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Nadejda A. Mirochnitchenko

Erica F. Stuber

Joseph J. Fontaine

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Biodiversity Scale-Dependence and Opposing Multi-level Correlations Underlie Differences among Taxonomic, Phylogenetic and Functional Diversity

Nadejda A. Mirochnitchenko, Erica F. Stuber, and Joseph J. Fontaine

Nebraska Cooperative Fish and Wildlife Research Unit, University of Nebraska–Lincoln, Lincoln, Nebraska, USA

Nadejda A. Mirochnitchenko, <https://orcid.org/0000-0002-5182-200X>

Erica F. Stuber, <https://orcid.org/0000-0002-2687-6874>

Joseph J. Fontaine, <https://orcid.org/0000-0002-7639-9156>

Corresponding author – Nadejda A. Mirochnitchenko, Nebraska Cooperative Fish and Wildlife Research Unit, University of Nebraska–Lincoln, Lincoln, NE, USA, email nmirochnitchenko@gmail.com

Abstract

Aim: Biodiversity is a multidimensional property of biological communities that represents different information depending on how it is measured, but how dimensions relate to one another and under what conditions is not well understood. We explore how taxonomic, phylogenetic, and functional diversity can differ in scale-of-effect dependence and habitat-biodiversity relationships, and subsequently how spatial differences among biodiversity dimensions may arise. **Location:** Nebraska, United States. **Taxon:** Birds. **Methods:** Across 2016 and 2017, we conducted 2,641 point counts at 781 sites. We modeled the occupancy of 141 species using Bayesian Bernoulli-Bernoulli hierarchical logistic regressions. We calculated species richness (SR), phylogenetic diversity (PD), and functional diversity (FD) for each site and year based on predicted occupancy, accounting for imperfect detection. Using Bayesian latent indicator scale selection and multivariate modeling, we quantified the

spatial scales-of-effect that best explained the relationships between environmental characteristics and SR, PD, and FD. Additionally, we decomposed the residual between-site and within-site biodiversity correlations using our repeated measures design. *Results:* Although relationships between specific land cover types and SR, PD, and FD were qualitatively similar, the spatial scales at which these variables were important in explaining biodiversity differed among dimensions. Between-site residual biodiversity correlations were negative, yet within-site biodiversity residual correlations were positive. *Main conclusions:* Our results demonstrate how spatial differences among biodiversity dimensions may arise from biodiversity-specific scale-dependent habitat relationships, low shared environmental correlations, and opposing residual correlations between dimensions, suggesting that single-scale and single-dimension analyses are not entirely appropriate for quantifying habitat-biodiversity relationships. After accounting for shared habitat relationships, we found positive within-site residual correlations between SR, PD, and FD, suggesting that habitat change over time influenced all biodiversity dimensions similarly. However, negative between-site residual correlation among biodiversity dimensions may indicate trade-offs in achieving maximum biodiversity across multiple biodiversity dimensions at any given location.

Keywords: Bayesian latent indicator, birds, land cover, multi-level correlations, multi-scale, multi-variate model, scale selection, scale-of-effect, species richness

1. Introduction

Biodiversity is a multifaceted property of biological communities emerging from the assembly of organisms shaped by ecological and evolutionary processes (Naeem et al., 2016; Swenson, 2011). Biodiversity is most commonly characterized by measures of taxonomic diversity (e.g., species richness, species evenness), which are often assumed to approximate other components of biodiversity, including phylogenetic and functional diversity (Naeem et al., 2016; Rodrigues et al., 2011). Although the multiple dimensions of biodiversity (i.e., taxonomic, phylogenetic, functional) are interrelated, the assumption that one dimension is a reliable surrogate for another does not necessarily follow from theory (Faith, 1992; Swenson, 2011) or empirical study (Chapman et al., 2018; Forest et al., 2007; Lyash-evska & Farnsworth, 2012; Mazel et al., 2018). Each biodiversity dimension clearly contains unique ecological and evolutionary information, thus it is not surprising that assuming perfect collinearity among biodiversity measures can lead to false inferences about unmeasured dimensions and limit our ability to identify the mechanisms driving biodiversity patterns (Naeem et al., 2016; Swenson, 2011; Swenson & Enquist, 2009). Dimensions of biodiversity are not completely independent, however, and understanding the extent to which one biodiversity dimension represents another has value for how we measure biodiversity, and how we think about community formation and function (Naeem et al., 2016; Pavoine et al., 2013).

One of the challenges in understanding the relationships among biodiversity dimensions is that the processes that shape ecological communities, and thus biodiversity, act at multiple spatial scales (Boyce, 2006; Chase & Myers, 2011; Levin, 1992; Sandel & Smith, 2009). Environmental features that predict the presence of a species at one spatial scale, for example, may perform poorly when considered at another scale (Robinson, 1950; Stuber et al., 2017). Not matching the scale of analysis with the scale of the underlying processes

affecting community composition can therefore obscure relationships among biodiversity dimensions, and between biodiversity dimensions and environmental features, contributing to poor model performance at best, and inappropriate inferences at worst (Henebry, 1995; Keitt et al., 2002; Stuber & Fontaine, 2018, 2019). Despite an awareness of the importance of spatially specific assessments of ecological relationships (Chalfoun & Martin, 2007; Horne & Schneider, 1995; Hurlbert & Jetz, 2007), few biodiversity studies address scales-of-effect when measuring, or more importantly, predicting biodiversity metrics (Jackson & Fahrig, 2014; Martin, 2018; McGarigal et al., 2016). Unlike biodiversity studies that seek to understand how biodiversity metrics themselves change across spatial scales (e.g., how alpha and beta biodiversity differ, or how local biodiversity compares to regional biodiversity), scale-of-effect studies consider biodiversity at a single scale (e.g., local biodiversity), and vary the scale (in either extent or resolution) that predictor variables explain variation in biodiversity. While scale-of-effect studies are increasing in wildlife and landscape ecology (referred to as multiscale studies; reviewed in McGarigal et al., 2016; Stuber & Gruber, 2020), only a few consider habitat-biodiversity relationships (reviewed in Martin, 2018).

Hierarchical models provide a means to disentangle sampling error from the ecological processes driving biodiversity and quantify the relationships among biodiversity dimensions and the environmental features that ultimately shape biodiversity (Kéry & Schaub, 2011; Rich et al., 2016). Using a multiscale approach that quantifies biodiversity-environment relationships within relevant spatial scales (Stuber et al., 2017), we quantified taxonomic, phylogenetic, and functional biodiversity dimensions of bird species across Nebraska, USA, and asked: (1) how correlated are biodiversity dimensions within- and between-study sites over time, (2) at which spatial scales do habitat predictors best explain variation in biodiversity dimensions, (3) do the shapes of habitat response curves differ between biodiversity dimensions, and (4) how might habitat responses and intercorrelations between dimensions lead to differences in predictions of biodiversity metrics among biodiversity dimensions. We expected positive between-site and within-site correlations among biodiversity dimensions due to some level of information sharing as all three metrics are calculated from the same underlying biological data, and ecological processes therefore may influence each biodiversity dimension to some degree (Pavoine et al., 2013; Stevens & Tello, 2014). We also expected negative biodiversity response curves for all biodiversity dimensions across agricultural land cover types, as land use intensification has been linked to biodiversity loss (Benton et al., 2003; Donald et al., 2001; Flynn et al., 2009). There is no theory yet to guide predictions of absolute scales-of-effect of biodiversity-environment relationships. However, we predict that the scales-of-effect relating to phylogenetic diversity will be relatively larger on average than those of functional diversity and taxonomic diversity, as phylogenetic diversity is shaped by the biogeographical history of sites, which are likely structured over broader spatial and temporal scales than functional and taxonomic diversity, both of which may be strongly shaped by local, density-dependent processes.

2. Materials and Methods

2.1. Avian point counts

We conducted 500 m fixed radius avian point count surveys during the breeding seasons (mid-April to late-June) of 2016 and 2017, on publicly accessible secondary and tertiary roads across Nebraska, USA (Fig. 1; McCarthy et al., 2012; Robbins et al., 1986). Survey sites were selected based on generalized random tessellation stratified sampling, which randomly distributed sampling sites across six a priori-selected land cover types (based on a 30 m resolution land cover product developed by the Rainwater Basin Joint Venture: Bishop et al., 2011) to spatially balance our sampling by mimicking the spatial variation across habitat gradients in Nebraska (Stevens Jr & Olsen, 2004). Sites were grouped into “routes” consisting of 7–19 point count locations such that all sites in each route could be visited within one morning. Additional routes were created in 2017 to include several of Nebraska’s Biologically Unique Landscapes, which are managed for declining rare species and unique natural communities (Fig. 1; Table S.1; Schneider et al., 2011). Trained observers visited each site up to four times (i.e., the “robust design” following Williams et al., 2002) during each sampling season. To reduce temporal correlation among visits, we randomized the order of route visitation and starting position. During surveys, observers recorded every bird seen or heard within a 3-minute period (i.e., a visit), which occurred between 15 min before sunrise and 10 A.M.: the time at which avian vocalizations are greatest and most consistent across species (Hutto et al., 1986). We did not perform surveys during inclement weather, including fog, drizzle, prolonged rain, and wind with speeds > 20 kmh.

