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A global map of the functionality of terrestrial ecosystems

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ABSTRACT

The functionality of ecosystems is important for energy dissipation, ecosystem service provisioning, resilience to global change and adaptive capacity. Ecosystem complexity and ultimately functionality depend on higher levels of biodiversity, biomass, heterogeneity and evolutionary potential, such as genes. These characteristics are also likely to promote system resilience and adaptive capacity, which are becoming increasingly important under global climate change. This paper proposes a global proxy-based index of ecosystem functionality (EFI). The results generated for all the main global biomes recorded highest index values for tropical and extratropical forest ecoregions. Out of the selected variables vegetation density, topographical heterogeneity and carbon storage demonstrated strong correlations with the ecosystem functionality index. It is argued that the ecosystem functionality index is not only useful for ecological research and conservation science but also as an effective prioritization scheme for biodiversity conservation at the landscape scale in times of rapid global environmental change. Furthermore, ecosystems that express high ecosystem functionality are also believed to have greater buffer and adaptive capacity and it is proposed that these parameters help to identify those ecosystems that will contribute toward global sustainability.

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1. Introduction

The Earth's ecosystems are open to material and energy exchange with the surrounding environment, but at the same time they self-organize towards maximum energetic, hydric and also material-related efficiency (Ripl, 2003; Ripl and Wolter, 2002). This efficiency-seeking behavior can be seen as a driving force to system organization and evolution (Hobson and Ibisch, 2012). Through the interaction between components the ecosystem is using a certain amount of energy to maintain its functionality over time, which minimizes the need for greater energy input by reducing any loss to heat. Evolutionary processes drive systems towards multiplication and complexification of energy and matter-transferring pathways and the establishment of cyclical processes. The maintenance of efficient functional processes is fundamental in ecosystems that do not only strive for higher efficiency, but also need to adapt to the stresses induced by environmental changes in order to sustain an optimal balance between efficiency and resilience (Patzek, 2008; Ulanowicz et al., 2009).

We define functionality as a state of ecosystems that is characterized by inherent structures, ecological functions and dynamics that provide ecosystems with both, the necessary efficiency and resilience to develop without abrupt change of system properties and geographical distribution, and to respond flexibly to external change. Ecosystems with a high level of functionality demonstrate a greater capacity for energy uptake and exergy storage (Schneider and Kay, 1994; Wagendorp et al., 2006). The inherent capability in ecosystems to self-order and regulate makes them less dependent on external conditions. For instance, they are able to buffer against the unpredictable availability of resources and also against climate variability (e.g., microclimatic regulation, water retention) (Norris et al., 2012). On a larger scale, more functional ecosystems develop climate-relevant emergent properties that contributes to the regulation of their environment (e.g., carbon sequestration and storage, water recycling and cloud formation, change of albedo) (Diaz and Cabido, 1997; Pielke et al., 2002).

The anthropogenic degradation of ecosystems signals a shift from an evolved state of self-ordering complexity toward a state where conditions reflect more simple structures and functions that are less efficient (Hobson and Ibisch, 2010; Rosen, 2009; Ryan et al., 2007). The simplification of ecosystems can lead to a lowering the levels of ecosystem internal complexity (e.g. Ryan et al., 2007; Wagendorp et al., 2001), with the loss of biodiversity and ultimate dysfunction in systems (e.g. Dolinar et al., 2010; Hassan, 2005; Hirsch, 2010).

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In this paper ecological complexity, is defined as the degree of spatial heterogeneity, historical contingency and organizational connectivity of ecosystems emerging from the interplay of behavioral, biological, physical and social interactions (Cadenasso et al., 2006; Michener et al., 2001). According to Cadenasso et al. (2006) ecological complexity can be measured through indicators of heterogeneity, connectivity and temporal contingencies.

At the same time, theories of non-equilibrium thermodynamics have been applied increasingly to address problems in ecosystem studies. Specifically, it has been proposed that exergy is an appropriate holistic indicator for assessing the environmental health of ecosystems (Jørgensen, 2006; Jørgensen and Fath, 2004; Jørgensen et al., 2000; Silow and Mokry, 2010; Szargut, 2005; Szargut et al., 2002). Other authors have adopted this concept to develop more effective approaches for assessing environmental impact, sustainable development and ecosystem service provisioning (Dincer and Rosen, 2007; Jørgensen, 2010; Rosen, 2009; Rosen and Dincer, 1997; Szargut et al., 2002). Principles of ecosystem complexity and functionality, including those of non-equilibrium thermodynamics can be applied to ecosystem science to better understand the effects of disturbance on processes and dynamics as well as to direct management practices (Silow and Mokry, 2010).

An important basis for growth and development in ecosystems is biodiversity. As early as 1969, Odum described trends toward greater biomass storage and community complexity, which, in turn promotes increasing ecosystem efficiency and functionality (Odum, 1969). Driven by evolution, biodiversity continuously generates new energy-dissipative structures to delay collapse and entropy (Jørgensen, 2006; Silow and Mokry, 2010). This leads on to increasing opportunities of interactions within and between systems and corresponding growth toward greater complexity and functionality (Hobson and Ibsch, 2010). The alteration in species composition and ecosystem structure is fundamental to survival and to maintaining a position as far as possible away from thermodynamic equilibrium. The evolution of compositional and conformational diversity provides ecosystems with the necessary resilience and adaptive capacity to change. It is also the fundament of basic ecosystem services. Thus, it can be concluded that the main aim of biodiversity conservation would be to promote ecosystem functionality. Underpinning the success of this strategy is the provision of a simple conceptual framework to enable practitioners to describe ecosystem complexity and functionality (White et al., 2010).

