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Preemption of space can lead to intransitive coexistence of competitors

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Intransitive competition has the potential to be a powerful contributor to species coexistence, but there are few proposed biological mechanisms that could create intransitivities in natural communities. Using a three-species model of competition for space, we demonstrate a mechanism for coexistence that combines a colonization–competition tradeoff between two species with the ability of a third species to preempt space from the other competitors. The combination of differential abilities to colonize, preempt, and overtake space creates a community where no single species can exclude both of its competitors. The dynamics of this kind of community are analogous to rock-paper-scissors competition, and the three-species community can persist even though not all pairs of species can coexist in isolation. In distinction to prior results, this is a mechanism of intransitivity that does not require nonhierarchical local interference competition. We present parameter estimates from a subtidal marine community illustrating how documented competitive traits can lead to preemption-based intransitivities in natural communities, and we describe methods for an empirical test of the occurrence of this mechanism.

Ecologists have described a variety of mechanisms by which species can coexist while competing for the same resources (Chesson 2000), but it remains an important challenge to apply these ideas to the full complexity of natural communities, where many species coexist presumably via many mechanisms (Agrawal et al. 2007). Models portraying coexistence are typically framed in terms of a tradeoff in competitive traits between two species, e.g. colonization ability versus competitive ability (Levins and Culver 1971), predator resistance versus resource exploitation (Leibold 1996), or resource use efficiencies for two essential resources (Tilman 1977). These insights are applied to more diverse communities by introducing additional species that experience the same tradeoff, or by assuming that multiple axes of competitive traits create multiple tradeoffs (Chase and Leibold 2003). This approach essentially builds diverse communities from two-species interactions, but it is possible for qualitatively new dynamics to emerge as communities become more complex. A simple example of such a qualitatively new dynamic is rock-paper-scissors competition in a three-species community (Gilpin 1975, May and Leonard 1975); here it is possible for three species to coexist despite no pair of species being able to coexist.

Despite several empirical examples of intransitive competition (Buss and Jackson 1979, Sinervo and Lively 1996, Kerr et al. 2002, Lankau and Strauss 2007), this phenomenon has received relatively little attention, perhaps because it seems to require an idiosyncratic arrangement of traits to generate such a counterintuitive loop of competitive outcomes, as opposed to the tradeoffs that are thought to have

an origin in resource allocation or ecological specialization (Strauss et al. 2002). In communities of sessile marine invertebrates intransitivity can occur in the ability of species to overgrow or encroach upon one another (Buss and Jackson 1979, Rubin 1982, Wootton 2001). In these communities the mechanism of intransitivity is based possibly upon allelopathy (Jackson and Buss 1975) or the morphological details of overgrowth (Buss 1980, Rubin 1982). In the case of allelopathy, species-specific allelochemical effects can allow for situations where species A overgrows species B, and species B overgrows species C, but species C can chemically inhibit species A (Jackson and Buss 1975). Similar forms of intransitivity involving allelopathy have been described for interactions between clones of bacteria (Kerr et al. 2002) and between genotypes and species of plant (Lankau and Strauss 2007). Mate competition between lizard morphs can also be intransitive, due to a rock–paper–scissors arrangement of the relative advantage of different mating strategies (Sinervo and Lively 1996). For all of these systems it has been argued or demonstrated that intransitivity contributes to the maintenance of diversity.

Here we describe a different mechanism for competitive intransitivity, one that arises from species differences that are commonly observed in communities where space is limited. In particular, we consider competitive communities with a colonization–competition tradeoff between two species and a third species that preempts space from the other competitors. Here preemption is defined as any case where species A grows more quickly into free space than it

does when displacing species B. Preemptive ability is therefore a continuous trait which measures how much the inferior competitor (species B) ‘resists’ displacement or overgrowth by the superior competitor. Calcagno et al. (2006) have shown that the inclusion of preemption into a model of competition for space can either enhance or deter coexistence, depending on whether the dominant competitor is colonization-limited. Our model differs from theirs in that we depict a scenario where one species is specialized at preempting space, while they modeled each species as preempting space to the same degree. Asymmetries in preemptive abilities are likely to be common in space limited communities, especially when competitors vary widely in morphology so that e.g. some species grow primarily vertically and others grow primarily horizontally (Buss and Jackson 1979, Sebens 1986). Consequently, it is important to understand how these asymmetries generate intransitivities in pairwise interactions and under what conditions they mediate coexistence.

We define intransitive competition more broadly than rock-paper-scissors competition, by stating that competition is intransitive whenever the pairwise outcomes between A and B, and between B and C, do not predict the outcome between A and C. Under this definition, intransitivities can involve pairwise coexistence, and this yields a variety of intransitive arrangements. For example, intransitivity occurs when A beats B, and B beats C, but C coexists with A. In this kind of community all three species can potentially persist by a network of indirect effects, such that the removal of one competitor may result in the loss of an additional competing species, contrary to an expectation based on the freeing of resources. This kind of competitive indirect effect has been noted before (Case 1999), and our model depicts one way in which this can occur.

Here we illustrate how intransitive outcomes can arise and affect coexistence, using a model of three species consisting of a good colonizer, a good preemptor, and a good overgrowth competitor. We then describe how these traits can occur in natural communities, using parameter estimates from a subtidal marine community as an example.

Model formulation

Our model is intended to represent three ‘strategies’ for competition in space. We will refer to these strategies as Fugitive, Preemptor and Overgrower. The inspiration for this framework comes from work in benthic marine communities, where it has been noted that some species are primarily good at colonizing free space, some species are primarily good at holding space once it is occupied, and some species are primarily good at encroaching onto space occupied by other species (Sebens 1986).

