Predictability and transferability of local biodiversity environment relationships

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Background: Biodiversity varies in space and time, and often in response to environmental heterogeneity. Indicators in the form of local biodiversity measures – such as species richness or abundance – are common tools to capture this variation. The rise of readily available remote sensing data has enabled the characterization of environmental heterogeneity in a globally robust and replicable manner. Based on the assumption that differences in biodiversity measures are generally related to differences in environmental heterogeneity, these data have enabled projections and extrapolations of biodiversity in space and time. However so far little work has been done on quantitatively evaluating if and how accurately local biodiversity measures can be predicted.

Methods: Here I combine estimates of biodiversity measures from terrestrial local biodiversity surveys with remotely-sensed data on environmental heterogeneity globally. I then determine through a cross-validation framework how accurately local biodiversity measures can be predicted within ("predictability") and across similar ("transferability") biodiversity surveys.

Results: I found that prediction errors can be substantial, with error magnitudes varying between different biodiversity measures, taxonomic groups, sampling techniques and types of environmental heterogeneity characterizations. And although errors associated with model predictability were in many cases relatively low, these results question - particular for transferability - our capability to accurately predict and project local biodiversity measures based on environmental heterogeneity. I make the case that future predictions should be evaluated based on their accuracy and inherent uncertainty, and ecological theories be tested against whether we are able to make accurate predictions from local biodiversity data.

1 **Predictability and transferability of local biodiversity environment relationships**

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Abstract

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29 biodiversity measures, taxonomic groups, sampling techniques and types of environmental

30 heterogeneity characterizations. And although errors associated with model predictability were in

31 many cases relatively low, these results question - particular for transferability - our capability to

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34 uncertainty, and ecological theories be tested against whether we are able to make accurate

35 predictions from local biodiversity data.

36

Introduction

38 Local biodiversity on land is known to vary with environmental heterogeneity (Hillebrand, 2004;

39 Stein & Kreft, 2015; Holt et al., 2017), often quantified as difference in availability and

40 variability of resources. These resources include the diversity of habitats and landscapes, or the

41 availability and structural complexity of vegetation or rocks (Stein & Kreft, 2015). Several
42 theories have been postulated as possible source of the relationship of environmental
43 heterogeneity with local biodiversity. These include, among others, the widely tested species-
44 energy (Hurlbert, 2004; Evans, Warren & Gaston, 2005; Duncan et al., 2015), the species
45 spectral-heterogeneity (Oldeland et al., 2010; Rocchini et al., 2010) or the species-geodiversity
46 hypotheses (Alahuhta, Toivanen & Hjort, 2020). However, despite a number of global meta-
47 analyses on the relationship between environmental heterogeneity and local biodiversity for
48 plant, bird and mammal species (Stein, Gerstner & Kreft, 2014; Duncan et al., 2015), it has
49 rarely been comprehensively investigated how predictable and transferable these relationships
50 are, especially across taxonomic and functional groups and different biodiversity measures more
51 generally.
52   Predictions made by statistical models are key for our understanding of the living world
53 and for the creation of outputs relevant for conservation management (Miller et al., 2004;
54 Houlahan et al., 2017). Because of the evermore increasing demand for scenarios and spatial
55 maps by policy makers and land managers, biodiversity modellers often need to rely on inter-
56 and extrapolations of model predictions across space and time (Miller et al., 2004). These
57 predictions need to be precise and accurate enough for the context and decisions they are meant
58 to inform (Santini et al., 2021). Thus model predictions should be investigated for their
59 predictability, e.g. a model's ability to accurately predict correlative relationships within the
60 same spatial and/or temporal context by withholding some parts of the data (as in cross-
61 validation procedures), and transferability, e.g. the capacity to produce accurate predictions for
62 conditions dissimilar to those of the data for which a model was trained (Petchey et al., 2015;
63 Yates et al., 2018; Tredennick et al., 2021). And yet, model predictability and transferability is
64 rarely consistently assessed and, when studied in more detail, results rarely look promising.
65   There is increasing evidence that models using variables of environmental heterogeneity,
66 e.g. soil condition, vegetation cover or microclimate, often fail to accurately predict and transfer
67 biodiversity environment relationships. Studies have found that the predictability of local
68 biodiversity as function of a difference in environmental heterogeneity are highly variable
69 between geographic regions (Phillips, Newbold & Purvis, 2017) and local contexts (Duncan et
70 al., 2015; Jung et al., 2017). Similarly, transferability of model predictions to spatial or
71 temporally distinct regions has long been recognized as key issue for species distribution models
72 (Zurell, Elith & Schröder, 2012; Mesgaran, Cousens & Webber, 2014; Regos et al., 2019) or
73 models using local and regional biodiversity measures (Parmentier et al., 2011; Schmidtlein &
74 Fassnacht, 2017). Despite the development of techniques for assessing the novel parameter space
75 of a model (Zurell, Elith & Schröder, 2012; Meyer & Pebesma, 2021), the limited uptake of
76 modellers to evaluate and present model uncertainty can hinder the application and affect trust in
77 biodiversity model predictions (Rapacciuolo, 2019).
78   An outstanding issue for assessing predictability and transferability of local biodiversity
79 environment relationships in macroecological studies has been the various ways in which
80 environmental heterogeneity is quantified (Stein & Kreft, 2015). Recent advances in remote

