On Testing the Competition-Colonization Trade-Off in a Multispecies Assemblage

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ABSTRACT: The competition-colonization trade-off has long been considered an important mechanism explaining species coexistence in spatially structured environments, yet data supporting it remain ambiguous. Most competition-colonization research examines plants and the dispersal-linked traits of their seeds. However, colonization is more than just dispersal because rapid population growth is also an important component of colonization. We tested for the presence of competition-colonization trade-offs with a commonly used artificial assemblage consisting of protozoan and rotifer species, where colonization was the ability of a species to establish populations in patches. By ranking species according to their colonization abilities and their pairwise competitive interactions, we show that these species exhibit competition-colonization trade-offs. These results reveal that the competition-colonization trade-off exists within nonplant assemblages and that even in a laboratory setting, species are constrained to be either good competitors or colonizers but not both.

Keywords: competitive exclusion, coexistence, dispersal, diversity, metacommunity, microcosm.

When it comes to mechanisms explaining species coexistence, the competition-colonization trade-off has long been considered one of the most important in spatially structured environments (Levins and Culver 1971). This trade-off predicts that better competitors are inferior colonizers and vice versa (fig. 1). Recently, significant doubt has been raised about the pervasiveness of these trade-offs (e.g., Jakobsson and Eriksson 2003).

The source of this doubt comes from the fact that many field studies fail to detect evidence for the competition-colonization trade-off (e.g., Harrison et al. 1995; Turnbull

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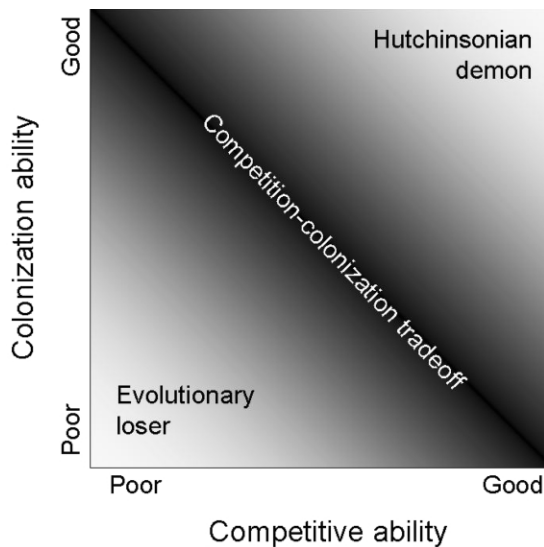
et al. 1999; Yu and Wilson 2001; Jakobsson and Eriksson 2003). Spatial heterogeneity may overwhelm trade-offs (Levine and Rees 2002), or the trade-offs simply do not exist in the expected form. Most work done on competition-colonization trade-offs has focused on plants, where seed attributes purportedly reveal the evolutionary outcome of this trade-off in the form of a trade-off between seed size and seed number (Rees 1995; Jakobsson and Eriksson 2000). Despite the presence of these seed characteristics, Jakobsson and Eriksson (2003) failed to find support for the existence of a competition-colonization trade-off in 15 wind-dispersed Asteraceae species. They concluded that doubt must be cast on models that assume this trade-off. This is a controversial conclusion, considering that numerous theoretical studies conclude that this trade-off is an important determinant of species coexistence (e.g., Levins and Culver 1971; Hastings 1980; Yu and Wilson 2001; Amarasekare et al. 2004). Furthermore, several authors believe that competition-colonization trade-offs are key for understanding patterns of coexistence at larger spatial scales (Amarasekare 2003; Kneitel and Chase 2004).

It seems, then, that there is a fundamental disconnect between empirical findings and theoretical assumptions. However, we contend that empirical studies are really measuring dispersal and not colonization per se. Dispersal describes the movement of individuals or propagules, while colonization also includes the ability to overcome Allee effects and successfully establish a population. Obviously, dispersal is important for establishing a population, and increasing the number of propagules likely increases the chances of establishing a population (Lockwood et al. 2005; Warren et al. 2006).

