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Long transients and dendritic network structure affect spatial predator–prey dynamics in experimental microcosms

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Abstract

1. Spatial dynamics can promote persistence of strongly interacting predators and prey. Theory predicts that spatial predator–prey systems are prone to long transients, meaning that the dynamics leading to persistence or extinction manifest over hundreds of generations. Furthermore, the form and duration of transients may be altered by spatial network structure. Few empirical studies have examined the importance of transients in spatial food webs, especially in a network context, due to the difficulty in collecting the large scale and long-term data required.

2. We examined predator–prey dynamics in protist microcosms using three experimental spatial structures: isolated, river-like dendritic networks and regular lattice networks. Densities and patterns of occupancy were followed for both predators and prey over a time scale that equates to >100 predator and >500 prey generations.

3. We found that predators persisted in dendritic and lattice networks whereas they went extinct in the isolated treatment. The dynamics leading to predator persistence played out over long transients with three distinct phases. The transient phases showed differences between dendritic and lattice structures, as did underlying patterns of occupancy.

4. Spatial dynamics differed among organisms in different trophic positions. Predators showed higher local persistence in more connected bottles while prey showed this in more spatially isolated ones. Predictions based on spatial patterns of connectivity derived from metapopulation theory explained predator occupancy, while prey occupancy was better explained by predator occupancy.

5. Our results strongly support the hypothesized role of spatial dynamics in promoting persistence in food webs, but that the dynamics ultimately leading to persistence may occur with long transients which in turn may be influenced by spatial network structure and trophic interactions.

KEYWORDS
colonization-extinction, connectivity, dendritic structure, metacommunities, networks, predator-prey interactions, spatial dynamics, transient dynamics

Matthew D. Green and Clara A. Woodie authors contributed equally to this manuscript and are listed alphabetically

1 | INTRODUCTION

Studies of spatial food webs have demonstrated the importance of spatial structure (Holyoak & Lawler, 1996; Huffaker, 1958; Pimentel et al., 1963) and heterogeneity (Leibold et al., 2004) on the dynamics of predators and their prey. Spatial structure can promote persistence in the face of potential local overexploitation through a variety of mechanisms: prey may find refuge in less-connected patches (Covich et al., 2009; Pillai et al., 2011) and expand their distributions through dispersal from sources to high predation sinks (Amezcua & Holyoak, 2000; Caudill, 2005; Livingston et al., 2017) while asynchrony among patches allow for rescue effects and regional stabilization (Briggs & Hoopes, 2004; Cooper et al., 2012; Fox et al., 2017; Holyoak, 2000a, 2000b; Holyoak & Lawler, 1996). More recent theoretical (Anderson & Hayes, 2018; Gilarranz & Bascompte, 2012; Hayes & Anderson, 2018; Holland & Hastings, 2008; Yeakel et al., 2014) and experimental (Arancibia & Morin, 2022; Carrara et al., 2012; Holyoak, 2000b) work has shown that the arrangement of dispersal connections among habitats can be important in persistence and stability through changes in colonization/extinction rates and asynchrony potential, even when dispersal rates are constant. Alteration of persistence mechanisms have also been shown by theory to have more complex dynamic effects that play out over longer temporal and spatial scales (Anderson & Hayes, 2018; Gilarranz et al., 2015; Hastings, 2001; Hayes & Anderson, 2018; Holland & Hastings, 2008). While there is extensive evidence that spatial processes promote metapopulation and predator–prey persistence, empirical understanding of their longer scale dynamic consequences in a network context is much less well developed (Francis et al., 2021).

One potential feature of longer scale spatial ecological dynamics are long transients (Francis et al., 2021; Hastings & Higgins, 1994; Holland & Hastings, 2008; Vortkamp et al., 2020), which are highly sensitive to network connectivity patterns (Holland & Hastings, 2008). Long transients are defined as non-asymptotic dynamics that persist for at least dozens of generations on an ecologically relevant scale (Francis et al., 2021; Hastings et al., 2018). Transients in high-dimensional systems such as spatial food webs are prone to sudden regime shifts that can push a system to an alternate state without any external perturbation or change in environmental conditions. There is emerging evidence that many natural systems remain in transient states indefinitely (Francis et al., 2021; Morozov et al., 2020). Transients can influence persistence negatively through sudden species extinctions during regime shifts or positively through dispersal mediated stability (Hastings, 2001; Holland & Hastings, 2008). Despite the potential importance of transient dynamics to predator–prey persistence, their exploration in the context of spatial food web ecology is vastly greater in theoretical rather than empirical contexts.

Regardless of scale, studies of spatial network effects on ecological dynamics have tended to focus on regular or random network topologies, potentially representing terrestrial or marine habitats (Arancibia & Morin, 2022; Gilarranz & Bascompte, 2012; Holland & Hastings, 2008; Holyoak, 2000a; Huffaker, 1958), although there has been an increasing interest in dendritic networks whose bifurcating patterns are used to characterize the branching nature of rivers (Campbell Grant et al., 2007; Tonkin, Altermatt, et al., 2018; Tonkin, Heino, & Altermatt, 2018). Dendritic networks, relative to linear or random networks, have been shown to increase the persistence of populations while also increasing variance in local population densities (Altermatt & Fronhofer, 2018; Yeakel et al., 2014). Experimental studies demonstrate that regular lattice structures harbour more homogeneous communities in comparison to dendritic structures, which have greater variability in species persistence within the metacommunity (Carrara et al., 2012). Field studies have confirmed that complexity introduced by dendritic network structure influences patterns of connectivity (Alther et al., 2021; Campbell Grant et al., 2010; Larsen et al., 2021), stability (Terui et al., 2018), and biodiversity (Altermatt et al., 2013; Brown & Swan, 2010; Green, Anderson, Herbst, et al., 2022; Henriques-Silva et al., 2019; Muneepeerakul et al., 2008). Despite these advances, most previous theoretical and experimental research has focused on the effects of spatial network structure on species interactions within similar guilds, particularly in dendritic networks. Limited theory suggests that dendritic structure reduces the tendency for consumers and resources to fluctuate and also affects food web structure (Campbell Grant et al., 2007; Cuddington & Yodzis, 2002). Asynchronous variability in the spatially isolated headwaters of river networks can drive statistical stabilization at regional scales (Anderson & Hayes, 2018). Trophic resource pulses can interact with dendritic structure to alter community composition (Harvey et al., 2020), although the importance of dendritic network structure on predator–prey interactions remains equivocal (Covich et al., 2009; Sepulveda & Lowe, 2011).

