Ecological drift and competitive interactions predict unique patterns in temporal fluctuations of population size

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Abstract. Recent studies have highlighted the importance of higher-order competitive interactions in stabilizing population dynamics in multi-species communities. But how does the structure of competitive hierarchies affect population dynamics and extinction processes? We tackled this important question by using spatially explicit simulations of ecological drift (10 species in a homogeneous landscape of 64 patches) in which birth rates were influenced by interspecific competition. Specifically, we examined how transitive (linear pecking orders) and intransitive (pecking orders with loops) competitive hierarchies affected extinction rates and population dynamics in simulated communities through time. In comparison to a pure neutral model, an ecological drift model including transitive competition increased extinction rates, caused synchronous density-dependent population fluctuations, and generated a white-noise distribution of population sizes. In contrast, the drift model with intransitive competitive interactions decreased extinctions rates, caused asynchronous (compensatory) density-dependent population fluctuations, and generated a brown noise distribution of population sizes. We also explored the effect on community stability of more complex patterns of competitive interactions in which pairwise competitive relationships were assigned probabilistically. These probabilistic competition models also generated density-dependent trajectories and a brown noise distribution of population sizes. However, extinction rates and the degree of population synchrony were comparable to those observed in purely neutral communities. Collectively, our results confirm that intransitive competition has a strong and stabilizing effect on local populations in species-poor communities. This effect wanes with increasing species richness. Empirical assemblages characterized by brown spectral noise, density-dependent regulation, and asynchronous (compensatory) population fluctuations may indicate a signature of intransitive competitive interactions.

Key words: community assembly; competition; density dependence; ecological drift; grid model; intransitive competition; neutral model; noise; spectral analysis; stability; Taylor's power law; time series.

Introduction

Analyses of empirical population time series have focused on the detection of ecologically important temporal patterns and processes (e.g., Turchin and Taylor 1992, Bjørnstad and Grenfell 2001, Brook and Bradshaw 2006), including community stability (Ives et al. 2003), the influence of environmental triggers (Coulson et al. 2004) and latitude on temporal variability (Doxford et al. 2013), and density-dependent population regulation (Turchin 2003, Ziebarth et al. 2010).

In a deterministic system without time lags, density dependence is characterized by a tendency for population trajectories to return toward a stable equilibrium point (such as the carrying capacity in a logistic growth model). In a simple stochastic system, equilibrium can be characterized by a system that approaches a stationary distribution, with a constant mean and variance (Turchin 2003). In contrast, even the simplest unregulated random walk will not achieve a stationary distribution because the variance increases through time (Berg 1993). A much richer array of possible outcomes is possible for more realistic stochastic models that include environmental stochasticity (temporal or spatial variation in vital rates), demographic stochasticity (fluctuations from random birth, death, or dispersal processes), and measurement error (uncertainty in the estimation of trajectories from empirical data). Constantino et al. (2005) extended studies of fluctuations in flour beetles (*Tribolium castaneum*) exemplify the complexity that can arise from the interactions of these different kinds of stochasticity.

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However, this fundamental corpus of literature, together with the many available studies dealing with single species-time series (Taylor 1961, Routledge and Swartz 1991), constitutes just a first step in the overly challenging path of discovery of the natural world's complexity. In fact, the individual temporal dynamics of a species in most real-world ecological settings cannot be simply regarded as self-regulated processes subjected to various sources of stochasticity. Instead, it is becoming increasingly clear that higher-level processes, including assemblage-level regulation (Gotelli et al. 2017) and pairwise species interactions, are important elements of species coexistence and community stability (e.g., Hart et al. 2016, Serván et al. 2018).

Simultaneous interactions within multi-species communities and their effects on temporal population variability have received relatively less attention than pairwise interactions, and have sometimes generated conflicting results (Godoy et al. 2017, Grilli et al. 2017). Models developed in this context have used a generalized Lotka-Volterra framework of first-order differential equations (Kokkoris et al. 2002, Dobramysl et al. 2018), or stochastic particle systems (Foley 1994) either with static (e.g., Cattin et al. 2004) or dynamic parameters (e.g., Cohen et al. 1990). In most of them, long-term stability requires specific parameter combinations and/or variable interaction strength (Taylor 1988, Allesina and Tang 2012, Serván et al. 2018). However, Grilli et al. (2017) made a convincing argument that diversity can be maintained even without assuming competitive equivalence between species (Gilpin 1975), showing how higher-order species interactions promote stable, long-term multi-species coexistence even when interaction coefficients are determined by a random draw from a uniform distribution.

Here we take a further step, by examining the different effects of nonrandom competitive hierarchies on community stability. Transitive competitive hierarchies are characterized by a linear pecking order (species A > B > C > D) whereas intransitive competitive hierarchies contain loops in the order of competitive strength (A > B > C > D > A; Laird and Schamp 2006). Soliveres et al. (2015), Laird and Schamp (2015), and Ulrich et al. (2018) demonstrated that competitive intransitivity can stabilize ecological communities and increase local species richness (but see Godoy et al. 2017). However, the impact of intransitive competition on the temporal variability of relative species abundance and community composition has not received sufficient attention so far.

