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RESEARCH PAPER

Teasing apart fine- and coarse-scale effects of environmental heterogeneity on tree species richness in Europe

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Abstract

The environmental heterogeneity–biodiversity relationship is generally hypothesised to be positive, with greater heterogeneity leading to greater biodiversity. However, the generality of positive environmental heterogeneity–species richness relationships is often debated, with some studies finding non-significant or even negative relationships. Negative relationships have primarily been found at fine spatial scales. Both negative and positive relationships have a basis in ecological theory. Environmental heterogeneity at coarse scales opens up niche space to allow more species to coexist; whereas high local heterogeneity, for instance in topography, may lead to increased local extinction due to micro-fragmentation, or dominance of species suited to heterogeneous conditions. However, it is difficult to attribute how much of the variance is explained at different scales within the same modelling framework.

Here, we use a new data-aggregation method which enables us to include both fine- and coarse-scale environmental heterogeneity within the same analysis. Using this method, we were able to tease apart the fine- and coarse-grain effects of topographic heterogeneity on European tree species richness. At the coarse scale (0.5 degrees), we found a positive effect of range in elevation on tree species richness. However, when measuring range in elevation using a fine-scale moving window of radius 500 m, we found a negative relationship with tree species richness. This supports existing research that has shown negative relationships between environmental heterogeneity and species richness at finer spatial grains. Because we were able to include a measure of both local and landscape-scale topographic heterogeneity in the same model, for the first time we could fully capture the effects of both scales on coarse-grain species richness while accounting for the effect of the other scale.

Keywords: Environmental heterogeneity; Tree species' richness; Topography; Scale; Data aggregation

Introduction

Environmental heterogeneity is widely recognised as a key driver of biodiversity, with variability in the spatial attributes

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of the environment attributed to gradients in species' richness globally (Stein et al., 2014). The hypothesised mechanism underlying this relationship is that high levels of environmental heterogeneity increase the niche space available to species (Hutchinson, 1957), enables coexistence of competing species (Shmida & Wilson, 1985), and opens up space for speciation (Hughes & Eastwood, 2006). Much empirical evidence of the environmental heterogeneity–diversity exists, but due to differences in measurement and study scale, the conclusions are varied (Stein et al., 2014)

In a meta-analysis of the evidence for the environmental heterogeneity–diversity relationship, Stein et al. (2014) found that while the relationship in general was positive, there was a wide range of variability in this relationship, in particular a positive interaction with scale resulting in neutral and negative effects at small scales. The conflicting relationships at different scales may result from the area–heterogeneity trade-off, which posits that the combined theories of environmental heterogeneity–diversity, and the species–area relationship may lead to unimodal or even negative relationships (Allouche et al., 2012). A related theory – microfragmentation effects – may also be at play. This is where increasing heterogeneity can increase isolation, and therefore stochastic extinctions (Laanisto et al., 2013; Tamme et al., 2010).

Evidence for the negative effects of microfragmentation has been building. For example a simulation modelling approach which combined island biogeography theory with niche theory showed that unimodal and negative environmental heterogeneity–diversity relationships were possible. Empirical evidence includes negative relationships between small-scale soil heterogeneity and plant diversity (Gazol et al., 2013); a unimodal relationship between heterogeneity in elevation and land-cover, and bird diversity (Chocron et al., 2015); and neutral effects in experimental zooplankton communities (Schuler et al., 2017).

Understanding the scale effect of heterogeneity on diversity can be challenging. This is because the opposing effects at fine, and coarse scales can be difficult to tease apart (Graham et al., 2019). Macroecological-scale studies of the environmental heterogeneity–diversity relationship show inconsistencies in the relationship due to the difficulties surrounding the representation of fine-grain environmental heterogeneity in coarse-grain models (Bellard et al., 2012). This is further complicated when examining differing hypotheses at different scales due to the need to harmonise fine-grain and coarse-grain data, leading to a loss of information about fine-scale spatial structure (Kitron et al., 2006).

