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Research article

Geographic and temporal distance–decay relationships across taxa

Tad A. Dallas, Lauren A. Holian and Cleber Ten Caten

Department of Biological Sciences, University of South Carolina, Columbia, SC, USA

Correspondence: Tad A. Dallas (tad.a.dallas@gmail.com)

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Communities that are farther away from one another in distance or time tend to be more dissimilar. These relationships are often referred to as 'distance–decay' relationships, relating compositional dissimilarity of communities to geographic distance or exploring compositional shifts through time at a single site. The data required to explore both relationships simultaneously – and their potential interactions – require standardized sampling through time across a set of geographically unique sites. We used data on five taxonomic groups sampled between 2013 and 2021 as part of the National Ecological Observatory Network (NEON) to explore evidence for geographic and temporal distance–decay relationships. Links between these relationships were explored by estimating the temporal consistency of geographic distance–decay relationships and estimating the strength of geographic patterns in temporal distance–decay relationships. Overall, we found evidence for geographic and temporal distance–decay relationships across the five studied taxa, but detected no temporal signal in geographic distance–decay relationships and no spatial signal in temporal distance–decay relationships. Together, this highlights that community composition changes across geographic and temporal gradients, but that the drivers of these changes may depend on different drivers at different scales.

Keywords: beta diversity, community dissimilarity, distance–decay, National Ecological Observatory Network

Introduction

Compositional shifts in ecological communities across space and time can be indicative of biodiversity change, homogenization of communities, the role of shared environmental responses, mobile predators, or dispersal connectivity to resulting community structure (Koenig 2002, Liebhold et al. 2004, Blowes et al. 2019). A common approach to exploring compositional turnover (β diversity) is to explore the role of geographic distance between sampled communities on the resulting dissimilarity in community composition (Whittaker et al. 1970). Doing this for a large set of sites can allow the estimation of a distance–decay relationship (Nekola and White 1999, Anderson et al. 2006, Morlon et al. 2008), the shape of which can be used to infer spatial distance

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thresholds to community similarity (Graco-Roza et al. 2022). Distance–decay relationships are foundational to community ecology (perhaps first conceptualized by Tobler 1970), and represent one of the most well-supported ecological patterns (Soininen et al. 2007, Graco-Roza et al. 2022), though variation exists, depending on spatial and taxonomic extent (Bell 2010, Steinbauer et al. 2012, Warburton et al. 2016).

A related line of inquiry aims at exploring compositional change through time (temporal β diversity; (Magurran et al. 2019). Temporal distance–decay relationships posit that sites closer together in time should be more similar to one another than across larger time spans (Dornelas et al. 2014, Magurran et al. 2019). These relationships can be assessed in at least three different ways. First, all pairwise combinations of communities across time can be used to explore the effect of the time difference between community states and community dissimilarity (Korhonen et al. 2010). Second, each community sampled at a given time could be compared to a reference time t, under the assumption that the chosen reference time is indicative of some natural state, with the typical relationship being a negative relationship between time interval and compositional similarity (Schmera et al. 2022). Finally, sites may be compared to one another with some time lag τ. If we consider a τ of 1, the community composition at time t would be compared to the community composition at $t - \tau$, in this case $t - 1$ (the current community is compared to the prior time period).

Both forms of distance–decay relationships (geographic and temporal) have been explored for a wide range of taxa (Blowes et al. 2019, Graco-Roza et al. 2022), but rarely at the same time (Dornelas et al. 2014, Blowes et al. 2019). The goal of this study was to link the two scales (geographic and temporal) together to provide an exploration of how geographic distance–decay relationships vary over time, and how temporal distance–decay relationships vary over space. That is, changes to the slope of the geographic distance–decay relationship might be indicative of the potential homogenization of local communities, and species losses or gains, and potentially lead to the ability to forecast change in community similarity through time. Meanwhile, a geographic signal in the slope of temporal distance–decay relationships could indicate that some sites are changing at a more dramatic rate than others, highlighting the need to understand what makes some sites remain compositionally similar through time, while others experience pronounced compositional shifts.

