Concurrent niche and neutral processes in the competition–colonization model of species coexistence

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The importance of neutral dynamics is contentiously debated in the ecological literature. This debate focuses on neutral theory's assumption of fitness equivalency among individuals, which conflicts with stabilizing fitness that promotes coexistence through niche differentiation. I take advantage of competition–colonization trade-offs between species of aquatic micro-organisms (protozoans and rotifers) to show that equalizing and stabilizing mechanisms can operate simultaneously. Competition trials between species with similar colonization abilities were less likely to result in competitive exclusion than for species further apart. While the stabilizing mechanism (colonization differences) facilitates coexistence at large spatial scales, species with similar colonization abilities also exhibited local coexistence probably due to fitness similarities allowing weak stabilizing mechanisms to operate. These results suggest that neutral- and niche-based mechanisms of coexistence can simultaneously operate at differing temporal and spatial scales, and such a spatially explicit view of coexistence may be one way to reconcile niche and neutral dynamics.

Keywords: competition–colonization trade-off; microcosm; niche versus neutral dynamics; spatial scale; species coexistence

1. INTRODUCTION

The idea that ecological communities are regulated by neutral processes (Bell 2001; Hubbell 2001) has had a profound effect on ecology, but this remains contentious (Gaston & Chown 2005). Data-driven studies generally refute some aspect of neutral patterns or processes (McGill 2003; Gilbert & Lechowicz 2004; Turnbull *et al.* 2005; Wootton 2005), denying that neutral dynamics can produce observable ecological patterns. Similarly, completely niche-based explanations have failed to adequately explain extant community patterns (Chave 2004; Holyoak & Loreau 2006). Consequently, a number of studies have attempted to reconcile neutral and niche dynamics (Chave 2004; Tilman 2004; Gravel *et al.* 2006; Holyoak & Loreau 2006; Adler *et al.* 2007). Chesson (2000) best anticipated the divergence and reconciliation between neutral and niche dynamics by explicitly viewing coexistence mechanisms as either equalizing or stabilizing (Chave 2004; Adler *et al.* 2007). Stabilizing coexistence describes species differences that result in reduced niche overlap, thus minimizing the impact of fitness inequalities on competitive interactions. Equalizing mechanisms promote similarities in species responses to environmental conditions (i.e. fitness equivalency) and reduce the rate of competitive exclusion as well as allow coexistence from weak stabilizing mechanisms. Often invoked as the fundamental assumption for neutral dynamics, equiv-alency does not mean that species are the same in all respects, rather that equalizing mechanisms diminish fitness inequalities.

Although Chesson (2000) viewed stabilizing and equal-izing mechanisms as small-scale resource competition, here

I view stabilizing and equalizing as contributions to coexistence in more general terms. Here I consider stabilizing mechanisms to be synonymous with any ecologi-cal difference that allows two species to stably coexist together at some definable spatial scale. Similarly, I define equalizing mechanisms as those that produce equivalent fitness responses to environmental conditions. Thus, equalizing coexistence is a product of environmental constraints and is observed at some finite spatial or temporal scale. It is important to note that in using Chesson's schema, I am explicitly viewing the outcome of neutral-type dynamics at the population level (i.e. persistence time) and not considering the more appropriate view of neutrality as stochasticity at the individual level (see Volkov *et al.* (2005) for a treatment on this difference).

With this more general definition, we can examine coexistence mechanisms at different spatial scales and specifically ask how dispersal and colonization play a role in our understanding of coexistence (McPeek & Holt 1992; Tilman 1994; Holt & McPeek 1996; Tilman & Kareiva 1997; Kinzig *et al.* 1999; Amarasekare 2003; Mouquet & Loreau 2003; Kneitel & Chase 2004; Holyoak *et al.* 2005). A number of coexistence models explicitly consider species as having a trade-off between their competitive and colonizing abilities (Levins & Culver 1971; Horn & Macarthur 1972; Tilman 1994; Pacala & Rees 1998; Yu & Wilson 2001; Yu *et al.* 2001; Levine & Rees 2002; Mouquet & Loreau 2003; Mouquet *et al.* 2006). I will argue in this paper that whether we view coexistence in a competition–colonization trade-off as stabilizing or equalizing probably depends on the scale of observation.

