





Temporal heterogeneity increases with spatial heterogeneity in ecological communities

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Abstract. Heterogeneity is increasingly recognized as a foundational characteristic of ecological systems. Under global change, understanding temporal community heterogeneity is necessary for predicting the stability of ecosystem functions and services. Indeed, spatial heterogeneity is commonly used in alternative stable state theory as a predictor of temporal heterogeneity and therefore an early indicator of regime shifts. To evaluate whether spatial heterogeneity in species composition is predictive of temporal heterogeneity in ecological communities, we analyzed 68 community data sets spanning freshwater and terrestrial systems where measures of species abundance were replicated over space and time. Of the 68 data sets, 55 (81%) had a weak to strongly positive relationship between spatial and temporal heterogeneity, while in the remaining communities the relationship was weak to strongly negative (19%). Based on a mixed model analysis, we found a significant but weak overall positive relationship between spatial and temporal heterogeneity across all data sets combined, and within aquatic and terrestrial data sets separately. In addition, lifespan and successional stage were negatively and positively related to temporal heterogeneity, respectively. We conclude that spatial heterogeneity may be a predictor of temporal heterogeneity in ecological communities, and that this relationship may be a general property of many terrestrial and aquatic communities.

Key words: *CommDyn Database; community dynamics; freshwater ecosystems; heterogeneity; lifespan; species abundance; terrestrial ecosystems.*

INTRODUCTION

Heterogeneity in space and time has long been recognized as an important feature of ecological systems (Levin 1992). Yet, ecologists now recognize the importance of understanding both the causes and consequences of heterogeneity in ecological communities (Kolasa and Pickett 1991, Carpenter et al. 2015). By heterogeneity, we refer specifically to variability in an ecological factor in space and/or time (McIntosh 1991). Global environmental change (e.g., nitrogen deposition, climate extremes) is a well-known driver of spatial and temporal heterogeneity in ecosystems (Smith et al. 2009, Hsu et al. 2012, Gossner et al. 2016). Thus, understanding the relationship between spatial and temporal heterogeneity would enhance our ability to predict how environmental drivers will alter the rate of change in ecological communities (Avolio et al. 2015). Although variability naturally decreases with scale (Levin 1992), theory predicts that regional stability can be understood by variability at local scales, and that diversity of

communities (heterogeneity) decreases ecosystem variability (Wang and Loreau 2014, 2016). Indeed, several case studies support these predictions (Hector et al. 2010, Koerner et al. 2016, Wilcox et al. 2017). Until recently, however, a lack of available ecological data has limited our ability to determine if a general relationship exists across scales between spatial heterogeneity and the degree to which communities change over time (temporal heterogeneity; Rose et al. 2017).

Recent observational studies suggest that increasing spatial and temporal heterogeneity tends to precede state change in ecosystems and has been proposed as an early indicator of regime shifts in alternative stable state theory (Pace et al. 2013, Ratajczak et al. 2017a). As an ecosystem approaches a tipping point, spatial heterogeneity tends to increase, creating a positive relationship between spatial heterogeneity at any point in time and temporal heterogeneity from one point in time to the next (Guttal and Jayaprakash 2008, Scheffer et al. 2009, 2012). For example, in small north-temperate lakes, increased spatial heterogeneity in phytoplankton abundance served as an early warning signal of a regime shift during an experimental reorganization of the food web (Carpenter et al. 2011, Cline et al. 2014). However, the relationship between

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spatial and temporal heterogeneity may not be restricted to regime shifts exclusively, but rather a general property of all ecosystems. This would imply that a positive relationship exists, in general, between spatial heterogeneity and how much a community changes from one time period to the next.

Indeed, an underlying principle of biodiversity and ecosystem function theory is that a positive relationship also occurs between spatial heterogeneity in community composition and ecosystem stability (Ives and Carpenter 2007, Isbell et al. 2009, Hector et al. 2010, de Mazancourt et al. 2013). For example, the portfolio effect predicts that high spatial community variability increases the stability (i.e., decreases variability) of net primary production (Figue 2004, Hector et al. 2010, Hallett et al. 2014, Hautier et al. 2014). That is, increased heterogeneity in species composition in space (greater community variability) leads to heterogeneity in species abundances through time in response to environmental variability, ultimately resulting in stability in ecosystem functioning (Wilcox et al. 2017). Temporal community variability may therefore engender stable ecosystem function even in the face of a temporally variable environment. Thus, high spatial and temporal community heterogeneity has implications for the provisioning of ecosystem services, like rangeland (McGranahan et al. 2016) and fisheries production (Schindler et al. 2010), crop pollination by wild native bees (Winfree and Kremen 2009), and other services (Duffy 2009, Balvanera et al. 2013).