We use an artificial species assemblage, often used in aquatic microcosm experiments (e.g., Warren 1996; Cadotte and Fukami 2005; Cadotte 2006), to examine the competition-colonization trade-off. This assemblage is referred to as artificial because these organisms have been collected at different times and places, have been in isolation for at least 1,000 generations, and have been placed together in controlled habitats. As a result, these species are not likely to face a strong evolutionary pressure maintaining relative competitive and colonization differences.

Figure 1: Hypothesized relationship between competitive and colonization abilities. If a trade-off exists, then species should fall along the diagonal line.

These species could conceivably be classified into one of three groups: those occurring along a trade-off diagonal; Hutchinsonian demons, with superior competitive and dispersal abilities (Kneitel and Chase 2004); or evolutionary losers, being poor competitors and dispersers (see fig. 1). If competition-colonization trade-offs in these species are based on a real trade-off between the ability to compete versus colonization ability, then we expect to see this trade-off maintained despite isolation.

Thirteen species were used in the two experiments, and they are listed in table 1. Several labs use these same or closely related organisms in experiments investigating the role of dispersal in regulating coexistence and species richness (e.g., Holyoak and Lawler 1996; Warren 1996; Holyoak 2000; Holt et al. 2004; Cadotte and Fukami 2005; Cadotte 2006; Cadotte et al. 2006), yet no study has examined whether there are in fact competition-colonization trade-offs exhibited by these organisms.

Methods

It is important to note that although laboratory microcosms lack the naturalness important for understanding ecological processes, they do offer some invaluable benefits (see Cadotte et al. 2005). Essentially, they allow researchers to control and manipulate variables, and they provide truly multigenerational data, something that is often essential for testing ecological theory (Hastings 2004; Cadotte et al.

2005), and in our case, both colonization and the outcome of competition are multigenerational processes.

We ran two separate experiments: one to determine relative colonization abilities and one to determine relative competitive abilities of the organisms involved. In both experiments, we used aquatic microfauna (table 1). Resource patches consisted of a nutrient solution of 0.55 g/L of protozoa pellets (Carolina Biological Supply, Burlington, NC), 0.05 g/L powdered vitamins, and a single sterilized wheat seed as a source of slow-release carbon in commercially available spring water (Crystal Springs, Flowery Branch, GA). Six days before initialization of local communities, the stock solution was inoculated with four bacterial species (*Bacillus cereus*, *Bacillus subtilis*, *Proteus vulgaris*, and *Serratia marcescens*) from stock cultures. Four days before initialization, microflagellates and associated unidentified bacteria were introduced.

It is important to note that these organisms interact in complicated ways. They do not all compete for a single resource in a single way. Instead, they may potentially use resources in species-specific ways such that applying resource competition theory can lead to ambiguous results or interpretations (e.g., Fox 2002). It is apparent that with species supplementing their bacterial diets with other ciliates, decomposing material, direct resource utilization, and photosynthesis, much potential for coexistence and niche partitioning exists (for actual food web, see Cadotte 2006). This could result in a decoupling of the competition-colonization trade-off because competition may depend more on niche requirements than on competition for a limiting resource. Regardless, it has been shown that negative interactions do limit coexistence with this assemblage to about five species (e.g., Cadotte 2006).

Experiment 1: Colonization Ability

We constructed a five-patch system, where local patches were 125-mL Nalgene bottles filled with 100 mL of the above-described nutrient solution. These bottles had two 4.76-mm holes drilled into opposite sides and were tapped to receive threaded barbed nylon tube fittings (Small Parts, Miami Lakes, FL), which were secured with pure silicone caulk. Dispersal corridors were 12.5 cm of clear Nalgene 4.76-mm PVC tubing. This entire landscape apparatus was completely autoclavable.