Here, we tested how regular and dendritic spatial structure influences the long-term persistence and spatial dynamics of a predator–prey protist metacommunity. Microcosm experiments allowed us to manipulate spatial structure at the scale that organisms experience space and at time scales over which complex phenomena such as transients and long-term cycles occur (Altermatt et al., 2015; Fraser & Keddy, 1997; Holyoak & Lawler, 2005). While previous studies have demonstrated effects of network structure on predator–prey persistence, these have focused on smaller networks and where metapopulation extinctions occur over relatively short time-scales (Holyoak, 2000b). We instead asked whether transient changes in abundances of predators and prey differed among network types as predicted by previous theory, and whether differences between network types and among transient phases were reflected in local occupancy patterns. Additionally, we explored the roles of connectivity and species interactions in observed dynamics. Because predators and prey may respond differently to network structure and influence each other's dynamics, we asked whether patterns of occupancy in each species could be explained by spatial network metrics, species-specific colonization and extinction probabilities, and local densities of the interacting species. We show that predator persistence was supported in realistic spatial networks through recovery from a long transient period of low occupancy. Furthermore, we found that transient patterns of occupancy differed among network types, potentially due to higher predator occupancy in more

highly connected local communities that made up a greater proportion of lattice networks. Our results strongly support the hypothesized role of spatial dynamics in promoting persistence in food webs, but that the dynamics ultimately leading to persistence may occur with long transients which in turn may be influenced by spatial network structure and trophic interactions.

2 | MATERIALS AND METHODS

2.1 | Study system and experimental assembly

We studied the predator–prey dynamics of two ciliated protists, *Euplotes eurystomus* and *Tetrahymena pyriformis* (Carolina Biological Supply, Burlington, N.C.) in spatial laboratory microcosms. *Tetrahymena* naturally feeds on bacteria while *Euplotes* feeds primarily on smaller protozoa such as *Tetrahymena*; both species naturally co-occur (McGrady-Steed et al., 1997). *Euplotes* can persist at low levels on bacteria, although in our cultures they show strong preferences for and substantially higher population growth feeding on *Tetrahymena* over bacteria (C.W. personal observation). Species of *Euplotes* and *Tetrahymena* are known to exhibit high-amplitude predator–prey cycles, with cycle troughs reaching densities close to zero (Fox et al., 2011; Vasseur & Fox, 2009).

Complete details on microcosm set-up and sampling are described in the Supplemental Methods (Appendix S1). Protist microcosms were assembled in two spatially unique network structure treatments. Local microcosm communities were 175 mL polypropylene Nalgene bottles linked by 11 cm long and 2 mm diameter silicon rubber tubing (Holyoak, 2000b; Holyoak & Lawler, 1996) that preliminary tests showed allowed both protist species to freely disperse between bottles at roughly similar rates. Each network contained fifteen connected local communities that were arranged in two different network structures (Figure 1). We replicated each network structure four times for a total number of 120 local communities comprising eight regional networks.

Each bottle was filled with 50 mL of high-productivity medium, inoculated with three species of freshwater bacteria, which promoted large amplitude cycles of *Euplotes* and *Tetrahymena* in pilot observations. We simultaneously inoculated bottles with random densities of the protist species, assigned with values from a random number generator (Appendix S1), to promote spatial asynchrony and long-term persistence. Following set-up, both species were counted under a light microscope from a 200 μL pipetted sample (Altermatt et al., 2015). Sampling was done three times a week until day 44, continuing twice a week throughout the rest of the experiment, with some sporadic interruptions. Additionally, we examined bacteria densities and environmental variables at the end of the
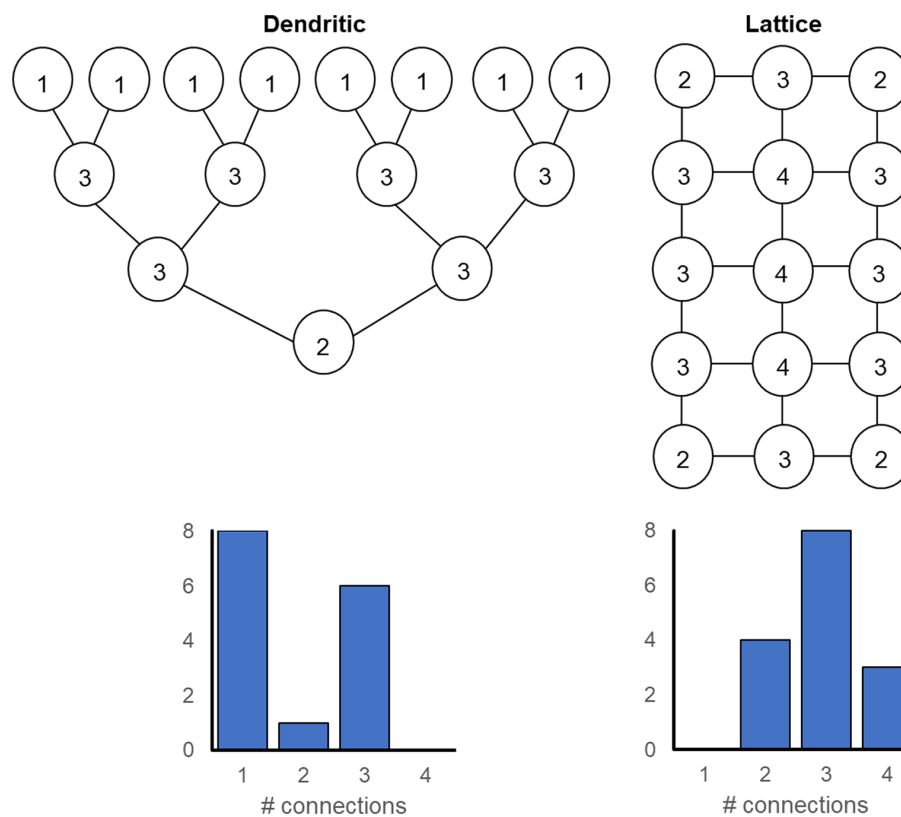

FIGURE 1 Experimental networks used for testing the effects of spatial network structure on predator–prey dynamics. Circles represent local communities, while the black lines are tubes that provide a direct connection between communities, allowing active movement. Numbers inside circles indicate the number of connections, or degree, to neighbouring bottles. The distribution of these connections are displayed below each network. Each network treatment of 15 local communities is replicated four times.

experiment for any emergent differences in resource levels and the local environment.

We additionally conducted a non-spatial comparison with isolated bottles of similar size and level of medium as individual bottles in the network treatments, replicated eight times (Appendix S1). Eight hundred *Tetrahymena* and 200 *Euplotes* individuals were added initially to each isolated bottle on the same day; these values were within the ranges of initial densities used for the network treatments. We sampled each species' density in the isolated communities three times a week for 56 days until *Euplotes'* extinction was confirmed, after which we recorded presence/absence of each species in ten drops of 20 μL for the rest of the experiment, a total of 236 days. To ensure *Euplotes* was fully extinct rather than surviving via encystment, we scanned for cysts during the entirety of the experiment. Additionally, at the end of the experiment, we removed 25 mL of medium and replaced it with 25 mL of fresh, sterile medium to promote excystment, although none was observed. Data from isolated communities are presented for comparison purpose but were not included in statistical analyses due to unbalanced replication.

2.2 | Data analyses

To describe the transients observed over the course of the experiment, our analyses consider dynamics across the entire experiment (days 0–236) as well as within three transient phases with distinct dynamics: Phase 1 (days 0–75), Phase 2 (days 76–150) and Phase 3 (days 151 through the final sampling day 236; Figure 2). While the phase breakpoints selected are somewhat arbitrary, they successfully encompassed the dynamic regimes of interest. Other phase definitions we tried did not lead to qualitatively different results.