With this set of three strategies in mind, the model can be written as:

$$\text{Fugitive } \frac{df_1}{dt} = \overbrace{b_1 f_1 (1 - f_1 - f_2 - f_3)}^{\text{colonization of free space}} - \overbrace{c_{12} f_1 f_2}^{\text{overgrowth}} - \overbrace{d_1 f_1}^{\text{mortality}} \quad (1)$$

$$\text{Overgrower } \frac{df_2}{dt} = b_2 f_2 (1 - f_1 - f_2 - f_3) + c_{12} f_1 f_2 - d_2 f_2 \quad (2)$$

$$\text{Preemptor } \frac{df_3}{dt} = b_3 f_3 (1 - f_1 - f_2 - f_3) - d_3 f_3 \quad (3)$$

where f_i is the fraction of total space occupied by species i , b_i is the per capita rate of colonization of free space, d_i is the per capita rate of mortality, and c_{ij} is the per capita rate at which species j overgrows species i (i.e. $c_{ij} = -c_{ji}$ and $c_{ij} \leq b_i$ for all i, j). The term $(1 - f_1 - f_2 - f_3)$ corresponds to the fraction of unoccupied space which is colonized at a rate $b_i f_i (1 - f_1 - f_2 - f_3)$ by species i , and $c_{ij} f_i f_j$ represents the net rate at which species j overgrows species i when c_{ij} is positive (or vice versa if c_{ij} is negative). We will refer to c_{ij} as an overgrowth rate, but this is only one biological interpretation and the term can be considered broadly as measuring relative competitive superiority. This model can be interpreted according to the formalism of Crowley et al. (2005), where the overgrowth term represents competition for space between clonal or colonial organisms. Equivalently this model can be interpreted as a patch model with one individual per patch (Hastings 1980, Tilman 1994), in which case the overgrowth term represents the rate at which the superior competitor colonizes and overtakes sites occupied by the inferior competitor. This model is constructed such that the Overgrower overgrows the Fugitive, while the Preemptor does not overgrow nor is overgrown by either species.

Model analysis

An important quantity associated with our competition model is the basic reproductive number of a species $\frac{b}{d}$ i.e. the average number of sites in essentially empty landscape colonized by its progeny during its lifetime. Since the fraction of occupied space

equals $\left(1 - \frac{d}{b}\right)$ at the equilibrium determined by a single species,

$\frac{b}{d}$ measures the ability of a species to occupy space in the absence of interspecific competition. In the absence of overgrowth, the basic reproductive number determines the outcome of pairwise interactions: the species with a higher reproductive number competitively excludes species with a lower reproductive number (Crowley et al. 2005). The inclusion of overgrowth can mediate coexistence for pairwise interactions provided there is a suitable tradeoff between overgrowth abilities and reproductive number (Crowley et al. 2005, Appendix 1).

Our analysis of Eq. 1–3 reveals that three species coexistence requires several life history tradeoffs (Appendix 1). First, the ability to overgrow must carry a cost of a lower basic reproductive number, and the ability to resist overgrowth must carry a similar but smaller cost. Therefore, the relative abilities to occupy space in the absence of overgrowth are given by the hierarchy: Fugitive > Preemptor > Overgrower (i.e. $\frac{b_1}{d_1} > \frac{b_3}{d_3} > \frac{b_2}{d_2}$).

Second, coexistence requires that the Fugitive have the greatest per-capita expansion rate, $b - d$, in addition to having the greatest reproductive number. This constraint seems biologically reasonable as it is only violated when the fugitive species exhibits a live-slow/die-old strategy and the other species exhibit a live-fast/die-young strategy.

In our model formulation the Preemptor does not overgrow and is not overgrown. Therefore, with the life history tradeoffs required for coexistence, the Preemptor excludes the Overgrower and is excluded by the Fugitive in pairwise competition. Consequently, in addition to the life history tradeoffs the conditions for three-species coexistence depend on the ecological outcome between the Fugitive and the Overgrower, and whether the Preemptor can invade the equilibrium determined by this outcome. Hence, we have three cases to consider.

Case 1: the Fugitive prevents invasion by the Overgrower

If the per-capita growth rate of the Overgrower is negative at the Fugitive equilibrium, then the Fugitive equilibrium is uninvadable by the other species (Fig. 1A, Appendix 1). Hence, coexistence for all initial conditions is not possible in this case.

Case 2: coexistence of the Fugitive and Overgrower

If the Fugitive and Overgrower coexist, then three-way coexistence will occur if the Preemptor can invade the equilibrium between Fugitive and Overgrower (Fig. 1B–C, Appendix 1). The Preemptor can invade if the following inequality holds:

$$\frac{b_3 - d_3}{b_3} > \frac{(b_1 - d_1) - (b_2 - d_2)}{b_1 - b_2 + c_{12}} \quad (4)$$

This inequality shows that invasibility of the equilibrium is favored by the Overgrower's relative ability against the Fugitive. Either increasing the Overgrower's reproductive number $\frac{b_2}{d_2}$ or increasing its overgrowth rate c_{12} favors

invasibility for the Preemptor by lowering the equilibrium abundance of the Fugitive. If this condition is fulfilled, then there is three species coexistence as all equilibria are invadable by a missing species and there is no rock–paper–scissor dynamic (Hutson and Law 1985).

Case 3: a cycle of pairwise exclusion

If the Overgrower excludes the Fugitive, then there is an intransitive cycle of competitive exclusion (Fig. 1D). For such a system, the fate of the community depends on the relative

size of the product of the invasion rates and the product of the exclusion rates (Hutson and Law 1985). If the product of the exclusion rates is greater than the product of the invasion rates, then the community dynamics can converge to the heteroclinic cycle of equilibria and ultimately two species go extinct. If the product of the invasion rates is greater than the product of the exclusion rates, then the three species coexist.

With the life history tradeoff $\frac{b_1}{d_1} > \frac{b_3}{d_3} > \frac{b_2}{d_2}$, the latter outcome always occurs (Appendix 1).

One way to envision the transition from case 1 to case 3 is by varying the overgrowth ability of the Overgrower as illustrated in Fig. 1. At low overgrowth abilities, the Overgrower is unable to halt the spread of the Fugitive species and the Fugitive species displaces its competitors. At intermediate overgrowth abilities, the Overgrower can coexist with the Fugitive, but is unable to facilitate the invasion of the Preemptor. At high overgrowth abilities, the Overgrower becomes sufficiently dominant against the Fugitive to facilitate the invasion of the Preemptor in which case there is three species coexistence.

