



# Spatial versus temporal heterogeneity in abundance of fishes in north-temperate lakes

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With 2 figures and 2 tables

**Abstract:** Probing relationships between spatial and temporal heterogeneity is a central pursuit in limnology and ecology, but until recently, data availability has constrained empirical tests of these patterns. In this study, I quantified spatial and temporal heterogeneity in fish species abundances within a landscape of north-temperate lakes and resolved an empirical relationship between heterogeneity dimensions. Across 18 species, there was an asymptotic relationship between spatial and temporal heterogeneity; thus spatial heterogeneity predicted temporal heterogeneity, but only at low heterogeneity levels. Some species expressed low levels of temporal-to-spatial heterogeneity while others, remarkably, had temporal heterogeneity  $\geq 100\%$  spatial heterogeneity. Relationships between spatial and temporal heterogeneity are likely useful for conservation and management. For example, species with low temporal:spatial heterogeneity ratios might benefit from landscape-scale management efforts (e.g., watershed management, hydrologic connectance, public land acquisitions). In contrast, species with high temporal:spatial heterogeneity ratios might be more successfully managed locally (e.g., via biomanipulation, hydrologic management, habitat restoration).

**Keywords:** biocomplexity; freshwater fisheries; landscape context; limnology; long-term ecological research; LTER; populations; scales; trophic cascades; variance

## Introduction

Understanding the dynamics of heterogeneity in ecosystems is a classic pursuit in limnology and ecology (Fathizadeh et al. 2014; Seiferling et al. 2014; Rodríguez & Kouki 2016; Hoffmann et al. 2017). Heterogeneity (i.e., diversity or variability in an ecological factor in space or time) is a direct product of ecogeomorphologic and evolutionary drivers (Kolasa & Rollo 1999; Rose et al. 2017). Ecologists have long recognized that ecological processes and patterns correlate positively in space and time (Preston 1960; Stommel 1963; Haury et al. 1978; Delcourt et al. 1982). For example, increased spatial heterogeneity of primary production

precedes temporal regime shifts in small lakes (Buttitta et al. 2017). And across diverse ecosystems, there is a weak to strongly positive relationship between spatial and temporal measures of community heterogeneity (Collins et al. 2018). Consequently, the study of heterogeneity is embedded into key theories including biogeography (Nelson 1978), general systems theory (von Bertalanffy 1950, Levins 1966), alternate stable states (Scheffer & Carpenter 2003; Brook et al. 2013; Dakos et al. 2015), and community ecology (Ben-Hur & Kadmon 2020).

Aquatic ecosystems are notable for their space and time heterogeneity (Kratz et al. 2005; Whiterod et al. 2015; Fullerton et al. 2018). However, lakes in particu-

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lar have been the focus of much research on this topic (Benson & Magnuson 1992; Mehner et al. 2005); presumably because of the problem associated with defining boundaries of many other aquatic ecosystems (Post et al. 2007). Dating back to Forbes (Forbes 1925), lakes have functioned as useful tools for understanding complex ecological and limnological phenomenon that might be more broadly generalized (Browne 1981; Carpenter et al. 1985; Carpenter et al. 2011). Yet until recently, myriad theories speculating on heterogeneity dimensions could not be tested because of limited data availability (Rose et al. 2017). As availability of replicated ecological data over space and time has grown, many previously intractable frameworks are increasingly testable. This may be especially true of freshwater environments that are notably fragile (Ricciardi & Rasmussen 1999; Eilers et al. 2007) and have magnificent and underutilized long-term ecological data (Magnuson 1990; Jeppesen et al. 2005; Carey et al. 2015). Indeed, empirical evaluations of long-standing heterogeneity theories are also timely for ecologists more generally, such as exploring causes, consequences and cures to global environmental change (Carpenter et al. 1992; Vitousek et al. 1997; Walther et al. 2002; Grimm et al. 2008). Changes in spatial heterogeneity might serve as an early warning indicator for ecosystem fragility and regime shifts in time, but existing work has only loosely supported this potential (Kéfi et al. 2014; Butitta et al. 2017; Sundstrom et al. 2017; Collins et al. 2018). Furthermore, patterns in spatial versus temporal heterogeneity may have some basis in the causes and consequences of life-history patterns (Aiba & Kohyama 1997; Collins et al. 2018). In fishes, life-histories evolved along axes of longevity, fecundity, and juvenile survivorship (Winemiller & Rose 1992). Thus, there may be expectation of heterogeneity in fish abundance being driven to some extent by life-history variations across space and time.