Early transient dynamics in Phases 1 and 2 were characterized by predator declines and prolonged periods at unobservably low densities. We defined a low occupancy period by when densities dropped below our sampling threshold (~2 individuals/mL, see also McGrady-Steed & Morin, 2000), as predator re-emergence indicated that they were persisting at extremely low, undetectable levels in the experimental networks. Regional time to low occupancy was calculated as the number of days until the last local community in a network reached a sampled predator density of zero; total low occupancy time was the day of the first local community in a network where the predator reappeared minus the day when predators could no longer be detected in any local community. Local community thresholds for low occupancy were calculated using a three sampling-day moving average of the entire time series; calculated low and high threshold values of predator density were used as certain bottles did not have a prolonged period of predator disappearance and/or a clear day of reappearance. The low threshold (2.27 individuals/mL) was measured as the average predator density in phase one after the peak, between Day 30 and Day 75. The high threshold (37.45 individuals/mL) was measured as the average density in Phase 2, between Day 75 and Day 150. Local community declines were calculated as the day that predator density dropped below the low threshold in each
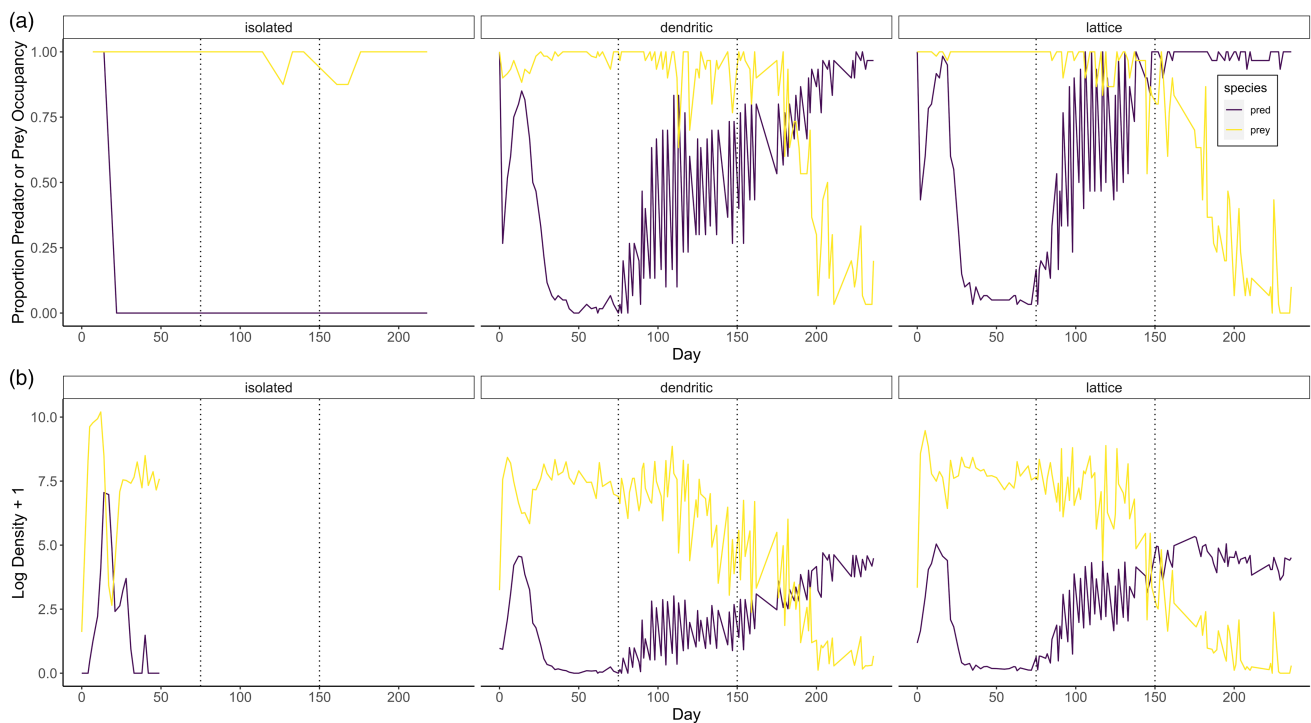

FIGURE 2 Time series of predator and prey a) occupancy and b) density (#ind./mL) for the three experimental treatments. Time series represent averaged values across replicates for each treatment. Dashed lines delineate the three phases of this experiment used in subsequent analyses (see Section 2 for details): Phase 1 (days 0–75), Phase 2 (days 75–150), and Phase 3 (days 150–275).

bottle. Total time at low occupancy was then calculated as the day predators increased past the high threshold density minus the day predators dropped below the low threshold.

We additionally examined predator–prey dynamics through occupancy patterns at both the local (i.e. bottle) and regional (i.e. network) level. Occupancy was defined as a binomial variable, where 0 indicated no occupancy (density = 0) and 1 indicated occupancy (density > 0). Mean occupancy was calculated as the average occupancy for each local community through a defined time period which included the entire experiment as well as each individual phase (i.e. incidence, e.g. Gilarranz & Bascompte, 2012). We also quantified occupancy at the regional network scale by calculating average occupancy across all local communities within a replicate and grouping those at the regional network level.

We explored mechanisms behind variability in occupancy dynamics by comparing them to those predicted by metapopulation theory. We used a spatially explicit metapopulation model that includes patterns of regional network connectivity to predict metapopulation level occupancy proportions p_R^* and local bottle level occupancy probabilities p_L^* from observed extinction e and colonization c probabilities for each species (Hanski & Ovaskainen, 2000). At the regional level, $p_R^* = 1 - \left(\frac{e_R}{c_R \, \lambda_m} \right)$ and λ_m is the leading eigenvalue of the network adjacency matrix that quantifies network structure, whereas at the bottle level, $p_L^* = \frac{c_L}{c_L + e_L}$. Extinction probability e_L was the probability a previously occupied bottle became unoccupied on the next sampling day. Similarly, colonization probability c_L was the probability a bottle that was previously unoccupied became occupied in the next sampling day. Extinction and colonization probabilities were then averaged at the regional level to obtain e_R and c_R.

Based on different observed responses to connectivity by prey and predators, we conducted a posteriori analyses to understand how trophic position influenced predator and prey dynamics based on observed differences among predator and prey occupancies. Local (bottle-level) relationships were examined among predator, prey, and final bacteria densities in the last phase of the experiment.

We assessed the effects of regional network treatments and local bottle connectivities as well as other variables on metrics describing population and trophic dynamics using generalized linear models (GLMs; McCullagh & Nelder, 2019) and generalized linear mixed models (GLMMs; Bolker et al., 2009). GLMs were used to model data at the whole experimental network (regional) level whereas GLMMs were used for analyses at the individual bottle (local) level. In the latter case, local dynamics were modelled using structure treatments (dendritic versus lattice) and bottle connectivity as fixed effects and replicate and spatially correlated random effects (Rousset & Ferdy, 2014). Spatial autocorrelated errors were based on patterns of connection among individual bottles within network replicates. Occupancy was modelled using binomial error distributions, temporal metrics using Poisson error distributions, and relationships between predators, prey, and bacteria densities using Gaussian distributions.

