



Multifunctionality and biodiversity: Ecosystem services in temperate rainforests of the Pacific Northwest, USA



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ARTICLE INFO

Article history:

Received 1 August 2013

Received in revised form 30 October 2013

Accepted 2 December 2013

Available online xxxx

Keywords:

Biodiversity conservation

Ecosystem management

Ecosystem service diversity

Multifunctional ecosystems

Temperate rainforests

ABSTRACT

Forests produce a myriad of ecosystem related benefits known as ecosystem services. Maximizing the provision of single goods may lead to the overexploitation of ecosystems that negatively affects biodiversity and causes ecosystem degradation. We analyzed the temperate rainforest region of the Pacific Northwest, which offers a multitude of ecosystem services and harbors unique biodiversity, to investigate linkages and trade-offs between ecosystem services and biodiversity. We mapped nine actual and potential ecosystem services, grouped into provision, supporting, regulating and cultural ecosystem service categories, as well as species richness of four taxonomic groups (mammals, birds, trees, and amphibians). We analyzed linkages and tradeoffs between ecosystem services, their overall diversity, and species richness as well as different levels of taxon diversity. We also tested if ecosystem service categories, in addition to climate and land cover parameters, could indicate species richness. We found significant positive linkages between ecosystem service diversity and species richness of all considered taxa. The provision of the majority of ecosystem services was higher in areas of high taxon diversity, indicating both positive relationships and slight trade-offs in maximizing single ecosystem services. In general, ecosystem service categories were a comparable indicator of species richness as climate. Our findings show that multifunctionality largely coincides with high levels of biodiversity within the study region. Hence, an integrative ecosystem management approach that incorporates ecosystem services and biodiversity concerns is needed to both provide diverse ecosystem benefits and conserve biological diversity.

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1. Introduction

Ecosystem services and biodiversity conservation have become the two dominant, and potentially conflicting (Bullock et al., 2011; Marrs et al., 2007; McShane et al., 2011) management aims in conservation science during the last decades. Ecosystem services are the numerous benefits people directly or indirectly appropriate from the functioning of ecological systems and provide the foundations for human well-being (Daily, 1997; Nelson et al., 2009). The ecosystem services concept combines resource use, ecosystem management – including adaptation to impacts of driving forces such as land use and climate change – and the valuation of nature (Maskell et al., 2013), making it a key concept that bridges social and ecological systems (Carpenter et al., 2009). Biodiversity is vital for maintaining ecosystem processes and functioning (Duffy, 2009; Hector and Bagchi, 2007). Its loss has been shown to cause ecosystem degradation (Hooper et al., 2012). Hence, biodiversity

is seen as essential requirement for the provisioning of ecosystem services (Diaz et al., 2006). Here it should be noted that as well as an instrumental value related to the provision of ecosystem services, the conservation of biodiversity is also a normative goal in its own right (Mace et al., 2012). Biodiversity conservation is therefore not solely contingent on the instrumental contribution to human well-being it may provide.

The increasing number of studies on the functional relationships between biodiversity and ecosystem services reveal mostly positive patterns (Gamfeldt et al., 2013; Hector and Bagchi, 2007; Maskell et al., 2013). However, many of these diversity-ecosystem services studies focus on a single facet of diversity such as one species group and a single ecosystem service, such as primary productivity (Costanza et al., 2007), pest control (Simon et al., 2010) or agricultural yields (Di Falco and Chavas, 2006). Managing an ecosystem for a single ecosystem service is potentially problematic as it may result in trade-offs in terms of associated biodiversity (Ingram et al., 2012; Ridder, 2008; Rodriguez et al., 2006) and thereby compromises conservation efforts. The interplay between the provision of multiple ecosystem services and biodiversity

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represents an important knowledge gap (Geijzendorffer and Roche, 2013; Sircely and Naem, 2012), potentially limiting our ability to effectively manage multifunctional landscapes for both ecosystem services provision and biodiversity conservation.

In this regard, it becomes vital to analyze ecosystems that are managed for diverse societal needs. Multifunctional ecosystems offer several services simultaneously to satisfy social, cultural, economic and environmental demands (O'Farrell et al., 2010). Hence, a diverse set of ecosystem services needs to be considered when assessing the relations between biodiversity conservation and ecosystem service provision in multifunctional ecosystems (Chan et al., 2006; Tallis and Polasky, 2009). This includes services that cannot be straightforwardly linked to specific ecosystem functions such as cultural services (Hernandez-Morcillo et al., 2013). Potential synergies between ecosystem services and biodiversity are expected, though they might vary across ecosystems and depend on the specific ecosystem services and aspects of biodiversity taken into consideration (Mace et al., 2012).

Forests are of immense global importance in delivering a myriad of benefits to humanity (Bonan, 2008; FAO, 2010; Schwenk et al., 2012). In particular, temperate rainforests represent an ecologically complex, unique ecosystem with high biodiversity importance, subjected to multiple human demands. We analyzed a region along the Pacific coastline of North America harboring the world's largest remaining extents of temperate rainforests (DellaSala, 2011). While currently offering a broad range of goods and services such as salmon (*Oncorhynchus* spp.), timber, water regulation and recreation, these rainforests are threatened by climate and land use changes (DellaSala, 2011; Fitzgerald et al., 2011).

We addressed three key questions to investigate linkages and trade-offs between ecosystem services and biodiversity across the temperate rainforest region of the Pacific Northwest: (1) How is ecosystem service diversity related to species richness across different taxonomic groups? (2) How are ecosystem services and their diversity linked to different diversity levels of the considered taxa? (3) In order to untangle the interrelations among the environment, ecosystem services and species richness we tested if the provision of ecosystem services, grouped by the millennium ecosystem service assessment (MA) categories, alongside environmental variables such as climate and land cover, indicate species richness. Here, we did not seek to explain the functional relations between biodiversity and ecosystem services categories. Rather, we described the patterns (Shmueli, 2010) between the types of ecosystem services provided, their diversity and biodiversity across the temperate rainforest region of the Pacific Northwest and discussed the implications of these patterns for multifunctional landscape management and conservation at a regional scale.

Recent studies focusing on the relationship between ecosystem services and biodiversity have taken a functional perspective and mostly considered limited ecosystem service categories such as provisioning or regulating services (e.g. Balvanera et al., 2006; Costanza et al., 2007; Schwenk et al., 2012) and single species groups such as plant species (e.g. Gamfeldt et al., 2013; Maskell et al., 2013; Tilman et al., 2012). By involving multiple taxa and multiple ecosystem services including supporting and cultural services, we aim to identify more comprehensive patterns relating ecosystem services to biodiversity.

Here we note that the direct quantification of ecosystem services is often problematic and that there might be considerable differences between the ecosystem services that potentially flow from a given ecosystem and the actual services that are appropriated at a given point in time. For example, timber harvest is an indicator for the appropriation of timber but provides limited information regarding the capacity of a given system to sustainably provide timber. Similarly it can be argued that benefits received

(i.e. the direct quantification of services) from physically appropriated goods such as timber must be related to how those physical goods contribute to human well-being (Fischer et al., 2009). Given the importance of both the actual appropriation and the potential capacity to supply ecosystem services and the difficulty in directly and accurately quantifying multiple ecosystem services across large spatial and temporal extents, we focus on the mapping of proxy datasets that indicate nine important potential and actual ecosystem services within the temperate rainforest region of the Pacific Northwest. The following proxy data for ecosystem services were modeled: timber harvest, salmon abundance, deer hunting, net primary productivity, carbon storage in vegetation, organic matter in soil, forest importance for drinking water supply, landscape aesthetics, and park visitation. These proxies for ecosystem services were grouped into the MA categories of provision, supporting, regulating, and cultural ecosystem services (MA, 2005). Biodiversity was quantified in terms of spatially explicit species richness data for higher taxa, including mammals, birds, trees and amphibians. Diversity metrics were derived for ecosystem services and the higher taxa. Subsequently, we computed univariate models to reveal the patterns between ecosystem service diversity and species richness. Potential and actual ecosystem services and their diversity were linked to the higher taxon diversity. Multivariate direct gradient analyses were performed to assess if the MA ecosystem service categories are able to indicate species richness in interaction with and untangled from environmental variables such as climate and land cover.

