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Patterns of landscape seasonality influence passerine diversity: Implications for conservation management under global change

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ABSTRACT

The importance of environmental heterogeneity for biodiversity across scales is widely recognized in ecological theory and profusely supported by evidence. However, our understanding of the effects of spatiotemporal patterns of landscape functional properties on biodiversity is still rather limited. We examined the relationship between common passerine species richness and ecosystem functioning dynamics, namely seasonality, measured by satellite remote sensing. We focused on rural landscapes of a mountain National Park in Portugal undergoing rapid reshaping from agro-pastoral mosaics to early successional landscapes. We applied multi-model inference to compare the hypothesis of landscape seasonality as a driver of species richness with three competing hypotheses representing structural habitat heterogeneity, disturbance, and availability of food resources. We found support for landscape seasonality and its spatial heterogeneity in explaining passerine richness in mountain rural landscapes. Conversely, no significant support of the remaining hypotheses was found. These results highlight the role of ecosystem functioning variability in space and time. They also stress the importance of considering species-energy relationships for conservation at the landscape level. Specifically, they provide support and guidance to the identification of meaningful functional attributes of the landscape that shape its biodiversity. Our results further demonstrate the utility of remote sensing approaches and products to measure those attributes and follow their trends through time. Spatially-explicit measures of energy variability, such as the functional amplitude between winter and summer retrieved from earth observations, can link global socio-environmental change to species' responses and support the inclusion of landscape seasonality on conservation and monitoring frameworks.

1. Introduction

Understanding the relationship between biological diversity and landscape patterns and dynamics is crucial to face ongoing environmental change. Mediterranean landscapes of Southern Europe, shaped by human management through a combination of fire, husbandry and agriculture, sustain diverse mosaics that promote the local increase of species richness (Grove and Rackham, 2001). These landscapes typically include patches of relatively natural habitat in a mosaic of human land uses. When compared to more uniform environments, these heterogeneous landscapes allow more species to coexist locally. In fact, both species richness and diversity of bird communities were shown to be higher in heterogeneous landscapes (Benton et al., 2003; Smith et al., 2010). The importance of this heterogeneity for biodiversity across scales is widely recognized in ecological theory and supported by abundant evidence (reviewed in (Rosenzweig, 1995; Statzner and Moss, 2004).

The positive relationship between biodiversity and habitat heterogeneity at landscape scales is generally accepted, particularly in agricultural landscapes (Benton et al., 2003; Fahrig et al., 2011). The relationship between structural habitat heterogeneity and species diversity is a well-documented pattern in landscape ecology (Tews et al., 2004). Moreover, structural modifications in habitat mosaics are known to develop alongside with important changes in functional attributes of ecosystems, such as energy balance, which may ultimately affect biodiversity (Hurlbert, 2004). Therefore, in addition to structural heterogeneity, energy variations in space and time may also influence species diversity in heterogeneous mosaics, especially in dynamic landscapes submitted to driving forces such as land use change (Evans et al., 2005; Hurlbert and Haskell, 2003).

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Mountain landscapes in southern Europe, at the northern edge of the Mediterranean region, are undergoing rapid reshaping as the abandonment of agro-pastoral mosaics trigger secondary vegetation succession, scrub encroachment and forest re-growth (Honrado et al., 2016a). This system provides a good context not only to study the impacts of land use change on biodiversity, but also to explore the responses of biodiversity to changes in landscape functioning. Descriptors of landscape functioning dynamics, and of its temporal and spatial variability, can provide a more profound insight of the proximal landscape conditions that support biological diversity (Carrara and Vázquez, 2010; Honkanen et al., 2010; Hurlbert, 2004). This will improve our understanding of how functional and structural multi-scale landscape heterogeneity affects biodiversity, supporting better predictions of species responses to future landscape change (Orme et al., 2005), at the interface between local and regional scales (Vicente et al., 2014), thus contributing to foster conservation management and monitoring (Honrado et al., 2016b).

In this study we examined the relation between species richness of passerine birds and landscape functional dynamics namely its seasonality component as measured by satellite remote sensing. We assessed this relation in a set of mountain rural landscapes located in a National Park in Portugal and undergoing abandonment of farming and husbandry. Based on a multi-model inference (MMI) framework, we compared the predictive power of landscape seasonality with three other hypotheses representing other components of those landscapes that may influence bird species richness (habitat heterogeneity, disturbance, and availability of food resources). Finally, we aimed to outline implications for conservation management of biodiversity under land use change.

