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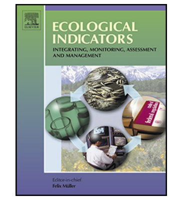

Disentangling the effects of land use and geo-climatic factors on diversity in European freshwater ecosystems

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ABSTRACT

Land use effects are considered among the main stressors on freshwater biodiversity, with up to 80% of land in Europe under intensive use. Here, we address the impact of arable and urban landscapes on taxon richness, Shannon–Wiener diversity, taxon rareness and taxonomic distinctness of eleven organism groups encompassing vertebrates, invertebrates and plants, occurring in five freshwater ecosystem types across Europe: rivers, floodplains, lakes, ponds and groundwater. In addition, nine geo-climatic descriptors (e.g. latitude, longitude, precipitation) were used to disentangle land use effects from those of natural drivers of biodiversity. Using a variance partitioning scheme based on boosted regression trees and generalised linear regression modelling, we sought: (i) to partition the unique, shared and unexplained variation in the metrics explained by both groups of descriptor variables, (ii) to quantify the contribution of each descriptor variable to biodiversity variation in the most parsimonious regression model and (iii) to identify interactions of land use and natural descriptors. The variation in biodiversity uniquely described by land use was consistently low across both ecosystem types and organism groups. In contrast, geo-climatic descriptors uniquely, and jointly with land use, explained significantly more variance in all 39 biodiversity metrics tested. Regression models revealed significant interactions between geo-climatic descriptors and land use for a third of the models, with interactions accounting for up to 17% of the model's deviance. However, no consistent patterns were observed related to the type of biodiversity metric and organism group considered. Subdividing data according to the strongest geo-climatic gradient in each dataset aimed to reduce the strength of natural descriptors relative to land use. Although data sub-setting can highlight land use effects on freshwater biodiversity, sub-setting our data often failed to produce stronger land use effects. There was no increase in spatial congruence in the subsets, suggesting that the observed land use effects were not dependent on the spatial extent of the subsets. Our results confirm significant joint effects of, and interactions between, land use and natural environmental descriptors on freshwater biodiversity, across ecosystem types and organism groups. This has implications for biodiversity monitoring. First, the combined analysis of anthropogenic and natural descriptors is a prerequisite for the analysis of human threats to biodiversity. Second, geo-climatically, but not necessarily geographically more homogeneous datasets can help unmask the role of anthropogenic descriptors. And third, whole community-based biodiversity metrics (including taxon richness) are not ideal indicators of anthropogenic effects on biodiversity at broad scales.

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1. Introduction

Although freshwaters cover only 1% of the earth's surface, almost 10% of the world's species live in freshwater ecosystems (Loh and Wackernagel, 2004). Freshwater biodiversity is declining faster than marine and terrestrial biodiversity (Dudgeon et al., 2006), most likely because human life and many human activities rely on fresh water. This results in high population densities, intense land and water uses and modification and pollution hotspots in the vicinity of freshwater bodies. Consequently, human impacts on freshwater biodiversity are numerous and wide-ranging. Dudgeon et al. (2006) identify five major stressors of biodiversity which affect different freshwater ecosystem types to varying degrees: (i) water overexploitation; (ii) water pollution; (iii) flow modification; (iv) habitat degradation; and (v) invasive species. While rivers are more affected by physical alterations (e.g. dams, impoundments, disconnection from the floodplain), lentic waters are more susceptible to nutrient enrichment (Wetzel, 2001; Schindler, 2006), with increasing adverse effects on lentic biota under climate change (Jeppesen et al., 2010, 2012).

Numerous stressors are linked to land use, which therefore is considered a composite (or proxy) stressor. Intensive agriculture, in particular, affects both lotic and lentic biodiversity through flow modification, pollution by fine sediment and pesticide fluxes (Allan, 2004; Feld, 2013), habitat degradation and eutrophication (Jeppesen et al., 2000). Urbanisation represents another intensive land use, with strong effects on freshwater biodiversity, resulting in "consistent declines in the richness of algal, invertebrate, and fish communities" (Paul and Meyer, 2001). In Europe, a very high proportion (up to 80%) of the land is intensively used for settlements, infrastructure and production systems (including agriculture and intense forestry: http://www.eea.europa.eu/themes/landuse/intro; accessed 11.05.15) and aquatic biodiversity is probably impoverished accordingly. Because of this cocktail of stressors, freshwater ecosystems and their biodiversity are currently among the most threatened on the planet, prompting scientists and politicians to develop strategies to sustain and improve biodiversity functioning and ecosystem service provisioning.