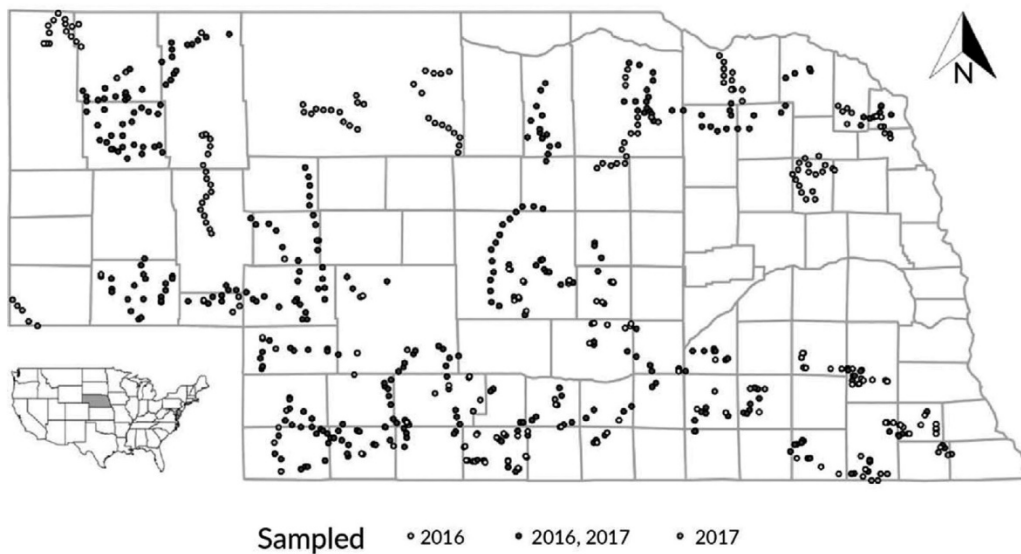


Figure 1. A map of the 2016–2017 survey points throughout the state of Nebraska, USA. Lightest gray points were visited only in 2016, medium gray points were visited only in 2017, and dark gray points were visited both years.

2.2. *Species occupancy modeling*

For each visit, species counts were collapsed into binary occurrence data. We modeled the occurrence of each species detected with a hierarchical logistic regression that jointly estimated occupancy and detection probabilities to account for imperfect detection (Kéry & Schaub, 2011). Specifically, we used a Bernoulli-Bernoulli hierarchical logistic regression, in which the probability of (latent) true site occupancy was modeled as a function of land cover predictors (linear and orthogonal quadratic effects of percentage grasses, small grains and woodland, and linear effects of percentage conservation reserve program grasses [CRP], and wetland within the 500 m radius of the point count surveys were included), with a fixed effect for year that allowed a sites' occupancy status to change between years. The observation process was reflected by a detection probability model. Detection probability was associated with visit-specific covariates, including observer identity as a random effect and linear and quadratic effects of wind speed, time of day, date, temperature, and cloud cover as fixed effects (Diefenbach et al., 2003; Kéry & Schaub, 2011; Royle & Kéry, 2007). See Table S.2 for JAGS code used to specify the model.

We estimated occupancy for each species via Bayesian posterior simulation with JAGS ("just another Gibbs sampler"; Plummer, 2003) via the *rjags* (Plummer & Stukalov, 2014) and *coda* packages (Plummer et al., 2005) in program R (R Core Team, 2018). We ran each model with one chain of 120,000 Markov chain Monte Carlo (MCMC) samples after a 5000-iteration burn-in period. We visually confirmed convergence and calculated the mean and 95% credible interval for each covariate, which represented our estimate and its uncertainty.

As many species were relatively rare, we maximized the number of detections available for model fitting and examined model performance for each species by comparing predicted versus observed detections. We turned each model's estimated probability of detecting a species at a visit into predictions of detection if the estimated probability of detecting a species at a visit was greater than the prevalence of the species across all point count visits (Crammer, 2003). This data-based prevalence thresholding for model checking was simple and effective at minimizing predictions of false negative and positive detections (Liu et al., 2005) and was used only to assess model performance.

To measure model fit, we compared predicted versus observed detections using the true skill statistic (TSS; $TSS = \text{sensitivity} + \text{specificity} - 1$) because TSS is largely insensitive to the threshold used to binarize data and is unbiased by unequal proportions of presences and absences, which is particularly important for rare species (Allouche et al., 2006). TSS values ranged from -1 to +1, where +1 indicated perfect agreement between predicted and actual detection. Values close to zero indicated that the predicted detection was no better than random, and negative values indicated that the predicted detection was opposite of the observed detection. We considered model fit to be excellent if the model's TSS was above 0.75, adequate if TSS was between 0.4 and 0.75, and poor if TSS was less than 0.4 (Allouche et al., 2006).

Semi-variograms of a random subset of single-species occupancy models did not suggest residual spatial autocorrelation. All species models were used in subsequent modeling steps.

2.3. Diversity dimensions quantified based on occupancy models

We took a two-step approach to estimating mean diversity metrics based on predicted species occupancy of sites by first estimating species occupancy independently (described above), then using the fitted models to simulate mean biodiversity metrics (i.e. taxonomic, phylogenetic, functional) based on the estimated occupancy models. Our simulation approach to estimate mean biodiversity (described below) is statistically equivalent to a point estimate from a multispecies occupancy model but computationally tractable for the large size of our dataset both in terms of number of species analyzed and the number of sampling locations (Calabrese et al., 2014; Devarajan et al., 2020). Our approach highlights the trade-off between model completeness and feasibility that limits our ability to estimate direct measures of uncertainty around diversity scores but instead relies on credible intervals around diversity point estimates and correlations to understand uncertainty.

2.3.1 Taxonomic diversity

We used species richness (SR) as our measure of taxonomic diversity, quantified as the number of species predicted to occupy a site within each year. A species was considered to occupy a site when the modeled occupancy probability was higher than the prevalence of the species across all visits (Allouche et al., 2006; Crammer, 2003).

2.3.2 Phylogenetic diversity

Because there was uncertainty associated with phylogenetic tree construction, we followed the consensus tree-building recommendations of Rubolini et al. (2015) to generate a phylogeny that included all species detected in our study. We downloaded 1,000 phylogenetic trees generated from a trimmed subset of the Hackett phylogeny, which was the most complete molecular phylogeny of extant bird species available (Hackett et al., 2008; Rubolini et al., 2015; compiled from <http://www.birdtree.org>; Jetz et al., 2012). Using the maximum clade credibility criterion (program BEAST: Bouckaert et al., 2014), we generated a consensus tree and assigned the median divergence to branch lengths on the consensus tree to represent time since speciation (Morrison, 2008; Fig. S.1). We then calculated Faith's (1992) phylogenetic diversity (PD), which is the sum of all the branch lengths on the phylogeny connecting the species occupying a site (R package "picante"; Kembel et al., 2010). The root of the phylogeny, which extended to include all taxa in the dataset, was included in calculations of PD so that any combination of clade members would include the evolutionary history since the root (Faith et al., 2004).

2.3.3 Functional diversity

Like a phylogenetic tree, a functional dendrogram hierarchically clusters species; however, species similarity is based on ecological trait similarities rather than genomic similarity. We built a functional dendrogram based on 23 functional traits: 4 reproductive traits, 10 diet traits, 1 binary activity trait, 1 body size trait, and 7 foraging strategy traits (Table S.3; Petchey et al., 2007). Trait information was compiled from the "Birds of North America" series from the American Ornithological Society (Rodewald, 2015), the "Elton Traits 1.0" species foraging characteristics database for extant birds (Wilman et al., 2014), and the *CRC Handbook of Avian Body Masses* (Dunning Jr, 2007). Each trait was standardized (mean =

zero, standard deviation = 1) so that all traits had equal influence in the construction of the functional dendrogram (Petchey & Gaston, 2002, 2006). We hierarchically clustered species using Gower's distance and an unweighted pair group method based on arithmetic mean (Mouchet et al., 2010; Petchey & Gaston, 2002; Podani & Schmera, 2006; Fig. S.2). Like PD, we quantified functional diversity (FD; Petchey & Gaston, 2002) using the total branch length connecting all co-occurring species at each site based on our functional dendrogram, including the dendrogram's root (R package "picante"; Kembel et al., 2010).

2.3.4 Predicted biodiversity

Because there is uncertainty and potential bias associated with stacking occupancy model predictions (Calabrese et al., 2014), we took a two-step, simulation approach to calculating biodiversity dimensions based on estimated single-species occupancy models. First, we simulated 1000 predictions from each single species occupancy model (i.e., for each study site we predict 1000 possible community assemblages based on overlaying 1000 single-species model predictions given the uncertainty in occupancy models). Then, we calculate the mean biodiversity for each site based on its 1000 simulations (i.e., calculate mean SR, mean PD, mean FD per site based on 1000 simulated communities from estimated occupancy models). This approach accounts for prediction uncertainty in occupancy models rather than using a thresholding procedure to binarize model predictions. Furthermore, by extracting the mean biodiversity, the simulation framework leads to the same biodiversity point estimate that would be produced by a multi-species occupancy model (Calabrese et al., 2014; Devarajan et al., 2020) in a way that is computationally feasible for the large size of our study.

