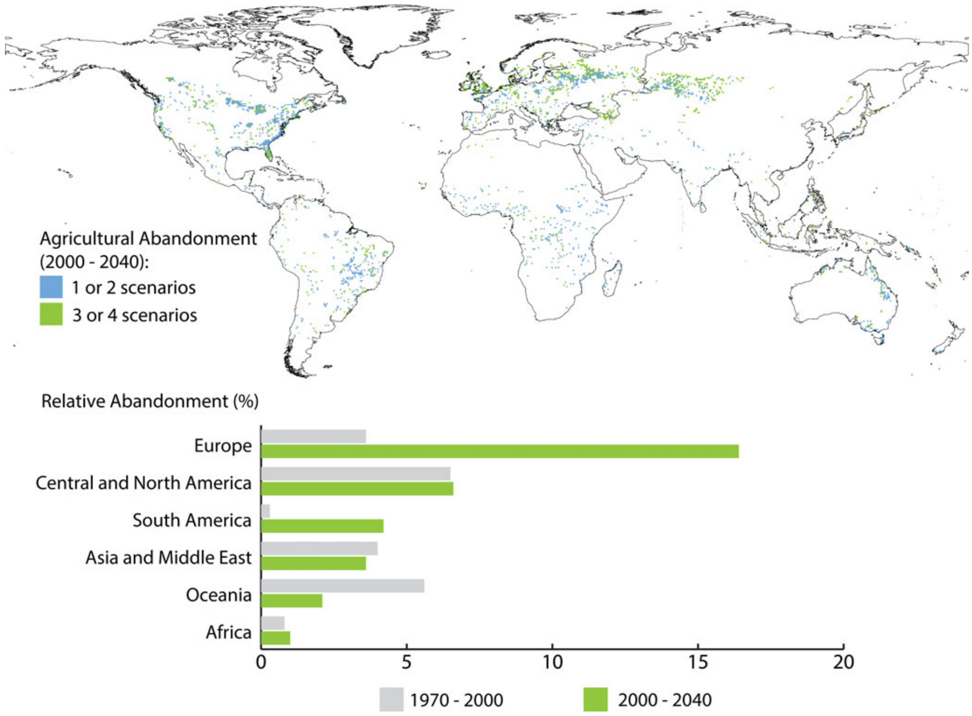

Figure 1. Areas projected to be converted from agriculture to natural areas between 2000 and 2040 based on the IMAGE 2.2 model at a 0.5×0.5 degree resolution (Alcamo et al. 2005) and 4 scenarios of the Millennium Ecosystems Assessment (Alcamo et al. 2005; Cork et al. 2005): Order from Strength (OS), Global Orchestration, TechnoGarden, and Adapting Mosaic. We used the OS scenario for the baseline projections of 2000. The bar graph shows the percentage of past and the projected future conversion from agriculture to natural areas in each world region based on the OS scenario.

(27 countries). We used 4 socio-economic VOLANTE scenarios that describe different policy and management choices in Europe (Paterson et al. 2012). We considered abandonment only if it was predicted in at least 3 of the scenarios.

We mapped 4 metrics of wilderness in Europe at a 4 km^2 resolution. We calculated the pHPP based on the potential net primary productivity and net harvested primary productivity data sets of Haberl et al. (2007). Net harvested primary productivity is the ecosystem productivity appropriated by humans through agriculture or forestry. We mapped accessibility based on travel time considering terrain ruggedness and land-cover data from transport infrastructure to each pixel (Carver & Fritz 1999; EUROSTAT 2006). The dPNV is an estimate of the similarity between the current land cover and the potential natural vegetation (PNV). We used the CORINE 2000 land-cover map for the current vegetation classes (EEA 2012*a*) and the map developed by Bohn et al. (2000) based on expert assessment as the reference PNV. We calculated the night light impact based on high resolution satellite imagery (NOAA National Geophysical Data Center 2012). The light impact score per pixel was the sum of impact scores from the surrounding light sources over a radius of approximately 10 km. These wilderness metrics partially overlapped with parameters used in the Dyna-CLUE model as determinants of land use allocation; therefore, our results should be interpreted carefully. For protected areas, we used the World Database of Protected Areas (World Conservation Union and UNEP-World Conservation Monitoring Centre 2007) and data on the Natura 2000 network (EEA 2012*b*).

We extracted the values of the metrics at the location of projected abandonment from the values calculated at continental level with a bivariate normal kernel function with a radius of approximately 10 km. We split the raster values for all wilderness metrics across the EU27 into quantiles to calculate the amount of farmland abandonment at different ranges of wilderness. We identified the percentage of abandonment areas that fell within the 10%, 25%, 50%, and 75% highest levels of wilderness for accessibility, pHPP, and dPNV. The division into quantiles of the night light data was less precise due to many ties in the values. Therefore, we used the 16.7%, 33.3%, 50%, and 83.3% of the area with the highest levels of wilderness for night light. Because the night light data set was restricted to areas south of 66°N parallel, the quantiles of all metrics were calculated after clipping each data set to this region. We mapped the overlap between dPNV and pHPP by calculating the difference between the normalized values of the 2 metrics. We calculated the projected abandonment around protected areas by

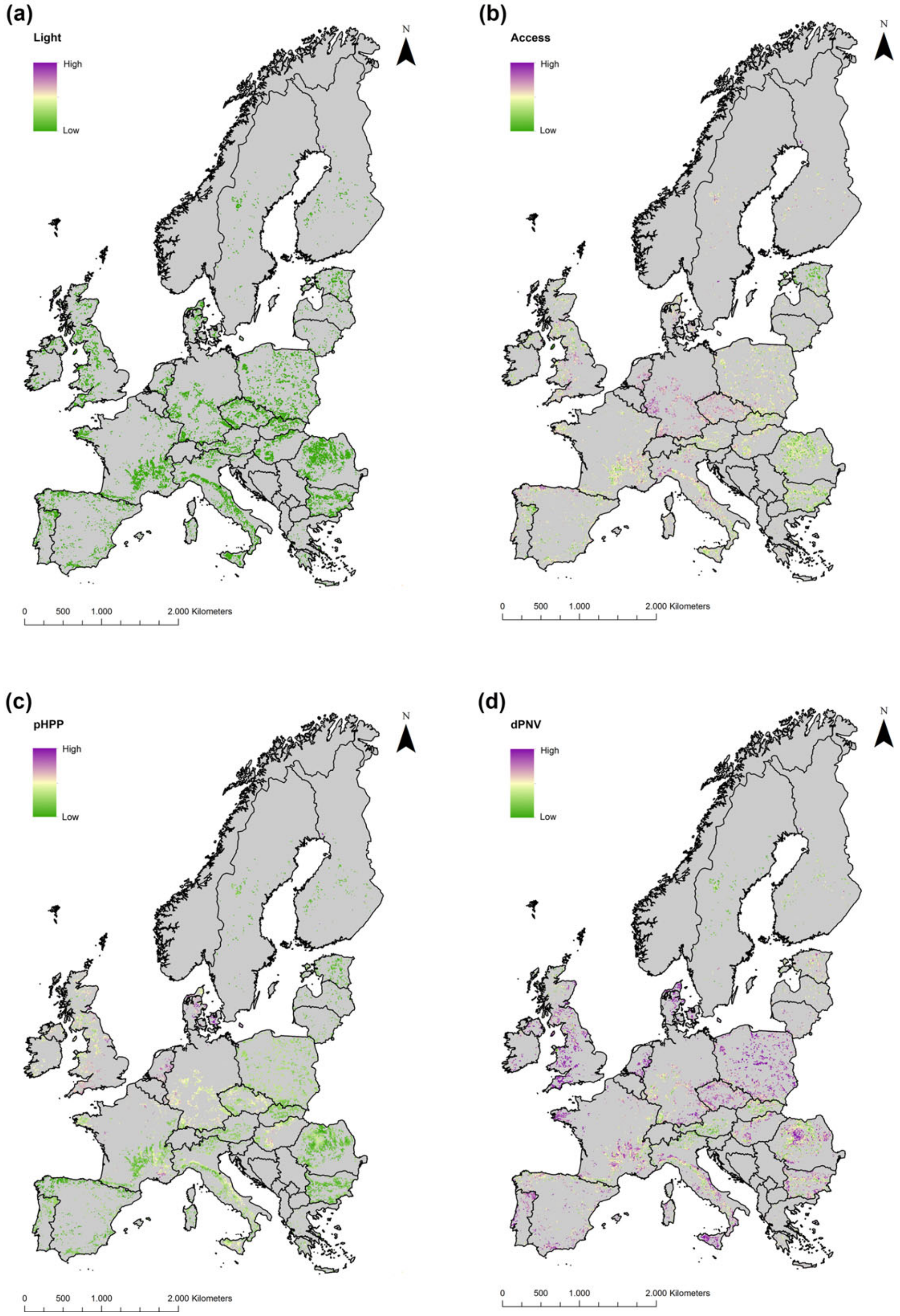

Figure 2. Wilderness value for areas of farmland abandonment based on (a) artificial night light, (b) human accessibility score, (c) proportion of harvested primary productivity, and (d) deviation from potential natural vegetation within a radius of 10 km. High scores of these metrics correspond to low wilderness. The initial resolution of the data sets was 1 km^2, but pixel size is 3 times larger to increase visibility of the considered areas.

Table 1. Percentage of projected agricultural abandonment within the upper 10%, 25%, 50%, and 75% of highest wilderness values calculated at continental level for the human access score, percentage of harvested primary productivity (pHPP), deviation from potential natural vegetation (dPNV), and night light.

Metric	*Quantiles of wilderness values*			
	10%	25%	50%	75%
Human access	4.4	17.4	47.1	77.7
pHPP	4.7	17.5	48.1	81.7
dPNV	0.6	8.4	43.4	82.1
Night light*	73.7	87.2	91.3	96.8

**For artificial night light, we used 16.7%, 33.3%, 50%, and 83.3% highest wilderness values because the clumping of data does not allow for exact quantile definition.*

measuring Euclidian distance to the borders of protected areas of IUCN category I and II and to Natura 2000 sites. A detailed description of the data sets and methods is in Supporting Information.

These wilderness metrics outline human impacts on biodiversity and ecosystem function. The effects of artificial light are documented for invertebrates (Davies et al. 2012), fish (Becker et al. 2013), birds (Gauthreaux Jr & Belser 2006), and mammals (Boldogh et al. 2007). The strongest effects are direct mortality, modification of community structure, and disruption of migratory routes (Rich & Longcore 2005; Gaston et al. 2013). Furthermore, artificial light produces a night glow effect at distances of several kilometers from the light sources (Kyba et al. 2011). Roads and human accessibility have impacts at individual, species, and community level through direct mortality of several taxa (Forman & Alexander 1998; Forman 2003). Roads and traffic can also cause pollution (Pagotto et al. 2001) and avoidance behaviors in mammals (Whittington et al. 2005; Kitzes & Merenlender 2014), and favor the expansion of invasive species (Vicente et al. 2010) and of human-favored predators (Alterio et al. 1998). The other two metrics, pHPP and dPNV, are indicative of the current ecological and vegetation structures and the amount of primary productivity available within trophic networks. Vegetation type is fundamental in the structuring of ecosystems (Bridgeland et al. 2010), and the amount of primary productivity available in the ecosystems has effects on species abundance (Madhusudan 2004) and richness (Haberl et al. 2005).

Wilderness metrics in abandonment areas

Farmland areas projected to be abandoned in at least 3 scenarios covered 4.2% of the land area in EU27. The maps of wilderness metrics offered snapshots of the current human impact in areas to become abandoned (Fig. 2). More than 87% of abandonment was predicted to occur in the 33% of the area with the highest wilderness as defined by night light (Table 1). In contrast, 8.4% of predicted abandonment occurred in the 25% of the area with the highest wilderness as defined by dPNV (Table 1). Accessibility and pHPP had intermediate values: 17.4% and 17.5% of abandoned areas were predicted to be, respectively, in the 25% highest wilderness areas as defined by these metrics. This confirms that farmland areas most prone to abandonment exhibit low to moderate levels of infrastructure development and low population density (Navarro & Pereira 2012). Areas of predicted abandonment in central Europe had higher accessibility due to higher infrastructure development than in other parts of Europe (Fig. 2b). Elsewhere on the continent, areas projected to be abandoned are relatively remote rural regions with a long history of landscape modification and low productivity and are often located in mountains, where limits to mechanization make it difficult to compensate for low productivity (MacDonald et al. 2000; Navarro & Pereira 2012).

Identifying areas of agreement and disagreement between pHPP and dPNV at continental and regional scales provides further information on the diversity of local contexts for rewilding (Fig. 3). Although both pHPP and dPNV are strongly related to farming activities, their spatial distribution was quite different (Fig. 3) as a result of underlying environmental drivers, land-use histories, and the degree to which agricultural activities create landscapes closer to or farther away from the natural reference points. Large urban areas such as London, Paris, and Berlin had very high dPNV and very low pHPP (Fig. 3a). In contrast, most mountainous areas showed low dPNV and relatively high pHPP (Fig. 3b), presumably as cattle grazing at high elevations does not produce a high deviation from the original alpine grasslands (Fig. 3b). Areas such as the Iberian Peninsula and large areas of Eastern Europe showed strongly modified vegetation but a lower pHPP than the intensive agricultural regions in Western Europe (Figs. 3a & 3c). This is expected because technological progress has allowed agriculture to gradually intensify in the most productive and easily mechanized lands, whereas climate and biophysical limitations have not allowed some systems, for example in Southern Europe, to increase their productivity above a certain threshold (Pinto-Correia & Mascarenhas 1999). Low levels of mechanization can also be due to economics in areas such as the former socialist countries (Müller et al. 2009) or to local socio-economic factors such as farm size or existing conservation policies. The continuation of low intensity agriculture has nevertheless maintained ecosystems in a modified state throughout many areas of Europe (Ceaușu et al. 2015).

Protected Areas and Abandonment

In Europe, nationally designated protected areas are based on classifications that often can be mapped to the International Union for Conservation of Nature (IUCN) categories. Protected areas of category I (strict nature reserves and wilderness areas) and II (national parks)

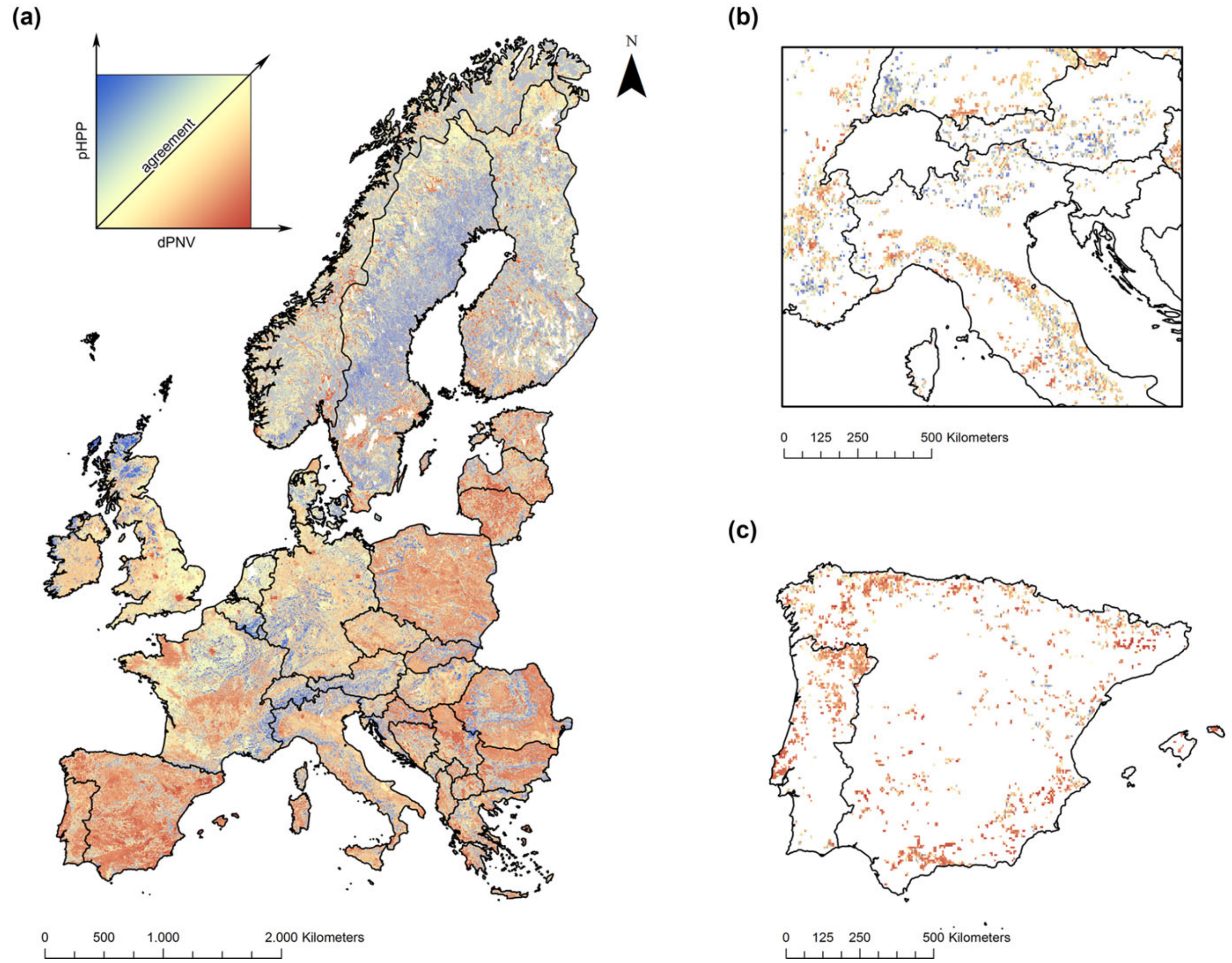

Figure 3. Areas of agreement between the proportion of harvested primary productivity (pHPP) and the deviation from potential natural vegetation (dPNV) in (a) Europe, (b) abandonment locations in the Alps and northern Apennines, and (c) abandonment locations in the Iberian Peninsula (in the online version, yellow represents areas where the normalized values of pHPP and dPNV are equal or close to equal; blue, pHPP is higher than dPNV; red, dPNV is higher than pHPP).
The initial resolution of the data sets was 1 km^2, but pixel size is 3 times larger to increase the visibility of areas considered in (b) and (c).

Table 2. Proportion of projected agricultural abandonment within a 5-km and a 10-km radius around the protected areas of International Union for Conservation of Nature (IUCN) category I and II and Natura 2000 sites.[a]

Type of protected area	*EU27[b] area*	*Abandonment inside*	*Abandonment in a 5 km radius*	*Abandonment in a 5–10 km radius*
IUCN category I and II	2.7	1.2	2.9	3.6
NATURA 2000	17.9	14.4	31.9	22.1

[a] *The areas of the radii are not overlapping and do not contain the areas inside the protected areas.*
[b] *European Union before 2013 (27 countries).*

directly address the maintenance and support of natural ecological processes and minimum human intervention (Dudley 2008) and therefore would be the most favorable to rewilding. However, protected areas of category I and II occupy only 2.7% of the EU territory (Table 2). These areas are biased toward large wilderness areas that have low human presence and thus no agriculture to be abandoned (Dudley 2008; Joppa & Pfaff 2009). As a result, approximately 4% of projected abandonment was inside or within a 5-km radius around protected areas of IUCN category I and II (Table 2).