Resolving the dimensionality of ecological heterogeneity dynamics might also aid in development of new conservation and management strategies (Loehle 1991; Holling & Meffe 1996; Crowder & Norse 2008). In general, low temporal heterogeneity measures are associated with increased 'stability' of assemblages or systems (Fischer et al. 2001; Zhao et al. 2020). Most conservation and management programs remain species-centric (Simberloff 1998; White et al. 2013; Bichet et al. 2016); thus examining patterns of spatial versus temporal heterogeneity in species abundances could be useful in aquatic ecosystems (Poff & Ward 1990; Boon 1992; Lodge et al. 2006; Arlinghaus et al. 2008). If temporal heterogeneity within single lakes is

low relative to spatial heterogeneity, landscape-scale factors may be more important in driving species dynamics (Collins & Glenn 1991; Jeffries 2008; Bertrand et al. 2016). In contrast, if temporal heterogeneity is high relative to spatial variance, local factors might be more critical (Brooks et al. 2008; Sibly et al. 2009). The relationship between temporal and spatial heterogeneity may also vary. Collins et al. (2018) demonstrated a broad linear trend between heterogeneity dimensions for ecological communities. There is little reason to expect that the same trend would hold in a similar analysis involving species abundance. Understanding dimensionality of species production patterns on a landscape can allow adoption of management approaches matched to these scales (Carpenter et al. 2017; Rypel et al. 2019).

The goals of this study were to 1) Quantify spatial and temporal heterogeneity and temporal:spatial heterogeneity ratios in fish abundances for north-temperate lakes; 2) Evaluate whether an empirical interspecific relationship exists between spatial and temporal abundance heterogeneity; 3) Test if species life-histories explain spatiotemporal patterns in heterogeneity.

## Methods

### Data

This analysis leveraged two datasets collected in conjunction with the North Temperate Lakes, Long-Term Ecological Research (NTL-LTER) program; <https://lter.limnology.wisc.edu/data>. Spatial heterogeneity values were estimated using data collected as part of the Biocomplexity at north-temperate lakes (BIOCOM) project. Temporal heterogeneity in fish population abundances were quantified using the NTL-LTER core datasets on fish abundances (Supplementary Datasets 1, 2). The general goal of the BIOCOM project was to survey a series of lakes in northern Wisconsin USA (Vilas County) to understand the extent to which landscape position and context influenced diversity and abundance metrics of aquatic organisms. In general the management status of the study lakes is complicated, with some lakes (e.g., Trout Lake) receiving significant management attention in the form of fish stocking. However, most of the study lakes remain either lightly managed or managed towards fisheries production as is typical for lakes in the region. Fish populations were surveyed across 55 glacial lakes in Vilas County, Wisconsin USA. Within each lake, littoral fishes were sampled at eight randomly selected sites using boom-mounted boat electrofishing at night.



All sampled fishes were counted and measured. Additional gears (e.g., minnow and crayfish traps) were also used in this study, but for consistency, all analyses in this paper use boat electrofishing; thus data are reflective of littoral (i.e., nearshore, or where water depths range from > 0 m and < 2 m depth) fish population dynamics.

For NTL-LTER, fish communities have been sampled annually and consistently since 1981 in seven northern Wisconsin (Vilas County) lakes (Allequash, Big Muskellunge, Crystal Lake, Sparkling Lake, Trout Lake, Trout Bog and Crystal Bog). In general, sampling is at the same sites/habitats within lakes over time. Thus temporal heterogeneity information was available for smaller spatial of lakes, but with excellent replication over time (36 y). Fish populations in NTL-LTER lakes are sampled annually various gears (e.g., fyke nets, gill nets, minnow traps, seines, electrofishing) and all captured fishes counted and measured. To simplify gear biases, and align NTL-LTER datasets with BIOCOM datasets, data here were limited to boat electrofishing. Boat electrofishing is not conducted in Trout Bog, Crystal Bog, or Crystal Lake; thus these lakes were dropped.