Jørgensen (2006) and Jørgensen et al. (2000) proposed three forms of growth and development of ecosystems as follows: the growth of biomass or the physical–biological structure; the growth of the network, referring to increasing connections between components in a system; and the growth of information that describes, for example, the building of communities toward higher proportional representation of K-strategy species rather than more generalist, r-strategy species (Hobson and Ibsch, 2010; Jørgensen, 2006). According to information theory both information and ecosystem dynamics are linked to trophic structure, and together, these attributes contribute to system development and complexity (Ulanowicz, 2003). In this model exergy increases with all three growth forms and collectively they are adopted as proxy measures of ecosystem functionality. Most studies on ecosystem complexity and function are based on research carried out on specific case studies (e.g. Lin et al., 2009; Norris et al., 2012), as well as problems of theoretical ecology and mathematical modeling (see Silow and Mokry, 2010 for review). Some of this research has produced detailed global maps presenting information on ecosystem service provisioning (e.g. Egoh et al., 2008; Naidoo et al., 2008) or evidence for the most undisturbed ecosystems (e.g. Frontier Forests from Bryant et al., 1997).

However, few studies have used a framework to evaluate the functionality of ecosystems as an effective means of informing land use practices and biodiversity conservation.

This study is a first attempt at applying complementary concepts of ecosystem functionality in order to generate a global map of a weighted, additive, dimensionless index based on a set of proxy indicators. The final algorithmic index and accompanying spatial image represents a relative proxy measure of ecosystem functionality. The results and final analysis favor more proactive strategies for conservation planning that take on board future risks associated with global change.

2. Materials and methods

2.1. Selection and explanation of proxies

Both vegetation density (percent ground coverage) (Hansen et al., 2003), and carbon storage (in kg carbon per m²) (Gumpenberger et al., 2010) are used as proxy indicators of living and non-living biomass accumulated over time and likely to continue into the future. Systems that record high values for primary producers and stored carbon are expected to return high readings for the amount of biomass. A greater abundance of primary producers is also likely to increase the capture of solar energy thus adding to the downloading of biomass and in so doing, improving the functionality of these systems.

Measures of ecosystem complexity and information are also incorporated into the map. Network complexity is represented using proxy indicators for structural diversity. In this study we use species richness of vascular plants (Kier et al., 2005), functional richness of plants (Reu et al., 2011), foliage canopy height (Lefsky, 2010) and topographic heterogeneity and slope (ESRI, 2008b) as indicators for ecosystem complexity and heterogeneity.

Ecosystems with greater species richness are also likely to support a more complex trophic structure with many more conformational linkages. Consequently, these systems appear to have higher cycling rates of biomass, energy and information. Equally, where there are more species there is also more biomass productivity and carbon storage in the system (Ho and Ulanowicz, 2005). However, there are exceptions to the rule and high species richness can also occur in highly disturbed regions (Wang et al., 2010) where linkages and connectivity are relatively low. Equally, high species richness can also occur in climax communities where productivity is not maximized (Wang et al., 2010).

Other indicators used as proxy measures of ecosystem complexity include tree canopy height and topographical heterogeneity. Landscapes with higher tree canopies are more likely to show old-growth forest conditions and complex vertical stratification (e.g. herbal, shrub, higher and lower canopy layer) (Zenner, 2004). Vertical stratification is not only a product of forest dynamics and biophysical processes but is also an indicator of enhanced biodiversity and ecosystem function (Spies, 1998). Foliage layering is important for wildlife habitat, and in moderating microclimatic conditions in forests. It also plays an important part in the absorption of solar radiation. Many species respond to patterns in vertical foliage structuring (Basset et al., 2001; Bourlière and Harmelin-Vivien, 1989; Brühl et al., 1998; Fermon et al., 2005; Intachat and Holloway, 2000; Sutton et al., 1983; Whitmore, 1993; Wolda, 1987). Structurally complex stands provide more diverse habitats for specialized late-succession species and communities (Begon et al., 1986).

Topographical heterogeneity indicated by slope also influences species richness at different scales. For instance, at macro-scale habitat diversity increases along altitudinal gradients, and geological barriers increase opportunities for allopatric speciation (Kerr and Packer, 1997; Rahbek and Graves, 2001).

Table 1

List of applied modes and procedures for sensitivity analysis including setting details and total number of generated modified index files for statistical evaluation.

Sensitivity analysis mode	Applied procedure	Setting details	No. of generated modified indices
Jackknifing	Iterative exclusion of each indicator	–	6
High and low case scenario	Adjustment of weighting scheme according to indicator distribution	Maximum weight 20%; minimum weight 10% for each indicator	2
Random weight variation	Random weight variation	Between 10% and 20% for all indicators all at a time	10
Systematic weight variation	Systematic weight variation	Between 10% and 20% for each indicator one at a time with a step size of 5%	18 (3 for each indicator)

Values for functional richness refer to the number of observed plant growth strategies and are related to the concept of plant functional types (Reu et al., 2011). Plant functional types identify those species that share similar growth strategies and physiological characteristics for specific environmental conditions and are likely to affect ecosystem processes in similar ways (Walker, 1992). Different plant growth types are likely to react differently to changes in conditions as a result of climate and environmental changes, with some species shifting their habitat or possibly going extinct whilst other species adapt to the changing conditions (Diaz and Cabido, 1997). High functional species richness that offers a diversity of plant growth strategies should be better placed to meet the challenges of future climate change by contributing to ecosystem functionality as well as enhancing the adaptive capacity of ecosystems (Diaz and Cabido, 1997).