National systems of protected areas coexist with Natura 2000, the European Union system of protected areas. The Natura 2000 network occupies almost 18% of the EU territory (Table 2) and aims to maintain specific species and habitats in a "favorable conservation status" (EC 1979, 1992). Many of the species and habitats under the Natura 2000 management guidelines are characteristic of extensive farmland and early successional habitats (Halada et al. 2011; Prach et al. 2013). Almost half of projected abandonment was predicted to occur in or within a 5-km radius of Natura 2000 sites (Table 2). Therefore, to potentiate rewilding in those regions, Natura 2000 management guidelines have to be expanded to include rewilding actions.

Policies and Management for Rewilding

The speed at which different dimensions of wilderness will respond to farmland abandonment varies. The pHPP will respond almost immediately (Fig. 4) because land abandonment, even if progressive or partial, corresponds to a decrease in the appropriation of ecosystem productivity. Decreased pHPP can lead to the restoration of natural vegetation and a decrease in dPNV. However, several obstacles make it difficult not only to predict the amount of time taken by ecosystems to reach a new equilibrium but also to predict how close the novel ecosystems will be to the PNV (Vera 2000; Rey Benayas et al. 2007) (Fig. 4). Climate change may lead to modified patterns of PNV (Hickler et al. 2012). Additionally, levels of natural herbivory and other disturbances to natural succession (e.g., fire, flood, wind) will be distinct in post-abandonment landscapes in present Europe from the Pleistocene or pre-agricultural Holocene (Fuhlendorf et al. 2009). Thus, management actions to increase populations of wild herbivores through no-hunting zones or reintroductions could promote the restoration of natural vegetation. Moreover, the recovery of forest vegetation is often hindered by the isolation of current seed banks (Rey Benayas et al. 2008). In some areas, local forest species have been replaced by non-native species planted mainly for commercial purposes, and the structure and composition of these communities differ from those of native communities (Proença et al. 2010). Planting of woodland islets with native trees could accelerate rewilding (Rey Benayas & Bullock 2015).

Other dimensions of wilderness may also have a delayed response to abandonment. Artificial light may decrease soon after abandonment, but due to the presence of public light infrastructure and the development of new activities in the landscape, such as tourism (Cerqueira et al. 2015), some degree of artificial light may persist for long periods. Policies can promote the progressive decrease of public lighting and foster tourism infrastructure that uses low light pollution architecture (Salmon 2006). Accessibility may be the slowest to respond to abandonment because roads will persist for a long time. Still, a decrease in traffic could lead to a decrease in the effects of road mortality on animal populations (Forman 2003) and a decrease in other negative effects such as noise and pollution (Summers et al. 2011). Policies could promote decreased accessibility by promoting road removal or implementing traffic limitations (Switalski et al. 2004).

Biodiversity Dynamics of Rewilding

Rewilding will often result in the increase of forest cover, leading to many specialist species of open areas becoming less abundant and more spatially restricted. Common farmland birds and grassland butterflies are already becoming less abundant (Tryjanowski et al. 2011; Van Swaay et al. 2012), although much of this decrease is probably attributable to agriculture intensification (Donald et al. 2006). At the same time, several species in Europe are taking advantage of the spaces and resources made available by land abandonment, such as the gray wolves (*Canis lupus*) and brown bears (*Ursus arctos*) (Enserink & Vogel 2006; Gehrig-Fasel et al. 2007; Chapron et al. 2014). This megafauna increase is also an outcome of decades of conservation policies (e.g., Hoffmann et al. 2010; Deinet et al. 2013; Navarro & Pereira 2015), including species protection regulations such as the Habitats and Birds Directives and national legislations; the implementation of national protected areas and the Natura 2000 network; and reintroduction programs of keystone and emblematic species, such as the European bison (*Bison bonasus*) (Kuemmerle et al. 2010) and the Iberian lynx (*Lynx pardinus*).

Current populations of megafauna spatially coincide with high values of wilderness metrics and with projected areas of abandonment, especially in mountainous areas, thus raising the possibility of migration into the newly available space (Ceaușu et al. 2015). Moreover, rewilding will increase connectivity of natural habitats, supporting the adjustment of ranges to climate change (Lindner et al. 2010).

How biodiversity dynamics will continue to evolve after abandonment and what rewilding strategies should be implemented are active areas of research. Timmermann et al. (2015) showed that despite management interventions to maintain extensive farmland in Denmark, vegetation structure continued to change. Some scientists argue that pre-farming levels of herbivory were sufficiently high to maintain a mosaic of woods and grasslands (Vera 2000; Sandom et al. 2014). Thus, several approaches to rewilding in Europe are based on filling the ecological role of extinct wild herbivores (Vera 2000; Monbiot 2013). However, several recent studies suggest that Europe was

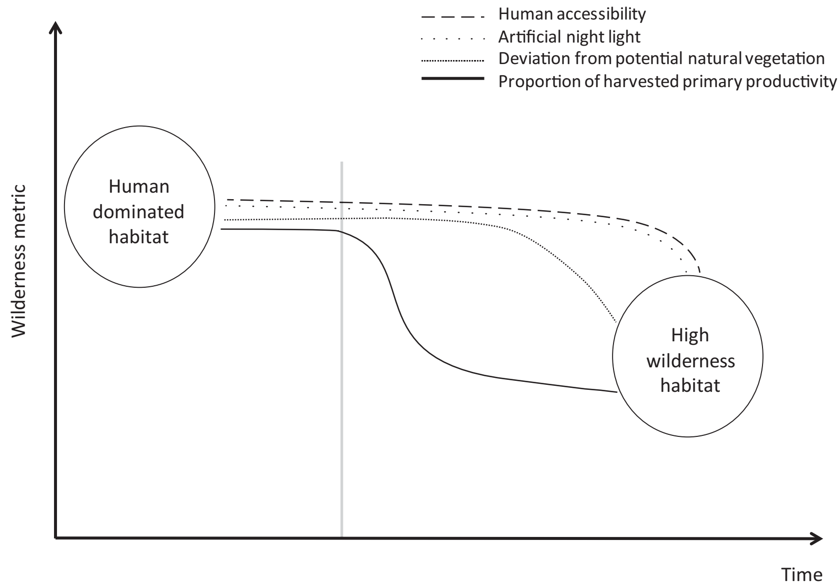

Figure 4. Conceptual illustration of the variation over time in wilderness value after abandonment based on 4 metrics (gray vertical line, beginning of farmland abandonment). High values of each metric correspond to low wilderness.

mostly covered by closed canopy forests until humans created open landscapes (Birks 2005; Mitchell 2005). We hypothesize that in former and novel landscapes, fire, storms, and diseases could generate a fluid mosaic of early successional habitats in a predominantly closed forest (Navarro et al. 2015). An open question is whether large herbivores can delay succession by selectively grazing open areas, particularly in the presence of predators. In any case, one would not expect a lack of open habitats in a post-abandonment Europe, including remaining agricultural areas and areas where abiotic factors limit tree recruitment, such as high elevation areas and wetlands.

A Global Perspective on Abandonment and Rewilding

Reponses to farmland abandonment differ across the world. In several regions, such as Australia, there are few agricultural subsidies (Productivity Commission 2005), and abandonment has been taken up as an opportunity for restoration of native vegetation (Cramer et al. 2007). In other countries, agricultural subsidies have been implemented to halt abandonment. Many of these subsidies are justified by environmental concerns but are also driven by socio-economic considerations (Mattison & Norris 2005; Batie 2009).

Agricultural policies have also changed over time, subject to globalization trends and protectionist tendencies (Mattison & Norris 2005). In the 19th century, the response to abandonment in the northeastern United States was the acquisition of land by government to encourage reforestation and restoration (McGrory Klyza 2001). During the economic depression of the 1930s, agricultural subsidies were designed as a support for farmers. In the more recent decades, they have also addressed environmental issues (Mattison & Norris 2005). In the past, the emphasis of these measures was to provide incentives for setting aside areas for wildlife habitat (Haufler et al. 2005). But funding has now shifted toward mitigating the impacts of agricultural intensification and the funding for wildlife habitat has decreased (Mayrand et al. 2003). Many previously set aside areas have now been brought back into production, especially for biofuels (Avery 2006).

Wilderness mapping can support the development of rewilding strategies in these different agricultural contexts. Our analyses confirmed our hypotheses that different wilderness metrics reveal different priorities and that abandonment areas in Europe are close to Natura 2000 sites. Rewilding actions can be prioritized toward improving the wilderness metrics lacking in a certain region (e.g., decreasing infrastructure in areas of high accessibility). The management of protected areas can also be used to facilitate rewilding in areas of high abandonment. In marginal agricultural regions where agricultural subsidies are politically difficult to remove, subsidies can be shifted to rewilding measures such as the creation of no-hunting zones and wildlife habitat (Merckx & Pereira 2014).

Conservation management in the face of anthropogenic change represents an issue of global importance. Soulé (1985) argues that the role of conservation should be to protect nature for its intrinsic value and ensure protection for the least disturbed ecosystems. Kareiva and Marvier suggest instead that conservation should focus on human modified systems because ecological dynamics are tightly connected to human dynamics (Kareiva & Marvier 2012). A rewilding approach recognizes that the majority of ecosystems have been modified by humans, but identifies opportunities for decreasing the human pressure on ecosystems and restoring the more natural biodiversity dynamics and ecosystem services associated with wilderness (Naidoo et al. 2008; Cerqueira et al. 2015).

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Supporting Information

A detailed description of the data sets and methods (Appendix S1) are available on-line. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

Literature Cited

Alcamo J, vanVuuren D, Cramer W. 2005. Changes in ecosystem services and their drivers across scenarios. Pages 297–373 in Carpenter SR, Prabhu LP, Bennet EM, Zurek MB, editors. Ecosystems and human well-being: scenarios. Island Press, Washington, D.C.

Alterio N, Moller H, Ratz H. 1998. Movements and habitat use of feral house cats *Felis catus*, stoats *Mustela erminea* and ferrets *Mustela furo*, in grassland surrounding yellow-eyed penguin *Megadyptes antipodes* breeding areas in spring. Biological Conservation **83:**187–194.

Avery DT. 2006. Biofuels, food, or wildlife? The massive land costs of US ethanol. Competitive Enterprise Institute, Washington, D.C.

Batie SS. 2009. Green payments and the US Farm Bill: information and policy challenges. Frontiers in Ecology and the Environment **7:** 380–388.

Becker A, Whitfield AK, Cowley PD, Järnegren J, Næsje TF. 2013. Potential effects of artificial light associated with anthropogenic infrastructure on the abundance and foraging behaviour of estuary-associated fishes. Journal of Applied Ecology **50:**43–50.

Birks HJB. 2005. Mind the gap: How open were European primeval forests? Trends in Ecology & Evolution **20:**154–156.

Bohn U, Gollub G, Hettwer C, Neuhäuslová Z, Raus T, Schlüter H, Weber H. 2000. Karte der natürlichen Vegetation Europas, Maßstab 1: 2 500 000. [Map of the Natural vegetation of Europe. Scale 1: 2 500 000]. Bundesamt für Naturschutz, Bonn.

Boldogh S, Dobrosi D, Samu P. 2007. The effects of the illumination of buildings on house-dwelling bats and its conservation consequences. Acta Chiropterologica **9:**527–534.

Bridgeland WT, Beier P, Kolb T, Whitham TG. 2010. A conditional trophic cascade: birds benefit faster growing trees with strong links between predators and plants. Ecology **91:**73–84.

Carver S, Comber A, McMorran R, Nutter S. 2012. A GIS model for mapping spatial patterns and distribution of wild land in Scotland. Landscape and Urban Planning **104:**395–409.

Carver S, Fritz S. 1999. Mapping remote areas using GIS. Landscape character: Perspectives on management and change. Natural Heritage of Scotland Series, HMSO. 112–126.

Ceauşu S, Carver S, Verburg PH, Kuechly HU, Holker F, Brotons L, Pereira HM. 2015. European wilderness in a time of farmland abandonment. Pages 25–46 in Pereira HM, Navarro LM, editors. Rewilding European landscapes. Springer, Netherlands.

Cerqueira Y, Navarro LM, Maes J, Marta-Pedroso C, Honrado J, Pereira HM. 2015. Ecosystem services: the opportunities of rewilding in Europe. Pages 47–64 in Pereira HM, Navarro LM, editors. Rewilding European landscapes. Springer, Netherlands.

Chapron G, et al. 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. Science **346:**1517–1519.

Cork S, Peterson G, Petschel-Held G, Alcamo J, Alder J, Bennet EM, Carr ER, Deane D, Nelson GC, Ribeiro T. 2005. Four scenarios. Pages 223–294 in Carpenter SR, Prabhu LP, Bennet EM, Zurek MB, editors. Ecosystems and human well-being: scenarios. Island Press, Washington, D.C.

Cramer VA, Standish RJ, Hobbs RJ. 2007. Prospects for the recovery of native vegetation in western Australian old fields. Pages 286–306 in VA Cramer, RJ Hobbs, editors. Old fields: dynamics and restoration of abandoned farmland. Island Press, Washington D.C.

Davies TW, Bennie J, Gaston KJ. 2012. Street lighting changes the composition of invertebrate communities. Biology Letters **8:** 764–767.

Deinet S, Ieronymidou C, McRae L, Burfield IJ, Foppen RP, Collen B, Bohm M. 2013. Wildlife comeback in Europe: the recovery of selected mammal and bird species. Final report to Rewilding Europe by ZSL, BirdLife International and the European Bird Census Council, London.

Donald PF, Sanderson FJ, Burfield IJ, VanBommel FP. 2006. Further evidence of continent-wide impacts of agricultural intensification on European farmland birds, 1990–2000. Agriculture, Ecosystems & Environment **116:**189–196.

Donlan CJ, Berger J, Bock CE, Bock JH, Burney DA, Estes JA, Foreman D, Martin PS, Roemer GW, Smith FA. 2006. Pleistocene rewilding: an optimistic agenda for twenty-first century conservation. The American Naturalist **168:**660–681.

Dudley N. 2008. Guidelines for applying protected area management categories. IUCN, Gland, Switzerland.

EC (European Council). 1979. Council Directive 79/409/EEC on the conservation of wild birds. Office for Official Publication of The European Union, Luxemburg.

EC. 1992. EU Habitats Directive (92/43/EEC). Consolidated Text. Office for Official Publication of The European Union. Luxemburg.

EEA (European Environment Agency). 2004. High nature value farmland. Characteristics, trends and policy challenges. Office for Official Publications of the European Communities, Luxemburg. Available from http://www.eea.europa.eu/publications/report_2004_1 (accessed August 2012).

EEA. 2012*a*. Corine Land Cover 2000 raster data. Available from http://www.eea.europa.eu/data-and-maps/data/corine-land-cover-2000-raster-2 (accessed February 12, 2015).

EEA. 2012*b*. Natura 2000 data - the European network of protected sites. Available from http://www.eea.europa.eu/data-and-maps/data/natura-3 (accessed July 5, 2013).

Enserink M, Vogel G. 2006. The carnivore comeback. Science **314:**7476–7749.

EUROSTAT. 2006. GEOSTAT population grid 2006.

Fischer J, Hartel T, Kuemmerle T. 2012. Conservation policy in traditional farming landscapes. Conservation Letters **5:**167–175.

Forman RT. 2003. Road ecology: science and solutions. Island Press, Washington, D.C.

Forman RT, Alexander LE. 1998. Roads and their major ecological effects. Annual Review of Ecology and Systematics **29:**207–231 + C2.

Fuchs R, Herold M, Verburg PH, Clevers J. 2012. A high-resolution and harmonized model approach for reconstructing and analyzing historic land changes in Europe. Biogeosciences **9:**14823–14866.

Fuhlendorf SD, Engle DM, Kerby J, Hamilton R. 2009. Pyric herbivory: rewilding landscapes through the recoupling of fire and grazing. Conservation Biology **23:**588–598.

Gaston KJ, Bennie J, Davies TW, Hopkins J. 2013. The ecological impacts of nighttime light pollution: a mechanistic appraisal. Biological Reviews **88:**912–927.

Gauthreaux Jr SA, Belser CG. 2006. Effects of artificial night lighting on migrating birds. Pages 67–93 in Rich C, Longcore T, editors. Ecological consequences of artificial night lighting. Island Press, Washington, D.C.

Gehrig-Fasel J, Guisan A, Zimmermann NE. 2007. Tree line shifts in the Swiss Alps: Climate change or land abandonment? Journal of Vegetation Science **18:**571–582.

Haberl H, Erb KH, Krausmann F, Gaube V, Bondeau A, Plutzar C, Gingrich S, Lucht W, Fischer-Kowalski M. 2007. Quantifying and mapping the human appropriation of net primary production in earth's terrestrial ecosystems. Proceedings of the National Academy of Sciences **104:**12942.

Haberl H, Plutzar C, Erb K-H, Gaube V, Pollheimer M, Schulz NB. 2005. Human appropriation of net primary production as determinant of avifauna diversity in Austria. Agriculture, Ecosystems & Environment **110:**119–131.

Halada L, Evans D, Romão C, Petersen JE. 2011. Which habitats of European importance depend on agricultural practices? Biodiversity and Conservation **20:**2365–2378.

Haufler JB, Galley KE, Rooney WR. 2005. Fish and wildlife benefits of Farm Bill conservation programs: 2000–2005 update. Wildlife Society, Washington, D.C.

Hickler T, et al. 2012. Projecting the future distribution of European potential natural vegetation zones with a generalized, tree species-based dynamic vegetation model. Global Ecology and Biogeography **21:**50–63.

Hoffmann M, et al. 2010. The impact of conservation on the status of the world's vertebrates. Science **330:**1503–1509.

Joppa LN, Pfaff A. 2009. High and far: biases in the location of protected areas. PLOS ONE **4** (e8273) DOI: 10.1371/journal.pone.0008273.

Kareiva P, Marvier M. 2012. What is conservation science? BioScience **62:**962–969.

Kitzes J, Merenlender A. 2014. Large roads reduce bat activity across multiple species. PLOS ONE **9** (e96341) DOI: 10.1371/journal.pone.009634.

Kuemmerle T, Perzanowski K, Chaskovskyy O, Ostapowicz K, Halada L, Bashta A-T, Kruhlov I, Hostert P, Waller DM, Radeloff VC. 2010. European bison habitat in the Carpathian Mountains. Biological Conservation **143:**908–916.

Kyba CC, Ruhtz T, Fischer J, Hölker F. 2011. Cloud coverage acts as an amplifier for ecological light pollution in urban ecosystems. PLOS ONE **6** (e17307) DOI: 10.1371/journal.pone.0017307.

Lindner M, et al. 2010. Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. Forest Ecology and Management **259:**698–709.

