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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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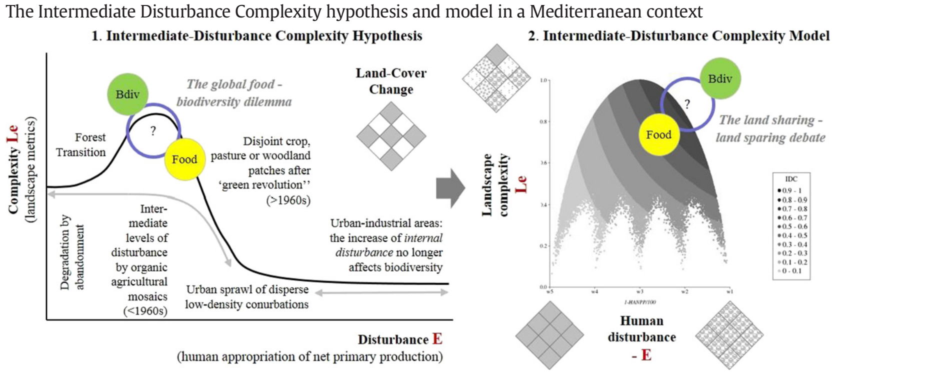
HIGHLIGHTS

- An Intermediate Disturbance Complexity (IDC) model is proposed at regional scale.
- IDC relies on human appropriation of net primary production and land cover change.
- The IDC is applied across a gradient of human-transformed landscapes.
- The IDC is used to assess the effects of land-use policies on biodiversity.
- Results are interpreted based on the land-sparing/land-sharing debate.

GRAPHICAL ABSTRACT

The Intermediate Disturbance Complexity hypothesis and model in a Mediterranean context



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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

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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.

1. Introduction

For millennia, global human-driven Land Use and Cover Changes (LUCC) have been increasingly affecting terrestrial ecosystems (Sterling and 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 and Lambin, 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 and 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 et al., 1997). 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 and 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 and 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 and Trosper, 2012) embedded in agro-ecological landscapes (Matthews and 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 explored 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.