In this five-patch system, the patches were linked serially so that community A was linked to B, B to C, C to D, D to E, and E back to A. Between 25 and 60 individuals of a single species were introduced into community A. All five communities were sampled weekly for species presence by removing 5 mL of solution, which was replaced with 5 mL of sterile solution. We equate an observed occurrence of individuals with patch colonization. Even if a single

Table 1: Mean time to colonize all five patches and the associated Monte Carlo mean colonization and competition ranks for each species used in this experiment

Species	Cell mass (g/cell)	Colonization time (weeks)	Mean colonization rank (2.5, 97.5 percentiles)	Mean competition rank (2.5, 97.5 percentiles)
Blepharisma americanum	2.27×10^{-7}	2.67	5.620 (3.5, 8.5)	11.055 (10, 12)
Chilomonas sp.	1.42×10^{-9}	1.33	9.766 (8, 12)	3.673 (2.75, 4.75)
Coleps sp.	2.02×10^{-8}	2.00	8.498 (7.5, 9.5)	6.719 (5.25, 8.25)
Colpidium striatum	1.52×10^{-8}	1.00	12.335 (12, 12.5)	3.532 (2.5, 5.25)
Euplotes sp.	8.05×10^{-8}	2.00	8.498 (7.5, 9.5)	7.136 (6.25, 8)
Lepadella sp.	9.68×10^{-8}	4.67	1.724 (1, 2.5)	8.379 (6.5, 9.75)
Paramecium aurelia	4.30×10^{-8}	2.00	8.498 (7.5, 9.5)	9.038 (8, 10)
Paramecium bursaria	1.96×10^{-7}	3.00	4.163 (3, 5.5)	9.259 (8.25, 10)
Paramecium caudatum	2.27×10^{-7}	3.00	4.163 (3, 5.5)	6.156 (4.25, 9)
Philodina sp.	1.34×10^{-7}	5.33	1.936 (1, 4.5)	11.836 (11.25, 12.25)
Spirostomum sp.	3.76×10^{-6}	2.33	7.052 (3.5, 9)	7.742 (4.75, 10.5)
Tetrahymena thermophila	4.77×10^{-9}	1.00	12.335 (12, 12.5)	1.83 (1.25, 2.5)
Uronema sp.	2.95×10^{-10}	2.67	6.41 (1.5, 9)	4.646 (3.75, 5.5)

Note: Larger ranks indicate greater speed of colonization or greater competitive ability. *Lepadella* sp. and *Philodina* sp. are rotifers; all other species are protozoa. All cell masses are taken from Fukami (2004), except *P. bursaria*, which is taken from McGrady-Steed and Morin (2000). Cell mass for *B. americanum* is taken from *P. caudatum* because it is a similarly sized species.

individual was observed in the 5-mL sample, the population would consist of approximately 20 individuals, yet none of our observations consisted of only a single individual in the 5-mL aliquot. We typically observed tens to hundreds of individuals.

During sampling, tube clamps closed dispersal corridors so that displaced solution did not cause the movement of solution with individuals among communities. This experiment was repeated three times for each of the 13 species. This experiment ran for a total of 8 weeks, enough time for all communities to be colonized. Colonization was measured as the time for any given species to colonize all patches.

Experiment 2: Competitive Ability

In isolated glass jars with 50 mL of nutrient solution, each species was introduced with one of the other 12 species. This was done for all 78 two-species combinations and was replicated three times.

Again, species presence/absence was sampled weekly by removing 5 mL of solution and replacing it with a 5-mL sterile aliquot. This experiment was again run for 8 weeks, but for purposes of this study, competitiveness was assessed with the results from the last sampling period.