Spatially implicit competition models (e.g. Hastings 1980; Caswell & Cohen 1991; Tilman 1994; Pacala & Rees 1998) show that in an environment where local

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disturbances (i.e. density-independent mortality) cause small-scale extinctions, a good colonizer/poor competitor and a poor colonizer/good competitor can stably coexist at larger spatial scales. Because there is a trade-off, neither strategy could replace the other in a moderately disturbed system and the relative occupancy of competitors depends upon disturbance frequency. However, in these models, local coexistence between these two strategies is impossible because the dominant competitor always replaces the better colonizer within a patch. The presence of any trade-off is often cited as evidence against the role of neutral dynamics in structuring communities (Turnbull *et al.* 2005; Ellis *et al.* 2006). Yet several recent publications suggest that even though relatively few strategies along a niche gradient can coexist, within any single niche strategy, multiple functionally similar or equivalent species can coexist, mimicking neutral-type dynamics (Hubbell 2005; Gravel *et al.* 2006; Holt 2006; Scheffer & van Nes 2006). Recently, Fukami *et al.* (2007) showed that adaptive radiation in *Pseudomonas* bacteria resulted in both the filling of empty niches and the evolution of ecological equivalents coexisting within niches. Thus, the presence of trade-offs may not necessarily refute neutral dynamics (Hubbell 2005). If we view the stabilizing mechanism (colonization ability) as part of a strict trade-off, then two species that have similar colonization abilities will also have similar competitive abilities within local patches. In the absence of any other local niche partitioning, these two, similarly competing species, should have similar fitness responses to local environmental conditions (Chesson 2000), meaning that either competitive exclusion takes many generations to occur or weak stabilizing mechanisms promote coexistence. I use data from aquatic microcosm experiments to test whether the risk of competitive exclusion decreases and time to local extinction increases as species become more similar.

2. A SIMPLE MODEL

With a competition–colonization trade-off, species can stably coexist at larger spatial scales despite competitive differences. However, within local patches, such coexistence is not possible if we assume that there is not any spatial subsidy effect enhancing one species birth rates over another (Mouquet *et al.* 2006). Furthermore, many competition–colonization models assume instantaneous competitive exclusion, but in considering a gradient from niche to neutral dynamics, the relative time for competitive exclusion is fundamentally important. Incorporating succession requires the addition of local niche dynamics to trade-off models (Pacala & Rees 1998). Here I assume that there is a strict trade-off between colonization and competitive ability. I am explicitly considering the dynamics of unicellular micro-organisms of a single trophic level inhabiting homogeneous, spatially discrete patches (e.g. Cadotte 2006, 2007). Given this simple system, the competition–colonization trade-off can be defined by two parameters: the intrinsic rate of increase for species i, r_i, and the strength of interspecific competition (b_{ij}, the effect of species j on i). Here I assume that intraspecific effects, b_{ii}, are constant. The population size of species i at time t is given by

$$N_{i,t} = r_i + b_{ii}N_{i,t-1} + b_{ij}N_{j,t-1} + \varepsilon, \qquad (2.1)$$
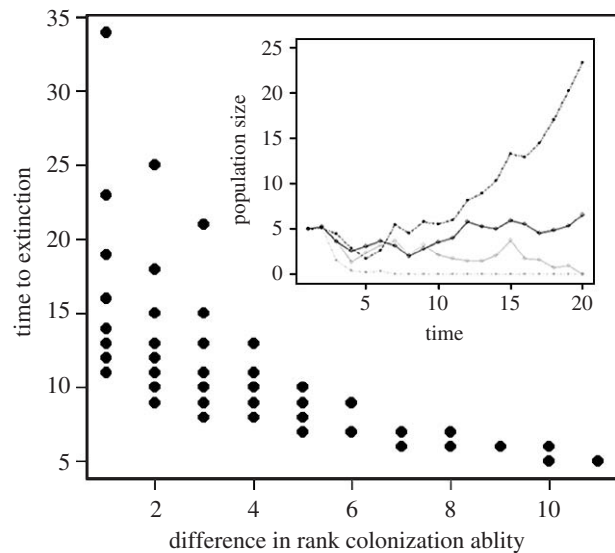
Figure 1. The time to observe a local extinction for pairwise species combinations from equation (2.1). Here 12 species are modelled with a strict competition–colonization trade-off. The best colonizer had $r_i = 1.325$ and was ranked 1, and subsequent species r's were decreased by 0.025, with the 12th ranked species having $r_i = 1.05$. The 12th ranked species was also the best competitor with $b_{i12} = 0.65$ and lower ranked species had lower b_{ij}'s by 0.05, with the best colonizer having $b_{i1} = 0.1$. The inset shows two example simulations: one simulation is between two species with similar abilities (solid lines) and the other is for two species with very different abilities (dashed lines). For the similar species: solid black line, species rank 5; solid grey line, species rank 4. For the different species: dashed black line, species rank 11; dashed grey line, species rank 3.