A further complication involved in identifying the effect of environmental heterogeneity at different scales is that environmental heterogeneity at fine and coarse scales tends to be highly correlated. This means that in order to avoid omitted variable bias, an approach which allows us to quantify the effect of one scale while accounting for the effect of the other is required (Larsen et al., 2019; Morrissey, 2018). It is therefore key that we incorporate both fine- and coarse-grain environmental heterogeneity, thus quantitatively estimating the effect of environmental heterogeneity at each scale without bias.

Here, we aim to tease apart the opposing effects of environmental heterogeneity on European tree species richness at fine and coarse scales using the 'grainchanger' methodology (Graham et al., 2019). Variation in topography has been shown to correlate with increased species richness due to increasing habitat variability (Simpson, 1964) and altering local climate patterns (O'Brien et al., 2000). Variation in topography has been found to be an important predictor in models of tree diversity (Irl et al., 2015; Kissling et al., 2008a; Svenning et al., 2010), so we predict that fine-scale topographic heterogeneity calculated using our approach will have a negative effect on tree species richness, and topographic heterogeneity calculated at the coarse-grain will have a positive effect.

Materials and methods

Data collection

We downloaded European species-level tree occurrences from the EU-Forest dataset (file Tree occurrences at species level; Mauri et al., 2017). This dataset is a compilation of multiple National Forest Inventories, which includes data from Forest Focus and Biosoil to fill some geographical gaps. In total, there are 1,000,525 occurrence records of 242 species (both native and non-native) collected from 260,707 plots (see Appendix A: Table 1 for details of species included). These data have previously been used to evaluate the 'naturalness' of European forests (Strona et al., 2016), and to improve understanding of European tree biogeography (Mauri et al., 2017).

We used the occurrence data, available at 1-km resolution, to calculate tree species richness at a resolution of 0.5 degrees (*sensu* Kissling et al., 2008; Mauri et al., 2017). Because this dataset is a collection of multiple National Forest Inventories which will have been compiled using different sampling methods, we applied a correction to the species richness using the Chao 2 measure (S_{Chao2}, Eq. 1). This is a bias-corrected species richness measure, which is suitable for replicated incidence data (Gotelli & Colwell, 2011).

$$S_{Chao2} = S_{obs} + \left(\frac{m-1}{m}\right)\frac{q_1(q_1-1)}{2(q_2+1)} \quad (1)$$

Where for each grid cell, S_{obs} is the total number of species observed, m is the sample size, and q_k is the number of species present in exactly k samples.

We obtained a 25-m resolution digital elevation model for Europe from the European Environment Agency (https://land.copernicus.eu/imagery-in-situ/eu-dem/eu-dem-v1.1?tab=download; EU-DEM v1.1). We calculated mean elevation at a resolution of 100 m (for input to the moving

Table 1. Results of the commonality analysis showing beta coefficients (β) with the 95% confidence interval, squared structure coefficients (r_s^2) and the total variance explained (r_s), partitioned into it's unique (U) and common (C) components.

Variable	β	2.5%	97.5%	r_s	r_s^2	U	C	Total
Fine-scale elevation (range)	-0.152	-0.240	-0.065	0.251	0.063	0.004	0.018	0.022
Coarse-scale elevation (range)	0.209	0.118	0.300	0.319	0.102	0.006	0.025	0.031
Mean elevation	0.188	0.125	0.250	0.323	0.104	0.011	0.018	0.029
Temperature	0.204	0.170	0.238	0.384	0.148	0.043	0.038	0.082
Precipitation	0.026	-0.018	0.069	0.217	0.047	0.000	0.026	0.026
Precipitation seasonality	-0.147	-0.180	-0.114	-0.530	0.281	0.024	0.057	0.081
Temperature (quadratic)	-0.261	-0.289	-0.233	-0.651	0.424	0.099	0.108	0.208
Precipitation (quadratic)	-0.071	-0.090	-0.053	-0.230	0.053	0.017	0.012	0.029

window) and 0.5 degree (mean elevation covariate) from EU-DEM. Climate variables (annual mean temperature, annual precipitation and precipitation seasonality) were downloaded at 0.5 degree resolution from WorldClim (Hijmans et al., 2005). We obtained a full set of response variables and covariates for n = 1915 0.5-degree cells (Fig. 1).

