

**Exploring the links between social metabolism and biodiversity distribution
across landscape gradients: a regional-scale contribution to the land-sharing
versus land-sparing debate**

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Abstract

The debate about the relative merits of the 'land-sparing' and 'land-sharing' approaches to biodiversity conservation is usually addressed at local scale. Here, however, we undertake a regional-scale approach to this issue by exploring the association between the Human Appropriation of Net Primary Production (HANPP) and biodiversity components (plants, amphibians, reptiles, birds and mammals) across a gradient of human-transformed landscapes in Catalonia, Spain. We propose an Intermediate Disturbance Complexity (IDC) model to assess how human disturbance of the photosynthetic capacity affects the landscape patterns and processes that host biodiversity. This model enables us to explore the association between social metabolism (HANPP), landscape structure (composition and spatial configuration) and biodiversity (species richness) by using Negative Binomial Regression (NBR), Exploratory Factor Analysis (EFA) and Structural Equation Modelling (SEM). The empirical association between IDC and landscape complexity and HANPP in Catalonia confirms the expected values of the intermediate disturbance hypothesis. There is some increase in biodiversity when high IDC values correspond to landscape mosaics. NBR and EFA show positive associations between species richness and increasing values of IDC and forest cover for all biodiversity groups except birds. SEM shows that total biodiversity is positively determined by forest cover and, to a lesser extent, by HANPP, and that both factors are negatively associated with each other. The results suggest that 'natural' landscapes (i.e. those dominated by forests) and agroforestry mosaics (i.e. heterogeneous landscapes characterized by a set of land uses possessing contrasting disturbances) provide a synergetic contribution to biodiversity conservation. This 'virtuous triangle' consisting of forest cover, HANPP and biodiversity illustrates the complex human-nature relationships that exist across landscape gradients of human transformation. This energy-landscape integrated analysis provides a robust assessment of the ecological impact of land-use policies at regional scale.

Keywords

Biodiversity conservation, cultural landscapes, food-biodiversity dilemma, global change, human appropriation of net primary production, intermediate disturbance hypothesis.

Introduction

For millennia, global human-driven Land Use and Cover Changes (LUCC) have been increasingly affecting terrestrial ecosystems (Sterling & Ducharne, 2008). They have led to unprecedented levels of landscape transformations worldwide that have greatly increased the amount of what are termed ‘anthropogenic habitats’ (Ellis et al., 2008). The past century was witness to particularly severe LUCC, which affected habitat and species conservation. The human population has continued growing, and the huge increase in global food production through increasingly industrialized and globalized production systems – necessary to satisfy population demands – has provoked many serious socio-ecological impacts and conflicts (Tilman et al., 2002; Mayer et al., 2015).

As a result, human-driven production systems are facing a global challenge amidst a scenario of socio-metabolic transition (Schaffartzik et al., 2014). The dilemma today is how to ensure that the increased land-use intensity required to meet the growing demand for food, feed, fibres and fuels (Godfray et al., 2010) remains compatible with efforts to avoid biodiversity loss (Cardinale et al., 2012). These global trends coexist with other important LUCC such as rural land abandonment at local-to-regional scales. The other face of agricultural intensification – and the abandonment of steep marginal lands – has led to forest transition (Meyfroidt et al., 2011). Another primary LUCC is landscape urbanization, widespread worldwide and concentrated in periurban and the most accessible areas, which competes with intensive cropping and farming for land (e.g. Basnou et al., 2013).

All these LUCC affect the photosynthetic capacity of ecosystems, which may have a serious impact on biodiversity. The Human Appropriation of Net Primary Production (HANPP) is a quantitative estimate of the potential annual biological productivity reduced by human activities such as row crops, timber harvesting, grazing, fire and changes in land use (Krausmann et al., 2013). Greater HANPP reduces the energy availability for other trophic chains and subsequently affects ecological functions and the provision of biodiversity-related ecosystem services. To date, however, HANPP has primarily been assessed at global and regional scales rather than at smaller (landscape) scales, which are more closely related to the

heterogeneous nature (and working scale) of both human and natural systems (Andersen et al., 2015; Marull et al., 2016a). On the other hand, HANPP patterns across landscape gradients and their association with landscape composition and biodiversity have been seldom explored, despite their relevance in regional planning and biodiversity conservation.

From a planning and conservation perspective, analysing HANPP effects on biodiversity across landscape gradients allows us to extend to regional scale the on-going ‘land-sparing’ *versus* ‘land-sharing’ debate (Perfecto & Vandermeer, 2010). The ‘land-sparing’ strategy consists of intensifying human land uses (e.g. cropping or urbanization) in certain areas to dedicate to nature conservation the freed-up (marginal) land (Matson & Vitousek, 2006). By contrast, the ‘land-sharing’ approach seeks to develop a synergistic interaction of human land uses and nature conservation areas within a complex landscape mosaic (Tscharntke et al., 2012). Even those who aim to combine these two approaches stress the need for more research to understand their respective effects on biodiversity conservation (Phalan et al., 2011).

For example, some studies underline the opportunity for biodiversity provided by rural land abandonment; this is the case of the forest transition approach (Rudel et al., 2005), which permits ecosystem recovery in combination with the designation of protected areas and other conservation policies (Grau & Aide, 2008). Conversely, other studies see land abandonment as a threat to the biodiversity found in traditional agroforestry mosaics of cultural landscapes, since it usually goes hand-in-hand with land cover homogenization and has negative consequences for open-habitat species (Preiss et al., 1997). Human-modified landscapes may in fact provide habitats and opportunities for certain species, above all multi-habitat and edge species (Benton et al., 2003), and create a more permeable land-matrix allowing for dispersion of local populations (Shreeve et al., 2004). Thus, thanks to a combination of the edge effect and high ecological connectivity, agroforestry mosaics may host greater biodiversity than more uniform landscapes (Harper et al., 2005).

The dilemma between HANPP and biodiversity conservation across landscape gradients requires further research into the disturbance regimes associated with land-use patterns and their effects on species

richness and ecosystem services (Fischer et al., 2008). More research at greater depth into the patterns and processes involved in landscape metabolism is still required (Pierce, 2014). Many studies highlight the importance for biodiversity conservation of keeping some degree of anthropic disturbance and landscape heterogeneity in cultural landscapes (Jackson et al., 2007). Indeed, an intermediate disturbance hypothesis has been frequently advocated to explain biodiversity maintenance (Huston, 2014), although there is no consensus about its applicability to all types of ecosystems (Fox, 2013). This hypothesis has contrasting lectures at landscape scale in the context of the ‘land-sharing’ *versus* ‘land-sparing’ debate, and its relevance to biodiversity conservation will depend to a great extent on the land-cover patterns generated by the diverse disturbance levels exerted by each anthropic type of land use (Chesson & Huntly, 1997).

On the one hand, intermediate disturbance patterns may generate high biodiversity in human-modified landscapes due to the coexistence of species with contrasting ecological requirements (Barnes et al., 2006). On the other hand, this will also depend on the vertical/horizontal complexity of land-use mosaics, as well as the intensity and direction of their associated socio-metabolic flows (Swift et al., 2004; Marull et al., 2016b). Therefore, understanding and correctly managing these patchy mosaics requires an interdisciplinary approach to the bio-cultural diversity (Parrotta & Trosper, 2012) embedded in agro-ecological landscapes (Matthews & Selman, 2006).

In light of the above, Marull et al. (2016a) have developed an Intermediate Disturbance Complexity (IDC) model to assess how landscape functional structure is affected by different levels of anthropogenic disturbance in ecosystems when altering Net Primary Production (NPP) through LUCC (Marull et al., 2017). The IDC is based on measures to describe the landscape patterns and processes, and uses HANPP as the basic measure of anthropic alteration of ecosystem energy flows. The model assumes that the conservation of heterogeneous and well-connected land matrices, where there is a positive interplay between human energy disturbances and landscape complexity, will ensure greater species richness in cultural landscapes. If this holds true, it will give rise to a hump-shaped relationship between both landscape complexity and available NPP and biodiversity. Yet, to date, these patterns have rarely been

assessed across landscape gradients. The main contribution of this paper is to provide an innovative analytical approach, based on a previous (IDC) model, of combined effects of energy appropriation and landscape structure on biodiversity. It then provides a basis for the energy-landscape integrated analysis of the ecological impact of land-use policies at regional scale.