81 sensing and cloud-processing have enabled the robust quantification of environmental
82 heterogeneity at high spatial and temporal resolution (Gorelick et al., 2017; Randin et al., 2020).
83 Through repeated satellite observations, measures of environmental heterogeneity, such as
84 differences in photosynthetic activity or spectral variability as proxies for vegetation cover,
85 vegetation condition and structure and overall variability of land surfaces (Rocchini et al., 2010;
86 Radeloff et al., 2019), can be robustly quantified. On their own they can be considered
87 continuous representations of contrasts in land cover and land use (Hansen et al., 2000; Jung,
88 Scharlemann & Rowhani, 2020), while also being related to key species population processes
89 (Pettorelli et al., 2005). Although those measures are not the only type of environmental
90 heterogeneity (Stein, Gerstner & Kreft, 2014), they can be exogenously quantified for different
91 points in term and have often been incorporated in statistical models for the prediction of species
92 distributions (Cord et al., 2013; He et al., 2015) or to infer differences in local biodiversity
93 measures (Oldeland et al., 2010; Goetz et al., 2014; Rocchini, Hernández-Stefanoni & He, 2015;
94 Jung et al., 2019; Jung, Scharlemann & Rowhani, 2020). Remote sensing data can therefore –
95 opposed to study-specific predictor variables commonly included in ecological meta-analysis –
96 serve as a globally consistent predictor for studies of biodiversity environment relationships
97 (Duncan et al., 2015). With the availability of new global databases on local biodiversity in-situ
98 observations (Hudson et al., 2017), it has become possible to investigate predictability and
99 transferability of biodiversity environment relationships in greater detail than what has been done
100 so far.
101   There are a number of shortcomings in previous analyses on the predictability and
102 transferability of local biodiversity environment relationships. Most studies have (a) focussed on
103 effect sizes among studies (e.g. strength of inference), rather than the predictability and
104 transferability of this relationships (Tredennick et al., 2021), (b) tended to focus mostly on
105 species richness (Stein, Gerstner & Kreft, 2014), thus ignoring other biodiversity measures such
106 as abundance or differences in species assemblage composition, (c) used variables of varying
107 origin to capture effects of changes in environmental heterogeneity on biodiversity (Supp &
108 Ernest, 2014; Shackelford et al., 2017) or have (d) focussed only on regional extents and single
109 taxonomic groups such as birds, butterflies or plants (Kerr, Southwood & Cihlar, 2001; Oldeland
110 et al., 2010; Goetz et al., 2014; Schmidtlein & Fassnacht, 2017). Quantitatively addressing these
111 issues is key, if we are to understand in which cases spatial and/or temporal predictions of local
112 biodiversity measures are reliable and accurate.
113   In this study I investigate the predictability and transferability of model-based predictions
114 on local biodiversity environment relationships. The expectation is that (i) predictability is
115 generally stronger than transferability, (ii) transferability of species-environment relationships
116 affects some biodiversity measures and taxonomic groups are less transferable than others, and
117 that (iii) unexplained variation is predominantly linked to differences in study design, e.g. spatial
118 scale and sampling duration. To test this, I combine local biodiversity data from globally
119 distributed surveys with remotely-sensed environmental predictors quantifying photosynthetic
120 activity (Evans, Warren & Gaston, 2005; Stein, Gerstner & Kreft, 2014; Duncan et al., 2015) and

121 spectral variability (Rocchini et al., 2010); predictors that represent a continuous characterization
122 of resource availability, habitat condition and land surface modifications. Using variations of
123 linear models, I assess the predictability, quantified as overall and within-study reduction in
124 prediction error, and transferability, quantified as reduction in prediction error between different
125 studies of comparable study design but identical taxonomic groups (Figure 1). The aim of this
126 work is thus to provide further insights into the generality of local biodiversity-environment
127 relationships at a global scale, which hopefully stimulates a debate on whether predicted local
128 biodiversity measures, such as total site-based abundance or richness, can accurately be predicted
129 or transferred to unsampled regions.

130

131 **Materials & Methods**

132 Biodiversity data preparation

133 For data on biodiversity I took species assemblage data from the global **P**rojecting **R**esponses of
134 **E**cological **D**iversity **I**n **C**hanging **T**errestrial **S**ystems (PREDICTS) database (Hudson et al.,
135 2017), which contains records of species occurrence and abundance at spatial-explicit sites
136 'sites' as reported in published 'studies'. PREDICTS includes only studies which differ in 'land-
137 use' and/or 'land-use intensity' and have spatial and temporal information associated with them,
138 e.g. sampling extent and date of sampling (Hudson et al., 2014). Studies in the PREDICTS
139 database vary widely in study properties, notably in taxonomic coverage (studies contain data on
140 terrestrial species of invertebrates, plants, birds, mammals, reptiles and amphibians), spatial grain
141 (0.05 – 39,150m, median = 60m), sampling start (1984 - 2013), sampling effort (>0 – 4,382 days,
142 median = 91 days) and methodology (flight traps, transects,…). Owing to these differences, a
143 hierarchical modelling framework is usually necessary when analysing biodiversity estimates
144 from databases such as PREDICTS (Purvis et al., 2018).
145   For each study j and site i in the PREDICTS database, I calculated four different site-
146 based measures of local biodiversity: total Species richness (S_i), total log-transformed abundance
147 ($\log_{10} A_i$), the arcsine square root transformed probability of interspecific encounter as measure
148 of assemblage evenness ($\sin^{-1}\sqrt{PIE_i}$) and the logit transformed pairwise Sørensen similarity
149 index as measure of difference in assemblage composition ($\text{logit } SIM_{i-i_n}$). Similar to previous

150 studies I assumed that, in the few cases where within-study study effort differs among sites, the
151 abundance of species individuals increases linearly with sampling effort (Newbold et al., 2015).
152 In cases where the sampling extent of a site is missing in the PREDICTS database, I
153 approximated the mean sampling extent using a heuristic that fills missing estimates with the
154 average used within studies of the same sampling method and/or taxonomic group. Earlier work
155 has shown that this approximation can accurately fill missing sampling extents (Jung et al.,
156 2019). Lastly, I created, based on the taxonomic group and sampling method attributed to a study
157 in the PREDICTS databased, a new factor variable that groups studies of comparable method,
158 unit and broad taxonomic grouping (SI Table 1), such as for instance studies involving bird

159 individuals that were counted using point counts. I realize that not all differences in sampling
160 techniques can attributed to this new contrast between sites and therefore post-hoc analyse the
161 contribution of differing sampling methods in explaining the cross-validated model error (see
162 statistical analysis).