MacDonald D, Crabtree JR, Wiesinger G, Dax T, Stamou N, Fleury P, Gutierrez Lazpita J, Gibon A. 2000. Agricultural abandonment in mountain areas of Europe: environmental consequences and policy response. Journal of Environmental Management **59:**47–69.

Madhusudan MD. 2004. Recovery of wild large herbivores following livestock decline in a tropical Indian wildlife reserve. Journal of Applied Ecology **41:**858–869.

Mattison EHA, Norris K. 2005. Bridging the gaps between agricultural policy, land-use and biodiversity. Trends in Ecology & Evolution **20:**610–616.

Mayrand K, Dionne S, Paquin M, Pageot-LeBel I. 2003. The economic and environmental impacts of agricultural subsidies: an assessment of the 2002 US Farm Bill & Doha Round. Unisféra International Centre. Available from http://www.ictsd.org/downloads/2008/04/usfarm.pdf (accessed February 2015).

McGrory Klyza C. 2001. Wilderness comes home: rewilding the Northeast. UPNE, Hanover, New Hampshire.

Merckx T, Pereira HM. 2014. Reshaping agri-environmental subsidies: from marginal farming to large-scale rewilding. Basic and Applied Ecology **16:**95–103.

Mitchell FJ. 2005. How open were European primeval forests? Hypothesis testing using palaeoecological data. Journal of Ecology **93:**168–177.

Monbiot G. 2013. Feral: searching for enchantment on the frontiers of rewilding. Penguin, United Kingdom.

Müller D, Kuemmerle T, Rusu M, Griffiths P. 2009. Lost in transition: determinants of post-socialist cropland abandonment in Romania. Journal of Land Use Science **4:**109–129.

Naidoo R, Balmford A, Costanza R, Fisher B, Green RE, Lehner B, Malcolm TR, Ricketts TH. 2008. Global mapping of ecosystem services and conservation priorities. Proceedings of the National Academy of Sciences **105:**9495.

Namgyel U, Siebert SF, Wang S. 2008. Shifting cultivation and biodiversity conservation in Bhutan. Conservation Biology **22:**1349–1351.

Nash R. 2001. Wilderness and the American mind. Yale University Press, New Haven, Connecticut.

Navarro LM, Pereira HM. 2015. Towards a European policy for rewilding. Pages 205–224 in Pereira HM, Navarro LM, editors. Rewilding European landscapes. Springer, Netherlands.

Navarro LM, Proença V, Kaplan JO, Pereira HM. 2015. Maintaining disturbance-dependent habitats. Pages 143–170 in Pereira HM, Navarro LM, editors. Rewilding European landscapes. Springer, Netherlands.

Navarro L, Pereira H. 2012. Rewilding abandoned landscapes in Europe. Ecosystems **15:**900–912.

NOAA National Geophysical Data Center, E. O. G. 2012. VIIRS Nighttime Lights - 2012. NOAA National Geophysical Data Center.

Pagotto C, Remy N, Legret M, LeCloirec P. 2001. Heavy metal pollution of road dust and roadside soil near a major rural highway. Environmental Technology **22:**307–319.

Paterson J, Metzger M, Walz A. 2012. Deliverable No: 9.1 - The VOLANTE scenarios: framework, storyline and drivers. VOLANTE - Visions of land use transitions in Europe.

Pereira HM, Navarro LM. 2015. Rewilding European landscapes. Springer, Netherlands.

Pinto-Correia T, Mascarenhas J. 1999. Contribution to the extensification/intensification debate: new trends in the Portuguese montado. Landscape and Urban Planning **46:**125–131.

Prach K, Jongepierová I, Řehounková K. 2013. Large-scale restoration of dry grasslands on ex-arable land using a regional seed mixture: establishment of target species. Restoration Ecology **21:**33–39.

Productivity Commission. 2005. Trends in Australian agriculture. Available from https://ideas.repec.org/p/ris/prodrp/0502.html (accessed February 2015).

Proença VM, Pereira HM, Guilherme J, Vicente L. 2010. Plant and bird diversity in natural forests and in native and exotic plantations in NW Portugal. Acta Oecologica **36:**219–226.

Queiroz C, Beilin R, Folke C, Lindborg R. 2014. Farmland abandonment: Threat or opportunity for biodiversity conservation? A global review. Frontiers in Ecology and the Environment **12:**288–296.

Ramankutty N, Foley JA, Olejniczak NJ. 2002. People on the land: changes in global population and croplands during the 20th century. AMBIO: A Journal of the Human Environment **31:**251–257.

Rey Benayas J, Martins A, Nicolau JM, Schulz JJ. 2007. Abandonment of agricultural land: an overview of drivers and consequences. CAB Reviews: Perspectives in Agriculture, Veterinary Science, Nutrition and Natural Resources **2:**1–14.

Rey Benayas JM, Bullock JM. 2015. Vegetation restoration and other actions to enhance wildlife in European agricultural landscapes. Pages 127–142 in Pereira HM, Navarro LM, editors. Rewilding European landscapes. Springer, Netherlands.

Rey Benayas JM, Bullock JM, Newton AC. 2008. Creating woodland islets to reconcile ecological restoration, conservation, and agricultural land use. Frontiers in Ecology and the Environment **6:**329–336.

Rich C, Longcore T. 2005. Ecological consequences of artificial night lighting. Island Press, Washington, D.C.

Rosati L, Marignani M, Blasi C. 2008. A gap analysis comparing Natura 2000 vs National Protected Area network with potential natural vegetation. Community Ecology **9:**147–154.

Salmon M. 2006. Protecting sea turtles from artificial night lighting at Florida's oceanic beaches. Pages 141–168 in Rich C, Longcore T, editors. Ecological consequences of artificial night lighting. Island Press, Washington, D.C.

Sanderson EW, Jaiteh M, Levy MA, Redford KH, Wannebo AV, Woolmer G. 2002. The human footprint and the last of the wild: the human footprint is a global map of human influence on the land surface, which suggests that human beings are stewards of nature, whether we like it or not. BioScience **52:**891–904.

Sandom CJ, Ejrnæs R, Hansen MD, Svenning J-C. 2014. High herbivore density associated with vegetation diversity in interglacial ecosystems. Proceedings of the National Academy of Sciences **111:**4162–4167.

Siebert SF, Belsky JM. 2014. Historic livelihoods and land uses as ecological disturbances and their role in enhancing biodiversity: an example from Bhutan. Biological Conservation **177:**82–89.

Sirami C, Brotons L, Burfield I, Fonderflick J, Martin J-L. 2008. Is land abandonment having an impact on biodiversity? A meta-analytical approach to bird distribution changes in the north-western Mediterranean. Biological Conservation **141:**450–459.

Soulé ME. 1985. What is conservation biology? BioScience **35:**727–734.

Summers PD, Cunnington GM, Fahrig L. 2011. Are the negative effects of roads on breeding birds caused by traffic noise? Journal of Applied Ecology **48:**1527–1534.

Switalski TA, Bissonette JA, DeLuca TH, Luce CH, Madej MA. 2004. Benefits and impacts of road removal. Frontiers in Ecology and the Environment **2:**21–28.

Timmermann A, Damgaard C, Strandberg MT, Svenning J-C. 2015. Pervasive early 21st-century vegetation changes across Danish seminatural ecosystems: more losers than winners and a shift towards competitive, tall-growing species. Journal of Applied Ecology **52:**21–30.

Tryjanowski P, et al. 2011. Conservation of farmland birds faces different challenges in Western and Central-Eastern Europe. Acta Ornithologica **46:**1–12.

VanSwaay C, et al. 2012. Dos and don'ts for butterflies of the Habitats Directive of the European Union. Nature Conservation **1:**73–153.

Vera FWM. 2000. Grazing ecology and forest history. CABI, Wallingford, United Kingdom.

Verburg PH, Overmars KP. 2009. Combining top-down and bottom-up dynamics in land use modeling: exploring the future of abandoned farmlands in Europe with the Dyna-CLUE model. Landscape Ecology **24:**1167–1181.

Vicente J, Alves P, Randin C, Guisan A, Honrado J. 2010. What drives invasibility? A multi-model inference test and spatial modelling of alien plant species richness patterns in northern Portugal. Ecography **33:**1081–1092.

Whittington J, St. Clair CC, Mercer G. 2005. Spatial responses of wolves to roads and trails in mountain valleys. Ecological Applications **15:**543–553.

World Conservation Union and UNEP-World Conservation Monitoring Centre. 2007. World database on protected areas. WCMC, Cambridge, United Kingdom.

Supplementary information

Description of datasets

Projections of farmland abandonment – Global scale

We used for Figure 1 global land-cover maps produced for the Millenium Ecosystems Assessment (MA) for 1970, 2000, and 2040 based on the IMAGE 2.2 model at a 0.5 by 0.5 degree resolution (Alcamo et al. 2005). We chose the Order from Strength maps as a baseline for 1970 and 2000, and used the projections with the four scenarios of the MA for 2040: Order from Strength, Global Orchestration, Technogarden, and Adapting Mosaic (Cork et al. 2005). For each scenario, we identified cells that were classified as agriculture in the baseline map of 2000, and were classified as natural in 2040. Thus, those cells represent the "agricultural abandonment and revegetation". Combining all four maps provides a global map of abandonment and revegetation indicating the level of agreement between scenarios, i.e. whether a cell was considered as abandoned and restored in one and two scenarios, or in three or four scenarios (see legend of Figure 1).

We calculated, per continent, the ratio between the number of cells classified as abandoned and restored in at least 3 scenarios in 2040, and the number of cells classified as agriculture in the 2000 baseline (see bar plot, white bars). The same ratio was calculated for the two baseline maps of 1970 and 2000 (see bar plot, black bars). Note that the projections do not distinguish between natural and planted forest.

Projections of farmland abandonment – European scale

We use the farmland abandonment projections of the Dyna-CLUE model (Verburg & Overmars 2009) based on four socio-economic scenarios (Paterson et al. 2012). Similarly to the well-known Special Report on Emissions scenarios of the Intergovernmental Panel on Climate Change (IPCC 2013) these scenarios range across two axes: regionalization versus globalization; and inclination versus aversion towards sustainable lifestyle choices and the level of regulation to achieve these. As an indicator of areas with a relatively high chance of facing abandonment, we chose for our analysis the areas of farmland abandonment predicted in at least three of the four scenarios.

The farmland abandonment projections of the Dyna-CLUE model (Verburg & Overmars 2009) have an initial resolution of 1 km^2. This model has a better resolution than the model used for Figure 1 and it was constructed specifically for the European context, thus we preferred to use it for our analyses. This model combines a land-use allocation module based on land demand at regional level, with a bottom-up module describing land-use conversions determined by local processes.

Wilderness metrics datasets

We calculate proportion of harvested primary productivity (pHPP) based on the datasets provided by Haberl et al. (2007) for net potential primary productivity (PP_0) and net harvested primary productivity (HPP). We calculated pHPP as the ratio between HPP and PP_0. Haberl et al. (2007) have derived potential primary productivity (PP_0) from the Lund-Potsdam-Jena dynamic global vegetation model (Sitch et al. 2003) and harvested primary productivity (HPP) based on the data of the Food and Agriculture Organization (FAO). The FAO data is based on national statistics which can have different degrees of accuracy (Haberl et al. 2007) and thus it presents some limitations.

For the deviation from potential natural vegetation (dPNV) dataset, we used the potential natural vegetation (PNV) map developed by Bohn et al. (2000) based on expert assessments. We used the CORINE 2000 land cover classes to compare PNV with current land cover and calculate the deviation from each other. In order to estimate the probability of coincidence, we classified the relationships between the current land classes and the PNV classes according to four different scores: 1 = assumed coincidence, 0.75 = most probable, 0.5 = probable and 0.1 = possible. To correct for anthropogenic pressure in terms of livestock grazing impacts on semi-natural grassland, we also integrated FAO data on grazing density that was linear transformed to the interval [0-1], with 1 representing a density of 20 heads/km² or more (FAO 2006). There are some criticisms regarding the PNV dataset. The more controversial regions are areas of the Iberian peninsula and of the Pannonian region (Hickler et al. 2012). These are areas in which our PNV data indicate forests as the natural vegetation but the dry climate in southern Europe, for instance, could also favor a shrubland type of vegetation (Hickler et al. 2012).

For the accessibility data, several datasets were aggregated: travel time as a measure of remoteness, night lights as a measure of the absence of artificial structures and population density (EUROSTAT 2006). The last two datasets were scaled directly to the [0-1] interval while. The travel time was calculated using a cost-distance approach based on the Naismith's Rule of different relative travelling times (Carver & Fritz 1999) based on the data from the Eurogeographics Roads and Open Street Map databases. The results were adjusted for terrain ruggedness based on data from the Shuttle Radar Topography Mission at 1 km resolution (SRTM) and for land cover based on CORINE 2000 and 2006. The adjustment of traveling times was done through a GIS-grid-based model in which steep slopes (>40°) have a negative impact on traveling time by forcing a traveller to circumvent them. The Naismith's Rule assumes that a person can walk at a speed of 5km/h on flat terrain and with decreasing speed for ascending and descending slopes, depending on the degree of the slope. Additionally, a relative cost surface is assumed for all land-cover types where, for instance, marshland and forests require longer travel times than grasslands and pastures. Heather and forest are assumed to have walking times of 3km/h while bogs would be crosses at 2 km/h. Rivers and water bodies were considered as absolute barriers, with the exception of the cases where a bridge exists. The travel time, night light and population density datasets were then combined with equal weights for the final human accessibility layer.

We mapped the impact of artificial night light within a spectral range of 0.5 – 0.9 µm by applying a normal kernel function over a radius of approximately 10 kilometers to account for both ecological and sensorial effects regarding the human perception of wilderness (Longcore & Rich 2004; Kyba et al. 2011). The data were obtained from the Visible Infrared Imaging Radiometer Suite (VIIRS) of the Suomi National Polar-orbiting Partnership (SNPP) for the year 2012 (NOAA National Geophysical Data Center 2012) with a spatial resolution of 15 arc seconds. Artificial night light data for the European areas north of approximately 66^{o} latitude is missing from the original dataset. We therefore excluded these areas also from the other wilderness metrics datasets when doing comparisons between these data.

Analyses

Extraction of wilderness values at the locations of potential abandonment and rewilding

All data extraction and analyses were performed in ArcGIS v10.2.1 (Esri, California, USA). We harmonized the resolution of all the wilderness metrics by bringing all dataset to the finest resolution, that of the light dataset of approximately 450mx300m. For the extraction of metrics values at abandonment locations, we applied to the harmonized datasets a bivariate normal kernel function that covers a circular area of a radius of approximately 10 km in order to account for the surrounding areas but give increasing importance to points closer to the locations of abandonment. We chose a radius of 10 km for our wilderness calculation in order to approximate the maximum typical distance for seed dispersal, taking into account the contribution of both biological and physical dispersers (Clark et al. 1999; Nathan & Muller-Landau 2000), from possible source populations into the newly abandoned areas (Rey Benayas et al. 2008). Such distances are also a good approximation for the dispersal of other species important for wild ecosystems such as carnivores and large herbivores (Sutherland et al. 2000). The weighting of the surrounding areas according to the distance from abandonment is due to the fact that closer areas will have a stronger effect in terms of species dispersal. We extracted the data at a resolution of 2x2 km. For the better visualization of patterns, the data were presented in Figure 2 and 3 at a resolution of 6x6km.

Combination of the functional wilderness metrics

We combined pHPP and dPNV by normalizing the values for both metrics for the [0, 1] interval according to the formula: $x_n = \frac{x - x_{min}}{x_{max} - x_{min}}$ where x_n is the normalized value, x is the initial value of the wilderness metrics, and x_{min} and x_{max} are the minimum and the maximum values for either of the metrics. We then performed the difference dPNV – pHPP. The results of this operation were then symbolized in Figure 2, with positive numbers (higher normalized dPNV) represented by the lower color ramp and the negative numbers (higher normalized pHPP) represented by the upper color ramp of the legend.

Calculation of abandonment levels in wilderness quantiles

In order to calculate the amount of farmland abandonment at different ranges of wilderness, we divided the overall raster values for all wilderness metrics at continental scale into quantiles. We identified the amount of abandonment points that falls within 10%, 25%, 50% and 75% highest wilderness levels for accessibility, pHPP, and dPNV. Due to the clustering of the night light data, the division into quantiles was less precise. Therefore, we used the highest 16.67%, 33.33%, 50% and 83.33% of the area for artificial night light.

Calculation of abandonment levels in protected areas

We calculated the Euclidean distance from places of farmland abandonment to the borders of protected areas of IUCN category I and II and to Natura 2000 sites (Table 2). Euclidian distance is a useful simplification for connectedness in our context but it is worth pointing out that from the point of view of ecological processes, a short Euclidian distance does not guarantee opportunities for dispersal and migration for taxa with different spatial requirements (Goldberg & Lande 2007).

Bibliography

Bohn, U., G. Gollub, C. Hettwer, Z. Neuhäuslová, T. Raus, H. Schlüter, and H. Weber. 2000. Karte der natürlichen Vegetation Europas, Maßstab 1: 2 500 000.[Map of the Natural vegetation of Europe. Scale 1: 2 500 000]. Bundesamt für Naturschutz, Bonn.

Carver, S., and S. Fritz. 1999. Mapping remote areas using GIS. Landscape character: Perspectives on management and change. Natural Heritage of Scotland Series, HMSO:112–126.

Clark, J. S., M. Silman, R. Kern, E. Macklin, and J. HilleRisLambers. 1999. Seed dispersal near and far: patterns across temperate and tropical forests. Ecology **80**:1475–1494.

EUROSTAT. 2006. GEOSTAT population grid 2006.

FAO. 2006. Health Atlas (GLIPHA). Global livestock production and health atlas of the FAO. Food and Agriculture Organization of the United Nations, Rome, Italy.

Goldberg, E. E., and R. Lande. 2007. Species' Borders and Dispersal Barriers. The American Naturalist **170**:297–304.

Haberl, H., K. H. Erb, F. Krausmann, V. Gaube, A. Bondeau, C. Plutzar, S. Gingrich, W. Lucht, and M. Fischer-Kowalski. 2007. Quantifying and mapping the human appropriation of net primary production in earth's terrestrial ecosystems. Proceedings of the National Academy of Sciences **104**:12942.

Hickler, T. et al. 2012. Projecting the future distribution of European potential natural vegetation zones with a generalized, tree species-based dynamic vegetation model. Global Ecology and Biogeography **21**:50–63.

IPCC. 2013. Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley (eds.)]. Page 1535. Intergovernmental Panel on Climate Change, Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Kyba, C. C., T. Ruhtz, J. Fischer, and F. Hölker. 2011. Cloud coverage acts as an amplifier for ecological light pollution in urban ecosystems. PLoS One **6**:e17307.

Longcore, T., and C. Rich. 2004. Ecological light pollution. Frontiers in Ecology and the Environment **2**:191–198.

Nathan, R., and H. C. Muller-Landau. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Trends in ecology & evolution **15**:278–285.

NOAA National Geophysical Data Center, E. O. G. 2012. VIIRS Nighttime Lights - 2012. NOAA National Geophysical Data Center.