Evidence from a natural subtidal community

We have shown that communities structured by both a colonization–competition tradeoff and significant preemption of space can have intransitive competitive outcomes that facilitate coexistence. Both of these conditions are common in natural communities, implying that intransitivities may be more common than currently realized. A potential example of a Fugitive–Preemptor–Overgrower system is described by Sebens (1982, 1986) for a rocky subtidal community in Massachusetts. This community includes tunicates, sponges, bryozoans and several other taxonomic groups that live attached to hard substrates. The colonial tunicate *Aplidium pallidium* (hereafter *Aplidium*) is an overgrowth dominant that spreads along the substrate and displaces or smothers most other species in the community. A number of species colonize space rapidly but are eventually overgrown, e.g. encrusting bryozoans. The preemptor strategy is represented by *Alcyonium siderium* (hereafter *Alcyonium*), an octocoral. This species grows away from the substrate and experiences a

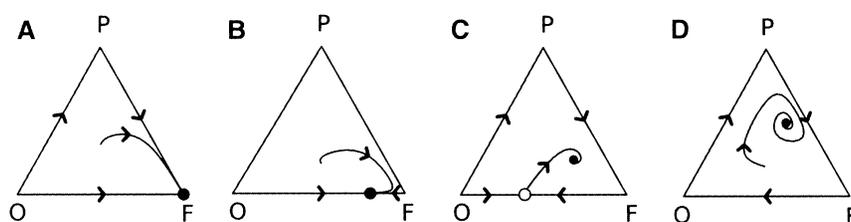


Figure 1. The four types of outcome under the Fugitive–Preemptor–Overgrower model. Each triangle is a ternary plot depicting the frequency of each species in the community. Arrows on the sides indicate the outcome of pairwise competition; if two arrows point inwards then those species coexist. An open circle represents an invadable equilibrium, a closed circle represents an uninvadable equilibrium. Curves inside the triangles indicate the community trajectory when all species are initially present. (A) an uninvadable Fugitive equilibrium. (B) the Fugitive and Overgrower coexist but the Preemptor cannot invade. (C) the Fugitive and Overgrower coexist, and the Preemptor can invade. (D) the Overgrower excludes the Fugitive, yielding a heteroclinic cycle between the single species equilibria. For these phase portraits, $b_1 = 3.6$, $b_2 = 2.6$, $b_3 = 1.9$, $d_1 = 0.9$, $d_2 = 1.5$, $d_3 = 0.63$. The parameter c_{12} is increased over the four outcomes, from (A) to (B) to (C) to (D).

size refuge from overgrowth by *Aplidium* once it has grown beyond a small juvenile stage. Furthermore *Alcyonium* is relatively long-lived compared to the rest of the community, and grows slowly in a primarily vertical direction, so that its impact on the rest of community is essentially via preemption.

The studies documenting this system are detailed enough to create rough estimates of the parameters of our model for *Aplidium*, *Alcyonium*, and the guild of encrusting bryozoans (Sebens 1982, 1986). These studies suggest that: 1) bryozoan colonization rate is an order of magnitude larger than the colonization rates of *Aplidium* and *Alcyonium*, which are similar, 2) the mortality rate of *Alcyonium* is an order of magnitude smaller than the mortality rates of *Aplidium* and the bryozoans, which are similar, and 3) *Aplidium* overgrows bryozoans easily, but cannot overgrow adult *Alcyonium*. We therefore assigned parameter values consistent with these constraints. Because *Aplidium* can decline significantly over one year, we set its mortality rate to 0.1 month^{-1} . We set its intrinsic rate of growth to 0.04 month^{-1} (i.e. $b = 0.14 \text{ month}^{-1}$), reflecting relatively slow growth after disturbance. We set the mortality rate of *Alcyonium* to be ten times less than *Aplidium* (0.01 month^{-1}), and we varied its colonization rate from 0.09 to 0.16 month^{-1} , to show how outcomes depend upon this species' reproductive number. We gave the bryozoans the same mortality rate as *Aplidium* and a colonization rate ten times greater (1.4 month^{-1}). We varied the overgrowth rate of *Aplidium* onto the bryozoans (from 0.08 to the maximum of 0.14 month^{-1}), to show how the outcome depends on how well the bryozoans preempt space. The overgrowth rates of *Aplidium* on *Alcyonium* and *Alcyonium* on bryozoans, were set to zero.

Figure 2 shows how the outcome of competition will vary depending on the rate at which *Aplidium* overgrows the bryozoans, and the reproductive number of *Alcyonium*. All

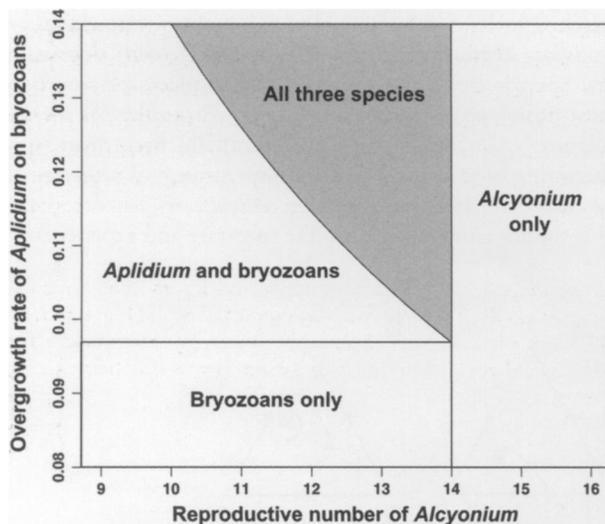


Figure 2. Predicted outcomes for the *Aplidium*–*Alcyonium*–bryozoan community. The parameters held constant for this figure are the growth and mortality rates of *Aplidium* ($b_{AP} = 0.14 \text{ month}^{-1}$, $d_{AP} = 0.1 \text{ month}^{-1}$) and the bryozoans ($b_{BR} = 1.4 \text{ month}^{-1}$, $d_{BR} = 0.1 \text{ month}^{-1}$). The overgrowth rate of *Aplidium* on bryozoans was constrained to be no greater than the growth rate of *Aplidium* into free space. The overgrowth rates of *Aplidium* on *Alcyonium*, and *Alcyonium* on bryozoans, were set to zero.

