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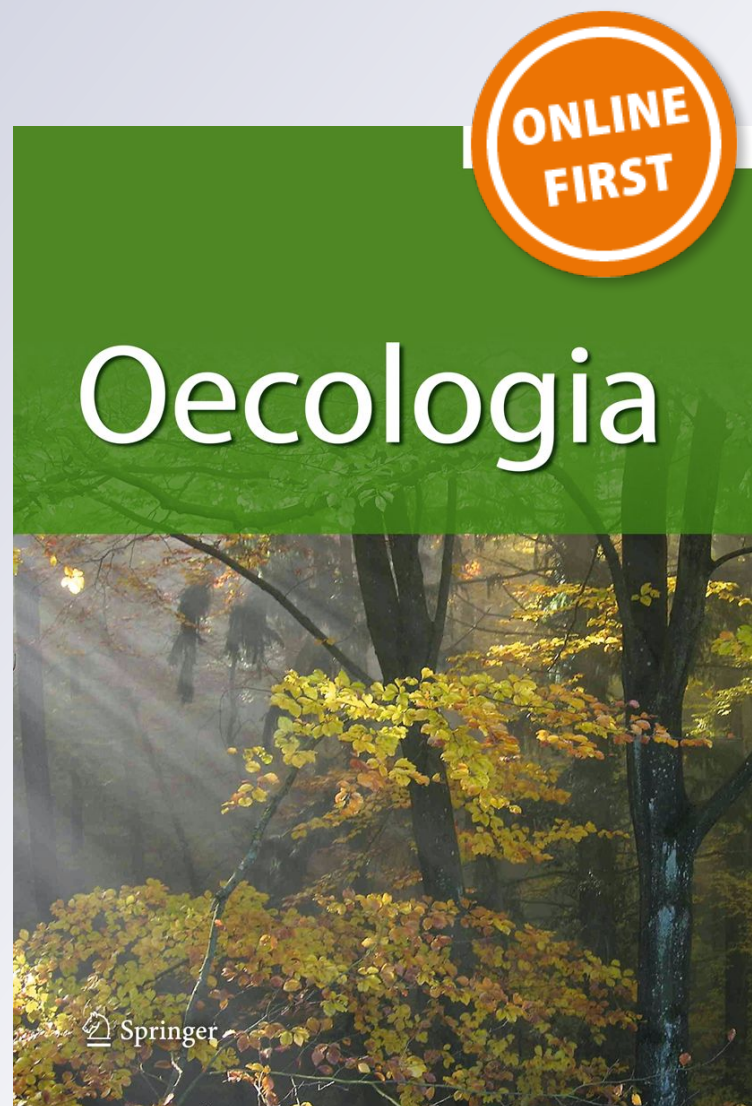
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Population synchrony decreases with richness and increases with environmental fluctuations in an experimental metacommunity

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Abstract Fluctuations of local but connected populations may show correlation or synchrony whenever they experience significant dispersal or correlated environmental biotic and abiotic variability. Synchrony may be an important variable in multispecies systems, but its nature and implications have not been explicitly examined. Because the number of locally coexisting species (richness) affects the population variability of community members, we manipulated richness under different regimes of environmental fluctuation (EF). We predicted that the temporal synchrony of populations in a species should decline with increasing richness of the metacommunity they live in. Additionally, we predicted that specialist species that are sensitive to a specific environmental factor would show higher synchronization when EF increases. We thus created experimental communities with varied richness, EF, and

species specialization to examine the synchronizing effects of these factors on three aquatic invertebrate species. We created four levels of richness and three levels of EF by manipulating the salinity of the culture media. Monocultures exhibited higher population synchrony than metacommunities of 2–4 species. Furthermore, we found that species responded differently to EF treatments: high EF enhanced population synchrony for the specialist and intermediate species, but not for the generalist species. Our findings emphasize that the magnitude of EF and species richness both contribute to determine population synchrony, and importantly, our results suggest that biotic diversity may actually stabilize metacommunities by disrupting synchrony.

Keywords Species richness · Population synchrony · Metacommunity · Environmental fluctuations · Cross-correlation function · Habitat specialization gradient

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Introduction

Population synchrony—the phenomenon in which the abundances of populations in individual habitats or different areas rise and fall simultaneously—is thought to contribute to species extinction, because it reduces the probability of effective rescue from neighboring patches (e.g., Paradis et al. 2000). According to prior research, an increase in migration rates among patches in a landscape (e.g., Ripa 2000), large-scale correlated environmental variability (e.g., Moran 1953; Hudson and Cattadori 1999), or predation and predator switching (e.g., Ims and Andreassen 2000) may act alone or together to synchronize fluctuations of populations that occupy distinct adjacent locations. Population synchrony occurs in many taxa,

including mammals, birds, fishes, and insects (e.g., Moran 1953; Paradis et al. 2000; Fontaine and Gonzalez 2005). In spite of this evidence, other studies have failed to support the proposition that population synchrony is driven by a correlation among shared local density-independent factors such as climatic, edaphic, or anthropogenic factors (Ranta et al. 2006, p 81).

