# Title

Predictability and transferability of local biodiversity environment relationships

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# Abstract

In a meta-analytical approach I combine data

Here I combine

**Keywords:** Spectral-diversity, productivity, transferability, PREDICTS, remote-sensing, extrapolation

# Introduction

Local biodiversity is known to vary with environmental heterogeneity (Hillebrand, 2004; Holt et al., 2017; Stein and Kreft, 2015), often quantified as differences in availability and variability of resources. These resources for instance include the diversity of habitats and landscapes or availability and structural complexity of vegetation or rocks (Stein and Kreft, 2015). Several theories have been postulated as possible source of the relationship with local biodiversity. These include, among others, the widely tested species-energy (Duncan et al., 2015; Evans et al., 2005; Hurlbert, 2004), the species spectral-heterogeneity (Oldeland et al., 2010; Rocchini et al., 2010) or the species-geodiversity hypotheses (Alahuhta et al., 2020; Theobald et al., 2015). However, despite a number of global meta-analyses on the relationship between environmental heterogeneity and local biodiversity (Duncan et al., 2015; Stein et al., 2014), it has rarely been investigated how predictable and transferable these relationships are, especially across taxonomic and functional groups, biomes and different biodiversity measures.

Predictions made by biological models are key for a better understanding of ecological theory and the creation of conservation management relevant outputs (Houlahan et al., 2017; Miller et al., 2004). Because of logistic and economic constrains and the evermore increasing demand for scenarios and spatial maps by policy makers and land managers, biodiversity modellers often need to rely on inter- and extrapolations of model predictions across space and time (Miller et al., 2004). These model predictions can and indeed should be investigated for their predictability, e.g. a model’s ability to accurately predict correlative relationships within the same spatial and/or temporal context, and transferability, e.g. the capacity to produce accurate predictions for conditions dissimilar to those for which a model was trained (Petchey et al., 2015; Yates et al., 2018). And yet model predictability and transferability is rarely consistently assessed and, when studied in more detail, results often do not look promising.

There is increasing evidence that models using variables of environmental heterogeneity often fail to accurately predict and transfer biodiversity environment relationships. Studies have found that the predictability of local biodiversity in response to differences in environmental heterogeneity caused by land use are highly variable between geographic regions (Phillips et al., 2017) and local contexts (Jung et al., 2017). Similarly, transferability of model predictions to spatial or temporally distinct regions has long been recognized as key issue for species distribution models (Mesgaran et al., 2014; Regos et al., 2019; Zurell et al., 2012) and models using local and regional biodiversity measures (Parmentier et al., 2011; Schmidtlein and Fassnacht, 2017). However few macroecological studies based on local biodiversity data report prediction accuracy, which can ultimately hinder their application (Rapacciuolo, 2019).

A key issue for assessing predictability and transferability of local biodiversity environment relationships in macroecological studies has been the various ways in which environmental heterogeneity is quantified (Stein and Kreft, 2015). However advances it remote sensing and cloud-processing now enable robust quantification of environmental heterogeneity at high resolution and global extent for inclusion in ecological models (Gorelick et al., 2017; Randin et al., 2020). Through repeated satellite observations, measures of environmental heterogeneity, such as differences in photosynthetic activity or spectral dissimilarity as proxies for vegetation productivity and condition or habitat structure respectively (Radeloff et al., 2019; Rocchini et al., 2010), can be robustly quantified. Subsequently, these measures have been incorporated in statistical models for the prediction of species distributions (Cord et al., 2013; He et al., 2015) or to assess differences in local biodiversity (Jung et al., 2019a, 2019b; Oldeland et al., 2010; Rocchini et al., 2015). Remote sensing data can therefore – opposed to study-specific predictor variables commonly included in ecological meta-analysis – serve as globally consistent predictor for studies of biodiversity environment relationships. Linked with new global databases on local biodiversity in-situ observations (Hudson et al., 2017), the time has come to investigate predictability and transferability of biodiversity environment relationships in greater detail.

There are a number of shortcomings in previous analyses on the predictability and transferability of local biodiversity environment relationships. Of the work known to the author most studies have (a) focussed on effect sizes among studies, rather than the predictability and transferability of this relationships, (b) tended to focus mostly on species richness (Stein et al., 2014), thus ignoring other biodiversity measures such as total abundance or differences in species assemblage composition, (c) have used variables of varying origin to capture effects of changes in environmental heterogeneity on biodiversity (Shackelford et al., 2017; Supp and Ernest, 2014) or have (d) focussed only on regional extents and single taxonomic groups such as butterflies or plants (Kerr et al., 2001; Oldeland et al., 2010; Schmidtlein and Fassnacht, 2017). I believe that accounting for these issues is key if we are to understand in which situations spatial and/or temporal projections of biodiversity change can be reliable and accurate.