Here we empirically evaluated whether spatial heterogeneity within a community predicted temporal heterogeneity of that community from one time step to the next. We combined both aquatic and terrestrial data sets because the portfolio effect is frequently applied to terrestrial systems whereas much of alternative stable state theory has been developed in aquatic systems (e.g., Carpenter et al. 2011). Based on the portfolio effect and alternative stable state theory, we predicted that spatial heterogeneity would be positively related to temporal heterogeneity within and across sites. We tested this hypothesis by conducting a synthesis of 68 data sets spanning aquatic and terrestrial systems that included replicate measures of species abundance over space and time. We also assessed the influence of community level characteristics, such as lifespan, species richness or trophic level that may mediate the relationship between spatial and temporal heterogeneity.

METHODS

Database description

The CommDyn Database (Collins et al. 2017, Data S1) contains 68 long-term community composition data sets from both primary producer and consumer communities. Data were gathered from publicly available portals as well as through author contacts where data were not publicly available. In order to be included in the database, a data set had to meet the following requirements: (1) species-level abundance data, (2) freshwater or terrestrial location, (3) a minimum of three replicate samples per sample period, (4) at least six sampling points through time, and (5) willingness of the data owners to allow us to publish the data. For most data sets, this meant annual sampling for six years or more. However, some data sets were gathered on

sub-annual scales while others were gathered once every few years. See Data S1 for a description of data sets including experimental and biotic predictors. Experimental predictors included $\ln(\text{plot size})$, number of plots (replicates), $\ln(\text{spatial extent in which the replicate samples occurred})$, length of the temporal data set, and time between sampling intervals. Biotic predictors included system type (aquatic/terrestrial), mean annual precipitation (MAP) and mean annual temperature (MAT) of the study location, successional system (yes/no), trophic level of the target community (primary/consumer), and lifespan of target community (sub-annual, annual/biennial, long-lived). MAP and MAT were calculated as the average over the 30-yr period from 1981 to 2010. Because precipitation and temperature were not measured at all sites, we acquired these variables from the PRISM Climate Group for all sites at a 1 km pixel size (Corvallis, OR; 2012), which accommodates the range of spatial scales among our data sets. Taxa of the target community (phytoplankton, plants, zooplankton, invertebrates, fish) as well as latitude, longitude, and a citation for each data set are also included in Data S1.

Relationship between spatial and temporal heterogeneity

Both spatial and temporal heterogeneity for a site were calculated using the Bray-Curtis index of dissimilarity. We used this index because it is the metric best suited for non-normal, multivariate data and is less sensitive to changes in rare species than other commonly used distance measures (Anderson and Walsh 2013). For spatial heterogeneity, we calculated pairwise combinations of Bray-Curtis dissimilarity for all plots within each year, and the mean value of all the pairwise comparisons was the measure of spatial heterogeneity for that year. For temporal heterogeneity, we first took the mean abundance of each species across all replicate plots in a year and then calculated Bray-Curtis dissimilarity between Time_x and Time_{x+1} .

To explore the drivers of temporal heterogeneity, we ran three mixed models using `lmer()` in the `lme4` library (Bates et al. 2015) in R v3.3.3 (R Core Team 2017). We assessed three linear mixed effects models to understand how spatial heterogeneity affects temporal heterogeneity. Random factors in all models represented the hierarchical structure of community type nested within a study nested within a long-term research site. An initial comparison of alternative models with different random factors was used to determine the most appropriate random factor design for this study (Zuur et al. 2009). Random factors in the final models included slopes and intercepts. Model 1 examined how spatial heterogeneity is correlated with temporal heterogeneity and was compared to a null model that included only random effects using AIC (Appendix S1: Table S1). Model 2 also included the experimental predictors as fixed effects (Table 1), while Model 3 included the biotic predictors (Table 2) as fixed effects.