163 Environmental predictors

164 In this work I exclusively used remotely-sensed environmental predictors, photosynthetic
165 activity and spectral variability, which are (1) available at medium to high spatial resolution, (2)
166 consistently quantified at global extent in comparable units, (3)temporally explicit, often
167 differing between years, (4) correlate with differences in local biodiversity (Duncan et al., 2015;
168 Jung et al., 2019) and land use (Mueller et al., 2014; Yin et al., 2014). These predictors can be
169 considered proxies of resources available to species (Pettorelli et al., 2005) as well as
170 characterizing differences in local habitat and land surface conditions on a continuous scale
171 (Rocchini et al., 2010; Jung et al., 2019; Randin et al., 2020). It should be noted that the aim of
172 this work is not identify best possible predictors of local biodiversity, but rather to evaluate most
173 commonly used ones for their predictability and transferability.
174 For each site in the PREDICTS databases, I calculated two different remotely sensed
175 predictors that reflect environmental heterogeneity. First, 16-day time series of atmospherically
176 corrected spectral observations (MCD43A v006, [Schaaf et al. 2002]) from the Moderate
177 Resolution Imaging Spectroradiometer (MODIS) sensor on board the Terra and Aqua satellites
178 were downloaded for each PREDICTS site from Google Earth Engine (Gorelick et al., 2017).
179 Time series of remotely sensed spectral observations often have data gaps caused by clouds or
180 sensor errors. To reduce the number of data gaps, I first aggregated (arithmetic mean) the
181 obtained time series to monthly estimates for each spectral observation (band 1 to 7). The overall
182 proportion of missing data in the aggregated time series was low (mean: 5.9% ± 10.5 SD),
183 nevertheless I subjected the aggregated time series to a missing value imputation using a Kalman
184 smoother on the whole time series (Hyndman & Khandakar, 2008) as implemented in the
185 'imputeTS' R package (Moritz & Bartz-Beielstein, 2017). Whenever the imputation did not
186 converge, a linear interpolation was used to impute missing observations among years. Only data
187 gaps smaller than five months were filled in that manner and sites with six or more missing
188 months were excluded from subsequent analyses. From the full time series, I then selected for
189 each site the first year (12 months) of data preceding biodiversity sampling as representation of
190 environmental heterogeneity (Jung et al., 2019).
191 Second, I calculated from the remaining time series of spectral observations, as proxy of
192 overall photosynthetic activity, the arithmetic mean of the two-band Enhanced Vegetation Index
193 (EVI, Jiang et al. 2008). Photosynthetic activity approximates the condition, structure and
194 availability of plant biomass. Variations in photosynthetic activity have previously been shown
195 to reflect continuous gradients in land cover (Huete et al., 2002; Radeloff et al., 2019) and
196 directly influence local biodiversity measures and life history (Pettorelli et al., 2005; He, Zhang
197 & Zhang, 2009; Oldeland et al., 2010; Jung et al., 2019; Jung, Rowhani & Scharlemann, 2019).

198   Furthermore, I also calculated a measure of overall spectral variability from the satellite sensor
199   data (Rocchini et al., 2010; Rocchini, Hernández-Stefanoni & He, 2015; Randin et al., 2020).
200   Spectral variability is expected to give a more nuanced view on land surface conditions than any
201   single vegetation index, given that it utilizes not two but all spectral bands of the satellite
202   (Rocchini et al., 2010). To capture spectral variability, I first calculated a principal component
203   analysis of all spectral observations (bands 1-7) and then calculated from the first two axes,
204   which on average explained 93% ± 5.92 SD of all variation, the centroid of the resulting
205   bivariate scatter plot. Spectral variability per site was then summarized as the mean Euclidean
206   distance to this centroid. Both environmental predictors, photosynthetic activity and spectral
207   variability are only weakly correlated (Pearson's r = -0.21, SI Figure 1). In total 21821 sites had
208   suitable remote sensing data for subsequent analyses, with the remainder (4028 sites) being
209   sampled either too long ago for sufficient remote sensing coverage from MODIS (2000 onwards)
210   or having too many data gaps.

Statistical analysis

212   In the context of this work, 'predictability' is defined as the ability to accurately infer a
213   biodiversity measure y_{ij} based on the environmental covariates x_{ij} among the sites i of a
214   PREDICTS study j (Figure 1b), and 'transferability' as the ability to accurately predict y_i based
215   on the environmental covariates x_i across studies of the same sampling methodology and
216   taxonomic group (Figure 1c).
217   In both predictability and transferability variants prediction accuracy is assessed by
218   calculating for each study the symmetric mean absolute percentage error ($sMAPE_j = \frac{100}{n}$
219    $\sum_{i=1}^{I} \left| \frac{y_{predicted} - y_{observed}}{(|y_{observed}| + |y_{predicted}|)} \right|$) between the observed biodiversity measures ($y_{observed}$) and the ones
220   predicted by the model ($y_{predicted}$) for a given site i. The sMAPE quantifies the percentage error
221   in a model prediction and is bounded between 0 and 100%. Alternative metrics to quantify
222   prediction precision and accuracy exists, however in this case the sMAPE is preferrable for
223   PREDICTS style data owing to its simplicity and inter-comparability between studies that use
224   biodiversity measures of different units and value ranges.
225   I constructed separate models for each study j and biodiversity measure y in site i, by assuming
226   that $y_i = \alpha_i + \beta_i x_i + \epsilon$, where α is the study specific intercept, β a slope coefficient, x the
227   environmental predictor and ϵ an error term. Models of S_i were assumed to have Poisson
228   distributed errors and a log-link function (log y), while models of A_i, PIE_i and SIM_{i-i_n} were
229   assumed to have Gaussian distributed errors. Pairwise similarities in species composition
230   (Sorensen Index) were related to differences in environmental predictors x in addition to pairwise
231   distance between sites, calculated as $\log_{10}(x + 0.05 \text{ km})$ from great circle distances between
232   sites. Here I calculated pairwise absolute difference in mean photosynthetic activity or between