2.2. Data processing and index calculation

All data sets were adjusted in resolution and projection to a 1 km raster before transforming to standardized measurements. Mean values were calculated for those original indicator measurements that exceeded 1 km grids. Each indicator was normalized (between 0 and 100) and weighted before adding to the index of ecosystem functionality (EFI). A simple weighted additive index formula was used to calculate the index as shown in formula (1). An equal weighting scheme was adopted as it was assumed that all indicators were of equal importance.

$$x = \sum_{i=1}^n g_i I_{N,i} \quad (1)$$

x = the calculated index value; n = the number of indicators; g_i = the relative weight for each indicator; $I_{N,i}$ = the normalized value of each indicator.

To account for the uncertainties that are manifest in the choice of indicators and weighting scheme a sensitivity analysis was performed using jackknifing and weighting variations within certain boundaries and according to different methodologies. Through the jackknifing procedure each variable was systematically excluded from the calculated index to assess the relative influence of each variable on the final index output. The methods used for weighting variation were based on high and low case scenario weighting and systematic and random variation. The high and low case scenario describes the adjustment made to the weighting scheme to account for the distribution patterns of each parameter. The weight of an indicator is adjusted downwards for a low case scenario if the indicator increases the value of the final index output (e.g. distribution is skewed to the right for positive indicators). In a low case scenario where the weightings of indicators depress the index output (e.g. distribution is skewed to the left for positive indicators) an upward adjustment of the weighting values is made. For random weighting variation as well as for high and low case scenario weighting variation the range of possible weights was set at 10% and 20% as a minimum and maximum weight respectively. Under the random weighting variation 10 additional modified index

files were generated. A further 18 modified index files were also created by applying systematic weighting variation with a step size of 5%, and between 10% and 20% (see Table 1 for details). Weighting variations were performed to take account of weighting uncertainties, and to calculate maps displaying statistics derived from all modified index files such as mean values, standard deviation and volatility (frequency of archiving high values under changing index settings).

The adjustment in resolution and projection of all indicator datasets was performed using the geographical information system software ArcGIS 9.3 (ESRI, 2008a). The normalization of all indicators, index calculation and sensitivity analysis was performed with Insensa-GIS (Biber et al., 2011).

Jørgensen (2010) calculated the annual production of exergy for a range of ecosystem types by multiplying the annual growth of biomass with an information factor. The estimated mean EFI values were compared with the data generated by Jørgensen (2010) for different ecosystem types. The selected ecosystems were extracted from the land cover classification system devised by Olson (1994). Using the results from Jørgensen's study (2010) it was possible to match this data against the mean EFI values calculated for the biomes chosen for this study. Incomplete data sets prevented a more comprehensive analysis of all global aquatic ecosystems. Nevertheless, it was possible to carry out effect statistical tests on available data within a selected number of ecoregions.

Finally, the spatial congruency between EFI and relative loss or growth of net primary production was analyzed to determine the level of impact of ecosystem functionality on net primary production. A ten-year data set was selected (2000–2010, Zhao and Running, 2010) to assess for possible relationships between the EFI values and relative net primary production increase or decrease.

3. Results

3.1. The ecosystem functionality index (EFI)

Fig. 1 represents the EFI values for all land cover types across the globe. Very high values are displayed in dark-green while very low values are presented in purple. At a coarse-filter scale both tropical and extra-tropical biomes comprise areas with the highest EFI values, with (sub-) tropical mountainous regions being especially prominent. More specifically, highest levels of “realized” ecosystem functionality were concentrated in the northern and western Amazon; the Congo basin; in subtropical and tropical forests of (South-) East Asia; and in boreal and temperate regions of northern Asia, North America and eastern part of Russia. Extra-tropical mountain chains such as the Appalachians, Alps, Balkans, and the Carpathians were also recorded as having a high EFI value. Notably, some temperate and boreal regions appeared to be as important as tropical forests. Predictably, both hot and cold desert landscapes such as the Sahel; parts of India; the United Emirates; western China; the Middle East; central Australia; Greenland; and the Antarctica appeared to exhibit low ecosystem functionality as defined here.