2.4 Biodiversity–land cover relationship modeling

To investigate the correlation structure between the predicted biodiversity metrics (scaled and centered) and identify the scale-of-effect of land cover covariates, we built a trivariate mixed-effects model with Gaussian error distributions for each biodiversity dimension. Multivariate hierarchical models are often used in behavioral ecology and quantitative genetics to decompose the variation in labile traits into their within- and among-individual components—for example, in studies in which repeated measures of plastic behavioral traits are measured in individuals over time (Dingemanse & Dochtermann, 2013). The example of repeatedly assaying behavioral traits on individuals is analogous to repeatedly measuring biodiversity at individual sites over time; in our case, individual field sites are repeatedly "assayed" for avian biodiversity that may change over time because of colonization or extirpation processes. In this case, biodiversity can vary both among (e.g., sites in forests have higher average biodiversity than sites in grasslands) and within sites (e.g., a field site may undergo a colonization event during the study such that biodiversity increases between the first and second field season). Because the structure of our data is similar to that of behavioral ecology and quantitative genetics data on individual subjects, we can use the same multivariate hierarchical models to gain insight to the multilevel nature of variation in biodiversity over time and across sites. Analytical procedures to identify scales-of-effect of predictor variables on the response of interest can be embedded within the multivariate framework (Stuber & Gruber, 2020).

We quantified relationships among taxonomic, phylogenetic, and functional dimensions of biodiversity and their relationships with six land cover gradients. Each biodiversity metric was allowed to have its own fixed effects of year and land cover covariates with random intercepts for sites that were jointly estimated to account for the nonindependence of multiple biodiversity metrics (Dingemanse & Dochtermann, 2013). We examined linear and orthogonal quadratic effects for row crops, small grain, grasses, and trees and linear-only effects for CRP and wetlands, which displayed a narrower range of variation across our study sites.

Because we did not know the spatial scales at which land cover variables influence biodiversity, we incorporated Bayesian latent indicator scale selection (BLISS; Stuber et al., 2017) in our trivariate model to determine which spatial scales of land cover variables best explained variation in each biodiversity metric. To save computational time, we used a two-step process to model land cover relationships at their optimal scales by first using BLISS to identify the optimal spatial scales for explaining land cover–biodiversity relationships from a set of candidate spatial scales, and then running a final model with only the BLISS-selected optimal spatial scales (Hooten & Hobbs, 2015). Previous work in this system investigating species abundance suggested the range of candidate scales used (500m–20km) is adequate for describing land cover scales-of-effect (Stuber & Fontaine, 2019), and we considered published suggestions for selecting candidate spatial scale ranges in similar exploratory studies (Jackson & Fahrig, 2014).

The BLISS procedure encoded each scale as a latent class indicator variable to sample land cover coefficients at each candidate spatial scale in proportion to its probability of being the most informative scale relevant to predicting each biodiversity metric (Stuber et al., 2017). We included all six land cover predictors because BLISS performed well with even highly correlated variables ($\geq \rho = 0.8$; Stuber et al., 2018; row crop and grasses were correlated at $\rho = -0.8$). We used uniform, discrete priors for each candidate spatial scale, which allowed BLISS to perform scale selection independently for each land cover variable and biodiversity metric combination (e.g., the optimal scale of the SR-row crop relationship could be 500 m, while the optimal scale of the PD-row crop relationship could be 2 km). BLISS evaluated both linear and quadratic effects of land cover variables at the same spatial scale at every sampling iteration. For each variable, we chose the scale with the highest posterior probability for each land cover type as the best spatial scale. Then, to better estimate the parameters for the habitat–biodiversity relationships at the optimal scales and save on computational time, we reran the same trivariate model with land cover covariates only at their selected scales (i.e., the same model formulation but without BLISS). See Table S.4 for JAGS code to specify the model.

We ran our models with one MCMC chain for 20,000 iterations after a 5000 burn-in period with mean-zero, normally distributed priors with a standard deviation of 0.1 on fixed effects and used a Wishart distribution for the precision parameter of the multivariate normal distribution. We visually assessed each parameter for convergence.

We quantified pairwise biodiversity correlations at the between-site and within-site levels based on the random intercepts and residual covariance between the three response variables in our multivariate model (Dingemanse & Dochtermann, 2013). A between-site correlation would be present when, for example, site-mean values of PD correlated with

site-mean values of FD. When considering measurements that change over time, such as biodiversity at a defined location, correlations can be decomposed into between-site and within-site components that jointly contribute to the raw pairwise correlations (Brommer, 2013; Dingemanse et al., 2012; Hadfield et al., 2007). A within-site correlation would be present when, for example, sites' change in PD between replicate measurements between years correlated with sites' change in FD between years. Because we calculated correlations from mixed-effect models, we consider instead, residual correlations (i.e., correlations between errors) after accounting for any fixed effects included in the model. After accounting for all fixed effects (here, land cover variables), the between-site residual correlation represents correlated deviations of site means from the expected value given shared relationships with fixed effects alone, and the within-site residual correlation represents correlated deviations of observations from their site-level means. For example, if sites that have higher mean PD than predicted by land cover alone also have higher mean FD than expected by land cover alone, we would find a positive between-site residual correlation. Only the between-site residual correlations reflect relationships between site-specific factors (e.g., permanent environmental effects, shared history), and raw correlations based on single measurements (i.e., based on only one visit to each field site) reflect only between-site correlations when within-site variation is low (Brommer, 2013). We refer interested readers to Pollock et al. (2014) for additional explanations of how to interpret shared environmental relationships separately from residual species correlations in a multispecies co-occurrence context.

We checked our models for homoscedasticity and normally distributed residuals and assessed the fit of our regression models using root mean square error (RMSE). We projected our fitted biodiversity model across Nebraska for each biodiversity dimension, using the empirical cumulative distribution function of each dimension to rescale each to range from 0 to 1, making the metrics comparable, and then calculated their pairwise differences spatially. Semivariograms did not indicate any residual spatial autocorrelation.

3. Results

3.1. *Avian point counts*

We detected 141 species across 2641 visits at 781 unique sampling sites; 548 and 549 sites were sampled in 2016 (eight observers) and 2017 (five observers), respectively, with 415 sites visited both years (Fig. 1). Site visitation averaged 2.4 ± 0.9 times per year. Of the 141 species detected, 83 were detected in less than 1% of the visits, and only 16 species were detected in more than 10% of visits. Across sites, average raw SR of detections was 9.69 ± 5.02 and 9.88 ± 3.90 in 2016 and 2017, respectively.

3.2. *Occupancy modeling*

Occupancy models for all 141 species attained visual convergence. Model fit for 124 species models was excellent ($TSS > 0.7$), 15 species models had good model fit ($0.7 > TSS > 0.4$), and two species models had poor model fit ($TSS < 0.4$). Across all sites, the simulated mean SR was 25.17 ± 2.39 species (not z-scored), mean PD was 845.44 ± 47.86 branch length (not z-scored), and mean FD was 1.03 ± 0.06 branch length (not z-scored).

3.3. Biodiversity modeling

3.3.1. Scale selection

Land cover varied across Nebraska, with grasses and row crops being the most abundant land cover variables across all scales, followed by grain, trees, CRP, and wetlands, respectively (Table S.1). BLISS revealed substantial variation in scale selection both among land cover types within each biodiversity dimension and among biodiversity dimensions within land cover types (Fig. 2), ranging from the smallest candidate scale (0.5 km radius) to 20 km radius. Probability distributions appeared largely unimodal; however, there were several bimodal patterns (e.g., FD CRP, SR wetland; Fig. 2, respectively) indicating the potential for two important scales for predicting these biodiversity-land cover relationships, and uniform distributions (e.g., SR, PD, FD small grains; Fig. 2) suggesting scale-insensitivity (Stuber & Fontaine, 2019).