In multi-species communities, the temporal variability in total abundance and species richness is often less than that of individual species (Doak et al. 1998), and may be regulated by a simple portfolio effect (Gotelli et al. 2017), in which stability is obtained from the sum of stochastic fluctuations (Loreau and de Mazancourt 2008). However, it is unknown how intransitive competitive interactions influence single species population dynamics and the stability of the whole community.

Because intransitivity may reduce local species extinction and increase species richness (Soliveres et al. 2015, Ulrich et al. 2017, 2018, but see Godoy et al. 2017), it should have a stabilizing effect on population dynamics and community structure.

Spectral analysis of time series, in which a time series is decomposed into a mixture of different sinusoidal functions, is commonly used to infer short- and long-term patterns in variability (Box et al. 2015). The slope of the respective power spectrum indicates the difference in short-term vs. long-term variation. A slope $z = 0$ indicates equal contribution of short-term and long-term fluctuations (white noise), whereas $z > 1$ indicates a greater importance of long-term fluctuations (brown and red noise). Many empirical time series exhibit red ($z \approx 1$) and brown noise (Pimm and Redfearn 1988), as do simple models of ecological drift (McGill et al. 2005). But what does the power spectrum of populations look like when competitive interactions are included?

Null model analysis could answer this question: observed patterns of temporal fluctuations are compared with randomized assemblages built according to specific ecological hypotheses (Gotelli and Ulrich 2012). Most previous studies of temporal fluctuations have used a random walk as a (null) frame of reference to identify nonrandom patterns in empirical time series (e.g., Bulmer 1975, Ulrich et al. 2017). In contrast, Gotelli and McGill (2006), He et al. (2012), and Rosindell et al. (2012) advocated neutral ecological drift (Hubbell 2001) as an appropriate null standard. However, neutral models have not been used in this way, in part because it is difficult to directly estimate their parameters (Gotelli and Ulrich 2012). However, even in the absence of direct comparisons with empirical data, stochastic simulations that are "null" with respect certain processes are still important for understanding what kind of patterns these mechanisms can generate.

Here, we use an individual-based spatially explicit neutral drift model (Hubbell 2001) enriched by transitive and intransitive competitive interactions (Ulrich et al. 2017) to infer the impact of competition on the form of population time series. In this simulation model, we have assumed the environment is constant in space and time, so there is no component of environmental stochasticity. We also did not incorporate measurement error because we are not trying to compare model results with empirical time series. Instead, our model isolates the effect of demographic stochasticity (random birth, death, and movement of individuals across a landscape) in combination with transitive and non-transitive competitive interactions.

Previously, we have used the same model to demonstrate that intransitivity is able to increase local richness and to generate nonrandom patterns of species co-occurrence (Ulrich et al. 2017). Here we ask (1) which patterns of population fluctuation are expected under pure neutral conditions? (2) How, if at all, do competitive interactions change these patterns? (3) Can intransitivity

generate compensatory fluctuations and density-dependent population regulation? And (4) do intransitive interactions modify local extinction probabilities?

<div style="text-align:center">METHODS</div>

<div style="text-align:center">*The ecological drift model*</div>

This analysis is based on a simulation platform for neutral community modeling that combines a spatially explicit ecological drift process with competitive species interactions (Ulrich et al. 2017). Here, we use a square grid of $N = 64$ contiguous patches initially populated randomly by $S = 10$ species (complete model settings are contained in the electronic Appendices S1 and S2). Smaller grids (≤ 32) might have generated possible edge effects, while in larger grids, edge effects are negligible (Ulrich et al. 2017). To investigate the potential effects of grid size, we also ran our models for a large grid of 144 patches. Because the results for both grid sizes were qualitatively identical, we present only results for the smaller grid (64 patches). We provide details and major results for the larger grid in Appendix S1. We tracked the population fluctuations of all species in the innermost patch only and did not analyze temporal trajectories from the other 63 patches in the grid (Appendix S1: Fig. S1).

Total meta-community size J (the total number of individuals in the grid) of the 64 patches grid ranged between 6,400 ($10 \times S \times N$) and 102,400 ($160 \times S \times N$), equivalent to an initial average of 10 to 160 individuals per species and patch. The subsequent birth/death and colonization/extinction dynamics in each patch followed the zero-sum rule of Hubbell (2001): each local birth, death, immigration, or emigration (all probabilities set to 0.01 leading to 64 to 1,024 such events at each time step) was immediately counterbalanced by a corresponding death, birth, emigration, or immigration (Appendix S2: Table S1, Fig. S1). Although these values are arbitrary, Ulrich et al. (2017) demonstrated that these migration probabilities ($P < 0.001$) did not influence patch species richness. We did not use very high probabilities to ensure that the same individuals were not selected several times at each time step.