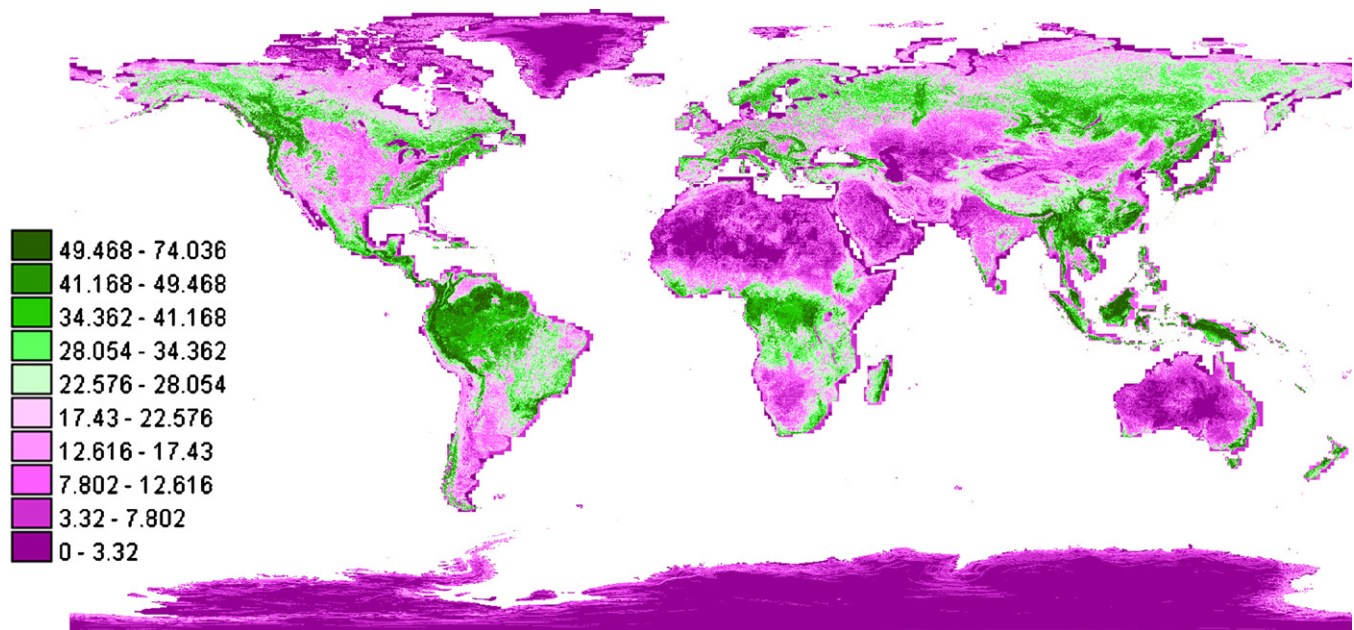


Fig. 1. Global map of the ecosystem functionality index (EFI) in 1 km resolution and WGS 1984 projection. High index values are colored green while low index values are colored purple. Class breaks were calculated using the Jenks natural breaks algorithm.

3.2. Sensitivity analysis

To understand the potential distortion to the data in the calculations a sensitivity analysis was carried out to determine the influence of each variable on the final results. The analysis was repeated to test for adherent uncertainty in the spatial distribution of the index.

3.2.1. Which variables are the most influential?

The use of environmental indicators to describe or measure quality or change to ecosystems is discussed extensively in the scientific literature. High or low correlation coefficient values generated in any analysis do not necessarily indicate that single

parameters should be excluded from the calculations. In this study, the results returned significant values for a positive Pearson and Spearman correlation between vascular plant species richness and plant functional richness as well as a high positive Spearman correlation between plant functional richness and vegetation density. High species richness corresponds to the richness of functional types. Similarly, high functional richness can be found in areas with complex structures and diversity of interactions. All indicators were positively correlated with the EFI but certain indicators showed higher correlation coefficients than others. Correlation between the EFI and vegetation density had a very high coefficient value of 0.841 for Pearson correlation and 0.841 for Spearman correlation as did the correlation between the EFI and

Table 2

Pearson (light gray) and spearman (dark gray) correlation coefficient matrix for different indicators for ecological functionality and the calculated ecosystem functionality index (EFI). Correlation coefficients higher than 0.6 are written in bold. All correlation coefficients are highly significant with $p < 0.0001$.

	Ecosystem Functionality Index	Tree Height	Vegetation Density	Species Richness of Vascular Plants	Slope	Plant Functional Richness	Carbon Storage
Ecosystem Functionality Index (EFI)	1.000	0.510	0.841	0.544	0.651	0.452	0.475
Tree Height	0.519	1.000	0.157	0.275	0.341	0.122	-0.228
Vegetation Density	0.842	0.190	1.000	0.388	0.250	0.482	0.397
Species Richness of Vascular Plants	0.519	0.364	0.499	1.000	0.146	0.692	-0.167
Slope	0.706	0.350	0.333	0.131	1.000	-0.028	0.111
Plant Functional Richness	0.435	0.218	0.608	0.732	-0.025	1.000	-0.101
Carbon Storage	0.622	-0.280	0.588	-0.040	0.142	0.078	1.000

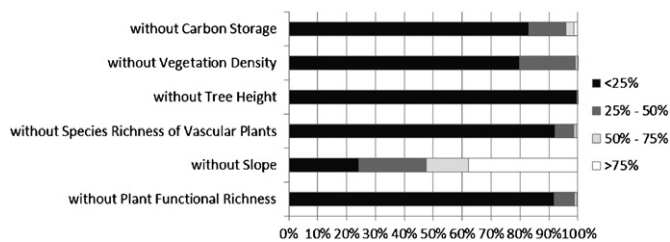


Fig. 2. Proportion of global area whose index value is changing less than 25%, 25–50%, 50–75% or >75% under the different settings applied to index calculation in sensitivity analysis.

slope (Pearson 0.651, Spearman 0.706). A high positive Spearman correlation coefficient for EFI and carbon storage (0.622) was also recorded although Pearson correlation was not as high (0.475). The results suggest that vegetation density, slope and carbon storage are the best single predictors of ecosystem functionality and appear to influence the index most (Table 2).

Different methods were used to explore the influence of the indicators and the weighting scheme on the final index output. Fig. 2 shows the proportion of the area that changes its index value by less than 25%; between 25% and 50%; between 50% and 75%; or more than 75% if the calculation settings are changed. This diagram does not only show patterns that reflect the relative change but also gives an idea of the magnitude of the change and therefore of the sensitivity of the index to a variable. About 38% of the area showed variations of more than 75% of the original index once slope was excluded from the index calculation. The exclusion of other variables resulted in a change of lower than 25% for most of the area. These numbers suggest that slope has a strong influence on a large number of sites.