We aggregated the elevation data from 100-m to 0.5-degree resolution in two ways: 1) calculating the range (the difference between the minimum and maximum elevation values) using the moving window approach in the 'grainchanger' R package (Graham et al., 2019, fine-scale elevation, radius 500 m) and 2) calculating range for the entire 0.5 degree cell (coarse-scale elevation). The `grainchanger` method applies a function in a moving window at an appropriate scale-of-effect for the process under study, and aggregates to the coarse grain by taking the mean of the values calculated in the moving window step. The scale of effect is that which we expect the predictor to influence the response variable. For fine-scale elevation, the scale-of-effect was a rectangular window of radius 500 m, the measure of environmental heterogeneity was range in elevation, and this was aggregated to the 0.5-degree resolution. We chose a 500-m resolution because this was equivalent to the finer-grain studies which displayed negative environmental heterogeneity−species richness relationships (Stein et al., 2014).

Statistical analyses

We modelled European tree species richness using a negative binomial generalised linear model, due to overdispersion in the data, using the MASS R Package version 7.3-55 (Venables & Ripley, 2002). We included fine-scale elevation, coarse-scale elevation, mean elevation, temperature, precipitation, precipitation seasonality, and the quadratic terms for annual mean temperature and annual precipitation as covariates. Due to skewed distributions and investigation of residual diagnostics, we log transformed all variables except temperature. In addition to the global model, we performed model selection using AIC and present results of this and model averaged coefficients. We calculated several measures for each model coefficient including interaction terms: beta coefficients (β), squared structure coefficients (r_s^2) and the total variance explained (r^2), partitioned into it's unique (U) and common (C) components (Ray-Mukherjee et al., 2014). β is the standardised partial regression

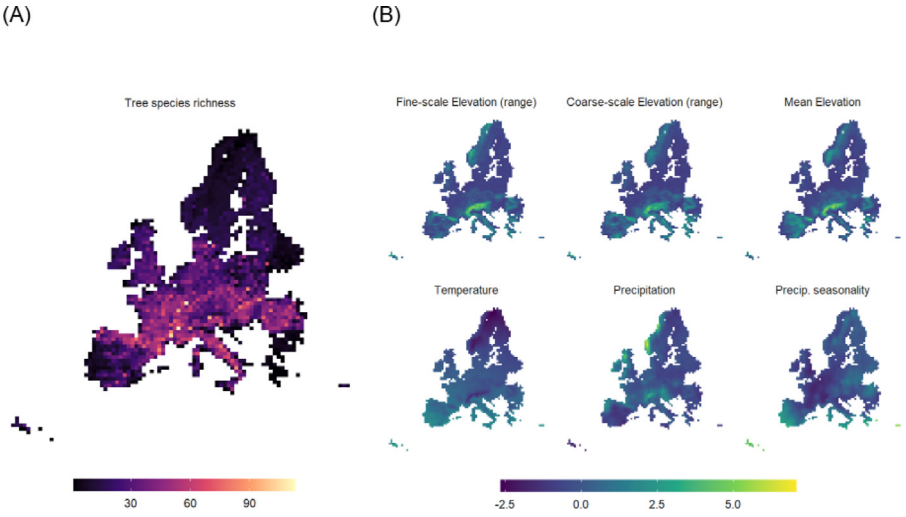

Fig. 1. Spatial distribution of (A) tree species richness, estimated using Chao 2, and (B) the climate and topography covariates used as input to the model. All data shown at 0.5 degree resolution.

coefficients and r_s^2 are the squared Pearson correlation between the variable and the fitted values from the model. Commonality analysis allows us to identify *U, C* and r^2. r_s^2, *U* and *C* are unaffected by multicollinearity.

All analyses were performed in R version 4.1.2 (R Core Team, 2021).

Results

There was a high correlation between fine-scale elevation and coarse-scale elevation (ρ = 0.94), however, the highest variance inflation factor within the global model was 10.37 for coarse-scale elevation. Given the large sample size, this is not problematic for the model (O'brien, 2007) because the variance inflation caused by collinearity between variables effectively reduces the sample size, so with a large data set omitted variable bias is a greater issue for correlated variables. Tree species richness was estimated using Chao2 ranged from 1 to 113 (median = 20, Fig. 1A).