Although most studies of synchrony employ multiple patches, they implicitly assume that populations of constituent species fluctuate independently of each other, irrespective of the richness and composition of a replicate community (see Loreau and de Mazancourt 2008). However, species richness is known to affect the population variability (temporal stability) of community members, even though its impact at the population level varies between single and multitrophic communities (Jiang and Zhichao 2009). Their review found that most studies support the notion of a stabilizing effect of species diversity at both the community and population levels in multitrophic communities, but that this effect was neutral in single-trophic communities. Beyond species richness, populations are also affected by other local processes via a range of species interactions, as well as by regional processes, as reflected in the effective dispersal of the focal and other species (Holyoak et al. 2005). Recognition of these potential influences raises the question of whether regional (dispersal) and local (community dynamics) factors leave a predictable stamp on population synchrony at the larger scale of the metacommunity. This is a particularly relevant question since theoretical studies (e.g., Earn et al. 2000) have shown that population synchrony increases the risk of global metapopulation extinction. By including the influences of other species, we place this problem explicitly within the metacommunity framework.

The metacommunity framework considers the combined effects of dispersal and local species interactions (Leibold et al. 2004; Holyoak et al. 2005) in a set of local communities that share a region. Thus, the metacommunity framework offers a context for jointly considering the metapopulation dynamics of different species. A theoretical study (Koelle and Vandermeer 2005) indicated that when population synchrony was induced in a metapopulation it did not propagate up to metacommunity scale; that is, it did not synchronize other members of the metacommunity. At the same time, their theoretical study found that reducing the effective distance between patches affected not only the focal species but all of the species that co-occurred with it. They further showed that a decrease in the effective between-patch distance may impede population synchrony, because changing the distance differentially modifies the migration patterns of other species. Possibly, the presence of other species affects the response of a

population to migration and environmental fluctuations by reducing its synchrony with other populations of same species. More direct evidence for the significant role of species interactions comes from experimental work by Vasseur and Fox (2009), who have demonstrated that both dispersal and the Moran effect (i.e., the correlated environmental variation that induces synchronization among initially independently fluctuating local populations; Royama 2005) increased the synchrony of the ciliate protist *Tetrahymena pyriformis* in a laboratory microcosm experiment, with synchrony being much stronger in the presence of predators, and dispersal having little or no effect on prey synchrony in the absence of predators.

Models showed that species richness decreases the synchrony in both per capita population growth rates and population sizes when interspecific competition is low (Loreau and de Mazancourt 2008). They further argued that the influence of demographic stochasticity should be greater in communities with many species, and thus cause a reduction in synchrony with increasing species richness. This is corroborated by observations that species-rich systems often show more stable ecosystem metrics than species-poor ones do (Teng and McCann 2004; McCann 2000). One reason for this could be the statistical averaging of population numbers when they fluctuate out of synchrony (Doak et al. 1998). Also, population synchrony can be expected to be lower in more diverse communities because such systems are likely to exhibit greater complexity of interactions. The presence of fast and slow energy channels in food webs is but one example of mechanisms that may link richness and interaction complexity to stability and synchrony (Rooney et al. 2006). Thus, we expect that higher species richness should lead to more complex interactions that, in turn, might interfere with synchrony through the diversification of local population dynamics. Based on this, we predicted that population synchrony in communities with fewer species would be higher than in more diverse communities.

In addition to species richness, Pandit et al. (2009) have recently shown that species with different specializations display different dynamics within the same metacommunity. Habitat generalists respond more to spatial factors, while specialist species respond more to local environmental factors. Because of such differences, we hypothesized that synchronization should also be greater when environmental fluctuation is large, with the size of the effect depending on the tolerance of the species to environmental factors. We tested the two above hypotheses relating to species richness and EF in relation to specialization in artificially assembled aquatic metacommunities consisting of microcrustaceans (two cladoceran, one ostracod, and one copepod species).

Methods

Experimental organisms

The experiment was conducted using four aquatic invertebrate species: *Daphnia magna*, *Ceriodaphnia rigaudi* (both cladocerans), *Potamocypris* sp. (an ostracod), and *Nitocra spinipes* (a copepod). The first species was collected from an old laboratory culture, while the remaining three species were originally collected from tropical rock pools, Jamaica (detailed information in Kolasa et al. 1996). *Ceriodaphnia*, *Daphnia* and *Nitocra* are planktonic algae feeders, while *Potamocypris* is a detritivore. We cultured these species in the laboratory in a large aquarium.

Microcosm system

The experiment was executed in plastic cups 8 cm in diameter and 15 cm deep. The cups were filled with medium to a depth of 10 cm (volume 500 ml), which is the minimum size of our natural rock pools (Jamaican rock pools, see Pandit et al. 2009). The medium used for the experiment was prepared according to Weber (1993) using 96 mg NaHCO₃, 60 mg CaSO₄, 60 mg MgSO₄, and 4 mg KCl per liter of distilled water. Every seven days, the medium of each microcosm was replaced with fresh medium of the same salinity. Single-cell green algae (*Chlorella*) were used as food for the experimental species. The algae were cultured in a 5 l glass jar placed in natural sunlight. The density of the algae was estimated in a hemocytometer to ensure that consistent amounts of food were provided. Fifty milliliters of water with algae at concentration of 1.5×10^6 cells/ml (i.e., food) were added along with the new medium every week. There were also some dead particles in the solution of algae, but we did not count them, as we assumed that the concentration of dead particles in the solution did not vary significantly from week to week. Saline solution for the experiments was prepared using analytical-grade NaCl.

