Ma de f f c e e f ec e ab d ce da a

We e U c , S a S e e , W c ec K e , Fe d T. Mae e d N c a J. G e

of intransitivity may change depending on environmental heterogeneity (Allesina and Levine 2011), successional stage (Worm and Karez 2002), or the presence of consumers (Paine 1984).

Despite the conceptual simplicity of intransitive competitive hierarchies, the empirical estimation of the strength of competition and of the frequency of competitive intran-

In general the probability $p_{j,i}$, with $1 \neq ... 3$, that species j is replaced by the species i is calculated as

$$p_{j,i} = \frac{1}{...} ... - ...$$

and for 1

$$\prod_{1,...} ... \frac{1}{1} \sum_{1,...} ... (1,..., \; 1, \; 1,..., \;)[\; \rightarrow \;]$$

(9)

Equation 8 and 9 generate the required transition matrix $\mathcal{P}$ for an arbitrary number of species in terms of competitive strength matrices for sets consisting of ($\mathbin{2} 1$) species.

The fact that the transition probability for two species (Eq. 8) contains terms that include other species means that a fully transitive competitive strength matrix $\mathbf{C}$ is not necessarily transitive with respect to the transition matrix $\mathcal{P}$ (Fig. 2). A fully transitive $\mathbf{C}$ matrix translates into a transitive $\mathcal{P}$ matrix only if competitive strengths of the off-diagonal elements in $\mathbf{C}$ are either constant or increase in each row from left to right (Fig. 2, C2, C3). This feature is equivalent to a fully quantitatively nested pattern of competitive strength (cf. Staniczenko et al. 2013). If this ordering is broken, a transitive $\mathbf{C}$ matrix translates always into an intransitive $\mathcal{P}$ matrix (Fig. 2, C4). Thus, it is important to quantify intransitivity in both the $\mathcal{P}$ matrix and in the underlying $\mathbf{C}$ matrix. Importantly, full transitivity (when defined by transition probabilities) does not necessarily imply competitive exclusion. Only $\mathbf{C}$ matrices that translate into absorbing $\mathcal{P}$ matrices cause competitive exclusion (Fig. 2, C1).

We note that the dominant eigenvector of the simple Markov chain model predicts the relative abundances of all

2) Spatial and environmental data

e second approach is based on spatial abundance data for
species collected at   1 to   sites for which environ-
mental variables are available. Assume a number of
homogeneous patches. If observed species abundance dis-
tributions were determined only by competition, we
could make a time-space substitution and interpret the
vector **A**

matrices matched the respective simulated matrices, we directly compared the simulated and the (best-fitting) predicted C_{test} and P_{test} matrices using Mantel correlations applied to the respective Euclidean distance matrices. We also used these best-fitting matrices to compare the degrees of transitivity t_i and t

approach used to recover competitive interactions from abundance data (Fig. 3). Our 'reverse-engineering' algorithm performed best for Þ matrices in combination with the spatial and environmental data (Fig. 3). In these analyses, the regression of estimated versus true transitivity explained 94% of the variance found in the data. Our methods were less successful at estimating pairwise competitive strength, and the respective regressions explained only between 51% (abundance data, Fig. 3F) and 53% (time series data, Fig. 3B) of the variance.

Despite variability in the prediction of the precise degree of transitivity, all three approaches were able to identify at least moderate degrees of intransitivity in test matrices (Table 1). For Þ matrices, each of our three approaches correctly recovered more than 94% (time series approach) of the moderately to highly intransitive test matrices, with t 0.95 (Table 1). For **C** matrices, at least 80% (times series) of them were correctly identified. Of the weakly intransitive matrices (0.95 t 1.0) between 74% (time series) and 94% (environmental data) were identified as being intransitive by the Þ matrices, and between 72% (time series) and 90% (environmental data) of them were identified as being intransitive by the **C** matrices.

ese methods were less successful in identifying perfectly transitive matrices (Table 1). For Þ matrices, between 36% (environmental data) and 60% (spatial data) of the upper 95% confidence limits of the t distributions of the 100 best-performing matrices included the value of 1.0 (full transitivity). For **C** matrices, between 49% (spatial data) and 61% (environmental data) were correctly identified as transitive. In all of the fully transitive test matrices, the predicted transitivity scores of the best-performing engineered Þ and

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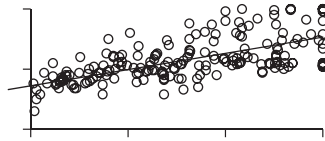
competitive strength (**C**) and the transition (**P**) matrices, with the latter showing a stronger pattern of intransitivity (Table 3).

For Hymenoptera, there was a trend towards increasing intransitivity (t) at higher slug weight (r ≳ 0.82, p 0.01, Table 2). e confidence limits of t of the 8 and 12 g carrion weight classes did not encompass 1.0 (Table 3). t was also negatively correlated with the degree of species segregation (r ≳ 0.78, p 0.01, Table 3). is trend was not obvious for t (Table 3).

Detailed comparisons of the competitive hierarchies of flies and parasitoid wasps (Table 2), revealed a reordering of species competitive strength between the di erent carrion weight classes. e average coe cient of correlation between all 45 combinations of predicted species rank orders of competitive strength was r 0.11 for Di). and

such as successional series. However, if conditions change through time (as in classic succession models; Connell and Slatyer 1977), the **P** matrix entries will be affected by both species interactions and abiotic conditions in each time step (Zaplata et al. 2013).

It is possible to construct other more complicated patch transition models, such as cellular automata models (Baltzer et al. 1998), but these models would require even more assumptions. Horn's (1975) patch transition model is the simplest way to convert the effects of pairwise species interactions into changes in relative abundance. One important caveat for this patch model is that it assumes the outcomes of species interactions are density independent.

is assumption is not unreasonable for many sessile invertebrates and plants that produce large quantities of mobile larvae or seeds and act effectively as a 'propagule rain'. is colonization scenario underlies classic models of island biogeography and metapopulation dynamics (Gotelli 2008).

As revealed by our benchmark testing, the methods introduced here successfully identify candidate competition matrices that predict abundance distributions that are very similar to the observed ones. Our approach recovers competitive hierarchies (Fig. 3), and intransitive test matrices always had predicted t and t values 0.95.

us, we propose this 0.95 value as a rule of thumb to separate communities with a strong transitive hierarchy in their competitive networks from those showing some degree of intransitivity (Fig. 1). Environmental heterogeneity can override these patterns (Fig. 3), but a pattern of consistent species rank abundances among sites is always a strong indicator of a high degree of competitive transitivity. However, the converse is not true. If species ranks vary widely among sites, it could indicate either the presence of intransitive networks and/or environmental heterogeneity

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