# Title:

Predictability and transferability of local biodiversity-environment relationships across the tree of life

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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:

- Introduction to species-environment relationships & Mechanisms

Biodiversity is known to vary along environmental gradients (Hillebrand, 2004; Holt et al., 2017).

This variation

Ecologists have long postulated a number of hypotheses as possible source of this variation. These include, among others, the widely tested species-energy hypothesis (Duncan et al., 2015; Evans et al., 2005; Hurlbert, 2004), the species spectral-heterogeneity hypotheses (Oldeland et al., 2010; Rocchini et al., 2010) and the species-geodiversity relationship (Alahuhta et al., 2020; Theobald et al., 2015).

And while a number of empirical studies exist that investigated these hypotheses using local biodiversity measures, such as species richness or abundance, rarely has been investigated whether those hypotheses hold across multiple taxonomic groups and/or geographic regions.

- Previous studies on the relationships

Spatial and temporal

- Predictability and transferability

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*.

Predictability

For a number of species-environment relationships there is increasing evidence that environmental covariates often fail to accurately predict local biodiversity in new areas (Parmentier et al., 2011; Schmidtlein and Fassnacht, 2017). With even pressures such as land use been found to be highly variable in geographic space and local setting (Jung et al., 2017; Phillips et al., 2017).

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, which might not necessarily be the case.

Because of logistic and economic constrains and the evermore increasing demand for spatialized information by policy makers and land managers, biodiversity modellers often need to rely on interpolations and extrapolations of model inferences across space and time (Miller et al., 2004).

Estimating predictability and transferability of biodiversity models is key to for our understanding of ecological relationships (Houlahan et al., 2017; Yates et al., 2018). Here

In spatial or temporal contexts ecological niche models (Moon et al., 2017; Petchey et al., 2015)

In order to be maximal useful for policy makers, Many

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

While spatial cross-validation can be used to robustly estimate uncertainty in predictor space (Roberts et al., 2017), few macroecological studies based on local biodiversity data report or map uncertainty, which can ultimately hinder their application (Rapacciuolo, 2019).

Advances it remote sensing and cloud-processing increasingly 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 measurements measures of environmental heterogeneity, such as differences in photosynthetic activity or spectral dissimilarity, which can serve as proxies for vegetation productivity and condition or habitat structure (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 predictors commonly included in ecological meta-analysis – serve as globally consistent predictor for studies of biodiversity environment relationships.

Understanding the predictability and transferability of biodiversity environment relationships is critical for our ability to make reliable predictions of changes in local biodiversity measures, especially if projected to novel, previously unsampled regions. Yet, previous work on the relationship between local biodiversity measures and environmental heterogeneity have (a) focussed on effect sizes among studies, rather than the predictability and transferability of this relationships, (b) tend 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 temporal projections of biodiversity change can be reliable and accurate.

In this study I investigate the predictability and transferability of two commonly found environmental relationships with biodiversity measures. 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 origins 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 or even extrapolated in 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).

### 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.

3 scenarios

Individual

Partial pooling per biome (SS|biome)

Pooling per

Predictability and transferability is assessed by calculating the Mean Absolute Error (MAE) between the observed biodiversity measures and the one predicted by the model for a given study.

Run through another 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.

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) 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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