Here, we used data from the National Ecological Observatory Network (NEON) for five taxonomic groups across terrestrial (birds, small mammals, and beetles) and aquatic (macroinvertebrates and fish) habitats sampled over time across a set of sites in the USA to explore the consistency of geographic and temporal distance–decay relationships. Additionally, we linked geographic and temporal scales by exploring the temporal change in geographic distance–decay relationships to address how these relationships may be changing over the course of the study period (2013–2021). We found differences among taxa in geographic distance–decay relationships, with consistent but weak relationships of compositional turnover with geographic distance across time. Temporal distance–decay relationships were nearly always positive (communities do differ more across larger periods of time), but relationships were similar in strength to geographic distance–decay relationships. Together, this highlights that community composition changes across geographic and temporal gradients, but that the drivers of these changes may depend on different drivers at different scales.

Material and methods

National Ecological Observatory Network data

The type of data required to explore both geographic and temporal distance–decay relationships consists of a set of geographically distributed sites sampled repeatedly over some length of time. Additionally, comparing across sites requires that the sampling procedure be standardized, such that community composition is comparable across sites. There are few data resources currently that fit these requirements entirely, though great strides have been made in collating exist-ing data resources into time series databases of community composition (e.g. the BioTime data Dornelas et al. 2018). However, these data come from independent studies, such that non-standardized sampling, and differences in detection probabilities and sampling effort, may influence estimates of compositional dissimilarity. Standardized sampling programs such as forest inventories (Smith 2002) and large-scale sampling programs (e.g. NEON; Nagy et al. 2021) offer a way to explore spatial and temporal distance–decay relationships simultaneously.

Data for three terrestrial (small mammals, carabid beetles, and birds) and two aquatic (macroinvertebrates and fish) taxa were obtained from NEON, a standardized sampling effort of 47 terrestrial (Kao et al. 2012, Thorpe et al. 2016) and 34 aquatic (Goodman et al. 2015, Balch et al. 2019) sites spread over 20 ecoclimatic domains across the USA. Some sites were as little as 30 km apart, while the mean distance between any two NEON sites was 2462 km, certainly large enough to see clear shifts in community composition, especially considering the range of taxonomic groups we considered and their corresponding capability for large-scale movement. The geographic extent considered has been found to change the shape of geographic distance–decay relationships, with smaller extents corresponding to a power-law relationship and larger extents having more exponential relationships. This is, of course, defined by the combination of the taxa considered and the geographic area sampled, where larger extents refer to the amount of variation in local versus regional species pools across sites (Graco-Roza et al. 2022).

The ‘neonDivData’ R package provided the NEON data in a standardized and cleaned format for sampling dates between 2013 and 2021 (Li et al. 2022). Some taxa were not sampled during this entire period (e.g. fish community sampling did not start until 2016). We opted to use all sampling effort within a given year to characterize communities across

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geographic sites and through time, as seasonality and species phenological variation, coupled with unequal sampling in some locations, made it difficult to compare communities at finer timescales. However, this still left standardized sampling of biological communities across the USA for five taxonomic groups for between six and nine years. Across sites, there was considerable variation in species richness, with macroinvertebrates having the highest mean species richness across sites ($\bar{n} = 229$), and birds ($\bar{n} = 84$), beetles ($\bar{n} = 51$), small mammals ($\bar{n} = 13$), and fish ($\bar{n} = 7$) having far fewer species. For this estimation, species richness was defined as the total number of unique species found at any point in time for a given taxonomic group. See the Supporting information for more detail on sampling times, geographic distributions, and community structure.

From these data, we assembled site-by-species tables (Fig. 1) that detail the occurrence of species in a given year across the set of sampled sites. We decided to not include information on species mean abundance in our estimation of community dissimilarity, as variation in sampling effort and the existence of rare species may introduce bias across differentially sampled geographic sites. Instead, we used a conservative threshold of detection, in which we proposed that a species was recorded at a site if at least one individual of that species was sampled in that year.