Experiment design and sampling

The main experiment was set up as an unbalanced factorial design, with four levels of species richness (in eight species combinations) and three amplitudes of environmental fluctuation [see Appendix 2 of the Electronic supplementary material (ESM) for the experimental design]. Prior to deciding which amplitude of EF to use, we ran a pilot experiment (see details in Appendix 1 of the ESM) to determine the population density of the experimental species under different salinity regimes. Based on the data from this experiment, we chose three amplitudes that allowed the survival of all species while imposing a stress

that would differentially affect their individual and population growths. The schedule of environmental variability was the same for each of the three amplitudes and consisted of alternating microcosm salinity and medium every seven days. With respect to salinity, we used the following fluctuation regimes:

1. No fluctuation (this treatment was also used as control): no change in salinity, salinity maintained at 0 ppt.
2. Low environmental fluctuation (low EF): salinity alternating between 0 and 3 ppt every seven days.
3. High environmental fluctuation (high EF): salinity alternating between 0 and 6 ppt every seven days.

The amplitude of salinity variation selected for the experiment was within the normal range of those encountered in the field by two (*Ceriodaphnia* and *Potamocypris*) of the three species occurring in Jamaica, with *Ceriodaphnia* preferring very low salinities. For example, based on long-term measurements in pools from which these species originated, the mean and standard deviation of the salinity concentration varied from 0.25 ± 0.7 to 7.93 ± 15.21 ppt. *Daphnia* is a common freshwater species but it did survive at high EF (6 ppt salt concentration) during the pilot experiment (Appendix 1 of the ESM), albeit with minimal population growth. Thus, *Daphnia* was considered an intermediate species, whereas *Ceriodaphnia* did not survive at high EF (6 ppt salt concentration), while the same salinity concentration did not affect *Potamocypris* density (Appendix 1 of the ESM). Thus, *Ceriodaphnia* was considered a specialist whereas *Potamocypris* was considered a generalist species with respect to salinity.

Each experimental unit (metacommunity) consisted of four communities (referred to as a “patch” or “beaker”). The metacommunity was formed by linking populations via manual dispersal, which was achieved by transferring a fraction of the individuals among cultures. We stirred the beaker contents, collected 10 ml of water with organisms (2 % of the culture volume) from communities within each cluster of four communities, mixed all of the samples together in one container, and then returned 10 ml of the water containing the mixture of organisms and propagules to the individual communities in each cluster of four communities.

Altogether we established 96 communities within 24 metacommunities. Among the eight species combinations, we had three single-species microcosms [*Daphnia* (D), *Ceriodaphnia* (C), and *Potamocypris* (P)], three two-species combination microcosms [*Ceriodaphnia* + *Daphnia* (C + D); *Daphnia* + *Potamocypris* (D + P); *Ceriodaphnia* + *Potamocypris* (C + P)], and one three-species combination [*Daphnia* + *Ceriodaphnia* + *Potamocypris* (D + C + P)]. In addition, we studied one (the only

possible) four-species combination, using *Nitocra* [*Daphnia* + *Ceriodaphnia* + *Potamocypis* + *Nitocra* (D + C + P + N)] to increase the range of species richness. *Nitocra* was not included in the pilot study since the species is common and shows adaptation to a wide range of salinity and temperature values (Bengtsson 1978). In this design for each species, there were two metacommunities with a species richness of two, and one metacommunity for all other species richness levels.

Each microcosm received 100 individuals, irrespective of the number of species. When a microcosm contained more than one species, all species were initially introduced in equal proportions (i.e., 50 + 50, 3 × 33, or 4 × 25 for two, three, and four species, respectively). Microcosms were sampled weekly prior to the scheduled salinity manipulations. First, the contents of each beaker were gently stirred with a glass rod to homogenize the distribution of organisms. Then, a small dip container was used to collect three aliquots 50 ml in volume from each microcosm, individuals of each species were counted under a dissecting microscope, and the mean of the counts obtained from three aliquots was recorded; thus, one record was obtained for each microcosm on each sampling date. Following the enumeration, live individuals were returned to their home microcosms to ensure that sampling did not affect the population dynamics. The experiment was conducted in the laboratory at room temperature (24–25 °C) from August 5 to October 28. Sampling started seven days after the experimental communities were assembled. Light was provided for 12 h per day by two fluorescent 40 W tubes placed 38 cm above the experimental microcosms. We changed the positions of the microcosms randomly every week to reduce any possible effects of differences in the intensity of the light reaching individual microcosms.

Statistical analysis

First, for each species, we calculated the population growth ($r_{i,t}$) as the differences between successive population estimates for each microcosm, such that $r_{i,t} = [(N_{i,t+1}) - (N_{i,t})] / (N_{i,t})$, where $N_{i,t}$ is the population estimate in microcosm i at time t . We tested whether the growth rates were significantly different among the species richness and EF treatments using a factorial ANOVA for each of three species separately. Although several methods are available to calculate the population synchrony (see Liebhold et al. 2004; Box et al. 1994; Ranta et al. 2006), we used cross-correlation coefficients, $\omega_{i,j}$, as a convenient and adequate method, given the goals of the study and the fact that they have been used by others in a similar context (e.g., Vasseur and Fox 2009; Bjørnstad et al. 1999), based on $r_{i,t}$ for each pair-wise combination of microcosms within each individual metacommunity. Estimates of synchrony were based on growth rates

of individual populations. We obtained all six possible cross-correlation coefficients for the growth rate of each species separately for each EF and species richness treatment (metacommunity of four microcosms). While changes in the growth rates of populations between the initial and stable phases could increase the calculated values of synchrony among population pairs, our major focus was differences in synchrony among treatments, not their absolute values. Hence, we used raw data on growth rate without any detrending. Averaging of the six coefficients was necessary to avoid pseudo-replication. However, as coefficient averaging may be misleading, we calculated the effective number of dimensions (see Jorgensen et al. 2000; Kirkpatrick 2009) in each metacommunity and used this number as a measure of the population synchrony in the metacommunity.