The objective of this paper is to discover the links that exist between social metabolism and biodiversity across gradients of landscape transformation at regional scale in a Mediterranean region (Catalonia), thereby assessing how ‘land-sharing/land-sparing’ approaches can contribute to explaining biodiversity in human-transformed landscapes. Using UTM 10-km cells, we account for the association between current landscape patterns (composition and spatial configuration), human disturbance (HANPP) and biodiversity (species richness of main biodiversity groups). First, we apply the IDC model, which combines a set of metrics of land-cover patterns, ecological processes and socio-metabolic changes. We then use Negative Binomial Regression (NBR), Exploratory Factor Analysis (EFA) and Structural Equation Modelling (SEM) to assess how these metrics affect the capacity of landscapes to host biodiversity.

1. Methods

1.1. Study area

The study is focused on Catalonia (NE Spain; 32,000 km²), part of the Mediterranean biodiversity hotspot and possessor of great ecosystem diversity due to its varied topography (with elevations ranging from 0 to 3,143 m a.s.l.) and important climatic gradients (Ninyerola et al., 2000). Landscape structure in Catalonia is the product of the long-term interaction between human activity and nature that characterizes Mediterranean bio-cultural regions (Grove & Rackman, 2001). Water resources are limited, as corresponding to a Mediterranean region, and dominated by the Ebro River (average water flow of 426 m³s⁻¹) whose catchment occupies 48% of Catalanian land. Other major rivers in the region are the Ter (25 m³s⁻¹), the Llobregat (21 m³s⁻¹) and the Fluvià (10 m³s⁻¹). In recent decades, the abandonment of steep, marginal agricultural areas has led to an upturn in the extent of forest cover (currently 40% of the land

surface area of Catalonia) (Fig. A1). The most favourable areas for human settlement – generally plains and other relatively flat areas – exhibit contrasting situations involving both growing crop intensification and greater urbanization. In drier areas, the water uses for agricultural, industrial or urban purposes entail an important stress for the river and riparian functioning and biodiversity, which play a key role as wildlife corridors. The central coastline of Catalonia around the city of Barcelona is one of the most populated and industrialized areas on the northern Mediterranean rim.

1.2.IDC model

Marull et al. (2016a) proposed the Intermediate Disturbance Complexity (IDC) model (Fig. 1) to explain how a combination of anthropogenic disturbance to ecosystem functioning and landscape structure may affect the capacity of the land matrix to host biodiversity (Fig. 2). In its initial version, IDC was conceived as the product of two variables that respectively summarize landscape patterns and human disturbance: the Shannon-Wiener index (H') of land cover and the remainder of the human appropriation of net primary production ($1-HANPP$).

The study was based on 251 UTM 10-km cells lying completely within the borders of Catalonia. The landscape structure of these cells was taken from the 2009 Land Cover Map of Catalonia (www.creaf.uab.es/mcsc/) reclassified into a set of principal land cover categories (Fig. A1). The land-cover percentage of each category was obtained for each UTM cell and these values were then used to calculate H' (Shannon & Weaver, 1949). HANPP values were also calculated for each UTM cell according to the approach used by Haberl et al. (2014):

$$HANPP = HANPP_{luc} + HANPP_{harv}; HANPP_{luc} = NPP_0 - NPP_{act}$$

where $HANPP_{harv}$ is the NPP appropriation due to harvests and $HANPP_{luc}$ is the change in the NPP due to human-induced land alteration. $HANPP_{luc}$ is defined as the difference between the NPP of the potential (NPP_0) and actual (NPP_{act}) vegetation. Thus, HANPP was calculated for each land-cover category and UTM cell as the weighted sum of fixed coefficients (w_i) multiplied by the proportion of the land surface-area occupied by each land cover type:

$$\text{HANPP} = \sum_{i=1}^k w_i p_i$$

where w_i is the weight and p_i the proportion of land cover i in a UTM cell. To estimate HANPP values it is necessary to assess different levels and amounts of NPP and harvests. Harvest ratios taken from each land cover were transformed into energy values. Conversion factors such as the residue/product ratio losses (Guzmán et al., 2014) were then applied to account for the unharvested biomass in each land-cover category.

Then IDC was improved by applying a previously developed index – the Le (Landscape Ecology metric) – that aims to describe a combination of landscape patterns and processes (Marull et al., 2016b):

$$\text{IDC} = \text{Le} (1 - \text{HANPP} / 100)$$

Le was obtained by orthogonalizing two landscape indices using canonical correlation analysis:

$$\text{Le} = \left(a L + b \frac{\text{ECI}}{10} \right) 1 / (a + b)$$

where a and b are the canonical coefficients. L is an improved index of landscape heterogeneity based on H' that subtracts the built-up areas (Marull et al., 2016a). ECI is an index of ecological connectivity that summarises landscape processes on a normalized scale from 0 to 10 (Marull & Mallarach 2005).

Fig. 1 depicts the shapes of all possible values for the theoretical relationship between human disturbance and landscape complexity wherever it is possible to represent the site-specific disturbance-complexity (IDC) values of a given territory. There is one H' (or Le) and one HANPP value for each sample cell. $1 - \text{HANPP}$ expresses the average energy available for non-domesticated species in each sample cell. Importantly, the same HANPP value can be obtained with different land-cover combinations (i.e. having one or various habitats composition). Likewise, Le can also be obtained using a number of land-cover categories, although the contribution of each land cover to biodiversity maintenance may vary (e.g. due to the variable amount of energy available for conserving trophic chains).

1.3. Biodiversity data

As a test of IDC against biodiversity data components, we used the observed species richness of different taxonomic groups (vascular plants, amphibians, reptiles, birds and mammals) and the total species richness per UTM 10-km cell in Catalonia (Fig. A2). These data were obtained from the Biodiversity Data Bank of Catalonia (BDBC; <http://biodiver.bio.ub.es/biocat>), a public data server that collates comprehensive records of biodiversity components in Catalonia. We then analysed the presence of taxa to obtain the species richness of each studied group per UTM cell.

1.4. Statistical analyses

Given that it is not disturbance as such but the disturbance-complexity interplay (IDC) that is determinant in biodiversity conservation at landscape scale, we did not assume any clear statistical relationship between species richness and HANPP when these two variables are taken separately. Rather, we expected that there would be a relationship between species richness and HANPP combined with Le (landscape connected-heterogeneity) as per the ‘land-sharing’ paradigm. Simultaneously, we also expected to find a relationship between great species richness (of certain biodiversity components) and the existence of homogeneous landscapes dominated by ‘natural’ categories of land covers (i.e. those with low human-driven disturbance) according to the ‘land-sparing’ paradigm. To test the association between landscape metrics, HANPP and biodiversity at UTM 10-km level, we performed three complementary statistical analyses:

First, we ran a Negative Binomial Regression (NBR) for the species richness of vascular plants, amphibians, reptiles, birds and mammals, and total biodiversity (including all the studied taxa) that took into account IDC and land-cover composition (in %) per UTM cell in 2009. The aim of this NBR (Hilbe, 2011) was to test the aggregated contribution to biodiversity of both the ‘land-sharing’ and the ‘land-sparing’ components.

Second, we performed an Exploratory Factor Analysis (EFA) with varimax rotation (Costello & Osborne, 2005) to explore the association between the measured variables of landscape, HANPP and biodiversity. The EFA was carried out using separately the taxa with most data (vascular plants, mammals

and birds) and total biodiversity, Le and HANPP (both components of IDC, treated independently), IDC, and the proportion of different land-cover categories in each UTM cell.

Finally, in order to disentangle the direct and indirect effects of landscape structure and HANPP on biodiversity, a Structural Equation Model (SEM) was constructed for each of the main biodiversity groups (vascular plants, birds and mammals) and total biodiversity. The SEM took into account the direct effects of Le and HANPP (the two IDC variables) and their indirect effects reflected in land-cover composition (Cm) controlled for elevation (MDE). The Model was conducted with the SEM package in R (Fox et al., 2016).