Geographic distance–decay relationships

Distance–decay relationships – quantifying the dissimilarity between two communities as a function of either geographic space or time – were estimated in two ways, consider-ing compositional change across geographic space, as well as compositional changes in a single site through time. To assess distance–decay in geographic space, we used the slope coefficient of a linear model between compositional dissimilarity (measured as Jaccard dissimilarity) and the log-transformed geographic distance (measured as Haversine distance) between sites, as well as the Mantel statistic, following previous explorations of distance–decay relationships (Graco-Roza et al. 2022). The log-transformation of the geographic distance between sites means that a linear model fit takes into account the non-linear relationship between geographic distance and dissimilarity that is commonly observed (Soininen et al. 2007). In concert, these estimate both the rate and strength of compositional change across geographic space. These statistics were measured annually for the set of sites sampled in that year, allowing the exploration of the temporal consistency of geographic distance–decay relationships.

The choice of dissimilarity measure is non-trivial and a subject of much research effort (Chao et al. 2005, Anderson et al. 2006, 2011, Tuomisto 2010, Baselga 2012, Chao et al. 2014). The Jaccard dissimilarity measure was used because of its ease of interpretation (i.e. the fraction of shared species between two sites) and continued use in similar large-scale analyses of distance–decay relationships (Graco-Roza et al. 2022) and as default methods for many R packages (e.g. 'vegan::vegdist' [Oksanen et al. 2022] and 'BAT::beta' [Cardoso et al. 2015]). However, it is important to note that the Jaccard statistic may be sensitive to species richness and sampling completeness (Chao et al. 2005, Beck et al. 2013), and estimating compositional dissimilarity between communities is an area of active research.

Temporal distance–decay relationships

Compositional turnover (temporal β diversity, Magurran et al. 2019) at a single site through time was estimated in a similar manner to geographic distance–decay relationships, where instead of geographic distance, the temporal distance between sites was the number of years inbetween sampling events at a single site. We recognize that this comes with the same issues as geographic distance–decay relationships, in that the resulting data are inherently non-independent because the community composition from a given year is being compared to all other years (see the Supporting information for more details).

To explore if this assumption influenced the detectability of temporal distance–decay relationships, we also calculated temporal distance–decay in two other ways which have been

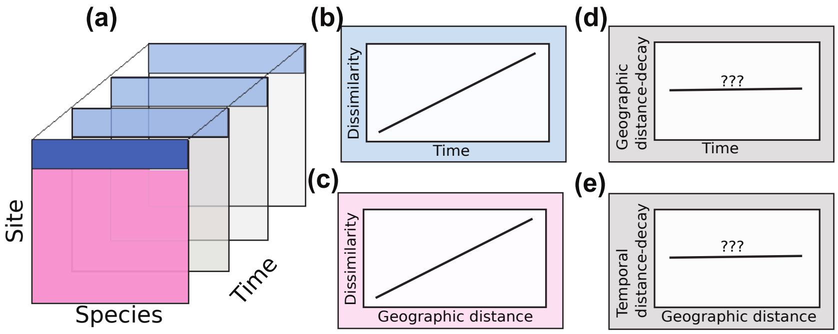

Figure 1. Community composition across a set of geographic sites and through time (panel a) provides at least two dimensions for exploring distance–decay relationships. Temporal distance–decay relationships (blue boxes in (a)) track the temporal change in community composition at a single site through time (b). Geographic distance–decay relationships (pink box in (a)) relate pairwise geographic distances between sites to compositional dissimilarity between communities (c). Exploring how geographic distance–decay relationships may change through time (d) as a function of non-random extinctions or biotic homogenization, and exploring how temporal distance–decay relationships may vary across geographic space (e), together serve to bridge geographic and temporal aspects of distance–decay relationships.

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previously used. First, we compared community composition in a given year to the previous year ($\tau = 1$, see Introduction) – using Jaccard dissimilarity as before. This means that in order to see a positive relationship (the community is becoming more dissimilar over time), it would require that the relative compositional change be greater in more recent years (i.e. there is an accelerating trend in compositional change). Second, we compared community composition for any given year to the first year of sampling. This means that temporal distance decay would be observed so long as the community is shifting away from the state it was at first sampling (for better or worse; Carroll et al. 2023). See the Supporting information for the results of these two approaches. In general we found no evidence for temporal distance–decay relationships as defined in this way.

As in the case of geographic distance–decay relationships, we used the slope coeficient from a linear model and the Mantel statistic to assess the rate and strength of compositional change of communities over time. We further explored spatial autocorrelation of temporal distance–decay correlation values using Moran's *I*, implemented in the 'ape' R package (Paradis and Schliep 2019).

