# 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.

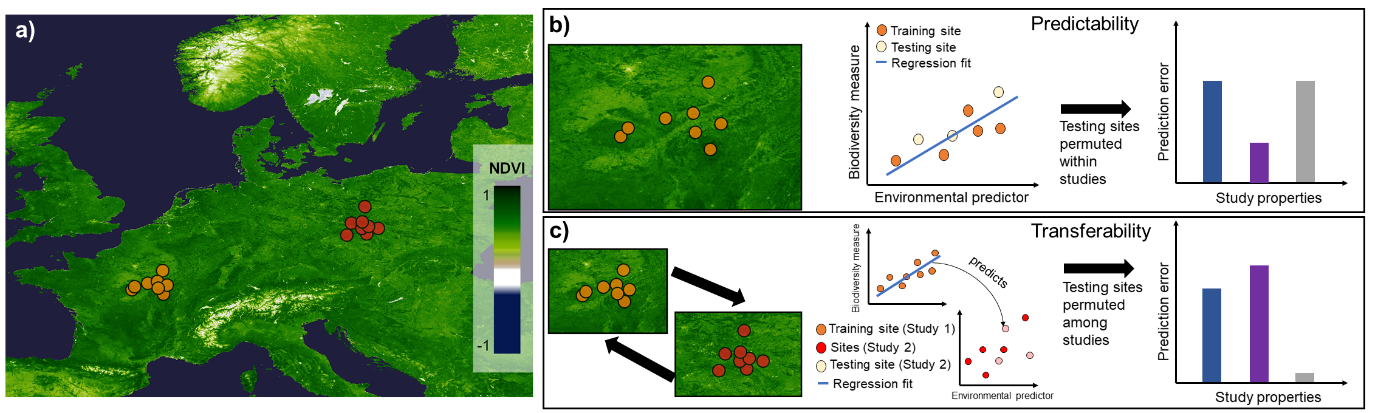
Predictions made by biological models are key for a better understanding of ecological theory and the creation of conservation management relevant outputs (Houlahan et al., 2017; Miller et al., 2004). Because of logistic and economic constrains and the evermore increasing demand for scenarios and spatial 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 (Goetz et al., 2014; 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 birds, butterflies or plants (Goetz et al., 2014; 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 cases 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 and transferred to unsampled regions.



**Figure 1:** (a) Distribution of two hypothetical studies (coloured in orange and red) and their sites at which a biodiversity measure and environmental predictor has been calculated. The Normalized Difference Vegetation Index (NDVI) is shown as example of remotely sensed environmental predictor. Simplified procedure for investigating the (b) predictability and (c) transferability of local biodiversity-environment relationships. For (b) testing sites are removed at random within studies, regressions refitted and the within-study prediction error quantified in relation to study properties. Contrastingly, in (c) regression fits from study 1 (orange) are used to predict permuted biodiversity estimates in study 2 (red), with the prediction error quantified in relation to study properties.

# Methods

### Biodiversity data preparation

In this study I aim to investigate whether environmental covariates can help to predict site-based biodiversity measures within and between studies. 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 study properties, notably in taxonomic coverage (e.g. invertebrates, plants, birds,…), spatial grain (0.05 – 39,150m, median = 60m), sampling start (1984 - 2013), sampling effort (>0 – 4,382 days, median = 91 days) and methodology (flight traps, transects,…). Owing to these differences, a hierarchical modelling framework is usually necessary when analysing biodiversity estimates from databases such as PREDICTS (Purvis et al., 2018).

For each study *j* in the PREDICTS database, I calculated four different site-based measures of local biodiversity: total Species richness (), total log-transformed abundance (, the arcsine square root transformed probability of interspecific encounter as measure of assemblage evenness () and the pairwise Sørensen similarity index as measure of difference in assemblage composition (). Similar to previous studies I assumed that, in the few cases where within-study study effort differs among sites, the abundance of species individuals increases linearly with sampling effort (Newbold et al., 2015). In cases where the sampling extent of a site is missing in the PREDICTS database, I approximated the mean sampling extent using a heuristic that fills missing estimates with the average used within studies of the same sampling method and/or taxonomic group. Earlier work has shown that this approximation can precisely fill missing sampling extents (Jung et al., 2019a). Lastly, I created, based on the taxonomic group and sampling method attributed to a study in the PREDICTS databased, a new factor variable that groups studies of comparable method and taxonomic grouping, such as for instance studies sampling bird individuals that were counted using point counts. I realize that not all differences in sampling techniques can attributed to this contrast and therefore post-hoc analyse the contribution of differing sampling methods in explaining the cross-validated model error (see statistical analysis).