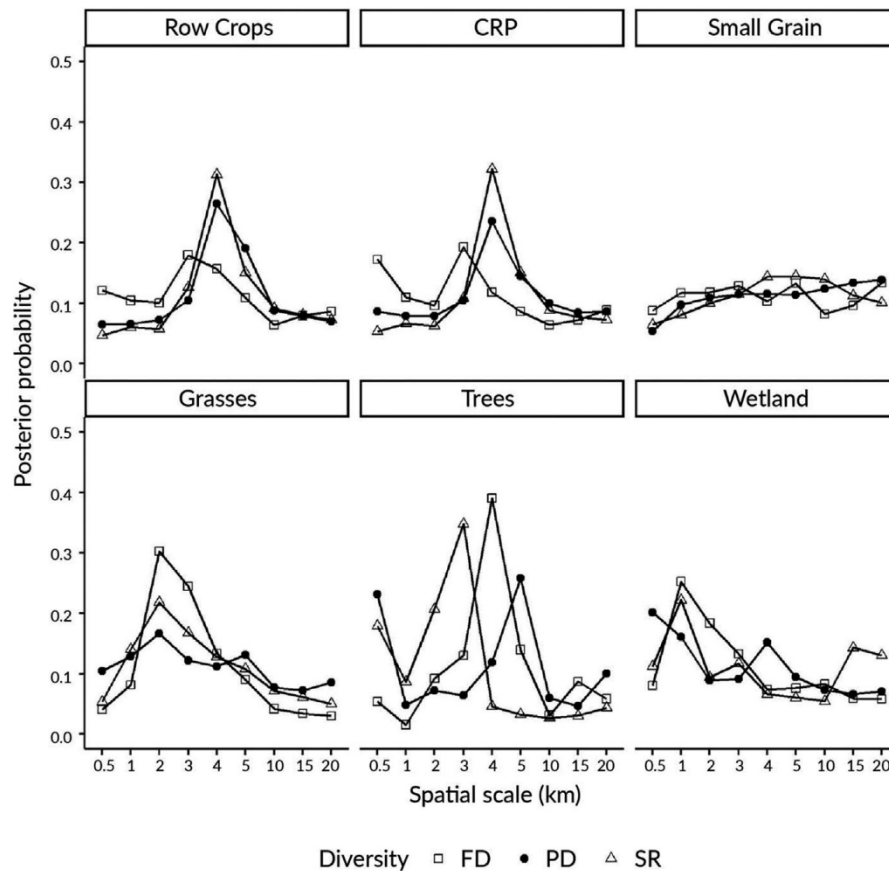


Figure 2. Posterior probability distributions for phylogenetic diversity (PD), species richness (SR), and functional diversity (FD) of breeding birds in Nebraska, USA, across candidate spatial scales (in km) of land cover predictors: row crops, CRP, small grain, grasses, trees, and wetlands as estimated by Bayesian latent indicator scale selection (BLISS). Lines are for visualization purposes only.

BLISS selected larger spatial scales for PD than FD for all land cover types except for grassland and wetland, and larger spatial scales for PD than SR for small grain and trees. BLISS selected equal numbers of smaller, larger and equivalent spatial scales for FD and SR with most optimal scales being within 1km of one another except for FD having a much larger optimal scale than SR for small grains (Table S.5; Fig. 2).

3.3.2. *Land cover relationships*

Within their selected scales, SR, PD, and FD generally displayed similar relationships across land cover gradients (Fig. 2a–f and j–i). FD and SR had similar negative relationships with proportions of wetlands, while PD had no relationship with proportion wetlands (Fig. 3g–i; Table S.5). While all metrics showed the same general relationships with the proportions of row crop and grassland (inverse-U and U-shaped, respectively), their intercepts differed (Fig. 2a–f; Table S.5). The most similar land cover relationships were often between biodiversity metrics for which BLISS selected a similar spatial scale (Fig. 2; Table S.5).

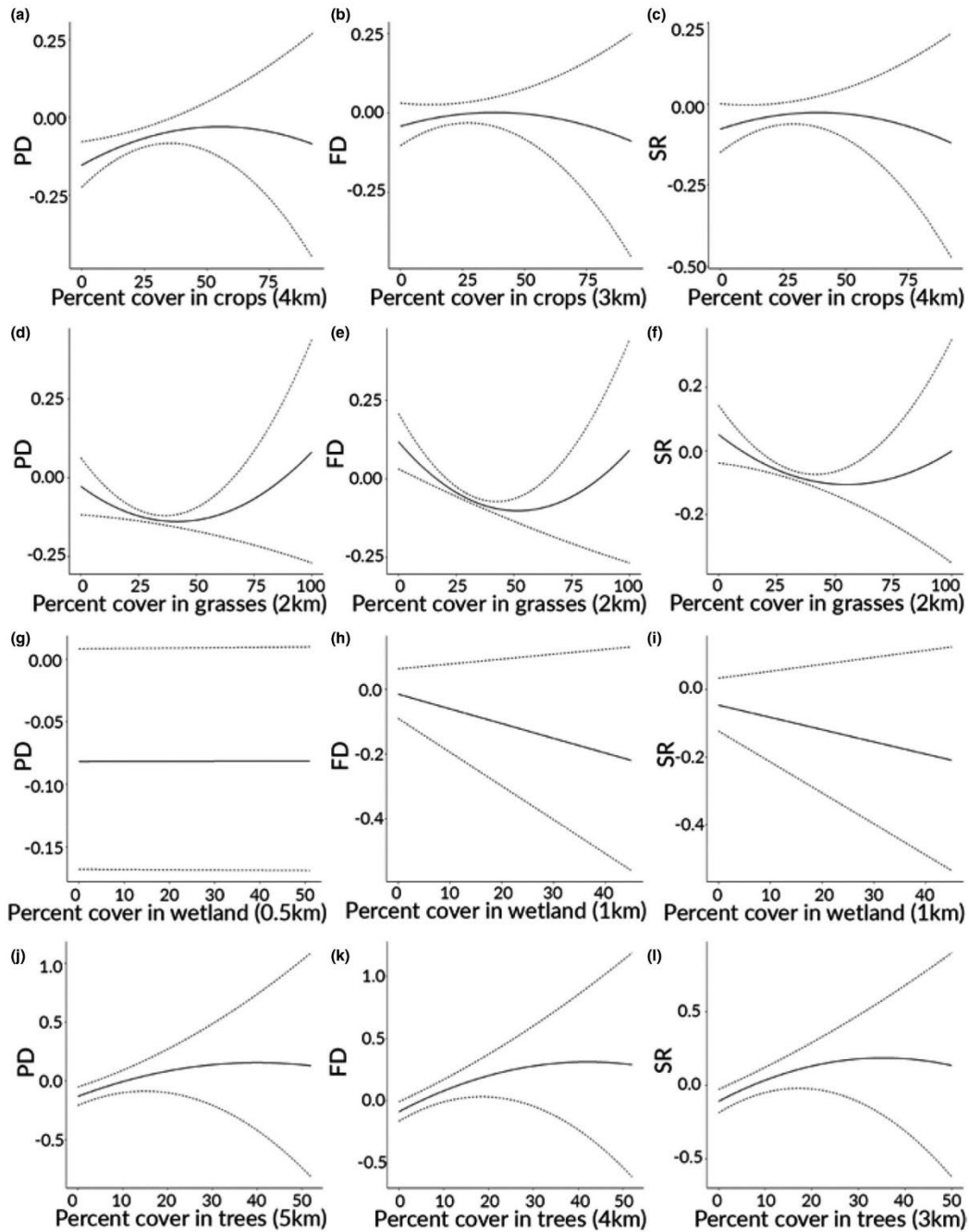


Figure 3. Estimated response curves (depicting z-scores) of phylogenetic diversity (PD), functional diversity (FD), species richness (SR) across gradients of row crops, non-CRP grass, wetlands, and trees within a radius of the most informative spatial scale as selected by BLISS. Solid line represents mean land cover relationships and dashed lines represent 95% credible intervals predicted out to the maximum range of that land cover within selected scales found within our study extent.

3.3.3. Biodiversity correlations

Our trivariate mixed-effect model provided strong support for nonzero residual correlations between biodiversity metrics that differed between the two hierarchical levels measured (between-site vs. within-sites). After accounting for shared responses to land cover covariates, sites that on average had higher biodiversity in any single metric than expected given the existing land cover, had lower than expected biodiversity scores in the remaining biodiversity metrics (i.e., negative between-site correlations in all pairwise biodiversity combinations; point estimates: -0.42 , -0.43 , and -0.60 for PD:FD, PD:SR, FD:SR, respectively; Table S.5). However, after accounting for shared responses to land cover covariates, the within-site correlations were strongly positive (point estimates: 0.98). From year to year, sites that either increased or decreased in one dimension of biodiversity showed a corresponding increase or decrease in both other dimensions of biodiversity.

3.3.4. Model checking

Visual residual analysis did not indicate model assumption violations. RMSE values were 18%, 17%, and 19%, for PD, FD, and SR, respectively.

3.3.5. Biodiversity projections

All three metrics were qualitatively similar across the grasslands of central Nebraska. Predicted PD, FD, and SR increased from west to east and all metrics had relatively high values in locations with relatively high percentage of woodland (e.g., eastern border of Nebraska; Fig. 4). Areas in the east, with the highest percent of agriculture in the state, were projected to have intermediate to high levels of all three biodiversity metrics. Based on land cover associations, when projected across Nebraska, values of biodiversity metrics were within 50% of each other with clusters of higher PD scattered in northwest and southeast Nebraska. FD was predicted to be higher than PD in the southwest corner of the panhandle of Nebraska, which has a large grassland and following rivers where there are more forest areas. Wooded areas in central and eastern Nebraska were associated with relatively higher SR than FD and higher FD than PD (Fig. 5).