Data Analysis

In order to assess relative performance of these species, we ranked their abilities. For colonization, we ranked species by the mean number of weeks needed to occupy all five patches. Competitive ability was also rank based but was based on two measures. First, we ranked species by the mean number of competition trials in which the species was still present at week 8. We also ranked species by the mean number of extinctions caused by that species by week 8. In both cases, smaller mean values were given smaller ranks. We then calculated mean rank for each species. Of course, competition could have been measured a number of different ways—most notably using abundance measures relative to control abundances. Abundance measures would have provided finer-scale measurements because two species could both persist while still having detectable competitive effects. However, we were constrained by the amount of time needed to sample each trial and therefore used persistence and extinctions caused as surrogates for competitive ability.

Lower values for both ranks correspond to poorer colonization or competitive abilities. We then plotted and used rank-based correlation to examine whether species corresponded to the relationship hypothesized in figure 1. To calculate confidence intervals, we used Monte Carlo techniques to generate 10,000 simulations. For each simulation, we randomly selected one replicate for each species and ranked species by colonization or competitive ability, as we did with mean scores. We calculated 95% confidence intervals by taking the 2.5 and 97.5 percentiles of the 10,000 simulations. All simulations were coded in Microsoft Visual C++, version 6.0 (Microsoft, Redmond, WA).

We also examined the role of body size on colonization and competitive abilities by regressing mean colonization

time and competition rank against cell mass (table 1). Cell mass was log transformed.

Results

Experiment 1: Colonization Ability

By the end of this experiment (week 8), all species had colonized all empty patches. There was significant among-species variation in the colonization rate of patches (repeated-measures ANOVA: $F = 20.09$, df $= 12, 26$, $P < .0001$). The best colonizers were able to colonize all patches within 1 week, while the poorest colonizers took 4 weeks or more (table 1). Log cell mass did not predict the time to colonize patches ($F = 1.763$, df $= 1, 11$, $P = .211$, $R^2 = 0.138$).

Experiment 2: Competitive Ability

By week 8, 10 species became extinct in at least one trial, and 11 species caused at least one extinction. There was a positive correlation between the number of extinctions caused and the number of trials in which a species survived (Pearson's $r = 0.317$, $P = .049$, $n = 39$). However, there was considerable scatter, so we combined these two variables into a single competition rank (table 1).

Unlike colonization ability, competitive ability is influenced by cell size. Competitive rank increases with increasing cell mass ($F = 7.753$, df $= 1, 11$, $P = .018$, $R^2 = 0.413$).

Competition-Colonization Trade-Off

Colonization ability and competitive ability were highly negatively correlated (Pearson's $r = -0.744$, $P = .004$, $n = 13$; fig. 2). Figure 2 conforms very well to the expectation highlighted in figure 1. Both of the competition ranks (resistance to extinction and extinctions caused) were individually negatively correlated with colonization rank when using Monte Carlo simulations (Pearson's $r = -0.855$ and -0.384, respectively).

Discussion

From these results, we can conclude that the poorest competitors were the best at colonizing new populations and vice versa. Although we view colonization as a process dependent on dispersal and population growth, this study does not attempt to quantify these aspects of colonization. Theory predicts that independent of species-specific dispersal-linked traits, species with high rates of population increase will colonize empty patches better (Warren et al. 2006), and those that maintain higher abundances
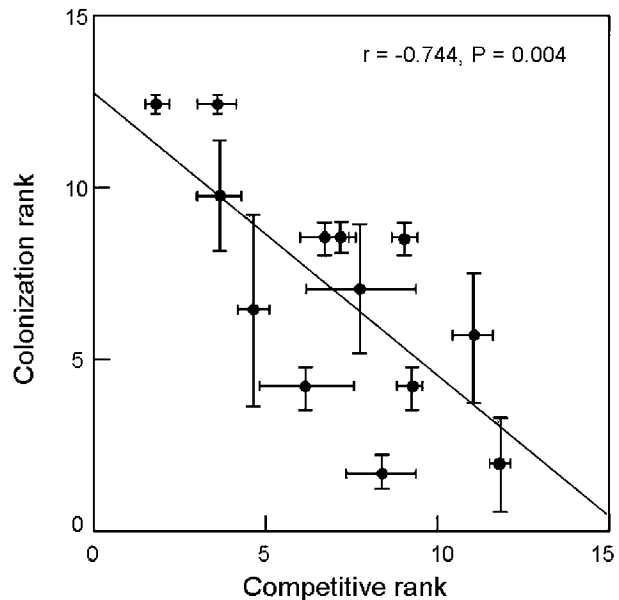