233   spectral centroids of each site (see environmental predictors). For each constructed full model I
234   furthermore calculate an R² measure as indication of overall variance explained.
235   To evaluate the predictability and transferability of local biodiversity environment
236   relationships, I constructed in total ten permutation sets, in each of which sites were split into
237   testing (33%) and training (66%) datasets. For evaluating predictability, I removed one third of
238   sites (33%) at random (Figure 1b), but weighted them by the mean distance to the study centroid,
239   therefore placing extra weight on sites that are less likely to be in close proximity (Roberts et al.,
240   2017). For transferability, instead of individual sites, I sampled and removed 33% of entire
241   studies and their sites from each set of comparable methodology in the PREDICTS database
242   (Figure 1c, methods above). However across all ten permutation sets, I iteratively weighted (0-1)
243   this sampling by whether a given study has been sampled before, therefore ensuring that each
244   study is part of both testing and training dataset at least once.
245   For each respective permutation set, predictability and transferability was then evaluated
246   by using the remaining training data to estimate the regression specified above for each study or
247   group of comparable methodology. I excluded combinations of taxonomic groups, sampling
248   method and sampling unit for which fewer than 2 studies where available. In total 77.3% of all
249   studies had a matching study of comparable methodology and unit for the same taxonomic
250   group. A table with all recategorized combinations (43) can be found in the supplementary
251   materials (SI Table 1). Using the fitted models I predicted y for the excluded 'hold-out' 33%
252   sites and then calculated the average sMAPE for each study in the permutation sets.
253   Lastly, I explored possible correlates of why sMAPE for some studies is larger than for others
254   for each of the four considered biodiversity measures. I considered a series of variables
255   commonly related to differences in sampling design, species and individual detectability and
256   errors in remotely-sensed environmental predictors. Specifically, I calculated for each study in
257   the permutation sets, the median sampling extent (m) as measure of sample grain, the median
258   sampling duration (days) of the study, the number of sites with a study as measure of effort for
259   the whole study, the average number of samples across sites as effort for area-based sampling
260   effort or the average time sampled (hours) for time-based sampling effort, average accessibility
261   to sites in the study (distance to nearest city in meters) from Weiss et al. (2018), and finally
262   factors related to possible errors in remotely-sensed environmental variables, including the
263   amount of missing data (before gap filling) and the average topographic ruggedness per study
264   using data from Amatulli et al. (2018). To make comparisons across these different units and
265   scales, I standardized all variables before model fitting by subtracting the mean and dividing by
266   one standard deviation.
267   I fitted linear models allowing partial pooling among studies j (Harrison et al., 2018) by
268   adding a random intercept α_k in addition to the overall intercept, e.g. $SMAPE_j = \alpha + \alpha_k + \beta_j$
269   $x_j + \epsilon$. These kind of models can borrow strength among studies by shrinking individual
270   estimates towards an overall population-wide average (Purvis et al., 2018; Harrison et al., 2018).
271   As random intercept k I used the methodology specific grouping (see methods and SI Table 1)
272   thus pooling possible correlates among studies of similar methodology. I fitted all possible

273   combinations between the above mentioned variables, including an interaction between sampling
274   extent and sampling effort, finally constructing an average ensemble model of the 5% best
275   performing models. Models were fitted in lme4 (Bates et al., 2015) using the 'MuMIn' package
276   in R for model averaging (Bartoń, 2015).
277
278   **Results**
279
280   The explanatory power of environmental predictors – photosynthetic activity and spectral
281   variability – in explaining differences in biodiversity varied across biodiversity measures and
282   individual studies. Models fitted with photosynthetic activity explained on average slightly more
283   variance than models fitted with spectral variability, the former having an average R^2 of 0.21 ($\pm$
284   0.285 SD) compared to an average R^2 of 0.19 ($\pm$ 0.284 SD) in the latter. There was considerable
285   variation of R^2 values across studies and biodiversity measures (Figure 2), with species richness
286   on average being best explained by photosynthetic activity (R^2=0.246 $\pm$ 0.311 SD) or spectral
287   variability (R^2=0.22 $\pm$ 0.306 SD). Notably, correlations with species abundance were particularly
288   low, with the R^2 being close to 0 ($R^2 < 0.001$) for more than a quarter of all studies (Figure 2).
289   Meanwhile the difference in explained variance between models using photosynthetic activity
290   compared to spectral variability was lowest for differences in assemble composition (Pearson's R
291   = 0.922). There were no obvious spatial (SI Figure 2) or directional patterns (SI Figure 3) in the
292   average explained variance, although some studies notably had high explanatory power
293   regardless of the considered biodiversity measure (SI Figure 2).
294
295   When applying local biodiversity models to known ('Predictability') or different
296   ('Transferability') contexts, the main issue is how accurately such models can predict local
297   biodiversity measures in unknown situations based on the covariates of interest (Figure 3).
298   Regardless of whether remotely-sensed photosynthetic activity or spectral variability was used as
299   covariate, linear models were reasonably accurate for known contexts in inferring species
300   richness (sMAPE of 19.1%), abundance (11.8%) and evenness (10.3%), but less so when
301   inferring differences in species assemblages (49.3%). Errors in predicting local biodiversity to
302   different contexts were expectedly larger (Figure 3), whereas particular species richness could be
303   extrapolated relatively poorly (relative error 43.3%) similarly to differences in species
304   assemblages (67.9%), compared to abundance (25.4%) or evenness (14.3%). Notably, when
305   local biodiversity models are used to extrapolate richness to different contexts, the sMAPEwas
306   larger than 50% in 35% of all studies, compared to 8.1% and 4.7% for abundance and evenness
307   (Figure 3).
308   There were also considerable differences in prediction error, as quantified by the sMAPE, among
309   taxonomic groups. Across taxonomic groups and biodiversity measures the sMAPE was larger
310   when predictions were extrapolated to novel contexts compared to predictability, particularly so
311   for reptiles (ΔsMAPE=21.3%) and mammals (ΔsMAPE=20.8%), with the greatest difference
312   being for reptile species richness (ΔsMAPE=33%) and abundance (ΔsMAPE=28%). The