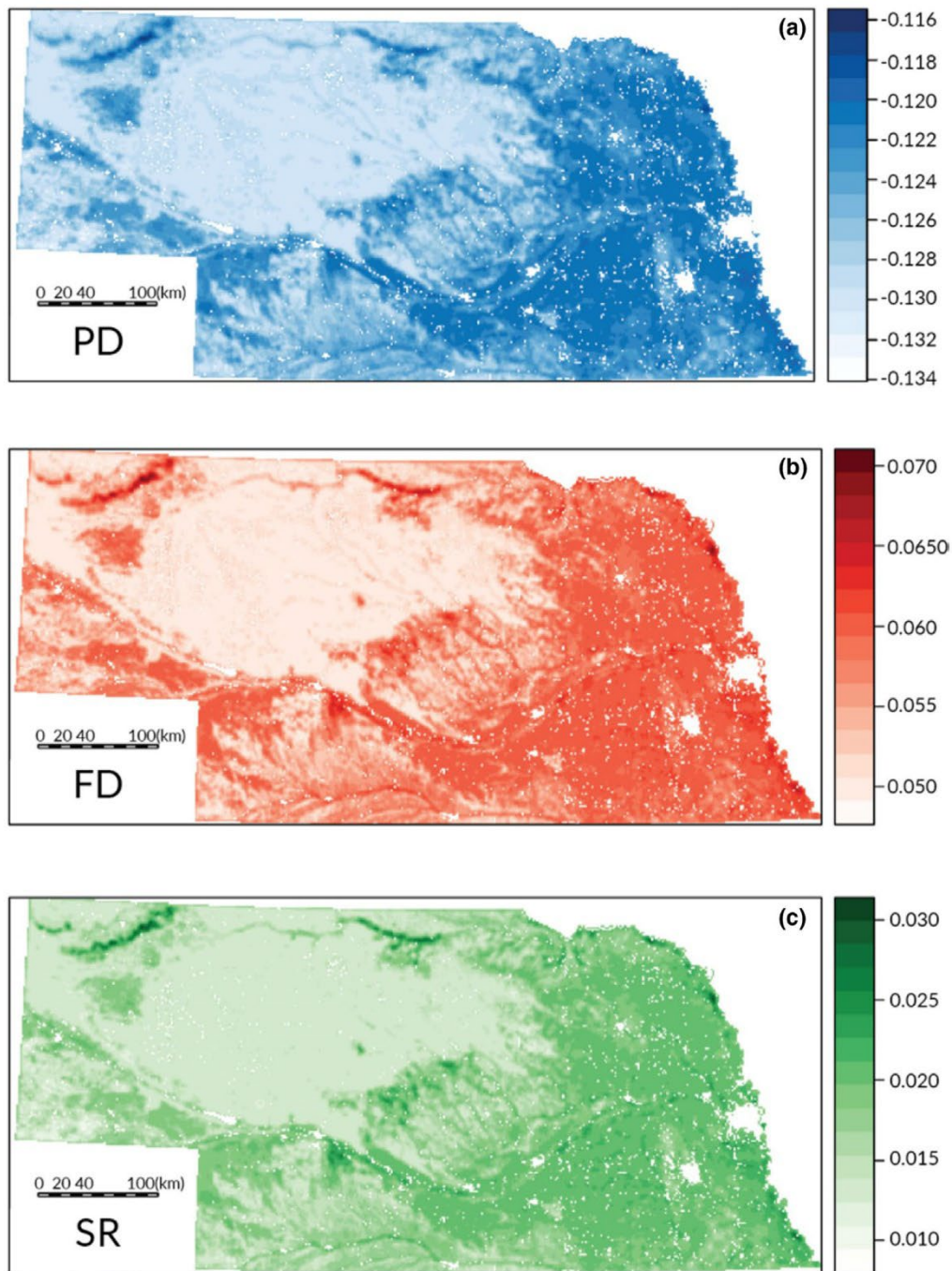


Figure 4. Map of predicted phylogenetic diversity (PD; blue (a)), functional diversity (FD; orange (b)), and species richness (SR; green (c)) of birds across Nebraska, USA. Results depict expected 2017 values based on estimated land cover relationship at the spatial scales selected by BLISS, using raster package (Hijmans 2017) in R.

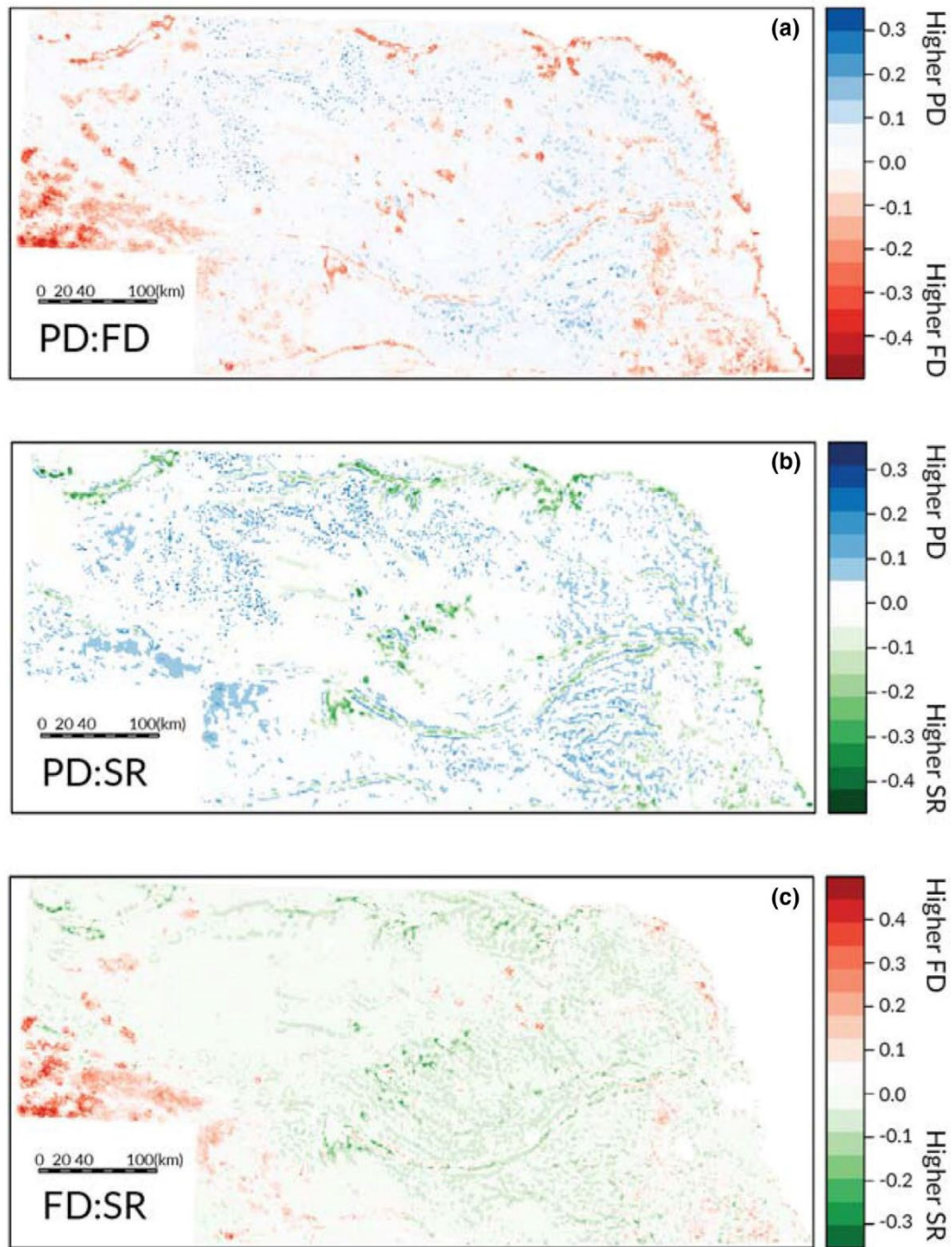


Figure 5. Map of pairwise differences between predicted relative phylogenetic diversity (PD), functional diversity (FD), and species richness (SR) of birds across Nebraska, USA. We rescaled each metrics' prediction map values to range from 0 to 1 and mapped the difference between each pair of biodiversity metrics in ArcMap (ESRI 2015).

4. Discussion

Understanding whether and how environmental context affects different dimensions of biodiversity and the relationships among dimensions can help inform when biodiversity dimensions can be used as surrogates for one another, elucidate drivers of biodiversity, and improve predictions of biodiversity trends. Here, we quantified relationships among taxonomic, phylogenetic, and functional dimensions of biodiversity and their relationships with six land cover gradients using a hierarchical approach. We identified the appropriate scales-of-effect of land cover predictor variables and described biodiversity correlations at the between-site and within-site levels after accounting for shared responses to land cover. We demonstrate variation in the ecological neighborhoods that are influential in shaping biodiversity dimensions and variation in the estimated response curves representing habitat-biodiversity relationships. Taken together, variation in scales-of-effect, habitat response curves, and correlations between biodiversity dimensions that were less than 1 translated to diverging predictions for each biodiversity dimension when projected onto a real landscape. Based on our findings, we suggest that surrogacy among biodiversity dimensions should be viewed with caution, particularly given negative correlations between biodiversity dimensions at the between-site level which suggest constraints in a site's ability to support maximal biodiversity in multiple dimensions and highlight the need for additional studies regarding the scale-dependence of response-environment relationships in biodiversity and conservation.