Results

Geographic distance–decay relationships and their consistency

We found general support for geographic distance–decay relationships across all years studied. However, the number of sampled years and sites varied across taxa, with as few as six years of sampling for fish communities and as many as nine years of sampling for mammals and carabid beetles. Fewer sites tended to be sampled in earlier years (e.g. in 2013 only four sites were sampled for mammals, while this increased to 42 by 2017). Despite variation in the number and timing of sampled sites, geographic distance–decay relationships tended to be consistently positive across taxa and years (Fig. 2). Estimating relationships using the slope coeficient of a linear model – most aligned to the estimation of the rate of decay – we found that beetles, mammals, and macroinvertebrates had significantly positive slopes for all years examined (Fig. 2). However, birds and fish had nearly no significant geographic distance–decay relationships, with the exception of very weak negative geographic distance–decay relationships in 2018 and 2020 for sampled bird communities (Supporting information). The lack of significant relationships for bird and fish communities also translated into low variance explained (adjusted R^2), while these estimates overall tended to be higher than in previous studies (Fig. 3; Graco-Roza et al. 2022). Estimating relationships using Mantel tests – most aligned with the estimation of the strength of decay – we found nearly identical results to the use of the linear model coeficients. That is, beetles, mammmals, and macroinvertebrates had significant positive geographic distance–decay relationships for all years except 2013 (an earlier sampling year when the number of sampled sites was quite low), while fish and bird communities showed no evidence of geographic distance–decay relationships (Fig. 2).

Temporal distance–decay relationships

Temporal distance–decay relationships were assessed in a comparable way to geographic distance–decay relationships, treating the number of years in between sampling points at a given site as a measure of distance. We found these relationships to be generally positive, though often weak (Fig. 4).

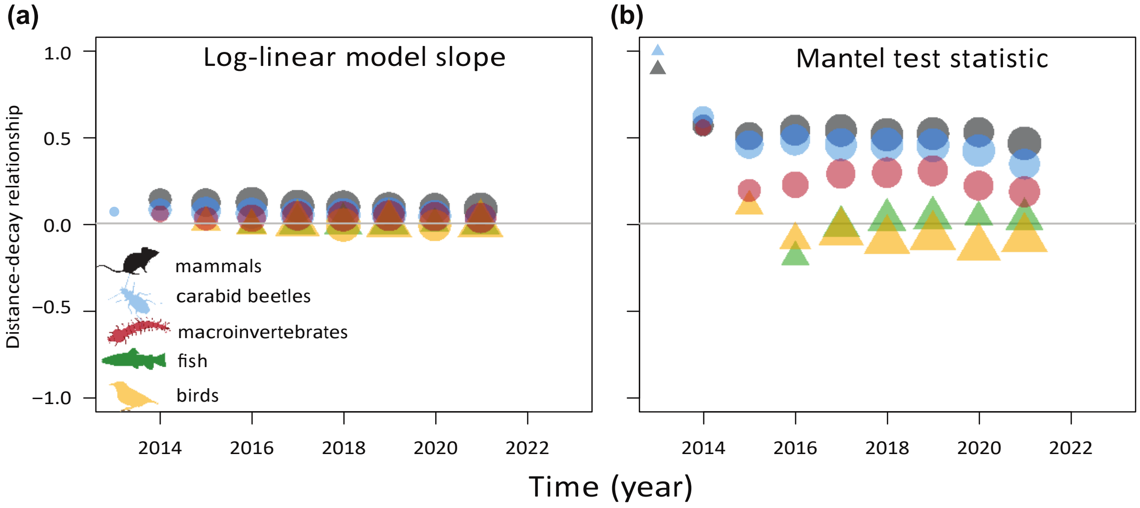

Figure 2. Geographic distance–decay relationships through time, estimated using the slope of a linear model (a) and the Mantel statistic (b) for five taxonomic groups. Points are colored by taxonomic group, shape indicates significance (circles were significant based on $\alpha = 0.05$), and point size is proportional to the number of sampled sites per year. During the early years of the National Ecological Observatory Network (NEON) (e.g. 2013), we can see an influence of the number of sites sampled on the resulting geographic distance–decay relation-ship strength for small mammals and carabid beetles.