three species are predicted to coexist for a significant fraction of possible trait values. As we described for the Fugitive–Preemptor–Overgrower model, coexistence requires that *Alcyonium* (the Preemptor) has a smaller reproductive number than the bryozoans (a Fugitive guild). Furthermore, *Aplidium* will coexist with the faster-growing bryozoans if its overgrowth rate is large enough, and *Alcyonium* can then invade this community depending on the magnitudes of its reproductive number and the *Aplidium*–bryozoan interaction. Therefore, the coexistence region in Fig. 2 corresponds to the community depicted in Fig. 1C. These predictions, although based on rough estimates, demonstrate a feasible role for this intransitive coexistence mechanism in natural communities. Moreover, the colonization–competition tradeoff displayed by these three kinds of species is present in the community more generally (Sebens 1986), so that the effect of including a strong preemptor species should hold generally as well.

Discussion

We have shown that the inclusion of preemption into a model of competition for space can create intransitive outcomes in a three-species community, and we have shown that these intransitive outcomes in combination with life history tradeoffs can allow three species to coexist despite the inability of all sub-communities to coexist. The competitive traits that underlie our results are observed commonly in space-limited communities, to the extent that competition–colonization tradeoffs are commonly observed during succession (Sebens 1986, Tilman 1994), while at the same time earlier colonizers typically inhibit the establishment of later colonizers to varying degrees (Connell and Slatyer 1977). Thus our results provide a plausible biological mechanism for intransitive competition, and an additional way by which diversity can be maintained in communities competing for a single resource. Coexistence of species with these traits is predicated on multiple life history tradeoffs that will need to be empirically quantified to further test the plausibility of this mechanism. More specifically, coexistence in this model requires that the ability to overgrow carries a large cost in reproductive number (a colonization–competition tradeoff), and that the ability to preempt space carries an intermediate cost in reproductive number (a colonization–preemption tradeoff). These tradeoffs apply as well in a more general analysis of three species competition for space (Appendix 2).

The mechanisms underlying coexistence of species specializing in overgrowth, preemption, and colonization can be understood in terms of the invasibility conditions illustrated in Fig. 1C–D. If the Fugitive is at high abundance then the Overgrower has a relative advantage because it can overtake space occupied by the Fugitive. If the Overgrower is at high abundance then the Preemptor has a relative advantage because it can resist overgrowth and colonize free space more quickly than the Overgrower. Finally, if the Preemptor is at high abundance then the Fugitive has a relative advantage because it can colonize free space more quickly than the Preemptor. This arrangement of relative abilities prevents any one species from becoming so abundant as to exclude the

others, allowing all three to persist. We have modeled these competitive strategies in tractable but simplified form, with the Preemptor having a zero probability of overgrowing or being overgrown. However, we have also simulated a more general three-species model where parameters were randomly chosen such that each species can exhibit a mixture of Fugitive, Preemptor, and Overgrower traits. In these simulations more than half of communities with three-species coexistence possessed intransitive Fugitive–Preemptor–Overgrower arrangements (Appendix 2).

Our results add to a growing literature on the ways that preemption and competitive asymmetry affect coexistence in spatial communities (Bolker and Pacala 1999, Adler and Mosquera 2000, Levine and Rees 2002, Calcagno et al. 2006). It has been shown that the effectiveness of a colonization–competition tradeoff in allowing coexistence varies with the degree of asymmetry in competitive effects (Adler and Mosquera 2000, Levine and Rees 2002). Coexistence of a large number of species is more difficult when superior competitors experience some negative effects when attempting to displace inferior competitors. In our framework, these negative effects are a form of preemption of space. Preemption was considered explicitly by Calcagno et al. (2006), using a model in which all species preempted space to the same degree. They showed that preemption in general could enhance or deter coexistence, depending on the degree to which superior competitors are colonization-limited. Our work adds to these results by examining a community in which the degree of preemption varies amongst the species. Our results suggest that the overall effect of preemption on the maintenance of diversity will depend upon the way that preemptive ability and other traits covary in natural assemblages.

How can we test whether this mechanism occurs in natural communities? Our example of a subtidal marine community demonstrates the kinds of ecological differences that need to be quantified. If there is a general negative relationship between colonization rate and overgrowth ability, and in addition some species are poor overgrowers but can resist overgrowth, intransitive dynamics may be present. A strong test of this mechanism is complicated by the way that intransitivities operate in concert with hierarchical overgrowth relationships and colonization–competition tradeoffs. For example, experimenters often clear patches in a community and observe succession for the surrounding area. If succession proceeds from fast colonizers that are poor competitors to slow colonizers that are superior competitors, this pattern is consistent with both a classic transitive model of coexistence, and the intransitive model presented here. Detection of intransitivities will therefore require a more direct analysis of pairwise interactions. One approach is to measure the appropriate demographic and competitive traits to parameterize a model of competition, similar to the approach we used for the *Aplidium–Alcyonium*–bryozoan community. Intransitive coexistence is present if the model predicts coexistence for the community as whole, but not for all subsets of the community. A second approach is to experimentally stage competition between pairs of species, as well as larger subsets of the community. This will allow a direct test of whether pairwise exclusion occurs, while at the same time larger subsets of the community are able to coexist. These

methods are data-intensive, but they will be necessary to determine whether natural competitors coexist in a transitive way, or whether coexisting communities are held together by a web of indirect effects. A weaker but revealing test for intransitivity is the removal of single species from a guild of competing species, followed by observation of whether any of the remaining competitors then go locally extinct. If this occurs, then the implication is that the removed species was maintaining additional diversity in the community by indirect interactions with other species.