4.1. Correlation and surrogacy

Evidence for taxonomic metrics being adequate surrogates for phylogenetic and functional metrics is equivocal and typically indicate only partial congruence (Huang et al., 2012; Pavoine et al., 2013; Rodrigues & Gaston, 2002). When the response variables of interest can change over time (e.g., species richness and phylogenetic diversity both may fluctuate over time), any correlations calculated based on only a single observation will be influenced by relationships at multiple hierarchical levels (i.e., the within- and between-subject levels). In our study, after accounting for shared responses to land cover covariates, three common biodiversity dimensions were positively correlated at the within-site level but negatively correlated at the between-site level. The general idea that biodiversity dimensions can act as surrogates for one another rests on the assumption that positive raw correlations specifically represent *between-site* correlations among biodiversity metrics, that is, sites with high average SR also have high average PD. However, positive raw correlations can also occur if biodiversity metrics are influenced by the same (unmeasured) environmental factors that fluctuate over time (within-site correlation). That is, we may observe a positive raw correlation between biodiversity metrics if we happen to measure a site that, on average, has low SR during a low predation-pressure year where uncommon species were able to colonize, resulting in higher than average SR during that observation. In observational studies, environmental heterogeneity is largely uncontrolled for, such that within-site correlations should be accounted for because they might be the major factor shaping raw correlations. Indeed, here we observe strong positive *raw* correlations of pairwise biodiversity metrics (point estimates: 0.96, 0.97, 0.98, PD:FD, PD:SR, FD:SR, respectively;

Table S.5); however, this is partly driven by PD and FD being mathematically linked to SR and partly by shared responses to land cover variables (correlation point estimates from land cover-based predictions: 0.12, 0.60, 0.63, for PD:FD, PD:SR, and FD:SR, respectively; Table S.5) and strong positive within-site correlations, rather than between-site correlations, which were negative (−0.42, −0.43, −0.60, PD:FD, PD:SR, FD:SR, respectively; Table S.5). Differences between raw correlations (i.e., not based on modeling) and correlations after adjusting for shared habitat responses and variation within and among study sites may be a general phenomenon. In particular, the opposing relationships we uncovered (i.e., differences in magnitude of correlations between biodiversity and land cover, and correlations that differed in direction at the within- and among-site levels) suggest that biodiversity studies, generally, should aim to collect repeated measurements of biodiversity at sites over time and account for variation in biodiversity at both within- and among-site levels to appropriately characterize variation in biodiversity.

The opposing relationships we uncover at the between- and within-site levels, after accounting for shared responses to land cover variables, suggest that different ecological processes may shape correlations at these two levels. Indeed, the processes that shape fluctuations in biodiversity at a site may have little relevance for understanding site-mean biodiversity values. Candidate mechanisms driving between-site correlations should be long-term, systematic environmental, ecological, or evolutionary factors that vary between sites and may be related to differential selection in past environments, species competition, or founder effects. Mechanisms driving within-site correlations may include fluctuations in local resources, local weather conditions, or correlated errors that unfold on shorter time-scales than the length of the study. The negative correlation among all biodiversity metrics at the between-site level, representing a trade-off, was masked in the raw correlation, driven by effects of fluctuating unmeasured variable(s). This scenario is not uncommon in life history studies in quantitative genetics (Reznick et al., 2000; Van Noordwijk & de Jong, 1986) and may be common in community ecology, although longitudinal investigations that decompose trait variation into hierarchical components are rare (Lasky et al., 2014).

Our results suggest that a single biodiversity dimension can be an unreliable predictor of another, echoing the conclusions of others that caution against surrogacy (Mazel et al., 2018; Pavoine et al., 2013). Although based on land cover alone we expect that “good” sites (i.e., with favorable land cover characteristics) will support relatively high biodiversity in multiple dimensions (land cover-only based biodiversity correlations: 0.12, 0.60, 0.63 for PD:FD, PD:SR, and FD:SR, respectively; Table S.5), negative between-site correlations suggest that biodiversity conservation based on programs that maximize biodiversity in a single metric likely do not represent maximal biodiversity in other metrics (e.g., while a site with “good” land cover characteristics may have relatively high expected PD and FD, unmeasured site-specific characteristics may result in higher than expected biodiversity in one dimension and lower than expected biodiversity in the remaining two dimensions). However, biodiversity conservation based on on-the-ground management action (e.g., through habitat restoration projects) could improve biodiversity simultaneously in multiple dimensions, if such management actions are reflected in the underlying within-site correlations. Understanding multilevel biodiversity correlations can help guide conservation

actions given specific target goals and practical constraints that warrant further study in community ecology and conservation science.

4.2. Scale selection

Despite the importance of considering scales-of-effect in understanding ecological relationships, our study is among the first to address scale-of-effect dependency across biodiversity dimensions (Martin, 2018; Miguet et al., 2016). We found substantial differences in the scales at which land cover covariates explain variation in each biodiversity dimension (Fig. 2; Table S.5). Our approach generally selected the largest spatial scales for PD, followed by FD, and then SR (Fig. 2; Table S.5). Although the study of scales-of-effect in biodiversity is relatively new, we might expect PD to respond to land cover covariates at larger spatial scales compared with FD and SR because the biological phenomena associated with changes in phylogenetic diversity likely occur over different temporal and spatial scales than the biological phenomena associated with taxonomic and functional diversity (Holling, 1992; Jackson & Fahrig, 2014; Miguet et al., 2016). Phylogenetic biodiversity is a snapshot of the outcomes of evolutionary processes associated with speciation and extinction that operate across large spatial and temporal scales (Jackson & Fahrig, 2014; Miguet et al., 2016; Swenson, 2011). In contrast, functional biodiversity is a snapshot of trait-based information that links species to ecological processes unfolding over relatively smaller spatial and temporal scales compared with evolution (Miguet et al., 2016; Mouchet et al., 2010). Taxonomic diversity is an outcome of colonization and extinction events (in the meta-population sense), which we expected to act on intermediate temporal and spatial scales to functional and phylogenetic diversity, although our results here are equivocal. Scale-of-effect dependence of biodiversity dimensions is among the most understudied in scale-of-effect analyses in ecology and substantial work is needed to develop a predictive framework to understand how and why particular ecological neighborhoods are influential to different dimensions of biodiversity, and how these neighborhoods might change over time.

4.3. Spatial predictions of biodiversity dimensions

Although our finding that there are spatial differences among biodiversity dimensions is not novel (Brum et al., 2017; Devictor et al., 2010; Quan et al., 2018; Safi et al., 2011), our study is the first to our knowledge that has attempted to tease apart scales-of-effect and biodiversity response curves. After accounting for the scale-dependence of biodiversity-habitat relationships, our results highlight response curves that are qualitatively similar between biodiversity metrics and the land cover variables investigated. Although the shapes of biodiversity-land cover relationships were broadly similar, the relationships manifested at different spatial scales, which can contribute to substantial differences in predicted biodiversity among different dimensions. When landscapes are homogenous across scale, we would expect to see similar biodiversity projections even when scales-of-effect differ, but when landscapes are nonhomogenous across scales, we would expect to see larger predicted differences among biodiversity dimensions under different scales-of-effect. Indeed, we saw larger differences among spatial predictions of biodiversity dimensions in areas with heterogeneous land cover (e.g., eastern edge of Nebraska where there

are more interspersed forest habitats) compared to areas where land cover is relatively homogenous (e.g., central Nebraska, which is characterized by extensive grassland cover; Fig. 5). Much of Nebraska was scattered with small areas with a high degree of difference, most of which were associated with rarer land cover types such as trees or wetlands (discussed below).

4.3.1. *Landscape drivers of variation in biodiversity dimensions*

Agricultural intensification is a major driver of biodiversity loss worldwide, including in birds (Benton et al., 2003; Donald et al., 2001; Flynn et al., 2009). However, we find only a weak relationship between avian biodiversity and the amount of row crop in the landscape, although biodiversity does decline as the amount of row crop increases (Fig. 3a–c; Table S.5). Furthermore, CRP, a program often used as a tool to increase wildlife biodiversity (Best et al., 1997; Johnson, 2005; Patterson & Best, 1996), showed a negative relationship with FD and SR (Table S.5). Species composition on CRP fields and other land cover types may also be influenced by climatic variation, interactions between surrounding habitat types, legacy effects, and the type and intensity of management (Johnson, 2005; King & Savidge, 1995), the inclusion of which may improve future models. Estimated land cover relationships may also vary between guilds of birds (e.g., species richness of grassland birds is expected to increase with addition of grassland, where richness of forest guild birds is not). Increasing the thematic resolution of land cover predictors (e.g., type of grassland, high/low stocked pasture, etc.) could increase the precision of our understanding of habitat-biodiversity relationships and would help to tailor recommendations regarding habitat set-aside or management action plans.

4.3.2. *Rare land cover types*

Woodlands and wetlands were relatively rare in our system (Bishop et al., 2011; Table S.1) and subsequently increased habitat heterogeneity where they were found, which has been cited as a driving factor that increases biodiversity (Benton et al., 2003; Stein et al., 2014). We observed a positive relationship between percent woodland and all three biodiversity dimensions that appeared to plateau around 30% woodland cover within 3–5 km radius areas (Fig. 3j–l; Table S.5), suggesting that biodiversity increases in all dimensions as the proportion of woodland cover increases, but only up to 30% cover. However, we observed negative relationships between wetlands and both SR and FD and no relationship with PD (Fig. 3h,i,g, respectively; Table S.5). Here, wetlands may act as an environmental filter that selects for species that have specific functional traits (e.g., piscivores, dabblers), yet those species could have relatively distant evolutionary relationships (e.g., waterfowl, cranes, shorebirds; Benton et al., 2003). The assemblages around wetlands are predicted to show large differences between PD and FD, where PD is large and FD is small (Fig. 5a). Thus, not all increases in habitat heterogeneity led to higher biodiversity, and biodiversity dimensions may respond asynchronously to habitat heterogeneity.

