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Research Article

Keywords: biodiversity indicators, community reassembly, Human Footprint, landscape context, spatial scale

Posted Date: November 10th, 2026

DOI: https://doi.org/10.21203/rs.3.rs-11152003/v1

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Additional Declarations: No competing interests reported.

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ABSTRACT

Context. Landscape–biodiversity associations depend on response and spatial extent. Taxon counts can remain stable as community composition changes.

Objectives. We compared five biodiversity indicators on identical sites across five natural-cover radii. We assessed associations with natural cover and infrastructure accessibility among studies.

Methods. We analysed 1,656 terrestrial PREDICTS sites from 31 studies in 18 countries; 1,641 had complete data for all five indicators. Models compared 1–50-km buffers with fixed accessibility, Human Footprint and ecological controls.

Results. Indicator choice changed association direction and magnitude. At 10 km, accessibility was negatively associated with richness and positively with dominance shift and effective-taxa loss. Natural cover was positively associated with reference-relative abundance redistribution. Across radii, natural-cover coefficients remained positive for redistribution, negative for richness and near zero for total abundance. Scale profiles changed modestly, while study slopes varied widely in sign and magnitude. Spatially conditioned and held-out checks showed weak transfer of the pooled relationship.

Conclusions. Response, extent and study context jointly shaped landscape inference. Complete indicator-by-scale profiles show these dependencies within a common sampling frame.

Keywords: biodiversity indicators; community reassembly; Human Footprint; landscape context; spatial scale

Introduction

Landscape ecology relates spatial variation in habitat and human modification to ecological responses. The estimated relationship also depends on what is measured. Taxon richness can remain stable while identities and relative abundances change (Hillebrand et al. 2018, Dornelas et al. 2019). Total abundance may likewise mask gains by some taxa and losses by others. Dominance, effective diversity and reference-relative abundance balance describe different parts of this reorganisation (McGill et al. 2015, Edmonds et al. 2024). Comparisons on identical sites and predictors can show whether indicator choice changes the landscape association itself. This matters where assessments rely chiefly on richness (Newbold et al. 2015, O'Reilly et al. 2025, McWilliam et al. 2026). Local taxon counts can remain unchanged as assemblages become more similar across places or reference-associated taxa decline (McKinney and Lockwood 1999, Olden and Rooney 2006, Socolar et al. 2016). Responses retaining taxon identity and relative abundance can reveal those changes. Direct tests of their slopes on the same sites reveal how each community property relates to identical landscape gradients. These responses also differ in the information required to construct them. Richness needs a taxon list, whereas dominance and redistribution use relative abundances; the latter additionally relies on local reference assemblages. Differences among model coefficients identify which biodiversity properties track each landscape gradient. Each coefficient can then be interpreted in relation to the ecological question and the observations used to construct its response. In a landscape analysis, a response can appear insensitive because opposing changes cancel in the summary measure. Comparing taxon identities across reference and modified sites reveals changes concealed by unchanged richness. Testing several responses

within one sampling frame identifies that dependence while holding the landscape data and communities constant.

Spatial extent is part of the same measurement problem. Natural cover close to a plot describes its immediate setting; broader buffers include more of the surrounding landscape. Habitat amount can have different associations across organisms, matrices and configurations (Fahrig 2013, Watling et al. 2020, Arroyo-Rodríguez et al. 2020). Roads and other infrastructure can create edges and disturbance, while verges or corridors provide resources or passage for some taxa (Forman and Alexander 1998, Benítez-López et al. 2010, Ouédraogo et al. 2020, de Jonge et al. 2022). We examine a fixed sequence of radii as a scale profile for every biodiversity response (Jackson and Fahrig 2015, Miguet et al. 2016, Monroe et al. 2022). Movement and habitat use differ among taxa, giving each radius a range of ecological meanings. The common sequence permits direct comparison of how estimated associations change as the measured landscape expands. Natural cover and infrastructure may also carry different spatial signals. Buffers describe spatial context around each sample, while movement ranges remain taxon specific. Holding each response fixed across radii clarifies how its association changes with measured landscape extent. Extending that comparison to several responses asks a further question: do apparent scale patterns reflect the landscape itself or the community property being described? If the relative positions of response curves persist, indicator choice may dominate the contrast; if they change, a single-scale comparison may miss the dependence. The contrast between the relative positions and the shapes of the response curves separates two sources of variation in a heterogeneous synthesis. The spatial extent determines which cover classes contribute to each site's landscape value and how much sites contrast within a study. Coefficients can therefore move with radius even when the sampled

communities do not change. Comparing several indicators over the same fixed sequence shows whether any such movement is shared across ecological responses or concentrated in one part of community structure.