2. Materials and methods

2.1. Study area

The study area was based on the original coastal temperate rainforest extent of the Pacific Northwest region (DellaSala, 2011) that shows an overall high proportion of forest coverage. All US counties that intersect the original coastal rainforest extent, including a buffer of 15 km, were incorporated into the study area of 325,614 km². This broad extent was chosen to ensure that climate and land cover gradients are well represented. Due to limited data availability, coastal rainforest regions located in British Columbia and Alaska were excluded from our analyses. All metrics related to species richness, ecosystem services and environmental data were mapped at a resolution of approximately 8 × 8 km – 3997 grid cells in total. It is important to note that the study extent, while dominated by forests, encompasses a spatially heterogeneous matrix of different land uses that in turn create spatially heterogeneous patterns of ecosystem service provision and biodiversity. The study extent comprised 55% forest, 33% scrub and grassland, 7% cultivated areas and 5% developed/urban regions. Public lands in this region are managed under the Northwest Forest Plan that governs ecosystem management and biodiversity conservation (DellaSala and Williams, 2006). However, non-federal landowners frequently focus on timber management as the primary ecosystem service. ARCGIS 10.1 was used for all geo-processing work.

2.2. Ecosystem service data

The proxy data used refer either to the actual goods or services people appropriate from nature, known as 'ecosystem services', or to the capacity of the ecosystem to deliver those goods and services to society, conceptualized here as 'potential ecosystem services' (Vira and Adams, 2009). The data were based on physical occurrence of actual and potential ecosystem services, rather than the monetary or non-monetary values associated with those services.

All data were gathered from publically available datasets, further processed and linked to spatial data or were readily available in a spatially explicit format. We compiled GIS-layers indicating the nine potential and actual ecosystem services, which were also grouped into MA categories – i.e. provisioning, regulating, supporting, and cultural ecosystem services (MA, 2005). Detailed descriptions of the datasets and data sources can be found in the online appendix (Online appendix, Table A1).

2.2.1. Provisioning services

2.2.1.1. Timber harvest. Timber is one of the most prominent resources derived from forest ecosystems and has been intensively harvested from temperate rainforests in this region. This layer depicts the total volume of timber harvested in 2010 measured in thousands of board feet. Derived tabular data are based on the county level.

2.2.1.2. Salmon abundance. Salmon are an important economic and food resource for the entire coastal rainforest region in North America and they are the key for trophic dynamics and energy transfer (DellaSala, 2011). The salmon abundance data are based on observed (1998–2005) and modeled data at the watershed level (Pinsky et al., 2009). Watershed based data were normalized and then converted into gridded data.

2.2.1.3. Deer hunting. Hunting has been taking place for millennia across the coastal temperate rainforest region of North America (Schoonmaker et al., 1997). Hence, hunting can be considered as a traditional source of local food resources. This layer indicates overall deer hunting successes for 2010 measured in counted deer kills. Census data are obtained and mapped based on hunting management units defined by State Departments of Fish & Wildlife.

2.2.2. Supporting services

2.2.2.1. Net primary productivity. The Pacific coastal rainforests belong to the most productive ecosystems worldwide (DellaSala, 2011), and primary productivity is a key ecological function from which many other, directly used, ecosystem services flow. Gridded information on NPP is derived from NASA's MODIS satellite data in a 10 km² grid cell resolution based on monthly values averaged for 2010 in gC m⁻² day⁻¹.

2.2.3. Regulating services

2.2.3.1. Carbon storage in vegetation. The storage of atmospheric carbon in biomass is essential to climate regulation and climate change mitigation. The coastal temperate rainforests in North America show high carbon densities compared to other forest ecosystems (DellaSala, 2011; Woodbury et al., 2007). Gridded data show total mean carbon content in vegetation for 1961–1990 and originate from outputs of the MC1 dynamic vegetation model (Bachelet et al., 2001a,b) in an 8.8 km² grid cell resolution.

2.2.3.2. Organic matter in soil. Organic matter strongly influences soil properties such as water retention, erodibility and fertility (Ontl and Schulte, 2012). Furthermore, soil represents a large carbon pool. The sequestration of atmospheric carbon in soil organic matter contributes to climate change mitigation (Lal, 2004). The data used indicates the total content of organic matter in soil expressed as percent by weight of the 2 mm soil fraction at the watershed level.

2.2.3.3. Forest importance for drinking water supply. Forests are known to serve as important regulators of drinking water, particularly in this region (DellaSala et al., 2011). This layer combines precipitation intensity, proportion of forests and population density per watershed and was derived from the USDA 'forests to faucets'

dataset (Barnes et al., 2009). We used these data as proxy for water regulation (Todd and Weidner, 2010).

2.2.4. Cultural services

2.2.4.1. Landscape aesthetics. The possibility to experience landscapes that are largely undisturbed by human pressure is usually accepted as a great benefit that ecological systems may offer in terms of recreation (Gobster et al., 2007). The compiled dataset consists of several spatial layers related to infrastructure such as roads, railroads and settlements, and natural elements such as lakes, rivers and forests that are undisturbed by human influences. All layers were weighted according to their naturalness. Terrain roughness was incorporated as proxy for physical landscape heterogeneity. Each layer was weighted either positively or negatively except for terrain roughness that was weighted based on three states, low roughness as negative, medium roughness as neutral and high roughness as positive. The resulted 'landscape aesthetics' layer is considered as a potential ecosystem service since the quantification of the actual cultural values associated with the landscapes of the study region was beyond the scope of our analysis.

2.2.4.2. Park visitation. State and national parks represent essential recreation areas in the US (Daniel et al., 2012), facilitating environmental education and sustainable tourism. We mapped the tabular park visitation data for 2010 on state and national parks, derived from the PAD-US protected area database (v. 1.2). Subsequently spatial data were aggregated on county level since most of the state parks do not match the working resolution and hence would not have been visible for the analyses. We used this dataset as proxy for the provision of space for recreation and cultural experiences.

All data based on unequally sized areas were normalized based on area. Thus, every layer refers to equal area units. For further analyses all potential and actual ecosystem service layers were transformed to a standardized scale based on their maximum values (Raudsepp-Hearne et al., 2010). Hence, all ecosystem service values range between 0 and 1.

2.3. Species data

Spatially explicit species richness data for higher taxa, including mammals (between 1 and 85 species recorded), birds (88–223 species), trees (1–50 species) and amphibians (2–38 species) were obtained as gridded layer from several resources (Online appendix, Table A2). For tree species, we compiled a richness layer through aggregating range polygon data (Little, 1978). Selected species groups represent major parts of the overall species diversity that exists across the Pacific coastal temperate rainforests and contain numerous species of economic, cultural and conservation importance. Reptiles, as a further terrestrial vertebrate group, were not included into the analyses since they are not well represented, nor particularly abundant, across the Pacific coastal temperate rainforests compared to other regions of their occurrence (Böhm et al., 2013).

2.4. Applied statistical approaches

All statistical analyses were undertaken using R 2.15, including the packages 'raster' (v. 2.1.12) for handling spatial data, 'car' (v. 2.0.16) for building generalized linear models (GLMs), 'spdep' (v. 0.5.56) for correcting autocorrelation patterns, 'vegan' (v. 2.0.6) to obtain diversity indices and to perform principal component analyses (PCAs) as well as redundancy analyses (RDAs).

2.4.1. Simpson diversity metrics

Diversity metrics were derived by using the Simpson diversity index for potential and actual ecosystem services (Raudsepp-Hearne et al., 2010) and higher taxa ranging between 0 (low diversity) and 1 (high diversity). The Simpson index is illustrated by the following formula:

$$D = 1 - \sum_{i=1}^R p_i^2$$

R is the richness of taxa/ecosystem services and p_i is the proportion of abundances for the i th taxon/ecosystem service.