We adopted an information-theoretic approach for model selection and inference (Burnham & Anderson, 2002). Our method involved creating a list of a priori candidate models describing the dependence of the response variables on the different levels of the predictor variables. For most bottle level analyses, the most-parameterized model included all fixed and random effects with other models using nested subsets of fixed effects. Random effects were kept in all candidate models. Candidate models were then ranked and weighted by AIC_c. All analyses and data visualizations were carried out using R version 4.2.2 (R Core Team, 2022). Statistical analyses were carried out using the 'stats' and spaMM packages.

3 | RESULTS

Dynamics across all treatments were complex and included long transient periods of low predator occupancy and subsequent recolonization in the network treatments (Figure 2). Phase 1 was characterized by a transient predator boom-and-bust cycle, where the predator increased in abundance followed by a sharp decline after which predators were not detected in most local communities. Phase 2 captured the predator's re-emergence from low occupancy and dispersal through the network treatments and its general coexistence with the prey; in this phase, the prey and predators both maintained fluctuations bounded far from zero. Lastly, Phase 3 was characterized by predator dominance and low prey abundances with frequent samples of zero prey occupancy.

Transient dynamics differed among network treatments, but the strength of these differences depended on the transient phase in question. The median time for predators to decline below the regional low occupancy threshold was approximately ~39 days for dendric networks and ~42 days for lattice networks (for comparison, declines for isolated communities were ~25 days, Figure 3a). Differences in regional declines among the treatments were not supported statistically, as the model that included separate predictor variables for lattice and dendritic networks with the most support and was <2 ΔAIC_c from the model that grouped networks together ($w_{structure} = 0.66$, $w_1 = 0.34$, Appendix S1: Table S2). Local communities took longer to decline below the low occupancy threshold when more highly connected ones and in lattice as opposed to dendritic networks (Figure 3b). The primary effects of connectivity and regional structure could not be disentangled as models with either and both spatial fixed effects receiving substantial support in model selection ($w_{connectivity} = 0.58$, $w_{structure} = 0.21$, $w_{connectivity + structure} = 0.13$; Appendix S1: Table S2). The model without either spatial effect however received virtually no support ($w \approx 0$).

Predators stayed at low occupancy for less time in lattice networks (median ~17 days) than dendritic networks (~37 days), while predators never re-emerged in the isolated communities (Figure 3c). Differences between lattice and dendritic networks were strongly statistically supported ($w_{structure} \approx 1$; Appendix S1: Table S3). Local communities also spent less time at low occupancy when part of lattice networks and when more highly connected (Figure 3d). These differences were adequately explained
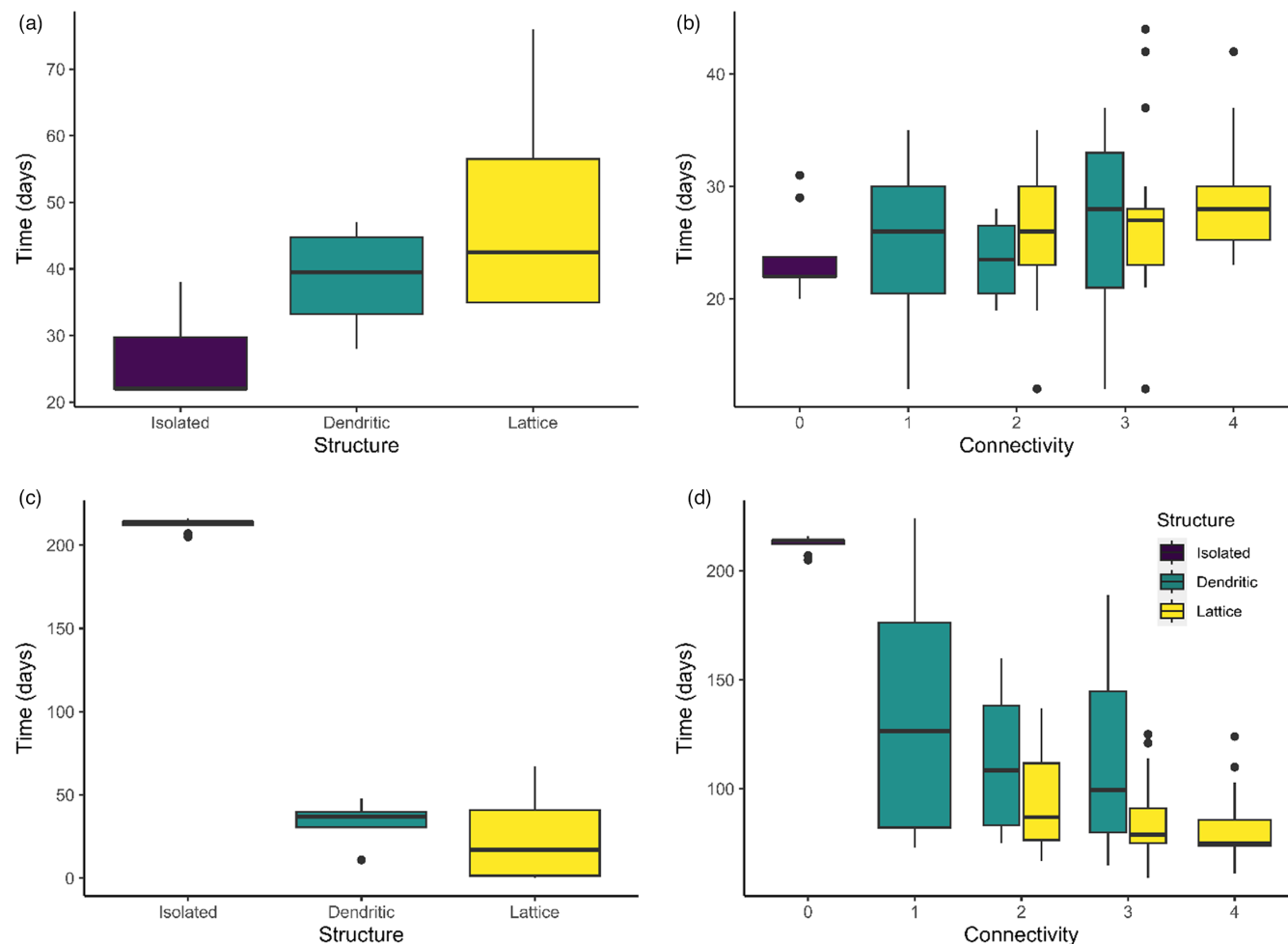
FIGURE 3 Transient dynamics of predator decline and re-emergence across regional network structures and local bottle connectivities. (a) The number of days for predators to decline below the regional low occupancy threshold, defined as the time until predators could not be detected in any bottle in a network. (b) The number of days for predators to decline below the low occupancy threshold in local communities (i.e. bottles) grouped by the number of connections to other bottles and regional network structure the bottle was in. The number of days that predators stayed consistently below detection before re-emerging is shown (c) region-wide and (d) for local communities.

by local connectivity with all top-ranked models containing connectivity as an effect, collectively accounting for ~99% of total model weight (Appendix S1: Table S3).