For a given species observed in a given metacommunity, the correlation values were described by a 4 × 4 matrix with ones on the diagonal. If the population densities of the species are correlated among the communities of a metacommunity, then the largest eigenvalue would be close to four, and the effective number of dimensions would be one (single dimension). We calculated the effective number of dimensions as the largest eigenvalue of the matrix divided by the sum of the eigenvalues. The effective number of dimensions of one would indicate perfect synchrony for a species in a given metacommunity. In an extreme case, if the population densities among the communities showed an equal amount of variation and were uncorrelated, each of the four eigenvalues would be equal to one and the effective number of dimensions would be 0.25.

We obtained one effective number of dimensions (for each metacommunity in each treatment). All together, we obtained 15 values for each species for three EF treatments and five species combinations, and these were normally distributed for each of three species (Wilks–Shapiro test; $P = 0.82$, $P = 0.66$, and $P = 0.51$ for *Ceriodaphnia*, *Daphnia*, and *Potamocypis*, respectively). We performed an unbalanced factorial analysis using the 15 effective numbers of dimensions, since replication of the two-species treatment in our experiment resulted in enough error degrees of freedom to test for an interaction effect between environmental fluctuation (EF) and species richness. We decided to use this unbalanced but replicated design because of time constraints. We were unable to implement a completely balanced design due to sample processing demands, which, for the sake of consistency, meant that all of the samples had to be counted within a short time frame.

Results

The population sizes of all three species varied over time in all six treatments of salinity variation and species richness

(Fig. 1). Notably, the populations stabilized after 24 (*Ceriodaphnia* and *Daphnia*) and 42 (*Potamocypris*) days at levels that were apparently independent of the initial densities. In addition, the population sizes of all three species varied over time in the EF treatments (control, low, and high) (see Fig. A3 in Appendix 3 of the ESM).

Population synchrony was significantly higher for the intermediate species and the specialist than for the generalist species, irrespective of EF treatment (Table 1; Fig. 2). Population synchrony significantly declined with species richness for all species in all experimental metacommunities (Fig. 2). The interaction effect between EF and species richness was not significant for all three species (Table 1). This was visually corroborated by the parallel lines in Fig. 2, which show that the effect of EF was independent of that of species richness. Since we found no significant interaction effect, we were able to conclude that the levels of EF were independent of species richness. As a result, we were able to average population synchrony across EF treatments to test for the main effect of species richness on population synchrony with multiple comparisons (see Underwood 1997, pp 331). We used a post hoc Student–Benjamini–Hochberg (BH) test (Verhoeven et al. 2005) for the comparison. Similarly, the levels of species richness were independent of EF, and population synchrony could thus be averaged across species richness.

For *Ceriodaphnia* and *Daphnia*, a significant increase in the population synchrony took place under high EF as compared to low and control EF, but population synchrony did not significantly differ between communities exposed to low and control EF (Fig. 3 panels a–c, Table 4a of Appendix 4 of the ESM). *Potamocypris* (generalist) showed no significant increase in the population synchrony

under high EF as compared to low and control EF (Fig. 3 panel c, Table 4a of Appendix 4 of the ESM).

In general, metacommunities with four species showed significantly lower population synchrony than those with one and two species (Fig. 3 panels d–f; Table 4b of Appendix 4 of the ESM). However, population synchrony did not significantly differ between metacommunities containing one and two species for *Ceriodaphnia* (specialist) and *Daphnia* (intermediate). On the other hand, for *Potamocypris*, population synchrony did significantly differ between metacommunities of one and two species (Fig. 3 panel f, Appendix Table 4b of the ESM).

We found no correlation between the average density and the species richness for any of the three species (*Daphnia*: $r^2 = 0.63$, $P = 0.10$; *Ceriodaphnia*: $r^2 = 0.29$, $P = 0.34$; and *Potamocypris*: $r^2 = 0.05$, $P = 0.71$), suggesting that the calculated population synchrony was not an artifact of the population dynamics being dominated by the increase in density. Further, one of our expectations was that the population synchrony among local populations declines as species richness increases, which may be due to an elevated interaction contingency when more species are present. Thus, we measured population growth rates, variability of population growth rate (growth rate variability), and population-level instability (coefficient of variation of population size, CV) in each treatment of species richness and EF as indices of interaction contingency. We tested whether these indices varied among the species richness and EF treatments for the three species. We found that population growth rates differed among the species richness and EF among the three species (Table 2a; Fig. 4 panels a–c). Further, Fig. 4 (panels a–c) and Table 2a indicate that the significant interaction term