Multi-study data add variation in ecological setting. Studies differ in taxa, biome, sampling extent and landscape matrix; a pooled slope may be driven by studies with many sites. Natural cover and infrastructure accessibility provide two ways to examine this variation. We estimate their associations after accounting for local land use and a nonlinear Human Footprint benchmark, which represents cumulative human pressure (Sanderson et al. 2002, Venter et al. 2016, Kennedy et al. 2019). These coefficients describe within-study associations after the benchmark and ecological controls are included. A study-level random slope reveals how far natural-cover relationships depart from one pooled value (Bolker et al. 2009, Harrison et al. 2018). Site-weighted estimates describe the assembled observations, while equal-study summaries and partially pooled slopes show how much the result depends on the distribution of sites among studies. A precise pooled coefficient can coexist with study slopes of different signs (Theobald et al. 2020, Mammides et al. 2022). The pooled and study-level summaries also describe different ecological populations. A large study can represent a particular taxon or landscape setting, so its many sites can make an overall coefficient precise even as slopes differ elsewhere. Comparing the pooled estimate with the distribution of study slopes addresses that ecological issue directly. It also sets an appropriate context for held-out validation: an association fitted across known studies may transfer poorly to a study with a different species pool or landscape matrix. In this synthesis, the Human Footprint benchmark remains in every model alongside the two focal descriptors. We assess the additional within-study associations of natural cover and accessibility beyond that broad

pressure gradient and the ecological controls. The same benchmark also provides a consistent reference for fit and validation checks in the Supplement.

We analysed terrestrial PREDICTS communities to address three questions. Does biodiversity indicator choice alter landscape associations on the same sites? Does the spatial scale of those associations depend on the indicator? How consistent are the associations among studies? We expected responses retaining taxon identity and relative abundance to reveal relationships that richness could miss, and expected study context to influence the natural-cover slope. The five radii were compared as a fixed sequence of observational associations. At each radius, the indicator comparison uses identical sites, a shared Human Footprint benchmark and the same ecological controls. The repeated radius sequence then shows how those response-specific patterns change as the measured surroundings expand.

Materials and Methods

Biodiversity data and study design

We used terrestrial site-level records from PREDICTS, which retains study identity across local biodiversity surveys (Newbold et al. 2015, Hudson et al. 2017). Samples were collected from 1993 to 2019. Positive, effort-corrected abundance records were summed for duplicate taxon-by-site entries before relative abundances were calculated. Strict-reference sites were primary vegetation under minimal use. For reference-based responses, studies needed at least five sites, two strict-reference sites, two non-reference sites and four active taxa. The source response table contained 1,848 sites from 37 studies. Complete cases for the abundance-redistribution anchor comprised 1,656 sites from 31 studies in 18 countries; 1,641 sites were complete for all five indicators and all

five radii (Table S1; Fig. 1). Reference-relative responses used strict-reference sites within the same study, retaining local taxonomic and sampling context.

The anchor population represented 1,271 coordinate pairs across four UN regions (Table S1; Fig. 1a). Birds contributed 1,012 of 1,656 sites; six other study-reported taxonomic groups made up the remainder (Table S2; Fig. 1b). Countries and studies contributed uneven numbers of sites (Fig. 1c). We retained study identity in every model and examined variation among studies directly. Coverage was uneven across terrestrial taxa and regions.

Reference-relative responses compare each site with strict-reference assemblages from its own study. This limits differences in regional species pools and survey protocols within the reference contrast (Hawkins et al. 2010). Eligibility rules were applied before model fitting. The resulting redistribution measure describes departure from the observed local reference assemblage.

Landscape predictors and spatial scales

Natural cover was the area-weighted proportion of seven vegetation classes in the EarthEnv 1-km consensus product (Tuanmu and Jetz 2014), measured within geodesic circular buffers of 1, 5, 10, 25 and 50 km. Infrastructure accessibility combined weighted GRIP4 road density with proximity to railways, airports, cities, urban areas and ports (Meijer et al. 2018; Natural Earth n.d.). Human Footprint for 2015 was the cumulative-pressure benchmark; mean annual temperature, annual precipitation, land use, use intensity and biome were controls (Fick and Hijmans 2017). Continuous predictors were centred within study and divided by the pooled standard deviation of their within-study deviations. The five radii were fixed before this comparison; 10 km served as the reporting reference. Extraction and construction details appear in Supporting texts S2–S4. The natural-cover measure represents surrounding cover aggregated from raster-cell fractions within

each buffer. Infrastructure accessibility is a single archived composite that remains fixed as natural-cover radius changes. Across the fully crossed analysis, each model changes the natural-cover extent while retaining the accessibility descriptor and adjustment set. Standardising within study makes each focal coefficient a change in the standardised response per pooled within-study standard deviation of the predictor.

Biodiversity responses

The five within-study standardised responses measured different features of community change. Taxon richness counted observed taxa, and total abundance summed effort-corrected individuals. Dominance shift was the maximum site-level relative abundance minus its strict-reference mean. Effective-taxa loss was the strict-reference mean Shannon diversity minus site-level Shannon diversity. Reference-relative abundance redistribution tracked whether relative abundance shifted toward taxa associated with non-reference conditions. For taxon k, we defined affinity as the log ratio of its mean relative abundance at non-reference (N) and strict-reference (R) sites:

$g_k = \log[(\bar{p}_{k,N} + 10^{-6})/(\bar{p}_{k,R} + 10^{-6})]$.

Taxa above the within-study 75th percentile of affinity were classified as operational non-reference winners; those below the 25th percentile were reference-associated losers. At each site, we subtracted the losers' summed relative abundance from the winners' summed relative abundance, then subtracted the strict-reference mean balance and standardised within study. Supporting text S3 gives the full construction and interpretation of all five responses.