Transient dynamics manifested as differences in occupancy patterns among local communities. Throughout the entire experiment, average predator occupancy was greater in local communities with higher connectivity (Figure 4). This in turn led to higher overall occupancy in lattice networks compared to dendritic ones due to differences in the connectivity of constituent local communities (Figures 2 and 4). Connectivity was sufficient to explain differences in both local and regional (treatment) occupancy for predators (Appendix S1: Table S4). Models with connectivity as the

sole fixed effect were the highest ranked across the experiment and in Phases 1 and 2, whereas models containing connectivity as at least one fixed effect always comprised the top three models with over >85% model weight (entire experiment: $w_{\text{connectivity}}=0.46$, $w_{\text{connectivity+structure}}=0.36$, $w_{\text{connectivity+structure+connectivity*structure}}=0.17$; Appendix S1: Table S4).

Prey occupancy patterns were opposite of those observed for predators, being higher in lower connectivity bottles and dendritic networks (Figures 2 and 4). These patterns were most pronounced in Phase 3 when predators had re-emerged from transient low occupancy. In contrast to predators, regional network structure rather than local connectivity most consistently explained

FIGURE 4 Occupancy patterns for predators and prey. Results are presented as the proportion of sampling times in a defined phase that a local bottle is occupied, grouped by the connectivity of a local community to other bottles in a network and by regional network treatment. Panels reflect different time segments occupancy was calculated for: (a) prey and (b) predators during the entire experiment, (c) prey and (d) predators during transient Phase 1, (e) prey and (f) predators during transient Phase 2, and (g) prey and (h) predators during the final Phase 3. Occupancy for isolated local bottles is shown for comparison.
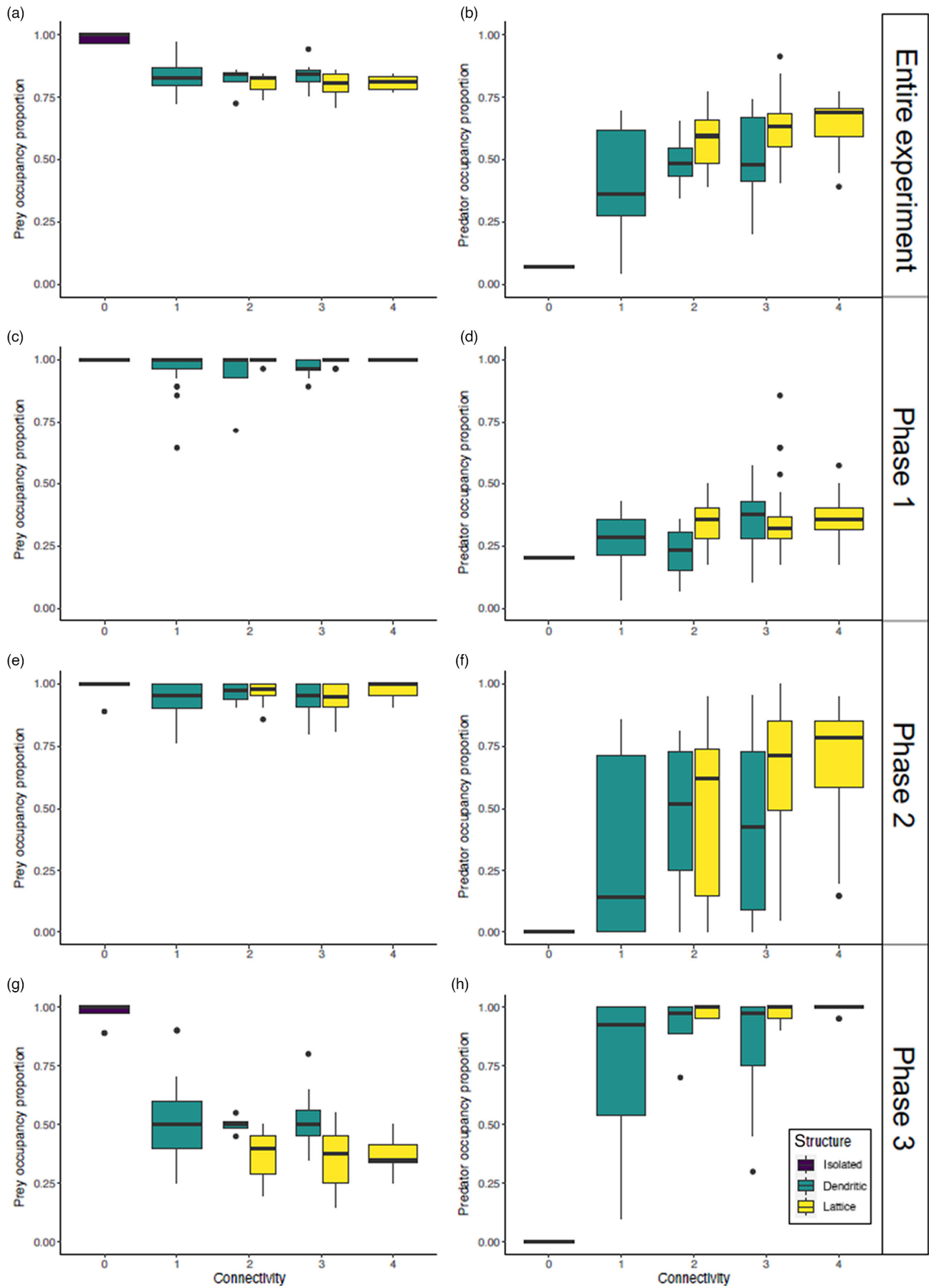
differences in prey occupancy. In Phases 1 and 3, when predator densities were relatively high, the top models of local prey occupancy all contained a fixed effect for regional network structure, in each case collectively responsible for >88% model weight (Phase 1: $w_{structure}=0.64$, $w_{connectivity+structure}=0.24$; Phase 3: $w_{structure}=0.58$, $w_{connectivity+structure}=0.23$; Appendix S1: Table S4). In Phase 2, prey occupancy was consistently high and predator occupancy low; during this phase the most parsimonious model did not contain either structure or connectivity fixed effects (Phase 2: $w_1=0.51$, $w_{connectivity}=0.20$, $w_{structure}=0.19$; Appendix S1: Table S4). Prey remained high in isolated treatments where predators were extinct (Figures 2 and 4).

Metapopulation theory strongly predicted average observed occupancy patterns for predators and prey at both the regional and local levels (Figure 5). Theoretical predictions performed better at the local level than at the regional level and for predators compared to prey. However, in all cases R^2 values were greater than 0.4 and for predators specifically greater than 0.9 (Figure 5).

Local prey densities were negatively related to bacterial (Figure 6a) and predator (Figure 6b) densities and predators were positively related to bacterial densities (Figure 6b) in the final phase

of the experiment. Univariate R^2 values for relationships between bacteria and both prey and predator densities were low (<0.1) and the effects of bacteria received low support (predators: $w_{bacteria}\approx0$; prey: $w_{bacteria}\approx0$; Appendix S1: Table S5). In contrast, the negative relationship between prey and predators was strongly supported (univariate $R^2=0.67$; predators: $w_{prey+bacteria}=0.59$, $w_{prey}=0.41$; prey: $w_{predators+bacteria}=0.28$, $w_{predators}=0.72$; Appendix S1: Table S5).