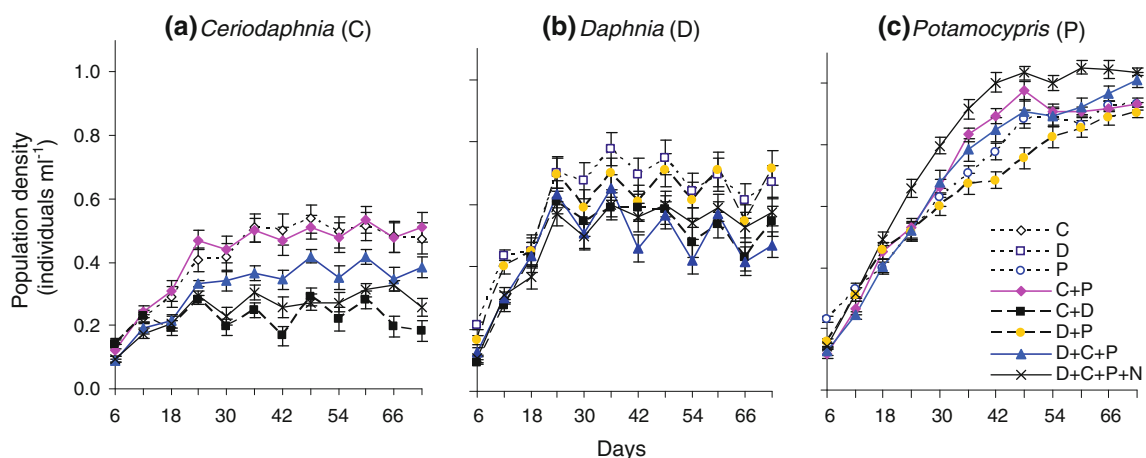


Fig. 1 Population densities (individuals ml^{-1}) of **a** *Ceriodaphnia*, **b** *Daphnia*, and **c** *Potamocypris* during the main experiment. Data points are the average population size (\pm SE) of each species in metacommunities exposed to three environmental fluctuation (salinity) treatments. There were three metacommunities with single

species; i.e., *Ceriodaphnia* (C), *Daphnia* (D), and *Potamocypris* (P), three metacommunities with two species (C + P), (C + D), and (D + P), one metacommunity with three species (D + C + P), and one metacommunity with four species (D + C + P + N)

Table 1 Summary of results of general linear models (two-way ANOVA table) for the effects of species richness, S , amplitude of environmental fluctuations (EF), and their interaction (EF \times S) on population synchrony of three species in metacommunities

Species	Treatment	SS	df	MS	F	p
<i>Ceriodaphnia</i> (specialist)	EF	0.050	2	0.025	12.824	0.034
	S	0.082	3	0.027	13.938	0.029
	EF \times S	0.003	6	0.001	0.255	0.927
	Error	0.006	3	0.002		
<i>Daphnia</i> (intermediate)	EF	0.030	2	0.015	17.981	0.021
	S	0.050	3	0.017	20.271	0.017
	EF \times S	0.001	6	0.000	0.273	0.918
	Error	0.002	3	0.001		
<i>Potamocypris</i> (generalist)	EF	0.000	2	0.000	0.018	0.982
	S	0.021	3	0.007	23.295	0.014
	EF \times S	0.002	6	0.000	1.249	0.463
	Error	0.001	3	0.000		

SS sum of squares, df degrees of freedom, MS mean squares; significant effects are shown in bold type

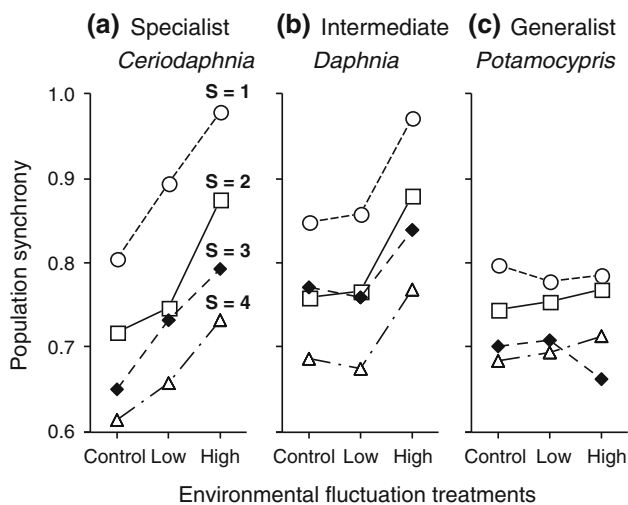


Fig. 2 Two-way interactions (species richness, S ; and the magnitude of environmental fluctuations) on population synchrony for three species: **a** specialist *Ceriodaphnia*, **b** intermediate *Daphnia*, and **c** generalist *Potamocypris*. The species richness of metacommunities varied from one to four ($S = 1$ –4). Mesocosms were exposed to no (con, control), low and high environmental fluctuation (treatments). In this analysis, we used the data for two metacommunities with a species richness of two ($S = 2$) and one metacommunity for all other species richness levels

for *Ceriodaphnia* resulted from the fact that its population growth was higher with high EF but only when the richness was 2–4, not for a richness of 1. For *Daphnia*, the growth rates were not significantly different among the species richnesses and levels of EF fluctuation. *Potamocypris* showed significant differences along the species richness gradient but not significant differences with changes in EF treatment (Table 2a; Fig. 4 panel c). Regarding the variance in the population growth rate, the growth rate variability increased in communities with higher species

richness, but it was not significant for two (intermediate and generalist species) of the three species (see Table 2b; Fig. 4 panels d–f). Similarly, population-level instability (percentage of coefficient of variation) increased with higher EF for the specialist and intermediate species (*Ceriodaphnia*, *Daphnia*), but decreased for the generalist (*Potamocypris*) (Table 2c; Fig. 4 panels g–i). In general, the instability declined for all species in communities with higher species richness, but this was significant only for *Potamocypris* (the generalist species) (Table 2c; Fig. 4 panels g–i).

Discussion

Our study shows that processes involved in the formation of metacommunities may challenge the current metapopulation paradigm because they involve two aspects that were largely overlooked. One is differences or gradients in the habitat specialization of species. The other is the effect of species richness (but see Loreau and de Mazancourt 2008). The species specialization gradient affects community structure and dynamics by differentiating growth rates, while species richness most likely does so through by systematically interfering with the predictions of metapopulation dynamics based on dispersal and Moran effects alone.