Statistical analysis

For indicator comparison, we fitted Gaussian models to the same 1,641 sites. The reduced model included three-degree-of-freedom natural splines for within-study Human Footprint, temperature

and precipitation, with categorical land-use, use-intensity, biome and study terms. The full model added linear natural-cover and infrastructure-accessibility terms. At 10 km, a stacked repeated-response model with study and site random intercepts estimated direct slope differences from richness; study-cluster resampling assessed their stability (Tables S11–S13). All coefficients describe within-study associations conditional on the common benchmark and controls.

The reduced and full models used identical complete cases within each comparison. We report focal coefficients with model-based 95% intervals and joint fit increments beyond the Human Footprint benchmark. Complete terms, fit statistics and uncertainty calculations appear in Supporting texts S4 and S9. The coefficients estimate landscape associations after adjustment for the benchmark and controls. Joint partial R^2 is the reduction in residual sum of squares relative to the benchmark, while the change in adjusted R^2 accounts for model complexity. The Supplement reports joint fit summaries for the two added terms, while Figure 2 presents their separate coefficients and directions.

The stacked model treated the five responses as repeated measurements of each site. Response-by-predictor interactions gave direct differences in standardised slopes. We report the prespecified redistribution-minus-richness contrasts for both landscape predictors and their study-cluster bootstrap intervals (Table S13).

For the multiscale indicator analysis, we repeated the same fixed-effect landscape model for each of the five responses at each of the five natural-cover radii. All 25 fits used the 1,641 sites complete for every response and radius. Within-study predictor standardisation, the Human Footprint benchmark and all controls were unchanged. Radii followed the prespecified sequence. Figure 3 shows every coefficient and 95% interval; Table S16 reports all 25 combinations. The

earlier single-response analysis on 1,656 sites remains in Tables S5 and S6 as a population comparison. At each radius, natural cover was re-centred within study and divided by the pooled within-study standard deviation, exactly as in the original model. This yields comparable standardised coefficients while retaining the actual spatial support of each buffer. Nested buffers yield correlated cover values, so we describe the radius-specific estimates as scale profiles. The identical site set separates changes in measured landscape extent from changes in sample composition.

Among-study heterogeneity was assessed at 10 km with a maximum-likelihood model containing a study random intercept and an independent natural-cover random slope. We report the population slope, its among-study standard deviation and the partially pooled study slopes (Tables S7 and S8; Fig. 4). The random-slope analysis addresses a different level of variation from the fixed-effect profiles. It measures how the 10-km natural-cover association for redistribution varies across the included studies. The population estimate and the distribution of conditional modes are therefore shown together, while the original site-weighted coefficient remains the summary of the assembled sites.

The random-slope model allows natural-cover associations to vary among studies while sharing information across them. Accessibility retained a fixed slope. Conditional study modes summarise the partially pooled study slopes. Supporting text S6 reports the model specification and variance components.

Sensitivity analyses covered equal-study weighting, study-cluster bootstrap, spatial conditioning, residual spatial dependence, spatially blocked validation, leave-one-study-out transfer and cross-fitted response construction. Procedures and full numerical results are in Supporting texts S4–S10,

Tables S5–S15 and Figs. S1–S2. Analyses used R with data.table, splines, lme4, performance and spdep.

Results

Indicator choice changed landscape associations

On the same 1,641 sites, the five indicators gave different landscape associations at 10 km (Fig. 2; Tables S11 and S12). Infrastructure accessibility was negatively associated with richness (−0.067, 95% CI −0.128 to −0.006), near zero for total abundance and redistribution, and positive for dominance shift and effective-taxa loss. Natural cover was positively associated with abundance redistribution (0.107, 0.061–0.153), while its richness estimate was −0.054 (−0.116 to 0.008). The joint landscape increment remained small for every response (Fig. S1a), alongside differences in the direction and magnitude of component associations.

The five indicators occupied distinct positions in the two-predictor comparison. Total abundance had little association with either component. Dominance shift and effective-taxa loss had positive accessibility coefficients, while redistribution had the clearest positive natural-cover coefficient. At 10 km, joint partial R^2 was 0.0034 for richness and 0.0141 for redistribution (Tables S11 and S12). These values quantify incremental in-sample fit beyond the benchmark.

Direct repeated-response contrasts supported an indicator difference (Fig. 2b; Table S13). The redistribution-minus-richness contrast was 0.088 (95% Wald CI 0.006–0.169) for accessibility and 0.166 (0.084–0.249) for natural cover. Study-cluster resampling retained a positive accessibility contrast (95% percentile interval 0.013–0.225), while the natural-cover contrast crossed zero (−0.099–0.340). The latter varied more with study composition. Wald and cluster-bootstrap intervals reflect different sources of uncertainty. The former describes the fitted repeated-response

model on the assembled sites; the latter varies which studies contribute to the contrast and captures between-study variation. Both contrasts were positive as model point estimates, but only the accessibility contrast retained a positive interval under study resampling. Table S13 reports the complete set of direct contrasts and uncertainty estimates.

The separate-response natural-cover coefficient for redistribution was positive in the common-site model, but the direct natural-cover contrast was less stable across sampled studies. The accessibility contrast retained its sign under study resampling. These two findings distinguish an association in the assembled sites from a contrast that recurs when whole studies are resampled.