Paterson, J., M. Metzger, and A. Walz. 2012. Deliverable No: 9.1 - The VOLANTE scenarios: framework, storyline and drivers. VOLANTE - Visions of land use transitions in Europe.

Rey Benayas, J. M., J. M. Bullock, and A. C. Newton. 2008. Creating woodland islets to reconcile ecological restoration, conservation, and agricultural land use. Frontiers in Ecology and the Environment **6**:329–336.

Sitch, S., B. Smith, I. C. Prentice, A. Arneth, A. Bondeau, W. Cramer, J. O. Kaplan, S. Levis, W. Lucht, and M. T. Sykes. 2003. Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. Global Change Biology **9**:161–185.

Sutherland, G. D., A. S. Harestad, K. Price, and K. P. Lertzman. 2000. Scaling of natal dispersal distances in terrestrial birds and mammals. Conservation Ecology **4**:16.

Verburg, P. H., and K. P. Overmars. 2009. Combining top-down and bottom-up dynamics in land use modeling: exploring the future of abandoned farmlands in Europe with the Dyna-CLUE model. Landscape Ecology **24**:1167–1181.

Chapter 5

No ecosystem services left behind: reconnecting ecosystem services and biodiversity

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No ecosystem services left behind: reconnecting ecosystem services and biodiversity

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Abstract

Not all ecosystem services have the same relationship to biodiversity. Some services, named here biophysical-based, rely on multiple ecosystem processes supported by complex biotic and abiotic interactions. For these services, it is difficult to establish links to species identities. Other services, named here biodiversity-based, rely on well-defined functional guilds and can be traced directly to certain species. Ecosystem services have been equated with biophysical-based services and assessments include frequently only this category. As a result, conservation policies and decision-making are based on incomplete information. We provide here a comprehensive assessment at European level of biodiversity-based services and we analyze whether these services are well represented by biophysical-based assessments. We use the concept of service providing units (SPU) and atlas data for vertebrates and plants to calculate estimates for 9 services. We show that areas prioritized based on biophysical-based services fail to capture 51% of the areas supplying high levels of biodiversity-based services. The spatial overlap between priority areas decreases further to 34% when we consider a national scale perspective. Regardless of the type of services considered, the relationship between biodiversity and services becomes stronger the more services are included. In conclusion, considering a biased set of services does not capture all the complexities of service supply. Assessments based on a low number of services risk underestimating the role of biodiversity.

Keywords: ecosystem services, biodiversity - ecosystem services relationship, multifunctionality, assessments of ecosystem services

Introduction

Ecosystem goods and services, from now on identified as services, have become increasingly influential in policy-making, and in linking biodiversity conservation and human development (COP 2010; EU Commission 2011; IPBES 2016). Despite the progress in the adoption of the concept, there are still lingering questions on the mechanisms of service supply. One of the most important questions is related to how biodiversity contributes to service supply. Most frameworks include a causal chain in which biodiversity drives ecosystem functions and processes, which in turn generate ecosystem services (Kremen 2005; Duncan et al. 2015). However, different services have different connections to biodiversity (Mace et al. 2012; Adams 2014) (Figure 1). Some services, we name them biophysical-based services, are generated usually by several ecological processes which are supported by complex interaction within ecological communities and between biotic components and abiotic components (Figure 1) (Mace et al. 2012). Thus, it is challenging to estimate the connections between species identities and service supply (e.g. carbon sequestration). For other services, we name them biodiversity-based services, well-defined functional guilds (e.g. scavengers) supply services (e.g. carcass removal) (Figure 1) without the mediation of processes (Mace et al. 2012). Instead, the influence of ecosystem processes is expressed in the composition of the community supplying these services. For biodiversity-based services, the species identities within a community has a direct impact (Karp et al. 2013).

Despite these differences, services in general have been consistently equated with biophysical-based services (Naidoo *et al.* 2008). Therefore, assessments and maps often include only this type of services, which are estimated based on methodologies that account for biodiversity at ecosystem level through land cover, vegetation types, or through ecosystem-level metrics such as carbon fractions (Chan *et al.* 2006; Naidoo *et al.* 2008; Maes *et al.* 2012). Although many experimental platforms address the connection between ecological functions and species identities or species richness (Hector and Bagchi 2007), these results are not yet integrated into large-scale assessments of biophysical-based services.

Comprehensive assessments and maps of biodiversity-based services are lacking and research efforts usually focus on a single service at small scales (Ricketts *et al.* 2004; Karp *et al.* 2013). These studies achieve important insights on functional relationships between species-level biodiversity and services, suggesting either a concave relationship where a few species ensure most service supply (Winfree *et al.* 2015) or a convex relationship where many species are necessary for service supply (Isbell *et al.* 2011). A concept that can support the large-scale assessments of biodiversity-based services is the service-providing unit (SPU). Luck *et al.* (2003) define SPU as a population unit or a functional guild within- or cross-taxa that provide services at some temporal or spatial scale. This concept is used at European level for pest control (Civantos *et al.* 2012) and implicitly applied for wild food (Schulp *et al.* 2014). However, these studies remain infrequent and disconnected. As a result, management and policy decisions are often based on incomplete assessments of services.

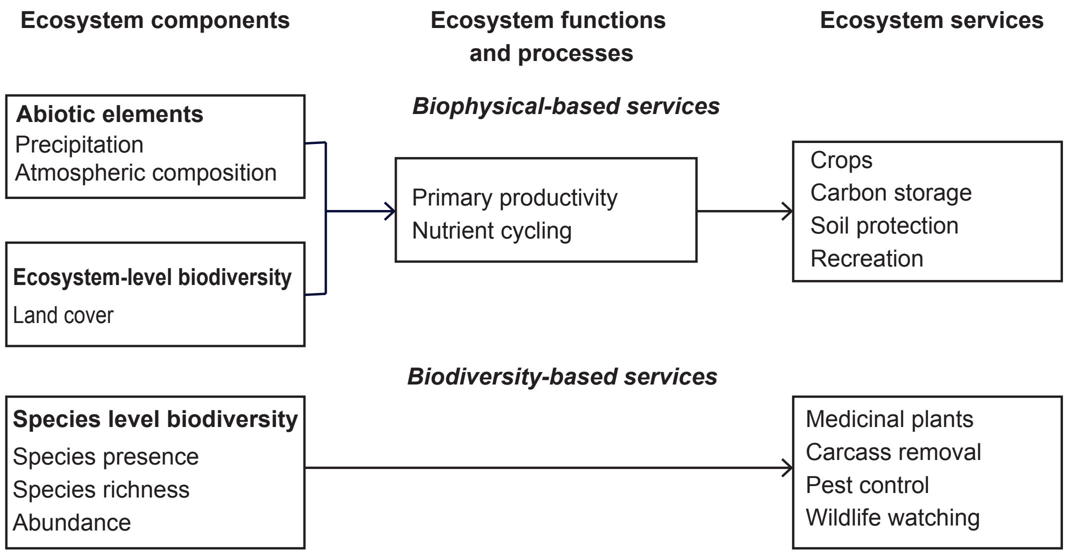

Figure 1 Conceptual figure of biodiversity-ecosystem services relationship. The *Biophysical-based services* rely often on several ecological functions and processes which are supported by complex interactions between biotic and abiotic elements. Ecosystem-level biodiversity measures are used to estimate *Biophysical-based services*. The *Biodiversity-based services* are supported by definable functional guilds, or service providing units (SPU), which supply functions easily translatable into services or directly services. Species identities can be more directly related to *Biodiversity-based services*.

Here, we provide an assessment at European level of 9 biodiversity-based services. Our study has three goals. First, we identify cross-taxa SPU for each biodiversity-based service and we calculate SPU richness by stacking the spatial distributions of species. We estimate service supply by considering three possible functional relationships with SPU richness: linear, convex and concave (Kremen 2005; Duncan *et al.* 2015). Second, we test whether priority areas for biodiversity-based services and variation patterns coincide with those for biophysical-based services. For this purpose, we use data for 9 biophysical-based services: 8 datasets developed by the Mapping and Assessment of Ecosystems and their Services (MAES) working group (Maes *et al.* 2015) and a map of carbon stocks (Ruesch and Gibbs 2008). We assess the spatial agreement between the areas supplying high biodiversity-based and biophysical-based services at two scales: European scale for a general assessment and a national scale for a management relevant perspective. We assess variation patterns by calculating the standard deviation (SD) of service estimates within each grid cell. Third, we assess how the relationship between services and species richness changes with increasing number of services. We calculate correlations based on repeated random sampling of spatial units in order to account for variation in local contexts. As supply and demand of services often have different spatial distributions (Burkhard *et al.* 2012), we included here the supply side for all services.

Methods

Biodiversity-based services

We selected 9 biodiversity-based services: wild food, medicinal plants, fodder, pest control, carcass removal, seed dispersal, existence value, wildlife watching and hunting (Table 1). We classified them into provisioning, regulating and cultural services based on definitions of the Millennium Ecosystem Assessment (MEA 2005). The geographical extent was continental Europe, including the Mediterranean islands but excluding Cyprus. The eastern borders of Finland, Estonia, Latvia, Lithuania, Poland and Romania represented the eastern limit of the extent. In the context of our study, a SPU represents all the populations on this territory of the species identified as suppliers of a biodiversity-based service. Estimating biodiversity-based services involved three steps (Figure 2): identifying the SPU for each service based on different sources, extracting and stacking the European distributions of the SPU species, calculating the service estimates based on three functional relationships.

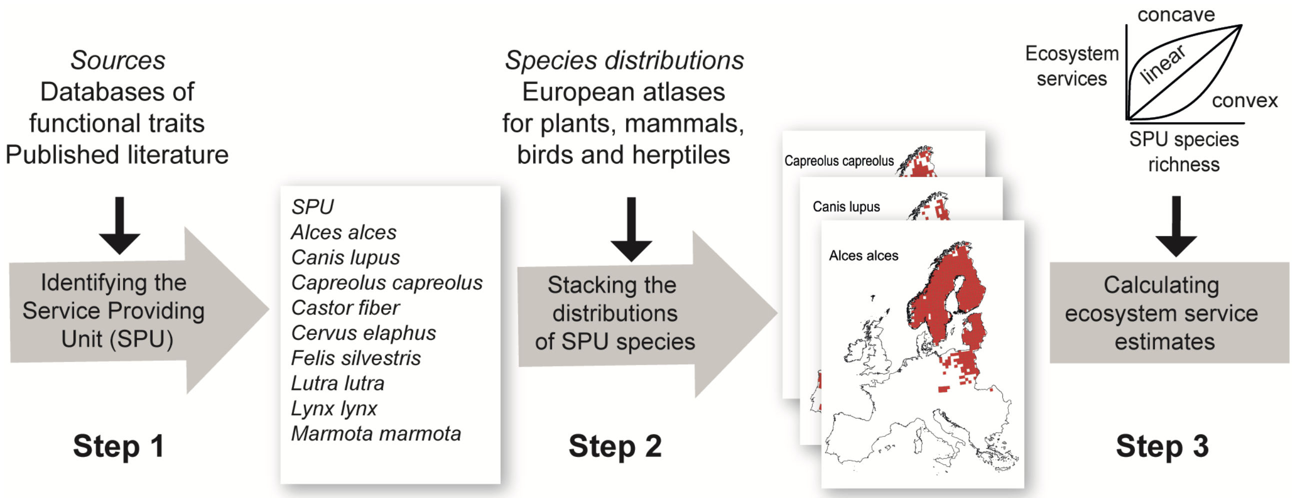

Figure 2 Methodology for estimating biodiversity-based services based on the service providing unit (SPU). We applied a three step approach. First, we defined SPU based on a variety of sources. Second, we extracted and stacked the atlas distributions of the SPU species. Third, we calculated estimates of services based on three possible functions: concave, linear and convex.

Identifying the SPUs

We assessed three provisioning services: medicinal plants, wild food and wild fodder (Table 1). We researched 6 databases (Lange 1998; WHO 1999; Green 2009; Wirth & Lichstein 2009; Kattge *et al.* 2011; Frenette-Dussault *et al.* 2012; Kew Royal Botanic Gardens 2014; USDA 2014; www.pfaf.org 2014) for medicinal plants. When the source contained medicinal ratings from 0 to 5 (www.pfaf.org), we selected from the respective databased only species with a rating of 4 or 5. We researched 4 databases (Lange 1998; Green 2009; Wirth & Lichstein 2009; Kattge *et al.* 2011; Frenette-Dussault *et al.* 2012; USDA 2014; www.pfaf.org 2014) for plant species representing wild food. The approach in extracting the information from databases was identical with the one used for medicinal plants. Additionally, we included in the wild food SPU the mammal and bird species hunted and consumed, as reported in Schulp *et al.* (2014). We identified the wild fodder SPU from TRY (Green 2009; Wirth & Lichstein 2009; Kattge *et al.* 2011; Frenette-Dussault *et al.* 2012) and BiolFlor (Kühn *et al.* 2004) databases. From TRY, we used data for the traits "Leaf palatability", "Plant palatability" and "Plant human usage types". When the fodder value was described according to a scale from 1 (lowest fodder value) to 10 (highest fodder value), we included species with a score of 7 or higher. When the fodder value was based on a categorical scale from "none" to "high", we included only the species rated as "high" or "variable (e.g. young plants palatable but adult plant not)".

We assessed three regulating services: pest control, carcass removal and seed dispersal (Table 1). In the pest control SPU, we included species reported as service providers for both mammal and invertebrate pests in Civantos *et al.* (2012). Carcass removal SPU contained mammal and bird species that rely on scavenging for at least 30% of their diet (Wilman *et al.* (2014). We defined the seed dispersal SPU as mammals and birds with at least 30% of their diet based on seeds and fruits (Wilman *et al.* 2014).

Table 1 Summary of biodiversity-based services, their description, references and sources for the respective species providing unit (SPU), and considered taxa.

Ecosystem service	Description	Sources/References	Taxa
Provisioning			
Medicinal plants	Wild plants that have been used in different forms (e. g. infusions, extracts) to cure or alleviate an illness.	www.pfaf.org; Lange and others (1998); World Health Organization (1999); Kew Royal Botanic Gardens (2014); Kattge *et al.* (2011); USDA (2014)	Plants
Fodder	Wild plants valuable in the diets of domestic herbivores.	Kattge *et al.* (2011); Kühn *et al.* (2004)	Plants
Wild food	Wild plants that have been used in different forms (e. g. raw, thermally processed, spices, drinks) in human diet and mammals and birds that are hunted and consumed in Europe.	www.pfaf.org; USDA (2014); Lange and others (1998); Kattge *et al.* (2011); Schulp *et al.* (2014)	Plants Mammals Birds
Regulating			
Carcass removal	Obligate or facultative scavengers that feed on animal waste	Wilman *et al.* (2014)	Birds Mammals
Seed dispersal	Species that, through their feeding habits, favor the spread of vegetation, important especially in restoration and forest recovery	Wilman *et al.* (2014)	Birds Mammals
Pest control	Vertebrates providing biological control of invertebrate and rodent pests in agricultural landscapes	Civantos *et al.* (2012)	Birds Mammals Amphibians Reptiles
Cultural			
Hunting	Vertebrate species considered game for hunting activities in Europe but which are not also consumed as food.	Schulp *et al.* (2014)	Birds Mammals
Existence value	Vertebrate and plant species whose individuals have a higher existence value because of their threatened status as a species. Such individuals benefit frequently from protection measures.	Temple and Terry (2007); Cox and Temple (2009); Temple and Cox (2009); Bilz *et al.* (2011); BirdLife International (2015)	Birds Mammals Amphibians Reptiles Plants
Wildlife watching	Species that are mentioned as attractions for tourism purposes of that are mentioned by tourists as reasons for travel to observe them or their traces.	Internet search conducted by authors	Birds Mammals

We assessed three cultural services: hunting, existence value and wildlife watching (Table 1). We included in the hunting SPU the species hunted in Europe but not consumed as food (Schulp *et al.* 2014). We used for this purpose a complete list of hunted species that was not published but was provided separately by the authors. The SPU of existence value was defined based on the European Regional Assessment of the RedList. We included species that were assessed as vulnerable, endangered or critically endangered at European level (Temple and Terry 2007; Cox and Temple 2009; Temple and Cox 2009; Bilz *et al.* 2011; BirdLife International 2015). We defined the wildlife watching SPU based on an internet search of the expression "Wildlife watching in <country>". We used the English expression because the internet searches in local languages were more difficult to process and they produced many results related to non-European wildlife tourism targeting national markets. We used the common names of 34 countries within our geographic extent. The search was conducted in the Google search engine by 5 of the co-authors. We searched webpages provided by the first 6 search pages, excluding the advertised web links. We selected the webpages that clearly refer to wildlife watching as a touristic activity and we recorded the species of interest. When species were likely to be listed on another webpage of the respective website, we navigated to that webpage. When referred by the common name, we included only wildlife that could be identified to species level with a reasonable level of certainty. We then pooled the results and summed them across all countries. We included in the wildlife watching SPU the species that were encountered 50 times or more.

Stacking the distributions of SPU species

We identified the distributions of the SPU species from atlas datasets containing 4174 plants (Lahti and Lampinen 1999), 498 birds (Hagemeijer and Blair 1997), 194 mammals (Mitchell-Jones *et al.* 1999), 133 reptiles and 70 amphibians (Sillero *et al.* 2014). The data are available at a resolution of 50x50 km. All datasets except the bird data were compiled in the Common European Chorological Grid Reference System (CGRS) agreed by the groups mapping European diversity. For bird species, the data were compiled in an earlier version of the grid at the same resolution. Analysis was subsequently conducted for the CGRS grid.

We extracted from the relevant atlas dataset the distribution of each species listed in SPUs. We then stacked the geographical distributions of all species from each SPU. For each grid cell:

$$SR_{ij} = \sum_{k=1}^{N} S(i,\ k) * E(j, k) \qquad (1)$$

where *SR* was the number of species providing service *j* in grid cell *i* and *S(j, k)* is one when species *k* is present in grid cell *i* and *E(j, k)* is one when species *k* is included in SPU of service *j*.

Calculating ecosystem service estimates

We considered three possible relationships between SPU richness and services (Figure 2, Step 3). The estimates of services (Figure 2, Step 3) in each grid cell was:

$$ES_{ij} = SR_{ij}^{a} \qquad (2)$$

where *ES* is the estimate of service *j* in grid cell *i*, SR_{ij} is the number of species providing the service *j* in grid cell *i* and *a* is a constant that modifies the relationship. When each new species supplied the same amount of service (linear relationship), *a* was equal to one. For a concave function (Figure 2, Step 3), when a small number of species supplies most of the service and each new species adds a decreasing amount of service, *a* was equal to 0.2. For a convex function (Figure 2, Step 3), when a minimum number of species is necessary for substantial supply and each new species adds an increasing amount, *a* was equal to 3. The values of a were chosen to visually approximate the function shapes proposed in the literature (Kremen 2005; Duncan *et al.* 2015).