In the pure neutral model, the individuals involved in these processes were selected at random irrespective of species identity. Any grid-wide species extinction was counterbalanced by a speciation event from a single point mutation of a randomly selected individual (Ulrich et al. 2017). We note that the zero-sum constraint is a simplifying assumption of the original neutral model of Hubbell (2001). However, our approach focuses on the abundance fluctuations of single species, making the community-wide zero-sum assumption less important. Moderate fluctuations of total community abundances do not influence our results because these fluctuations affect all species similarly.

Second, we incorporated the effects of direct pairwise competition on birth rates using the Markov chain approach of Ulrich et al. (2014, 2017). This method uses the fact that a pairwise species interaction matrix $\mathbf{C}$ (as defined by Laird and Schamp 2006) can be translated into a unique column stochastic transition matrix $\mathbf{P}$ (Appendix S1: Fig. S1). The inner product $\mathbf{PA_0} = \mathbf{A_1}$ provides the vector of expected species abundances $\mathbf{A_1}$ after one time step, given initial abundances $\mathbf{A_0}$. Within a neutral model framework, birth probabilities (population increase) are proportional to current abundances. Therefore, the inner product

$$\mathbf{PA_0} = \mathbf{A_1} \propto \mathbf{B_1} \qquad (1)$$

generates the vector $\mathbf{B}$, which (after normalization) contains the local birth probabilities of an individual in the community. In this way, our model incorporates effects of direct (pairwise) competition on birth rates (Appendix S1: Fig. S1). Thus, birth rates are affected by the density of competing species, but do not contain an intraspecific density effect. Therefore, our model is no longer strictly neutral.

<div style="text-align:center">*Simulation protocol*</div>

To assess the influence of interspecific competition on otherwise neutral communities, we created a factorial design and crossed two levels of dispersal limitation (unconstrained, all cells are equally likely to be the target of dispersal; limited dispersal, only the adjacent eight cells [Moore neighborhood] can reach in a single dispersal step), with four levels of competitive interactions (no interaction, fully transitive, intransitive, complex; the respective competition matrices are contained in Appendices S1 and S2).

In the fully transitive competition matrices, competitively inferior species were assigned a fitness value of zero, leading to an upper triangular matrix of interaction coefficient containing only 1s (Appendix S2: Table S2). In the intransitive case, the fitness of the four most competitive species was set to zero with respect to the least competitive species (Appendix S2: Table S2), thus forming a competitive loop. Finally, we used a complex transitive competition matrix forming a competitive network (Allesina and Levine 2011), in which competitively superior species were assigned high, but not maximum, fitness with respect to competitively inferior species (Appendix S2: Table S2).

In the pure neutral case, we used five meta-community sizes; in the models with competitive interactions, we used only two (high and low) meta-community sizes (Appendix S2: Table S1). Because variability in the model output within parameter sets was low in comparison to the variability between neutral and competitively structured communities, we achieved consistent, repeatable results by replicating each parameter combination only 10 times.

To ensure equilibrium conditions were achieved, we ran for all models an initial burn-in (cf. Ulrich et al.

2017) that incorporated between 32,000 (for the lowest total meta-community size, i.e. $J = 6,400$) and 5,120,000 (for the highest meta-community size, i.e. $J = 102,400$) birth/death, immigration/emigration, speciation/extinction events. This burn-in corresponded to approximately 50 cycles of complete turnover in species composition. After this burn-in, total species richness per patch did not show any systematic change through time.

Within this modeling framework, we defined a generation as the number of single birth/death steps needed to replace all individuals of the grid that is the meta-community size J. After the burn-in, we ran the different models for another $T = 150$ generations and recorded the abundances of all species in each time step. This resulted for each of the 18 different models (Appendix S2: Table S1) in a 10 (species) $\times$ 150 (time steps) matrix of time series.

Analyzing temporal variability

To study the average amplitude in population fluctuations we calculated for each species the dispersion index of (Lloyd 1967):

$$L = \frac{\sigma^2}{\mu^2} - \frac{1}{\mu} + 1 \qquad (2)$$

where μ and σ^2 are the mean and variance, respectively, of the species-time series. A Poisson random process yields $L = 1$. The empirical Taylor's power law states that the species population fluctuations within a community follow a proportional rescaling pattern ($\sigma^2 \propto \mu^z$) with exponent $z \approx 2$ (Giometto et al. 2015). Exponents $z \approx 1$ are equivalent to a Poisson resampling process. We calculated z from the slope of the power function $\sigma^2 = f(\mu)$ relationship across of a given model community. We also measured total local extinction rates as the number of times in which a species reached zero patch abundance divided by matrix size ($S \times T$).