3.2.2. Which areas of the globe record the highest levels of ecosystem functionality on average?

Using the sensitivity analysis the average EFI was calculated for the main terrestrial ecosystems (Fig. 3). The highest average index values are displayed in green while very low values are presented

in purple. Once again, the tropical and extra-tropical biomes displayed the highest EFI values, with (sub-) tropical mountainous regions recording very high average index values. Especially high index values were recorded for the Amazon, the Congo basin, in forests of South-East Asia, North America and eastern Russia. Hot and cold deserts achieved very low average index values.

3.2.3. How does variation of index values distribute globally?

Although it was difficult to statistically validate the global ecosystem functionality model it was possible to demonstrate by modifying input parameters that the robustness of the results varied globally. The coefficient of variation is calculated as the standard deviation divided by the mean. Since high EFI values are naturally characterized by higher standard deviation the coefficient of variation represents a better estimate of the uncertainty distribution. The results revealed in Fig. 4 represents the coefficient of variation calculated over all modified index files. Highest levels of uncertainty occurred in those regions with lower EFI values while areas characterized by high EFI values achieved low coefficients of variation. Extreme high values for coefficient of variation occurred in those areas where there was little or no data, for example at both poles, Greenland, and for large bodies of inland water (the Great Lakes in the USA, the Caspiann Sea, the Aral Sea and Lake Victoria).

3.2.4. Which areas recorded the greatest frequency of high index values?

A volatility test on the different sensitivity analysis indices was calculated to determine which areas were most frequently targeted in the analysis (Fig. 5). This included a count of the number of times each area was recorded as having the highest EFI values (achieving at least 60% of the maximum index value). Those areas that were selected most frequently are displayed in green and show the lowest uncertainty of being characterized as particularly ecologically functional. After resetting the index algorithm the results indicated that the western Amazonian region and much of South-East Asia were selected more often than other regions. To a lesser extent parts of the boreal

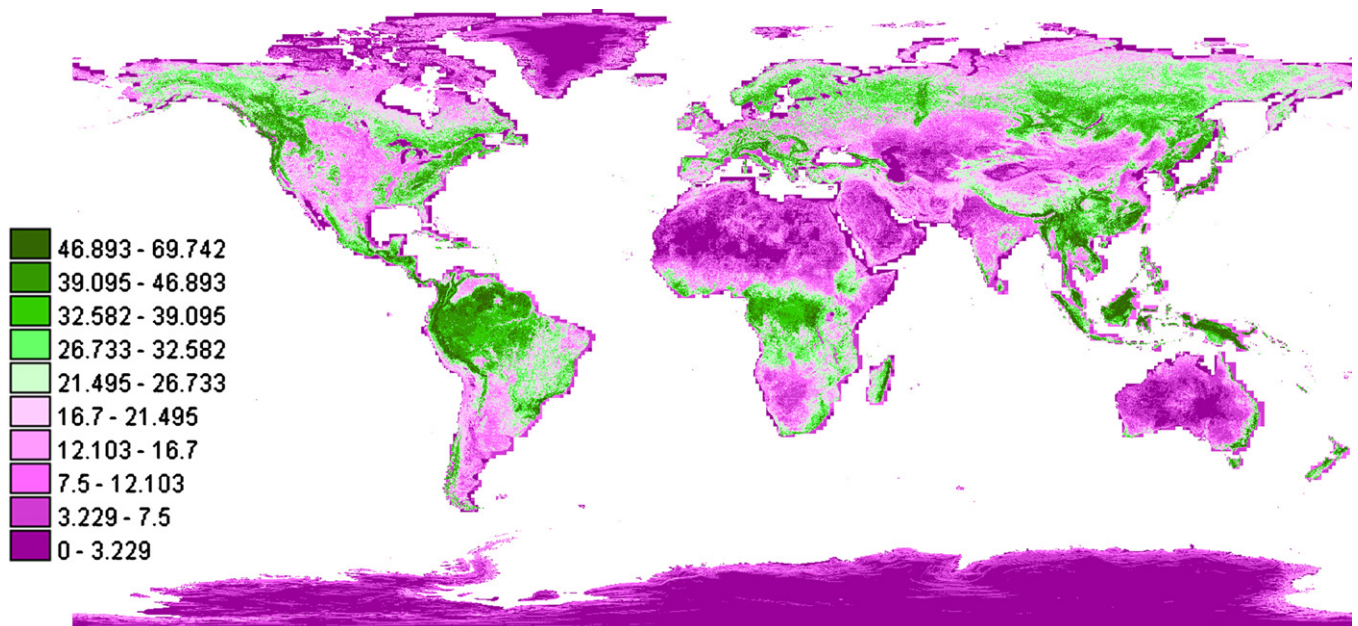


Fig. 3. Global map of mean index values in 1 km resolution and WGS 1984 projection. High index values are colored green while low index values are colored purple. Class breaks were calculated using the Jenks natural breaks algorithm. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