The Simpson diversity measure takes abundances into account and equals the probability that two entities taken at random from the dataset represent the same type (Simpson, 1949). The Simpson diversity of higher taxonomic groups was used as biodiversity metric that is comparable to the Simpson diversity of ecosystem services. A color map was compiled illustrating the degree of spatial correspondence between the diversity metrics across the study area.

2.4.2. Univariate linkage modeling: ecosystem service diversity – species richness

In order to model the relationship between ecosystem service diversity and species richness, we chose a univariate model approach using GLMs (Crawley, 2007). Due to the non-normalized distribution of model residuals, we opted for GLMs with Poisson error structure. Species richness data were selected as dependent variables and ecosystem service diversity as independent variable since Poisson-GLMs require real count data. Hence, we follow a descriptive approach rather than explaining the causal relationship between biodiversity and ecosystem services. GLMs also included quadratic terms and were reduced based on the Akaike information criterion (AIC), to avoid overfitting (Sakamoto et al., 1986). Since model residuals revealed patterns of spatial autocorrelation, we applied spatial eigenvector filtering to incorporate spatial autocorrelation structures (Dray et al., 2006; Griffith and Peres-Neto, 2006). Spatial eigenvectors are derived from a neighborhood matrix spanning a distance of 100 km, which was chosen due to highest spatial autocorrelation values within that distance. The number of incorporated spatial eigenvectors was based on Moran's I significance values for each GLM. Eigenvectors were included until they exceeded a significant Moran's I value ($p < 0.05$).

2.4.3. Ordination techniques: ecosystem service categories, land cover and climate – species richness

A multivariate direct gradient analysis was applied to investigate the proportion of species richness variances captured by potential as well as actual ecosystem services grouped into the MA categories and environmental variables. Initial analyses of data distribution and gradient lengths showed that linear models are a correct general assumption for our data. Hence we used a PCA to reduce multicollinearity inherent to the climatic parameters applied and a partially constrained RDA as overall multivariate model (Legendre and Legendre, 2012) to partition the explained variance of four different variable groups, such as potential and actual ecosystem services for each MA category, 'climate', 'land cover' and 'geography'. Species richness data from the considered taxonomic groups served as response variables and were subjected to Hellinger transformations as proposed for analyzing heterogeneous community datasets (Legendre and Gallagher, 2001). Climatic data were derived by performing a PCA, including 19 BIOCLIM variables that were obtained as downscaled spatial grids in a 2.5 arc-min resolution (Hijmans et al., 2005). The PCA scores from the first two principal components were extracted and subsequently used as 'climate' variable group for the RDAs (Hanspach et al., 2011). Land cover data were derived from the USGS land use survey 2006 comprising 16 land cover classes, including developed, forested, cultivated, wetland, herbaceous, scrubland and barren land cover types at a grid cell resolution of 30 meters. The original dataset was spatially downscaled to match the working resolution. To account for spatial autocorrelation effects, we defined latitude and longitude as a further variable group named 'geography'.

3. Results

3.1. Ecosystem service diversity and species richness

The compiled spatial layers of potential as well as actual ecosystem services, the derived Simpson diversity metrics of the considered taxa and ecosystem services varied across the study area (Fig. 1). The diversity of taxa and the diversity of ecosystem services were highly correlated, indicated by Spearman's $\rho = 0.719$ ($p < 0.001$). Species richness maps for mammals, birds, trees and amphibians are shown in online appendix (Fig. A1).

Ecosystem service diversity showed significant positive interactions with the richness of mammal, bird, tree, and amphibian

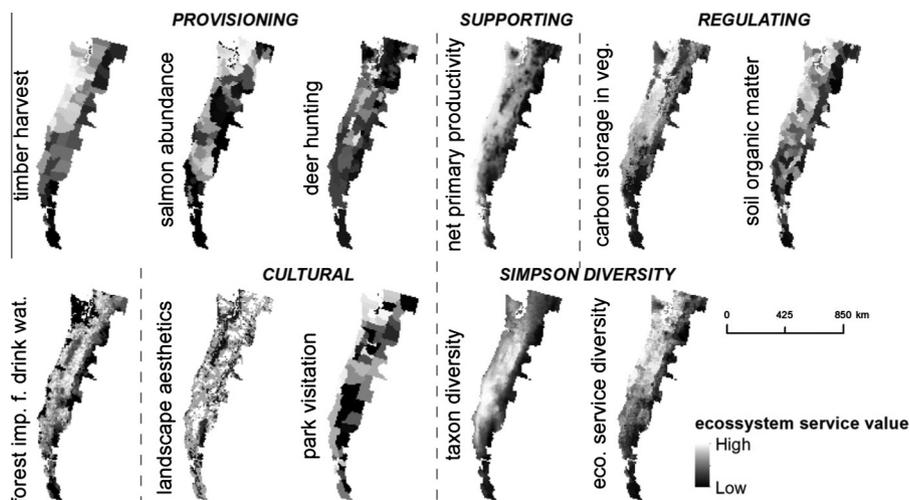


Fig. 1. Spatial distribution of nine potential and actual ecosystem services as well as the Simpson diversity of considered taxa and ecosystem services across the coastal temperate rainforest region of the Pacific Northwest, USA.

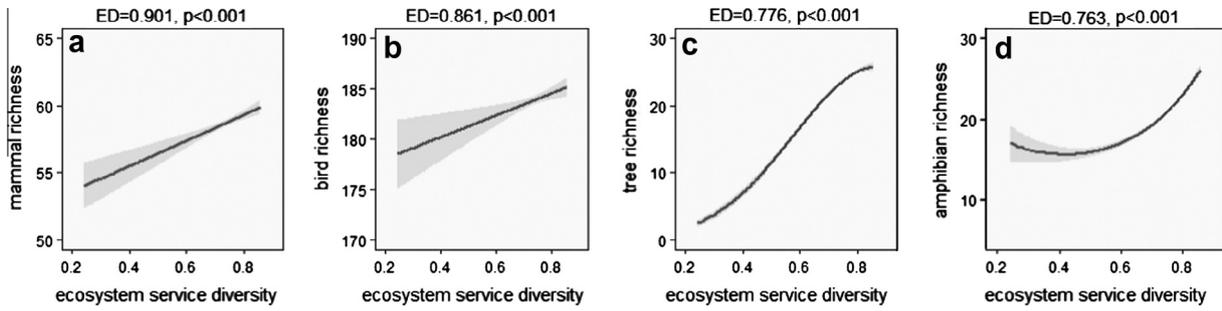


Fig. 2. GLM results for linkages between ecosystem service diversity and mammal, bird, tree, and amphibian richness. Incorporated spatial eigenvectors were kept at mean level. Light gray areas indicate the 95% confidence intervals of prediction errors (ED = explained deviance).

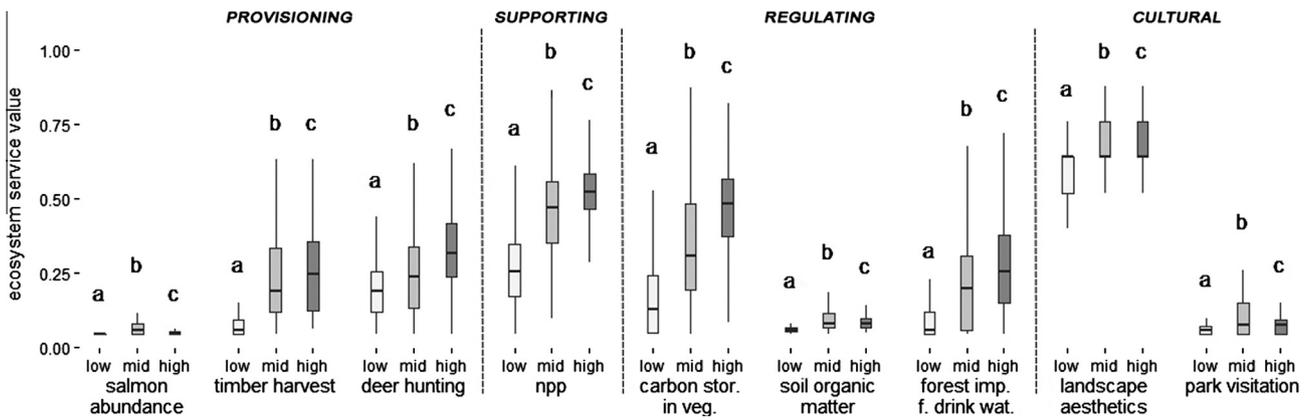


Fig. 3. Potential and actual ecosystem services for three levels of overall Simpson diversity of considered taxa (low = 0.335–0.514, mid = 0.514–0.573, high = 0.573–0.634). Grouping maintained equal sample sizes within each level. A Wilcoxon rank sum test was performed to assess the mean differences between Simpson diversity levels ($p < 0.001$). P -values were Bonferroni corrected to account for multiple testing.