2. Material and methods

2.1. Study area

The study area comprises the mountain catchment of river Vez (252 km^2), in the northwest of Portugal (Fig. 1). Parts of the catchment are included in *Peneda-Gerês*, the only National Park in the country, and in the *Natura 2000* network of European conservation areas. During the study period (1999–2008), the average annual precipitation and temperature were 1500 mm/year and 13.8 °C, respectively. Still, annual precipitation ranged from *ca.* 1000 mm/year in lowlands up to ca. 3000 mm/year in highlands. Rainfall is mainly concentrated in autumn, winter and early spring, especially in the lowlands, which hold a Mediterranean type of rainfall regime. In highlands, rainfall seasonality is not so sharp and the climate is considered Temperate Atlantic with a sub-Mediterranean rainfall regime (Mesquita and Sousa, 2009). Elevation ranges from 30 to 1400 m, and slopes above 25% shape 58% of the catchment. On top of this environmental heterogeneity, humans have shaped a highly diversified and dynamic landscape that was maintained by a traditional agro-pastoral land management regime. In recent decades, however, the region has suffered marked rural abandonment, scrub encroachment and afforestation. Fire regime has changed accordingly, and wildfires are nowadays an important driver of landscape change in the region (Honrado et al., 2016a).

2.2. Data collection

2.2.1. Sampling design

A two-stage sampling design (Fig. 1) was implemented to select locations for bird counts and habitat surveys (De Gruijter et al., 2006; Köhl et al., 2006; Voříšek, 2008). This scheme accounted for two main objectives: (i) the first stage aimed to distribute sample locations across the major gradients of spatial heterogeneity and land cover/use patterns; (ii) in the second stage, the aim was to reduce the total sampling effort by concentrating surveys in smaller, representative sample units.

Thus, in the first stage a stratified random sampling approach

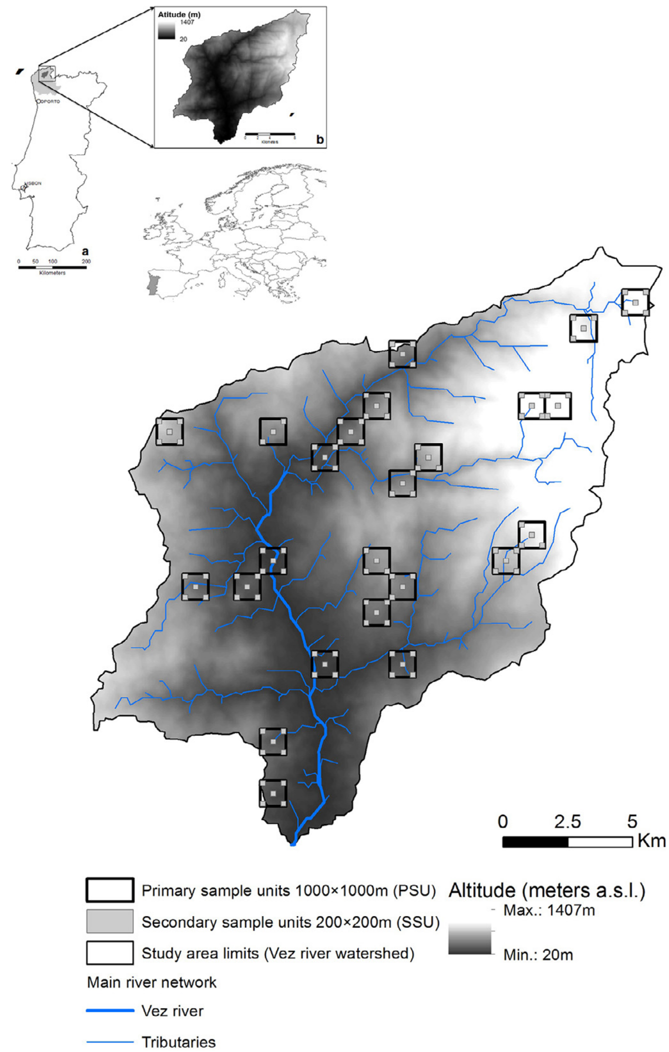

Fig. 1. Study area and sampling units used during field survey.

identified Primary Sample Units (hereafter PU) from a regular grid with 1 km^2 square units (Fig. 1). To obtain an environmental stratification of the study area for selecting PUs, four types of data layers related to environmental conditions: climate, topography, soil types, and protection regime protected areas, were combined in the Partition Around Medoids clustering algorithm (Maechler et al., 2016). Considering the Silhouette Index as the criterion to assess clustering validity and to select an adequate number of clusters (Rousseeuw, 1987), a total of six strata were obtained as the optimal solution. Based on the resulting stratification, 24 PUs were selected, with PU allocation proportional to the area of each environmental stratum and with a minimum of three PUs per stratum. In the second stage, and to reduce the costs of surveying the entire PU area, we used a systematic sampling approach to select five Secondary Sample Units (hereafter SU; with an area equal to 0.04 km^2) located at the corners and the centre of each PU (Fig. 1). This spatial positioning was used to maximize the distance between SUs and avoid overlaps in bird counts. A total of 120 SUs were initially selected, but nine were not surveyed due to physical inaccessibility. For further details on sampling design see Supplementary Material – Appendix S2.

2.2.2. Bird and habitat surveys

Species richness of passerine birds was the focal response variable, and the sample plots (n = 111 SUs) were surveyed using a 100 m fixed-radius point-count approach (Bibby, 2000). Surveyed plots were separated at least by 400 m to minimize the probability of sampling the