Effect of lifespan and sampling time step on the space–time relationship

Sampling intervals could have a strong impact on the relationship between spatial and temporal heterogeneity. To test whether relationships between spatial and temporal

TABLE 1. Mixed model results for Model 2 examining the effects of spatial heterogeneity and experimental variables on temporal heterogeneity.

Parameter	Estimate	SE	<i>t</i>
Intercept	0.17	0.08	2.00
Spatial heterogeneity	0.22	0.08	2.88
Plot size	0.01	0.01	-1.20
Number of plots	0.00	0.00	0.56
Spatial extent	0.01	0.00	2.09
Data set length	0.00	0.00	-1.52
Time step	-0.04	0.04	-1.03

Notes: Model 2 had a hierarchical structure, which included community nested within experiment nested within site as a random effect, and had random slopes and intercepts, as well. Spatial extent and plot size were ln-transformed prior to analysis.

TABLE 2. Mixed model results for Model 3 examining the effects of spatial heterogeneity and biotic variables on temporal heterogeneity.

Parameter	Estimate	SE	<i>t</i>
Intercept	0.20	0.07	2.95
Spatial heterogeneity	0.16	0.08	2.08
Lifespan, long lived	-0.05	0.04	-1.09
Lifespan, sub-annual	0.23	0.06	3.50
Mean annual precipitation	0.00	0.00	-2.11
Mean annual temperature	0.01	0.00	1.92
Successional (yes)	0.12	0.06	2.17
Trophic level (primary)	0.01	0.04	0.31
System (terrestrial)	-0.60	0.06	-1.04

Note: Model 3 had a hierarchical structure, which included community nested within experiment nested within site as a random effect, and had random slopes and intercepts, as well.

heterogeneity shifted by time interval between sample periods we calculated temporal heterogeneity over successively longer time lags. For example, a data set with six time intervals resulted in values for five one-interval Bray-Curtis distances (Time_{*x*} and Time_{*x+1*}; Time_{*x+1*} and Time_{*x+2*}, etc.), four two-interval distances (Time_{*x*} and Time_{*x+2*}; Time_{*x+1*} and Time_{*x+3*}, etc.) and so forth (Collins et al. 2000, code adapted from Hallett et al. 2016). To include all data sets, we set the maximum lag to be six sampling periods (the minimum number of time points in our data set). We used linear mixed effects models to compare how the relationship between spatial heterogeneity in the initial year and temporal heterogeneity shifted over increasing lag times. Because lifespan was the primary explanatory variable in earlier models (see *Results*) and because we expected the effect of time scale to differ with life history, we conducted separate model runs based on the dominant lifespan at a site. Our focus was on how the slope of the relationship between spatial and temporal variability changed with increasing lag times; therefore we included spatial heterogeneity, time interval (as an ordered factor), and an interaction between spatial heterogeneity and time interval as fixed effects. Similar to above, random factors in the models represented the hierarchical structure of community type nested within a study nested within a long-term research site; to avoid over-fitting this model, random

factors only included random intercepts. All data and R scripts are in Collins et al. (2017).

RESULTS

The complete data set contained information on aquatic and terrestrial communities spanning a range of taxa, spatial extent, and time. We found that the model incorporating spatial heterogeneity better predicted temporal heterogeneity than a null model ($\Delta\text{AIC} = 2.9$, $\chi^2 = 4.9$, $P = 0.027$). Overall, spatial heterogeneity was positively related to temporal heterogeneity (Model 2; Fig. 1, Table 1). Thus, communities with higher spatial heterogeneity changed more through time on average compared to communities with lower spatial heterogeneity. Of the 68 communities, 55 (81%) had weak to strongly positive slopes between spatial and temporal heterogeneity while the remaining communities were weak to strongly negative (19%) (Fig. 1b, c). The only other experimental predictor that positively influenced temporal heterogeneity was ln(spatial extent) (Model 2; Fig. 2a, Table 1 and Appendix S1: Table S1).

In the biotic model (Model 3), spatial heterogeneity was again significant, however lifespan was the strongest predictor of temporal heterogeneity (Fig. 2b, Table 2). Temporal heterogeneity was lower for communities with longer-lived species and higher in communities with sub-annual or annual species (Fig. 3a–c). Additionally, succession was positively, and MAP was negatively predictive of temporal heterogeneity in the biotic model (Fig. 2b, Table 2 and Appendix S1: Table S1).