2. Results

The IDC empirical results obtained for Catalonia show a hump-shaped relationship (Fig. 2a) in which the highest value of IDC is attained when 1-HANPP and Le tend to 60%, thereby confirming the intermediate disturbance hypothesis. Furthermore, there is no clear relationship between ‘natural’ landscapes (i.e. homogeneous landscapes dominated by land-cover categories with the highest values for 1-HANPP) and total biodiversity (Fig. 2b). Conversely, there is a certain tendency for biodiversity to increase when high IDC values are obtained in heterogeneous landscapes.

The NBR was applied to all the selected taxonomic groups. We used Principal Component Analysis (PCA) to identify two main factors (Table A1a): the first factor (34.8% of variance) showed higher loadings for IDC (‘land-sharing’) and forest cover (‘land-sparing’), while the second factor (22.9% of variance) had greater loadings for scrubland, pastureland, river corridors and unproductive land-cover categories. Then, we used these factors and the species richness of each taxonomic group to perform a NBR (Fig. 3). The NBR results show a positive association between species richness and increasing values for the first factor (corresponding to IDC and forest land cover) for all biodiversity groups except birds and reptiles (Chi-Square test at $p < 0.05$). These results highlight the synergetic contribution to biodiversity conservation made by both ‘natural’ landscapes (i.e. those dominated by forests) and agroforestry mosaics (i.e. heterogeneous landscapes with a set of land uses of contrasting disturbances).

The EFA (Fig. 4) confirms the positive association between IDC and forest cover, and the negative association between these variables and cropland and HANPP, which are, in turn, positively associated one another. By contrast, Le is positively associated in the landscape with several land-cover categories of minor importance but is negatively associated with built-up areas and road and rail networks affecting landscape structure and function. In terms of biodiversity components, total biodiversity is more closely associated with IDC (especially vascular plants) and forest cover (especially mammals). No relationship between these factors and species richness in birds was detected.

The SEM was applied for the main taxonomic groups and total biodiversity, showing all the paths significant (Tables A2-A5). A PCA with land-cover composition was conducted to reduce the number of predictors and their redundancy in the SEM (Table A1b). The first axis (38.5% of variance) was mainly correlated with forest (positively) and crop (negatively) cover, while the second axis (31.2% of variance) was most closely associated with non-urban (positively) and urban (negatively) cover. The SEM results (Fig. 5) show that total biodiversity was positively affected by the first landscape factor (forest-cropland gradient) and, to a lesser extent, by HANPP (scores of 2.08 and 1.82, respectively). It is worth noting that HANPP and this landscape component are negatively associated (coefficient: -0.97). Le probably has no important effect due to the fact that in the SEM two contrasting factors affect this variable: large forest patches (landscape homogeneity) and land cover mosaics. Indeed, SEM shows that overall biodiversity in Catalonia is associated with ‘natural’ spaces (or ‘land-sparing’) but also with the intermediate disturbance hypothesis (or ‘land-sharing’). SEM has been tested for several taxa (vascular plants, mammals and birds) and has always provided consistent results.

3. Discussion

3.1. Contribution to the ‘land-sharing/land-sparing’ debate at regional scale

This study confirms the validity of IDC as a proxy for assessing how different levels of HANPP affect the functional landscape structures that host biodiversity (Fig. 2). We have extended IDC from a formerly local approach (Marull et al., 2016a) to regional scale via the use of a gradient of landscapes with

contrasting degrees of HANPP. The empirical association between IDC and landscape complexity (Le) and human disturbance (HANPP) confirms the values predicted by the intermediate disturbance hypothesis, and corroborates that there is an optimal combination of landscape heterogeneity and HANPP that hosts the highest total biodiversity.

From a ‘land-sharing/land-sparing’ standpoint, our results suggest the importance of combining both approaches as a means of maintaining high biodiversity levels in landscapes of human-transformed regions. NBR (Fig. 3) results show a positive association between forest cover and landscape complexity for all biodiversity groups except birds. EFA (Fig. 4) ones indicate that overall biodiversity is associated with IDC (especially vascular plants) and forest (especially mammals). Finally, the SEM test (Fig. 5) shows that the resulting ‘virtuous triangle’ between forest cover, HANPP and total biodiversity can clearly explain the complex human-nature relationship inherent to human transformation across landscape gradients. All these results confirm the synergistic contribution to biodiversity maintenance made by ‘natural’ landscapes (i.e. those dominated by forests) and agroforestry mosaics (i.e. heterogeneous landscapes characterized by a set of land uses possessing contrasting disturbances). Hence, the restoring of cultural landscape heterogeneity via more sustainable farming systems could potentially be of great interest in the future.

The combination of spatially uneven disturbances and land-cover heterogeneity in cultural landscapes offers habitats for species and ecological communities associated with these human-modified landscapes. As a result, β -diversity at landscape scale increases and compensates for the fall in α -diversity at local (plot) level in croplands, the typical impact of organic farming on biodiversity at local scale (Gliessmann, 1990). A recent global review by Tscharntke et al. (2012) has stressed that spatial heterogeneity creates an ecological dissimilarity that determines landscape-wide biodiversity kept in human modified landscapes. Provided that farming disturbances – and the novel farm-associated biodiversity (Altieri, 1999) – do not threaten the survival of the species richness sheltering in the most undisturbed land units, this whole process could even entail an increase in γ -diversity at regional scale.

Our results show that landscape patterns and HANPP levels affect biodiversity groups in different ways depending on their contrasting ecological requirements and dispersal abilities. This is an obvious result, yet one that is rarely supported by empirical data in regional analyses. On the one hand, mismatches between richness of different biodiversity groups have been attributed to contrasting ecological filtering (Flather et al., 1997; Gaston, 2000). On the other hand, the role of landscape structure and composition in biodiversity distribution in human-modified regions has started to be explored. Herrera et al. (2016) recently emphasized the importance of forest cover and landscape complexity in vertebrate responses at both species (i.e. abundance) and community (i.e. richness) levels in a regional approach.

In Catalonia, regional-scale biodiversity patterns remain largely unexplored despite the abundance of biodiversity databases. Based on correlational approaches, Pausas et al. (2003) and Pino et al. (2005) found that the species richness per UTM 10-km square of native and alien plants depends, respectively, on environmental and human-driven landscape heterogeneity, and the latter is presumably associated with intermediate levels of HANPP. In addition, Santos et al. (2008) have highlighted the importance of agroforestry landscape mosaics (providing intermediate-to-high habitat heterogeneity and contrasting HANPP levels) for explaining bird species richness in UTM 1-km squares, a finding that has been confirmed in a study carried out at European scale (BirdLife International, 2004). Unfortunately, no previous information is available for mammal species. Nevertheless, our study does highlight the fact that mammal species richness positively responds to low levels of disturbance and human-driven landscape heterogeneity. This statement is supported by previous studies showing that habitat loss and degradation is the greatest threat to terrestrial mammals in Europe (Temple & Terry 2007).

3.2. Implications of the ‘land-sharing/land-sparing’ approach for land-use policy

Our results suggest that a combination of ‘land-sparing’ and ‘land-sharing’ approaches is especially indicated for protecting high biodiversity levels in human-transformed regions. Planning initiatives aimed at including cultural landscapes should not be regarded as incompatible with more mainstream policies designed to create networks of natural protected areas including pristine undisturbed landscapes, whose

ultimate aim is the preservation of specific habitats and/or charismatic species. The combination of traditional integrated land uses and heterogeneous well-connected habitats in urbanized regions facilitates spatial and temporal insurance, and provides greater resilience to ecological processes (Loreau et al., 2003). Consequently, a wildlife-friendly agro-ecological matrix could be a useful strategy for enhancing both biodiversity and food security. Cultural landscapes are greatly threatened in Europe with the contrasting trends of land abandonment and forest encroachment in marginal areas, as well as of crop intensification and urbanization in lowlands (Basnou et al., 2013). Both trends lead to degradation and rarefaction of heterogeneous landscape mosaics.