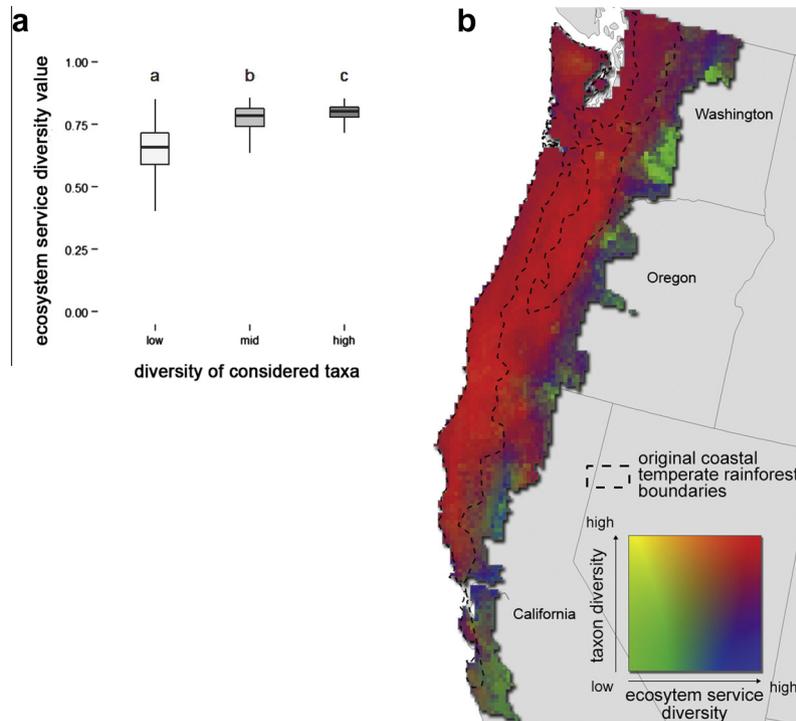


Fig. 4. (a) Ecosystem service diversity for three levels of overall Simpson diversity of the four considered taxonomic groups (low = 0.335–0.514, mid = 0.514–0.573, high = 0.573–0.634). Grouping maintained equal sample sizes within each level. A Wilcoxon rank sum test was performed to assess the mean differences between Simpson diversity levels ($p < 0.001$). P -values were Bonferroni corrected to account for multiple testing. (b) Spatial correspondence between ecosystem service diversity and diversity of four considered taxa. Mapped pixel colors were assigned based on a RGB color space defined by ecosystem service diversity on the x-axis and diversity of four considered taxa on the y-axis.

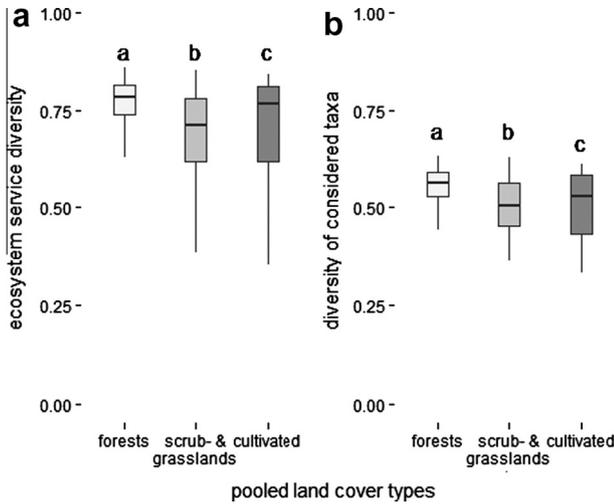


Fig. 5. Ecosystem service diversity (a) and diversity of considered taxa (b) for three pooled land cover types: forests, scrub- and grasslands, and cultivated areas. Developed land cover types were excluded due to minor relevance for the provisioning of analyzed ecosystem services.

species (Fig. 2, $p < 0.001$). Mammal and bird species richness increased linearly with higher ecosystem service diversity (Fig. 2a and b), tree richness showed a sigmoidal relationship indicating a saturation effect of tree species richness at the highest levels of ecosystem service diversity (Fig. 2c). Amphibian richness increased steeply with elevated ecosystem service diversity (Fig. 2d). The GLM on mammal richness had the highest model fit expressed as explained deviance (ED = 0.901), the model that considered amphibian richness the lowest (ED = 0.763).

3.2. Ecosystem services and taxon diversity

Higher values of ecosystem services were related to higher levels of the overall Simpson taxon diversity for most of the applied potential and actual ecosystem services across all MA categories (Fig. 3). However, salmon abundance, soil organic matter and park visitation differed from that pattern, indicating trade-offs between maxima of single ecosystem services and diversity of involved taxa. No pronounced ecosystem service gradient could be detected based on a PCA, including all modeled ecosystem services (not shown). The first two PCA axes together explained 46% of the overall variance.

Higher ecosystem service diversity was significantly linked to elevated taxon diversity (Fig. 4a, $p < 0.001$). However, less pronounced differences between medium and high levels of taxon diversity suggested a nonlinear relationship resulting in a saturation effect for ecosystem service diversity in areas of high taxon diversity. High spatial correspondence between ecosystem service diversity and the diversity of included taxa was shown within coastal temperate rainforest regions throughout most of the Pacific Northwest (Fig. 4b).

3.3. Ecosystem service categories as indicators for species richness

To assess both the distribution of ecosystem service diversity and the diversity of higher taxa for major land cover types, we pooled the detailed land cover types into three groups, namely, ‘forests’, ‘scrub- and grasslands’, and ‘cultivated areas’. Highest diversity values for ecosystem services as well as considered taxa were significantly higher for forests (Fig. 5a and b, $p < 0.05$). Groups differed significantly as assessed through a one-way analysis of