Our model explained 38% of the deviance in tree species richness (calculated using D-squared; Guisan & Zimmermann, 2000). All variables had a significant association with the bias-corrected estimate of tree species richness. Of the key variables of interest, the partial coefficients (i.e. after accounting for the other covariates and scale) coarse-scale elevation had a positive association (β = 0.21, 95% confidence interval = 0.12 to 0.30), and fine-scale elevation had a negative association (β = -0.15, 95% confidence interval = -0.24 to -0.07, Figure 2). Climate variables also had

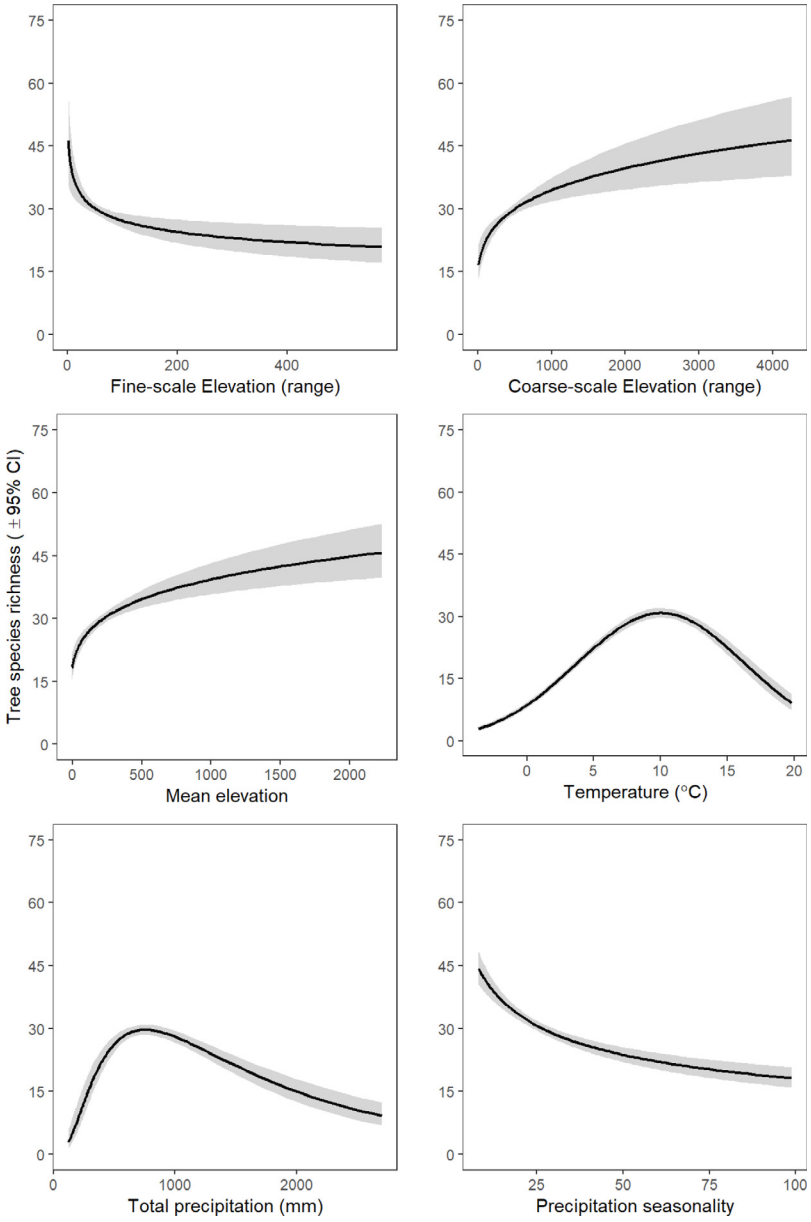

Fig. 2. Partial effect plots for European tree species richness. In each plot, all other variables are held at their mean.

significant effects on tree species richness, with a primarily negative influence of total precipitation above ~800 mm, a negative influence of precipitation seasonality, and a quadratic relationship with mean annual temperature (Fig. 2, full results in Appendix A: Table 2). Here we present the results of the global model, which was the second ranked model by selection by AIC (both fine-scale and coarse-scale elevation were included in the top two models). Results of model selection and model averaged coefficients are presented in Appendix A (Tables 3 and 4).