### Heterogeneity analyses

Heterogeneity in fish abundance was quantified as the coefficient of variation (CV) in catch-per-unit-effort (CPUE,  $n\ h^{-1}$ ) for each species. Thus CV was calculated as:

$$CV = \frac{SD}{\bar{X}}$$

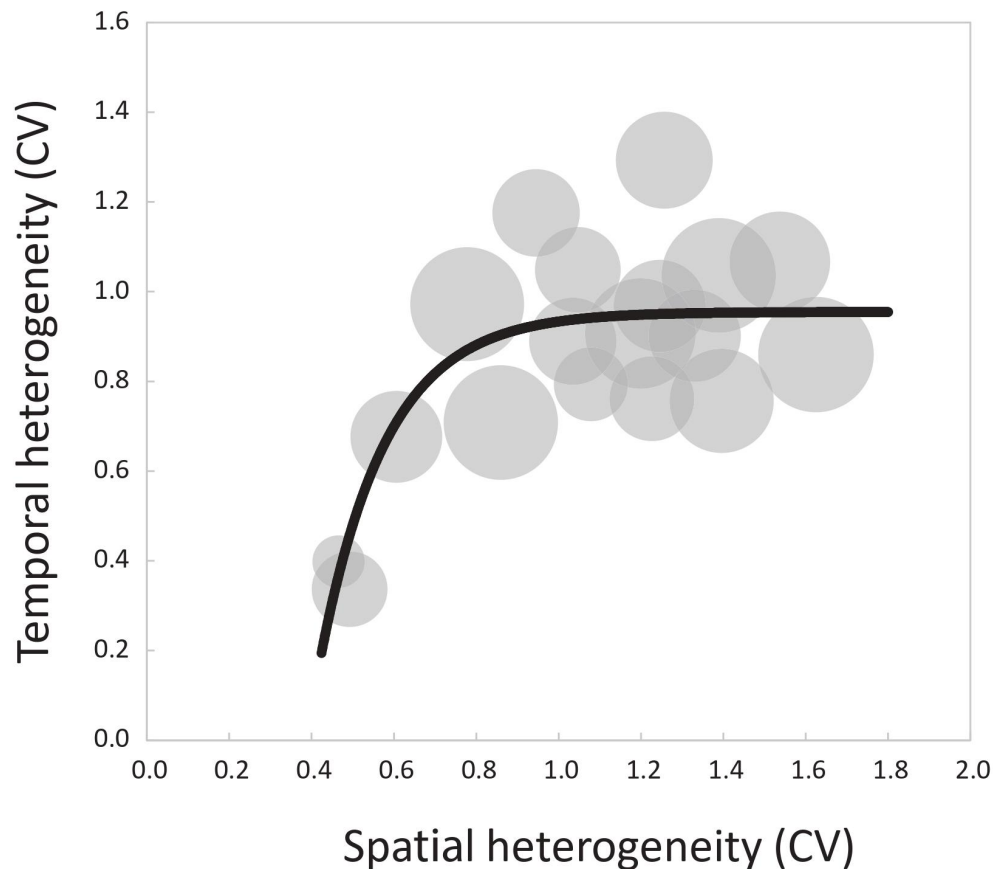
where CV is the coefficient of variation of the sample, SD is the sample standard deviation, and  $\bar{X}$  is the sample mean.

Spatial heterogeneity was estimated as CV in boat electrofishing CPUE for a species across 55 Vilas County WI BIOCOM lakes. Similarly, temporal heterogeneity in species CPUE was estimated as CV in boat electrofishing CPUE across all 36 y of boat electrofishing in each of four NTL-LTER lakes. Yet even with strong replication over space and time, data limitations for rare species remained. Thus, a power analysis was conducted for each species in each NTL-LTER lake, and each species over space in the BIOCOM dataset, to estimate minimum sample size to estimate heterogeneity. For each species dataset (spatial, or temporal in a lake), CPUE data were bootstrapped with replacement to create 100 new synthetic datasets on CPUE of each species. CV values were estimated from each of the 100 new synthetic datasets, whether

over space or through time within a lake. For each of the 100 series, total sample size at which the CV was maximized (i.e., a saturation point in CV vs number of samples) was estimated as the value at which CV approached 95% of observed maximum CV (Supplementary Fig. 1). Thus for each species series, 100 minimum sample size estimates were available, and final minimum sample size for each species series estimated as the mean minimum sample size +1 SD. Species with insufficient replication based on estimated minimum sample sizes were removed. All further spatial and temporal heterogeneity estimates and analyses are based on bootstrapped heterogeneity (CV) estimates to control for effect of N on CV (Huber 1975).