European policies designed to increase food production and safeguard protected areas (e.g. Common Agricultural Policy and Habitats/Birds Directives) have not generally taken into account the sustainability of these cultural landscapes. Thus, agricultural intensification threatens many regulatory and sustenance ecosystem services (i.e. water cycle and soil fertility, ecological processes and biodiversity) provided by cultural landscapes, while urban sprawl arising from the real-estate boom in recent decades has caused a substantial loss of landscape functions in lowland areas. By contrast, the abandoning of croplands and subsequent forest regrowth are leading to a recovery in forest biodiversity in remote upland areas, but also to a substantial losses in certain biodiversity components of great conservation concern (Melero et al., 2016).

The upshot is the abandoning of traditional agricultural activities, forest transition and urban sprawl. Traditional agro-ecosystems had organized their land usages in terms of different gradients of energy turnover, which kept an integrated management of multifunctional landscapes given that their survival depended on this land-use efficiency. In order to offset the energy lost in the inefficient human exploitation of animal bioconversion (Guzmán & González de Molina 2009), traditional organic farmers carefully ensured that livestock breeding was closely integrated with croplands, pastures and forest spaces (Krausmann, 2004). These traditional landscape mosaics, and their closed energy cycles, ensured that the ‘land-sharing’ strategy worked in favour of biological conservation (Tscharntke et al., 2012). Today, the socio-ecological transition to agro-industrial farm systems that rely on external inputs from underground

fossil fuels has enabled society to overcome the age-old energy dependency on renewable bioconverters (Schaffartzik et al., 2014).

The lack of an integrated management of energy flows and land uses, differentiated at diverse spatial scales and temporal rhythms, is part of the current global ecological crisis and ought to persuade societies to recover their lost landscape efficiency (Marull et al., 2016b). Industrial farming and animal breeding has cut off energy efficiency, raised the amount of agricultural greenhouse gas emissions, and generated widespread pollution by agrochemicals. Society is increasingly demanding more sustainable foodscapes that, together with healthier and nearer food provision, could be able to maintain a relevant share of species richness able to provide the whole range of ecosystem services. Despite the loss of traditional agro-forest mosaics, our results show that agroecosystems still contribute to a relevant extent to the overall biodiversity found in Catalonia (Cervera et al., 2016). Hence, if we can raise this contribution in future, we may take advantage of the farmland landscapes' capacity– still largely underused –for improving biodiversity and biodiversity-related ecosystem services.

3.3. Concluding remarks

By using both the Human Appropriation of Net Primary Production (HANPP) and the Landscape Ecology metric (Le) as proxies of biodiversity across landscape gradients of human transformation, the IDC model here proposed has proven to be statistically robust to apply the concept of intermediate disturbance complexity to landscape ecology assessment performed at regional scale (Catalonia, NE Spain). IDC metrics may assist to appraise the impact of land-use policies on ecological landscape functioning, especially in human-modified regions, thus helping to resolve the global food-biodiversity dilemma (Cardinale et al., 2012).

Our results have brought to light an interesting synergy between the classical 'land-sparing' approach, that promotes natural reserves for biodiversity conservation, and the newer 'land-sharing' approach, that highlights the key role that a wildlife-friendly mosaic of land uses can play in biodiversity maintenance in human-transformed landscapes (Fisher et al., 2008). 'Land-sparing' is based on homogeneous landscapes,

either abandoned or intensively used with important inputs of fertilizers and agrochemicals that usually attain very high agricultural yields, and might help to reduce the need to convert natural ecosystems into farmland to meet food production targets (Grau et al., 2013). However, our results back the claim that high biodiversity can also be achieved through correct landscape management that combines traditional rural knowledge and new agro-ecological practices in cultural landscapes (Agnoletti, 2014).

The HANPP-based approach to social metabolism proposed here needs to be adapted and enlarged in order to give account of the cyclical character of agroecosystems. While HANPP can be a useful indicator for studies performed at global or regional scales, it becomes inadequate at local scales. It is important to note that the use of HANPP as a measure of disturbance might have limitations in specific situations (in particular as HANPP values can become negative when $NPP_{act} > NPP_0$ due to fertilizer input or irrigation). The energy-landscape integrated analysis developed at local scale by Marull et al. (2016b) is aimed at meeting this challenge by using a graph modelling of energy turnover in agroecosystems to capture the interlinked complexity and information embedded in the pattern of flows that become imprinted in cultural landscapes.

The long-term decrease of energy efficiency, including non-renewable external inputs (fertilizers, pesticides, fuel); can be related with the deterioration of agroecosystems' in terms of farm-associated biodiversity and related ecosystem services. Confirming or rejecting this interpretation requires applying the energy-landscape integrated analysis to different biomes and time periods, and using large biodiversity datasets to find out where the critical thresholds in energy throughputs and landscape complexity interplay are located.

A key avenue for further research using these novel methods is to assess how land-use policies could favour more synergistic relationships among anthropic energy flows patterns, landscape ecological functioning and biodiversity as a means of achieving more sustainable landscapes.

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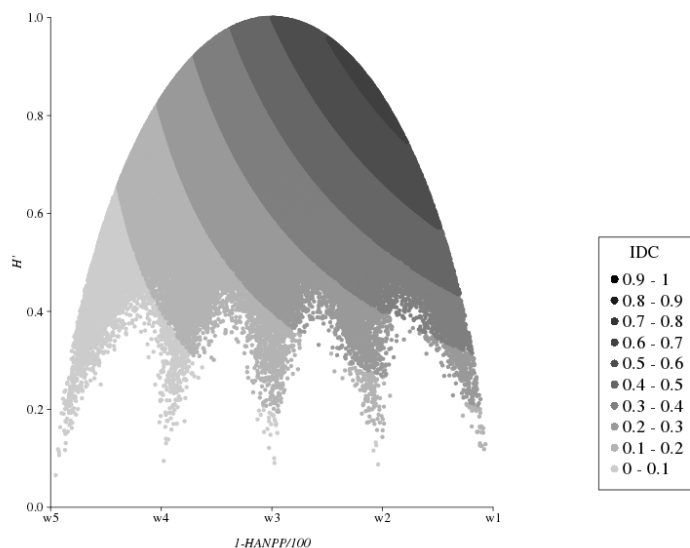
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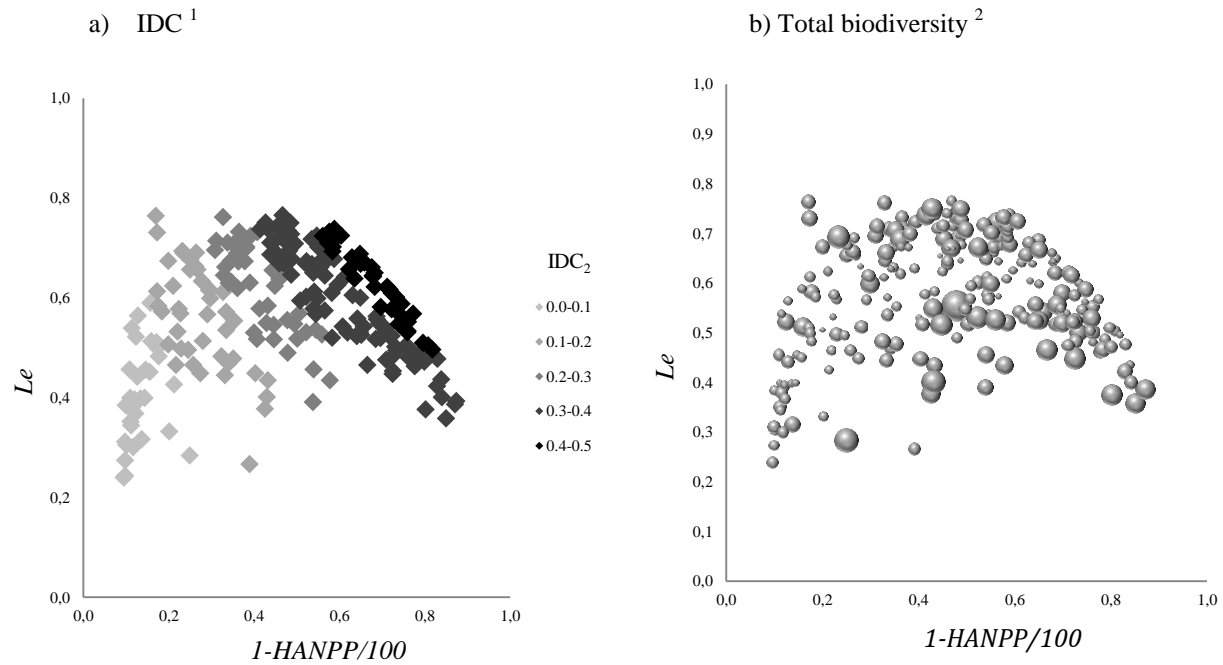
Figures

Figure 1. Theoretical values of the Intermediate Disturbance Complexity (IDC) model. Relationship between Shannon-Wiener Index (H') and Human Appropriation of Net Primary Production (HANPP). The model depicts the shape of all possible values adopted by the 'landscape complexity' and the 'land-use disturbance' wherever it is possible to represent the site-specific disturbance-complexity values of a given territory.