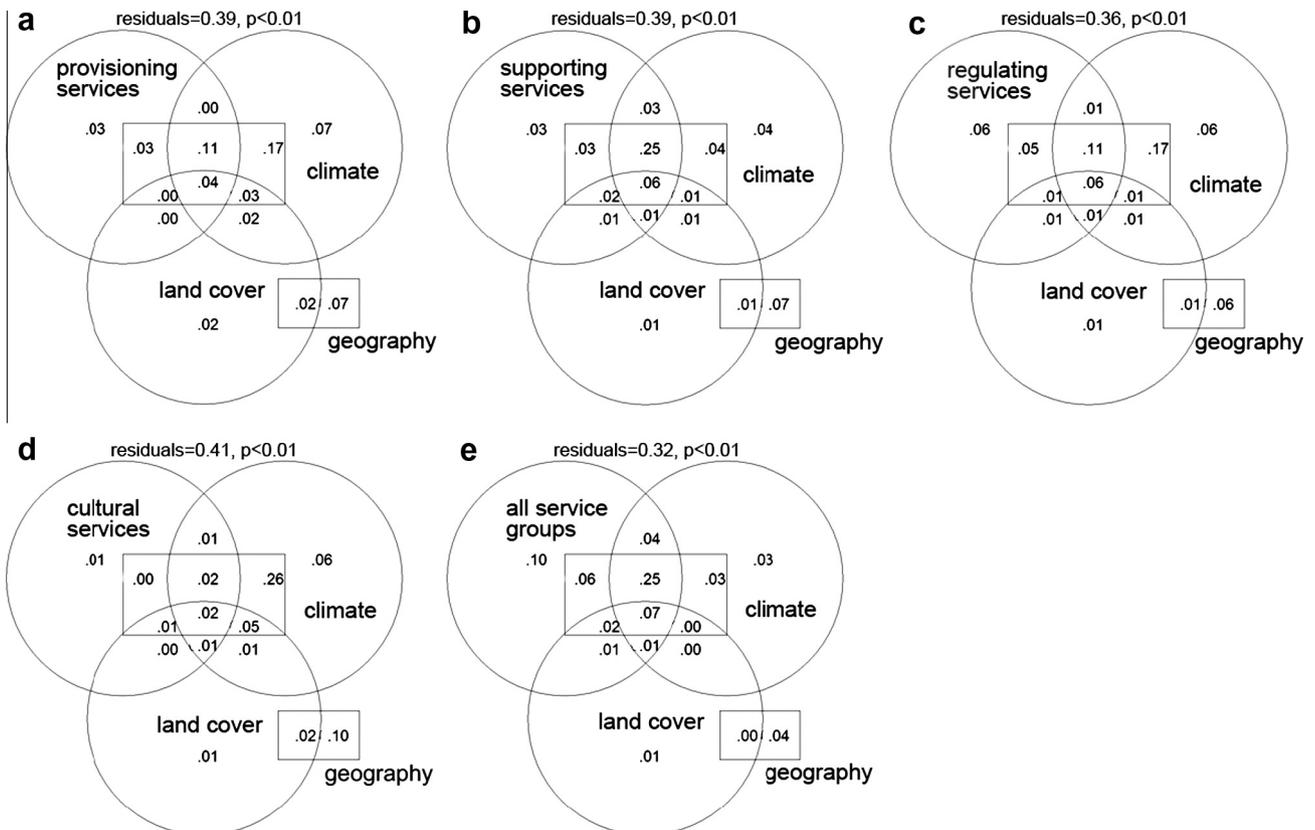


Fig. 6. RDA variance partitioning results for species richness including mammals, birds, trees and amphibians separately indicated by different ecosystem service categories: (a) provisioning, (b) supporting, (c) regulating, (d) cultural and (e) all potential and actual ecosystem services, climate, land cover (circles) and geography (rectangle). Displayed values show captured variances as adjusted R^2 for all single (non-overlapping parts of circles and the rectangle) and combined effects (overlapping parts of circles and the rectangle).

variance and a subsequent paired *t*-test ($p < 0.05$). *P*-values were Bonferroni corrected to account for multiple testing.

Constrained RDAs revealed that ecosystem service categories significantly indicated species richness in a comparable magnitude of land cover and climate (Fig. 6, $p < 0.001$). Among the RDAs that were fitted with single ecosystem service categories, the RDA with regulating services showed the lowest model error (Fig. 6c, residuals = 0.36) and the one that included cultural services the highest error (Fig. 6d, residuals = 0.41). The RDA incorporating the entire set of potential and actual ecosystem services as variable group showed the lowest model error among all RDAs (Fig. 6e, residuals = 0.32). However, for the majority of RDAs the climatic space was, after geography, the variable group that captured most of the species richness variances. This reflected both the prevailing climatic gradient that shapes diversity patterns across the temperate rainforests of the Pacific Northwest and an inherent autocorrelation pattern. Focusing on interactions between variable groups the climate-geography interactions showed the strongest effects followed by the ecosystem service category–climate interactions.

4. Discussion

4.1. Ecosystem service diversity and species richness

We found broad, positive relationships between ecosystem service diversity and species richness. Such a pattern confirms the findings of Egoh et al. (2009) who illustrated a spatial congruency between ecosystem services and biological diversity in South Africa. No trade-offs were observed in our study between ecosystem service diversity and species richness. Other studies reported both trade-offs and concordances between ecosystem service hotspots and biodiversity or its conservation (Chan et al., 2006; Turner et al., 2007). Our results clearly show that high levels of biodiversity are found in areas that provide diverse actual and potential ecosystem services across the coastal temperate rainforest region of the Pacific Northwest. This pattern was also apparent when all considered taxa were combined to one diversity index, particularly within the original coastal temperate rainforest boundaries. Though, some minor areas showed a contrasting pattern of low biodiversity but high ecosystem service diversity. These scattered areas were mostly distributed at the inland edges of our study region indicating transition zones to other ecosystems that might start to harbor different species inventories not included in our study.

Saturation effects were revealed for tree species and overall taxon diversity suggesting that further ecosystem service increases in regions of highly diverse ecosystem service provision coincide with marginally higher biodiversity levels. This might relate to redundancies of present species in terms of the necessary ecosystem functions that are required to maintain considered ecosystem services (Duffy, 2009; Hector and Bagchi, 2007). Notwithstanding, including more services and thus more ecosystem functions would probably incorporate more biodiversity needed to sustain these functions (Gamfeldt et al., 2008). Moreover, biodiversity reduces the vulnerability of ecosystems to disturbances, serving both as a backup for functional degradation and to ensure diverse and fast responses to perturbations hence improving overall ecosystem resilience (Mori et al., 2013).

4.2. Ecosystem services and their diversity for different levels of taxon diversity

The majority of our results indicate positive relationships between single ecosystem services included and the overall diversity of the considered taxa. Similar patterns are found in recent studies (Balvanera et al., 2006; Schneiders et al., 2012), in particular for

productivity and biodiversity (Gamfeldt et al., 2013; Tilman et al., 2012) – though Costanza et al. (2007) found a temperature dependent relationship. The relation between timber harvest and taxon diversity was most surprising and probably, in part, resulted from a scale artifact inherent to the data used. It is important to note here that the established relationships do not imply causality. Yet, intense forest management is usually considered to have negative impacts on biodiversity (Bengtsson et al., 2000). The data used in our study did not include any information on how the forests are managed for timber harvest on a local scale. Hence, it is beyond the scope of our analyses to assess the effects of forest practices on biodiversity patterns.

Despite the largely positive patterns found, a few trade-offs were noticeable in our results. Salmon abundance, soil organic matter and park visitation were highest in areas with moderate levels of taxon diversity. Non-supporting patterns or trade-offs among ecosystem services are postulated (Bennett et al., 2009) and reported on a regional (Raudsepp-Hearne et al., 2010), continental (Haines-Young et al., 2012) and global scale (Naidoo et al., 2008). Though, in our case, no clear trade-offs among the studied ecosystem services could be detected.

4.3. Ecosystem service categories as indicators for species richness

Both, ecosystem service diversity and taxon diversity were highest in forested extents within the study region. Although the differences among land cover types were only marginal, it suggests that forests provide conditions most suited for supplying ecosystem services and biodiversity.

Using a multivariate approach, including the nine actual and potential ecosystem services grouped into MA categories as well as environmental variables showed that the different MA ecosystem service categories indicated species richness of the four different taxa in a comparable magnitude to climate and land cover. The capability of all ecosystem service categories, in interaction with climate, to indicate species richness illustrates that a management focusing on multiple ecosystem-based benefits and the current climatic conditions are synergistic for both ecosystem services and biodiversity. These findings support the idea that the ecosystem service approach could be used to monitor and manage biodiversity (Egoh et al., 2009). However, cultural services showed an overall weak link, probably due to the most indirect relationship to richness for instance compared to the considered regulating ecosystem services. Nevertheless, the management of ecosystems based on providing a diversity of ecosystem services might have co-benefits in terms of biodiversity conservation.

4.4. Ecosystem service approach and multifunctional ecosystems

Temperate rainforests of the Pacific Northwest simultaneously offer a multitude of ecosystem-based benefits. We were able to show that such a multifunctional ecosystem might serve as indicator of biodiversity and its conservation while delivering important goods and services to society. Our results are restricted to one region and spatial scale as well as one point in time. Thus, extrapolating these results to other regions featuring different ecosystem properties and species should be done with considerable caution. However, high biodiversity levels in multifunctional landscapes also have been shown before for areas with heterogeneous land use or agricultural regions (O'Farrell et al., 2010; Schneiders et al., 2012; Sircely and Naem, 2012). Managing for multiple ecosystem services may also create conditions for higher levels of biodiversity. Given the co-occurrence of biodiversity and diverse ecosystem service provision, we suggest that biodiversity conservation should be integrated into the management of

multifunctional ecosystems and not only take place in areas explicitly designated for conservation.