In this study I investigate the predictability and transferability of model-based predictions on local biodiversity environment relationships. The expectation is that (1) predictability is generally larger than transferability, (2) species-environmental relationships are less transferable between different environmental spaces than between taxonomic groups, and that (3) unexplained variation is predominantly linked to differences in study design, e.g. spatial scale and sampling duration, and biogeography, rather than differences in functional or taxonomic groups. To test this, I combine local biodiversity data of multiple taxonomic origin with remotely-sensed environmental predictors quantifying photosynthetic activity (Duncan et al., 2015; Evans et al., 2005; Stein et al., 2014) and spectral variability (Rocchini et al., 2010). Using hierarchical Bayesian models, I then assess the predictability, quantified as overall and within-study reduction in prediction error, and transferability, quantified as reduction in prediction error between different studies of comparable study design that fall within the same or different environmental space and taxonomic group (Figure 1). I expect that the results of this work provide further insights into the generality of local biodiversity-environment relationships at a global scale, which hopefully stimulates a debate on whether local biodiversity measures, such as abundance or richness, can accurately be predicted to unsampled regions.

<Figure 1: Schematic of approach. Show missing and permutated data. Link to remote sensing data and spatial differences in assemblages. Use a globe illustration with phylopic icons to illustrate prediction within and among studies>

# Methods

### Biodiversity data preparation

I took species assemblage data from the global **P**rojecting **R**esponses of **E**cological **D**iversity **I**n **C**hanging **T**errestrial **S**ystems (PREDICTS) database (Hudson et al., 2017), which contains records of species occurrence and abundance at spatial-explicit sites ‘sites’ as reported in published ‘studies’. Only studies which differ in ‘land-use’ and have spatial and temporal information associated with them, e.g. sampling extent and date of sampling, were included in the PREDICTS database (Hudson et al., 2014).

Studies in the PREDICTS database vary widely in scope, notably in taxonomic coverage (e.g. invertebrates, plants, birds, … ), spatial grain (0.05 – 39,150m, median = 60m), sampling start (1984 - 2013) and effort (>0 – 4,382 days, median = 91 days) or methodology (flight traps, transects, …). Because of these differences, previous models utilizing PREDICTS data have exclusively relied on relative comparisons between studies (Purvis et al., 2018), where site-based biodiversity measures are typically compared against a (discrete) reference site within the same study (Gray et al., 2016; Jung et al., 2019b; Newbold et al., 2015). Comparisons of relative differences in biodiversity have obvious limitations, in that they require baselines, which often vary with local factors (Jung et al., 2017), and furthermore easily cause misinterpretations of the magnitude of effect.

In this study I aim to investigate whether environmental covariates can help to predict site-based biodiversity measures within and between studies. I created groups of comparable studies based on the taxonomic information and study methodology, for instance birds that were counted through point counts.

To account for differences in spatial grain and sampling effort, I used the Mobr package (REF) to create cross-validated species accumulation curves. Previous studies using PREDICTS data assumed that within-study abundance of species individuals increases linearly with sampling effort (Newbold et al., 2015). Finally, I calculated for each site *j* two commonly used measures of local biodiversity, a rarefied estimate of the total number of species r and the rarefied log10-transformed abundance r of all species.

### Environmental predictors

For each PREDICTS site I calculated two different remotely-sensed predictors that reflect the overall heterogeneity of environmental conditions. First, 16-day time series of atmospherically corrected spectral data (MCD43A v006, [Schaaf *et al.* 2002]) from the Moderate Resolution Imaging Spectroradiometer (MODIS) sensor on board the Terra and Aqua satellites were downloaded for each PREDICTS site from Google Earth Engine (Gorelick et al., 2017). From the obtained time series, I then selected the study and site specific first year of spectral data before biodiversity sampling.

Gap filling

No gap filling of missing spectral data was conducted as overall proportion of missing data was low (mean: 21.9% ± 22.7 SD) and aggregated in sub-sequential steps of the analysis. Nevertheless we removed sites with more than half of remote sensing measures missing, assuming that aggregated annual statistics are less precise, resulting in a total of 19954 sites for analyses.

Second, I then calculated from the acquired time series, as proxy of overall photosynthetic activity, the arithmetic mean of the two-band Enhanced Vegetation Index (EVI, Jiang *et al.* 2008). Variations in photosynthetic activity have previously been shown to reflect continuous gradients in land cover (Huete et al., 2002; Radeloff et al., 2019) and directly influence local biodiversity measures and life history (Jung et al., 2019a, 2019b; Oldeland et al., 2010; Pettorelli et al., 2005). Furthermore, I also calculated a measure of overall spectral heterogeneity from the spectral data (Randin et al., 2020; Rocchini et al., 2015, 2010). Spectral heterogeneity is expected to give a more nuanced view on habitat structure and condition than any single vegetation index. To capture spectral heterogeneity I first conducted a principal component analysis of all spectral bands (1-7) and then from the first two bands, which on average explained 91.3% ± 5.93 SD of the variation, calculated the centroid of the resulting scatter plot. Spectral heterogeneity per site was then summarized as the mean Euclidean distance to this centroid. Both environmental predictors were reasonably uncorrelated (SI Figure 1).