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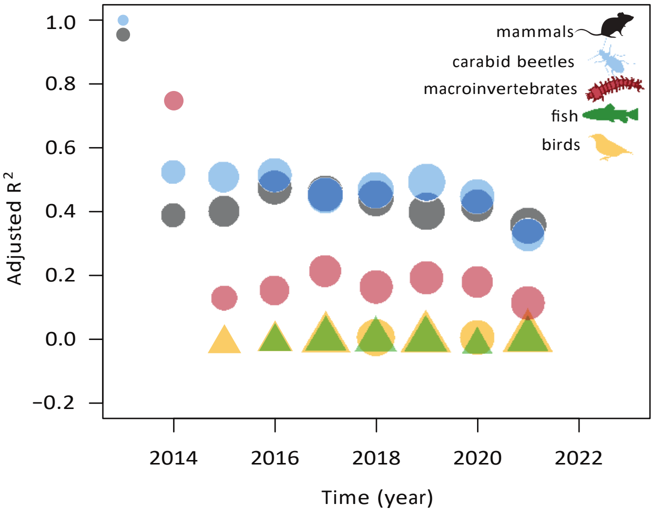

Figure 3. The adjusted R^2 from linear models fit to geographic distance by compositional dissimilarity highlight the role of the number of sites sampled on resulting linear fits, where point color indicates taxonomic group, point shape indicates significance (circles were significant based on $\alpha = 0.05$), and point size is proportional to the number of sampled sites per taxonomic group. Differences in numbers of species per taxa do not account for the taxonomic variation observed, as macroinvertebrates were much more species-rich than small mammals or beetles.

Nevertheless, we observed significant temporal distance–decay relationships for carabid beetles (17 out of 45 sites), small mammals (12 out of 43 sites), birds (9 out of 46 sites), macroinvertebrates (21 out of 33 sites), and fish (6 out of 16 sites). Further, the amount of variance explained (R^2 from linear model fits) was similar between geographic and temporal distance–decay relationships, if not slightly greater for temporal distance–decay relationships. We found no evidence for a spatial signal in temporal distance–decay relationships (Table 1), except for small mammals, which showed the opposite of a spatial signal (temporal distance–decay relationships were less spatially autocorrelated than expected under the null model). When we estimated temporal distance–decay relationships comparing communities to the sampling event before ($\tau = 1$) or to the first period of sampling, we saw very little evidence for temporal distance–decay relationships (Supporting information).

Discussion

Communities may become more compositionally dissimilar across geographic space or through time. For geographic distance–decay relationships, this assumes more geographically close sites also have the capability of dispersal and/or more similar environmental conditions compared to more geographically distant sites. For temporal distance–decay relationships, this assumes that shifting environments, community drift, or competitive dynamics lead to compositional changes over time. We found evidence for both geographic and temporal distance–decay relationships for our five taxonomic groups. However, we found almost no evidence for a temporal signal in geographic distance–decay relationships or a spatial signal in temporal distance–decay relationships. Together, this highlights that communities turnover as a function of both geographic distance and time, but that these two forces may not inherently be linked, suggesting the role of different forces that may be leading to the observed patterns. For example, dispersal and environmental conditions will constrain geographic distance–decay relationships, while stochasticity in community processes such as drift, and differential land use at a site, may influence temporal distance–decay relationships. Understanding how these forces interact, and how large-scale land use change and disturbance regimes may combine to entangle these relationships, is an intriguing open question.

Geographic and temporal distance–decay relationships have traditionally been explored independently. However, there have been some attempts to link the patterns. For instance, Collins et al. (2018) explored the relationship between temporal heterogeneity and spatial heterogeneity – corresponding to the mean dissimilarity across all sites within a year and the temporal dissimilarity between averaged sites (time lag of 1, Supporting information) – finding a weak positive scaling between these two measures of community dissimilarity. Other researchers have found latitudinal patterns in temporal distance–decay relationships (Korhonen et al. 2010) in aquatic systems, again considering temporal turnover with a time lag of 1 (e.g. each sampling is compared to the previous sampling period). In our exploration of the NEON data, we did not find a similar connection between geographic and spatial processes, highlighting the importance of spatial scale (Collins et al. 2018) and taxonomic group (Korhonen et al. 2010). To date, the focus of much research has been on linking patterns of temporal community turnover to aspects of the environment, which is an important next step for considering the different drivers of geographic and temporal distance–decay relationships. That is, we might expect temporal distance–decay relationships in a site to be driven by compositional drift, successional patterns, or changing environments in a given site. Meanwhile, geographic distance–decay patterns may be more linked to aspects of the regional pool (e.g. these may fundamentally differ across large spatial extents), community drift and environmental filtering (Graco-Roza et al. 2022).