4.5. Threats to ecosystem services and biodiversity: land use and climate change

North America's temperate rainforests are fragmented by logging, road building, and other human disturbances (DellaSala, 2011). Coinciding biodiversity loss and the degradation of ecosystem functions are expected due to habitat fragmentation and increasing land use intensity (Foley et al., 2005). However, sustainable trajectories of land use changes and restoration efforts have been positively linked to ecosystem service provision and biodiversity conservation (Nelson et al., 2009; Rey Benayas et al., 2009).

Ecosystem services in this region are threatened by a changing climate regime and projected vegetation shifts in Western North America (Wang et al., 2012). Dominant tree species and vegetation types in our study area are predicted to shift substantially until the end of the 21st century (Coops and Waring, 2011; Gonzalez et al., 2010; McKenney et al., 2007), probably detrimentally affecting both current ecosystem service and biodiversity patterns. Hence, an adaptive ecosystem management approach is needed to mitigate estimated impacts.

5. Conclusions

Our results confirm that multifunctional landscapes, here largely covered by temperate rainforests, co-occur with high levels of biodiversity. Thus, the management of ecosystem services should not substitute, but rather incorporate, biodiversity conservation since the two concepts are interdependently related through maintaining the functioning of ecosystems on the one hand and the management for goods and services on the other hand (Ingram et al., 2012; Mace et al., 2012). Based on our results, we derive the following management and research recommendations for the coastal temperate rainforest region across the Pacific Northwest.

1. The concepts of ecosystem services and biodiversity are not only linked, they act in concert. Based on our analysis, an integrative approach of ecosystem management that incorporates both ecosystem services and biodiversity is indeed beneficial in providing goods and services to society while maintaining biodiversity. We therefore support the perspective that multifunctional ecosystems should become a key for sustainable ecosystem management in this region, particularly in a way that optimizes land-use and strives for compatibility in management among different ecosystem services.
2. Our findings generally show that land managers who are interested in the provisioning of diverse ecosystem services are also able to maintain biodiversity. For instance, large landscape level management efforts inherent to the Northwest Forest Plan (DellaSala and Williams, 2006) represent approaches in which ecosystem management and biodiversity conservation on public lands are capable to produce multiple ecosystem benefits and, hence, help to maintain multifunctionality.
3. Research at finer spatial scales, incorporating time series data and information on how local forest management practices determine possible relationships between timber harvest, other ecosystem services and biodiversity would be useful for our study region. Standardized surveys and sampling protocols are required and data on socio-economical dynamics and ecosystem service valuations should be linked to assess the compatibility of (potentially competing) provisioning ecosystem services at the local and regional scale. Scenario driven analyses

(Carpenter et al., 2006; Nelson et al., 2009) that consider climate and land-use changes are necessary since they may offer valuable insights about possible future trajectories of biodiversity and ecosystem service patterns in this region.

Acknowledgements

We thank the Leuphana University Lüneburg for providing the project fund. We are also very grateful to all governmental and non-governmental organizations that made available the data needed for our analyses. Finally we thank Pascal Fust for his contribution to the manuscript.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2013.12.003>.

References

- Bachelet, D., Lenihan, J.M., Daly, C., Neilson, R.P., Ojima, D.S., Parton, W.J., 2001a. MC1: A Dynamic Vegetation Model for Estimating the Distribution of Vegetation and Associated Ecosystem Fluxes of Carbon, Nutrients, and Water. Technical Documentation. Version 1.0.
- Bachelet, D., Neilson, R.P., Lenihan, J.M., Drapek, R.J., 2001b. Climate change effects on vegetation distribution and carbon budget in the United States. *Ecosystems* 4, 164–185.
- Balvanera, P., Pfisterer, A.B., Buchmann, N., He, J.S., Nakashizuka, T., Raffaelli, D., Schmid, B., 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecol. Lett.* 9, 1146–1156.
- Barnes, M., Todd, A., Whitney, L.R., Barten, P., 2009. Forests, Water and People: Drinking water supply and forest lands in the Northeast and Midwest United States.
- Benayas, J.M.R., Newton, A.C., Diaz, A., Bullock, J.M., 2009. Enhancement of biodiversity and ecosystem services by ecological restoration: a meta-analysis. *Science* 325, 1121–1124.
- Bengtsson, J., Nilsson, S.G., Franc, A., Menozzi, P., 2000. Biodiversity, disturbances, ecosystem function and management of European forests. *For. Ecol. Manage.* 132, 39–50.
- Bennett, E.M., Peterson, G.D., Gordon, L.J., 2009. Understanding relationships among multiple ecosystem services. *Ecol. Lett.* 12, 1394–1404.
- Böhm, M., Collen, B., Baillie, J.E.M., Bowles, P., Chanson, J., Cox, N., Hammerson, G., Hoffmann, M., Livingstone, S.R., Ram, M., Rhodin, A.G.J., Stuart, S.N., van Dijk, P.P., Young, B.E., Aftang, L.E., Aghasyan, A., Garcia, A., Aguilar, C., Ajtic, R., Akarsu, F., Alencar, L.R.V., Allison, A., Ananjeva, N., Anderson, S., Andrés, C., Ariano-Sánchez, D., Arredondo, J.C., Auliya, M., Austin, C.C., Avci, A., Baker, P.J., Barreto-Lima, A.F., Barrio-Amorós, C.L., Basu, D., Bates, M.F., Batistella, A., Bauer, A., Bennett, D., Böhme, W., Broadley, D., Brown, R., Burgess, J., Captain, A., Carreira, S., Castañeda, M.D.R., Castro, F., Catenazzi, A., Cedeño-Vázquez, J.R., Chapple, D.G., Cheylan, M., Cisneros-Heredia, D.F., Cogalniceanu, D., Cogger, H., Corti, C., Costa, G.C., Couper, P.J., Courtney, T., Crnobrnja-Isailovic, J., Crochet, P.-A., Crother, B., Cruz, F., Daltry, J.C., Daniels, R.J.R., Das, I., de Silva, A., Diesmos, A.C., Dirksen, L., Doan, T.M., Dodd Jr., C.K., Doody, J.S., Dorcas, M.E., Duarte de Barros Filho, J., Egan, V.T., El Mouden, E.H., Embert, D., Espinoza, R.E., Fallabrino, A., Feng, X., Feng, Z.-J., Fitzgerald, L., Flores-Villela, O., França, F.G.R., Frost, D., Gadsden, H., Gamble, T., Ganesh, S.R., Garcia, M.A., García-Pérez, J.E., Gatus, J., Gaulke, M., Geniez, P., Georges, A., Gerlach, J., Goldberg, S., Gonzalez, J.-C.T., Gower, D.J., Grant, T., Greenbaum, E., Grieco, C., Guo, P., Hamilton, A.M., Hare, K., Hedges, S.B., Heideman, N., Hilton-Taylor, C., Hitchmough, R., Hollingsworth, B., Hutchinson, M., Ineich, I., Iverson, J., Jaksic, F.M., Jenkins, R., Joger, U., Jose, R., Kaska, Y., Kaya, U., Keogh, J.S., Köhler, G., Kuchling, G., Kumlatas, Y., Kwet, A., La Marca, E., Lamar, W., Lane, A., Lardner, B., Latta, C., Latta, G., Lau, M., Lavin, P., Lawson, D., LeBreton, M., Lehr, E., Limpus, D., Lipczynski, N., Lobo, A.S., López-Luna, M.A., Luiselli, L., Lukoschek, V., Lundberg, M., Lymberakis, P., Macey, R., Magnusson, W.E., Mahler, D.L., Malhotra, A., Mariaux, J., Maritz, B., Marques, O.A.V., Márquez, R., Martins, M., Masterson, G., Mateo, J.A., Mathew, R., Mathews, N., Mayer, G., McCranie, J.R., Measey, G.J., Mendoza-Quijano, F., Menegon, M., Métrailler, S., Milton, D.A., Montgomery, C., Morato, S.A.A., Mott, T., Muñoz-Alonso, A., Murphy, J., Nguyen, T.Q., Nilson, G., Nogueira, C., Núñez, H., Orlov, N., Ota, H., Ottenwalder, J., Papenfuss, T., Pasachnik, S., Passos, P., Pauwels, O.S.G., Pérez-Buitrago, N., Pérez-Mellado, V., Pianka, E.R., Pleguezuelos, J., Pollock, C., Ponce-Campos, P., Powell, R., Pupin, F., Quintero Díaz, G.E., Radder, R., Ramer, J., Rasmussen, A.R., Raxworthy, C., Reynolds, R., Richman, N., Rico, E.L., Riservato, E., Rivas, G., da Rocha, P.L.B., Rödel, M.-O., Rodríguez Schettino, L., Roosenburg, W.M., Ross, J.P., Sadek, R., Sanders, K., Santos-Barrera, G., Schleich, H.H., Schmidt, B.R., Schmitz, A., Sharif, M., Shea, G., Shi, H.-T., Shine, R., Sindaco, R., Slimani, T., Somaweera, R., Spawls, S., Stafford, P., Stuebing, R., Sweet, S., Sy, E., Temple, H.J., Tognelli, M.F., Tolley, K.,