Weighted regression models were used to evaluate the empirical interspecific relationship between spatial and temporal heterogeneity. Four models were fit to the heterogeneity data: linear, power, logistic and asymptotic and the best fit model (asymptotic) selected using Akaike information criterion (AIC). Weighting was based on sample size of lakes constituting each species heterogeneity value.

Life-history data, reflecting critical drivers in evolution and management of these species (Winemiller & Rose 1992; Winemiller 2005), were collated (see Supplementary Dataset 3). A variety of life-history data were collated from the literature for the focal species studied. Data included mean size, mean maximum size, mean weight, mean maximum weight, maximum age, Von Bertalanffy average maximum size (i.e.,  $L_{\infty}$ ), Von Bertalanffy growth rate (i.e.,  $K$ ), minimum fecundity, maximum fecundity, median fecundity, and average trophic position. Collated life-history parameter data were as locally-relevant as possible. Data on species mean size, mean maximum size, mean weight, and mean maximum weight were calculated from the actual BIOCOM and NTL-LTER datasets described above. A “mean of means” approach was used to estimate mean lengths and mean maximum weights. Thus for each survey (lake-year combination), a mean size or max size (i.e., the largest fish captured) was calculated; then a mean was estimated across these survey specific max calculations. Von Bertalanffy growth parameters, and minimum, maximum and median fecundity values were based on data published in *Fishes of Wisconsin* (Becker 1983). Thus “Wisconsin-average” Von Bertalanffy growth curves were fitted for each species using a mean of all reported lengths-at-age in each species description. Maximum age estimates were interpreted as the highest reported age. Fecundity values were based on the range of fecundity values reported in each species description in Becker (1983).



**Fig. 1.** Relationship between spatial and temporal heterogeneity in abundance of fishes from north temperate lakes. Each bubble represents a single species, and size of the bubble scales to the number of lakes with temporal data (and thus confidence of temporal heterogeneity patterns). Dark blue line denotes a weighted non-linear (asymptotic) regression, and weighting was based on the number of lakes used in the mean temporal heterogeneity calculation.

Thus, the lowest fecundity was taken as “minimum fecundity”, the highest value taken as “maximum fecundity”, and the median between these two values estimated as “median fecundity”. Average trophic position by species was based on trophic position values reported in FishBase ([www.fishbase.org](http://www.fishbase.org)). A final summary of fish life-history data are available in Supplementary Dataset 3.

A principle components analysis (PCA) reduced these variables to a set of uncorrelated variables for further analysis. A scree plot was used to identify PCs explaining the bulk of variance in fish life-histories (PCs 1 and 2). Statistical relationships between heterogeneity measures and life-history characteristics were examined using three models (one GLM and two mixed effect models). In model one, spatial heterogeneity in fish abundances (quantified as described above) was examined as a linear function of PC1 and PC2. Model two was a mixed model and examined

temporal heterogeneity in fish abundances as a function of PC1 and PC2, and lake as a random effect. Finally, model 3 was another mixed model that examined temporal:spatial heterogeneity ratios as a function of PC1 and PC2, and again used lake as a random effect. Statistics were conducted in SAS statistical software (Version 9.4, SAS Institute Inc, Cary North Carolina, USA) and considered significant at  $\alpha < 0.05$ .