Scale profiles were broadly consistent in shape across indicators

The 25-model comparison kept the same 1,641 sites and controls at all five radii (Fig. 3; Table S16). Natural-cover coefficients for abundance redistribution were positive throughout, increasing from 0.102 at 1 km to 0.130 at 50 km. Richness coefficients were negative at every radius (−0.071 to −0.094), while total-abundance coefficients stayed near zero (−0.008 to 0.026). Dominance shift and effective-taxa loss showed positive natural-cover estimates, generally smaller than those for redistribution. At 10 km, the estimates exactly reproduced the common-site indicator comparison. The indicator ordering was broadly retained across radii; changes within individual profiles were modest relative to the between-indicator differences. For effective-taxa loss, the natural-cover coefficient ranged from 0.059 to 0.093; its model intervals straddled zero at 10 km but did not at 1, 5, 25 or 50 km. Dominance-shift coefficients were positive and smaller, with intervals spanning zero at every radius. The dominant pattern is a persistent difference among community properties, with modest movement across spatial extents. Figure 3 displays the full sequence of estimates and intervals. The intervals for redistribution excluded zero at all five radii,

whereas those for total abundance included zero throughout. Richness intervals excluded zero at 1, 5, 25 and 50 km, but included zero at 10 km. At 10 km, lower precision widened the interval around a consistently negative richness estimate. Table S16 reports every indicator-radius combination and its uncertainty.

Infrastructure accessibility showed a similarly stable ordering across radii (Fig. 3b; Table S16). Richness estimates stayed negative, dominance shift and effective-taxa loss stayed positive, and abundance redistribution and total abundance remained close to zero. Natural-cover estimates varied somewhat more with radius, particularly for redistribution and effective-taxa loss, but the fitted profiles provide no single radius supported across all responses. Confidence intervals describe uncertainty within each model, while the nested buffers make neighbouring radius estimates correlated. The infrastructure coefficient for richness ranged from −0.067 to −0.084, while dominance-shift estimates ranged from 0.078 to 0.091 and effective-taxa-loss estimates from 0.083 to 0.102. These ranges are descriptive across the fixed radii. The near-constant infrastructure term helps show that most between-radius movement in a given profile comes from replacing the surrounding natural-cover measurement and re-estimating the joint model. The infrastructure measure itself remains fixed across the five models. All five indicators are displayed against the same radius sequence. This reveals the relative stability of the infrastructure profiles alongside the somewhat larger movements in the natural-cover coefficients. Overlapping natural-cover buffers link neighbouring estimates, so Figure 3 emphasises profile shape and interval width.

The earlier single-response scale analysis used 1,656 redistribution sites and yielded a similar positive natural-cover profile (Tables S5 and S6). Equal-study weighting reduced some estimates.

Spatially blocked prediction showed small pooled gains at 25 and 50 km, but study-average intervals crossed zero at every radius (Table S10A; Fig. S1b). These checks show how predictive performance varies among studies across the fixed radii. The close agreement between the 1,656-site and 1,641-site redistribution profiles is useful for interpreting the new comparison. It shows that restricting the analysis to sites complete for every indicator did not create the positive redistribution pattern. The common-site population supports indicator comparison, while the larger anchor population supports the archived study-level and validation analyses. We keep their sample sizes explicit throughout the manuscript and Supplement.

Landscape associations varied among studies

The site-weighted positive natural-cover association concealed substantial among-study variation. In the 10-km random-slope model, the population slope was −0.064 (95% CI −0.222 to 0.093), the among-study slope standard deviation was 0.269, and partially pooled modes ranged from −0.680 to 0.277 (Fig. 4; Tables S7 and S8). Only eight of 31 modes were positive. The study-level slopes therefore differed in magnitude and direction, even though the pooled site-weighted coefficient was positive.

The site-weighted model gives larger studies more influence and assumes a common natural-cover slope. The hierarchical model allows each study to depart from a shared distribution. Its conditional modes are partially pooled estimates of fitted study slopes. The wider study-cluster interval around the pooled natural-cover coefficient reinforces the sensitivity to study composition (Table S7A).

Robustness and transferability

Cross-fitted response construction retained the positive site-weighted natural-cover association in its eligible subset (Table S15). The 10-km joint fit increment lay within the spatially conditioned null distribution (empirical P = 0.864; Table S9A; Fig. S2b), and residual spatial structure persisted (Table S9B). Spatially blocked gains varied among studies (Fig. S1b). Average leave-one-study-out transfer at 10 km was negative and uncertain (mean ΔRMSE −0.044, 95% interval −0.115 to 0.016; Table S10B; Fig. S2a). These results limit support for a broadly transferable pooled landscape relationship. The leave-one-study-out summary covered 27 estimable studies and 1,456 sites; four held-out studies contained a biome level absent from the training data and were not scored under the declared model specification (Table S10C). The spatially blocked analysis covered 1,317 held-out sites in 29 studies. These transfer checks concern the redistribution model and use populations distinct from the common-site indicator comparison in Figure 3.

The robustness analyses answer different questions. Cross-fitting checks construction of the redistribution response; the spatial null asks whether the joint fit increment exceeds a geographically conditioned baseline; held-out validation evaluates prediction. Together, they show a positive in-sample redistribution association alongside weak spatial and across-study transfer of the pooled landscape model.