313   transferability of fungi (sMAPE=7.5%), and bird (sMAPE=9.1%) assemblage evenness was
314   overall the lowest, while predictability was best for evenness and abundance of fungi
315   (sMAPE=5.11%) and plants (sMAPE = 9.65%). Fungi and Plants had across biodiversity
316   measures the lowest sMAPE in predictability and transferability (Figure 4). Overall, assemblage
317   composition of vertebrates was the most poorly predicted with sMAPE estimates well over 50%
318   throughout (Figure 4).
319   I also explored across studies which factors helped explain differences in prediction error, as
320   quantified by the sMAPE (Figure 5). Across biodiversity measures, having a greater number of
321   samples per site most effectively reduced the sMAPE ($\Delta\beta$=-3.14) for transferability, and so did
322   sample duration but to a lesser degree ($\Delta\beta$=-0.98). Meanwhile a greater number of sites per study
323   on average increased the sMAPE ($\Delta\beta$=2.23). Patterns of comparison results were broadly similar
324   between transferability (Figure 5) and predictability (SI Figure 5), although notably a study being
325   more accessible resulted in an average larger reduction in the sMAPE ($\Delta\beta$=-1.02) for
326   predictability (SI Figure 5). Overall variance explained by these factors in the average model was
327   relatively low ($R^2_{marginal} = 0.08$, $R^2_{conditional} = 0.14$).
328

Discussion

330   In this work I comprehensively evaluate the predictability and transferability of biodiversity-
331   environment relationships, e.g. the ability of models to infer local biodiversity measures in
332   known and novel contexts. Particular emphasis is placed on differences among biodiversity
333   measures, taxonomic groups and sampling circumstances. I found that the explanatory power of
334   biodiversity-environment was relatively low for most studies (Figure 2). This aligns with a
335   previous meta-analysis that found that relationships between biodiversity measures and
336   photosynthetic activity cannot always be established (Duncan et al., 2015). I also discovered that
337   prediction errors are on average lowest for evenness and abundance, and, maybe unsurprisingly,
338   generally larger when models predictions are transferred to novel contexts (Figure 3).
339   Biodiversity measures of sessile organisms were on average more precisely predicted (Figure 4),
340   although not by much with predictions errors generally larger than 25% compared to observed
341   values, particularly so for differences in species assemblage composition. Overall these results
342   shed some doubts on the predictability and transferability of biodiversity measures, although
343   they have to be interpreted in the context of the individual studies (Figure 5) and ultimately in
344   what is an acceptable accuracy to achieve with such predictions.
345   Indeed, it is not formerly defined what makes a prediction better or worse based on
346   quantitative measures such as the cross-validated error metrics used in this study. According to
347   Yates et al. (2018) 'transferability' is broadly defined as the capacity of a model to produce
348   predictions for a new set of predictor values that differ from those on which the model was
349   trained. Similarly predictability can be understood as the capacity of a model to infer held-out
350   observations (Figure 1). In this context a good precision could be understood as a model that
351   demonstrates transferability errors smaller or comparable to errors inherent in model inferences
352   or that don't exceed an apriori set threshold. I found that the predictability of local biodiversity

353   measures was overall reasonable good with errors being smaller than 25% in most cases (Figure
354   3), although particularly differences in assemblage composition were poorly predicted. This
355   might indicate that photosynthetic activity and spectral variability are useful predictors for
356   quantifying differences in local biodiversity measures, although the variance explained varied
357   considerably across studies (Figure 2). In contrast I found that errors associated with
358   transferability of biodiversity measures can be considerable, exceeding 50% relative to the
359   original measure for species richness and differences in assemblage composition in many studies
360   (Figure 3). This is especially relevant, since a number of studies spatially extrapolated local
361   biodiversity estimates, e.g. species richness or abundance, to unsampled areas based on
362   environmental predictors (König, Weigelt & Kreft, 2017; Phillips et al., 2019; van den Hoogen et
363   al., 2019). These approaches assume that local biodiversity-environment relationships are
364   transferable to new, unsampled environments and the results by this work indicate that this often
365   entails considerable errors. Ideally models are evaluated on their ability to accurately reproduce
366   their data in novel contexts (Jung et al., 2017), quantify the uncertainty in doing so, or
367   alternatively limit predictions to areas within the models applicability (Mesgaran, Cousens &
368   Webber, 2014; Meyer & Pebesma, 2021).
369   Biodiversity measures for certain taxonomic groups might be easier to predict than others owing
370   to the dynamics, drivers and mechanisms underlying them (Magurran, 2004). Indeed previous
371   studies have found species abundance to be stronger correlated with photosynthetic activity than
372   other measures (Oldeland et al., 2010; Duncan et al., 2015). Similarly, I found that abundance-
373   based biodiversity measures – e.g. abundance and evenness – had overall lowest precision errors
374   (Figure 3). A potential mechanism could be that a greater photosynthetic activity or spectral
375   variability is indicative of resources available to species populations, facilitating population
376   growth (Hurlbert, 2004; Pettorelli et al., 2006). While species richness had the largest average
377   explained variance compared to other biodiversity measures, it performed considerably poorer
378   when evaluated in predictions (Figure 3). Possibly, the processes underlying patterns of local
379   species richness, such as colonization and extinction, might cause simple predictions to fail
380   (Chase, 2003), unless the spatial-temporal dynamics of environmental predictors are taken into
381   account (Fernández, Román & Delibes, 2016). Similarly, the fact that both predictability and
382   transferability errors were on average lowest for more sessile organisms such as Fungi and Plants
383   (Figure 4), likely indicates that similar important processes mediate biodiversity-environment
384   relationships. Overall this study highlights the benefit of comparing relationships across a range
385   of studies and biodiversity measures (Stein, Gerstner & Kreft, 2014; Duncan et al., 2015),
386   revealing that biodiversity-environment relationships are not universally strong.
387   Investigating as to what factors best explain prediction errors can help to improve future
388   monitoring and modelling efforts. Among the most important factors that resulted in overall
389   smaller prediction errors was the average number of samples per sites (Figure 5), which can be
390   considered a simplified metric of sampling completeness. Given that errors were smaller for sites
391   with many samples, it could be that many species communities in the PREDICTS database have
392   not been comprehensively sampled, if one assumes that biodiversity-environment relationships