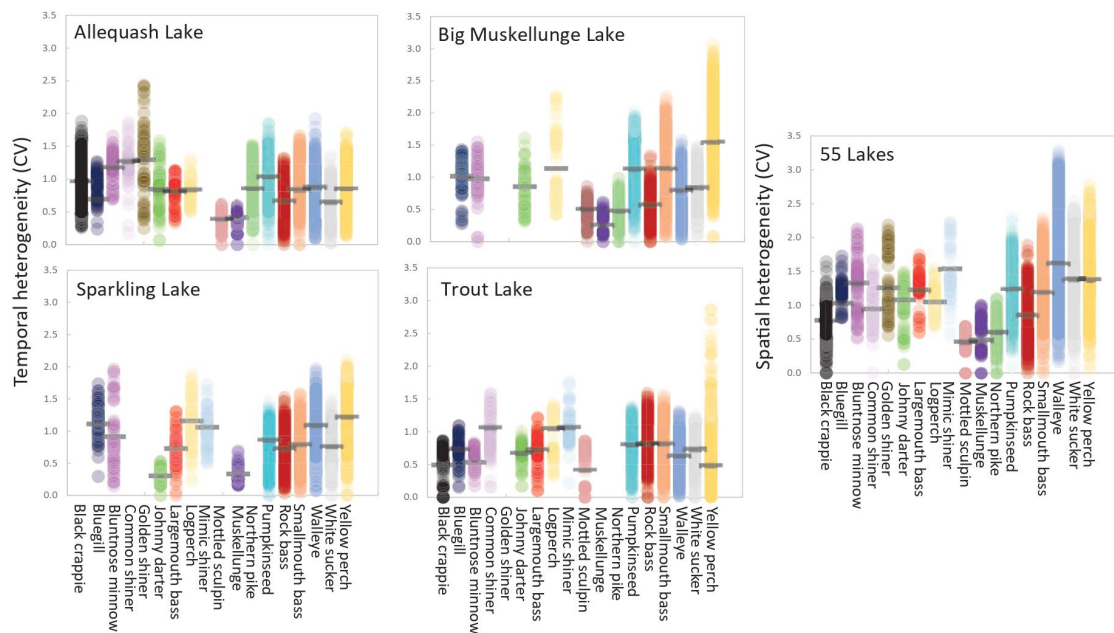
## Results

18 species had sufficient data replicated over space and time to test the overall relationship between spatial and temporal heterogeneity in abundance (Table 1). These species constituted a range of life-histories, but reflect the typical dominant components of fish communities in north-temperate lakes in Wisconsin USA. As predicted, some species were highly heterogeneous in



**Table 1.** Temporal, spatial, and temporal:spatial heterogeneity estimates for 18 freshwater fish species from north-temperate glacial lakes in Wisconsin, USA.

Species	Scientific name	Temporal heterogeneity (CV)	Spatial heterogeneity (CV)	Temporal: Spatial heterogeneity (%)
Black Crappie	<i>Pomoxis nigromaculatus</i>	0.97	0.78	125
Bluegill	<i>Lepomis macrochirus</i>	0.89	1.03	86
Bluntnose Minnow	<i>Pimephales notatus</i>	0.90	1.33	68
Common Shiner	<i>Luxilus cornutus</i>	1.18	0.95	124
Golden Shiner	<i>Notemigonus crysoleucas</i>	1.29	1.26	103
Johnny Darter	<i>Etheostoma nigrum</i>	0.79	1.08	74
Largemouth Bass	<i>Micropterus salmoides</i>	0.76	1.23	62
Logperch	<i>Percina caprodes</i>	1.05	1.05	100
Mimic Shiner	<i>Notropis volucellus</i>	1.07	1.54	69
Mottled Sculpin	<i>Cottus bairdii</i>	0.40	0.47	85
Muskellunge	<i>Esox masquinongy</i>	0.34	0.49	68
Northern Pike	<i>Esox lucius</i>	0.68	0.61	112
Pumpkinseed Sunfish	<i>Lepomis gibbosus</i>	0.97	1.25	78
Rock Bass	<i>Ambloplites rupestris</i>	0.71	0.86	82
Smallmouth Bass	<i>Micropterus dolomieu</i>	0.91	1.20	76
Walleye	<i>Sander vitreus</i>	0.86	1.62	53
White Sucker	<i>Catostomus commersonii</i>	0.76	1.40	54
Yellow Perch	<i>Perca flavescens</i>	1.04	1.39	75

**Fig. 2.** Bootstrapped temporal heterogeneity measures for 18 fish species in each of four lakes compared to bootstrapped spatial heterogeneity measures for the same species across 55 lakes regionally. Species like walleye were less heterogeneous in individual lakes over time relative to patterns observed spatially. Conversely, black crappie and yellow perch had high temporal heterogeneity in lakes relative to observed spatial heterogeneity.

time, while others were more heterogeneous in space. For example, several small-bodied fishes (common shiner *Luxilus cornutus*, golden shiner *Notemigonus crysoleucas*, mimic shiner *Notropis volucellus*, log-

perch *Percina caprodes*) showed high temporal heterogeneity in abundances whereas others (muskellunge *Esox masquinongy*, mottled sculpin *Cottus bairdii* and northern pike *Esox lucius*) had low temporal heteroge-

**Table 2.** Principal component (PC) loadings and % contributions extracted from PCA of life-history characteristics for 18 study species. Eigenvalues were 9.0 and 0.7 for PCs 1 and 2, respectively.