4 | DISCUSSION

Integrating spatial and trophic processes remains an ongoing challenge in ecology because spatial foodwebs can produce complex dynamics that are difficult to disentangle over experimental timescales. Our microcosm experiment demonstrated persistence in an extinction prone predator–prey system as part of long, complex transient dynamics that differed among network types. Predators dropped to extremely low densities in both spatial treatments after an initial prey exploitation cycle. However, predators re-emerged and spread in spatial networks with differences in these subsequent transient phases among treatments (Figure 2). This spread subsequently led
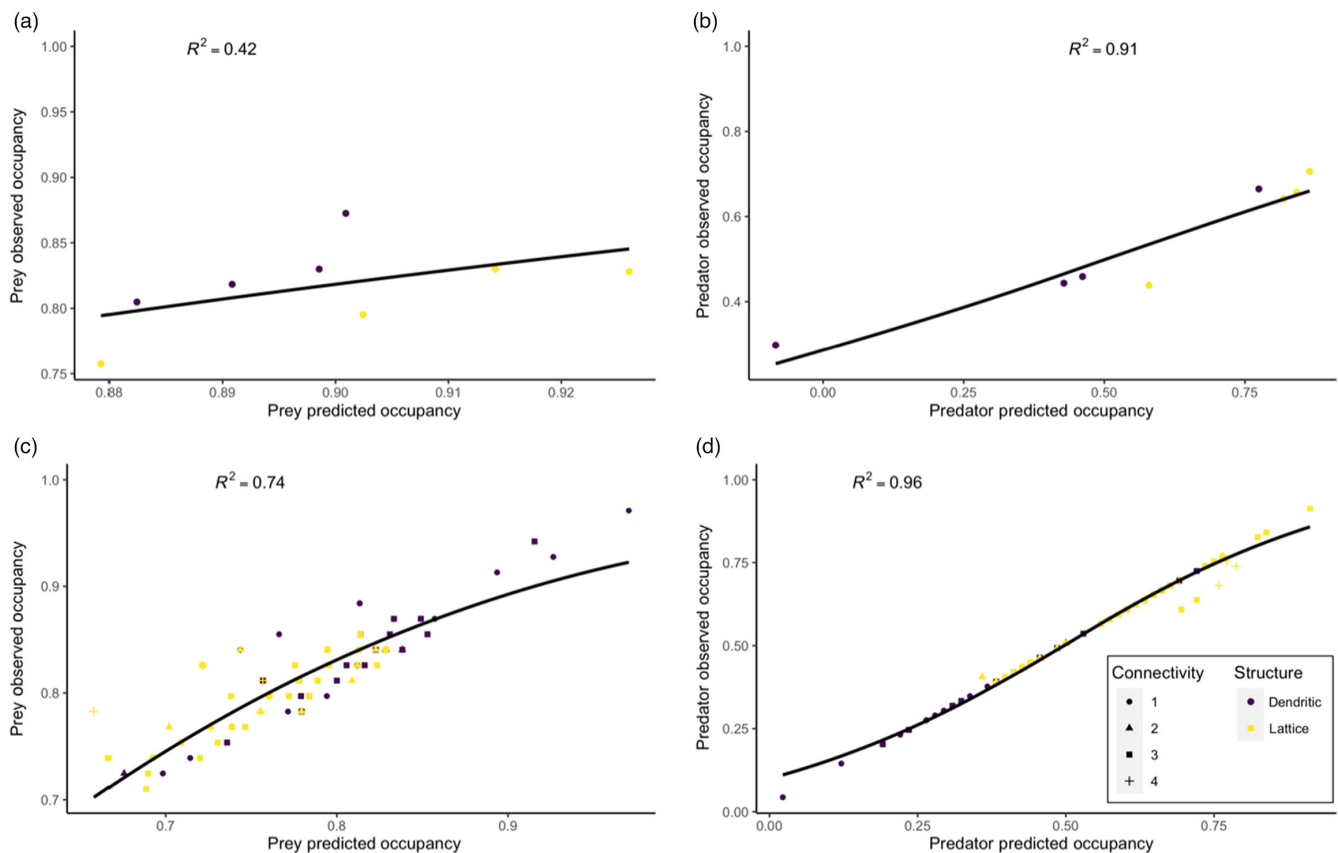

FIGURE 5 Predictions from metapopulation theory strongly predict observed occupancy patterns for predators and prey at both the regional and local levels. Average regional occupancy for (a) prey and (b) predators were predicted using the relationship $p_R^* = 1 - \left(\frac{e_R}{c_R \lambda_m} \right)$ where e_R and c_R are the observed average extinction and colonization rates respectively for each network replicate (see Section 2 for details). Local average occupancy for (c) prey and (d) predators were predicted by $p_L^* = \frac{c_L}{c_L + e_L}$, where e_L and c_L are the observed average extinction and colonization rates respectively for each bottle. Lines represent predictions across the observation range, with R^2 values being calculated from the difference between observed and predicted occupancies.
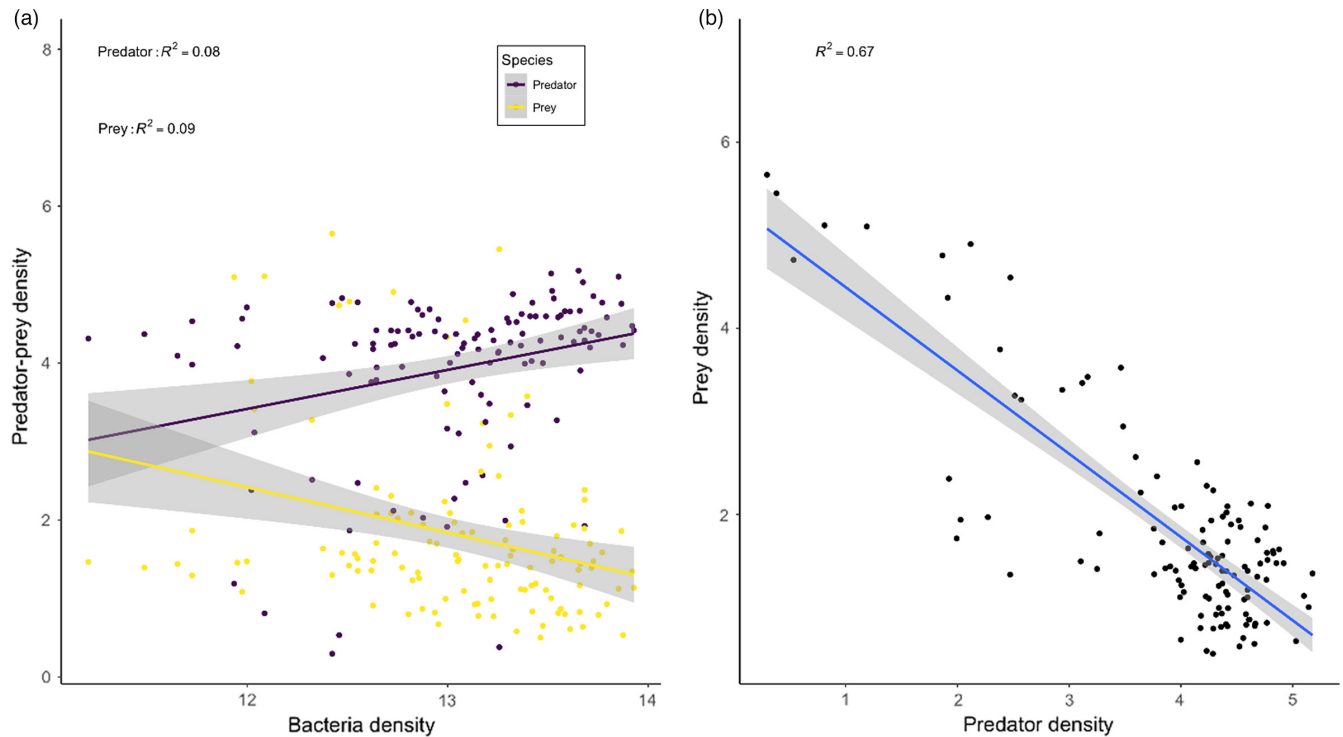
FIGURE 6 Relationships between (a) local predator or prey, and bacterial densities (log +1) and (b) prey and predators densities in spatial network treatments. Prey and predator densities are averages for Phase 3 of the experiment whereas bacterial densities were taken on the final day. Density units are #ind./mL. Lines and R^2 values are shown for univariate relationships; full analyses are presented in Supporting Information Table S5.