393   are strongest in equilibrium. There are ways to account for detectability and observation biases
394   (Royle, Nichols & Kéry, 2005), which however was not feasible for the studies in the
395   PREDICTS database given the heterogeneity of sampling information. Thus better standards for
396   sampling techniques and monitoring are advisable to enable better comparability (Montgomery
397   et al., 2021).
398   Interestingly, and in contrast to previous studies (Chase & Knight, 2013), differences in
399   sample grain, e.g. the linear scale of sampling, did not help to explain why biodiversity measures
400   could be better predicted in some studies. A likely explanation is that the contrasts between
401   sampling extents are relatively small (most studies in the PREDICTS database were sampled at
402   scales between ~1m and 4000m). Scale-dependent effects might only become apparent at spatial
403   scales that go beyond the local scale. A spatial mismatch at the lower end, e.g. that the grain of
404   the used MODIS data is too coarse to be matched to the extent of sampling in PREDICTS
405   studies, could be another explanation, however previous studies that used very-high resolution
406   satellite imagery (<10m) did not find much more accurate predictions than presented here
407   (Dalmayne et al., 2013; Hofmann et al., 2017). Other, non-explored factors could further explain
408   differences in prediction error, such as for instance preceding changes in environmental
409   predictors (Jung et al., 2019; Jung, Rowhani & Scharlemann, 2019) or a better accounting of
410   differences in species traits (Duncan et al., 2015; Regos et al., 2019). Future efforts could
411   evaluate if inter- and intra-specific variability of species traits can be more precisely linked to
412   differences in environmental heterogeneity.
413   In this work I used photosynthetic activity and spectral availability as measures of
414   environmental heterogeneity, acknowledging that other characterizations of environmental
415   variability (e.g. soil, micro-climate) could be more important (Stein & Kreft, 2015). The finding
416   that prediction errors were lowest for plants and fungi could be related to the fact that
417   photosynthetic activity is more closer related to the abundance of these taxa, than for other
418   taxonomic groups, where only indirect correlations (resources for herbivores, differences in land
419   cover) could be the most likely explanation. However focussing solely on remotely-sensed
420   variables ensures global consistency and is frequently used to predict local biodiversity measures
421   (Dalmayne et al., 2013; Hofmann et al., 2017; Randin et al., 2020). The key limitation is that
422   environmental heterogeneity is not necessarily related to differences in land use and land-use
423   intensity, for which the PREDICTS database was explicitly designed (Purvis et al., 2018). Indeed
424   it could be that the potential of remotely sensed environmental heterogeneity in predicting local
425   biodiversity measures has been exaggerated, and better characterizations of land use and its
426   management from remote sensing have to be developed. Further, given the complexities of local
427   species community assembly (Chase, 2003; Leibold et al., 2004), any claim that a direct
428   prediction of 'biodiversity' through remotely-sensed proxies (Rocchini et al., 2016; Randin et al.,
429   2020) should thus be taken with a grain of salt. Remote sensers are at best able to measure
430   changes in habitat extent or condition; and those changes do not necessarily correlate strongly
431   with changes in biodiversity measures. Future work should ideally focus on the principal

432 mechanisms of species community assembly, their practical incorporation into models and how
433 remote sensing can assist in capturing relevant predictors.

434

Conclusions

436

437 The findings presented in this study have particular implications for spatial projections of local
438 biodiversity-environment relationships. Ecological models can and should be used for
439 predictions (Houlahan et al., 2017; Tredennick et al., 2021), however caveats and limitations
440 should be better identified, communicated and hopefully build upon. We need to create models
441 that enable biodiversity-environment relationships to be more predictable across scales and
442 novel contexts, especially when applied to conservation contexts (Santini et al., 2021). Given
443 the considerable drops in precision for transferability, key recommendations from this work
444 could be that spatial projections of local biodiversity measures at least provide estimates of
445 uncertainty or limit their projections to areas of model applicability (Meyer & Pebesma, 2021).
446 To improve future biodiversity predictions I further propose that models (a) should be evaluated
447 comprehensively based on their ability to create accurate predictions, (b) account better for
448 underlying hierarchies and sampling effects, (c) ensure that environmental predictors are
449 quantified in a globally replicable and transparent way. Quantitative correlative models might not
450 be the most precise in many situations, but that does not invalidate their use if
452 shortcomings are appropriately communicated.

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Figure 1

Schematic of the analysis framework showing the distribution of two hypothetical studies and their sites at which a biodiversity measure and environmental predictor has been calculated.

(a) Hypothetical studies are coloured in orange and red and the Normalized Difference Vegetation Index (NDVI) is shown as example of a remotely sensed environmental predictor. Shown is a simplified procedure for investigating the (b) predictability and (c) transferability of local biodiversity-environment relationships. For (b) 'testing' sites within a studies are removed at random, regressions refitted and the within-study prediction error quantified in relation to study properties. Contrastingly, in (c) regression fits from one study (orange) are used to predict permuted biodiversity estimates in another study (red) that have been removed (beige), with the prediction error quantified in relation to study properties.
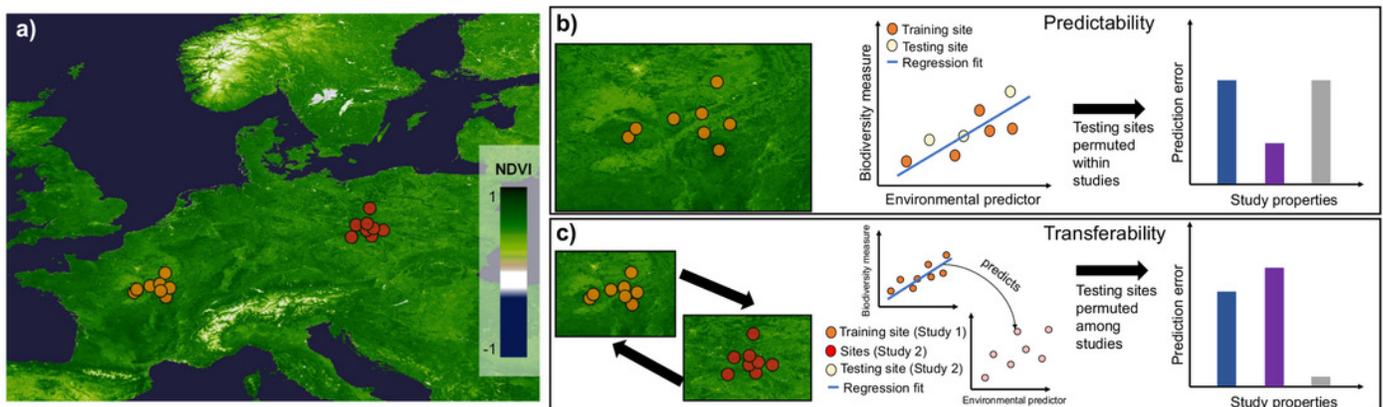
Figure 2

Explained variance (R²) calculated from models fitted between different biodiversity measures and either photosynthetic activity or spectral variability.