where $N_{i,t-1}$ is the population size at time $t-1$ and ε is the normally distributed stochasticity with a mean of 0 and standard deviation of 1.

If there is a trade-off, then as r_i increases, its effect on the other species, b_{ji}, must decrease. As the difference increases, the disparity between competitive effects also increases. Thus, within patches, increasing D means that the inferior competitor goes extinct faster (figure 1). Species with identical r's (and thus b's) will persist indefinitely, but even species with small D may persist for many generations if the magnitude of the difference in b's is less than demographic stochasticity (ε in equation (2.1)).

3. A TEST USING MICRO-ORGANISMS

Here I use data from the competition–colonization experiment of Cadotte *et al.* (2006). Using an artificial system of aquatic micro-organisms (protozoans and rotifers; see figure 2 for species list), Cadotte *et al.* (2006) revealed that species exhibited competition–colonization trade-offs, where the best competitors were generally poor colonizers and the best colonizers were typically poor competitors (figure 2). Colonization was measured as the relative time for species to colonize every patch in a discrete five-patch system, whereas competition was measured as the extinction probability in pairwise combinations with every other species (see Cadotte *et al.* (2006) for detailed methods). The patches in the colonization experiment were 125 ml Nalgene bottles filled with 100 ml of bacterialized nutrient solution, and with 4.76 mm threaded holes having nylon tube fittings
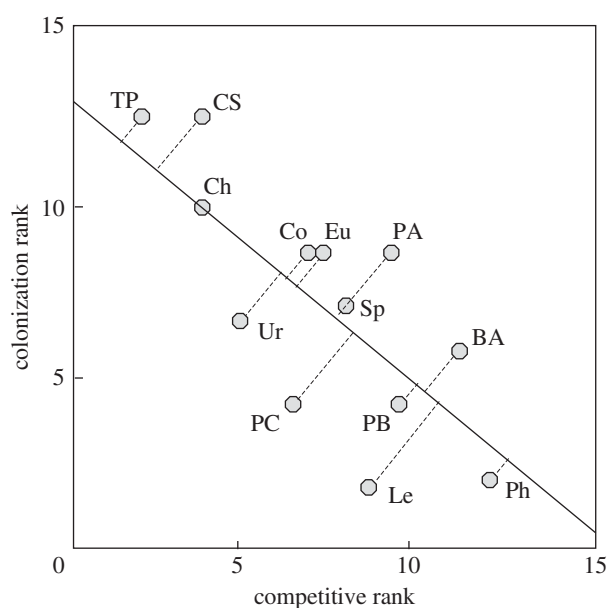
Figure 2. The relationship between competitive and colonization abilities, showing a competition–colonization trade-off (adapted from Cadotte *et al.* (2006)). Dashed lines show species locations along regression line. Species with similar colonization abilities are assumed to have similar fitnesses given laboratory conditions and resource availability. BA, *Blepharisma americanum*; Ch, *Chilomonas* sp.; Co, *Coleps* sp.; CS, *Colpidium striatum*; Eu, *Euplotes* sp.; Le, *Lepadella* sp.; PA, *Paramecium aurelia*; PB, *P. bursaria*; PC, *P. caudatum*; Ph, *Philodina* sp.; Sp, *Spirostomum* sp.; TP, *Tetrahymena pyriformis*; Ur, *Uronema* sp.