Anthropogenic stress intensity and thus its influence on biodiversity differs regionally, impacting large-scale biodiversity patterns, originally shaped by natural drivers. These natural drivers are considered in macro-ecological and other broad-scale studies highlighting the role of (i) energy/climate (e.g. Mittelbach et al., 2007; Pearson and Boyero, 2009; Heino, 2011), (ii) area/habitat heterogeneity (e.g. Vinson and Hawkins, 1998; Oberdorff et al., 2011) and (iii) history (e.g. Leprieur et al., 2011; Vinson and Hawkins, 2003). The influence that energy and climate have on biodiversity are primarily driven by temperature, precipitation and evapo-transpiration, all of which influence ecosystem energy supply and thus control or support biophysical processes operating within the system (Wright, 1983; Hawkins et al., 2003; Evans et al., 2005; Mittelbach et al., 2007; Field et al., 2009). However, temperature and evapo-transpiration vary with altitude, and more importantly, freshwater biodiversity is also found to increase with altitude (see Vinson and Hawkins, 1998 for a review on benthic invertebrates). This suggests temperature is unlikely to be the main co-variate of the energy/climate driver in freshwater ecosystems, and in more general terms, the role of energy/climate differs between terrestrial and aquatic systems (Field et al., 2009).

Area/habitat heterogeneity refers to the size and heterogeneity (habitat diversity) of an area under consideration, with the assumption that larger and more heterogeneous areas exhibit higher biodiversity (*sensu* MacArthur and Wilson, 1967; Guégan et al., 1998; Davies et al., 2007). Lastly, historical events (i.e. previous and often long-term events dating back for centuries or even millennia) may continue to shape contemporary biodiversity patterns (Mittelbach et al., 2007; Leprieur et al., 2011; Tisseul et al., 2013). The expansion of Pleistocene glaciers and their subsequent contraction followed by recolonisation, for example, are considered a key factor in explaining much of the variation in the distribution of contemporary biodiversity across Europe (Reyjol et al., 2007; Araújo et al., 2008; Baselga et al., 2012), with formerly glaciated regions (e.g. Scandinavia) generally exhibiting less diversity than non-glaciated regions (e.g. Mediterranean peninsula). Over more recent timescales land use practices dating back decades may continue to shape contemporary biodiversity even if land use has subsequently changed or been abandoned (Harding et al., 1998).

Both the natural drivers of freshwater biodiversity and multiple stressors resulting from human land and water uses have been addressed in many studies (see Stendera et al., 2012 for a recent summary of 368 papers), although few have considered these in an integrated way. Studies that investigate the combined effects of natural and anthropogenic descriptors are rare, but are necessary to address metacommunity aspects in ecosystem assessment studies (Heino, 2013). Furthermore, Stendera et al. (2012) found that the majority of studies on natural drivers were rather broad-scale (continental and global), whereas studies on anthropogenic stressors tend to focus on much finer (regional and local) spatial scales. The spatial resolution (grain size) also often differs, with the catchment 'grain' prominent in broad-scale studies, but single sites within one or several catchments foremost in fine-scale studies. The mechanisms driving biodiversity, however, are likely to vary with spatial grain (local ecosystem vs. catchment) and extent (Field et al., 2009; Heino, 2011). Few studies addressed the impacts of both natural drivers and anthropogenic stressors on freshwater biodiversity (Irz et al., 2008; Argillier et al., 2013; Brucet et al., 2013) and there remains a limited understanding of the synergies between both groups of descriptors.

In this study, we developed a stepwise analysis to determine the independent, overlapping and interacting effects of land use and geo-climatic variables (hereafter referred to as descriptors) on the European biodiversity patterns of eleven organism groups in five lotic and lentic ecosystem types (rivers, lakes, floodplains, ponds and groundwater). We used a machine-learning technique to partition the variance and to quantify the independent and overlapping effects of both descriptor groups in each ecosystem. In line with previous studies at continental scale (e.g. Brucet et al., 2013), we hypothesised a strong influence of natural descriptors on biodiversity (e.g. latitude, mean annual temperature), but a much weaker role of agricultural and urban land uses. As land use, however, is not independent of, for example, altitude (i.e. slope), temperature and precipitation, we expected strong joint effects. This was analysed by variance partitioning, and further tested by means of significant interaction terms between single land use and geo-climatic descriptor variables in regression modelling. To decrease the effect of the most influential geo-climatic descriptor in the regression models, we generated subsets of the data and quantified the proportion of variance attributable to land use separately for each subset. This procedure was driven by the hypothesis that geo-climatically more homogeneous data (with shorter natural gradients) would reveal a stronger influence of land use on biodiversity. In order to account for the response of different aspects of biodiversity, we compared the results of four widely used biodiversity metrics: taxon richness, Shannon–Wiener diversity, taxon rareness and taxonomic distinctness (Clarke and Warwick, 1998). The first two metrics quantify the number and equal distribution of species within a community and thus represent very basic concepts of diversity, i.e. richness and equity. The latter two metrics add the aspects of relative rareness of taxa and their phylogenetic relationships to each other within a community. We hypothesised that taxa are not equally sensitive to human impact and that in particular