While taxonomic groups did not differ in the detectability of temporal distance–decay relationships, there were differences among groups for geographic distance–decay relationships, with small mammals and beetles consistently having stronger geographic distance–decay relationships relative to fish and birds, with macroinvertebrates in the middle. These relationships stayed consistent over time, and were not simply a function of species richness, as the most species-rich groups – macroinvertebrates (n = 1372), beetles (n = 768), and birds (n = 576) – were quite different in the detectability of geographic distance–decay relationships, while small mammals showed the strongest support and had lower species richness (n = 149). One potential driver of geographic

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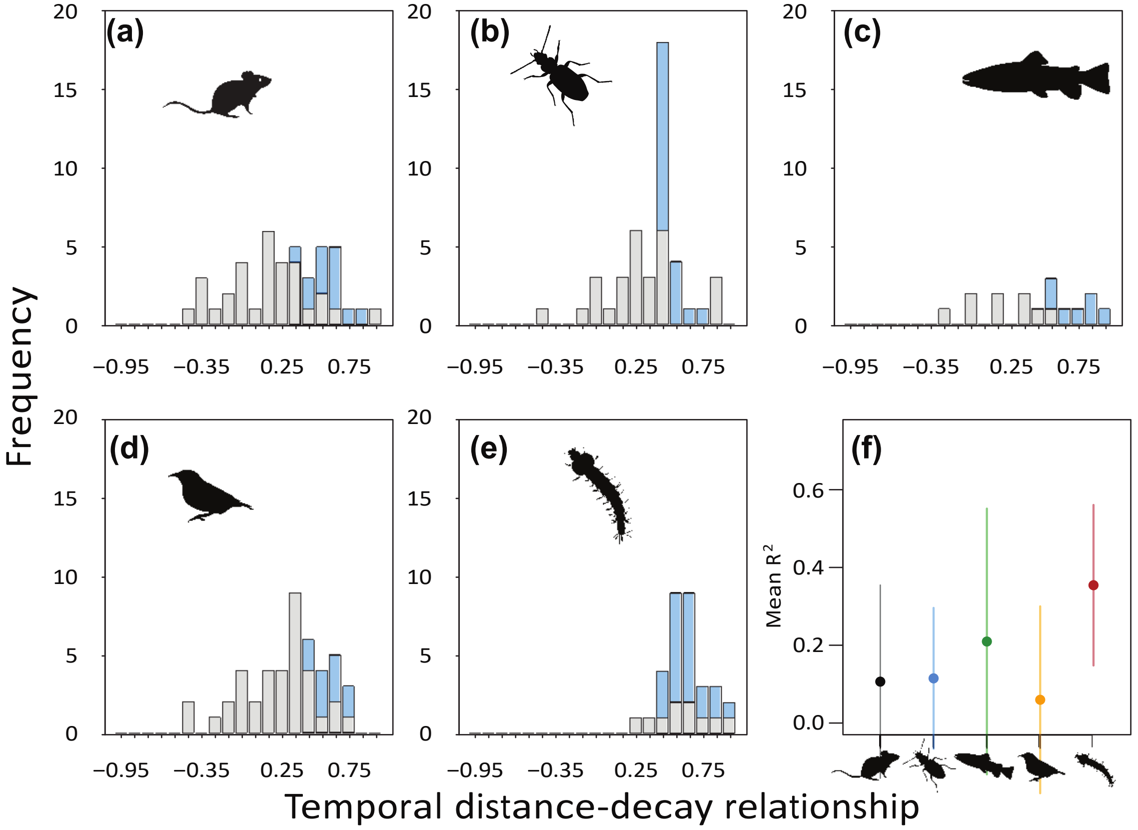