An additional factor that could influence temporal heterogeneity is the scale of the time step upon which the heterogeneity metric was calculated. Indeed, we found communities dominated by taxa with sub-annual life-cycles were sensitive to the time step of the calculation (Fig. 3d–f). For example, sub-annual plankton communities showed a positive relationship between spatial and temporal heterogeneity over short time intervals, and the slope of this relationship weakened with longer time steps (Fig. 3, statistics reported in Appendix S1: Table S1). For communities with longer lifespans than sub-annual plankton, the slope of the relationship between spatial and temporal heterogeneity did not appear to depend on the time interval between measurements (statistics reported in Appendix S1: Tables S2 and S3).

DISCUSSION

The role of variability in structuring ecological communities and processes has long been recognized (Kolasa and Pickett 1991, Levin 1992, Benedetti-Cecchi 2003, Rose et al. 2017). Consistent with our hypothesis, we found a significant positive relationship between spatial heterogeneity and temporal heterogeneity using a diverse suite of aquatic and terrestrial data sets. Importantly, these relationships were found across a range of species richness and therefore are not an artifact of statistical averaging (e.g., Doak et al. 1998). Furthermore, this pattern was consistent across trophic levels, scales, ecosystem types, and sampling methodologies. Therefore, we suggest that the positive relationship between spatial and temporal heterogeneity may be a general property of many ecological communities.