We studied spectral properties of the time series using the power function slopes β of the spectrograms:

$$\sigma^2(f) = (1/f)^{\beta} \qquad (3)$$

where f denotes the time interval (band width) and $\sigma^2(f)$ is the associated variance in mean abundance. For the time series of 150 generations, we calculated for each species the exponent β from seven time intervals (1, 2, 4, 8, 16, 32, 64). We excluded species absences from calculations. Below we present community-wide averaged values of β. $\beta = 0$ (white noise) means that the variance in abundance is similar for all frequencies. Higher variability at longer band widths returns $\beta \gg 0$ (red and brown noise).

We note that the precise estimation of spectral exponents requires long time series. Short series are prone to increased estimation errors. However, we were not mainly interested in precise spectral data for single

species but in community-wide patterns. Therefore, we used community averages. To exclude a possible bias due to variation in species abundance and temporal species absences, we always compared competitively structured communities with the neutral standard. This comparison is similar to a mechanistic null model approach (Gotelli and Ulrich 2012) and provides a reliable baseline for measuring the effects of competition on species temporal variability.

Bulmer's (1975) first autocorrelation method has been widely used as a sensitive test of density-dependent population regulation with low type I and II errors rates (Pollard et al. 1987, Fox and Ridsdill-Smith 1995). However, Bulmer's test, as well as more recent state space Gompertz models (Dennis et al. 2006), can yield biased results in cases of temporal trends in abundance (Fox and Ridsdill-Smith 1995), census errors and undersampling (Freckleton et al. 2006, Knape 2008), unequal time intervals (Dennis and Ponciano 2014), and strong Allee effects (Stephens et al. 1999). Our model time series had no detection errors, were assessed at equal time intervals and, stemming from random drift, did not include any Allee effects. Moreover, the burn-in period ensured that population data were taken at equilibrium conditions. Therefore, these series fully met the constraints of the random walk assumption on which Bulmer's and other autocorrelation tests are based. Nevertheless, a random walk implies that some populations might exhibit short-term stochastic temporal trends. To ensure that such trends did not affect the results, we additionally detrended each series using a linear regression on the log-transformed abundances

$$x_t = \ln(a_t + 1) - (mt + b) \qquad (4)$$

where a_t is the abundance at time t and m and b are the slope and the intercept, respectively, of the linear regression between $\ln(a_t + 1)$ and time t. The quotient

$$R = \frac{V}{U} = \frac{\sum_{t=1}^{T-1} (x_{t+1} - \bar{x})^2}{\sum_{t=1}^{T-1} (x_{t+1} - x_t)^2} \qquad (5)$$

was compared to the lower boundary $R_L = 1/4 + (T - 2)\xi_L$. Here, we used $\xi_L = 0.017$, which denotes the empirical 0.1% margin of the V/T^2 random distribution. Importantly, we used this lower boundary only as an additional criterion as we compared the time series with competitive interactions to those of pure neutrality. The latter served in all tests as the baseline null standard (Rosindell et al. 2012).

To infer the degree of temporal synchrony in abundance between species, we used the index of Loreau and de Mazancourt (2008) and calculated the quotient

$$\varphi = \frac{\sigma_t^2}{\left(\sum_i \sigma_i\right)^2} \qquad (6)$$

where σ_i^2 denotes the total variance through time in the summed abundance of all species, and σ_i is the standard deviation of species i along the time series. Values of $\varphi < 1$ indicate compensatory effects in abundance, whereas $\varphi > 1$ points to synchrony in abundance variation and lack of compensation. Again, we compared time series incorporating competitive interactions with those generated by pure neutral drift. For each of the four metrics (Eqs. 1–4), we used community averages and their respective variances in subsequent analyses.

To explore temporal variability in community composition, we calculated the average degree of species co-occurrences in time using the abundance-based weighted C score (WCS) introduced by Ulrich and Gotelli (2010). This metric is the abundance analogue of the familiar incidence-based C score (Stone and Roberts 1990) and is a normalized count of the number of abundance checkerboards of the form $CA = \begin{pmatrix} a & b \\ c & d \end{pmatrix}$, where $a > b$, $a > c$, $d > b$, $d > c$ or $a < b$, $a < c$, $d < b$, $d < c$

$$\text{WCS} = \frac{n(\text{CA})}{S(S-1)T(T-1)} \quad (7)$$

where $n(\text{CA})$ is the total number of abundance checkerboards.