Discussion

Biodiversity indicators reveal different landscape relationships

Indicator choice changed the estimated landscape relationship on the same sites. Richness counts taxa; abundance-sensitive measures describe shifts in their relative abundance. Total abundance can remain steady when gains and losses balance. Dominance shift, effective-taxa loss and

reference-relative redistribution retain different aspects of community structure (Jost 2006, Hillebrand et al. 2018, Dornelas et al. 2019). The observed coefficients trace those distinct properties of community structure. Richness had a negative accessibility association, while dominance shift and effective-taxa loss had positive estimates. Natural cover was more clearly associated with redistribution than with richness, although the direct contrast depended on study composition. The appropriate response depends on the biodiversity property the question addresses.

These differences also affect what a survey can recover after sampling. A taxon list supports richness, while taxon-level abundance data support dominance, effective diversity and reference-relative balance. Redistribution additionally needs strict-reference assemblages within the same study, so the affinity groups reflect the local species pool and sampling protocol. Collecting these observations together allows the five responses to be estimated for the same sites. This common design distinguishes changes in taxon membership from changes in the distribution of individuals among taxa, even when overall abundance varies little.

The infrastructure contrast illustrates the value of comparing slopes directly. Richness declined along the adjusted accessibility gradient, while the redistribution estimate was close to zero. Their difference remained positive under study resampling. The stable contrast shows that taxon counts and abundance balance can describe different associations with the same landscape structure.

Spatial extent changes the measured association, with similar indicator ordering

The fully crossed analysis showed a stable broad ordering among indicators across the five radii. Redistribution remained positively associated with natural cover, richness negatively associated, and total abundance close to zero. The redistribution coefficient rose modestly with buffer radius;

other natural-cover profiles varied and reached their extrema at different radii. Accessibility coefficients changed little with the natural-cover radius. Response definition had a clearer influence on direction than the chosen extent within this fixed 1–50-km sequence. Movement, habitat association, matrix structure and study extent can affect the scale at which landscape cover matters (Miguet et al. 2016, Watling et al. 2020, Monroe et al. 2022), and their separate contributions remain unresolved in this synthesis. The dominant pattern is a persistent indicator contrast with modest radius dependence. The 25 coefficients share overlapping landscape summaries, which links their variation across buffers. The plotted intervals express precision within each fit, while the study-level analyses show the wider variation in ecological settings. The five-radius sequence displays the persistence and variation of the association across measured extents. Richness and abundance redistribution also differ in what their signs mean. A negative richness coefficient describes fewer observed taxa along a measured gradient after adjustment. A positive redistribution coefficient describes a shift in the balance of taxa classified against local reference assemblages; its ecological meaning follows the taxa and reference assemblages involved. Together, the curves show that changes in taxon counts and abundance balance can have different directions across the measured landscape gradients. Their persistent separation across radii is the more direct indicator-dependent finding.

Changing radius also changes the predictor distribution within a study. Small buffers preserve contrasts among nearby plots; large buffers average over more land-cover cells and can expose broader differences among landscapes. Standardisation places each radius on the same within-study scale, while the underlying cover values reflect different spatial supports. A coefficient profile therefore describes sensitivity to measured context across a fixed sequence. In this

365 analysis, that sensitivity was generally smaller than the persistent difference between richness and
366 redistribution across radii.
367 Fixed radii create comparable measurements of surrounding cover across birds and other taxa,
368 whose movement ranges and habitat use differ. The modest changes in coefficients also need to be
369 viewed alongside uncertainty across studies and the weak validation gains. Reporting the whole
370 profile presents the magnitude and uncertainty at every radius.
371 **Average relationships mask among-study heterogeneity**
372 Natural-cover slopes varied substantially among studies. The random-slope model gave partially
373 pooled values on both sides of zero, with a population estimate whose interval included zero.
374 Study weighting and cluster resampling likewise reduced support for a common positive mean.
375 These differences reflect the uneven number of sites per study and the range of ecological settings
376 represented. Taxon, biome, landscape matrix and sampling extent could contribute to the
377 variation, and the present study-level replication leaves their separate contributions unresolved.
378 Explaining those sources would require adequately replicated study-level comparisons. The study
379 distribution defines the scope of the positive site-weighted redistribution coefficient. A site-
380 weighted model assigns more influence to studies that sampled many plots; a random-slope model
381 asks how relationships vary across the represented studies. Both are useful summaries, but they
382 answer different questions. The conditional modes make that distinction concrete, and their spread
383 accords with the weak average gain when a whole study is withheld. Heterogeneity is the clearest
384 study-level result; its ecological drivers remain an open question.
385 The difference between site-weighted and equal-study summaries matters when applying the
386 synthesis beyond its sampled sites. Site weighting describes the observed collection of plots;