5. Conclusions

Taxonomic, phylogenetic, and functional dimensions of biodiversity are lenses to examine different aspects of biological variation, yet the relationships among biodiversity dimensions are not well understood and can lead to false inferences if we fail to account for multiscale, spatial, and hierarchical relationships when measuring or predicting biodiversity metrics. Our study is one of the first to take a multiscale, scale-of-effect optimization approach to characterize habitat-biodiversity relationships and thus one of the first to demonstrate spatial scale-of-effect dependence across relationships between land cover predictor variables and taxonomic, phylogenetic, and functional biodiversity, and hierarchical dependence of biodiversity correlations (i.e., opposing residual correlations at the between-site and within-site levels) contributing to spatial differences among biodiversity metrics. Scale-dependence coupled with opposing multilevel correlations among dimensions provide strong evidence cautioning against the use of one metric as a surrogate for another. Rather, substantial work is needed to compile assessments of scales-of-effect and uncover the drivers of opposing between-site and within-site correlations in biodiversity-related responses such that general patterns may be documented and eco-evolutionary hypotheses tested.

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Biosketch

Nadejda Mirochnitchenko studies spatial ecology, including biodiversity, aquatic-terrestrial linkages, and community composition. She works with many taxonomic groups (e.g., birds, herpetofauna, arthropods, plants) and focuses on applying interdisciplinary approaches to improve conservation biology and wildlife management.

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SUPPLEMENTARY MATERIALS

Table S.1. Summary statistics of the proportion of land cover surrounding survey points at considered candidate scales in Nebraska, USA.

Statistic	Min Percentile (25)		Median Percentile (75)		Max	Median	St. Dev.
Crop 0.5km	0	0	16	50	96	16	30.457
Crop 1km	0	0	18	52	95	18	30.117
Crop 2km	0	5	23	51	94	23	28.412
Crop 3km	0	6	26	50.5	93	26	27.885
Crop 4km	0	7	26	52	92	26	27.288
Crop 5km	0	7	26	52	90	26	26.902
Crop 10km	0	9	26	51	87	26	26.002
Crop 15km	0	11	25	53	86	25	25.567
Crop 20km	0	11	25	53.5	85	25	25.129
CRP 0.5km	0	0	0	0	65	0	9.010
CRP 1km	0	0	0	3	55	0	7.025
CRP 2km	0	0	0	3	50	0	5.000
CRP 3km	0	0	1	3	44	1	4.087

CRP 4km	0	0	1	3	33	1	3.480
CRP 5km	0	0	1	3	33	1	3.211
CRP 10km	0	0	1	3	27	1	2.599
CRP 15km	0	0	1	3	22	1	2.220
CRP 20km	0	0	1	3	20	1	2.039
Grain 0.5km	0	0	0	4	96	0	18.637
Grain 1km	0	0	0	9	95	0	18.735
Grain 2km	0	0	0	10.5	91	0	17.897
Grain 3km	0	0	1	11	91	1	17.590
Grain 4km	0	0	1	12	88	1	17.255
Grain 5km	0	0	1	13	88	1	16.884
Grain 10km	0	0	1	14	76	1	15.605
Grain 15km	0	0	1	15	71	1	14.610
Grain 20km	0	0	1	14	62	1	13.540
Grass 0.5km	0	13	43	75.5	100	43	32.334
Grass 1km	0	16	43	72	100	43	31.250
Grass 2km	0	17	40	70	100	40	30.006

Grass 3km	0	18	39	70	99	39	29.384
Grass 4km	0	19	38	69	99	38	29.032
Grass 5km	1	20	37	68.5	99	37	28.695
Grass 10km	2	22	38	65	98	38	27.419
Grass 15km	3	21	40	63	97	40	26.773
Grass 20km	4	21	43	62	97	43	26.392
Tree 0.5km	0	0	0	4	56	0	7.588
Tree 1km	0	0	1	5	48	1	7.197
Tree 2km	0	0	1	6	49	1	6.861
Tree 3km	0	0	1	6.5	50	1	6.469
Tree 4km	0	0	1	7	52	1	6.021
Tree 5km	0	0	2	7	52	2	5.762
Tree 10km	0	1	2	6	33	2	4.889
Tree 15km	0	1	2	6	24	2	4.489
Tree 20km	0	1	3	7	21	3	4.045
Wetlands 0.5km	0	0	0	0	51	0	6.023
Wetlands 1km	0	0	0	1	45	0	5.212

Wetlands 2km	0	0	0	1	36	0	4.411
Wetlands 3km	0	0	0	1	27	0	3.938
Wetlands 4km	0	0	0	1	26	0	3.610
Wetlands 5km	0	0	0	1	23	0	3.444
Wetlands 10km	0	0	0	1	19	0	2.948
Wetlands 15km	0	0	0	1	16	0	2.637
Wetlands 20km	0	0	0	1	13	0	2.413

Table S.2. Species occupancy model used with JAGS to determine the occupancy and land cover associations for bird species detected in Nebraska, USA.

```

model{
  # Land cover occupancy priors
  betayear1 ~ dnorm(0,0.1)
  betayear2 ~ dnorm(0,0.1)
  betag ~ dnorm(0,0.1)
  betag2 ~ dnorm(0,0.1)
  betacrp ~ dnorm(0,0.1)
  betagr ~ dnorm(0,0.1)
  betagr2 ~ dnorm(0,0.1)
  betat ~ dnorm(0,0.1)
  betat2 ~ dnorm(0,0.1)
  betaw ~ dnorm(0,0.1)

```

```

# Detection probability priors

alpha0 ~ dnorm(0,0.1)

alphad ~ dnorm(0,0.1)

alphad2 ~ dnorm(0,0.1)

alphaw ~ dnorm(0,0.1)

alpham ~ dnorm(0,0.1)

alpham2 ~ dnorm(0,0.1)

alphat ~ dnorm(0,0.1)

alphat2 ~ dnorm(0,0.1)

alphac ~ dnorm(0,0.1)


#Hyperprior for random effect precision on observers in detection model

tau.observer~ dgamma(4,1)


#Random effect variance

sigma2.observer <- 1/tau.observer

sigma.observer <- sqrt(sigma2.observer)


#Random effect observer

for (o in 1:nobservers){

  u.observer[o] ~ dnorm(0, tau.observer)

}


# Occupancy model

for (y in 1:nyears) {

  for (i in 1:npoints){

```



```

logit_occ[y,i] <- betayear1 * Year1[i] + betayear2 * Year2[i] + betag * grass500l[i] +
betag2 * grass500q[i] + betacrp * crp500l[i] + betagr * grain500l[i] + betagr2 * grain500q[i] + betat *
tree500l[i] + betat2 * tree500q[i] + betaw * wet500l[i]

```

```

logit(occ[y,i]) <- logit_occ[y,i]

Psi[y,i] ~ dbern(occ[y,i])

}

}

```

```

# Detection probability model

for (j in 1:nsurveys) {

logit_pr[j] <- alpha0 + alphad * Season_Datel[j] + alphad2 * Season_Dateq[j] + alphaw *
Windspeedl[j] + alpham * Minutes_since_midnightl[j] + alpham2 * Minutes_since_midnightq[j] + alphas *
Templ[j] + alphas2 * Tempq[j] + alphac * Cloudsl[j] + u.observer[Obs_n[j]]

```

```

logit(prob[j]) <- logit_pr[j]

```

```

# Occupancy * detection

```

```

mu_p[j] <- Psi[Year.id[j], Route.Point.id[j]] * prob[j]

```

```

# Observation model

```

```

Cluster[j] ~ dbern(mu_p[j])

```

```

}

}

```

Table S.3. Traits included in the creation of the functional dendrogram.