Specifically, we found that both species richness and the amplitude of environmental fluctuations affect population synchrony among the microcosms constituting a metacommunity. However, the degree of population synchrony differed depending on the ecological specialization of the species. Our expectation that population synchrony would

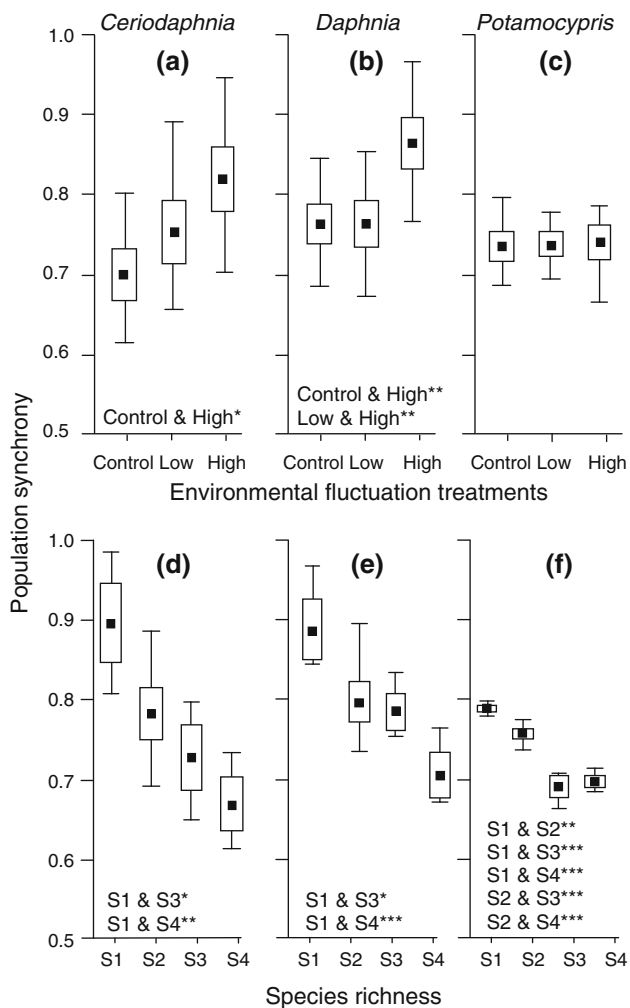


Fig. 3 Population synchrony using a post hoc Student–Benjamini–Hochberg (BH) test for the effects of (a–c) no (control), low and high environmental fluctuations, and (d–f) species richness ($S = 1–4$). Boxes represent the interquartile range, central points represent the mean, and whiskers represent minimum and maximum values. Asterisks identify groups that were significantly different at $P \leq 0.01$ (***), $P \leq 0.05$ (**), and $P \leq 0.1$ (*); see the Appendix in the ESM for all values of P

be higher in metacommunities exposed to high environmental fluctuations was upheld for the specialist and intermediate species, but not for the generalist. It is possible that these results were caused by species-specific differences in growth rates, as species with higher growth rates are also able to better track environmental changes. We checked whether the growth rates under the control conditions without other species were species-specific, but found no significant differences in growth rates between the different species in the control monocultures (Table A5a in Appendix 5 of the ESM). Further, the results for the effects of specialization could have been influenced by the fact that the species may have differed in their competitive abilities. We checked whether the growth rate

of *Ceriodaphnia* (specialist species) in the metacommunity with *Daphnia* present differed from that in the metacommunity without *Daphnia*, but found no significant differences in the growth rates of *Ceriodaphnia* in the metacommunity containing *Ceriodaphnia* and *Daphnia*; or in the metacommunity containing *Ceriodaphnia* and *Potamocyparis* in the control EF treatment (Table A5b in Appendix 5 of the ESM).

Previous studies predicted that the degree of synchrony should depend on the relative strength of the environmental fluctuation (e.g., Ranta et al. 1997a), with stronger fluctuation producing higher synchrony. However, our study identifies a possible general effect that the degree of synchrony also depends on how a particular species perceives the strength of the environmental fluctuation, since our study found that the correlated environmental fluctuation has differing effects on the synchrony of species with different specializations. This implies in particular that lower levels of environmental fluctuation are required to alter the population dynamics of specialist and intermediate species than those of generalist species. Since a metacommunity consists of a mix of generalist and specialist species (Pandit et al. 2009), we predict distinctly unequal levels of synchrony among the species forming a metacommunity.

Moran (1953) assumed that, for a linear model of population density, populations would synchronize to the same degree as the environment. This was not the case in our study, where population synchrony never matched the level of correlation of environmental fluctuation for any of the species. Our result is in agreement with other research involving natural (Grenfell et al. 1998) and experimental (Benton et al. 2001; Fontaine and Gonzalez 2005) communities. For example, Grenfell et al. (1998) examined synchrony in populations of feral sheep on two neighboring islands where there was no dispersal between islands, and found that an environmental correlation of ~ 0.9 was required to produce the observed population synchrony of 0.685. Similarly, experiments involving soil mites revealed levels of synchrony of about 0.75, even when environmental noise was perfectly correlated among patches (Benton et al. 2001). Although the salinity fluctuation treatment was strong enough to change the population dynamics for specialist species in our experiment, fluctuations of population growth rates showed limited synchrony. Fontaine and Gonzalez (2005) suggested that the Moran effect and dispersal interacted to increase population synchrony. However, Vasseur and Fox (2009) recently argued that the Moran and dispersal effects depend on the trophic position of the species. They found that the Moran effect significantly induced synchrony of the prey (*Tetrahymena pyriformis*), but that dispersal was able to induce synchrony of the prey species only in the presence of