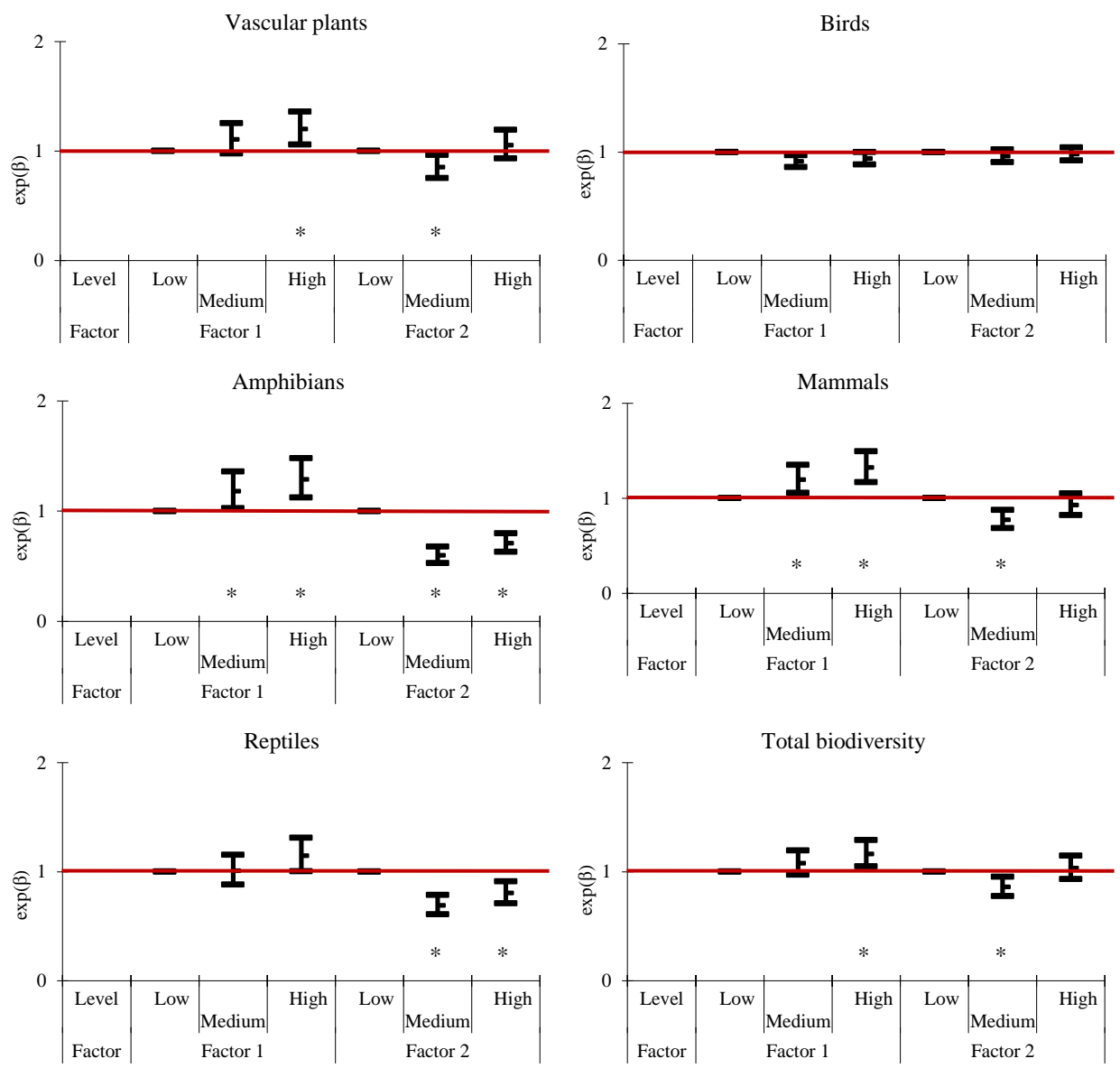
Note: $IDC = H'(1 - HANPP/100)$

Figure 2. Empirical values of the Intermediate Disturbance Complexity model (IDC) (a). Relationship between Landscape Ecology metric (Le), Human Appropriation of Net Primary Production (HANPP) and total biodiversity (b) in UTM 10-km sample cells in Catalonia (2009). The empirical results seem to confirm the intermediate disturbance hypothesis that explains how anthropogenic control of energy fluxes and landscape structure affect the capacity of ecosystems to host biodiversity.



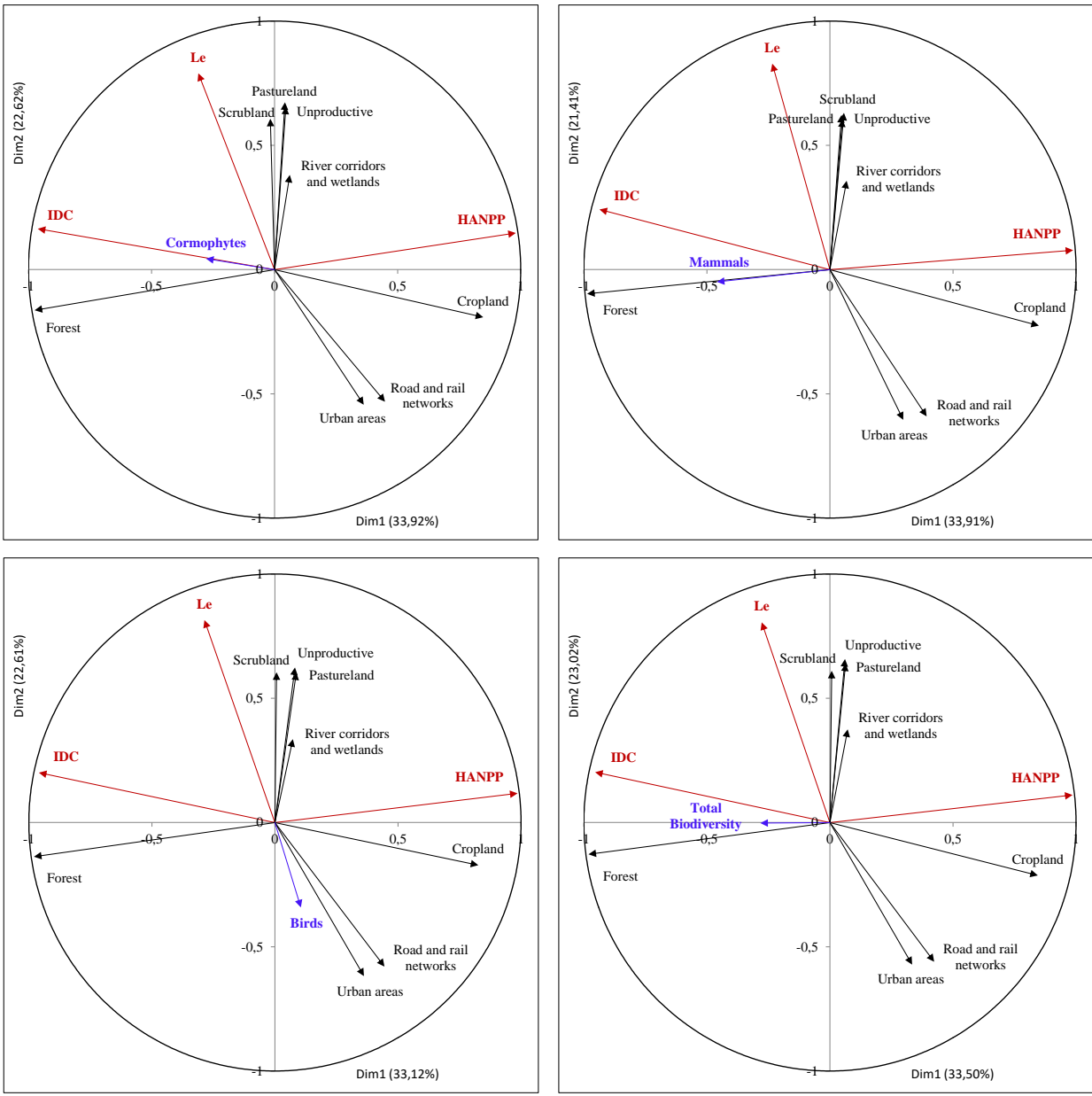
Notes: ¹ IDC = Le (1 - HANPP/100); ² Total biodiversity in Catalonia (including vascular plants, reptiles, amphibians, birds and mammals; the size of the dot is proportional to the species richness) –the dispersion of values are mainly produced by birds.