Each point is an individual study in the PREDICTS database with point size indicating the number of sites per study and the colour being a visual indication of density in the plot. A map of the average R² per study and biodiversity measure can be found in SI Figure 2.
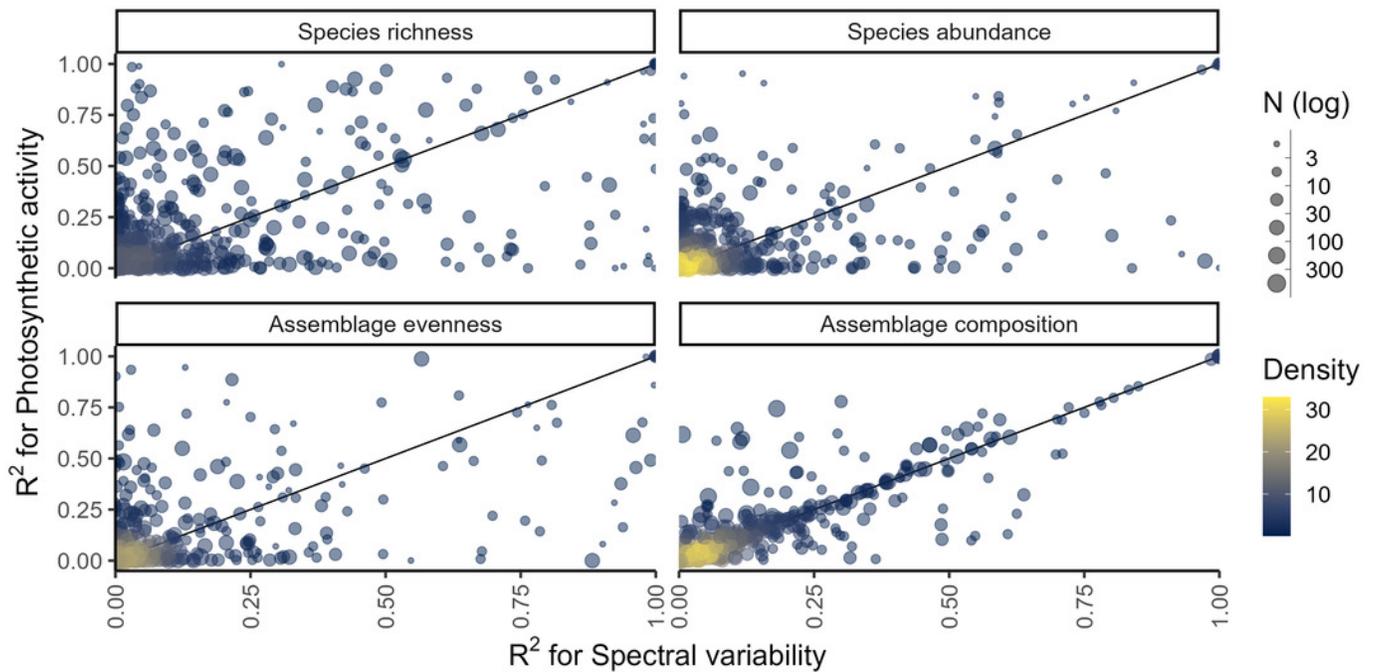
Figure 3

Distribution of the symmetric mean absolute percentage error (sMAPE) of biodiversity measures calculated from models using photosynthetic activity or spectral variability

Larger values (range 0 to 100) indicate a larger prediction error. Colours differentiate between models that evaluate Predictability and Transferability (see Methods). Point error ranges show the arithmetic mean and standard deviation of the sMAPE.
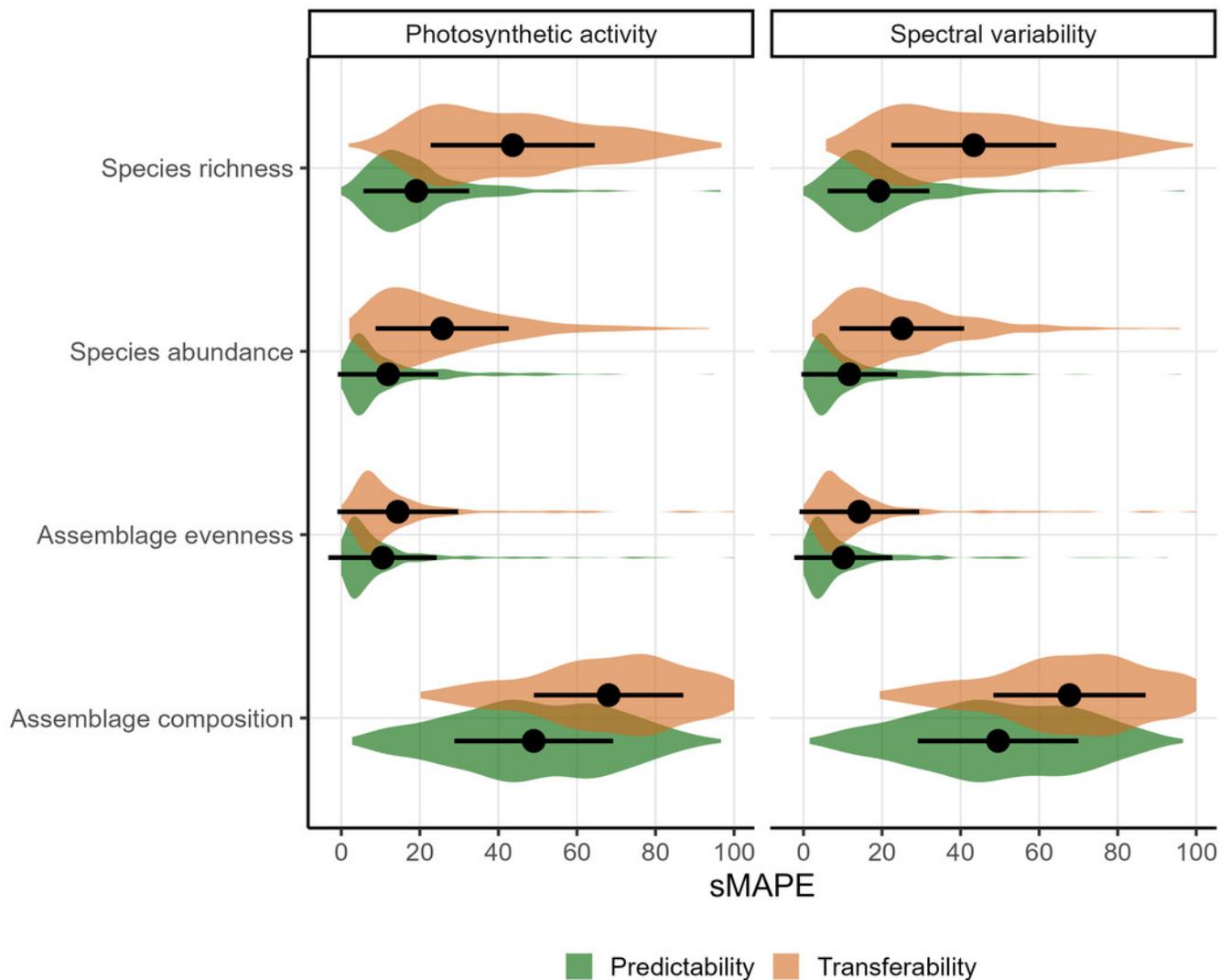
Figure 4