- Tolson, P.J., Tuniyev, B., Tuniyev, S., Üzümlü, N., van Buurt, G., Van Sluys, M., Velasco, A., Vences, M., Vesely, M., Vinke, S., Vinke, T., Vogel, G., Vogrin, M., Vogt, R.C., Wearn, O.R., Werner, Y.L., Whiting, M.J., Wiewandt, T., Wilkinson, J., Wilson, B., Wren, S., Zamin, T., Zhou, K., Zug, G., 2013. The conservation status of the world's reptiles. *Biol. Conserv.* 157, 372–385.
- Bonan, G.B., 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science* 320, 1444–1449.
- Bullock, J.M., Aronson, J., Newton, A.C., Pywell, R.F., Rey-Benayas, J.M., 2011. Restoration of ecosystem services and biodiversity: Conflicts and opportunities. *Trends Ecol. Evol.* 26, 541–549.
- Carpenter, S.R., Bennett, E.M., Peterson, G.D., 2006. Scenarios for ecosystem services: an overview. *Ecol. Soc.* 11.
- Carpenter, S.R., Mooney, H.A., Agard, J., Capistrano, D., DeFries, R.S., Diaz, S., Dietz, T., Duraiappah, A.K., Oteng-Yeboah, A., Pereira, H.M., Perrings, C., Reid, W.V., Sarukhan, J., Scholes, R.J., Whyte, A., 2009. Science for managing ecosystem services: beyond the millennium ecosystem assessment. *Proc. Natl. Acad. Sci. USA* 106, 1305–1312.
- Chan, K.M.A., Shaw, M.R., Cameron, D.R., Underwood, E.C., Daily, G.C., 2006. Conservation planning for ecosystem services. *Plos Biol.* 4, 2138–2152.
- Coops, N.C., Waring, R.H., 2011. Estimating the vulnerability of fifteen tree species under changing climate in Northwest North America. *Ecol. Model.* 222, 2119–2129.
- Costanza, R., Fisher, B., Mulder, K., Liu, S., Christopher, T., 2007. Biodiversity and ecosystem services: a multi-scale empirical study of the relationship between species richness and net primary production. *Ecol. Econom.* 61, 478–491.
- Crawley, M.J., 2007. *The R Book*. John Wiley & Sons, West Sussex.
- Daily, G., 1997. *Nature's Services: Societal Dependence on Natural Ecosystems*. Island Press, Washington DC.
- Daniel, T.C., Muhar, A., Arnberger, A., Aznar, O., Boyd, J.W., Chan, K.M.A., Costanza, R., Elmqvist, T., Flint, C.G., Gobster, P.H., Gret-Regamey, A., Lave, R., Muhar, S., Penker, M., Ribe, R.G., Schauppenlehner, T., Sikor, T., Soloviy, I., Spierenburg, M., Taczanowska, K., Tam, J., von der Dunk, A., 2012. Contributions of cultural services to the ecosystem services agenda. *Proc. Natl. Acad. Sci. USA* 109, 8812–8819.
- DellaSala, D.A., 2011. *Temperate and Boreal Rainforests of the World: Ecology and Conservation*. Island Press, Washington DC.
- DellaSala, D.A., Williams, J.E., 2006. Special section: the northwest forest plan: a global model of forest management in contentious times. *Conserv. Biol.* 20, 274–276.
- DellaSala, D.A., Karr, J.R., Olson, D.M., 2011. Roadless areas and clean water. *J. Soil Water Conserv.* 66, 78A–84A.
- Di Falco, S., Chavas, J.P., 2006. Crop genetic diversity, farm productivity and the management of environmental risk in rainfed agriculture. *Eur. Rev. Agric. Econom.* 33, 289–314.
- Diaz, S., Fargione, J., Chapin, F.S., Tilman, D., 2006. Biodiversity loss threatens human well-being. *Plos Biol.* 4, 1300–1305.
- Dray, S., Legendre, P., Peres-Neto, P.R., 2006. Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecol. Model.* 196, 483–493.
- Duffy, J.E., 2009. Why biodiversity is important to the functioning of real-world ecosystems. *Front. Ecol. Environ.* 7, 437–444.
- Egoh, B., Reyers, B., Rouget, M., Bode, M., Richardson, D.M., 2009. Spatial congruence between biodiversity and ecosystem services in South Africa. *Biol. Conserv.* 142, 553–562.
- Nations, F.A.O.o.t.U., 2010. *Global Forest Resources Assessment 2010, Main report*, Rome.
- Fischer, B., Turner, R.K., Morling, P., 2009. Defining and classifying ecosystem services for decision making. *Ecol. Econom.* 68, 643–653.
- Fitzgerald, J., DellaSala, D.A., McNeely, J., Grumbine, E., 2011. A global strategy for rainforests in the era of climate change. In: DellaSala, D.A. (Ed.), *Temperate and Boreal Rainforests of the World: Ecology and Conservation*. Island Press, Washington DC, pp. 260–274.
- Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N., Snyder, P.K., 2005. Global consequences of land use. *Science* 309, 570–574.
- Gamfeldt, L., Hillebrand, H., Jonsson, P.R., 2008. Multiple functions increase the importance of biodiversity for overall ecosystem functioning. *Ecology* 89, 1223–1231.
- Gamfeldt, L., Snäll, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P., Ruiz-Jaen, M.C., Froberg, M., Stendahl, J., Philipson, C.D., Mikusinski, G., Andersson, E., Westerlund, B., Andren, H., Moberg, F., Moen, J., Bengtsson, J., 2013. Higher levels of multiple ecosystem services are found in forests with more tree species. *Nat. Commun.* 4.
- Geizendorfer, I.R., Roche, P.K., 2013. Can biodiversity monitoring schemes provide indicators for ecosystem services? *Ecol. Indicators* 33, 148–157.
- Gobster, P.H., Nassauer, J.I., Daniel, T.C., Fry, G., 2007. The shared landscape: what does aesthetics have to do with ecology? *Landscape Ecol.* 22, 959–972.
- Gonzalez, P., Neilson, R.P., Lenihan, J.M., Drake, R.J., 2010. Global patterns in the vulnerability of ecosystems to vegetation shifts due to climate change. *Global Ecol. Biogeogr.* 19, 755–768.
- Griffith, D.A., Peres-Neto, P.R., 2006. Spatial modeling in ecology: the flexibility of eigenfunction spatial analyses. *Ecology* 87, 2603–2613.
- Haines-Young, R., Potschin, M., Kienast, F., 2012. Indicators of ecosystem service potential at European scales: mapping marginal changes and trade-offs. *Ecol. Indicators* 21, 39–53.
- Hanspach, J., Kuhn, I., Schweiger, O., Pompe, S., Klotz, S., 2011. Geographical patterns in prediction errors of species distribution models. *Global Ecol. Biogeogr.* 20, 779–788.
- Hector, A., Bagchi, R., 2007. Biodiversity and ecosystem multifunctionality. *Nature* 448, 188–U186.
- Hernandez-Morcillo, M., Plieninger, T., Bieling, C., 2013. An empirical review of cultural ecosystem service indicators. *Ecol. Indicators* 29, 434–444.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* 25, 1965–1978.
- Hooper, D.U., Adair, E.C., Cardinale, B.J., Byrnes, J.E.K., Hungate, B.A., Matulich, K.L., Gonzalez, A., Duffy, J.E., Gamfeldt, L., O'Connor, M.L., 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* 486, U105–U129.
- Ingram, J.C., Redford, K.H., Watson, J.E.M., 2012. *Applying Ecosystem Services Approaches for Biodiversity Conservation: Benefits and Challenges*. S.A.P.I.E.N.S 5, pp. 1–10.
- Lal, R., 2004. Soil carbon sequestration impacts on global climate change and food security. *Science* 304, 1623–1627.
- Legendre, P., Gallagher, E.D., 2001. Ecologically meaningful transformations for ordination of species data. *Oecologia* 129, 271–280.
- Legendre, P., Legendre, L., 2012. *Numerical Ecology*. Elsevier Science BV, Amsterdam.
- Little, E.L., Jr., 1978. *Atlas of United States trees*. Department of Agriculture Miscellaneous Publication 1361.
- MA, 2005. *Millennium Ecosystem Assessment. Ecosystems and Human Well-being: Synthesis*, Washington DC.
- Mace, G.M., Norris, K., Fitter, A.H., 2012. Biodiversity and ecosystem services: a multilayered relationship. *Trends Ecol. Evol.* 27, 19–26.
- Marrs, R.H., Galtress, K., Tong, C., Cox, E.S., Blackbird, S.J., Heyes, T.J., Pakeman, R.J., Le Duc, M.G., 2007. Competing conservation goals, biodiversity or ecosystem services: element losses and species recruitment in a managed moorland-bracken model system. *J. Environ. Manage.* 85, 1034–1047.
- Maskell, L.C., Crowe, A., Dunbar, M.J., Emmett, B., Henrys, P., Keith, A.M., Norton, L.R., Scholefield, P., Clark, D.B., Simpson, I.C., Smart, S.M., 2013. Exploring the ecological constraints to multiple ecosystem service delivery and biodiversity. *J. Appl. Ecol.* 50, 561–571.
- Mckenney, D.W., Pedlar, J.H., Lawrence, K., Campbell, K., Hutchinson, M.F., 2007. Potential impacts of climate change on the distribution of North American trees. *Bioscience* 57, 939–948.
- McShane, T.O., Hirsch, P.D., Trung, T.C., Songorwa, A.N., Kinzig, A., Monteferrri, B., Mutekanga, D., Thang, H.V., Dammert, J.L., Pulgar-Vidal, M., Welch-Devine, M., Brosius, J.P., Coppolillo, P., O'Connor, S., 2011. Hard choices: making trade-offs between biodiversity conservation and human well-being. *Biol. Conserv.* 144, 966–972.
- Mori, A.S., Furukawa, T., Sasaki, T., 2013. Response diversity determines the resilience of ecosystems to environmental change. *Biol. Rev.* 88, 349–364.
- Naidoo, R., Balmford, A., Costanza, R., Fisher, B., Green, R.E., Lehner, B., Malcolm, T.R., Ricketts, T.H., 2008. Global mapping of ecosystem services and conservation priorities. *Proc. Natl. Acad. Sci. USA* 105, 9495–9500.
- Nelson, E., Mendoza, G., Regetz, J., Polasky, S., Tallis, H., Cameron, D.R., Chan, K.M.A., Daily, G.C., Goldstein, J., Kareiva, P.M., Lonsdorf, E., Naidoo, R., Ricketts, T.H., Shaw, M.R., 2009. Modeling multiple ecosystem services, biodiversity conservation, commodity production, and tradeoffs at landscape scales. *Front. Ecol. Environ.* 7, 4–11.
- O'Farrell, P.J., Reyers, B., Le Maitre, D.C., Milton, S.J., Egoh, B., Maherry, A., Colvin, C., Atkinson, D., De Lange, W., Bignaut, J.N., Cowling, R.M., 2010. Multi-functional landscapes in semi arid environments: implications for biodiversity and ecosystem services. *Landscape Ecol.* 25, 1231–1246.
- Ont, T.A., Schulte, L.A., 2012. Soil carbon storage. *Nat. Education Knowledge* 3, 35.
- Pinsky, M.L., Springmeyer, D.B., Goslin, M.N., Augerot, X., 2009. Range-wide selection of catchments for pacific salmon conservation. *Conserv. Biol.* 23, 680–691.
- Raudsepp-Hearne, C., Peterson, G.D., Bennett, E.M., 2010. Ecosystem service bundles for analyzing tradeoffs in diverse landscapes. *Proc. Natl. Acad. Sci. USA* 107, 5242–5247.
- Ridder, B., 2008. Questioning the ecosystem services argument for biodiversity conservation. *Biodiv. Conserv.* 17, 781–790.
- Rodriguez, J.P., Beard, T.D., Bennett, E.M., Cumming, G.S., Cork, S.J., Agard, J., Dobson, A.P., Peterson, G.D., 2006. Trade-offs across space, time, and ecosystem services. *Ecol. Soc.* 11.
- Sakamoto, Y., Ishiguro, M., Kitagawa, G., 1986. *Akaike Information Criterion Statistics*. D. Reidel Publishing Company, Dordrecht/Tokyo.
- Schneiders, A., Van Daele, T., Van Landuyt, W., Van Reeth, W., 2012. Biodiversity and ecosystem services: complementary approaches for ecosystem management? *Ecol. Indicators* 21, 123–133.
- Schoonmaker, P.K., von Hagen, B., Wolf, E.C., 1997. *The Rain Forests of Home: Profile of a North American Bioregion*. Island Press, Washington DC.
- Schwenk, W.S., Donovan, T.M., Keeton, W.S., Nunery, J.S., 2012. Carbon storage, timber production, and biodiversity: comparing ecosystem services with multi-criteria decision analysis. *Ecol. Appl.* 22, 1612–1627.
- Shmueli, G., 2010. To Explain or to Predict? *Statistical Sci.* 25, 289–310.
- Simon, S., Bouvier, J.C., Debras, J.F., Sauphanor, B., 2010. Biodiversity and pest management in orchard systems. A review. *Agronomy Sustain. Develop.* 30, 139–152.
- Simpson, I.C., 1949. Measurement of diversity. *Nature* 163, 688.