Figure 3. Negative Binomial Regression (NBR) for the variables: vascular plant, amphibian, reptile, bird and mammal species richness, and total biodiversity; taking into account the Intermediate Disturbance Complexity model (IDC), and land covers of Catalonia in 2009 (UTM 10-km sample cells)¹. The results show the synergetic contribution of ‘natural’ landscapes and agroforestry mosaics (heterogeneous landscapes with land uses of contrasting disturbances) to biodiversity conservation.



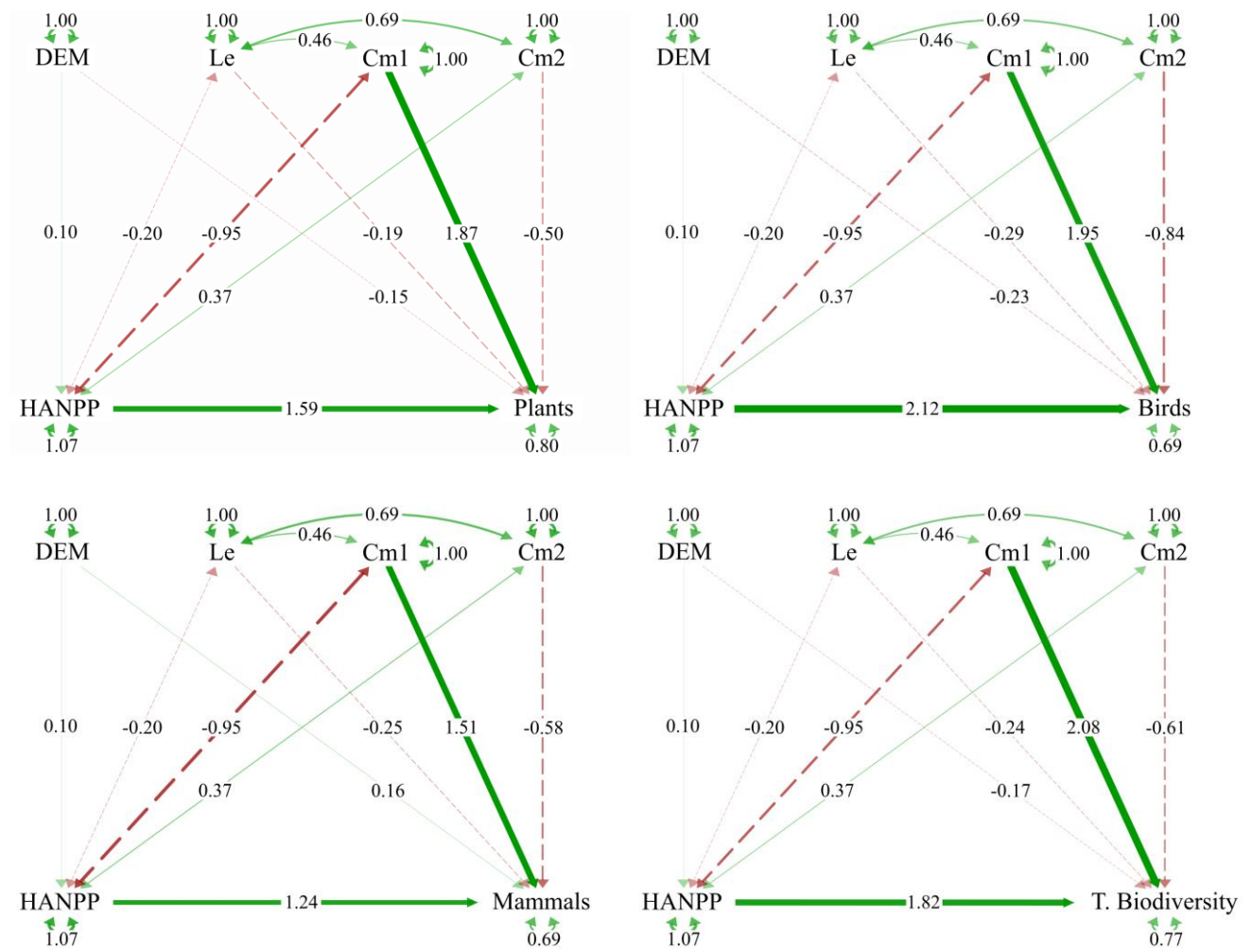
Note: ¹ Principal Component Analysis in Table A1. * Indicates a significant association of each factor with the response variable for the associated Chi-Square test at $p < 0.05$.

Figure 4. Exploratory Factor Analysis (EFA) applied to the variables: vascular plant, bird and mammal species richness, and total biodiversity; taking into account the variables Le, HANPP and IDC¹, and the land covers of Catalonia in 2009 (UTM10-km sample cells). Landscapes dominated by forests but also landscape mosaics are relevant for biodiversity conservation.



Notes: ¹ Landscape Ecology metric (Le), Human Appropriation of Net Primary Production (HANPP), and Intermediate Disturbance Complexity model (IDC).