Because this metric depends on matrix fill and size, we compared observed scores with a null model that resamples individuals proportional to observed marginal totals until, for each row and column, the observed total number of individuals is reached (the IT null model in Ulrich and Gotelli (2010)). Ulrich and Gotelli (2010) advocated this null model because it is least affected by matrix fill, shape, and size. We measured effect sizes $\Delta \text{WCS} = \text{WCS} - \text{WCS}_{\text{exp}}$ and standardized effect sizes $\text{SES} = \Delta \text{WCS}/\sigma_{\text{WCSexp}}$, where WCS_{exp} and σ_{WCSexp} are the mean and the standard deviation, respectively, of the null model distribution. When used in this form, ΔWCS is an averaged matrix-wide measure of the degree of temporal synchrony in abundance ($\Delta \text{WCS} < 0$) or of temporal segregation ($\Delta \text{WCS} > 0$). Under the assumption of an approximately normal null model distribution, $|\text{SES}| > 2$ indicate statistically significant deviations from the null model expectation at roughly the two-sided 5% error level.

Results

Competitive interactions, but not the degree of dispersal limitation, had a strong influence on the temporal fluctuations of the model communities (Table 1, Figs. 1, 2). Transitive competition caused rapid extinction of the weaker species and leading to the persistence of only the strongest competitors (Appendix S1: Table S1). Therefore, we did not use these transitive simulations in the following analyses of the impact of competition on community patterns.

Extinction rates per patch decreased with increasing meta-community size by power functions (Fig. 1a). Intransitive competitive loops decreased species extinction rates (Fig. 1a), while complex competitive interactions also decreased extinction rates, but only at large meta-community size (Fig. 1a). Grid size did not affect this result. For a larger grid of 144 cells, we obtained qualitatively identical results (Appendix S1: Fig. S2).

Competitive effects decreased Taylor's z (Fig. 1b) with respect to the neutral baseline, implying more synchrony in abundance fluctuations irrespective of average abundance. The variability in population fluctuations quantified by the Lloyd index of dispersion strongly differed with respect to the type competition (Table 1).

Lloyd's index was lowest in cyclic intransitive communities (Fig. 2a). Communities governed by complex competitive interactions did not significantly differ from the pure neutral ones in the degree of dispersion (Fig. 2a). In pure neutral and complex competitive communities, but not in intransitive communities, the degree of dispersion decreased with increasing meta-community size (Fig. 2a). The variability in dispersion among the model communities was lowest in the case of cyclic intransitive interactions (Fig. 3a). Again, this result was not influenced by grid size (Appendix S1: Fig. S4).

Neutral communities exhibited pink-to-red noise ($0.3 < \beta < 1.5$) abundance fluctuations (Fig. 2b). Color changed from red to pink with increasing meta-community size (Fig. 2b). Competitive interactions strongly changed this pattern irrespective of grid size (Table 1, Fig. 2b, Appendix S1: Fig. S3b). Cyclic intransitive competition shifted the spectrum toward brown ($\beta > 1.5$) noise. In turn, the opposite shift appeared when comparing the variability among communities (Fig. 3b): cyclic

TABLE 1. Estimated coefficients and the explained variance r^2 for a general linear model of six time series metrics as a function of different models of competitive interaction and the degree of dispersal.

Variable	df	ES WCS	Taylor's z	Dispersion	Noise	Density dependence	Synchrony
Competition	2	0.22**	0.45***	0.76***	0.88***	0.76***	0.28**
Dispersal	1	<0.01	0.01	<0.01	0.01	<0.01	<0.01
Competition × Dispersal	2	0.01	0.02	0.01	0.02	0.01	0.02
ln J	1	0.02	0.02	0.01	0.01	0.06	<0.01
Extinctions	1	0.01	<0.01	0.61***	0.06	0.05	0.08
r^2 (model)		0.26**	0.44***	0.91***	0.88***	0.79***	0.48***

Notes: Error df = 82. WCS, weighted C score
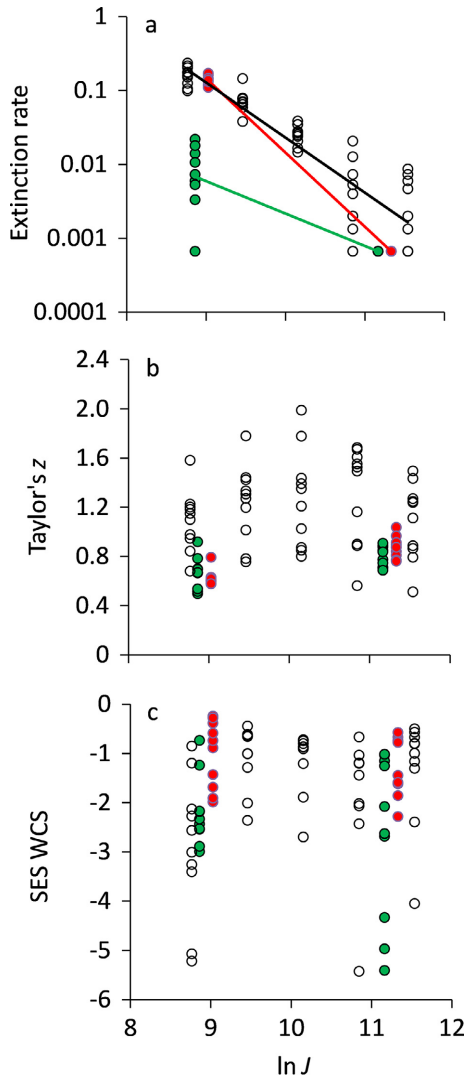**$P < 0.01$, ***$P < 0.001$ (Bonferroni-corrected parametric values).