Although we have used a simple model of competition between three strategies, we expect our results to hold more generally. Our simulation results indicate that intransitivity can frequently contribute to coexistence, and that the strategies we have described occur naturally in randomly drawn coexisting communities (Appendix 2). Preliminary work has shown that these mechanisms are not restricted to three-species systems, but rather that complex networks of intransitive pairwise outcomes can occur as more speciose communities are assembled (Edwards unpubl.). Preliminary work has also shown that these mechanisms occur in spatially explicit representations of competition, and we therefore expect that our conclusions are not model-specific. Likewise, we have taken inspiration from benthic marine communities in constructing our model, but the results are applicable in general for spatially structured competition, as described e.g. for grassland communities (Tilman 1994), ant communities (Adler et al. 2007), and lichen communities (Crowley et al. 2005).

In conclusion, our results highlight that understanding the maintenance of diversity may require approaches that go beyond pairwise interactions. Acquisition of a limiting resource may be achieved in multiple ways; in our model this occurs by rapid colonization of free space, by capturing occupied space, or by preempting occupied space from being captured. The interaction of more than two strategies can result in intransitive coexistence, and if communities are maintained by intransitive interactions the extinction of a single species can result in a cascade of secondary extinctions. Understanding the prevalence of intransitive coexistence therefore has implications both for how diversity is maintained and how communities respond to large perturbations.

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References

- Adler, F. R. and Mosquera, J. 2000. Is space necessary? Interference competition and limits to biodiversity. – *Ecology* 81: 3226–3232.
- Adler, F. R. et al. 2007. Maintaining diversity in an ant community: modeling, extending, and testing the dominance–discovery tradeoff. – *Am. Nat.* 169: 323–333.
- Agrawal, A. A. et al. 2007. Filling key gaps in population and community ecology. – *Front. Ecol. Environ.* 5: 145–152.

- Amarasekare, P. 2003. Competitive coexistence in spatially structured environments: a synthesis. – *Ecol. Lett.* 6: 1109–1122.
- Bolker, B. M. and Pacala, S. W. 1999. Spatial moment equations for plant competition: understanding spatial strategies and the advantages of short dispersal. – *Am. Nat.* 153: 575–602.
- Buss, L. W. 1980. Competitive intransitivity and size–frequency distributions of interacting populations. – *Proc. Natl Acad. Sci. USA* 77: 5355–5359.
- Buss, L. W. and Jackson, J. B. C. 1979. Competitive networks: nontransitive competitive relationships in cryptic coral reef environments. – *Am. Nat.* 113: 223–234.
- Calcagno, V. et al. 2006. Coexistence in a metacommunity: the competition–colonization tradeoff is not dead. – *Ecol. Lett.* 9: 897–907.
- Case, T. J. 1999. An illustrated guide to theoretical ecology. – Oxford Univ. Press.
- Chase, J. M. and Leibold, M. A. 2003. Ecological niches: linking classical and contemporary approaches. – Univ. of Chicago Press.
- Chesson, P. 2000. Mechanisms of maintenance of species diversity. – *Annu. Rev. Ecol. Syst.* 31: 343–366.
- Connell, J. H. and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. – *Am. Nat.* 111: 1119–1144.
- Crowley, P. H. et al. 2005. A general model of local competition for space. – *Ecol. Lett.* 8: 176–188.
- Gilpin, M. E. 1975. Limit cycles in competition communities. – *Am. Nat.* 109: 51–60.
- Hastings, A. 1980. Disturbance, coexistence, history and competition for space. – *Theor. Popul. Biol.* 18: 363–373.
- Hofbauer, J. and Sigmund, K. 1998. Evolutionary games and population dynamics. – Cambridge Univ. Press.
- Hutson, V. and Law, R. 1985. Permanent coexistence in general models of three interacting species. – *J. Math. Biol.* 21: 285–298.
- Hutson, V. and Schmitt, K. 1992. Permanence and the dynamics of biological systems. – *Math. Biosci.* 111: 1–71.
- Jackson, J. B. C. and Buss, L. 1975. Allelopathy and spatial competition among coral reef invertebrates. – *Proc. Natl Acad. Sci. USA* 72: 5160–5163.
- Kerr, B. et al. 2002. Local dispersal promotes biodiversity in a real-life game of rock–paper–scissors. – *Nature* 418: 171–174.
- Laird, R. A. and Schamp, B. S. 2006. Competitive intransitivity promotes species coexistence. – *Am. Nat.* 168: 182–193.
- Lankau, R. A. and Strauss, S. Y. 2007. Mutual feedbacks maintain both genetic and species diversity in a plant community. – *Science* 317: 1561–1563.
- Leibold, M. A. 1996. A graphical model of keystone predators in food webs: trophic regulation of abundance, incidence and diversity patterns in communities. – *Am. Nat.* 147: 784–812.
- Levine, J. M. and Rees, M. 2002. Coexistence and relative abundance in annual plant assemblages: the roles of competition and colonization. – *Am. Nat.* 160: 452–467.
- Levins, R. and Culver, D. 1971. Regional coexistence of species and competition between rare species. – *Proc. Natl Acad. Sci. USA* 68: 1246–1248.
- May, R. M. and Leonard, W. J. 1975. Nonlinear aspects of competition between three species. – *Siam J. Appl. Math.* 29: 243–253.
- Rubin, J. A. 1982. The degree of intransitivity and its measurement in an assemblage of encrusting cheilostome Bryozoa. – *J. Exp. Mar. Biol. Ecol.* 60: 119–128.
- Sebens, K. P. 1982. Competition for space: growth rate, reproductive output and escape in size. – *Am. Nat.* 120: 189–197.
- Sebens, K. P. 1986. Spatial relationships among encrusting marine organisms in the New England subtidal zone. – *Ecol. Monogr.* 56: 73–96.
- Sinervo, B. and Lively, C. M. 1996. The rock–paper–scissors game and the evolution of alternative male strategies. – *Nature* 380: 240–243.
- Strauss, S. Y. et al. 2002. Direct and ecological costs of resistance to herbivory. – *Trends Ecol. Evol.* 17: 278–285.
- Tilman, D. 1977. Resource competition between planktonic algae: an experimental and theoretical approach. – *Ecology* 58: 338–348.
- Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. – *Ecology* 75: 2–16.
- Wootton, J. T. 2001. Causes of species diversity differences: a comparative analysis of Markov models. – *Ecol. Lett.* 4: 46–56.