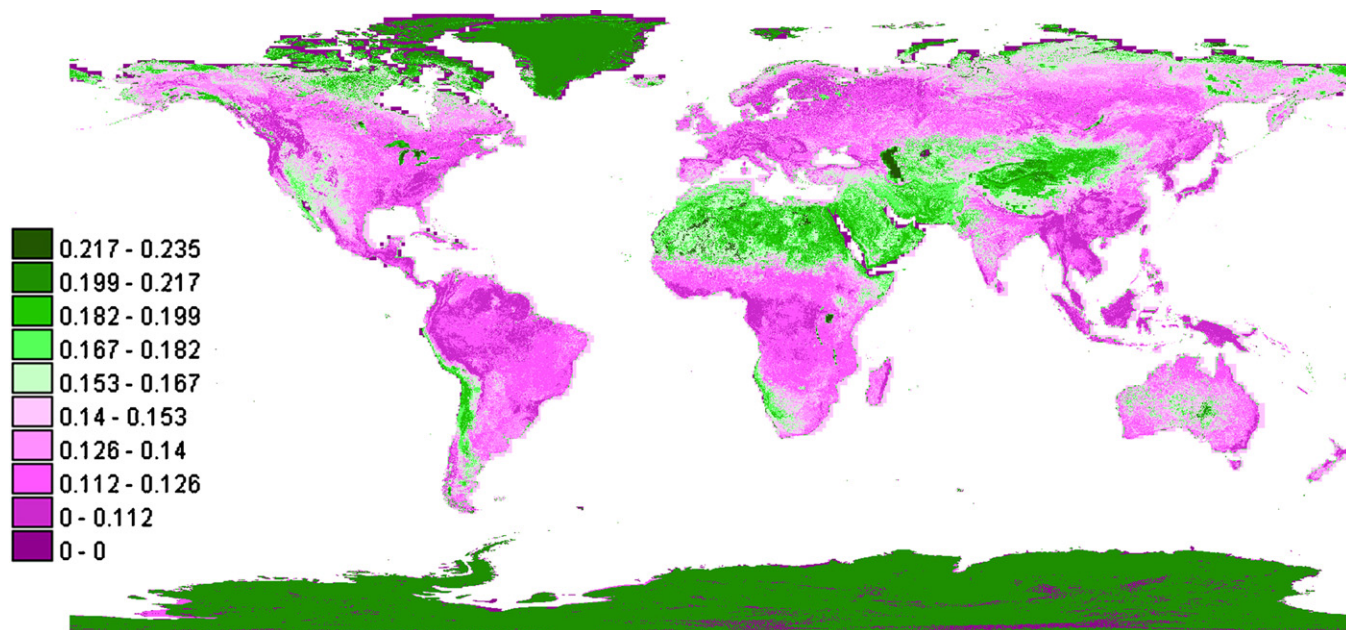


Fig. 4. Mean statistical sensitivity of the ecosystem functionality index (EFI) as overall coefficient of variation of all modified index values in 1 km resolution and WGS 1984 projection. High coefficient of variation values are colored green while low values are colored purple. Class breaks were calculated using the Jenks natural breaks algorithm. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

region in northwestern North America, and northeastern Asia were also selected more frequently than other regions across the globe.

3.3. How do our results compare to measures of ecosystems' exergy growth?

Table 3 indicates that the findings of this analysis are generally in accordance with the values given for eco-exergy growth in the study by Jørgensen (2010). A Spearman correlation analysis revealed consistency with a positive but not significant correlation

coefficient of 0.62 ($p = 0.054$). Highest mean EFI values and highest eco-exergy were recorded for forested regions.

3.4. Does higher ecosystem functionality prevent climate-change-induced net primary production loss?

The ecosystems in the southern hemisphere have been characterized by drought induced NPP loss rates that may be related to global climate change. This contrasts with the results for a number of landscapes in the northern hemisphere where relative growth of NPP was observed to increase. In the map that visualizes

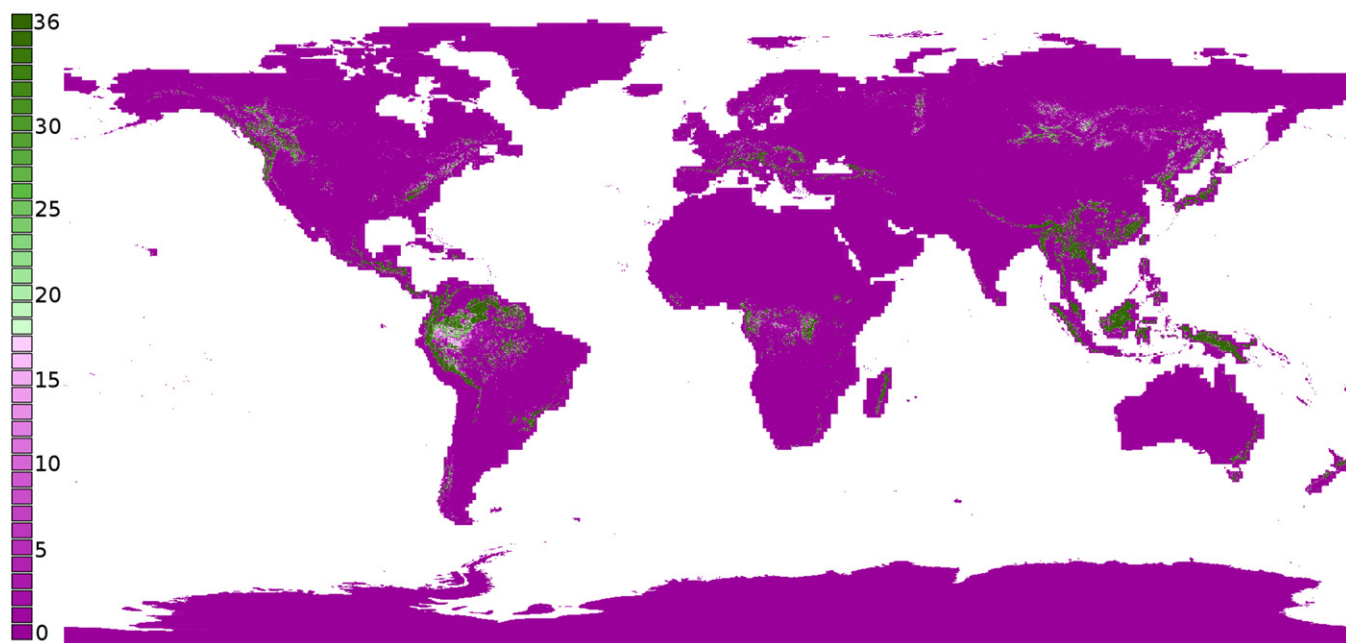


Fig. 5. Global map of the volatility (frequency of that the index value achieved at least 60% of the maximum index value over all indices of sensitivity analysis) in 1 km resolution and WGS 1984 projection. High frequency values are colored green while low index values are colored purple. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