We then normalized service estimates based on the equation:

$$ESn_{ij} = \frac{ES_{ij} - ES_{j\,min}}{ES_{j\,max} - ES_{j\,min}} \qquad (3)$$

where *ESn* is the normalized estimate for service *j* in grid cell *i*, ES_{ij} is the initial estimate of service *j* in grid cell *i*, $ES_{j\,min}$ and $ES_{j\,max}$ represent the minimum and maximum estimates of service j across all grid cells, respectively. We used equation (3) also for subsequent normalizations to [0, 1].

Ecosystem services based on biophysical data

We selected 9 biophysical-based services for which European-wide data were available (Table 2). The MAES data represent a comprehensive set of services estimated for 2010 by the Joint Research Centre, which aims to provide scientific support for European policies (Maes *et al.* 2015). We also included data on biomass carbon stocks for 2000 based on outputs developed at global level (Ruesch and Gibbs 2008). Carbon stocks in Europe are estimated to have changed only slightly in the decade between 2000 and 2010. For instance, forest carbon potential grew by 1.7% during this timeframe (Maes *et al.* 2015). Thus, we considered the temporal mismatch between datasets minor. The spatial extents differed between data. We mapped most services to the territory of the European Union at the current extent (EU28) without Cyprus. The recreation potential map did not include Croatia.

Table 2. Summary of biophysical-based services, their description, references, data used for calculating estimates, and measurement units

Ecosystem service	Description	Type of data used for the estimation	Sources/References	Unit
Provisioning services				
Cultivated food	Harvested production of food crops	National, European or global statistics	Maes *et al.* (2015)	ton x year-1
Cultivated fodder	Harvested production of fodder crops	Land use/cover		ton x year-1
Energy crops	Harvested production of energy crops		Maes *et al.* (2015)	ton x year-1
Harvested timber	Total timber removal			m3 year-1
Grazing livestock	Reared animals		Maes *et al.* (2015)	Heads
Regulating services				
Water Retention capacity	Capacity of ecosystems to reduce runoff and capture water	Land use/cover Soil properties Topography Vegetation functional traits (Leaf area index)	Maes *et al.* (2014, 2015)	Dimensionless
Capacity of ecosystems to avoid soil erosion	Capacity of ecosystems to provide soil protection	Soil properties Topography Land use/cover	Maes *et al.* (2014, 2015)	Dimensionless
Carbon stocks	Biomass carbon stored by living vegetation in above and belowground	Land use/cover Vegetation functional traits (root-to-shoot ration, carbon fraction)	Ruesch and Gibbs (2008)	ton C x ha-1
Cultural services				
Recreation	Potential of outdoor recreation for resident population and reachable by short traveling	Land use/cover National, European or global statistics Spatial extent of protected areas Water bodies properties	Maes *et al.* (2014); Paracchini *et al.* (2014); Maes *et al.* (2015)	Dimensionless

Maes *et al.* (2015) estimated the provisioning services considered here based on aggregated statistical data compiled in the Common Agricultural Policy Regionalised Impact Modelling System (CAPRI) model (http://www.capri-model.org/) which includes agricultural and timber output data from the statistical office of the European Union (Eurostat) and the Food and Agriculture Organization of the United Nations (FAO). These data were downscaled using a proportionally distributed model that assigned a value to each 10X10 km grid cell based on the proportion of relevant land-cover (e. g. forest for timber removal) in the respective grid cell. This land-cover proportion was calculated using a refined version of the Corine Land Cover (CLC) for 2006 (Batista e Silva *et al.* 2013). The land-cover classes used for downscaling and further details are presented in Maes *et al.* (2015).

The Water Retention Index is a dimensionless indicator that considers water retention in vegetation, soil and groundwater. Additionally, the index considers slope and percentage of sealed area as factors influencing water retention (Maes *et al.* 2015). The capacity of ecosystems to avoid soil erosion is also represented as a dimensionless indicator capturing the capacity of land cover types to mitigate soil loss (Guerra *et al.* 2014; Maes *et al.* 2015). The indicator is calculated based on the refined CLC (Batista e Silva *et al.* 2013) and a process-based model which takes into account the interaction between precipitation, soil attributes, topography and land cover (Maes *et al.* 2015). Both datasets were calculated at 100x100 m resolution. Ruesch and Gibbs (2008) estimated vegetation carbon stocks based on globally consistent values for aboveground biomass and root to shoot ratios for belowground biomass provided by the Intergovernmental Panel on Climate Change (IPCC). Based on carbon fractions for each vegetation types, Ruesch and Gibbs (2008) compiled 124 carbon zones or regions that were then mapped based on land cover, continental regions, ecofloristic zones and forest age at 1x1 km resolution.

Paracchini *et al.* (2014) mapped recreation potential based on components linked to recreation preferences: degree of naturalness, presence of protected areas as indicator of high natural value and water bodies accounting for water attractiveness (Maes *et al.* 2012; Paracchini *et al.* 2014). The three components were given equal weights in the calculation of the final indicator at 100x100 m resolution.

For the comparison with the biodiversity-based services, we aggregated the data to the CGRS grid through averaging. Finally, we normalized all services to [0, 1].

Analysis

Mapping priority areas and variation patterns

The priority areas were define based on the total service value (TSV) for both biodiversity-based and biophysical-based services. We calculated TSV for biodiversity-based services assuming a linear relationship (*a* equal to one in equation 2) between SPU species richness and biodiversity-based services. For both biodiversity-based and biophysical-based services, we first summed separately the normalized values of provisioning, regulating and cultural services (Table 1 and 2). We then normalized the summed values of the three categories to [0, 1]. Finally, we summed the three categories to obtain the TSV for each category of services. We then selected the highest quartiles of each TSV. For the national level, we selected for each country the grid cells covering the respective country and we calculated the highest quartiles only for those values. We estimated variation patterns between the service estimates by calculating the SD of normalized estimates at grid cell level.

Correlation with species richness

When considering separately biodiversity-based and biophysical-based services, we randomly sampled combinations of the 9 services (500 selections of one service, 500 selections of 2 services, and so on). When we considered all services together, we sampled combinations of the 18 services. For each selection, we then randomly selected 100 cells from the 2377 grid cells containing values for all 18 services. We summed the normalized values of services for the 100 grid cells and we performed a rank correlation with the corresponding normalized species richness. In the case of biodiversity-based services, we additionally randomly chose between the three possible function shapes: linear, convex and concave.

Results

Ecosystem services based on biodiversity data had a strong pattern of high values in central Europe. This was driven by plant and bird species richness patterns (Figures 2 and 1S). This pattern was similar with the distribution of biophysical-based services (Figure 4). Biodiversity-based services such as carcass removal, pest control and especially existence value had a more diversified pattern with higher value for southern Europe, mainly Iberia (Figure 3).

Of the designated priority areas, 49% of grid cells were supplying high TSV for both biodiversity-based and biophysical-based services (Figure 5a). Therefore, more than half of the quartile area supported the highest values for only one type of services. The non-overlapping areas for the biodiversity-based services extended in the eastern part of the continent, while for biophysical-based services they covered the western part of the continent. The prioritization at national level led to markedly different spatial results from the total estimates. The high TSV areas of central Europe split at national level, with the southern mountainous areas becoming particularly important for concomitantly high supply of the two types of services. Only 34% of the quartile area selected at national level supplied the highest estimates for both biodiversity-based and biophysical-based services. However, these results were geographically differentiated (Figure 5b). Thus, almost 60% of the quartile area in Spain and 45% in Italy supplied the highest level for both biodiversity-based and biophysical-based services. In Finland, only 2% of the quartile area represented high supply for both types of services (Figure 5b).

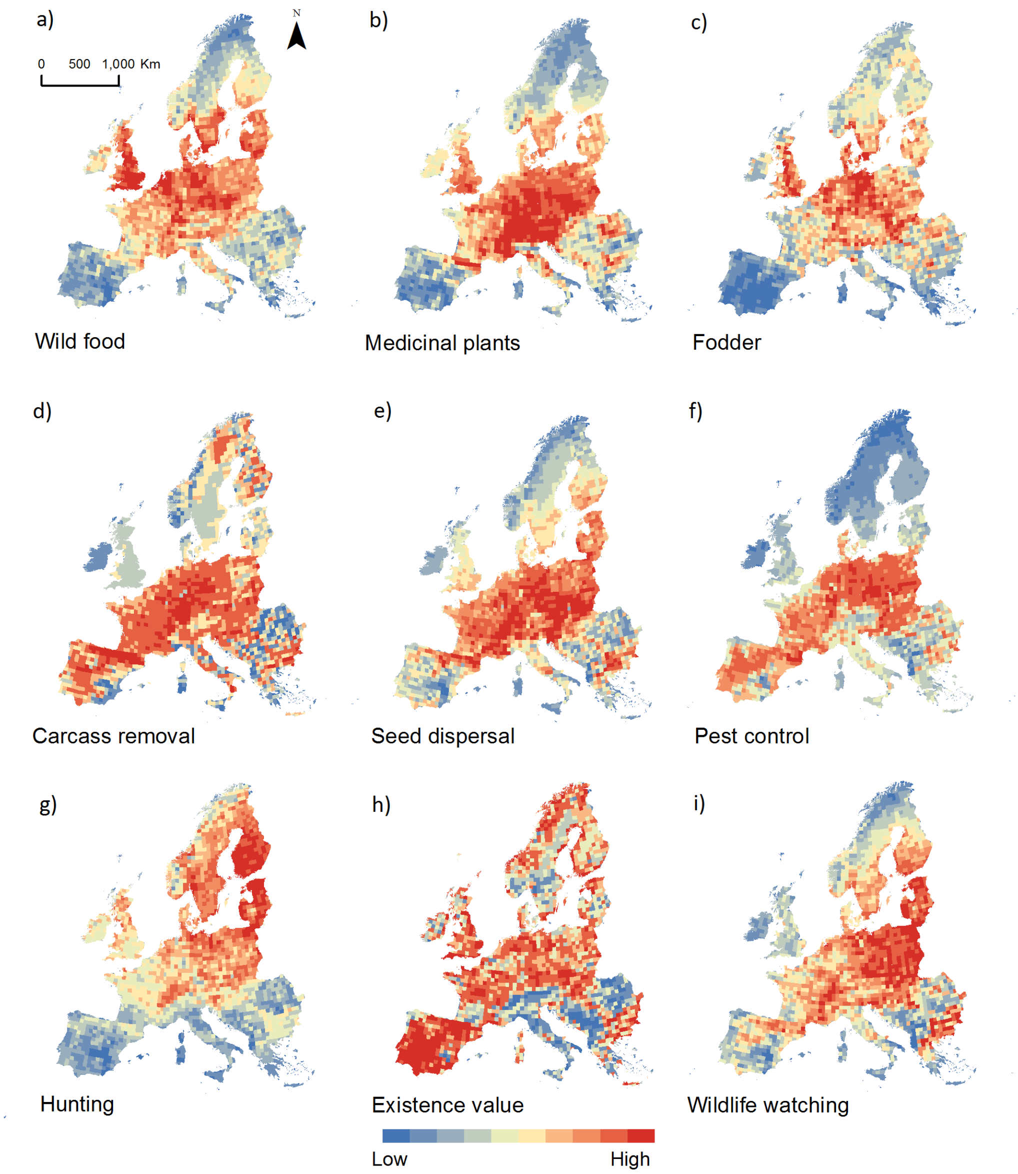

Figure 3 Spatial distribution of ecosystem services based on biodiversity data at 50x50 km resolution.

The patterns of variation between the two types of services were also considerably different. For instance, in the Iberian peninsula, areas that presented a high variation between biodiversity-based services had low variation of biophysical-based services (Figure 6). Meanwhile, fewer areas had similar patterns. For example, the Alps had high variation in both types of services.

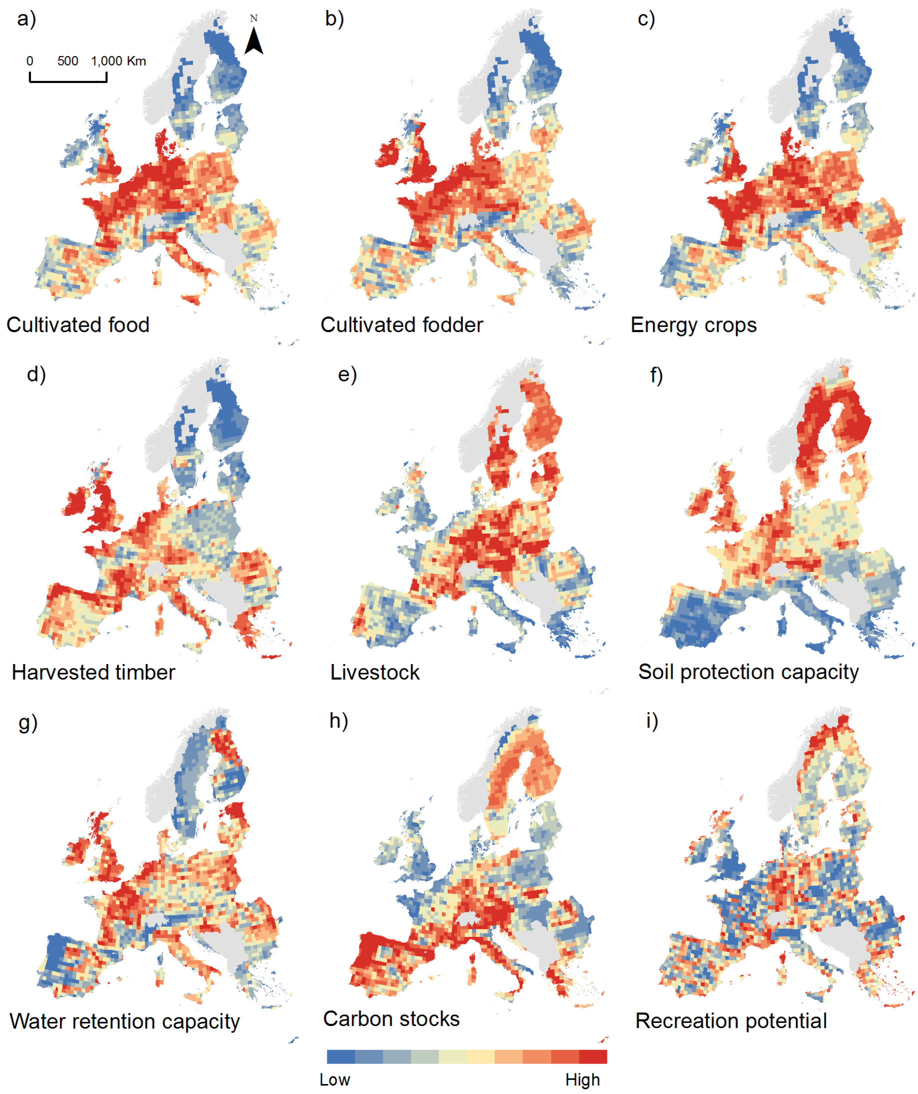

Figure 4 Spatial distribution of ecosystem services based on biophysical data at 50x50 km resolution.

Correlation with species richness increased with the increase of number of services for all services together, as well as for the biodiversity-based and biophysical-based services separately (Figure 7). Moreover, the distribution of correlation results became narrower with the increase of number of services. For example, the average Spearman's rho between one biodiversity-based service and species richness was 0.55, the 95th percentile between 0.08 and 0.87. The average rho for all biodiversity-based services was 0.79, 95th percentile between 0.67 and 0.87 (Figure 7a). The pattern was similar for biophysical-based services (Figure 7b) and for all services considered together (Figure 7c).

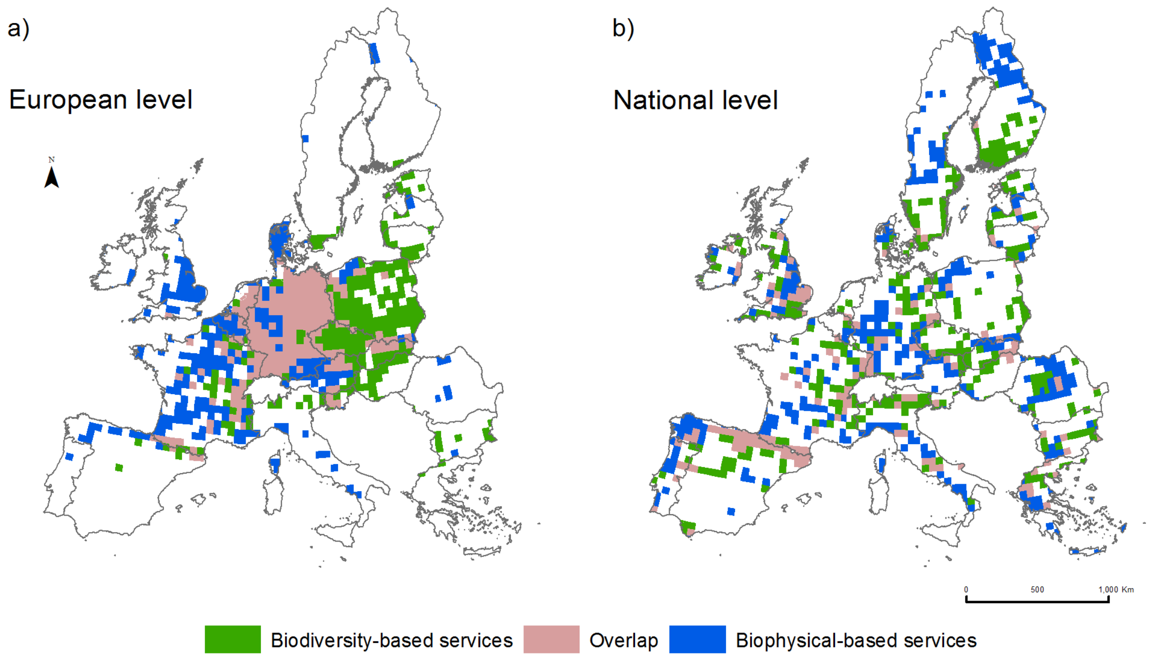

Figure 5 Spatial overlap between the 25% highest values of the two sets of ecosystem services (biodiversity-based and biophysical-based) at: a) European level, b) National level.

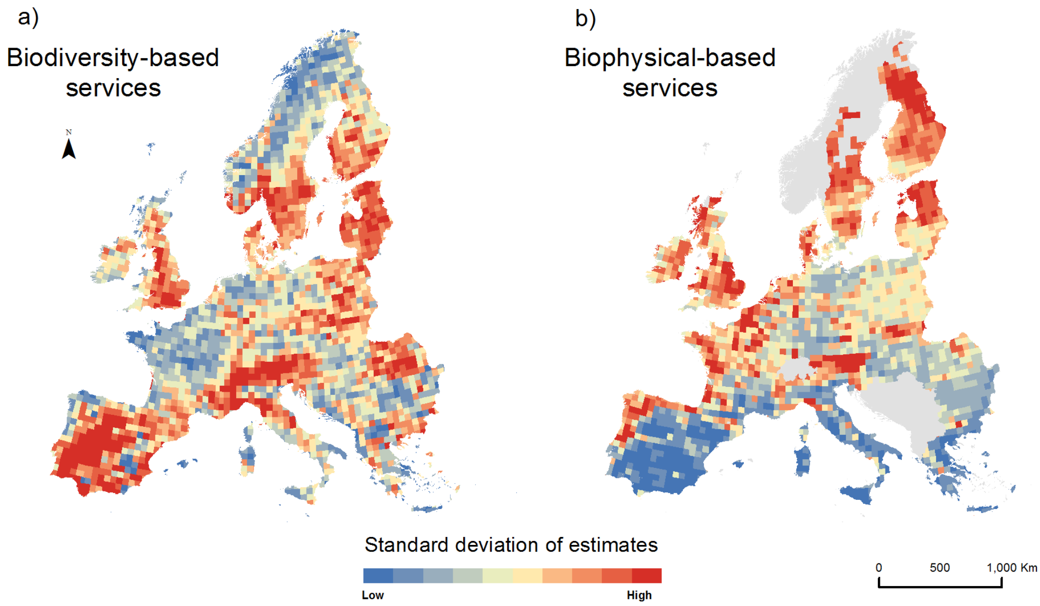

Figure 6 Standard deviation of estimates calculated at the level of the 50x50 km grid cells for: a) biodiversity-based and, b) biophysical-based services.