Life history variable	Factor loadings		% Contribution	
	PC1	PC2	PC1	PC2
Mean length (mm)	0.920	0.034	9.405	0.163
Maximum length (mm)	0.983	0.022	10.745	0.065
Mean mass (g)	0.978	0.033	10.638	0.153
Maximum mass (g)	0.976	0.006	10.591	0.005
Maximum age (y)	0.897	0.062	8.940	0.529
Asymptotic length (Linf)	0.940	-0.145	9.830	2.903
Growth rate (K)	-0.672	0.678	5.023	63.592
Min Fecundity (n eggs)	0.946	0.122	9.945	2.059
Max Fecundity (n eggs)	0.915	-0.016	9.312	0.036
Median Fecundity (n eggs)	0.929	0.000	9.595	0.000
Trophic Level	0.733	0.470	5.975	30.495

neity. Similarly, the most spatially heterogeneous species were walleye *Sander vitreus*, mimic shiner, and white sucker *Catostomus commersonii*, while the least spatially heterogeneous species were mottled sculpin, muskellunge and northern pike. Yet when temporal heterogeneity was linked with spatial heterogeneity, patterns changed in key ways. For example, walleye had the lowest temporal:spatial heterogeneity ratio, and similar patterns applied to white sucker, large-mouth bass *Micropterus salmoides*, and bluntnose minnow *Pimephales notatus*. In contrast, Black crappie *Pomoxis nigromaculatus*, common shiner, northern pike, golden shiner, and logperch showed temporal heterogeneity  $\geq$  spatial heterogeneity (Table 1).

Across species, there was a significant asymptotic relationship between temporal and spatial heterogeneity (Fig. 1, weighted non-linear regression, DF = 15,  $R^2 = 0.42$ , RMSE = 0.16,  $p = 0.001$ ). The equation of the fitted model was: Temporal heterogeneity (CV) =  $-10.6 * e^{(-6.2 * \text{Spatial heterogeneity})} + 0.95$ . Thus, spatial heterogeneity predicted temporal heterogeneity, but only at low levels of heterogeneity. Once spatial heterogeneity exceeded CV  $\approx 1$ , predictability of temporal heterogeneity based on spatial heterogeneity quickly eroded.

Temporal heterogeneity was variable across the four NTL-LTER lakes (Fig. 2). For example, temporal heterogeneity in yellow perch abundance was high in both Big Muskellunge and Trout Lake, in both cases, representing the most time heterogeneous species in either lake. However, in Allequash and Sparkling Lake, while yellow perch *Perca flavescens* temporal heterogeneity was high, there were other species that had near or higher levels of temporal heterogeneity (e.g., golden shiner in Allequash Lake, or walleye and

bluntnose minnow in Sparkling Lake). Across the 55 lake landscape, high spatial heterogeneity in walleye abundance was clear whereas spatial heterogeneity in bluegill *Lepomis macrochirus*, mottled sculpin, muskellunge or northern pike numbers was low.

Life-history characteristics were poor predictors of all heterogeneity measures. The PCA explained 82 % of the cumulative variation in life-history characteristics examined. PCs 1 and 2 had eigenvalues of 9.0 and 0.7, respectively: thus most variation was explained by PC1 (Table 2). Life-history characteristics were not a significant predictor of spatial heterogeneity in fish abundances in the study lakes (multiple regression, df = 15;  $F = 0.21$ ;  $p = 0.82$ ,  $R^2 = 0.03$ ). Life-history characteristics were also not a significant predictor of temporal heterogeneity in species abundances across lakes (Mixed effect model, -2 Res Log(Likelihood) = 52.2,  $p > \text{Chi}^2 = 0.70$ ) or within individual lakes (Mixed effect model, lake effect  $p = 0.65$  (Trout Lake), = 0.73 (Allequash Lake), = 0.92 (Big Muskellunge Lake), = 0.58 (Sparkling Lake). Finally, life-history characteristics were not a significant predictor of temporal:spatial heterogeneity ratios across lakes (Mixed effect model, -2 Res Log(Likelihood) = 10.1,  $p > \text{Chi}^2 = 0.76$ ) or again within individual lakes (Mixed effect model, lake effect  $p = 0.51$  (Trout Lake), = 0.51 (Allequash Lake), = 0.63 (Big Muskellunge Lake), = 0.89 (Sparkling Lake).