- Sircely, J., Naeem, S., 2012. Biodiversity and ecosystem multi-functionality: observed relationships in smallholder fallows in Western Kenya. *Plos One* 7.
- Tallis, H., Polasky, S., 2009. Mapping and valuing ecosystem services as an approach for conservation and natural-resource management. *Ann. New York Acad. Sci.* 1162, 265–283.
- Tilman, D., Reich, P.B., Isbell, F., 2012. Biodiversity impacts ecosystem productivity as much as resources, disturbance, or herbivory. *Proc. Natl. Acad. Sci. USA* 109, 10394–10397.
- Todd, I.H., Weidner, E., 2010. Valuing drinking water as an ecosystem service. *The Pinchot Letter* Winter 2010, 1–13.
- Turner, W.R., Brandon, K., Brooks, T.M., Costanza, R., da Fonseca, G.A.B., Portela, R., 2007. Global conservation of biodiversity and ecosystem services. *Bioscience* 57, 868–873.
- Vira, B., Adams, W.M., 2009. Ecosystem services and conservation strategy: beware the silver bullet. *Conserv. Lett.* 2, 158–162.
- Wang, T.L., Campbell, E.M., O'Neill, G.A., Aitken, S.N., 2012. Projecting future distributions of ecosystem climate niches: uncertainties and management applications. *For. Ecol. Manage.* 279, 128–140.
- Woodbury, P.B., Smith, J.E., Heath, L.S., 2007. Carbon sequestration in the U.S. forest sector from 1990 to 2010. *For. Ecol. Manage.* 241, 14–27.