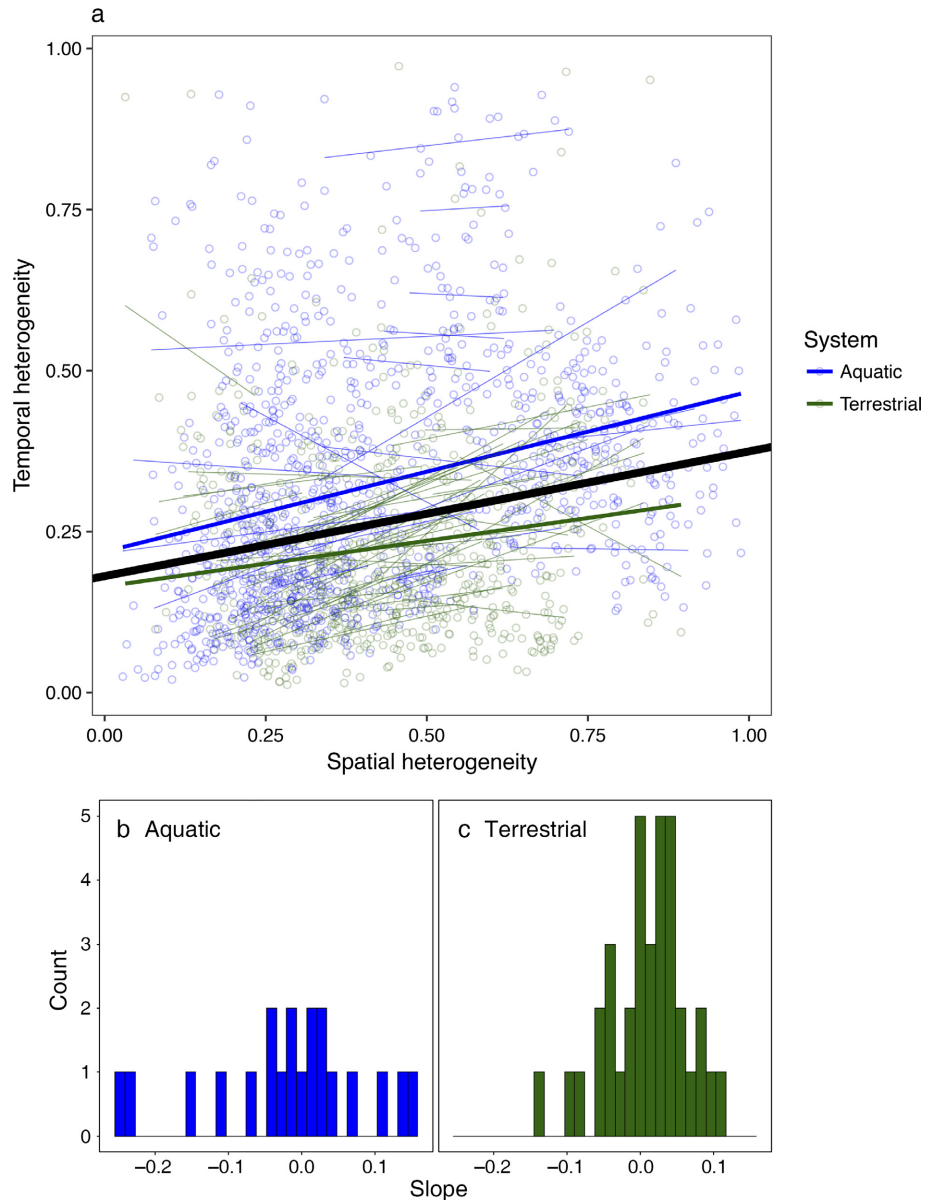


FIG. 1. (a) Relationship between spatial heterogeneity and temporal heterogeneity in aquatic (blue points, heavy blue line) and terrestrial (green points, heavy green line) systems. The solid black line represents the overall relationship (fixed effect) between spatial heterogeneity and temporal heterogeneity. Each thin line represents the relationship between temporal and spatial heterogeneity during the course of a study at a long-term site (random effect). Each data point represents temporal variation over one time interval as a function of spatial variation among plots at a single time point. See Methods for calculations of heterogeneity. Lines represent predictions of Model 2 (Table 1). (b, c) Histograms show distribution of slopes for aquatic and terrestrial sites.

The positive relationship we observed between spatial and temporal heterogeneity is implicit in both the portfolio effect (Tilman et al. 2014) and alternative stable state theories (Scheffer et al. 2009, 2012). However, this positive community-level relationship differs from the patterns observed for heterogeneity and stability of ecosystem processes. For example, the portfolio effect predicts that asynchronous species responses create temporal community heterogeneity and these responses are negatively related to variability in ecosystem function (i.e., negative species covariance increases functional stability; Hallett et al. 2014, Hautier et al. 2014). Indeed, McGranahan et al. (2016) showed that increased spatial variability in community composition in tallgrass

prairie reduced temporal variability in aboveground net primary production. Furthermore, variability in annual Bristol Bay salmon returns was less than half when composed of several hundred discrete, asynchronous populations rather than a single homogenous population (Schindler et al. 2010). Thus, asynchrony in community dynamics assists in stabilizing ecosystem function in many systems. In contrast to the negative relationship between spatial community heterogeneity and temporal variation in ecosystem function, we observed a positive relationship between spatial heterogeneity and temporal heterogeneity in community composition that appears to be generalizable across ecosystems and trophic levels. This relationship is consistent with alternative