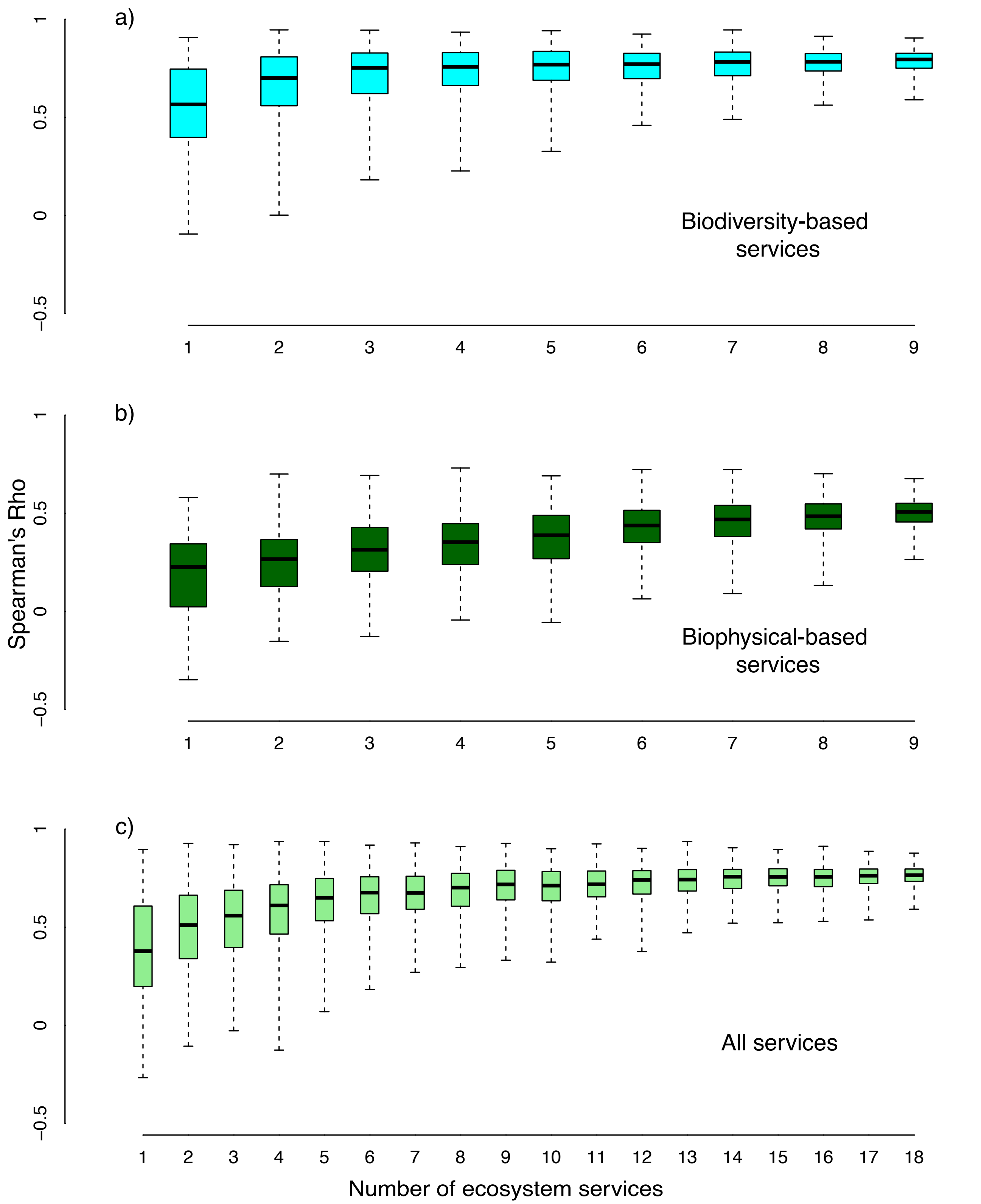

Figure 7 Results of rank correlations between species richness normalized per taxa and random combinations of an increasing number of a) biodiversity-based, b) biophysical-based, and c) all services. The random combinations were repeated 500 times for each number of ecosystem services. The black band inside each box represents the median, the boxes represent 50% of values around the median, the whiskers extend to the most extreme values.

Discussion

Our study provides a comprehensive assessment of biodiversity-based services, a category overlooked by large-scale assessments (Chan *et al.* 2006; Naidoo *et al.* 2008; Maes *et al.* 2012; Schröter *et al.* 2016). We show that this can be a damaging approach as it provides incomplete results for prioritization and management of conservation areas (Chan *et al.* 2006). Focusing limited resources on areas identified based only on biophysical-based services risks reducing resources for protecting biodiversity-based services and biodiversity (Schröter *et al.* 2014). Meanwhile, the large overlap between high-supplying areas also suggests effortless synergies in some regions between priorities of biodiversity-based and biophysical-based services. For example, areas prioritized for crop production can benefit from pest control (Karp *et al.* 2013). Spatial overlaps have also important consequences for management. For instance, forest management has to pay particular attention to biodiversity in areas of high supply of wild foods or medicinal plants to avoid damaging these services (Gamfeldt *et al.* 2013). Assessing variation patterns in service estimates is novel within service research but it is highly relevant as it can provide insights on where management has to target multiple services at the same time. Our results on variation patterns further highlight the differences between the two types of services and the need to consider them complementarily in assessments for policy and management decisions.

Changing the scale of the assessment in our study modified dramatically the spatial distribution of areas of high supply of services as well as overlap between services (Figure 5b). This shows that analyses at a single extent can be misleading, especially as relevant extents for policy-making and demand differ among services. For instance, soil protection (Guerra *et al.* 2014), pest control (Karp *et al.* 2013) or carcass removal (Duško Ćirović *et al.* 2016) have to be consumed at the point of production and lower extents are more relevant for analysis. Other services have integrated regional markets and policies, such as the European agricultural system (European Commission 2005). Still other services are of global interest such as carbon stocks (Ruesch and Gibbs 2008). For these, analyses at large extents are of higher relevance.

Our results also highlight the important role biodiversity plays for the multifunctionality of landscapes. This relationship is strengthened by the addition of biodiversity-based services (Figure 6c). But biophysical-based services present a similar pattern, in accordance with previous research suggesting that increasing number of species are necessary for supplying an increasing number of functions in diverse contexts (Tilman *et al.* 2014). At our coarse grain which covers wide ranges of environmental conditions, the functional relationship between species richness and services supply is likely to fit the relationship suggested by Isbell *et al.* (2011) rather than the one found in specific contexts, especially in the case of pollination (Winfree *et al.* 2015). Thus, the goals of conserving biodiversity and services, especially at large scales, should not be approached separately, as suggested previously (Adams 2014). Conserving biodiversity is the highest insurance for guaranteeing long-term supply of multiple services (Isbell *et al.* 2011).

Among the issues limiting progress in the research of biodiversity-based services at large scales are the scarcity and biases in biodiversity data (Collen *et al.* 2008). Although European biodiversity atlases are among the most complete datasets at continental level, biases are still present. The plant distributions are affected by geographical biases, especially in the southern part of the continent (Hanspach *et al.* 2011), although Ronk *et al.* (2015) suggest that variation in plant diversity is well represented. The compilation of the atlas of amphibians and reptiles was limited by different approaches to data-sharing of data owners across Europe (Sillero *et al.* 2014). The quantity and quality of estimates of biophysical-based services also differed between countries and, in some cases, within countries (Maes *et al.* 2015). Considering a wide range of sources and services is an approach towards mitigating biases (Isbell *et al.* 2011; Milt *et al.* 2014) but improving monitoring for both biodiversity (Pereira and Cooper 2006) and services (Tallis *et al.* 2012) is a priority for conservation science.

Furthermore, presence data offer limited information on the potential of ecological communities to supply ecosystem services as species roles are strongly dependent on abundances (Winfree *et al.* 2015). Integrating abundance in model estimating service supply raises, however, important challenges in terms of available data and models for such integration. In addition to the costs of acquiring such biodiversity data (Turner *et al.* 2003), estimating a species effectiveness at performing a service at different abundances would likely require significant research resources (Kremen 2005).

Nevertheless, these limitations should not impede us from conducting compreensive assessments of ecosystem services. Our results indicate that considering few services of any type distorts our understanding of the relationships between biodiversity and service supply. Moreover, comprehensive assessments can provide crucial information on opportunities for synergies (Maes *et al.* 2012) and avoidable damages in service management (Thomas *et al.* 2013). Therefore, we call here for further research and increased efforts for a balanced assessment of both biodiversity-based and biophysical-based services.

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References

Adams WM. 2014. The value of valuing nature. *Science* **346**: 549–551.

Batista e Silva F, Lavalle C, and Koomen E. 2013. A procedure to obtain a refined European land use/cover map. *J Land Use Sci* **8**: 255–283.

Bilz M, Kell SP, Maxted N, and Lansdown RV. 2011. European red list of vascular plants. Publication Office of the European Union Luxembourg.

BirdLife International. 2015. European Red List of Birds. Luxembourg: Office for Official Publications of the European Communities.

Burkhard B, Kroll F, Nedkov S, and Müller F. 2012. Mapping ecosystem service supply, demand and budgets. *Ecol Indic* **21**: 17–29.

Chan KM., Shaw MR, Cameron DR, *et al.* 2006. Conservation planning for ecosystem services. *PLoS Biol* **4**: e379.

Civantos E, Thuiller W, Maiorano L, *et al.* 2012. Potential impacts of climate change on ecosystem services in Europe: the case of pest control by vertebrates. *BioScience* **62**: 658–666.

Collen B, Ram M, Zamin T, and McRae L. 2008. The tropical biodiversity data gap: addressing disparity in global monitoring. *Trop Conserv Sci* **1**: 75–88.

COP. 2010. Decision Adopted by the Conference of the Parties to the Convention on Biological Diversity at its Tenth Meeting. Nagoya: Convention on Biological Diversity.

Cox NA and Temple HJ. 2009. European Red List of Reptiles. Luxembourg: Office for Official Publications of the European Communities.

Duncan C, Thompson JR, and Pettorelli N. 2015. The quest for a mechanistic understanding of biodiversity–ecosystem services relationships. In: Proc. R. Soc. B. The Royal Society.

Duško Ćirović, Aleksandra Penezić, and Miha Krofel. 2016. Jackals as cleaners: Ecosystem services provided by a mesocarnivore in human-dominated landscapes. *Biol Conserv* **199**: 51–5.

EU Commission. 2011. Our Life in Insurance, our Natural Capital: An EU Biodiversity Strategy to 2020. *COM 2011* **244**.

European Commission. 2005. Agri-environment measures. Overview on General Principles, Types of Measures, and Application.

Frenette-Dussault, C., Shipley, B., Léger, J.-F., Meziane, D. & Hingrat, Y. 2012. Functional structure of an arid steppe plant community reveals similarities with Grime's C-S-R theory. *J. Veg. Sci.*, 23, 208–222

Gamfeldt L, Snäll T, Bagchi R, *et al.* 2013. Higher levels of multiple ecosystem services are found in forests with more tree species. *Nat Commun* **4**: 1340.

Green, W. 2009. USDA PLANTS Compilation, Version 1, 09-02-02.

Guerra CA, Pinto-Correia T, and Metzger MJ. 2014. Mapping soil erosion prevention using an ecosystem service modeling framework for integrated land management and policy. *Ecosystems* **17**: 878–889.

Hagemeijer WJ and Blair MJ. 1997. The EBCC atlas of European breeding birds: their distribution and abundance. T. & AD Poyser London.

Hanspach J, Kühn I, Schweiger O, *et al.* 2011. Geographical patterns in prediction errors of species distribution models. *Glob Ecol Biogeogr* **20**: 779–88.

Hector A and Bagchi R. 2007. Biodiversity and ecosystem multifunctionality. *Nature* **448**: 188–190.

IPBES. 2016. Summary for policymakers of the assessment report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services on pollinators, pollination and food production. Bonn, Germany: Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services.

Isbell F, Calcagno V, Hector A, *et al.* 2011. High plant diversity is needed to maintain ecosystem services. *Nature* **477**: 199–202.

Karp DS, Mendenhall CD, Sandí RF, *et al.* 2013. Forest bolsters bird abundance, pest control and coffee yield. *Ecol Lett* **16**: 1339–1347.

Kattge J, Diaz S, Lavorel S, *et al.* 2011. TRY–a global database of plant traits. *Glob Change Biol* **17**: 2905–2935.

Kew Royal Botanic Gardens. 2014. Medicinal Plant Names Services Portalhttp://www.kew.org/kew-science/people-and-data/resources-and-databases/medicinal-plant-names-services. Viewed

Kremen C. 2005. Managing ecosystem services: what do we need to know about their ecology? *Ecol Lett* **8**: 468–479.

Kühn I, Durka W, and Klotz S. 2004. BiolFlor: a new plant-trait database as a tool for plant invasion ecology. *Divers Distrib* **10**: 363–365.

Lahti T and Lampinen R. 1999. From dot maps to bitmaps: Atlas Florae Europaeae goes digital. *Acta Bot Fenn* **162**: 5–9.

Lange D. 1998. Europe’s medicinal and aromatic plants: their use, trade and conservation. Traffic International.

Luck GW, Daily GC, and Ehrlich PR. 2003. Population diversity and ecosystem services. *Trends Ecol Evol* **18**: 331–6.

Mace GM, Norris K, and Fitter AH. 2012. Biodiversity and ecosystem services: a multilayered relationship. *Trends Ecol Evol* **27**: 19–26.

Maes J, Fabrega N, Zulian G, *et al.* 2015. Mapping and Assessment of Ecosystems and their Services Trends in ecosystems and ecosystem services in the European Union between 2000 and 2010. *JRC Sci Policy Rep Publ Off Eur Union Luxemb Httpdx Doi Org102788341839 SBN 978-92-79-46206-1 PDF*.

Maes J, Paracchini ML, Zulian G, *et al.* 2012. Synergies and trade-offs between ecosystem service supply, biodiversity, and habitat conservation status in Europe. *Biol Conserv* **155**: 1–12.

Maes J, Teller, Anne, Erhard, M., *et al.* 2014. Mapping and Assessment of Ecosystems and their Services: Indicators for ecosystem assessments under Action 5 of the EU Biodiversity Strategy 2020. European Union.

MEA. 2005. Ecosystems and human well-being. *Wash DC*.

Milt AW, Palmer SR, and Armsworth PR. 2014. Updating conservation priorities over 111 years of species observations. *J Appl Ecol* **51**: 1515–1524.

Mitchell-Jones AJ, Amori G, Bogdanowicz W, *et al.* 1999. The atlas of European mammals.

Naidoo R, Balmford A, Costanza R, *et al.* 2008. Global mapping of ecosystem services and conservation priorities. *Proc Natl Acad Sci* **105**: 9495.

Paracchini ML, Zulian G, Kopperoinen L, *et al.* 2014. Mapping cultural ecosystem services: A framework to assess the potential for outdoor recreation across the EU. *Ecol Indic* **45**: 371–385.

Pereira HM and Cooper HD. 2006. Towards the global monitoring of biodiversity change. *Trends Ecol Evol* **21**: 123–129.

Ricketts TH, Daily GC, Ehrlich PR, and Michener CD. 2004. Economic value of tropical forest to coffee production. *Proc Natl Acad Sci U S A* **101**: 12579–12582.

Ronk A, Szava-Kovats R, and Pärtel M. 2015. Applying the dark diversity concept to plants at the European scale. *Ecography* **38**: 1015–25.

Ruesch A and Gibbs HK. 2008. New IPCC Tier-1 Global Biomass Carbon Map for the Year 2000http://cdiac.ornl.gov/epubs/ndp/global_carbon/carbon_documentation.html#datafiles. Viewed 2 Jun 2016.

Schröter M, Albert C, Marques A, *et al.* 2016. National Ecosystem Assessments in Europe: A Review. *BioScience*: biw101.

Schröter M, Rusch GM, Barton DN, *et al.* 2014. Ecosystem services and opportunity costs shift spatial priorities for conserving forest biodiversity. *PloS One* **9**: e112557.

Schulp CJE, Thuiller W, and Verburg PH. 2014. Wild food in Europe: A synthesis of knowledge and data of terrestrial wild food as an ecosystem service. *Ecol Econ* **105**: 292–305.

Sillero N, Campos J, Bonardi A, *et al.* 2014. Updated distribution and biogeography of amphibians and reptiles of Europe. *Amphib-Reptil* **35**: 1–31.

Tallis H, Mooney H, Andelman S, *et al.* 2012. A Global System for Monitoring Ecosystem Service Change. *BioScience* **62**: 977–86.

Temple HJ and Cox NA. 2009. European Red List of Amphibians. Luxembourg: Office for Official Publications of the European Communities.

Temple HJ and Terry A. 2007. The Status and Distribution of European Mammals. Luxembourg: Office for Official Publications of the European Communities.

Thomas CD, Anderson BJ, Moilanen A, *et al.* 2013. Reconciling biodiversity and carbon conservation. *Ecol Lett* **16**: 39–47.

Tilman D, Isbell F, and Cowles JM. 2014. Biodiversity and ecosystem functioning. *Annu Rev Ecol Evol Syst* **45**: 471.

Turner W, Spector S, Gardiner N, *et al.* 2003. Remote sensing for biodiversity science and conservation. *Trends Ecol Evol* **18**: 306–14.

USDA. 2014. Grin Taxonomy for Plants. United States Department of Agriculture (USDA). *Agric Res Serv ARS Available Httpwww Ars-Grin Govcgi-Binnpgshtmltaxgenform Pl Accessed Oct 2014*.

Wilman H, Belmaker J, Simpson J, *et al.* 2014. EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology* **95**: 2027–2027.

Winfree R, W Fox J, Williams NM, *et al.* 2015. Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. *Ecol Lett* **18**: 626–635.