(Cadotte *et al.* 2006). Patches were linked serially, connected with 12.5 cm of clear Nalgene 4.76 mm PVC tubing. For the competition experiment, the two species were added to 50 ml of bacterialized solution in 250 ml glass jars. For both experiments, the presence of species was assessed with weekly 5 ml samples (and replaced with 5 ml of sterile nutrient solution). All experiments were replicated three times.

Here I assume that the outcomes of species competition in Cadotte *et al.* (2006) result from fitness inequalities. I also assume that species inhabit a stable environment, are limited by a single resource and have colonization abilities that reflect maximal population growth rates (Warren *et al.* 2006). Competitive interactions are estimated in an extremely conservative manner: whether one of the two populations goes extinct, ostensibly due to competitive exclusion. Colonization ability was ranked by time to colonize all patches. Rank was calculated as the mean rank from 10 000 random draws of the individual replicates (see Cadotte *et al.* 2006). Since I observed exclusions over an eight-week interval, with weekly samplings, the data are said to be right-censored. Right-censored data are common in 'time to' experiments where observations end at some arbitrary time and therefore represent a biased sampling where parameter estimation does not conform to widely used parametric estimations (Hosmer & Lemeshow 1999). Which species went extinct is not important here because as long as there was extinction, then these two species are said to exhibit fitness inequalities. Therefore, to estimate the probability of coexistence, I used the Kaplan–Meier product-limit estimator (Hosmer & Lemeshow 1999), which calculates the probability that a given population will persist beyond time *t*. The
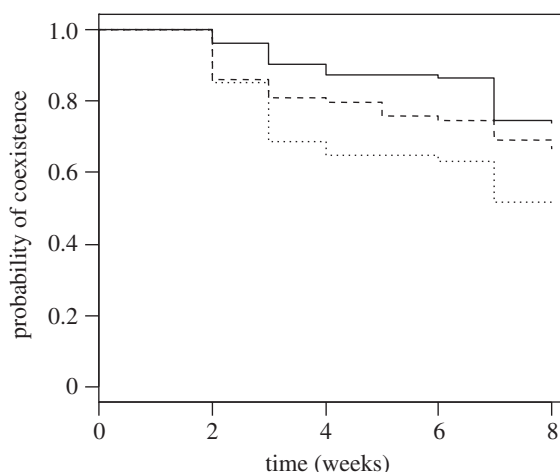

Figure 3. The Kaplan–Meier product-limit estimator of the probability of coexistence over time. The three lines refer to species classified by differences in colonization rank (*D*). Small (solid line), $D < 3$; medium (dashed line), $3 \leq D \leq 6$; large (dotted line), $D > 6$. For clarity, 95% CIs were removed.

maximum-likelihood estimate of this probability is given by

$$\hat{S}(t) = \prod_{t_i < t} \frac{n_i - d_i}{n_i}, \tag{3.1}$$

where n_i is the number of surviving populations and d_i is the number of deaths at time t_i. I used a parametric regression fitting the probability of coexistence to a Weibull distribution against the absolute difference in colonization rank, and evaluated the model using a likelihood ratio test (presented as χ^2-value) comparing this model with a model containing only an intercept. Survival analysis was performed using the SURVIVAL Package, v. 2.31 with R v. 2.4.1 maintained by Thomas Lumley (www.r-project.org).

4. RESULTS

The regression analysis reveals that the probability of successful coexistence between any two species is negatively related to the difference in their colonization rank ($\chi_1^2 = 7.56$, $p = 0.006$; coefficient $\pm$ s.e. $= -0.07892 \pm 0.0289$). To best illustrate this relationship, I grouped the colonization differences into three classes: (i) difference in colonization rank < 3.00, (ii) difference ≥ 3.00 and ≤ 6.00, and (iii) difference > 6.00. The probability of coexistence as a function of time is shown in figure 3, and the relationship between the probability of coexistence and the colonization difference classes is very similar to that for the continuous model above ($\chi_1^2 = 8.75$, $p = 0.003$; coefficient $\pm$ s.e. $= -0.2814 \pm 0.0976$).