to both higher densities and higher occupancy of predators with concomitant declines in prey. These patterns were indicative of long transient dynamics, as the time scale over which predators initially crashed, re-emerged and spread throughout the networks represents >100 predator and >500 prey generations for the species used in the experiment rather than several generations expected for simple consumer-resource systems (Murdoch et al., 2002).

Experimental demonstrations of long transients is limited (Cushing et al., 1998; Fukami, 2004) though transients have been observed in a variety of ecosystems (Frank et al., 2011; Hastings et al., 2018; van Geest et al., 2007). Transient dynamics may manifest as regime shifts (Hastings, 2001; Holland & Hastings, 2008), changes in distributions of prey relative to predators (Tobin & Bjørnstad, 2003) or temporal correlations across species (Klapwijk et al., 2018). In our study, these effects manifested as a transient, widespread dominance by prey that transitioned to predator dominance through a period of variable densities and occupancy. Hastings (2001) showed theoretically that long transients can occur when a single patch of a two-patch system starts off unoccupied, and additional theory shows that regular extinctions in patches can disrupt the final endpoint of community assembly (Cottenie, 2005; Leibold & Loeuille, 2015). These results may help explain why our Phase 1 dynamics were very similar across regional networks but later dynamics were not. Initially, all patches were inoculated with large numbers of individuals of each species; patches then exhibited fairly similar dynamics resembling overexploitation cycles with

rapid increases and then decreases in predator numbers (Bonsall & Hassell, 2007). Networks in our experiment began to display more complex and diverging dynamics in Phase 2 after extinctions had occurred in Phase 1. Resulting heterogeneous recolonization of predators in different patches at different times may have then contributed to the long transient dynamics seen throughout the experiment.

Evidence from our experiment suggests differences between the dynamics of dendritic and lattice networks were related to underlying patterns of spatial connectivity and trophic interactions that lead to variability in extinctions and recolonizations. More highly connected bottles had higher predator persistence, recolonization probabilities and occupancies (Figures 2 and 4). Highly connected bottles were more prevalent in lattice networks, potentially explaining why lattice networks exhibited longer times to extinction and shorter total extinction times in Phase 1 (Figures 2 and 3) at both the local and regional level compared to dendritic networks, although the statistical support for these differences was somewhat equivocal. Local communities in lattice networks also showed faster predator re-colonization and overall higher total occupancy in Phases 2 and 3 (Figures 2 and 5), which were strongly supported effects. Early predator persistence as well as colonization and occupancy in later phases were particularly reduced in the low connectivity bottles on the terminal branches of dendritic networks (Figures 3 and 4). Variation in predator densities were also highest in these low connectivity bottles (Appendix S1: Figures S1 and S2).

Trophic interactions potentially influenced variation in the way species were spatially structured; predators had higher persistence in more connected bottles, while prey maintained high densities longest in bottles that were more spatially isolated. Furthermore, predator occupancy tightly followed patterns among local communities and regional networks predicted by theory (Figure 5). These relationships were much weaker for prey. Predators and prey have been shown to strongly influence each other's distributions in a variety of ecosystems (Fahimipour & Anderson, 2015; Howeth & Leibold, 2010; Livingston et al., 2017; Orrock et al., 2008; Petchey, 2000), and spatial complexity can reduce local predation pressure (Bellmore et al., 2015; Cuddington & Yodzis, 2002; Pillai et al., 2011). It is possible spatially isolated local communities in dendritic networks acted as spatial prey refuges in our study due to predators' lower abundances in these patches. Covich et al. (2009) found similar results where predator-free headwaters provided spatial refuge for shrimp prey in river networks. Predatory fish experienced geographic barriers to dispersal in their study; though our experiment offered equal dispersal opportunity to both predator and prey, the less-connected patches where predators were less abundant potentially provided space for prey populations to maintain higher densities and local persistence. Other experiments have similarly shown decreased predator presence and thus decreased predation in more isolated patches (Belmaker et al., 2009; Scheffer et al., 2006). Previous experiments with *Tetrahymena* have shown it capable of benefiting from dispersal by exhibiting higher densities in higher connectivity communities (Altermatt & Fronhofer, 2018). In contrast, the additional trophic interaction could explain why *Tetrahymena* did not benefit from high connectivity local communities in our study as these communities supported higher abundances of the predator *Euplotes*.

Occupancy and density patterns in spatial networks reflected an apparent trophic cascade at the local level, where *Euplotes* suppressed *Tetrahymena* populations, leading to increased bacteria densities (Figure 6). There is a possibility that competition for bacteria, rather than predation, was responsible for *Tetrahymena's* decline. *Euplotes* exhibits omnivorous tendencies and some species can persist on just bacteria alone (Zubkov & Sleigh, 1996). However, the strong preference that *Euplotes* shows in our cultures for *Tetrahymena* over bacteria make the trophic cascade mechanism the more likely driver of local density patterns among trophic levels.

In addition to persisting at low, undetectable levels in Phase 1 of our experiment, it is possible that *Euplotes* could have encysted in a state of dormancy before excysting and recolonizing the metacommunity, promoting longer transients. Dormancy may co-vary with dispersal in metacommunities in a way that influences community variability (Wisnoski et al., 2019). There is evidence of *Euplotes* sp. encysting to withstand unfavourable environmental conditions and excysting when conditions are more favourable (Garnjobst, 1928; Verni & Rosati, 2011). However, we did not find any evidence of dormancy in our experiment and did not detect any visible cysts in any treatment. Furthermore, we replaced half the medium in some isolated bottles with fresh medium to improve environmental conditions

and promote population growth and excystment. *Euplotes* did not return, indicating that it went extinct in isolated bottles and likely persisted at densities below our sampling threshold in spatial ones.