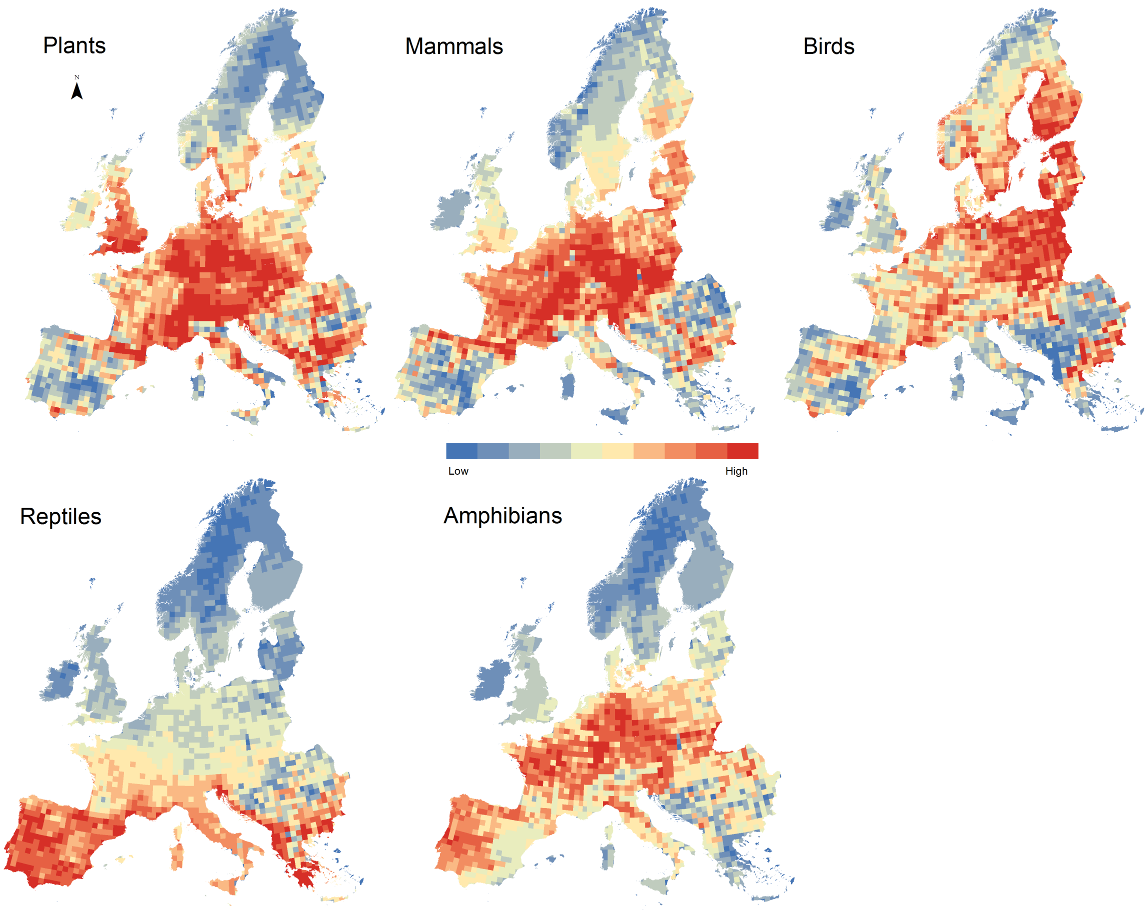
Wirth, C. & Lichstein, J.W. 2009. The imprint of species turnover on old-growth forest carbon balances-insights from a trait-based model of forest dynamics. In: *Old-growth forests*. Springer, pp. 81–113.

World Health Organization. 1999. WHO monographs on selected medicinal plants. World Health Organization.

www.pfaf.org. Plants for a Futurehttp://www.pfaf.org/user/default.aspx. Viewed 1 Oct 2014.

Supplementary material

Figure S1. Species richness in Europe at a resolution of 50x50 km (Lahti and Lampinen 1999, Hagemeijer and Blair 1997, Mitchell-Jones *et al.* 1999, Sillero *et al.* 2014).



Chapter 6

Synthesis

This thesis contributes to several crucial areas for achieving the Aichi Biodiversity Targets for 2020. It also contributes to a more integrative biodiversity science by considering multiple dimensions of biodiversity for addressing conservation challenges.

6.1 Target 11

Current studies suggest that we will reach 17% of global area under a protection regime by 2020 (Leadley *et al.* 2014). However, this progress is spread unequally among biomes and ecoregions, with almost 30% of terrestrial ecoregions having less than 5% coverage of protected areas (Watson *et al.* 2014). Moreover, the coverage of areas representing different management categories as defined by the International Union for Conservation of Nature (IUCN) also differs among biomes (Figure 6.1, Leadley *et al.* 2014). For instance, western United States is dominated by strict protection areas (category I and II) while the European Natura 2000 network of protected areas covers mainly habitats and species characteristic of human dominated habitats (Figure 6.1, EC 1992; Halada *et al.* 2011). This suggests that methods for prioritizing areas for conservation are unequally applied in different regions.

Imbalances in applying prioritization approaches can lead to the underrepresentation of some biodiversity dimensions, as different approaches maximize different biodiversity targets (Chap. 2). Many studies dealing with prioritizing areas for conservation focus on one biodiversity dimension such as species conservation. For instance, species richness, rarity or threat have been at the center of many prioritization studies (Williams *et al.* 1996; Orme *et al.* 2005). Although ecosystem services have recently been integrated in conservation prioritization (Schröter *et al.* 2014), the discussion usually focuses on the trade-offs between conserving different biodiversity dimensions. While the biodiversity conservation literature has strongly focused on species preservation, the ecosystem services literature has increasingly moved away from species-level biodiversity (Chap. 5). Thus, most studies on prioritizing areas for ecosystem services use biophysical data to estimate supply (Maes *et al.* 2012). These divergent focuses in area prioritization risks undermining interlinked biodiversity targets (Marques *et al.* 2014). Although studies attempting to integrate biodiversity goals usually highlight the challenges raised by the different spatial distributions and ecological mechanisms (Karp *et al.* 2015), such efforts are necessary for finding conservation solutions for all biodiversity dimensions in protected areas and beyond.

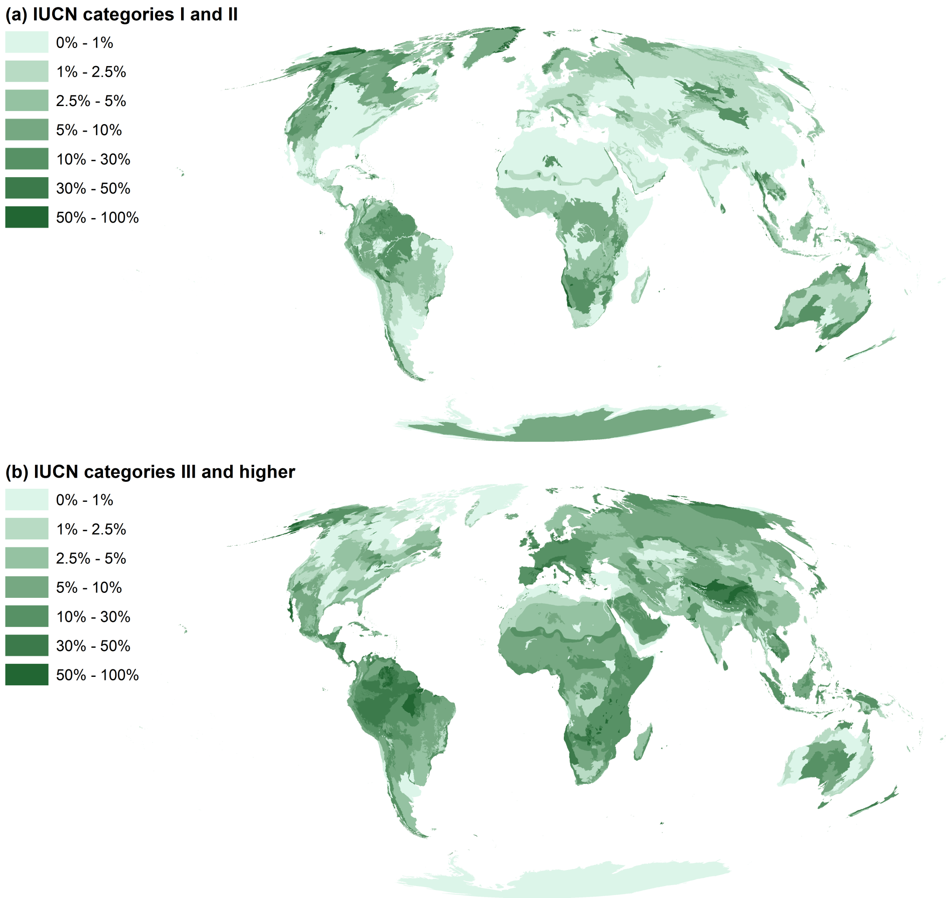


Figure 6.1 The distribution of protected areas in IUCN categories I and II (a) and in all other categories (III, IV, V, VI, including areas with no information on category) (b) across world ecoregions. The different shades of green represent the proportion of each ecoregion's land surface covered by protected areas. Source: World Database of Protected Areas (IUCN-WCPA/UNEP-WCMC 2015) and Terrestrial Ecoregions (WWF; http://maps.tnc.org/gis_data.html).

An area of particular importance for Target 11 is also the management of protected areas. Several recent studies addressed effectiveness of protected areas and results suggest that urgent progress is necessary to improve results. In a global analysis of over 3000 protected areas, Leverington *et al.* (2010) found that the management of 40% of areas showed major deficiencies. Moreover, protected areas seem to be effective at conserving forest habitat but not as successful at conserving species populations (Geldmann *et al.* 2013). This highlights the complexity of factors that influence the maintenance of ecological communities and the need to address the multiple layers of human impact present on a landscape (Chap. 3, Chap. 4). Additionally, as human appreciation has always represented a strong driver towards conservation, integrating perceptions of solitude and naturalness (Chap. 4) into management can attract higher support from stakeholders and thus higher chances of conservation success.

Another issue affecting the results of conservation management in protected areas and beyond is the static image of biodiversity based on which decisions are taken (Heller and Hobbs 2014). In Europe, the management of protected areas is focused on maintaining human-dependent habitats in the face of farmland abandonment (Prach *et al.* 2013, Chap 4). Despite these efforts, ecological communities continue to change under the current drivers (Timmermann *et al.* 2015) because the targeted ecosystems are not self-sustaining in the absence of continuous human-management. This represents a result of the selective removal of trophic links (Ripple *et al.* 2014) and the alteration of ecological functions and disturbance regimes (Navarro *et al.* 2015) during centuries of human occupation. Taking a prescriptive view of conservation can increase the instances of conservation-reliant species for which continuous management in necessary to ensure survival (Scott *et al.* 2010; Goble *et al.* 2012). In order to reduce conservation costs to achievable levels (McCarthy *et al.* 2012) and benefit from ecosystem services (Cerqueira *et al.* 2015), conservation has to aim for self-sustaining ecosystems and to take advantage of the conservation opportunities arising in formerly managed landscapes. Based on the differences between regions in terms of human impacts, targeted management can address specific contexts with the overall aim of reducing the amount of human management in order to allow the development of resilient ecosystems (Chap. 4).

6.2 Target 14

Several authors have concluded that the connections between services and biodiversity are too weak to justify the common pursuit of these goals in conservation (Adams 2014; Kleijn *et al.* 2015). Such a conclusion can have serious consequences for the achievement of conservation targets and thus, it deserves careful examination. Current assessments describe the supply of all ecosystem services in the same terms: complex interactions between biotic and abiotic components support ecosystem processes and these in turn supply services (Duncan *et al.* 2015). However, there is a variation in how services are produced and some services arise directly from species-level biodiversity (Mace *et al.* 2012). Nevertheless, most assessments estimate service supply based only on biophysical data (e.g. land cover), while ignoring the services which rely directly on species identities (Naidoo *et al.* 2008). We show that biodiversity-based services are particularly strongly correlated to species richness at European level and that incomplete assessments can lead to underestimating the role of biodiversity in service supply (Chap. 5).

Moreover, scale and the number of assessed services can shift the conclusions regarding the relationship between biodiversity and services (Chap 2, Chap. 5). Irrespective of their type, the more services we included in the calculation, the stronger and more consistent was the correlation with species richness in Europe at 50 x 50 km resolution (Chap. 5). This aligns with previous research that suggests that an increasing number of species is necessary to supply multiple services in different years and environmental conditions (Isbell *et al.* 2011). At finer extents species richness seems to be a poor proxy for ecosystem services (Winfree *et al.* 2015, Chap. 2). This can have at least two explanations. First, coarse spatial units are more likely to contain very different environmental conditions that require contributions from different species for adequate supply of services (Isbell *et al.* 2011). Second, as previously stated, the analysis of a reduced set of services can lead to an underestimation of the relationships between species richness and services (Chap. 5). In conclusion, assessments should include a wide array of services, both dependent on species-level and ecosystem-level biodiversity. However, restoration and safeguarding of services should also take into account different spatial relationships at different scales.

The spatial prioritization of areas supplying high levels of services changes dramatically from continental to national scales (Chap 5.). In an increasingly globalized world, global assessments of ecosystem services are relevant for coordinated policies and sharing experiences in managing services successfully (IPBES 2016). Moreover, several services have now global and continental markets (European Commission 2005; Tilman *et al.* 2011) and the impact of their loss is global (IPCC 2013). However, in the case of many other services, the safeguarding and management is done at national or local scales. Thus, national and regional perspectives should be actively encouraged for an efficient restoration and safeguarding of ecosystem services (Chap. 2, Chap. 5).

The common analysis of biodiversity-based and biophysical-based services reveals also large areas of overlap (Chap. 5). These areas could favor synergies in managing both types of services and thus, contribute to maximizing the supply of essential services. This is the case especially for agriculture-based services that can benefit highly from pest control or pollination services (Ricketts 2004; Karp *et al.* 2013). Conversely, management should also take into account these areas in order to avoid inadvertently reducing some services while trying to maximize others. For instance, forestry management can lead to a decrease in species richness which can result in the reduction of non-timber products (Gamfeldt *et al.* 2013). Areas that provide only biodiversity-based services indicate where further resources should be invested to safeguard these services, especially considering that biodiversity-based services such as wild food and medicinal plant benefit the most vulnerable social categories (Leadley *et al.* 2014).

6.3 Target 15

Many areas with severely damaged biodiversity and services require costly, intensive restoration efforts aimed at returning ecosystems to prior states (Suding *et al.* 2004). Undeniably, such efforts are necessary in order to remove the most serious effects of human activities. However, these efforts do not always achieve resilience (Klötzli and Grootjans 2001) and long-term species preservation (Scott *et al.* 2010). Maintaining a non-prescriptive approach to restoration allows for a better adjustment of ecosystems to new environmental conditions and better use of conservation resources (Balaguer *et al.* 2014). Thus, restoration should also focus on increasing resilience and ecosystem functions while reducing the impact of human presence (Chapt. 3, Chap. 4).

By analyzing wilderness metrics in the areas projected to be abandoned, adequate responses can be designed for restoration in Europe (Chap. 3, Chap. 4). For instance, the recovery of the deviation from potential natural vegetation (dPNV) is conditioned by several factors, such as the absence of seed banks (Rey Benayas *et al.* 2007) or low abundances of herbivores and large carnivores (Chap. 4). These gaps in the trophic network can lead to a homogeneous vegetation structure that impacts the diversity of ecological communities (Navarro *et al.* 2015). Moreover, changes produced by climate change to the patterns of the potential natural vegetation (Hickler *et al.* 2012) can lead to ecosystems farther from the potential natural vegetation than expected. Management and policy actions can support effective restoration through planting of vegetation islets to increase seed banks (Rey Benayas *et al.* 2008). The recovery of local populations of wild herbivores and their predators can be achieved through no-hunting zones and reintroductions (Ripple *et al.* 2016) while combating the effects of climate change can be addressed through building and maintaining ecological corridors for dispersal processes (Nuñez *et al.* 2013; Pauli *et al.* 2014). Such combined restoration strategies would lead both to the recovery of formerly-persecutes species (Enserink and Vogel 2006) and to enhancing the supply of certain ecosystem services (Cerqueira *et al.* 2015).

Some of the biggest opportunities for restoration are the established conservation infrastructures. For instance, a large proportion of farmland projected to be abandoned in Europe is located in and around the Natura 2000 sites (Chap. 4, Table 2). Thus, restoration actions could be integrated within the management plans of these areas. In general, restoration actions can take advantage of existing management structures and connections to local communities of established protected areas in order to ensure positive results (Andam *et al.* 2013). However, in the case of Natura 2000 sites, the management guidelines require the maintenance in a "favorable conservation status" of many species and habitats characteristic of extensive farmland or early successional habitats (Prach *et al.* 2007; Halada *et al.* 2011). This limits the range of restoration actions and an adjustment of policies is necessary in order to potentiate rewilding across Europe (Chap. 4, Merckx and Pereira 2014). Similarly, other fields of restoration depend on policy changes such as the implementation of biodiversity offsets and clear restoration targets included in environmental impact assessments (Pereira *et al.* 2014; Gonçalves *et al.* 2015).

6.4 Final remarks

The field of conservation experienced bitter controversies regarding which biodiversity dimensions and contexts should receive the most efforts (Sarkar 1999; Kareiva 2014; Soulé 2014). However, many studies show that we need to look at the big, integrative picture in order to understand and effectively protect biodiversity (Mittermeier *et al.* 2003; Isbell *et al.* 2011). I expect that such conclusions will increasingly emerge from research. Conservation management in the context of global change and increased anthropogenic pressures will work by taking into account multiple dimensions of biodiversity. A research priority is, of course, understanding the relationships between the different biodiversity dimensions (Balvanera *et al.* 2006; Naidoo *et al.* 2008; Tilman *et al.* 2014). This thesis addresses this priority and uncovers important synergies from which conservation can benefit. Above all, we need to also look at conservation successes and emphasize the cases where we have achieved our targets in order to build momentum for a sustainable, biodiverse world.

Bibliography

Adams WM. 2014. The value of valuing nature. *Science* **346**: 549–551.

Andam KS, Ferraro PJ, and Hanauer MM. 2013. The effects of protected area systems on ecosystem restoration: a quasi-experimental design to estimate the impact of Costa Rica's protected area system on forest regrowth. *Conserv Lett* **6**: 317–23.

Balaguer L, Escudero A, Martín-Duque JF, *et al.* 2014. The historical reference in restoration ecology: Re-defining a cornerstone concept. *Biol Conserv* **176**: 12–20.

Balvanera P, Pfisterer AB, Buchmann N, *et al.* 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecol Lett* **9**: 1146–56.

Cerqueira Y, Navarro LM, Maes J, *et al.* 2015. Ecosystem services: the opportunities of rewilding in Europe. In: Rewilding European landscapes. Springer.

Duncan C, Thompson JR, and Pettorelli N. 2015. The quest for a mechanistic understanding of biodiversity–ecosystem services relationships. In: Proc. R. Soc. B. The Royal Society.

EC. 1992. EU Habitats Directive (92/43/EEC). *Consol Text Off Off Publ Eur Union CONSLEG 1992LOO43–0105–2004*.

Enserink M and Vogel G. 2006. Wildlife conservation: the carnivore comeback. *Science* **314**: 746.

European Commission. 2005. Agri-environment measures. Overview on General Principles, Types of Measures, and Application.