Table 3

Production of eco-exergy and ecosystem service utilization by humanity according to Jørgensen (2010) in comparison to mean values for ecosystem functionality for different ecosystem types.

Ecosystem types (Jørgensen, 2010)	Grouped ecosystem types (Olson, 1994) from USGS Vers.2.0 ^a	GJ/ha year eco-exergy (Jørgensen, 2010)	Mean values of ecosystem functionality
Desert	Bare desert, semi desert trees and shrub, glacier ice, sand desert, polar and alpine desert	2070	4.56
Open Sea	No land cover classes assigned	2380	NA
Coastal Zones	Coastal wetland, mangroves, coastal fringe, beaches and dunes, bare coastal dunes, residual dunes and beaches, compound coastlines	4830	24.02
Coral Reefs, Estuaries	No land cover classes assigned	960	NA
Lakes, Rivers	No land cover classes assigned	93.5	NA
Coniferous Forests	Coniferous forest, deciduous conifer boreal forest, cool conifer forest, conifer forest, narrow conifers, southern hemisphere conifers	539	31.28
Deciduous Forests	Deciduous broadleaf forest, deciduous and mixed boreal forest, deciduous tree crop	1.0 mill.	33.99
Temperate Rainforest	Cool rain forest	1.5 mill.	44.00
Tropical Rainforest	Tropical rain forest, tropical degraded forest, rain green tropical forest	3.0 mill.	41.15
Tundra	Upland tundra, arctic tundra	7280	19.00
Croplands	Cool crops and towns, crops and towns, corn and beans cropland, rice paddy and field, hot irrigated cropland, cold irrigated cropland, crop and water mixtures	420	19.81
Grassland	Low sparse grassland, tall grasses and shrubs, hot and mild grasses and shrubs, grass crops	18	18.14
Wetlands	Wooded wetlands and swamp, marsh wetland	45	25.73

^a Several land cover categories of Olson (1994) are not listed as it was not possible to assign them to one land cover classification of (Jørgensen, 2010) or because data for ecosystem functionality were insufficient. These categories were omitted during analysis.

the relationship between ecosystem functionality and loss of net primary production (between 2000 and 2010; Fig. 6) the areas with high EFI values and relative growth of NPP are displayed in blue while areas with high EFI values and relative loss of NPP are

displayed in purple. Although EFI and NPP loss are not strongly correlated with $r = -0.05$ ($p < 0.0001$), broad global patterns linking the two measures are apparent in the bivariate map (Fig. 6). Blue areas with high EFI values and NPP growth were