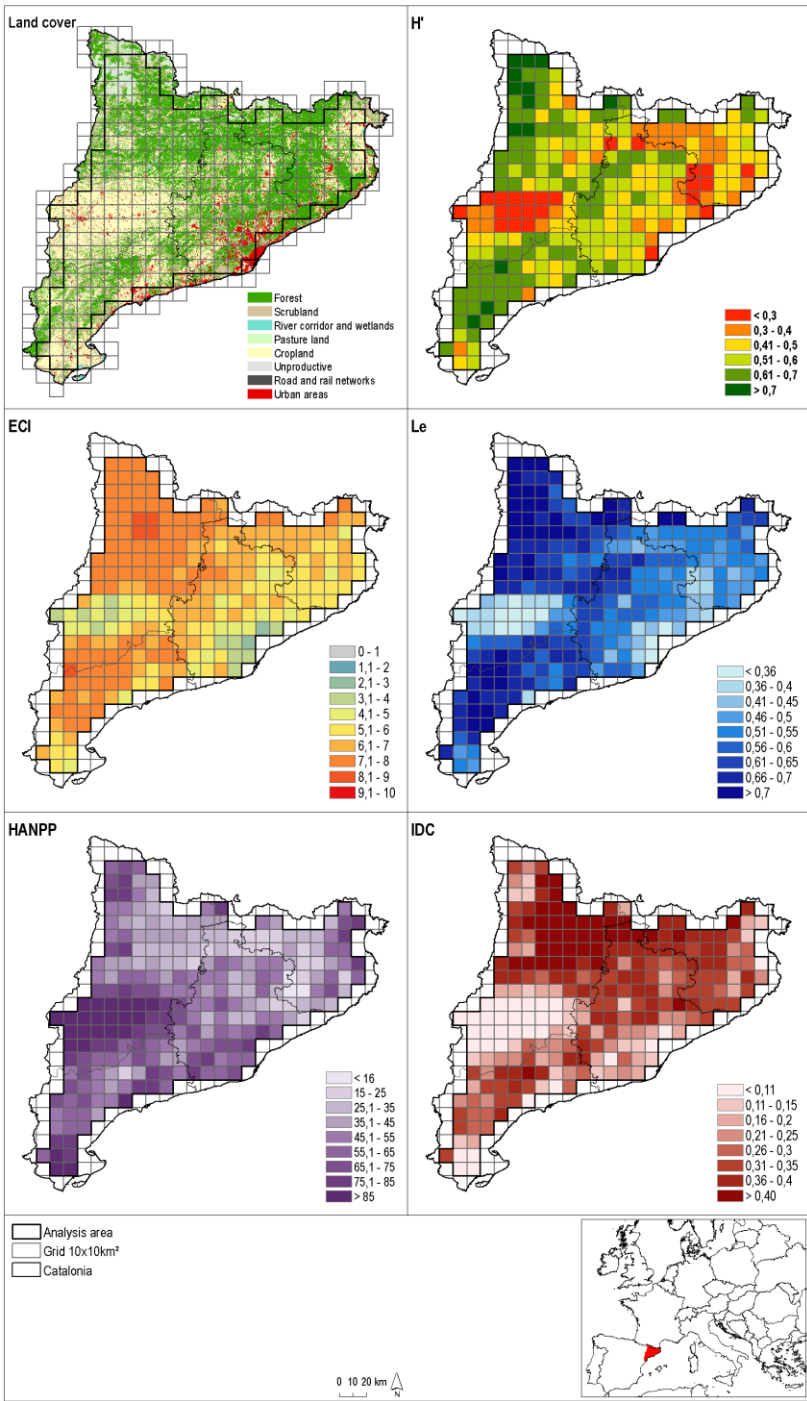
Figure 5. Structural Equation Model (SEM) applied to the variables vascular plant, bird and mammal species richness, and total biodiversity taking into account the direct effects of Le and HANPP (the two components of IDC)¹, as well as their indirect effects via land-cover composition (Cm)², and controlling for elevation (MDE) of Catalonia in 2009 (UTM 10-km sample cells). The resulting ‘virtuous triangle’ between forest cover, HANPP and total biodiversity describes the complex human-nature relationship across landscape gradients of human transformation.



Notes: ¹ Landscape Ecology metric (Le), Human Appropriation of Net Primary Production (HANPP) and Intermediate Disturbance Complexity model (IDC). ² Principal Component Analysis in Table A1.

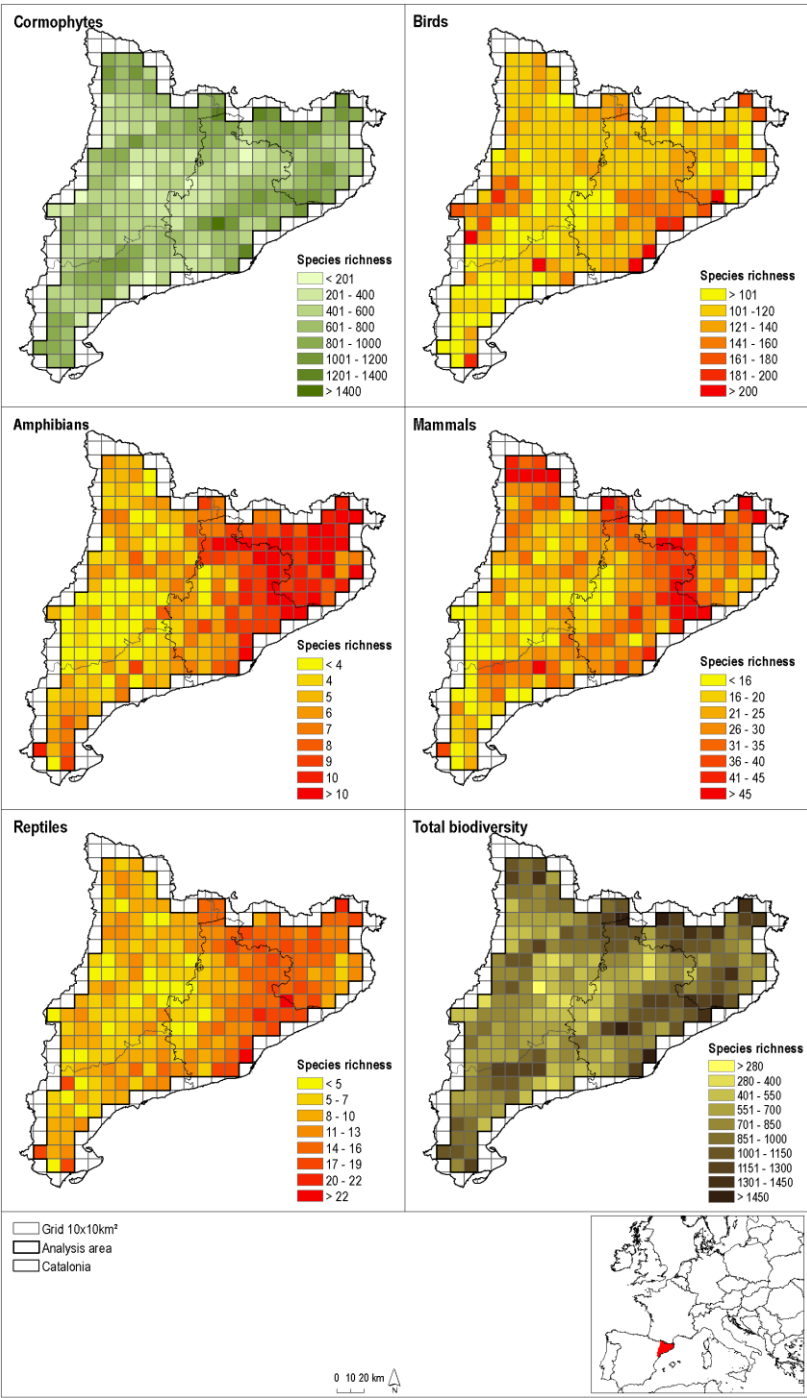
Appendices

Figure A1. Land-cover categories and landscape ecology metrics (H' , ECI, Le, HANPP and IDC)¹ for UTM 10-km cells in Catalonia (data from 2009).



Notes: ¹ Shannon-Wiener Index (H'), Ecological Connectivity Index (ECI), Landscape Ecology metric (Le), Human Appropriation of Net Primary Production (HANPP) and Intermediate Disturbance Complexity model (IDC).

Figure A2. Total species richness and species richness of the studied biodiversity groups (vascular plants, amphibians, reptiles, birds and mammals) per UTM 10-km cells in Catalonia (data from 2009).