5. IMPLICATIONS: HOW NICHE AND NEUTRAL PROCESSES CAN COEXIST

One of the earliest axioms of ecology was that two species occupying the same niche results in competitive exclusion of the inferior competitor (Grinnell 1904, 1917; Gause 1934). However, this 'competitive exclusion principle' was quickly cast into doubt as examples of coexistence in ecologically similar species surfaced (Ross 1957; Udvardy 1959; den Boer 1986). Since then, the idea that species coexist due to their similarities rather than their differences has repeatedly surfaced, primarily by ecologists studying tropical forests (e.g. Webb 2000; Hubbell 2006) and freshwater algae (Hutchinson 1967; Lewis 1977;

McCormick 1996). The debate, whether coexistence results from ecological differences or similarities, is almost as old as the science of ecology. Hubbell (2006) rightly noted that experimental evidence of equivalency was lacking. I would argue that this is largely due to the fact that experimenters have not been explicitly looking for equalizing mechanisms, especially in concert with niche processes.

To look for niche versus neutral (i.e. stabilizing versus equalizing) processes, Adler *et al.* (2007) recently suggested quantifying intra- versus interspecific effects on vital rates, or measuring frequency-dependent population growth. Here I look at the outcome of negative interspecific effects on vital rates by enumerating population extinctions. The results reveal that the more similar two species are in their colonization ability, the more likely that they persist together for long periods, ostensibly due to fitness equivalency. Fitness similarities allow for coexistence from weak stabilizing mechanisms.

These results also suggest that whether apparent coexistence is due to strong stabilizing or equalizing mechanisms depends upon the spatial and temporal scales at which observations are being made. From Chesson's (2000) framework, equalizing coexistence is ultimately unstable since fitness equivalency results in intrinsic rates of population increase that equal zero. Therefore, a population affected by a density-independent mortality event will not be able to recover when in the presence of a competitor with equivalent fitness. For inferior competitors, equalizing coexistence is trumped by the inevitable eventual immigration of the superior competitors (Cadotte 2006).

However, stabilizing coexistence from a competition–colonization trade-off occurs over large spatial and temporal scales. For superior competitors, periodic disturbances or environmental changes eventually eliminate local populations. Species distributed along a competition–colonization trade-off have differing strategies where coexistence depends on chance events happening at larger spatial and temporal scales than within patch dynamics alone (Amarasekare 2003; Kneitel & Chase 2004). In the absence of disturbance, dominant competitors will eventually exclude the inferior ones even at large spatial scales (Cadotte 2007), and in the microcosm system, space appears necessary for coexistence, contrary to Adler & Mosquera (2000).

Recently, Turnbull *et al.* (2005) concluded that the presence of a trade-off necessarily negates the possibility that neutral processes structure communities. They examined the potential for coexistence among grassland pioneer species and nicely showed that an 'establishment/colonization' trade-off best explained coexistence patterns (Turnbull *et al.* 2005). This trade-off describes the fact that species with larger seeds (i.e. poorer dispersers) can tolerate a greater range of environmental hazards while small-seeded species are more susceptible to hazards, but they have a better chance of dispersing to optimal microsites (Turnbull *et al.* 2005). The current results are completely compatible with Turnbull *et al.* (2005), in that in a strict stabilizing trade-off, only species with differing strategies should coexist. However, given the fact that Turnbull *et al.* (2005) were able to group species according to seed mass in their analyses, the question becomes: do species with similar seed sizes coexist, and if so, is this

coexistence best explained by similar fitnesses as opposed to strong stabilizing mechanisms? Other plant community studies have shown that while several stabilizing traits appear to allow for coexistence, species composition within any trait appears haphazard and historically contingent (Fukami *et al.* 2005; Ejrnaes *et al.* 2006)

With a competition–colonization trade-off, coexistence is often thought of as the product of non-equilibrium, spatially dependent processes (Connell 1978; Huston 1979), where these chance events present different niche opportunities for species. Connell's (1978) intermediate disturbance hypothesis viewed local richness as dependent on the time since disturbance, where soon after a disturbance colonizing species establish populations. A result of the logic in this hypothesis is that if immigration ceased, then succession would be arrested and species richness would cease to change. The mechanism that allows coexistence within any successional stage was attributed to microhabitat niche partitioning (Connell 1978). The current results support the notion that species show equivalency and thus neutral processes probably dominate within successional stages, while niche processes drive patterns among successional stages (Denslow 1980; Ellner & Fussmann 2003; Cadotte 2007).

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