Table 2 Summary of the results of general linear models (two-way ANOVA table) for the effects of species richness (*S*), amplitude of environmental fluctuations (EF), and their interaction (EF × *S*) on (a) the population growth rate, (b) the variance in the population growth rate, and (c) the population-level instability (coefficient of variation in population size, CV)

Treatment	(a) Population growth rate					(b) Var. in pop. growth rate				(c) Population-level instability			
	<i>df</i>	SS	MS	<i>F</i>	<i>P</i>	SS	MS	<i>F</i>	<i>P</i>	SS	MS	<i>F</i>	<i>P</i>
<i>Ceriodaphnia</i> (specialist)													
EF	2	0.545	0.272	23.233	0.000	8.415	4.207	4.710	0.014	1431.43	715.72	13.95	0.00
<i>S</i>	3	0.141	0.047	4.011	0.013	7.509	2.503	2.802	0.050	315.28	105.09	2.05	0.12
EF × <i>S</i>	6	0.266	0.044	3.775	0.004	5.565	0.927	1.038	0.413	445.72	74.29	1.45	0.22
Error	48	0.563	0.012			42.883	0.893			2463.57	51.32		
<i>Daphnia</i> (intermediate)													
EF	2	0.079	0.039	1.834	0.171	2.082	1.041	1.972	0.150	1330.79	665.39	16.42	0.00
<i>S</i>	3	0.114	0.038	1.775	0.164	2.233	0.744	1.410	0.251	50.59	16.86	0.42	0.74
EF × <i>S</i>	6	0.162	0.027	1.261	0.293	3.413	0.569	1.077	0.389	174.26	29.04	0.72	0.64
Error	48	1.029	0.021			25.339	0.528			1945.58	40.53		
<i>Potamocypis</i> (generalist)													
EF	2	0.011	0.005	0.612	0.546	0.637	0.318	1.132	0.331	237.41	118.71	5.29	0.01
<i>S</i>	3	0.171	0.057	6.547	0.001	1.005	0.335	1.191	0.323	327.66	109.22	4.87	0.01
EF × <i>S</i>	6	0.014	0.002	0.262	0.952	1.632	0.272	0.967	0.457	88.70	14.78	0.66	0.68
Error	48	0.418	0.009			13.501	0.281			1076.64	22.43		

SS sum of squares, *df* degrees of freedom, *MS* mean squares; significant effects are shown in bold type

predators. They predicted that the Moran effect combined with predator synchrony would induce a prey synchrony that would be greater than that of its predator. Such propagation of effects down the food chain did take place in their study system when dispersal was present, but not when it was absent. In our study, the mismatch between population synchrony and environmental correlation likely results from strong nonlinearities in the growth rate of each species in most of the treatments.

The nonlinearities in the growth rates of species may have reduced the effects of the environmental forcing, as explained by Grenfell et al. (1998, 2000) and others (Benton et al. 2001; Greenman and Benton 2001; Royama 2005). These studies explained the loss of correlation between environmental and population synchrony as being due to nonlinearities in the density dependence. Such nonlinearities, by changing the rate or direction of population growth, may produce different behaviors in different patches and thus de-synchronize populations in spite of the correlated environmental forcing. Another reason for the poor correlation may be the dual nature of strong environmental noise, as explained by Ranta et al. (1997b), who noted that a strong environmental fluctuation that was correlated among locations may create synchrony in population fluctuations, but it may also modify or disrupt interspecific population dynamics over the long term.

Our expectation that population synchrony among local populations declines as the species richness increases was upheld by the analysis. In general, the findings are

consistent with theoretical results. Loreau and de Mazancourt (2008) suggested that population synchrony should be lower in communities with many species and provided a possible mechanism: demographic stochasticity is higher in communities with many species, and a higher demographic stochasticity reduces synchrony. However, such a reduction should depend on the strength of demographic stochasticity relative to the effect of environmental forcing in the community as a whole. Density vagueness—a stochastic variation of density increases in small populations (Melbourne and Hastings 2008; Reed 2008)—may have a similar effect to population synchrony. However, we found no consistent relationship between density and species richness in the experimental communities.

Another possible mechanism for this decline in synchrony may be an elevated interaction contingency when more species are present. Greater contingency is likely to disrupt the synchronization of populations among communities. Furthermore, if population growth rates are lower in higher species richness communities, the population synchrony might also decline even if populations tended to change in the same direction. Thus, we initially expected that the population growth rate would be lower in higher species richness communities, which might reduce the population synchrony. However, we found no support for this mechanism, since the three species differed in how their population growth rates decreased in response to increasing species richness (Table 2a). More specifically, for *Daphnia*, there were no significant changes in the