Appendix 1

Analysis of the Fugitive–Preemptor–Overgrower model

In this Appendix, we determine under what conditions three species coexistence is possible for the Fugitive–Preemptor–Overgrower model. We determine coexistence using the criterion of permanence. Permanence requires that the densities of all species are bounded away from zero for all initially positive trajectories (Hutson and Schmitt 1992). For the three species competition models of the type used here, permanence is ensured if (1) each single-species and two-species equilibrium is invadable by at least one missing species and (2) if there is no two species equilibrium and each single species equilibrium is invadable (i.e. there is a rock–paper–scissor dynamic), then the product of the invasion rates is greater than the product of the exclusion rates (Hutson and Law 1985). Our analysis begins with recalling basic results for the single and two species subsystems of our three species model.

Single species and pairwise interactions

Species i has a positive intrinsic rate of growth provided that $b_i - d_i > 0$. Equivalently $R_i > 1$ where $R_i = \frac{b_i}{d_i}$ is the

basic reproductive number of species i . Throughout the Appendix, we assume that $R_i > 1$. Under this assumption, species i has the positive equilibrium abundance $f_i^* = 1 - 1/R_i$. For pairwise interactions, our model corresponds to a reparameterization of the classical Lotka–Volterra competition equations. Consequently, generically, there are three possible outcomes: coexistence, bistability, and exclusion. For the Fugitive–Preemptor and the Preemptor–Overgrower interactions, the species with the lower R_i value is excluded. For the Fugitive–Overgrower interaction, the per-capita growth rate of the Overgrower at the Fugitive equilibrium $(f_1, f_2) = (f_1^*, 0)$ is given by $b_2/R_1 - d_2 + c_{12}(1 - 1/R_1)$ and the per-capita growth rate of the Fugitive at the Overgrower equilibrium $(f_1, f_2) = (0, f_2^*)$ is given by $b_1/R_2 - d_1 - c_{12}(1 - 1/R_2)$. Exclusion occurs when these per capita growth rates have opposite signs, coexistence occurs when both of these per capita growth rates are positive, and bistability occurs when both of these per capita growth rates are negative. In the cases of coexistence and bistability, there is a positive equilibrium $(f_1, f_2) = (f_1^{**}, f_2^{**})$ supporting both species. At this equilibrium, the fraction of unoccupied space equals

$$1 - f_1^{**} - f_2^{**} = \frac{c_{12} + d_1 - d_2}{c_{12} + b_1 - b_2}$$

Permanence for the full model

Our analysis continues by proving that three species coexistence requires the life history constraints: $R_1 > R_3 > R_2$. By the Poincaré–Hopf index theorem (Hofbauer and Sigmund 1998), permanence is only possible if there is a positive equilibrium for the model. For the Fugitive—Preemptor—Overgrower model, a positive equilibrium $(\hat{f}_1 - \hat{f}_2 - \hat{f}_3)$ must satisfy

$$\begin{aligned} 0 &= b_1(1 - \hat{f}_1 - \hat{f}_2 - \hat{f}_3) - d_1 - c_{12} \hat{f}_2 \\ 0 &= b_2(1 - \hat{f}_1 - \hat{f}_2 - \hat{f}_3) - d_2 + c_{12} \hat{f}_1 \\ 0 &= b_3(1 - \hat{f}_1 - \hat{f}_2 - \hat{f}_3) - d_3 \end{aligned}$$

The third equation implies that $1 - \hat{f}_1 - \hat{f}_2 - \hat{f}_3 = 1/R_3$. Substituting this expression into the first equation yields $b_1/R_3 - d_1 = c_{12} \hat{f}_2$. Equivalently, $R_1 = R_3(1 + c_{12} \hat{f}_2)$. Hence, $R_1 > R_3$ at any positive equilibrium. Similarly, substituting $1 - \hat{f}_1 - \hat{f}_2 - \hat{f}_3 = 1/R_3$ into the second equation yields that $R_3 > R_2$ at any positive equilibrium. Thus, we have shown that three species coexistence requires that $R_1 > R_3 > R_2$ and we assume this relationship holds for the remainder of this Appendix.

Due to this ordering of the basic reproductive numbers, the Fugitive excludes the Preemptor and the Preemptor excludes the Overgrower in pairwise interactions. Therefore, determining three species coexistence reduces to considering three cases based on the outcome of competition between the Fugitive and the Overgrower.

Case 1: the Overgrower can not invade the Fugitive equilibrium

If the per capita growth rate of the Overgrower is negative at the Fugitive equilibrium i.e. $b_2/R_1 - d_2 + c_{12}(1 - 1/R_1) < 0$, then the Fugitive equilibrium $(f_1, f_2, f_3) = (1 - d_1/b_1, 0, 0)$ is uninvadable and the system is not permanent.

Case 2: coexistence between the Fugitive and Overgrower

Coexistence occurs when the per-capita growth rates $b_2/R_1 - d_2 + c_{12}(1 - 1/R_1)$ and $b_1/R_2 - d_1 - c_{12}(1 - 1/R_2)$ are both positive. Equivalently,

$$b_1 - d_1 > (d_1 d_2)(R_1 - R_2)/c_{12} \tag{A1}$$

$$b_2 - d_2 < (d_1 d_2)(R_1 - R_2)/c_{12} \tag{A2}$$

Recall, at this equilibrium, the fraction of unoccupied space is $1 - f_1^{**} - f_2^{**} = \frac{c_{12} + d_1 - d_2}{c_{12} + b_1 - b_2}$. Hence, the per capita growth rate of the Preemptor at this equilibrium is $b_3 \frac{c_{12} + d_1 - d_2}{c_{12} + b_1 - b_2} - d_3$

$$\text{which is positive when } \frac{b_3 - d_3}{b_3} > \frac{((b_1 - d_1) - (b_2 - d_2))}{(b_1 - b_2 + c_{12})} \tag{A3}$$

Therefore permanence in this case requires that conditions A1–A3 hold.