FIG. 1. Dependencies of (a) extinction rates, (b)the slope z of Taylor's power law, and (c) the standardized effect sizes SES of weighted C score (WCS) measure of temporal co-occurrence on ln-transformed meta-community size J. Open circles, ecological drift only; green circles, ecological drift + cyclic intransitive competition; red circles, ecological drift + complex competition. $N = 10$ replicates simulated for each value of J. Power function regression between extinction rates and J in panel a) black (pure neutral) $r^2 = 0.81$, slope $z = -1.71$; green $r^2 = 0.75$, $z = -1.01$; red $r^2 = 0.99$, $z = -2.31$.

intransitive competition resulted in a low variability among communities of identical parameter settings (Fig. 3b).

In spite of the zero-sum assumption, pure neutral communities did not exhibit a density-dependent regulation of abundances (Fig. 2c, Appendix S1: S3c). For all meta-community sizes, Bulmer's R was above the significance threshold for density dependence (Fig. 2c) and increased with increasing meta-community size. Competitive interactions, irrespective of type, introduced a

significant (Fig. 2c, $P < 0.001$) signal of density-dependent regulation. The strength of this signal did not change with meta-community size. Again, the variability in the degree of density-dependent regulation was lowest in communities governed by cyclic intransitive competition (Fig. 3c).

We used two measures of temporal synchrony in species abundances. In all model communities, segregation in abundance was lower than expected from the null model (Table 1, Fig. 1c). The three community types significantly differed with respect to SES WCS (Fig. 1c, one-way ANOVA $P(F_{2,87}) < 0.001$). The φ metric (Table 1, Fig. 2d, Appendix S1: Fig. 3Sd) pointed to a significantly lower degree of temporal abundance compensation (temporal asynchrony) in the communities governed by cyclic intransitive competition in comparison to pure neutral ones. Communities with complex competitive interactions did not differ from the pattern observed in the pure neutral communities (Fig. 2d).

DISCUSSION

Results from our simulations on neutral and non-neutral model meta-communities provide important insights on the ecological mechanisms affecting temporal patterns of population fluctuations. First, we asked which patterns of population fluctuation are expected under pure neutral conditions. This question has no simple answer because the degree of fluctuation strongly depends on the length of the time interval used to infer variability. In our analysis, we measured population abundances and community structure after each complete turnover of individuals, that is, approximately, every generation. We consider this temporal resolution as the most ecologically meaningful for the purposes of the study. At the temporal scale of one generation in our model, neutral population variability appeared to be equivalent to a random walk constrained by patch size. McGill et al. (2005) neutral model also generated brown noise, but these authors did not relate their findings to the model parameter settings and the spectrogram slope. Our simulations point to a range of possible slopes and consequently colors, even at identical initial parameter settings. Spectral color changed from brown to pink with increasing community size.