## Discussion

Heterogeneity in species abundance is one of the more prominent features of ecosystems (Preston 1960; Collins et al. 2018). Lakes express high degrees of het-



erogeneity (Hall & Burns 2002; Brämick et al. 2008; Soininen & Weckstrom 2009), though perhaps not to the same degree as rivers and streams (Power 1992; Zeug & Winemiller 2008). Here, some fish species showed high heterogeneity in space relative to time, while other species had high temporal heterogeneity. Walleye, white sucker and largemouth bass had 1.5–2X spatial heterogeneity in abundances relative to temporal heterogeneity. In contrast, five species (black crappie, common shiner, golden shiner, logperch, and northern pike) exhibited  $\geq 100\%$  temporal heterogeneity within ecosystems relative to spatial heterogeneity. This degree of temporal heterogeneity is remarkable, but speaks to the value of long-term datasets in capturing empirical heterogeneity dynamics through time (Magnuson et al. 1990; Schlesinger et al. 1990; Kratz et al. 2003; Collins & Smith 2006; Czeglédi & Erős 2013).

Patterns in temporal versus spatial abundance heterogeneity might be useful in freshwater conservation and management. Many conservation and management agencies remain intensely species-centric (White et al. 2013; Bichet et al. 2016); thus new information on the heterogeneity in species dynamics is useful. More specifically, management may be more successful if it aimed at the scale upon which key ecological dynamics occur, i.e., local versus regional scales (Glenn et al. 1992; Angermeier & Winston 1998; Liu et al. 2007). As one example, walleye in this study was the most heterogeneous species in space relative to time. This pattern supports the finding that production rates of walleye vary by over an order of magnitude across Wisconsin lakes (Rypel & David 2017; Rypel et al. 2018; Embke et al. 2019). Population dynamics of species like walleye and largemouth bass (another species more variable in space versus time) are driven by recruitment potential which can be strongly temperature dependent (Hansen et al. 2017). Managing populations and ecosystems where dynamics are so strongly influenced by temperature, and where temperatures are changing (e.g., due to climate change; De Stasio et al. 1996; Magnuson et al. 2000; Winslow et al. 2015; Till et al. 2019) is challenging because lake temperatures are largely unmanageable at local scales. Therefore, management must focus on more readily manipulatable factors, like harvest and habitat (Carpenter et al. 2017; Rypel & Magnuson 2019). Whereas walleye heterogeneity in abundances is greater in space versus time, it is possible that landscape-level conservation measures represent the best management practice for walleye. Some examples might include landscape-scale adaptive fisheries manage-

ment (Beard et al. 2003), watershed management of nutrients that influence oxythermal conditions (Evans et al. 1996; Schindler & Scheuerell 2002), or restoration of hydrologic connectance and dispersal potential for fragmented populations (Rypel & Layman 2008; Moody et al. 2017).

In contrast, species with high temporal heterogeneity might be best managed locally. Black crappie appear to exemplify this pattern. Within-population recruitment and abundance of this species is notoriously variable (Mitzner 1984; Maceina & Stimpert 1998; Isermann et al. 2002). Species exhibiting extreme temporal relative to spatial heterogeneity are likely good candidates for local or ecosystem-scale manipulation. For example, recruitment of black crappie in reservoirs is strongly influenced by reservoir hydrology (Maceina & Stimpert 1998; Sammons et al. 2002), macrophyte communities (Weaver et al. 1997), other in-lake habitats (Bassett 1994), and biomanipulation (Shapiro 1990; VanMiddlesworth et al. 2017). Indeed, some research has outright stated black crappie are best managed locally (Guy & Willis 1995).

The asymptotic relationship between spatial and temporal heterogeneity was an unexpected but intriguing pattern. Asymptotic relationships between spatial and temporal heterogeneity in abundance may arise from a combination of factors:

1) *Species life-history*. Life-history characteristics can be a driver of temporal and spatial heterogeneity in abundance (Hamrick et al. 1979; Pimm 1991; Townsend & Hildrew 1994; Polis et al. 1996). Yet in this case, available life-history data were poor predictors of all three heterogeneity measures (spatial, temporal and time:space heterogeneity ratios). Life-history characteristics might become more predictive of heterogeneity if a larger suite of species or spatial scales were examined. Of the three heterogeneity measures, temporal heterogeneity should logically be most linked to species life histories, as temporal heterogeneity is often inversely related to species life span (Pimm 1991). It is possible that this study, while 35 years in length, was still not long enough to actuate this pattern for longer-lived fishes. Research frameworks that replicate ecological data over space and time (e.g., LTER, eLTER, NEON and others) will be increasingly critical for detecting these patterns.