387 equal-study weighting gives each included study the same influence, and the hierarchical model
388 estimates a distribution of slopes. Their divergence has ecological meaning because studies
389 represent different taxa, landscapes and sampling designs. The weak average leave-one-study-out
390 performance is consistent with that spread. For applications, the study-slope distribution provides
391 a starting range alongside the pooled mean, with local observations establishing the direction in a
392 target setting.
393 A pooled coefficient remains a description of the assembled sites. When study slopes differ in
394 sign, its value depends on the distribution of observations among studies. The partially pooled
395 modes and equal-study summaries show a range of associations across the sampled landscapes.
396 This variation is part of the ecological result.
397 **Implications and limitations**
398 Natural-cover and infrastructure coefficients were estimated after a Human Footprint benchmark
399 and local controls (Sanderson et al. 2002, Venter et al. 2016). The added fit was small. The
400 spatially conditioned null placed the joint 10-km increment within its expected range, and residual
401 spatial autocorrelation persisted. Held-out locations showed inconsistent gains; average transfer to
402 an unseen study did not improve. These checks limit how far the pooled associations can be
403 generalised (Roberts et al. 2017, Yates et al. 2018). The indicator contrast and the study
404 heterogeneity are stronger findings than a common transferable landscape coefficient. The spatial
405 null is particularly relevant because neighbouring sites can share unmeasured environmental
406 structure. The observed joint increment fell below the mean of its conditioned null distribution,
407 offering little evidence of spatially distinctive information. The joint test assesses added predictive

information from the two landscape components as a pair. Direct indicator contrasts address how biodiversity response definitions differ on the same sites.

Spatial blocking tests prediction at separated locations within represented studies. Leaving out a study changes the taxonomic and sampling context. Cross-fitting instead tests whether each site contributed to the affinity classification used to score it. The distinction matters for applications: in-sample association and transfer to a new landscape require distinct evidence (Wenger and Olden 2012, Roberts et al. 2017, Yates et al. 2018).

The sample spans 18 countries but is concentrated in birds and several well-sampled regions. Surveys from 1993 to 2019 were paired with global landscape layers that differ in temporal alignment. Infrastructure accessibility and natural cover describe structural context, and the models estimate observational associations. Reference-relative groups depend on observed within-study affinities. Cross-fitting supported the in-sample association in its eligible subset; repeated surveys and time-varying landscape data would be needed to test the response contrasts and study-level explanations more directly.

For monitoring, the biodiversity response and spatial extent should be chosen together. Richness serves questions about taxon counts; abundance-based responses address dominance and shifts in taxon identity. Reference-relative redistribution additionally requires local reference sites and taxon-level abundance data. Reporting several indicator-by-scale profiles can show whether an inference changes with the property or extent measured. For application to a new study, the weak average holdout performance calls for local validation. Results tables should show the fitted radii and the numbers of sites and studies contributing to each response, making profiles comparable as future syntheses expand to additional taxa and regions. Recording taxon-level abundance and local

reference assemblages at the design stage preserves the information needed to revisit indicator choice as monitoring questions develop.

Conclusion

Biodiversity indicators revealed contrasting landscape associations on the same terrestrial sites. These differences persisted broadly across five natural-cover radii, with modest changes in the scale profiles. Natural-cover slopes also varied in magnitude and direction among studies. Landscape inference therefore depends on the community property measured, the spatial extent used to describe context and the ecological settings represented; the pooled association had limited support for transfer to new studies. Monitoring programmes can use these profiles to match response measures to their ecological questions and test pooled relationships against local observations before applying them elsewhere.