Our second question was how, if at all, do competitive interactions change these patterns? Transitive and intransitive competitive interactions had opposite effects. Intransitivity shifted the spectral colors toward long-term brown noise, whereas transitive competition shifted the spectral colors toward short-term white noise (Fig. 1). Intransitivity strongly reduced the variability in spectral colors among species (Fig. 3b) in comparison to transitive interactions. Therefore, intransitive competition reduced temporal population fluctuation (Figs. 1a, 2a) and consequently stabilized local populations. This lower variability decreased local extinction rates, irrespective of meta-community size (Fig. 1b). Based on the
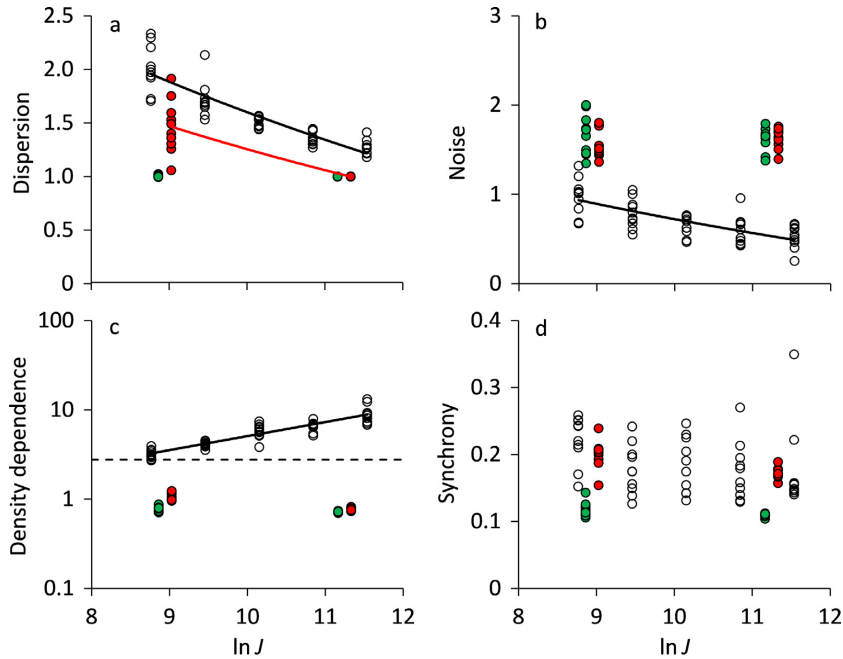
FIG. 2. Dependencies of the average values of (a) temporal dispersion in abundance, (b) spectral density noise, (c) temporal density dependence, and (d) temporal synchrony as a function of ln-transformed meta-community size J. Open circles, ecological drift only; green circles, ecological drift + cyclic intransitive competition; red circles, ecological drift + complex competition. $N = 10$ replicates for each value of J. The broken black line in panel c denotes the lower R value for density dependence at the 1% error level according to Bulmer's (1975) test. The respective variability (except for synchrony) for each metric is given in Fig. 3. Power function regressions between the metric and J in (a) black (pure neutral) $r^2 = 0.79$, slope $z = -2.70$ and red $r^2 = 0.66$, $z = -2.05$; (b) black $r^2 = 0.51$, $z = -1.63$; (c) black $r^2 = 0.85$, $z = 0.36$.
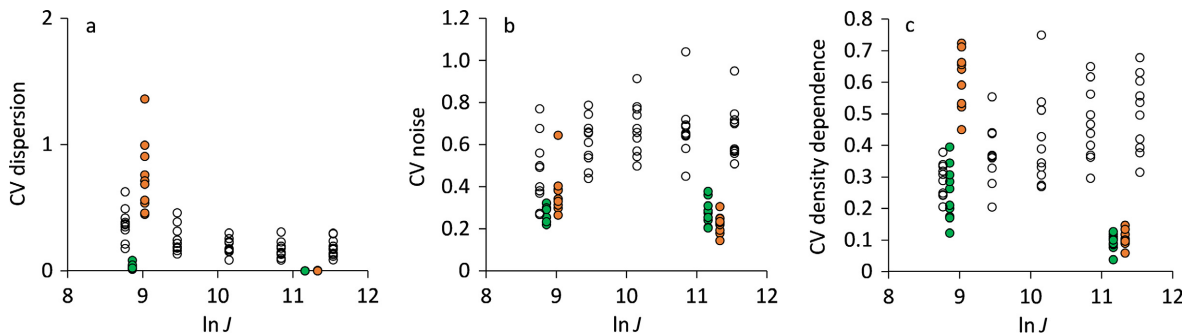

FIG. 3. Dependencies of the coefficients variation (CV) of (a) temporal dispersion in abundance, (b) spectral density noise, and (c) temporal density dependence on ln-transformed meta-community size J. Open circles, ecological drift only; green circles, ecological drift + cyclic intransitive competition; red circles, ecological drift + complex competition. $N = 10$ replicates for each value of J.

analysis of a species-poor interaction models, Laird and Schamp (2006) and Grilli et al. (2017) found that intransitive competition and dynamic species interactions tend to increase local species richness, and to stabilized species abundances. In empirical studies conducted in grasslands and salt marshes, Soliveres et al. (2015, 2018), Stouffer et al. (2018), and Ulrich et al. (2018) have found empirical support for this hypothesis. However, Dormann (2016) questioned the claims of Soliveres et al. (2015), and pointed to the lack of testing of alternative hypotheses to the mechanism of intransitive

competition. Indeed, in earlier studies intransitivity might have actually been a side effect of small-scale habitat variability, leading, in turn, to environmentally induced changes in species' competitive strength.

In this respect, our simulations should be interpreted as an initial proof of concept. Future studies will have to explore the potential effects of environmental change on species competitive interactions, and how this, in turn, may affect population dynamics and community stability (Strona and Lafferty 2016). Importantly, the patterns we detected were strongest in case of the competitive

loop used in earlier simulation studies to infer the behavior of intransitive competitive networks (Laird and Schamp 2006, Allesina and Levine 2011, Grilli et al. 2017). However, these strong, perfect cycles might be uncommon in nature. Contrary to the argument of Grilli et al. (2017), the more realistic complex networks produced much weaker effects. Laird and Schamp (2006) and Grilli et al. (2017) used three to five species for their simulations while our study was based on 10 species. We speculate that the size of the competitive network might affect the stabilizing power. In this respect, it has long been known that complex food webs become eventually unstable (May 2001, Allesina and Tang 2012). Competitive networks and food webs are essentially governed by the same types of interactions and should obey similar stability criteria. Further studies have to determine the relationships between richness effects and complexity in competitive networks. Nevertheless, the results of Allesina and Levine (2011) and Grilli et al. (2017) might not be as general as supposed and rather refer to simple model settings.