Gamfeldt L, Snäll T, Bagchi R, *et al.* 2013. Higher levels of multiple ecosystem services are found in forests with more tree species. *Nat Commun* **4**: 1340.

Geldmann J, Barnes M, Coad L, *et al.* 2013. Effectiveness of terrestrial protected areas in reducing habitat loss and population declines. *Biol Conserv* **161**: 230–238.

Goble DD, Wiens JA, Scott JM, *et al.* 2012. Conservation-Reliant Species. *BioScience* **62**: 869–73.

Gonçalves B, Marques A, Soares AMVDM, and Pereira HM. 2015. Biodiversity offsets: From current challenges to harmonized metrics. *Curr Opin Environ Sustain* **14**: 61–67.

Halada L, Evans D, Romão C, and Petersen JE. 2011. Which habitats of European importance depend on agricultural practices? *Biodivers Conserv* **20**: 2365–2378.

Hickler T, Vohland K, Feehan J, *et al.* 2012. Projecting the future distribution of European potential natural vegetation zones with a generalized, tree species-based dynamic vegetation model. *Glob Ecol Biogeogr* **21**: 50–63.

IPBES. 2016. Summary for policymakers of the assessment report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services on pollinators, pollination and food production. Bonn, Germany: Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services.

IPCC. 2013. Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA: Intergovernmental Panel on Climate Change.

Isbell F, Calcagno V, Hector A, *et al.* 2011. High plant diversity is needed to maintain ecosystem services. *Nature* **477**: 199–202.

IUCN-WCPA/UNEP-WCMC. 2015. World Database on Protected Areas.

Kareiva P. 2014. New conservation: setting the record straight and finding common ground. *Conserv Biol* **28**: 634–636.

Karp DS, Mendenhall CD, Callaway E, *et al.* 2015. Confronting and resolving competing values behind conservation objectives. *Proc Natl Acad Sci* **112**: 11132–7.

Karp DS, Mendenhall CD, Sandí RF, *et al.* 2013. Forest bolsters bird abundance, pest control and coffee yield. *Ecol Lett* **16**: 1339–1347.

Kleijn D, Winfree R, Bartomeus I, *et al.* 2015. Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. *Nat Commun* **6**.

Klötzli F and Grootjans AP. 2001. Restoration of Natural and Semi-Natural Wetland Systems in Central Europe: Progress and Predictability of Developments. *Restor Ecol* **9**: 209–19.

Leadley PW, Krug CB, Alkemade R, *et al.* 2014. Progress towards the Aichi Biodiversity Targets: An Assessment of Biodiversity Trends, Policy Scenarios and Key Actions. Montreal, Canada: Secretariat of the Convention on Biological Diversity.

Leverington F, Costa KL, Pavese H, *et al.* 2010. A global analysis of protected area management effectiveness. *Environ Manage* **46**: 685–698.

Mace GM, Norris K, and Fitter AH. 2012. Biodiversity and ecosystem services: a multilayered relationship. *Trends Ecol Evol* **27**: 19–26.

Maes J, Paracchini ML, Zulian G, *et al.* 2012. Synergies and trade-offs between ecosystem service supply, biodiversity, and habitat conservation status in Europe. *Biol Conserv* **155**: 1–12.

Marques A, Pereira HM, Krug C, *et al.* 2014. A framework to identify enabling and urgent actions for the 2020 Aichi Targets. *Basic Appl Ecol* **15**: 633–8.

McCarthy DP, Donald PF, Scharlemann JPW, *et al.* 2012. Financial Costs of Meeting Global Biodiversity Conservation Targets: Current Spending and Unmet Needs. *Science* **338**: 946–9.

Merckx T and Pereira HM. 2014. Reshaping agri-environmental subsidies: From marginal farming to large-scale rewilding. *Basic Appl Ecol*.

Mittermeier RA, Mittermeier CG, Brooks TM, *et al.* 2003. Wilderness and biodiversity conservation. *Proc Natl Acad Sci* **100**: 10309.

Naidoo R, Balmford A, Costanza R, *et al.* 2008. Global mapping of ecosystem services and conservation priorities. *Proc Natl Acad Sci* **105**: 9495.

Navarro LM, Proença V, Kaplan JO, and Pereira HM. 2015. Maintaining Disturbance-Dependent Habitats. In: Rewilding European landscapes. Springer Netherlands.

Nuñez TA, Lawler JJ, Mcrae BH, *et al.* 2013. Connectivity Planning to Address Climate Change. *Conserv Biol* **27**: 407–16.

Orme CD., Davies RG, Burgess M, *et al.* 2005. Global hotspots of species richness are not congruent with endemism or threat. *Nature* **436**: 1016–1019.

Pauli H, Gottfried M, and Grabherr G. 2014. Effects of climate change on the alpine and nival vegetation of the Alps. *J Mt Ecol* **7**.

Pereira HM, Navarro LM, Ceausu S, *et al.* 2014. Target 15 - Ecosystem Resilience. In: Technical Report of the Global Biodiversity Outlook 4. Secretariat of the Convention on Biological Diversity.

Prach K, Jongepierová I, and Řehounková K. 2013. Large-Scale Restoration of Dry Grasslands on Ex-Arable Land Using a Regional Seed Mixture: Establishment of Target Species. *Restor Ecol* **21**: 33–39.

Prach K, Lepš J, and Rejmánek M. 2007. Old field succession in Central Europe: local and regional patterns. *Old Fields Dyn Restor Abandon Farml*: 180–201.

Rey Benayas JM, Bullock JM, and Newton AC. 2008. Creating woodland islets to reconcile ecological restoration, conservation, and agricultural land use. *Front Ecol Environ* **6**: 329–36.

Rey Benayas JM, Martins A, Nicolau JM, and Schulz JJ. 2007. Abandonment of agricultural land: an overview of drivers and consequences. *CAB Rev Perspect Agric Vet Sci Nutr Nat Resour* **2**: 1–14.

Ricketts TH. 2004. Tropical forest fragments enhance pollinator activity in nearby coffee crops. *Conserv Biol* **18**: 1262–1271.

Ripple WJ, Chapron G, López-Bao JV, *et al.* 2016. Saving the world's terrestrial megafauna. *BioScience*: biw092.
Ripple WJ, Estes JA, Beschta RL, *et al.* 2014. Status and ecological effects of the world's largest carnivores. *Science* **343**: 1241484.
Sarkar S. 1999. Wilderness preservation and biodiversity conservation—keeping divergent goals distinct. *BioScience* **49**: 405–412.
Schröter M, Rusch GM, Barton DN, *et al.* 2014. Ecosystem services and opportunity costs shift spatial priorities for conserving forest biodiversity. *PloS One* **9**: e112557.
Scott JM, Goble DD, Haines AM, *et al.* 2010. Conservation-reliant species and the future of conservation. *Conserv Lett* **3**: 91–7.
Soulé M. 2014. The "new conservation." In: Keeping the Wild. Springer.
Suding KN, Gross KL, and Houseman GR. 2004. Alternative states and positive feedbacks in restoration ecology. *Trends Ecol Evol* **19**: 46–53.
Tilman D, Balzer C, Hill J, and Befort BL. 2011. Global food demand and the sustainable intensification of agriculture. *Proc Natl Acad Sci* **108**: 20260–20264.
Tilman D, Isbell F, and Cowles JM. 2014. Biodiversity and ecosystem functioning. *Annu Rev Ecol Evol Syst* **45**: 471.
Timmermann A, Damgaard C, Strandberg MT, and Svenning J-C. 2015. Pervasive early 21st-century vegetation changes across Danish semi-natural ecosystems: more losers than winners and a shift towards competitive, tall-growing species (J Bennett, Ed). *J Appl Ecol* **52**: 21–30.
Watson JE, Dudley N, Segan DB, and Hockings M. 2014. The performance and potential of protected areas. *Nature* **515**: 67–73.
Williams P, Gibbons D, Margules C, *et al.* 1996. A comparison of richness hotspots, rarity hotspots, and complementary areas for conserving diversity of British birds. *Conserv Biol* **10**: 155–174.
Winfree R, W Fox J, Williams NM, *et al.* 2015. Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. *Ecol Lett* **18**: 626–635.

Appendix

Curriculum Vitae

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PERSONAL INFORMATION

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Address: c/o German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig
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EDUCATION/ACADEMIC EMPLOYMENT

Current position

2012-present — ***Doctoral student (under the supervision of Henrique M. Pereira)***
German Centre for Integrative Biodiversity Research (iDiv)
Martin Luther University Halle-Wittenberg (MLU), Germany
transferred in 2013 from
Centre of Environmental Biology, Faculty of Sciences of the University of Lisbon, Portugal

Previous positions

2010-2012 — ***Research Fellow***
Centre of Environmental Biology, Faculty of Sciences of the University of Lisbon, Portugal

2007-2009 — ***M.Sc. in Environmental Sciences, Policy and Management***
Central European University (CEU), Hungary, Lund University, Sweden;

2005-2007 — ***M.Sc. in Systems Ecology***
University of Bucharest, Romania

2001-2005 — ***B.Sc. in Ecology***
"Ovidius" University Constanța, Romania

Other employment

2006-2010[1] — **Counselor**
Romanian National Environmental Protection Agency

FELLOWSHIPS AND GRANTS

2012-2013 — PhD fellowship from Fundação para a Ciência e a Tecnologia, Portugal. The application included a research proposal.

[1] Includes two leaves of absence, totaling two years and 6 months, to pursue graduate studies

	The studentship was awarded for 4 years. It was suspended following my transfer to the German Centre for Integrative Biodiversity Research (iDiv), as a result of my supervisor's new position at iDiv.
2007-2009	Central European University full master scholarship for 2 years
Oct.2008 – Feb.2009	Socrates/Erasmus Mobility Program grant

ACADEMIC ACTIVITIES

Reviewing:

2016	Journal of Environmental Management
2014	Ecography, Ecosystems

Teaching:

2015	Teaching Assistant (R programming), Spatial Ecology course for the master program, taught by Prof. Henrique Pereira at Martin Luther University of Halle-Wittenberg
2012	Teaching Assistant (R programming), Theoretical Ecology course for the undergraduate program, taught by Dr. Henrique Pereira, Faculty of Sciences of the University of Lisbon, Portugal

Supervising:

September 2016	Esther Sossai (8 weeks collaboration)
June 2016	Marlen Schmid (6 weeks internship)
December 2016	Marlen Schmid (6 weeks internship)
February 2014	Max Hofmann (6 weeks internship)

Involvement in multi-party projects:

- Global Biodiversity Outlook 4 (GBO4 - A mid-term assessment of progress towards the implementation of the Strategic Plan for Biodiversity 2011-2020) - Lead author for Target 15 - Ecosystem restoration and resilience
- Land Use – BioDiversity – Ecosystem Services trade-offs (LUBDES) (supported by SESYNC, Helmholtz Centre for Environmental Research and Synthesis Centre for Biodiversity Sciences - sDiv)
- Harmonizing Global Biodiversity Modelling (HarmBio) (European Cooperation in Science and Technology – COST Action)
- Agricultural abandonment, fire and the future of biodiversity - ABAFOBIO Project PTDC/AM/73901/2006

Other activities:

2014 – 2015	PhD student representative in the yDiv board. yDiv is the graduate school of the German Centre for Integrative Biodiversity Research (iDiv).

Halle (Saale), den 12.12.2016

Silvia Ceaușu

List of publications and conference participations

Publications of the dissertation

- **Ceaușu, S.**, Hofmann, M., Navarro, L. M., Carver, S., Verburg, P. H., Pereira, H. M. 2015. Mapping opportunities and challenges for rewilding in Europe, *Conservation Biology* 29(4) 1017-1027.
- **Ceaușu, S.**, Gomes, I., Pereira, H. M. 2015. Conservation planning for biodiversity and wilderness: a real-world example, *Environmental Management* 55(5) 1168-1180.
- **Ceaușu, S.**, Carver S., Verburg P. H., Kuechly H. U., Hölker F., Brotons L., and Pereira H. M., European wilderness in a time of farmland abandonment, in Pereira H.M. and Navarro L.M. *Rewilding European Landscapes*, pp. 25–46, Springer Netherlands, 2015.
- **Ceaușu, S.**, Apaza, A., Schmidt, M., Martín-López, B., Cortés-Avizanda, A., Maes, J., Brotons, L., Queiroz, C., Pereira, H. M. *in preparation*. No ecosystem services left behind: reconnecting ecosystem services and biodiversity.

Peer-reviewed journals

- **Ceaușu S.**, Borda-de-Água L., Merckx T., Sapage M., Miranda M., Pereira H. M. *in preparation*. High-impact journals publish papers with high statistical significance.
- Beckmann M., Gerstner K., Akin-Fajiye M., **Ceaușu S.**, Kambach S., Kinlock N. L., Phillips H. R. P., Verhagen W., Gurevitch J., Klotz S., Newbold T., Verburg P. H., Winter M., Seppelt R. *submitted*. The simultaneous effects of land-use intensification on biodiversity and production: A global meta-analysis.
- Santini L., Belmaker J., Costello M. J., Pereira H. M., Rossberg A. G., Schipper A. M., **Ceaușu S.**, Dornelas M., Hilbers J., Hortal J., Huijbregts M. A. J., Navarro L. M., Katja H. Schiffers K. H., Visconti P., Rondinini C. *in press, available online*. Assessing the suitability of diversity metrics to detect biodiversity change, *Conservation Biology*.
- Seppelt R., Beckmann M., **Ceauşu S.**, Cord A. F., Gerstner K., Gurevitch J., Kambach S., Klotz S., Mendenhall C., Phillips H. R. P., Powell K., Verburg P. H., Verhagen W., Winter M., Newbold T. 2016. Harmonizing biodiversity conservation and productivity in the context of increasing demands on landscapes, *BioScience,* biw004.

Book chapters and technical reports

- Pereira H. M., Navarro L. M., **Ceaușu S.**, Gonçalves B., Marques A. and ten Brink B., Target 15: ecosystem restoration and resilience, in Leadley, P.W., Krug, C.B., Alkemade, R., Pereira, H.M., Sumaila U.R., Walpole, M., Marques, A., Newbold, T., Teh, L.S.L, van Kolck, J., Bellard, C., Januchowski-Hartley, S.R. and Mumby, P.J. *Progress towards the Aichi Biodiversity Targets: An Assessment of Biodiversity Trends, Policy Scenarios and Key Actions*, Secretariat of the Convention on Biological Diversity, Montreal, Canada, 2014.
- Bhave A., **Ceaușu S.**, Deshmukh A., Jewell J., Pan W., Timm J., Vision statement for the planet in 2050, in Costanza R. and Kubiszewski I. (ed.) *Creating a Sustainable and Desirable Future: Insights from 45 Global Thought Leaders*, World Scientific Publishing Company, pp. 51-53, 2014.

- **Ceaușu S.**, Steger T., Environmental issues in the animated TV series: South Park, The Simpsons, and The Family Guy, in Drummond P. (ed.) *The London Film and Media Reader 1: Essays from FILM AND MEDIA 2011, the First Annual London Film and Media Conference*, The London Symposium, United Kingdom, pp. 87-97, 2013.

Talks and posters in international conferences (selection)

- 2016 - **iDiv conference**, Leipzig, Germany - No ecosystem services left behind: reconnecting ecosystem services and biodiversity (talk)
- 2016 - **GEO BON Open Science Conference & All Hands Meeting**, Leipzig, Germany - No ecosystem services left behind: reconnecting ecosystem services and biodiversity (talk)
- 2015 - **27th International Congress for Conservation Biology, 4th European Congress for Conservation Biology**, Montpellier, France - Mapping opportunities and challenges for rewilding in Europe (talk)
- 2013 - **University of Cambridge, Student Conference on Conservation Science 2013**, Cambridge, UK - Conserving the wild and the tamed: a comparison of reactive and proactive approaches in Peneda-Gerês National Park, Portugal (poster)
- 2012 - **3rd European Congress of Conservation Biology**, Glasgow, UK - The wilder the better in biodiversity conservation? Comparison of three biodiversity prioritization approaches in Peneda-Gerês National Park, Portugal (talk).
- 2011 - **IALE World Congress: Landscape Ecology for Sustainable Environment and Culture**, Beijing, China - The wilder the better in nature conservation? Comparing two prioritization approaches in Peneda-Gerês National Park, Portugal (talk)

Authors' contributions

Chapter 2

Ceaușu, S., Gomes, I., Pereira, H. M. 2015. Conservation planning for biodiversity and wilderness: a real-world example, *Environmental Management* 55(5) 1168-1180.

Analysis: Ceaușu, S. (60%), Gomes, I. (30%), Pereira, H. M. (10%)

Writing: Ceaușu, S. (90%), Pereira, H. M. (10%), Gomes, I. (corrections)

Chapter 3

Ceaușu, S., Carver S., Verburg P. H., Kuechly H. U., Hölker F., Brotons L., and Pereira H. M., European wilderness in a time of farmland abandonment, in Pereira H.M. and Navarro L.M. *Rewilding European Landscapes*, pp. 25–46, Springer Netherlands, 2015.

Analysis: Ceaușu, S. (90%), Pereira H. M. (10%), Carver S., Verburg P. H., Brotons L. (data contributions)

Writing: Ceaușu, S. (90%), Pereira H. M. (10%), Carver S., Verburg P. H., Kuechly H. U., Hölker F., Brotons L. (corrections)

Chapter 4

Ceaușu, S., Hofmann, M., Navarro, L. M., Carver, S., Verburg, P. H., Pereira, H. M. 2015. Mapping opportunities and challenges for rewilding in Europe, *Conservation Biology* 29(4) 1017-1027.

Analysis: Ceaușu, S. (40%), Hofmann, M. (40%), Navarro, L. M.(10%), Pereira H. M. (10%), Carver S., Verburg P. H (data contributions)

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Chapter 5

Ceaușu, S., Apaza, A., Schmidt, M., Martín-López, B., Cortés-Avizanda, A., Maes, J., Brotons, L., Queiroz, C., Pereira, H. M. No ecosystem services left behind: reconnecting ecosystem services and biodiversity. Manuscript

Data collection: Ceaușu, S. (30%), Apaza, A.(30%), Schmidt, M.(20%), Martín-López, B. (10%), Cortés-Avizanda, A. (10%)

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Halle (Saale), 12.12.2016

Silvia Ceaușu

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Eigenständigkeitserklärung

Hiermit erkläre ich, dass die Arbeit mit dem Titel „Conserving species and wilderness to achieve the Aichi Biodiversity Targets“ bisher weder bei der Naturwissenschaftlichen Fakultät I Biowissenschaften der Martin-Luther-Universität Halle-Wittenberg noch einer anderen wissenschaftlichen Einrichtung zum Zweck der Promotion vorgelegt wurde.
Ferner erkläre ich, dass ich die vorliegende Arbeit selbstständig und ohne fremde Hilfe verfasst sowie keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe. Die den Werken wörtlich oder inhaltlich entnommenen Stellen wurden als solche von mir kenntlich gemacht.
Ich erkläre weiterhin, dass ich mich bisher noch nie um einen Doktorgrad beworben habe.

Halle (Saale), den 12.12.2016

Silvia Ceaușu