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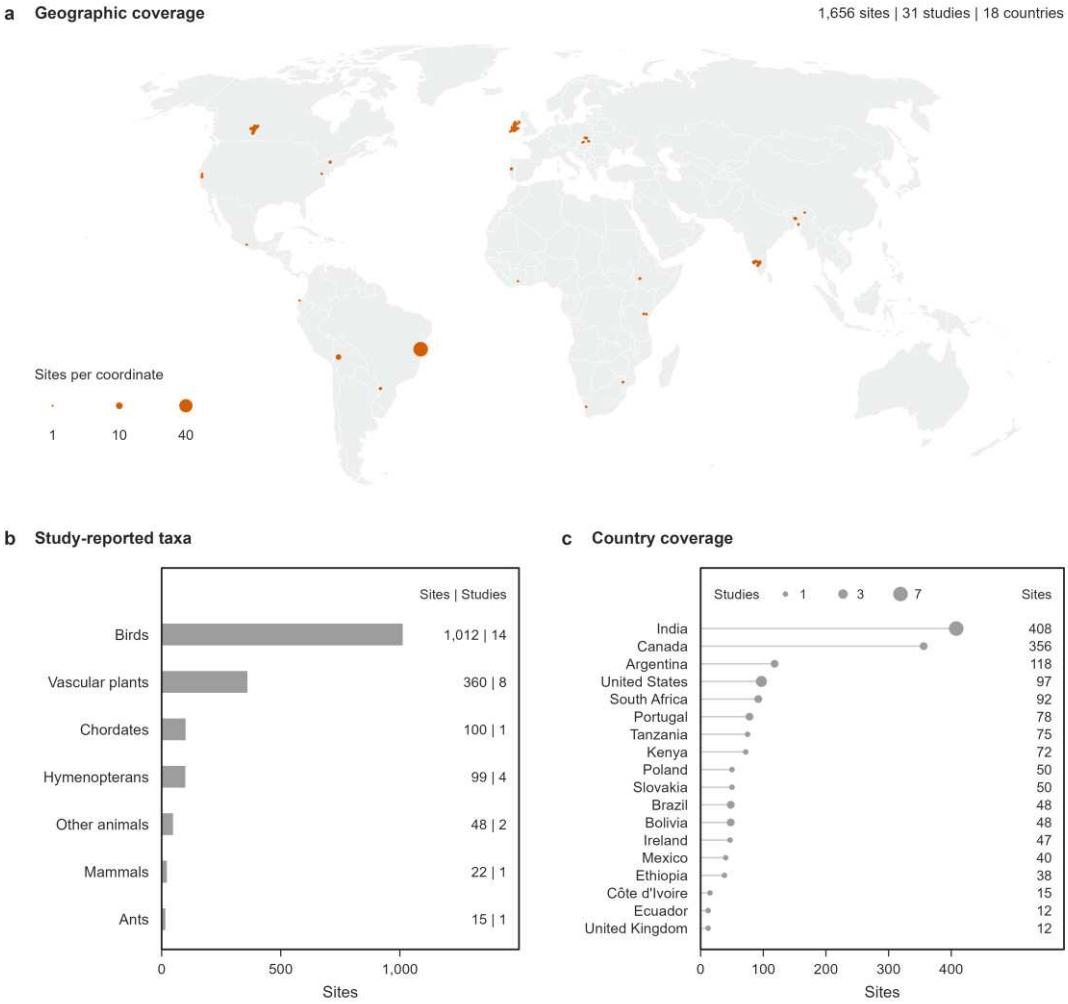
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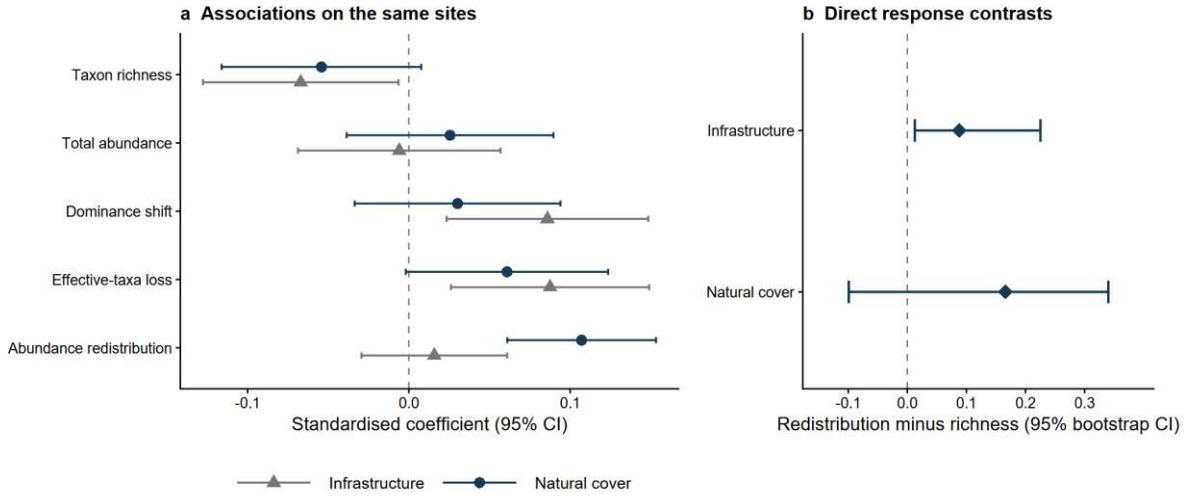
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616 Figure 1. Spatial and taxonomic coverage of the anchor analysis set. (a) Locations of 1,656 sites

617 from 31 studies in 18 countries, in the Robinson projection. Point area denotes sites sharing a

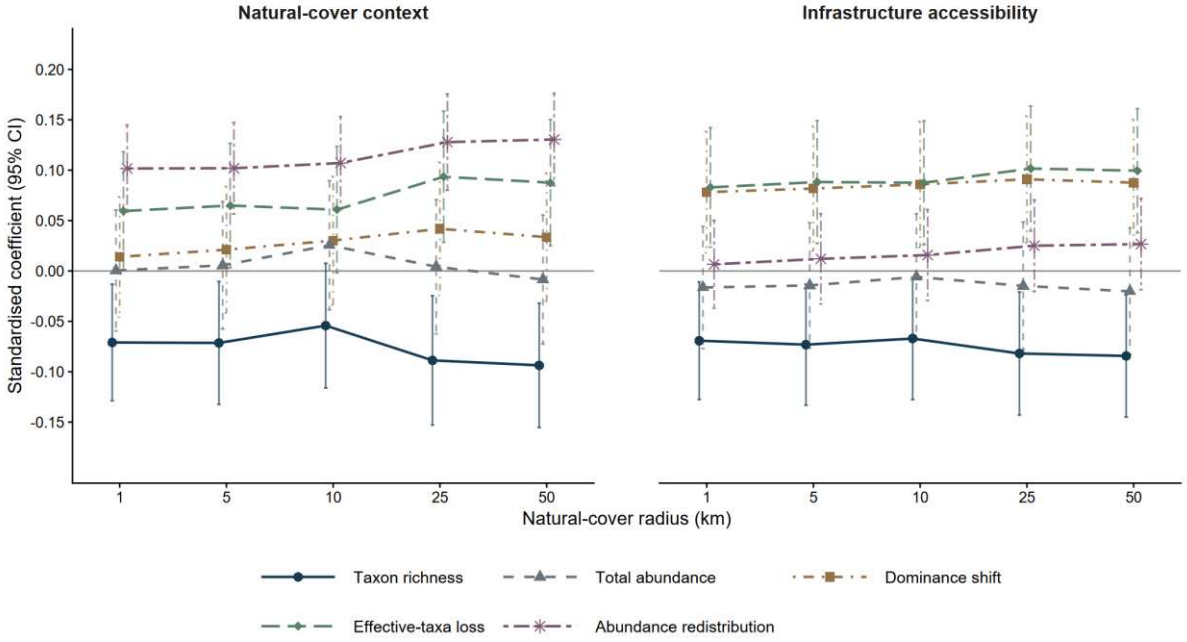
618 coordinate. (b) Site counts for seven study-reported taxonomic groups, with site and study counts.

