

**Ecological drift and competitive interactions predict unique patterns
in temporal fl**

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 vari-

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

METHODS

The ecological drift model

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

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):

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

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'

where σ

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).

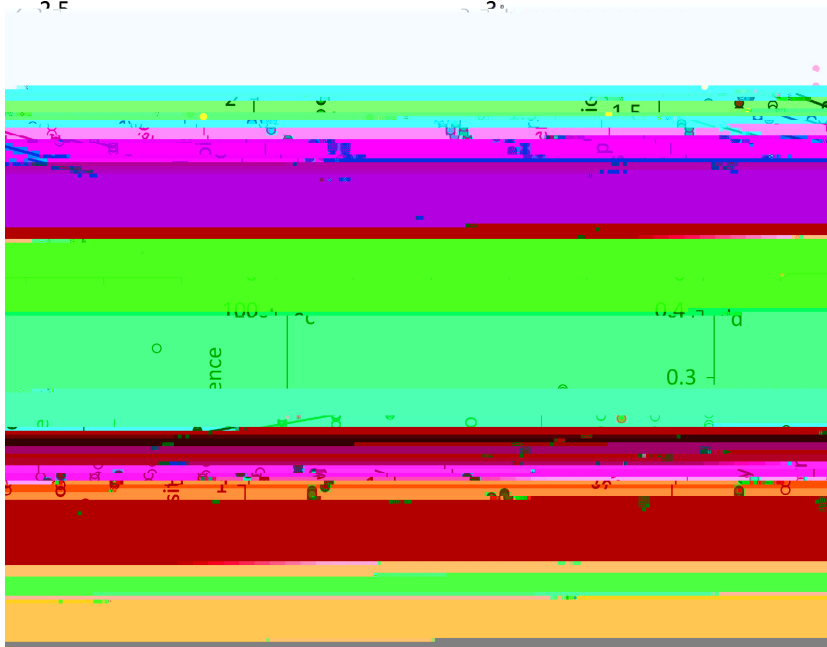
We used two measures of temporal synchrony in species abundances. In all model communities, segregation in abundance was lower than expected from the null model (Table 1, Fig. 1c). The three community types significantly differed with respect to SES WCS (Fig. 1c, one-way ANOVA $P(F_{2,87}) < 0.001$). 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

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



FIG

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.

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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LITERATURE

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