Case 3: the Overgrower excludes the Fugitive

If the Overgrower excludes the Fugitive, then the community forms a heteroclinic cycle. The asymptotic dynamics of this heteroclinic cycle are determined by the per capita growth rates at the singles-species equilibria. Define the invasion rate of species j at the equilibrium determined by species i as

$$I_{ij} = \frac{b_j}{R_i} - d_j + c_{ij}(1 - 1/R_i)$$

where $c_{12} = -c_{21}$, $c_{23} = c_{32} = 0$, $c_{13} = c_{31} = 0$ for our model. It has been shown by Hofbauer and Sigmund that a three-dimensional Lotka–Volterra system will be permanent, i.e. the heteroclinic cycle will be repelling, if the product of the three positive invasion rates is greater than the product of the absolute values of the three negative invasion rates (Hofbauer and Sigmund 1998). For our model, the product of the positive invasion rates is given by

$$I_{12} I_{23} I_{31} = (b_2/R_1 - d_2 + c_{12}(1 - 1/R_1)) (b_3/R_2 - d_3) (b_1/R_3 - d_1)$$

the product of the negative invasion rates is given by

$$I_{13} I_{32} I_{21} = (b_3/R_1 - d_3) (b_2/R_3 - d_2) (b_1/R_2 - d_1 - c_{12}(1 - 1/R_2))$$

and permanence requires that $\frac{R_1 R_2 R_3}{d_1 d_2 d_3}$. Equivalently after

multiplying both sides by and simplifying this yields

$$(R_2 - R_1 + c_{12}(R_1 - 1)/d_2)(R_3 - R_2)(R_1 - R_3) > (R_1 - R_3)(R_3 - R_2)(R_2 - R_1 + c_{12}(R_2 - 1)/d_1)$$

Equivalently, permanence requires that

$$b_1 - d_1 = (R_1 - 1)d_1 > (R_2 - 1)d_2 = b_2 - d_2$$

Conversely, if $b_1 - d_1 < b_2 - d_2$, then the heteroclinic cycle on the boundary is an attractor and the system is not permanent.

Appendix 2

Preemption, intransitivities, and coexistence in a more general model

We use a variant of the general model of spatial competition formulated by Crowley et al. (2005). The n -species version of the model can be written as:

$$\frac{df_i}{dt} = \underbrace{b_i f_i}_{\text{colonization of free space}} \left(1 - \sum_{j=1}^n f_j \right) - \underbrace{\sum_{j \neq i} c_{ij} f_j f_i}_{\text{overgrowth}} - \underbrace{d_i f_i}_{\text{mortality}}, \tag{A4}$$

with the parameters interpreted as in the text. Some commonly cited models of competition for space can be derived as special cases of this general model (Levins and Culver 1971, Hastings 1980, Tilman 1994, reviewed by Amarasekare 2003). For instance, Tilman's model of the competition-colonization tradeoff is given by $c_{ij} = \text{sign}(i - j)b_j$, which assumes for analytic simplicity that a superior competitor experiences no competitive effect from an inferior competitor. In contrast, the more general model allows inferior competitors to preempt space (i.e. resist being overgrown from another competitor), to a degree determined by the overgrowth parameters. Here we study coexistence for the three species version of Eq. A4 using a combination of analytic and numerical methods.

Analysis of the Fugitive–Preemptor–Overgrower model has shown that species with these traits can coexist, and this coexistence results from intransitivities and life history tradeoffs that stabilize the outcomes of pairwise competition. We now ask how these life history trade-offs and intransitivities contribute to coexistence in general. The general model eliminates the parameter constraints that defined the Fugitive–Preemptor–Overgrower system, creating a three-species community with no a priori relationship between colonization ability, preemption ability, and overgrowth ability. We used random draws to search the parameter space for this model, and we used permanence criteria to determine whether coexistence occurs (Appendix 3). Our primary constraint in drawing parameters was to force overgrowth abilities to be transitive, because the effects of intransitive overgrowth have been investigated elsewhere (Laird and Schamp 2006).

The parameters were chosen as follows: (1) the reproductive number $\frac{b}{d}$ of each species is a uniformly distributed random number on the interval (1, 25). (2) The intrinsic rate of growth $b - d$ of each species is a uniformly distributed random number on the interval . (3) If we define species 2 as the superior overgrowth competitor, and species 1 as the weakest overgrowth competitor, then c_{12} is chosen randomly on the interval (0, b_2), c_{32} is chosen randomly on the interval (0, c_{12}), and c_{13} is chosen randomly on the interval (0, $\min(c_{12}, b_3)$).

These conditions ensure that each species has positive growth when alone ($b > d$), and that overgrowth is hierarchical with species 3 overgrowing species 1, and species 2 overgrowing both species 3 and 1. Furthermore, the rates of overgrowth are hierarchical in the sense that $c_{12} > c_{32}$ and $c_{12} > c_{13}$. We performed 10^6 draws in our search of parameter space. Similar results were obtained for different parameter constraints on b and d , e.g. a lower ceiling for $\frac{b}{d}$ and $b - d$, or

a requirement that the greatest $\frac{b}{d}$ implies the greatest $b - d$.

Results of numerical search of parameter space

We gauge the importance of intransitivity by classifying each parameter set in which coexistence occurred, according to the corresponding outcomes of pairwise competition (Fig. A1).

Out of the fifteen possible coexistence configurations, all except one (no. 15) involve some kind of intransitivity in pairwise outcomes. The frequencies of the different configurations suggest that the parameter space for coexistence involving intransitivity is much larger than the parameter space for coexistence when all pairs of competitors can coexist; the fully transitive case only occurs in 2% of draws where coexistence occurs.