2) *Niche breadth*. Hutchinson classically conceptualized the species niche as an “n-dimensional hypervolume” such that environment, evolutionary history, density-dependence and other factors affected species persistence (Hutchinson 1957; Holt 2009; Senthilnathan & Gavrillets 2021). Species with large niche

widths are more likely to be widely distributed (Slatyer et al. 2013) and thus more likely to have high spatial heterogeneity in abundance. In this study, widely distributed species (e.g., walleye, largemouth bass, and pumpkinseed sunfish) indeed had increased spatial heterogeneity. In contrast, species with smaller niches might have reduced spatial heterogeneity because only narrow and stable conditions would promote persistence. However, low spatial heterogeneity species in this study were somewhat generalist species (e.g., mottled sculpin, muskellunge and rock bass) suggesting little support for this hypothesis.

3) *Alternate stable states*. Within a single ecosystem, increasing temporal heterogeneity in the abundance of consumers can be an early indicator of trophic cascades (Bell et al. 2003; Carpenter et al. 2008). In small north temperate lakes, fishes exhibit high interannual variance in recruitment, and when recruitment is high, effects can cascade to lower trophic levels (Carpenter et al. 1985; Carpenter 1989). In small lakes, ecosystems sometimes oscillate between bass and minnow dominated states, with divergent outcomes for lower trophic levels (Carpenter et al. 1987; Seekell et al. 2013). Thus lakes exhibiting oscillating states should express high temporal heterogeneity in abundances and vice versa. Dominance of ecosystems with high temporal heterogeneity species may suggest a general vulnerability to regime shifts. Keystone species or critical functional groups are often temporally dynamic (Folke et al. 2004; Collie et al. 2008). In this study, an intriguing converse to this pattern is that certain species were slow changers (e.g., muskellunge, mottled sculpin and rock bass) and thus less temporally heterogeneous. Muskellunge are the ultimate apex predator in Wisconsin lakes (Rypel 2010), and previous research has shown that predator diversity can stabilize food webs (Polis & Strong 1996; Finke & Denno 2004). Furthermore, both rock bass and mottled sculpin are productive species that can dominate fish community biomass (Hile 1942; Rypel & David 2017). These patterns beg the question: Are low temporal heterogeneity species “ecosystem stabilizers”? That is, could presence or dominance of these species have a stabilizing effect on food webs such that they slow down or block regime shifts overall? In contrast, are food webs composed of high temporal heterogeneity species “born to be wild?”

4) *Density-dependence*. Density-dependence is common in fish populations (Fowler 1981; Post et al. 1999); thus asynchronous patterns between spatial heterogeneity and temporal heterogeneity might result strictly as a product of varying densities or its impact

on food webs (see 3). For example, density dependence could amplify spatial heterogeneity, but within a single system, whereas density-dependent effects in other populations could be strong or weak. Thus species with high spatial heterogeneity might simply reflect species experiencing varying degrees of constraint and release following density-dependence.

## Conclusions

Understanding relationships between spatial and temporal heterogeneity in ecosystems is a classic theme of limnology and ecology, but until recently, these patterns were largely untestable (Rose et al. 2017). This study provides an example for how availability of spatially and temporally replicated data are useful for exploring the dimensionality of heterogeneity in ecosystems and landscapes. An asymptotic relationship between spatial and temporal heterogeneity found in this study for fishes, combined with recent work by McGranahan et al. (2016) and Collins et al. (2018), highlights that space-time heterogeneity relationships can take a variety of forms depending on question, taxa and scale. Future work might explore the generality of this relationship across additional taxa and ecosystem types. Furthermore, experimental work might be useful in testing hypothesized mechanisms for heterogeneity dimensionality as outlined above.

One of the central challenges in freshwater conservation and management is that information is lacking on most species to best inform management practices. However, in some cases (e.g., at LTER or NEON sites), abundance data on species are available over space and time. Temporal and spatial heterogeneity measures can be calculated using these data, and this information may be valuable for conservation. In particular, the level of temporal heterogeneity in abundance expressed relative to spatial heterogeneity for that species appears to have implications for conservation. Species and populations with large spatial heterogeneity relative to temporal heterogeneity may benefit more from landscape-scale management efforts while species with high temporal heterogeneity might be more successfully managed locally.

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