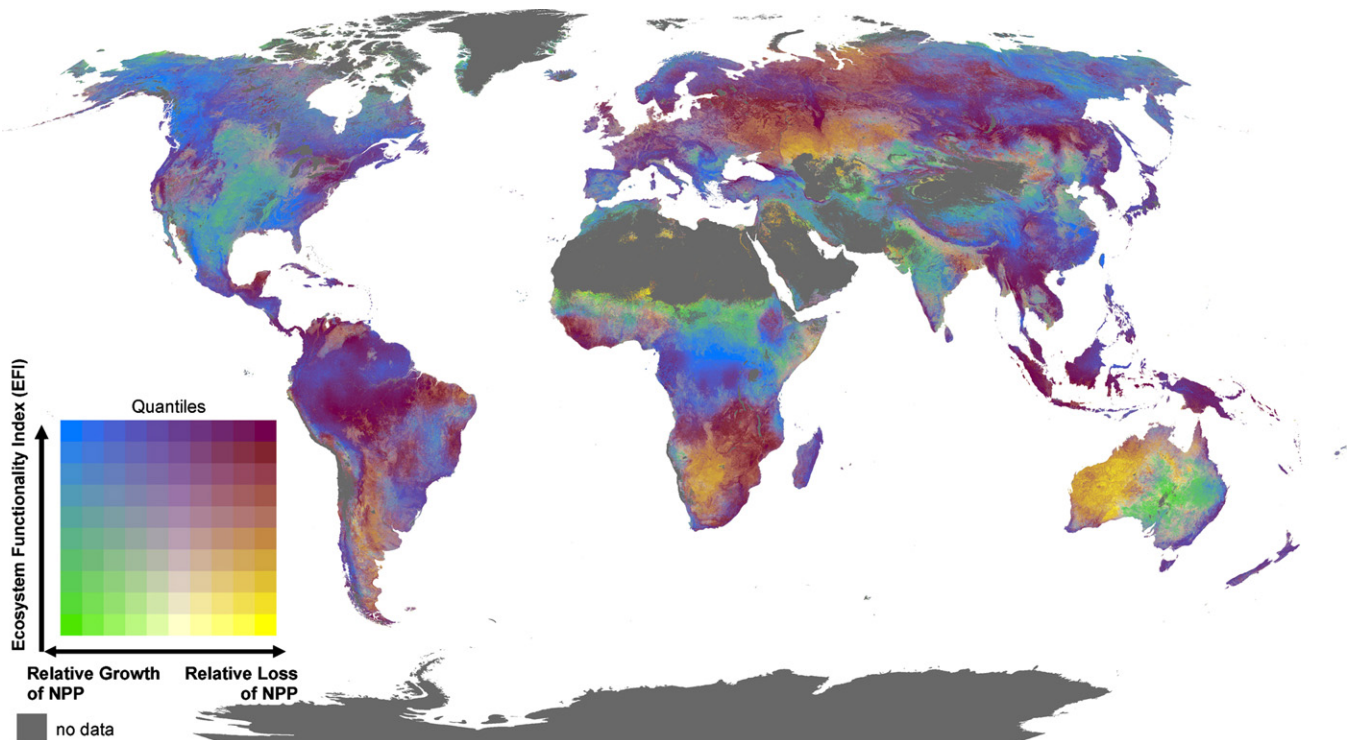


Fig. 6. Global choropleth bivariate map of the ecosystem functionality index (EFI) and the relative loss and growth of net primary production between 2000 and 2010 (Zhao and Running, 2010) in 1 km resolution. Class breaks were calculated using quantile breaks.

recorded mainly in North America and northern Asia as well as in some parts in central Africa and South-East Asia. Purple areas with very high EFI values and high NPP loss were distributed all over the world but mainly in South America, parts of southern Africa, South-East Asia and central Eurasia. These results suggest that there is no simple link between net primary production loss and ecosystem functionality.

4. Discussion

Most scientific studies on ecosystem behavior and concepts that inform conservation policy focus on compositional diagnostics and linear interactions under prevailing conditions rather than attempt to capture systemic function and processes. In this study, a metasytemic approach identifies the specific relationships between the constituent parts of an ecosystem and the contribution this makes to the function and resilience of an ecosystem. These links are captured in the form of an index and then projected onto a global map. A number of expected outcomes are derived including the high values for tropical regions and forests in general. That said a number of noticeable differences between these results and the more conventional maps representing global biodiversity are evident. For instance, this model awards higher values to boreal and certain northern temperate forest regions partly due to the high weighting given to contributing factor of biomass. The importance of this factor in the function and regulation of ecosystems is argued extensively in the various studies on non-equilibrium thermodynamics and ecosystem exergy by Jørgensen et al. (2000) and Jørgensen (2006). Biodiversity and carbon storage (biomass) are inexorably linked and cannot be treated as separate entities as is so often portrayed in recent studies and debates on climate change. Standard measures of biodiversity used in strategies for conservation include diversity, rarity, endemism and representativeness. However, these are most often applied without consideration for the wider function or structure of ecosystems. In this study attributes of diversity and structure are used in the context of ecosystem complexity and complementary functionality. The findings of this research represent a marked departure from a species-orientated strategy towards a more process-driven and functional approach to prioritizing areas for conservation.

There are caveats to using this index. The patchy and inconsistent nature of global data can distort the empirical and cartographic outcomes. Most of the indicators used in the algorithm are model-based. Global forcing functions such as solar radiation and precipitation that are relevant to the global distribution of the indicators are not taken into account in the construction of the index. Furthermore, the index only provides proxy measures of ecosystem function and complexity, as an 'equation of everything' does not yet exist. Nevertheless, the combined effects of the different factors influencing energy dissipation in ecosystems are presented that then allow comparisons to be made between the different ecosystems and biogeographical regions.

The sensitivity analysis is incorporated in to the model to lend a certain amount of robustness against charges of over-simplifying ecosystem functionality. The relative influence of different indicators does not imply that the index settings are unfavorable but provides information on the importance of the various indicators of data quality. The purpose of comparing the results with the findings from Jørgensen's research (Jørgensen, 2010) was to provide a certain degree of external validation of the method. The authors would argue that this study builds on the work by Jørgensen (2010) in that proxy indicators for exergy growth are spatially represented for the major global ecosystems and that this is a more appropriate format for landscape planning.

The value of using principles of ecosystem complexity and functionality goes beyond just an ease of understanding and application. Frequently, conservation action is frustrated by conflicting interests and ambiguity that often leads to compartmentalized micromanagement for species or habitats. This does little to address the sort of global problems that now manifest in extreme ecosystem dynamics. Ultimately, all of life is determined by energy intake and use, and measures of ecosystem structure and function that reflect this are likely to provide more useful and relevant platforms on which to build effective conservation strategies.

More specifically, in conservation, despite encouraging moves toward more coarse-filter, top-down strategies for protecting biodiversity (Chan et al., 2006; Kapos et al., 2008; Naidoo et al., 2008), compositional representations of nature continue to drive strategies for protecting biodiversity. Examples include the Global Biodiversity Hotspots (Myers, 2003; Myers et al., 2000), Centers of Plant Diversity (Davis et al., 1994–1997), Endemic Bird Areas (Stattersfield et al., 1998), Alliance for Zero Extinction Sites (Ricketts et al., 2005) or the Global 200 terrestrial ecoregions (Olson and Dinerstein, 1998).

The ecosystem functionality model presented in this paper attempts to break away from this mold and offers a more realistic approach for proactive strategies to conserve the buffer and adaptive capacity of ecosystems under the stresses of climate change. By adopting a coarse-filter, whole systems approach to conservation the problems of fragmented policy and action inherent in some of the existing strategies for dealing with climate-induced ecological problems can be avoided (compare Brooks et al., 2006).

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