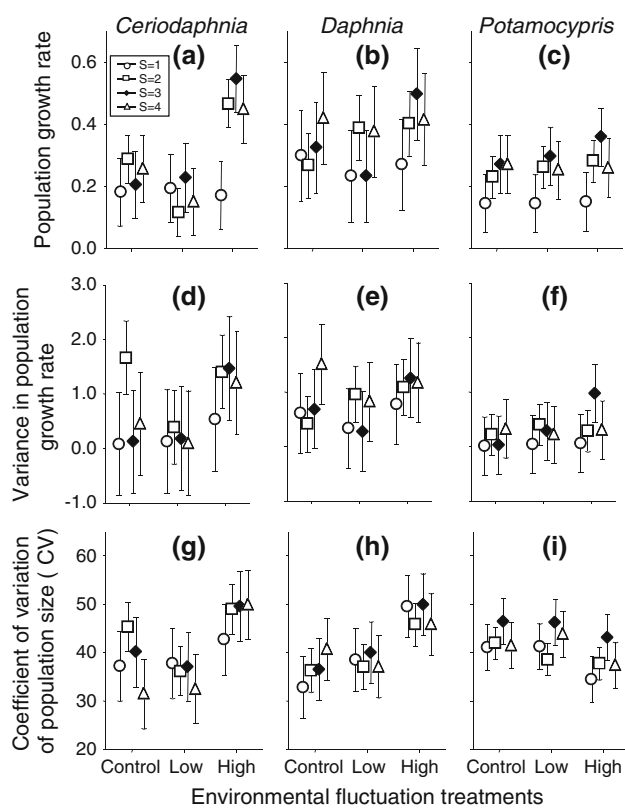


Fig. 4 Two-way interactions of species richness and the magnitude of environmental fluctuations ($S \times EF$) on **a–c** the population growth rate, **d–f** the variance in the population growth rate, and **g–i** the population-level instability (CV coefficient of variation of population size) for *Ceriodaphnia*, *Daphnia*, and *Potamocypris*. Symbols represent the mean; symbol shapes represent metacommunities of different species richness, S . Vertical bars denote 95 % confidence interval

population growth rate with different species richnesses, whereas there were for *Ceriodaphnia* and *Potamocypris* (Table 2a). In addition, we used the variance in population growth rates as an index of interaction contingency. The study shows that the variability in growth rates increased with species richness, even though this increase was significant for *Ceriodaphnia* only. Whether in response to species richness or by chance, the variance in growth rates was higher in replicates with more species. We thus suggest that increasing interaction contingency may have contributed to synchrony reduction in the communities with more species, thus providing a plausible mechanism for the observed pattern.

Another possible mechanism by which species richness might reduce synchrony is through the higher stability of population size generated by statistical averaging (cf. Doak et al. 1998). In fact, the growth response of each species to the environmental fluctuations, but also indirectly on changes in the abundances of each of the species in the

community (Ives 1995). For instance, compensatory effects—where an increase in the population of one species results in a decline in the population of the other—are frequently observed in plant and animal communities with high species richness (e.g., Naeem and Li 1997; Bai et al. 2004). As such, the dynamics of the monoculture populations and those of multispecies communities might be expected to differ, because the density of one species in a monoculture may decline rapidly under harsh environmental conditions, but it will recover rapidly once favorable conditions are restored, without any impact of interspecific competition or facilitation. In contrast, a natural metacommunity is more likely to include species with a range of environmental tolerances that will allow them to respond differently to environmental fluctuations. If these species compete or participate differently in a food processing chain, the recoveries of species may exhibit different dynamics in different populations, disrupting any synchrony among populations that environmental fluctuation might promote. This compensatory mechanism would be the case if there were consistent effects of the experimental treatments on population level instability and species growth rate. However, we found no evidence for such effects under higher species richness conditions (Table 2; Fig. 4). In fact, a recent meta-analysis (Jiang and Zhichao 2009) supports our results by showing that the temporal stability at community level increases with diversity, but that the effect of diversity on population level stability is neutral. Thus, the compensatory mechanisms invoked to explain the reduction in population synchrony under elevated species richness may not be generalizable to all species. By analogy, recent research finding indicates that environmental disturbances and noise may disrupt compensatory dynamics that could otherwise generate periods of correlated interspecific fluctuation at one or more temporal scales (see Vasseur and Fox 2007; Keitt 2008; Gouhier et al. 2010).

The observation that correlated environmental fluctuation has differing effects on the synchrony of species with different specializations but the same dispersal regime has implications for how we may interpret the dynamics of different species in the context of metacommunity. We have already shown (Pandit et al. 2009) that variation in the abundances of habitat specialists in a system of natural microcosms is best accounted for by the species sorting model (cf., Leibold et al. 2004). By contrast, either neutral or patch dynamics models apply to habitat generalists. Therefore, many species in communities that conform to the species sorting type of dynamics (e.g., Leibold et al. 2004; Ellis et al. 2006) should be synchronized primarily by synchrony of the important environmental variables. Many species in communities that conform to patch or neutral dynamics models should be much more influenced

by dispersal rates and factors affecting dispersal such as spatial configuration, connectivity, and dispersal barriers among patches (Cottenie 2005). This study thus supports the idea (Pandit et al. 2009; Pandit and Kolasa 2012) that the population dynamics of specialists are described better by species sorting models, since their population fluctuations were more affected by the environmental regime than those of the generalist.

Furthermore, the synchronizing roles of environment (on specialists) and of dispersal (on specialists and generalists) can be reduced by increasing the species richness of a target metacommunity. Consequently, one should expect different metacommunity dynamics under different levels of species richness. Differences in metacommunity dynamics due to richness may introduce variation into the performances of fitted metacommunity models.

Our findings potentially have some conservation implications. If population synchrony tends to be higher among specialists than generalists in habitats with spatially correlated EF, this raises a serious concern. Theoretical studies (e.g., Heino et al. 1997; Earn et al. 2000) have already shown that higher synchrony increases the risk of global metapopulation extinction, which adds one more factor to the increased vulnerability of specialists. However, we show that the effects of synchrony decline when species richness increases. If confirmed in natural systems, the richness may have positive impact on reducing the risk of extinction of habitat specialists. Thus, the finding provides yet another argument on behalf of biodiversity conservation.

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