Trait type		Trait	Value type
Resource quantity	1	Body mass	Continuous
	2	Clutch size	Continuous
	3	Mean (no. clutches)	Continuous
	4	Egg length	Continuous
	5	Egg breadth	Continuous
Diet	6	Invertebrates	Percent
	7	Mammals	Percent
	8	Reptiles	Percent
	9	Fish	Percent
	10	Vertebrates (unknown)	Percent
	11	Scavenge	Percent
	12	Fruit	Percent
	13	Nectar or pollen	Percent
	14	Seeds	Percent
	15	Other plant material	Percent
Foraging Strategy	16	Below water	Percent
	17	On water	Percent
	18	On ground	Percent
	19	Below understory	Percent
	20	In middle levels of trees/ bushes	Percent
	21	In canopy	Percent
	22	Aerial	Percent
Foraging period	23	Nocturnal	Binary

Table S.4. The trivariate biodiversity model used with JAGS to determine optimal spatial scales for each land cover type with BLISS and the biodiversity response curves at the optimal spatial scales.

```

model{

  # Land cover coefficients for PD

  alphayear1 ~ dnorm(0,0.1)

  alphayear2 ~ dnorm(0,0.1)

  alphag ~ dnorm(0,0.1)

  alphag2 ~ dnorm(0,0.1)

  alphacrop ~ dnorm(0,0.1)

  alphacrop2 ~ dnorm(0,0.1)

  alphacrp ~ dnorm(0,0.1)

  alphagr ~ dnorm(0,0.1)

  alphagr2 ~ dnorm(0,0.1)

  alphas ~ dnorm(0,0.1)

  alphas2 ~ dnorm(0,0.1)

  alphaw ~ dnorm(0,0.1)


  # Land cover coefficients for FD

  betayear1 ~ dnorm(0,0.1)

  betayear2 ~ dnorm(0,0.1)

  betag ~ dnorm(0,0.1)

  betag2 ~ dnorm(0,0.1)

  betacrp ~ dnorm(0,0.1)

  betacrop ~ dnorm(0,0.1)

  betacrop2 ~ dnorm(0,0.1)

```

betagr ~ dnorm(0,0.1)

betagr2 ~ dnorm(0,0.1)

betat ~ dnorm(0,0.1)

betat2 ~ dnorm(0,0.1)

betaw ~ dnorm(0,0.1)

Land cover coefficients for SR

gammayear1 ~ dnorm(0,0.1)

gammayear2 ~ dnorm(0,0.1)

gammag ~ dnorm(0,0.1)

gammag2 ~ dnorm(0,0.1)

gammacrp ~ dnorm(0,0.1)

gammacrop ~ dnorm(0,0.1)

gammacrop2 ~ dnorm(0,0.1)

gammagr ~ dnorm(0,0.1)

gammagr2 ~ dnorm(0,0.1)

gammag ~ dnorm(0,0.1)

gammag2 ~ dnorm(0,0.1)

gammaw ~ dnorm(0,0.1)

BLISS priors

scale.pd.grass ~ dcat(c(1,1,1,1,1,1,1,1,1))

scale.pd.grain ~ dcat(c(1,1,1,1,1,1,1,1,1))

scale.pd.crop ~ dcat(c(1,1,1,1,1,1,1,1,1))

scale.pd.tree ~ dcat(c(1,1,1,1,1,1,1,1,1))

scale.pd.wet ~ dcat(c(1,1,1,1,1,1,1,1,1))

```
scale.pd.crp ~ dcat(c(1,1,1,1,1,1,1,1,1))
```

```
scale.fd.grass ~ dcat(c(1,1,1,1,1,1,1,1,1))
```

```
scale.fd.grain ~ dcat(c(1,1,1,1,1,1,1,1,1))
```

```
scale.fd.crop ~ dcat(c(1,1,1,1,1,1,1,1,1))
```

```
scale.fd.tree ~ dcat(c(1,1,1,1,1,1,1,1,1))
```

```
scale.fd.wet ~ dcat(c(1,1,1,1,1,1,1,1,1))
```

```
scale.fd.crp ~ dcat(c(1,1,1,1,1,1,1,1,1))
```

```
scale.sr.grass ~ dcat(c(1,1,1,1,1,1,1,1,1))
```

```
scale.sr.grain ~ dcat(c(1,1,1,1,1,1,1,1,1))
```

```
scale.sr.crop ~ dcat(c(1,1,1,1,1,1,1,1,1))
```

```
scale.sr.tree ~ dcat(c(1,1,1,1,1,1,1,1,1))
```

```
scale.sr.wet ~ dcat(c(1,1,1,1,1,1,1,1,1))
```

```
scale.sr.crp ~ dcat(c(1,1,1,1,1,1,1,1,1))
```

```
# covariance/precision priors
```

```
tau ~ dwish(R, 5)
```

```
# Bivariate response model
```

```
for (i in 1:npoints) {
```

```
  mu_PD[i] <- alphayear1 * Year1[i] + alphayear2 * Year2[i] + alphag * l_grass[i, scale.pd.grass] +  
  alphag2 * q_grass[i, scale.pd.grass] + alphacrp * l_crp[i, scale.pd.crp] + alphacrop * l_crop[i,  
  scale.pd.crop] + alphacrop2 * q_crop[i, scale.pd.crop] + alphagr * l_grain[i, scale.pd.grain] + alphagr2 *  
  q_grain[i, scale.pd.grain] + alphas * l_tree[i, scale.pd.tree] + alphas2 * q_tree[i, scale.pd.tree] + alphaw *  
  l_wet[i, scale.pd.wet]
```

```

mu_FD[i] <- betayear1 * Year1[i] +betayear2 * Year2[i]+ betag * l_grass[i, scale.fd.grass] + betag2 *
q_grass[i, scale.fd.grass] + betacrp * l_crp[i, scale.fd.crp] + betacrop * l_crop[i, scale.fd.crop] +
betacrop2 * q_crop[i, scale.fd.crop] +betagr * l_grain[i,scale.fd.grain] + betagr2 *
q_grain[i,scale.fd.grain] + betat * l_tree[i,scale.fd.tree] + betat2 * q_tree[i,scale.fd.tree] + betaw *
l_wet[i,scale.fd.wet]

```

```

mu_SR[i] <- gammayear1 * Year1[i] +gammayear2 * Year2[i]+ gammag * l_grass[i, scale.sr.grass] +
gammag2 * q_grass[i, scale.sr.grass] + gammacrp * l_crp[i, scale.sr.crp] + gammacrop * l_crop[i,
scale.sr.crop] + gammacrop2 * q_crop[i, scale.sr.crop] +gammagr * l_grain[i,scale.sr.grain] + gammagr2
* q_grain[i,scale.sr.grain] + gammat * l_tree[i,scale.sr.tree] + gammat2 * q_tree[i,scale.sr.tree] +
gammaw * l_wet[i,scale.sr.wet]

```

```

mu[i,1] <- mu_PD[i]

```

```

mu[i,2] <- mu_FD[i]

```

```

mu[i,3] <- mu_SR[i]

```

```

diversity[i,] ~ dmnorm(mu[i,], tau)

```

```

}

```

```

}

```


Table S.5. Selected spatial scale-of-effect for each land cover-diversity relationship, posterior probability associated with the selected spatial scale as estimated by BLISS, coefficient estimates (posterior mean) and their associated 95% credible intervals (CI) within the most informative spatial scale for phylogenetic diversity (PD), functional diversity (FD), and species richness (SR), and correlations between biodiversity dimensions. Coefficients are associated with orthogonal values of land cover for the biodiversity models and are not back transformed here.

Diversity	Spatial Scale (km)	Scale Posterior Probability	Coefficient	Posterior mean (95% CI)
PD	4	0.26	Crops	1.13 (-0.9, 3.07)
			Crops ²	-0.88 (-2.44, 0.63)
	4	0.24	CRP	-1.72 (-2.99, -0.42)
	2	0.17	Grasses	0.72 (-1.45, 2.93)
			Grasses ²	1.62 (-0.25, 3.47)
	20	0.14	Small Grains	0.12 (-1.04, 1.27)
			Small Grains ²	-0.39 (-1.11, 0.33)
	5	0.26	Trees	1.91 (0.65, 3.15)
			Trees ²	-0.5 (-1.49, 0.51)
	0.5	0.2	Wetland	0 (0, 0.01)
			Year 1	0.08 (-0.01, 0.16)
			Year 2	-0.08 (-0.17, 0.01)
FD	3	0.18	Crops	-0.11 (-2.29, 1.76)
			Crops ²	-0.67 (-2.16, 0.76)
	3	0.19	CRP	-1.57 (-2.82, -0.32)
	2	0.3	Grasses	-0.71 (-2.98, 1.47)
			Grasses ²	2.06 (0.17, 3.9)
	20	0.13	Small Grains	-0.29 (-1.33, 0.79)
			Small Grains ²	-0.53 (-1.2, 0.16)
	4	0.39	Trees	2.65 (1.42, 3.85)
			Trees ²	-0.65 (-1.64, 0.35)
	1	0.25	Wetland	-0.76 (-1.73, 0.25)
			Year 1	0.02 (-0.07, 0.1)
			Year 2	-0.02 (-0.11, 0.07)

SR	4	0.31	Crops	-0.04 (-1.98, 1.74)	
			Crops ²	-0.72 (-2.22, 0.72)	
	4	0.32	CRP	-1.78 (-2.99, -0.52)	
	2	0.22	Grasses	-0.79 (-2.96, 1.36)	
			Grasses ²	1.3 (-0.56, 3.12)	
	5	0.14	Small Grains	-0.66 (-1.91, 0.57)	
			Small Grains ²	-0.34 (-1, 0.33)	
	3	0.35	Trees	2.24 (1.03, 3.47)	
			Trees ²	-0.69 (-1.63, 0.26)	
	1	0.22	Wetland	-0.6 (-1.52, 0.34)	
Year 1			0.05 (-0.04, 0.13)		
Year 2			-0.05 (-0.14, 0.04)		
PD.FD			Within-site correlation	0.977 (0.973, 0.981)	
			Between-site correlation	-0.42 (-0.47, -0.35)	
PD.SR		Within-site correlation	0.979 (0.975, 0.982)		
		Between-site correlation	-0.43 (-0.49, -0.37)		
FD.SR		Within-site correlation	0.985 (0.982, 0.987)		
		Between-site correlation	-0.59 (-0.64, -0.54)		