The commonality analysis allows us to show the unique and common proportion of the variance explained by the fine-scale (unique = 0.004, common = 0.018) and coarse-scale elevation (unique = 0.006, common = 0.025, Table 1).

Discussion

The generality of positive environmental heterogeneity−species richness relationships is often debated, with some studies finding non-significant or negative relationships (Stein et al., 2014). Using our data-aggregation method, we were able to tease apart the fine- and coarse-grain effects of topographic heterogeneity on European tree species richness by including both in the same model. At the coarse scale, we found a positive effect of range in elevation on tree species richness. However, when measuring using a moving window of radius 500 m, we found a negative relationship with tree species richness. Both relationships are supported by theory, but it has previously been difficult to identify the independent effects using existing aggregation methods.

We found a positive effect of range in elevation at coarse-scale on tree species richness. This is in agreement with previous studies, which found an overall positive relationship between topography and plant species richness (Currie & Paquin, 1987; Kissling et al., 2008b; Lundholm, 2009; Thuiller et al., 2006), and species richness more generally (Stein et al., 2014). The theoretical underpinning behind this relationship is that topographic heterogeneity at coarse scales opens up niche space to allow more species to coexist (Levins, 1979; Lundholm, 2009).

Once the positive effect of coarse-scale range in elevation had been controlled for, we found a slightly weaker negative effect of fine-scale resolution on tree species richness. Negative heterogeneity−diversity relationships have primarily been found at fine spatial scales (Gazol et al., 2013; Tamme et al., 2010). High local heterogeneity in topography may lead to increased local extinction due to micro-fragmentation (Tamme et al., 2010), or dominance of species suited to heterogeneous conditions (Gazol et al., 2013). Additionally, increased environmental heterogeneity at fine scales can have similar effects to fragmentation at landscape scales, meaning that the influence it has depends on a species' level of specialism or dispersal ability (Laanisto et al., 2013).

Both climate and topography are key drivers of tree species richness, and previously it has been noted that models containing only climate may not perform as well as those which also incorporate topography (Irl et al., 2015). Our results suggest that it is also important to include topography at different scales, due to the aforementioned competing mechanisms.

Our results should be viewed in the context of a heavily managed ecosystem. Europe has been under human management for millenia (Strona et al., 2016) and therefore tree planting decisions are likely to influence species richness. This is reflected in the lack of naturalness found in many areas of Europe (Strona et al., 2016). While the relationship we find at the coarse grain may reflect management practices, such as more monocultures in topographically homogeneous areas, at the 0.5-degree resolution of our analysis, this is unlikely to be a key driver. At the fine scale, our results run counter to this expectation, reflecting similar patterns to those of Strona et al. (2016) who found lower species richness in areas of high topographical heterogeneity (e.g. in Scandinavia) when compared to Potential Natural Vegetation. Additionally, factors such as land cover and soils may have an influence, but the former is spatially less heterogeneous and tied to tree cover, and data for the latter is less readily available.

Because we were able to include a measure of both local and landscape-scale topographic heterogeneity in the same model, we could fully capture the effects of both scales on coarse-grain species richness while accounting for the effect of the other scale. This allows us to tease apart the independent effects of fine- and coarse-scale heterogeneity on species' richness. For heterogeneity measures such as elevation range, included here, this is an exercise in testing theory around the existence of both negative and positive heterogeneity−diversity relationships. The same approach could, however, be used to examine the influence of land use and land cover heterogeneity on other species groups, and therefore unpick the scales at which human activity influences species diversity (Graham et al., 2019).

Declaration of Competing Interest

None.

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Supplementary materials

Supplementary material associated with this article can be found in the online version at doi:10.1016/j.baae.2022.12.002.

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