619 (c) Site counts for all 18 countries; point area denotes study count.



620

621 Figure 2. Indicator-specific landscape associations at 10 km. All estimates use the same 1,641
622 sites from 31 studies and identical controls. (a) Standardised natural-cover and infrastructure-
623 accessibility coefficients with 95% Wald confidence intervals for five biodiversity responses. (b)
624 Direct abundance-redistribution-minus-richness slope contrasts from a stacked repeated-response
625 model. Diamonds are model estimates; intervals are 95% percentiles from 499 study-cluster
626 bootstrap draws. Positive values indicate a larger slope for redistribution. Joint partial R^2 is shown
627 in Fig. S1a.



628

629 Figure 3. Biodiversity indicator-by-spatial-scale associations on 1,641 common sites from 31
630 studies. The same model was fitted for each of five responses at natural-cover radii of 1, 5, 10, 25
631 and 50 km. Panels show coefficients for natural-cover context (left) and infrastructure
632 accessibility (right). Points and lines denote the response; vertical bars are model-based 95% Wald
633 confidence intervals. Radius changes the natural-cover predictor, while infrastructure accessibility
634 and the controls retain the same definitions. Shapes and line types distinguish responses in
635 monochrome. Complete values are in Table S16.

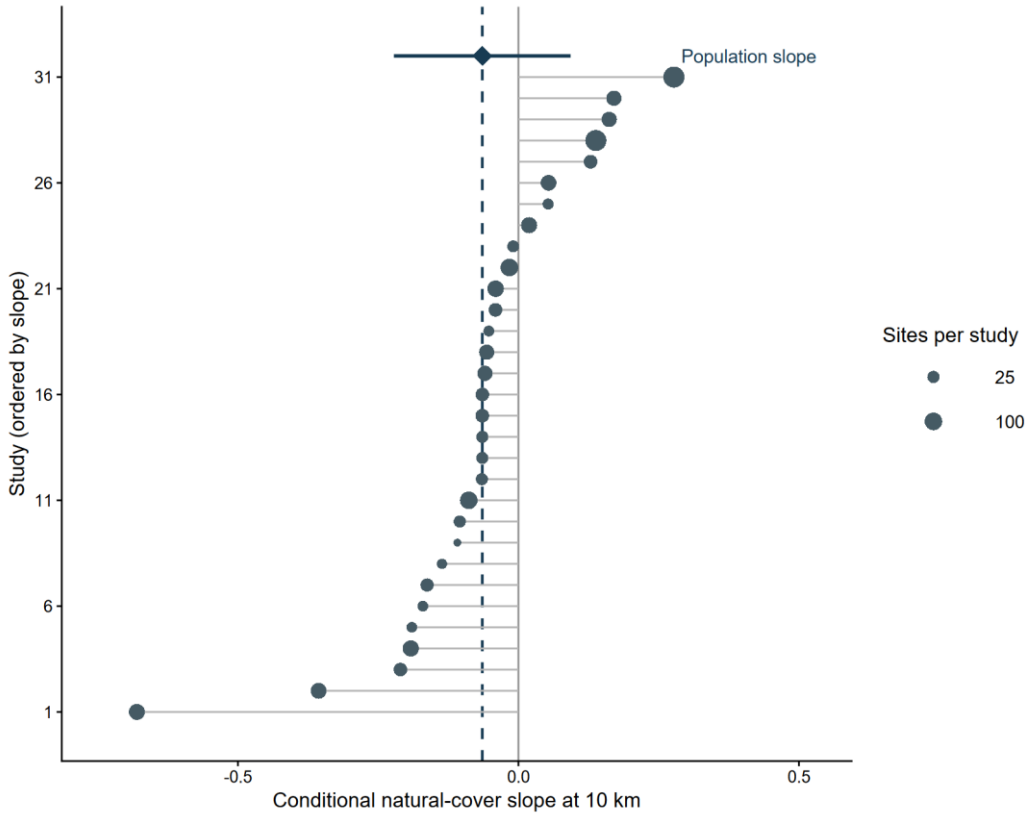


Figure 4. Among-study heterogeneity in the 10-km natural-cover association with abundance redistribution. Points are partially pooled conditional modes for 31 studies, ordered by slope; point size indicates study sample size. The diamond and horizontal interval at the top give the population slope (−0.064) and its 95% Wald interval (−0.222 to 0.093). The study modes are point estimates. Leave-one-study-out transfer and the spatially conditioned null appear in Fig. S2.

Supplementary Files

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