We investigated the mechanism of coexistence in these communities by quantifying a colonization–competition tradeoff. To describe the colonization–competition tradeoff we calculated an ‘overgrowth factor’ for each species that averages its overgrowth performance against the other two species. For instance, the overgrowth factor for species 1 is $\frac{c_{12} + c_{13}}{2}$, which averages the per capita rates at which species 1 is overgrown by species 2 and 3 respectively. A colonization–competition tradeoff corresponds to a negative correlation between the reproductive number and the overgrowth factor for each species. Calculation of the mean overgrowth factor for each community configuration showed that all community types had an average correlation between -0.85 and -0.99 , while for non-coexisting communities the average correlation was zero. These results suggest that a colonization–competition tradeoff is necessary for coexistence in this model.

To further understand the maintenance of coexistence in these randomly drawn communities, we can compare these results to the model of the Fugitive, Preemptor and Overgrower. In that case the Preemptor excluded the Overgrower, the Fugitive excluded the Preemptor, and the Overgrower either excluded or coexisted with the Fugitive. This arrangement of outcomes is consistent with the direction of the arrows in configurations 1–7 in Fig. A1. The Preemptor strategy was defined by the fact that this species did not overgrow and was not overgrown. For the more general model, we can define a corresponding ‘preemption factor’ $= 1 - \frac{(c_{13} + c_{32})}{2c_{12}}$, where species 2 is the superior overgrower,

species 1 is the poorest overgrower, and species 3 is intermediate. This quantity increases when species 3 is poor at overgrowing species 1 and/or resists overgrowth from species 2, measured relative to the rate at which species 1 overgrows species 2. The maximum of this quantity is 1, in which case species 3 cannot be overgrown (i.e. has parameters equivalent to those of the Preemptor). The minimum of this quantity is 0, in which case all species resist overgrowth to the same extent (i.e. $c_{12} = c_{32} = c_{13}$). We calculated the average preemption factor for each configuration of pairwise outcomes (Fig. A1).

This analysis supports the intuition that configurations 1–7 from Fig. A1 correspond to the kind of community described under the rubric of Fugitive–Preemptor–Overgrower. For these, species 3 typically has trait values corresponding to what we have called a preemption strategy (i.e. a preemption factor close to 1). In contrast, for configurations 8–14 the outcomes of pairwise competition are reversed. These pairwise outcomes occur when the preemption factor is close to 0 and correspond to communities where the superior overgrower can dominate the intermediate overgrower and the intermediate overgrower can dominate the poorest overgrower. However, the superior overgrower cannot overgrow the poorest overgrower fast

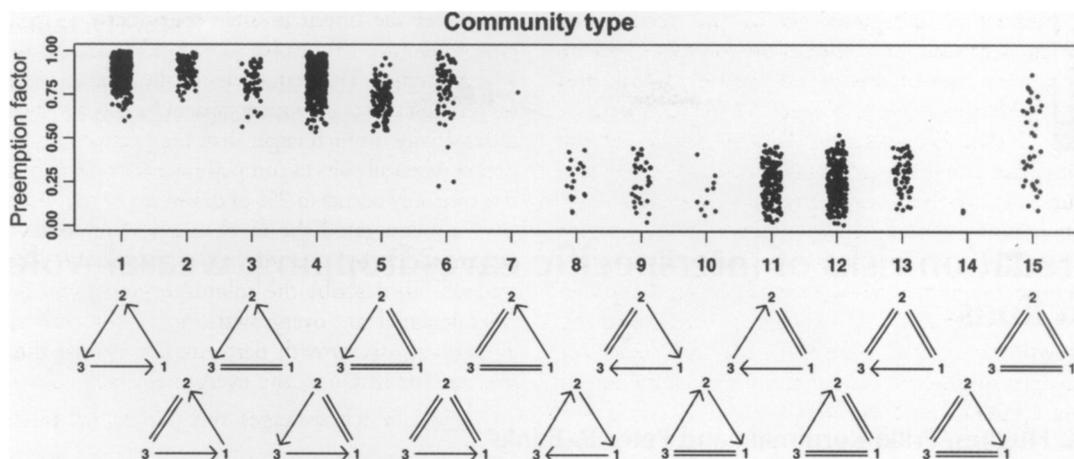


Figure A1. Results of the random draws from the general model. Below, the fifteen possible configurations of pairwise outcomes for a coexisting community. Arrows point to the winner in pairwise competition, double lines indicate stable coexistence. Species numbers follow those in the text. Above, a plot of preemption factor grouped by community configuration. Each point represents one randomly drawn coexisting community. Points have been jittered along the x-axis to illustrate the frequency of the different configurations.

enough, relative to its reproductive number, to dominate. Biologically this could occur if the outcomes of overgrowth competition are hierarchical while the rates of overgrowth do not vary greatly over the hierarchy. In other words species 2 may overgrow both 3 and 1, but overgrow each at relatively the same rate. If species 1 has a colonization advantage this allows for a cycle of outcomes that again sets up a balance of indirect effects among the three species. It is important to note that preemption of space is still critical for this kind of community, because it allows the best colonizer to potentially dominate the best overgrower. In general, the simulation results confirm the relevance of the simplified model described in the text, and indicate a second way in which varying degrees of competitive asymmetry can lead to intransitive coexistence.

Appendix 3

Algorithm for determining permanence

Permanence in a three-dimensional Lotka–Volterra system requires either that all single-species and two-species

equilibria are invadable by at least one missing species (Hutson and Law 1985), or in the special case of a heteroclinic cycle the product of the positive invasion rates must be greater than the negative of the product of the negative invasion rates (Hofbauer and Sigmund 1998, Appendix 1). We accordingly used this algorithm in determining whether a random draw of parameters fulfilled the permanence criteria:

- 1) Is there a positive three-species equilibrium? If yes go to (2), if no the system is not permanent.
- 2) Check each single-species equilibrium. Is each invadable by at least one missing species? If yes go to (3), if no the system is not permanent.
- 3) Are there any positive two-species equilibria? If yes go to (4), if no go to (5).
- 4) Are all two-species equilibria invadable by the missing species? If so, the system is permanent.
- 5) Is the product of the invasion rates greater than the product of the extinction rates? If so, the cycle is repelling and the system is permanent. If no, the cycle is attracting.