Source: Biodiversity Data Bank of Catalonia (BDBC; biodiver.bio.ub.es/biocat)

725 Table A1. Principal Component Analysis (PCA) applied in the Negative Binomial Regression (NBR; a –

a)	Variable	Factor1	Factor2
NBR	IDC	0.318	0.077
	Forest	0.304	-0.164
	Cropland	-0.256	-0.042
	Scrubland	0.038	0.147
	Pastureland	-0.028	0.407
	River corridor / Wetland	-0.027	0.256
	Unproductive	-0.027	0.426
	Road and rail networks	-0.188	-0.114
	Urban areas	-0.162	-0.104
	Variance	34.8%	22.9%

726 Figure 3) and in the Structural Equation Model (SEM; b –Figure 5).

b)	Variable	Cm1	Cm2
SEM	Forest	0.649	-0.395
	Cropland	-0.674	0.027
	Grassland / Scrubland	0.180	0.816
	Urban/roads	-0.301	-0.422
	Variance	38.5%	31.2%

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728

729 Table A2. Standardized coefficients (estimate; a –and for total, direct and indirect effects of each variable;
730 b), standard error and P-value for each path in the Structural Equation Model (SEM) for total biodiversity.

a)	Estimate	Std Error	Pr(> z)	
beta1	-0.1722	0.0576	2.76e-03	Total <— MDE
beta2	1.8188	0.2768	4.98e-11	Total <— HANPP
beta3	-0.2392	0.0937	1.07e-02	Total <— Le
beta4	2.0826	0.2610	1.46e-15	Total <— Cm1
beta5	-0.6051	0.1428	2.25e-05	Total <— Cm2
beta8	0.0995	0.0105	2.38e-21	HANPP <— MDE
beta10	-0.1997	0.0537	2.03e-04	Le <—> HANPP
beta11	-0.9461	0.0776	3.51e-34	HANPP <—> Cm1
beta12	0.4617	0.0491	5.60e-21	Le <—> Cm1
beta13	0.3737	0.0322	3.95e-31	HANPP <—> Cm2
beta14	0.6941	0.0647	7.59e-27	Le <—> Cm2
e1	0.7738	0.0629	8.15e-35	Total <—> Total
e2	1.0698	0.0768	4.57e-44	HANPP <—> HANPP
e3	1.0000	0.0724	2.28e-43	Le <—> Le
e4	1.0000	0.0812	8.15e-35	MDE <—> MDE
e5	1.0000	0.0812	8.15e-35	Cm1 <—> Cm1
e6	1.0000	0.0812	8.15e-35	Cm2 <—> Cm2

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b)		MDE	Le	HANPP	Total	Cm1	Cm2
Total	Total	0.00875	-2.39e-01	1.82	0	2.08	-0.605
	HANPP	0.09951	-1.53e-17	0.00	0	0.00	0.000
Direct	Total	-0.1722	-0.239	1.82	0	2.08	-0.605
	HANPP	0.0995	0.000	0.00	0	0.00	0.000
Indirect	Total	0.181	-2.78e-17	0	0	0	0
	HANPP	0.000	-1.53e-17	0	0	0	0

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734 Table A3. Standardized coefficients (estimate; a –and for total, direct and indirect effects of each variable;
735 b), standard error and P-value for each path in the Structural Equation Model (SEM) for plants
736 biodiversity.

a)	Estimate	Std Error	Pr(> z)	
beta1	-0.1503	0.0587	0.0104	Plants <--- MDE
beta2	1.5870	0.282	1.87e-08	Plants <--- HANPP
beta3	-0.1937	0.0956	0.0426	Plants <--- Le
beta4	1.8705	0.266	2.08e-12	Plants <--- Cm1
beta5	-0.4995	0.146	0.000602	Plants <--- Cm2
beta8	0.0995	0.0105	2.38e-21	HANPP <--- MDE
beta10	-0.1997	0.0537	0.000203	Le <--> HANPP
beta11	-0.9461	0.0776	3.51e-34	HANPP <--> Cm1
beta12	0.4617	0.0491	5.6e-21	Le <--> Cm1
beta13	0.3737	0.0322	3.95e-31	HANPP <--> Cm2
beta14	0.6941	0.0647	7.59e-27	Le <--> Cm2
e1	0.8046	0.0654	8.15e-35	Plants <--> Plants
e2	1.0698	0.0768	4.57e-44	HANPP <--> HANPP
e3	1.0000	0.0724	2.28e-43	Le <--> Le
e4	1.0000	0.0812	8.15e-35	MDE <--> MDE
e5	1.0000	0.0812	8.15e-35	Cm1 <--> Cm1
e6	1.0000	0.0812	8.15e-35	Cm2 <--> Cm2

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b)		MDE	Le	HANPP	Total	Cm1	Cm2
Total	Plants	0.00765	-0.194	1.59	0	1.87e+00	-0.5
	HANPP	0.09951	0.000	0.00	0	1.40e-16	0.000
Direct	Plants	-0.1503	-0.194	1.59	0	1.87	-0.5
	HANPP	0.0995	0.000	0.00	0	0.00	0.000
Indirect	Plants	0.158	0	0	0	2.22e-16	0
	HANPP	0.000	0	0	0	1.40e-16	0

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740 Table A4. Standardized coefficients (estimate; a –and for total, direct and indirect effects of each variable;
741 b), standard error and P-value for each path in the Structural Equation Model (SEM) for mammals
742 biodiversity.

a)	Estimate	Std Error	Pr(> z)	
beta1	0.1570	0.0542	0.00381	Mammals <--- MDE
beta2	1.2380	0.261	2.08e-06	Mammals <--- HANPP
beta3	-0.2532	0.0883	0.00415	Mammals <--- Le
beta4	1.5115	0.246	8.01e-10	Mammals <--- Cm1
beta5	-0.5762	0.135	1.86e-05	Mammals <--- Cm2
beta8	0.0995	0.0105	2.38e-21	HANPP <--- MDE
beta10	-0.1997	0.0537	0.000203	Le <--> HANPP
beta11	-0.9461	0.0776	3.51e-34	HANPP <--> Cm1
beta12	0.4617	0.0491	5.6e-21	Le <--> Cm1
beta13	0.3737	0.0322	3.95e-31	HANPP <--> Cm2
beta14	0.6941	0.0647	7.59e-27	Le <--> Cm2
e1	0.6875	0.0559	8.15e-35	Mammals <--> Mammals
e2	1.0698	0.0768	4.57e-44	HANPP <--> HANPP
e3	1.0000	0.0724	2.28e-43	Le <--> Le
e4	1.0000	0.0812	8.15e-35	MDE <--> MDE
e5	1.0000	0.0812	8.15e-35	Cm1 <--> Cm1
e6	1.0000	0.0812	8.15e-35	Cm2 <--> Cm2

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b)		MDE	Le	HANPP	Total	Cm1	Cm2
Total	Mammals	0.2802	-0.253	1.24	0	1.51	-0.576
	HANPP	0.0995	0.000	0.00	0	0.00	0.000
Direct	Mammals	0.1570	-0.253	1.24	0	1.51	-0.576
	HANPP	0.0995	0.000	0.00	0	0.00	0.000
Indirect	Mammals	1.23e-01	0	0	0	0	0
	HANPP	1.39e-17	0	0	0	0	0

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746 Table A5. Standardized coefficients (estimate; a –and for total, direct and indirect effects of each variable;
747 b), standard error and P-value for each path in the Structural Equation Model (SEM) for birds biodiversity.

a)	Estimate	Std Error	Pr(> z)	
beta1	-0.232	0.0542	1.77e-05	Birds <--- MDE
beta2	2.12	0.26	3.94e-16	Birds <--- HANPP
beta3	-0.289	0.0882	0.00106	Birds <--- Le
beta4	1.95	0.246	2.02e-15	Birds <--- Cm1
beta5	-0.837	0.134	4.57e-10	Birds <--- Cm2
beta8	0.0995	0.0105	2.38e-21	HANPP <--- MDE
beta10	-0.2	0.0537	0.000203	Le <--> HANPP
beta11	-0.946	0.0776	3.51e-34	HANPP <--> Cm1
beta12	0.462	0.0491	5.6e-21	Le <--> Cm1
beta13	0.374	0.0322	3.95e-31	HANPP <--> Cm2
beta14	0.694	0.0647	7.59e-27	Le <--> Cm2
e1	0.685	0.0557	8.15e-35	Birds <--> Birds
e2	1.07	0.0768	4.57e-44	HANPP <--> HANPP
e3	1	0.0724	2.28e-43	Le <--> Le
e4	1	0.0812	8.15e-35	MDE <--> MDE
e5	1	0.0812	8.15e-35	Cm1 <--> Cm1
e6	1	0.0812	8.15e-35	Cm2 <--> Cm2

b)		MDE	Le	HANPP	Total	Cm1	Cm2
Total	Birds	-0.0215	-0.289	2.12	0	1.95	-0.837
	HANPP	0.0995	0.000	0.00	0	0.00	0.000
Direct	Birds	-0.2325	-0.289	2.12	0	1.95	-0.837
	HANPP	0.0995	0.000	0.00	0	0.00	0.000
Indirect	Birds	0.211	0	0	0	0	0
	HANPP	0.000	0	0	0	0	0

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