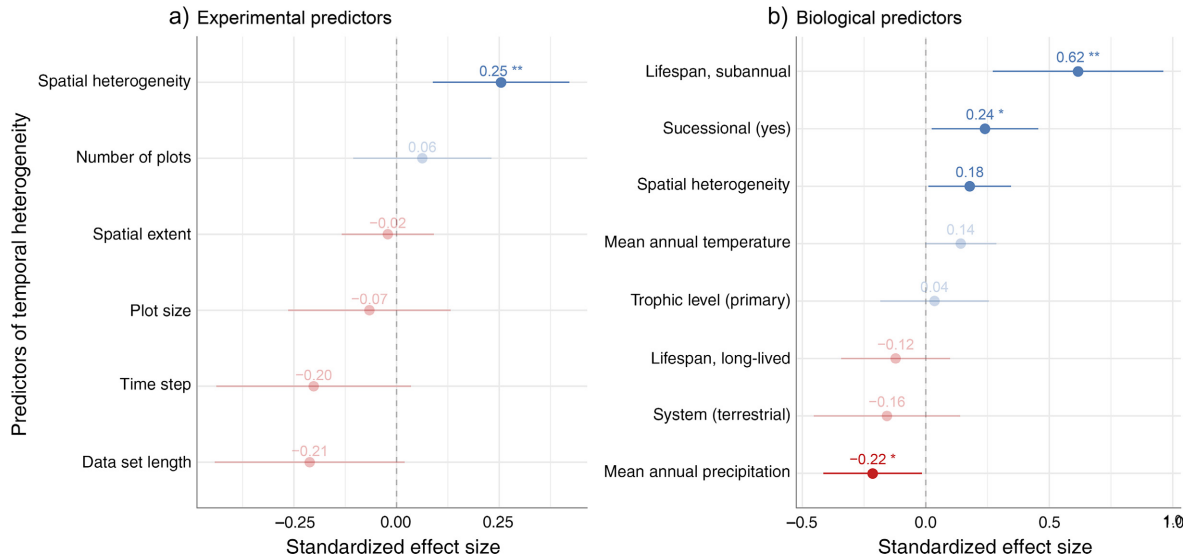


FIG. 2. Effects of spatial heterogeneity and (a) experimental or (b) biological predictors on temporal heterogeneity. Predictors with a positive effect on temporal heterogeneity are in blue, while negative are in red. Additionally, non-significant predictor color is muted compared to significant predictors. Asterisks indicate factors that differ significantly from zero (Tables 1, 2; * $P \leq 0.05$, ** $P \leq 0.01$).

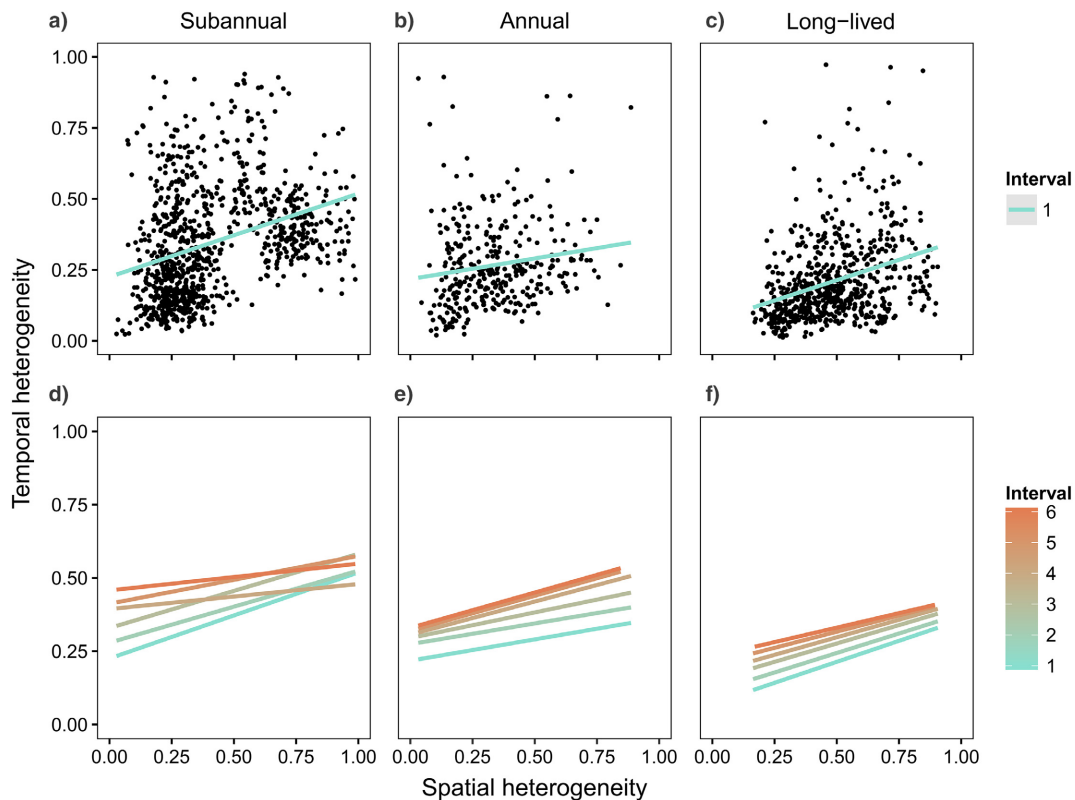


FIG. 3. (a–c) Relationship between spatial heterogeneity and temporal heterogeneity by lifespan and over time. Columns correspond to species' lifespans. Black points represent temporal variation at a long-term research site over one time interval as a function of spatial variation among plots within that site at a single time point; regression line is across sites. (d–f) Shifts in the relationship between spatial and temporal heterogeneity over successively longer time intervals. Interval 1 is calculated between Time_x to Time_{x+1} , interval 2 between Time_x to Time_{x+2} , etc. The positive relationship between spatial and temporal heterogeneity decays rapidly for short-lived species but persists for long-lived species. See Appendix S1: Tables S1–S3 for statistics.

stable state theory whereby increasing spatial heterogeneity can serve as an early warning indicator of impending state change (Ratajczak et al. 2017a).