Specifically, the complex competitive structure (the one with several competitive loops) was characterized by several competitive loops, reduced extinction rates only at large meta-community size (Fig. 1a). Hubbell (2001) argued that drift alone is able to maintain high local species diversity. However, even small departures from pure ecological drift dramatically shorten coexistence time, leading to low local diversity (Zhang and Lin 1997, Yu et al. 1998). Zhang et al. (2012) applied a lottery model and showed that a certain degree of reproductive trade-off among species (low reproduction in one species gives another species the chance for higher reproduction) can decrease local extinction rates and consequently increase diversity. However, He et al. (2012) noted that the high species coexistence times of strict neutral meta-community models do not match the transient coexistence observed in empirical studies. Here, we clarify the precise mechanism behind this effect. Reproductive trade-offs are comparable (although not identical) to an intransitive situation in which reproductive output does not decrease linearly with competitive strength in a transitive hierarchy (Ulrich et al. 2014). Here, we show that only extreme intransitivity that reverse the competitive order of the most and least competitive species, is able to reduce extinction probabilities. More complex competitive hierarchies only reduce extinction probabilities at large meta-community sizes (Fig. 1a). Therefore, intransitivity can increase the stability of community structure only if a limited number of species at the top and the bottom of the competitive pecking order is involved (Fig. 1a). This result might explain contrasting reports about the effect of intransitivity on community stability (Vandermeer 2011, Soliveres et al. 2015, Gallien et al. 2017, Godoy et al. 2017).

Our third question was whether intransitivity can generate compensatory fluctuations and density-dependent population regulation? The answer appears to be yes (Fig. 2c). Density dependence has long been known to stabilize populations (Murdoch 1994), decrease local extinction rates (Drake 2005), and increase local species richness (LaManna et al. 2017). Most evidence comes from simulation studies within the Lotka-Volterra framework (Wangersky 1978) and from experimental studies involving small numbers of species (reviewed in Laird and Schamp 2015). These studies have focused on intraspecific regulation or predator–prey dynamics. Here we show that interspecific competition might also be a mechanism generating density dependence. We note that transitive competition caused low local richness, and the density effect was a statistical artefact due to the constraint on the local abundances. More important are the results of both of the intransitive simulations, which generated sustained high diversity at the local patch scale. Both forms of intransitivity increased the strength of density-dependent regulation (Fig. 2c) and reduced the variability in population fluctuations (Fig. 1b). These results contrast with an early study by May and Leonard (1975), who found that three competing species lead to instable population cycling and rapid extinction. On the other hand, Stouffer et al. (2018) found evidence in annual plants that cyclic intransitivity, in which competitive strength depends on population size, might cause density-dependent population regulation. In our models, competitive strength was fixed but nevertheless induced strong density-dependent population regulation.

The pure neutral models assessed at the scale of a generation returned variance–mean ratio (as covered by the slopes of Taylor's power spectrum) comparable to those of a Poisson random process and in line with previous analyses of the temporal behavior of neutral models (e.g., Azaele et al. 2016, Faust et al. 2018). Slopes between $z = 1$ and $z = 2$ are typical for many vertebrate and plant communities (Taylor 1988). However, many arthropod time series follow a proportional rescaling pattern characterized by a variance that is proportional to the square of the mean abundances ($\sigma^2 \propto \mu^2$; Ballantyne and Kerkhoff 2007). In this respect, Ballantyne (2005) argued that the key factor for determining the slope value is the effective reproduction rate. Reproduction rates in the classical neutral model used here are low and constrained to maintain population size. This might be a crucial restriction for their applicability to serve as random standards in community ecology (Mutshinda et al. 2008, Rosindell et al. 2012).

In multispecies communities, compensation in abundances might be a strong stabilizing factor (Wilcox et al. 2017). A standard test for compensation, also used here, compares community abundance variability with the average variability of its constituent species (Loreau and de Mazancourt 2008). However, our results strongly indicate that this test might be biased toward detection of asynchrony. Irrespective of meta-community size, the pure neutral communities returned φ values much below unity, the random expectation. Apparently the zero-sum constraint of the neutral model constrains the sample

space for total abundance variation in neutral communities, leading to similar bias as for Taylor's z. This may reduce the value of neutral models as a benchmark standard. Nevertheless, the low φ values observed here in communities characterized by intransitive competition clearly indicate that cyclic, but not complex, intransitive competition is a strong compensatory agent. As complex intransitivity should be quite common in the real world, particularly in species-rich communities, a simple mechanism of strong intransitivity may not be the most likely explanation for the maintenance of high local diversity.

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