Figure 2: Relationship between competitive and colonization abilities, which supports a competition-colonization trade-off. Error bars represent 95% confidence intervals from 10,000 Monte Carlo simulations.

should occupy more patches (Holt et al. 1997). Regardless of whether dispersal ability or population dynamics controls colonization for any particular species, it is safe to assume that overall colonization patterns are likely the outcome of both processes.

We believe that these results are significant for three reasons. First, as mentioned, most work on this trade-off has been done with plants. Further, many studies focus on seed traits (e.g., Rees 1995) to detect dispersal ability, which does not actually measure colonization because, as pointed out above, colonization includes the ability to form larger populations quickly. This study is the first to show a competition-colonization trade-off in an assemblage where colonization is measured by the occupancy of previously empty patches.

Second, these species reveal potential evolutionary constraints. Constraints are the basis of any trade-off because no single species should be both a superior local competitor and a superior colonizer. The species used in this experiment have various origins. Some were ordered from Carolina Biological Supply Company, some were obtained from other labs, and others were obtained from ponds around Knoxville, Tennessee. This, accompanied by the fact that these species have been cultured in isolation for at least 1,000 generations, indicates that any observed trade-off is not the product of recent evolutionary interactions among these species. Rather, this trade-off seems to be a product of robust traits not subject to short-term

releases from competitive selection pressures. However, we can only speculate, albeit with circumstantial evidence, on the currency of this trade-off. It seems that energetics play a major role in this trade-off. Superior colonizers appear to move faster and for longer periods of time, while superior competitors move intermittently and for shorter durations of time (M. W. Cadotte, personal observations). Colonizers appear to find and colonize open patches quickly, while competitors require fewer available resources or use resources more thoroughly than colonizers. The fact that body size is positively correlated with competitive ability likely means that large-bodied organisms secure and store food better than small-bodied ones. Thus, small-bodied species must adopt other strategies, such as rapidly colonizing empty patches in order to coexist.

Finally, as mentioned in the introduction to this note, a number of laboratories use these organisms to test ecological hypotheses and theories, including the role of space and species movement and metacommunity dynamics (e.g., Holyoak and Lawler 1996; Warren 1996; Holyoak 2000; Holt et al. 2004; Cadotte and Fukami 2005; Cadotte 2006). Yet, even in these well-studied species, the presence of competition-colonization trade-offs has not been observed or tested experimentally. In a recent article by Cadotte (2006), dispersal rate and patch connectivity were manipulated, and competition-colonization trade-offs were hypothesized as an important mechanism affecting the results. The current results reveal that the dominant species in Cadotte's (2006) no-dispersal control are superior competitors/inferior colonizers. However, some dispersal treatments enhanced richness, and the species benefiting most from these treatments are those that are intermediate in the trade-off. Superior colonizers still eventually lost out, likely because there were no disturbances in Cadotte's (2006) experimental design. We would hypothesize that inferior competitors/superior colonizers would benefit from nonequilibrial conditions imposed by local disturbances, much like weedy species in an agricultural landscape.

Conclusion

While competition-colonization trade-offs are an important tool in explaining species coexistence at larger spatial scales (Amarasekare 2003; Kneitel and Chase 2004), we feel that studies thus far actually measure dispersal and not colonization. We here show that when measuring colonization, the competition-colonization appears to be potentially robust. Further, most studies of this trade-off use plants; we show its existence in a nonplant system.

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