In addition to spatial heterogeneity, species lifespan was also a significant predictor of temporal community heterogeneity, as others have observed (Haury et al. 1978, Levin

1992). Not surprisingly, ecological communities dominated by species with sub-annual lifespans have higher rates of temporal turnover than communities dominated by long-lived taxa (Winemiller and Rose 1992, García et al. 2008, Cleland et al. 2013). However, within these sub-annual communities we further found that temporal heterogeneity decreased with longer time steps (i.e., across years). This pattern was likely due to the more frequent sampling of these communities (e.g., monthly sampling), and may reflect seasonal phenology (April to September) rather than annual trends (April to April) in these systems (Gaedke 1992, Anneville et al. 2004). Additionally, we found a negative relationship between MAP and temporal heterogeneity, likely because terrestrial sites with higher MAP tend to support forested vegetation dominated by long-lived species and therefore have lower temporal heterogeneity. Furthermore, we found the time step upon which temporal heterogeneity is calculated affects the space–time relationship. This is the temporal equivalent of distance decay in ecological communities (Nekola and White 1999, Soininen et al. 2007). Therefore, lifespan and the time step at which samples are collected are critical aspects of temporal heterogeneity and need to be considered when assessing temporal change in ecological communities.

Successional stage was also a significant predictor of temporal community heterogeneity in our model. Succession can both increase and decrease temporal heterogeneity. Across successional stages, species are transient, resulting in high temporal heterogeneity (Tilman 1987, del Moral and Ellis 2004, Baer et al. 2016). This pattern was found in most successional communities in our data set resulting in a positive effect of succession on temporal heterogeneity. However, within a successional stage, a dominant species may increase in abundance through time (Inouye and Tilman 1988), reducing both spatial and temporal heterogeneity. In fact, four of the sixteen successional communities in our analysis exhibited a negative relationship between spatial and temporal heterogeneity. Therefore, when considering temporal heterogeneity, ecological context, such as successional state, can influence the direction of the relationship.

In addition to a few successional communities, seven aquatic communities and two desert grasshopper communities also exhibited a negative relationship between spatial and temporal heterogeneity. These negative relationships could arise due to high sampling efficiency relative to the species pool in these systems. If a high proportion of the species pool was captured every year, temporal heterogeneity would be low (e.g., low turnover in species composition), as might occur with the localized grasshopper data sets from the Sevilleta in our analysis. A similar explanation may also be applicable to aquatic ecosystems because aquatic community samples typically integrate over area and depth dimensions (e.g., as is common with integrated plankton samples in lakes). Yet by and large, negative relationships between spatial and temporal heterogeneity were uncommon in our analysis.

The unprecedented scale and rate of global environmental change is likely to alter both the spatial and temporal heterogeneity of ecological communities (Vitousek et al. 1997, Sala et al. 2000). Under increasing environmental change, such as higher temperature and atmospheric CO₂ concentration (Smith et al. 2009), metrics will be needed to assist in predicting

gradual or sudden state shifts in ecosystems (Fuhlendorf et al. 2006, Carpenter and Turner 2017); spatial heterogeneity may be one such tool to predict the likelihood and rate of community change over time. This resulting temporal heterogeneity may be desirable or undesirable depending on context. For example, it could indicate a state change to an undesirable state (Ratajczak et al. 2017b) or it could indicate increased stability of ecosystem processes (Brown 2003, Isbell et al. 2009, Hector et al. 2010, de Mazancourt et al. 2013). In either case, prediction of temporal heterogeneity is an important consideration for the management of ecosystem structure and function. We showed that spatial heterogeneity was a significant, albeit weak, general predictor of temporal heterogeneity across terrestrial and aquatic ecosystems that varied in spatial scale, lifespan and taxa. Therefore, we conclude that the relationship between spatial and temporal heterogeneity is not confined to diversity–stability relationships or alternative stable state theory, but instead may be a general property of many ecological communities.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecs.2154/supinfo>

DATA AVAILABILITY

Data associated with this study are available from the Environmental Data Initiative: <https://doi.org/10.6073/pasta/ef4dbad515813be74404a6a87af98f00>