### Environmental predictors

In this work I exclusively used remotely-sensed environmental predictors, which – opposed to commonly-used differences in climate or topography – have (1) medium to high spatial resolution, (2) are consistently quantified at global extent in comparable units, (3) are temporally explicit, often differing between years, (4) correlate with differences in local biodiversity (Duncan et al., 2015; Jung et al., 2019a) and land use (Mueller et al., 2014; Yin et al., 2014).

For each site in the PREDICTS databases, I calculated two different remotely sensed predictors that reflect environmental heterogeneity. First, 16-day time series of atmospherically corrected spectral observations (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). Time series of remotely sensed spectral observations often have data gaps caused by clouds or sensor errors. To reduce the length of overall data gaps, the obtained time series were first aggregated (arithmetic mean) to monthly estimates for each spectral observation (band 1 to 7). The overall proportion of missing data in the aggregated time series was low (mean: 5.9% ± 10.5 SD), nevertheless we subjected the aggregated time series to a missing value imputation using a Kalman smoother on the whole time series (Hyndman and Khandakar, 2008) as implemented in the ‘imputeTS’ R package (Moritz and Bartz-Beielstein, 2017). Whenever the imputation did not converge, a linear interpolation was used to impute missing observations among years. Only data gaps smaller that five months were filled in that manner and sites with six or more months were excluded from subsequent analyses. From the full time series, I then selected for each site the first year (12 months) of data preceding biodiversity sampling as representation of environmental heterogeneity.

Second, I calculated from the remaining time series of spectral observations, 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 calculated a principal component analysis of all spectral observations (bands 1-7) and then calculated from the first two axes, which on average explained 93% ± 5.92 SD of all variation, the centroid of the resulting bivariate scatter plot. Spectral heterogeneity per site was then summarized as the mean Euclidean distance to this centroid. Both environmental predictors, photosynthetic activity and spectral heterogeneity are only weakly correlated (Pearson’s r = -0.21, SI Figure 1). In total 21821 sites had suitable remote sensing data for subsequent analyses, with the remainder (4028 sites) being sampled either to long ago for sufficient remote sensing coverage or having too many data gaps.

### Statistical analysis

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

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

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 assessed using Bayesian R² and error (XXX) metrics and compared them between taxonomic groups and biomes.

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

MCMC stats, parameters

To evaluate the predictability and transferability of local biodiversity environment relationships, I constructed in total five spatially structured permutation sets of sites (Roberts et al., 2017), with the total number of sites removed differing between studies. In the case of evaluating predictability, I removed 33% of sites split equally over spatial blocks nested within the same study (Figure 1b). Not every study in the PREDICTS has a spatially blocked sampling design (Hudson et al., 2014) and in cases where such blocking is missing, I removed sites at random, but weighted by the mean distance to the study centroid, therefore placing extra weight on sites that are less likely to be in close proximity. The remaining 66% of sites were then used to refit the regression formulas outlined above and applied to the excluded sites to predict the local within-study biodiversity measures. For transferability, I removed 33% of sites within a given study, however only for the subset of studies in the PREDICTS database, where a matching study of comparable methodology is available (Figure 1c). In addition, the following random effect structure was added to the regression formula: , thus allowing partial pooling of effect strengths among studies of the same sampling methodology and taxonomic group (see above) and nested within the same biome (Harrison et al., 2018). A new regression fit for this reduced set of sites was then created and used to predict the biodiversity measures of the permuted sites.

In both predictability and transferability scenarios the prediction precision is assessed by calculating per study the mean absolute percentage error (MAPE = ) between the observed biodiversity measures () and the ones predicted by the model ( for a given site *i* in study *j* .

I realize that alternative metrics able to quantify model precision exists, however for the sake of simplicity, the MAPE is used as metrics that is interpretable and comparable between studies with response variables of varying units and value range.

Results shown by biodiversity measure and broad taxonomic group (e.g. Plantae, Invertebrates, Mammals, Amphibians, .

Lastly, I posthoc investigated possible sources of study intrinsic and extrinsic factors that might explain the prediction error in both predictability and transferability scenario. Since the XX is a relative measure of prediction error, it can be compared between studies. Using a random forest regression, I aimed to find the most influential groups of variables that might explain any site-specific prediction error. I considered four wider groups of variables: (1) study-specific factors such as the study sampling method, rescaled sampling effort, the broadest taxonomic group, sampling duration, sampling extent; (2) habitat characteristics such as predominant land use and use intensity according to PREDICTS, the coefficient of variation of EVI2 values as measure of dispersion and mean elevation sampled from a highly-resolved Digital Elevation model (Danielson, J.J., Gesch, 2011); (3) biogeographic factors such as the biome and realm (Dinerstein et al., 2017) and (4) uncharacterized factors. Random forest regressions were fitted using the ‘ranger’ package in R (REF).

# 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.

Indicators

https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0041128

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).

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.

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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