Average error (sMAPE) across models for predictability and transferability.

Errors were averaged (lines indicating standard deviation) across models with different biodiversity measures (shapes) and taxonomic group (colours). Shown only for models using photosynthetic activity as predictor as spectral variability results were broadly comparable in overall patterns (SI Figure 4).
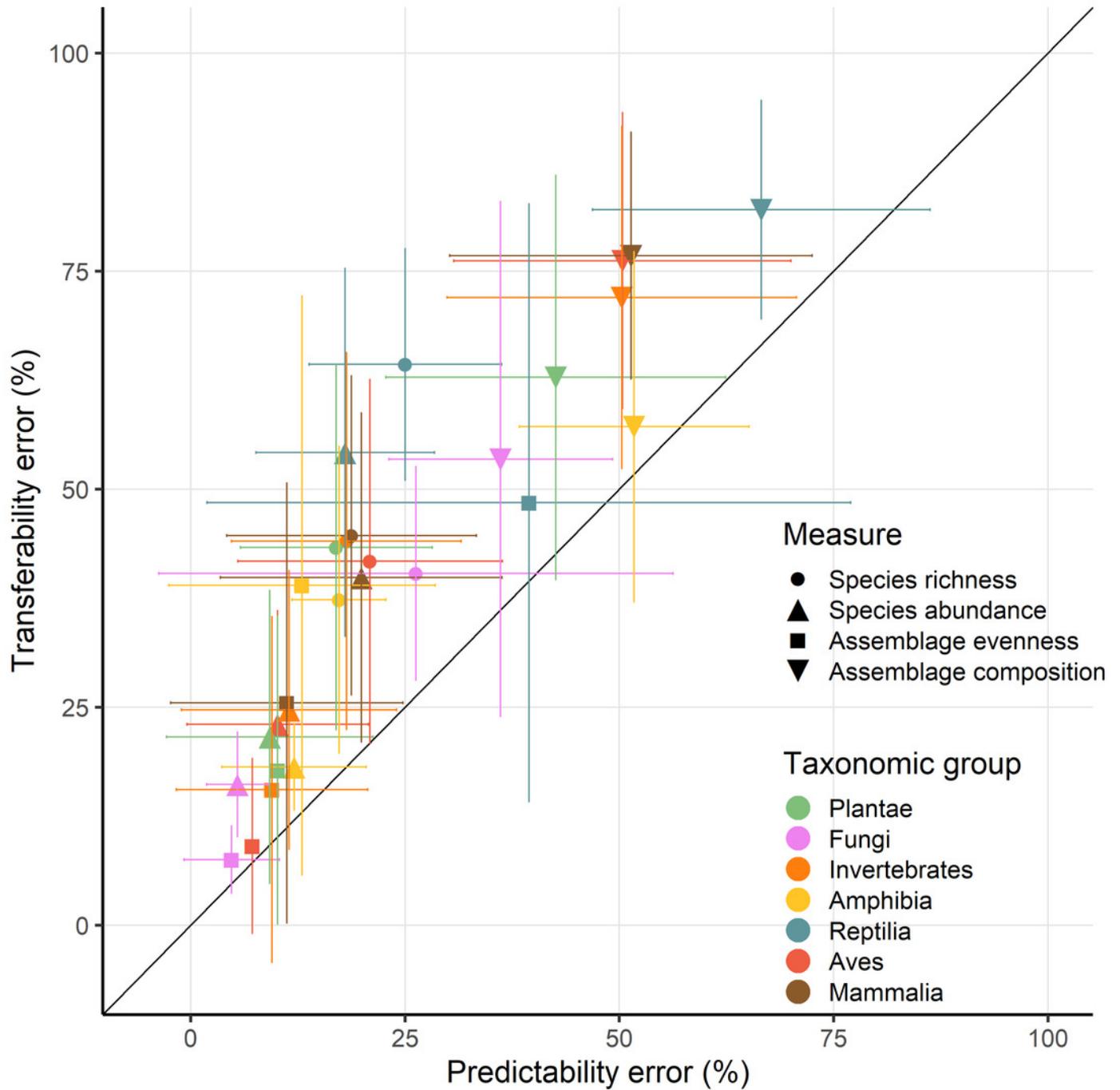
Figure 5

Averaged and standardized model coefficients of variables that best explain differences in sMAPE.

Standardized coefficients smaller than zero indicate that increases in a given variable reduce study-specific prediction errors, while coefficients greater than zero increase the error. Shapes distinguish different biodiversity measures (as in Figure 3). Standardized coefficients shown for transferability permutations only as predictability results follow similar patterns (SI Figure 5).

Figure showing forest plot of standardized coefficients.