Long transients in our experiment may have been influenced by change in both abiotic and biotic conditions. Despite having homogeneous conditions at setup, environmental changes may have emerged from endogenous processes such as waste or metabolite build-up. Average environmental conditions did not appear to notably differ among networks at the end of the experiment (Appendix S1: Table S1), and side experiments showed similar predator–prey dynamics in "fresh" and "used" medium (Appendix S1: Supplementary Methods), thus yielding little evidence that a changing environment played a role in observed dynamics. It is also possible that phenotypic or evolutionary changes occurred, particularly in allowing the predator *Euplotes* to spread and replace the prey *Tetrahymena* after an extended period of very low density. Evolutionary responses of protists have been shown to alter trophic interactions in systems strongly influenced by dispersal (terHorst, 2010, 2011). While we observed no obvious trait changes during the experiment, untangling the influence of non-stationary environmental conditions, phenotypic plasticity and evolutionary responses on trophic dynamics remains a fertile ground for future inquiry.

Our demonstration of long transient dynamics that differ among network configurations in an empirical predator–prey system adds to recent considerations of trophic dynamics in metacommunity theory (Amarasekare, 2008; Beger et al., 2010; Gravel et al., 2011; Guzman et al., 2019; Holt, 2002; Pillai et al., 2011). In our system, transients emerged as typical predator overexploitation cycles; patterns of subsequent predator re-emergence from low occupancy and spread differed among regional network types, leading to altered occupancy patterns for both predators and prey (Figures 2 and 3). Other studies have also shown spatial structure shown to affect species on higher trophic levels more strongly than their prey (Barter & Gross, 2016; Liao et al., 2017; Pillai et al., 2011; Ryser et al., 2019), which then drives spatial variation in prey occupancy dynamics as seen in our system. Responses to spatial structure may be introduced by differences in body size and other life history traits such as dispersal that differ among trophic levels. Such differences can lead members of each trophic level to experience the environment at different spatial and temporal scales (Anderson & Fahimipour, 2021; McCann et al., 2005). Differential space use is one of the key reasons why the loss of top predators can have significant and unexpected consequences on food web stability (Woodward et al., 2012).

Understanding how the dynamics of populations and communities are reflected in patterns of occupancy is a longstanding focus of ecological research Occupancy patterns are extensively used to study the drivers of species distributions (MacKenzie, 2018; Passy, 2012) and project how species will respond to climate change and management actions (Franklin et al., 2016; Keppel et al., 2012). Traditional species distribution models have typically been based on establishing relationships between abiotic variables and occurrences (Franklin, 2010). These approaches however omit important biotic processes, and there are an increasing number of attempts

to link occupancy patterns to spatial connectivity (Radinger & Wolter, 2015), population dynamics (Bonebrake et al., 2014; Conner et al., 2016; Fandos et al., 2021), and species interactions (Holland et al., 2018; Singh et al., 2022). At the same time, there has been development of theory for occupancy dynamics in metacommunities (Gravel et al., 2011; Guzman et al., 2019). Microcosm studies such as ours provide a means for testing the effects of trophic interactions in spatially complex environments on regional occupancy patterns, bridging theory and wider-spread empirical application (Altermatt et al., 2015).

Our study in particular suggests that maintaining connectivity and, importantly, variability in connectivity, appears particularly necessary given that species on different trophic levels maintain persistence by responding to network structure differently. In river ecosystems, this requires management of the entire watershed from the isolated headwaters downstream to the mainstem where connectivity is highest (Patrick et al., 2021). While our study focused largely on dendritic branching structure, microcosm studies can replicate other aspects of river metacommunities such as biased dispersal (Altermatt et al., 2011), relationships between branching position and habitat size (Carrara et al., 2014), and resource exchanges between aquatic and terrestrial ecosystems (Harvey et al., 2020). Experiments that link such processes to predator–prey dynamics over long time-scales may provide additional insights into the importance of long transients for river ecosystems. More generally, future studies of spatial food web responses to spatio-temporal environmental heterogeneity and variation in traits among organisms will improve our understanding of their dynamics and how to effectively manage them.

AUTHOR CONTRIBUTIONS

Kurt E. Anderson developed the original concept for the study; Kurt E. Anderson, Matthew D. Green and Clara A. Woodie designed the study; Clara A. Woodie and Megan Whitesell collected and archived the data; Matthew D. Green, Clara A. Woodie and Megan Whitesell performed data analyses; Matthew D. Green and Clara A. Woodie wrote the initial draft of the manuscript with input from Kurt E. Anderson and Megan Whitesell; Kurt E. Anderson wrote subsequent drafts of the manuscript with input from Matthew D. Green, Clara A. Woodie and Megan Whitesell All authors gave final approval for publication.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository http://doi.org/10.5061/dryad.3j9kd51kx (Green, Anderson, Woodie, et al., 2022).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Spatial representation of predator (a–d, i–l) and prey (e–h, m–p) mean occupancy for dendritic (a–h) and lattice (i–p) spatial structures. The mean occupancy of Phase 1 (days 0–75) is indicated by: a, e, i, m. The mean occupancy of Phase 2 (days 75–150) is indicated by: b, f, j, n. The mean occupancy of Phase 3 (days 150–236) is indicated by: c, g, k, o. The mean occupancy throughout the entire experiment (days 0–236) is indicated by: d, h, l, p.

Figure S2. Spatial representation of the percent Coefficient of Variation (% CV) for predator (a–d, i–l) and prey (e–h, m–p) in the dendritic (a–h) and lattice (i–p) spatial structures. The % CV of Phase 1 (days 0–75) is indicated by: a, e, i, m. The % CV of Phase 2 (days 75–150) is indicated by: b, f, j, n. The % CV of Phase 3 (days 150–236) is indicated by: c, g, k, o. The % CV throughout the entire experiment (days 0-236) is indicated by: d, h, l, p.

Table S1. Summary environmental data taken at the conclusion of the experiment. Values are presented as regional averages (± SD) for each fifteen-bottle spatial structure.

Table S2. Results from GLMs and GLMMs comparing the experimental network treatments on the time of predator decline to low occupancy in Phase 1 of the experiment averaged at the regional (network) and local (individual bottle) scales. For regional models, the ~structure GLM includes separate predictor levels for each individual treatment (i.e. dendritic vs. lattice) whereas the ~1 model only contains one predictor level for combined treatments. For local GLMMs, the connectivity models include a fixed effect that models bottle occupancy based on the number of connections to other bottles without considering overall network structure, whereas structure is a fixed effect for the network structure treatment the

bottle belongs to. Terms (1|rep) and adjacency(1|bottle) are replicate and spatial autocorrelation random effects, respectively. Spatial autocorrelation random effects were based on an adjacency matrix specifying connections among individual experimental bottles in each treatment and replicate. Each model is presented with AIC, the number of parameters *k*, and Akaike weights w_i. AIC values reported for GLMMs are marginal AICs and *k* is calculated as the effective degrees of freedom for the fixed effects portion of each model. Models are ranked by ΔAIC.

Table S3. GLMs and GLMMs comparing the experimental network treatments on predator total time at low occupancy in phase 1 of the experiment averaged at the regional (network) and local (individual bottle) scales. Model definitions and outputs are as defined in Table S2.

Table S4. GLMMs comparing the experimental network treatments on predator and prey occupancy. Models are presented for occupancy across the entire experiment as well as for each of three phases. Fixed and random effects and as defined in Table S2.

Table S5. GLMMs analyzing the effects of local species densities on one another. Specifically, we analyzed the effects of final bacteria density (bac) on predator density (pred), the effects of final bacteria density on prey density (prey), and the effects of predator density on prey density. Random effects are as defined in Table S2.