### Predictability and transferability scenarios

To evaluate the predictability and transferability of local biodiversity environment relationships, I construct five cross-validated sets

Individual

Partial pooling per biome (SS|biome)

Pooling per

These were conducted using a ‘blocked’ cross-validation procedure (Roberts et al., 2017), where

Remove from each set of variables, values at the rear end (extrapolation) and centre (interpolation).

### Statistical analysis

For the statistical analysis I relied on hierarchical Bayesian linear models using a

with intercepts varying per study and/or sampling methodology and taxonomic grouping.

Predictability and transferability is assessed by calculating the Relative Mean Absolute Error (MAE) between the observed biodiversity measures and the one predicted by the model for a given study. Used relative owing to difference in measure and making this comparable

mean percentage error (MPE)

‘Because actual rather than absolute values of the forecast errors are used in the formula, positive and negative forecast errors can offset each other; as a result the formula can be used as a measure of the bias in the forecasts.’

Run through CART model to detect most important variables

Bayesian

Need to vary random intercepts

Study level intercepts makes prediction impossible across studies. Find replacement through accounting for sampling methodology.

Or study as random slope! Nested within habitat type

Biodiversity and environmental heterogeneity relationships can

Cross-validation

In the context of this study, I define ‘Predictability’ as the ability to accurately infer *y* based on environmental predictors *x* within a PREDICTS study and ‘Transferability’ as the ability to predict *y* with *x* across studies with the same sampling methodology and taxonomic group (Figure 1). The explained variance and precision of both predictions was assed using Bayesian R² and Root-Mean-Square Error (RMSE) metrics and compared them between taxonomic groups and biomes.

Classification tree on residuals -> find most influential variables on errors

Variables: Habitat type dominant, climate, traits (body size, taxonomic group), scale, time period, sampling duration

All Bayesian statistical models were fitted constructed using the ‘brms’ package (Bürkner, 2017) and

MCMC stats, parameters

# Results

Figure 2: Overall correlation strength within study and across studies

Figure 3: Across taxonomic groups with their R-square

Figure 4: Path Model? Or classification tree of residuals

Figure 5: MESS or similar globally for all predictors. Insert points. Below the 3 maps show a simple boxplot (vertical) highlighting the proportion of terrestrial land area outside the environmental surface. Or scatterplot of environmental surface with the points highlightedg

* Show average fitted R2 across combinations
* Show cross-validated prediction

# Discussion

Do not quantify land-use as used by many common models, however the situation should be similar

Ecological models can and should be used for predictions (Houlahan et al., 2017), however caveats and limitations should be better identified, communicated and hopefully build upon. According to Yates *et al.* (2018) ‘transferability’ is broadly defined as the capacity of a model to produce *predictions for a new set of predictors that differ from those on which the model was trained*.

Especially recently predicted global relationships of local data across scales can be problematic. Uncertainty unknown!

Data was not specifically gathered to test these hypotheses

Species environment relationships do not equate relationships to pressures.

This is especially relevant, since a number of studies spatially extrapolated local biodiversity estimates, e.g. species richness or abundance, to unsampled areas (König et al., 2017; Newbold et al., 2016; Phillips et al., 2019; van den Hoogen et al., 2019). These approaches thus assume that local biodiversity-environment relationships are transferable to new environments.

The question of transferability has also long been investigated in the context of species distribution modelling (Mesgaran et al., 2014; Regos et al., 2019), where tools have been developed to quantify and visualize the uncertainty introduced by projecting models to novel environments in space and time (Mesgaran et al., 2014; Roberts et al., 2017; Zurell et al., 2012).

Our findings also have major implications on broad-scale extrapolations.

Modelled local biodiversity responses to land use, e.g. regression coefficients towards differences in discrete land-use variables, such

of local biodiversity data from the PREDICTS databases have frequently been projected upon land use or climate data (Newbold et al., 2016, 2015), even in regions

Similarly, approaches such as the generalised dissimilarity modelling (Ferrier et al., 2007; König et al., 2017) rely heavily on the assumption that spatial turnover in assemblage composition is transferable as a function of environmental variables such as climate and soil.

Or work aiming to predict species traits at large scales often show considerable uncertainty in areas that have low sample density or are outside the environmental space of included data (Boonman et al., 2020).

Another limitation of the presented results is that preceding changes in remotely-sensed environmental predictors have generally been ignored. In previous work I have found that observed differences in local biodiversity tend – to a measurable degree – be influenced by preceding changes in remotely-sensed vegetation availability (Jung et al., 2019b, 2019a).

# Conclusion

Improve existing models to account for underlying hierarchies

Ensure covariates are based on globally replicable and transparent way, e.g. no

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