Figure 4. Temporal distance–decay relationships – quantified using the Mantel test statistic for our five taxonomic groups – were nearly always non-significant (grey), though some sites did show significant positive (blue) temporal distance–decay relationships (y-axis represents the frequency of National Ecological Observatory Network (NEON) sites for a given taxa in each temporal distance–decay relationship bin on the x-axis). Panels correspond to each taxonomic group: small mammals (a), carabid beetles (b), fish (c), birds (d), and macroinverte-brates (e). Variance explained from linear model fits (mean $R^2 + -$ SD) were comparable with geographic distance–decay relationships (f).

distance–decay relationships would be dispersal limitation leading to distinct communities through geographic space (Tornero et al. 2018, Graco-Roza et al. 2022). This would mean that more vagile taxa would tend to show lower support for geographic distance–decay relationships (completely ignoring the role of differences in species niches and the role of environmental filtering). This is potentially an explanation for bird communities not showing strong geographic distance–decay relationships, though this is quite tenuous and requires further testing.

Table 1. There was no evidence of spatial autocorrelation in estimates of temporal distance–decay relationships for any taxonomic group apart from small mammals, shown here by calculating Moran's *I* for each taxonomic group, considering geographic distance as Haversine distance between sites. However, the spatial signal observed for small mammals suggests that a null model would produce greater spatial autocorrelation than is actually observed. Significant p-values ($\alpha = 0.05$) are highlighted in bold.

Taxonomic group	Observed	Expected	SD	p value
Beetles	−0.02	−0.02	0.01	0.68
Small mammals	−0.08	−0.02	0.01	< **0.001**
Birds	−0.03	−0.02	0.01	0.83
Macroinvertebrates	−0.04	−0.03	0.02	0.45
Fish	−0.05	−0.03	0.03	0.56

Finally, there could be a role for disturbance on both geographic and temporal distance–decay relationships. This could be especially true when using a community dissimilarity index that considers species relative abundances. By disturbing a set of sites to the point where local extinction of some species occurs (e.g. through natural enemies, Smith et al. 2009), the geographic distance decay relationship would be affected (likely causing a decreased slope for one year in Fig. 2). Likewise, even an isolated disturbance at a single site would markedly change temporal distance–decay relationships, again likely reducing the slope. The consistency of a geographic distance–decay relationship slopes through time for all taxa, signaling that disturbance may not be a strong driver, but this is certainly an area worth further exploration. This is yet another strength of the NEON data, as site management and major disturbance events are recorded and publicly released (data product DP1.10111.001; National Ecological Observatory Network (NEON) 2023).

Distance–decay relationships are based on the common observation that community composition changes over geographic space and through time (Soininen et al.

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2007, Graco-Roza et al. 2022). We demonstrate – as others have (Graco-Roza et al. 2022) – the generality of geographic distance–decay relationships. However, considering geographic and temporal scales independently hinders our overall understanding of distance–decay relationships generally, as we might expect geographic distance–decay relationships to weaken in the face of dispersal barrier reduction or invasion of widespread species. On the other hand, local species extirpations driven by land use change or other factors might lead to stronger geographic distance–decay relationships, depending on the spatial structure of the change. This suggests that linking geographic and temporal scales is important. We found geographic distance–decay relationships to be quite stable over time, suggesting a generality of geographic distance–decay relationships within our time window of 2013–2021. The degree to which this stability holds across different datasets and across longer time periods is an open question. Finally, temporal distance–decay relationships were similarly detectable as geographic distance–decay relationships and contained no spatial signal, suggesting that communities do become more dissimilar as a function of time, but that this change does not have an inherent spatial structure given the data. It is important to note – as we move forward to reconcile geographic and temporal scales of community compositional shifts – the relationships between geographic and temporal scales, and the relative effects of geographic space and time to changes in community composition.

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Author contributions

Tad A. Dallas: Conceptualization (equal); Formal analysis (equal); Investigation (equal); Project administration (equal); Resources (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Lauren Holian**: Conceptualization (equal); Investigation (equal); Writing – review and editing (equal). **Cleber Ten Caten**: Conceptualization (equal); Investigation (equal); Writing – review and editing (equal).

Data availability statement

R code is available on figshare at https://doi.org/10.6084/m9.figshare.22666234. NEON data were accessed through the 'neonDivData' R package (Li et al. 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

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