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From simple rules to cycling in community assembly

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Simulation studies of community assembly have frequently observed two related phenomena: (1) the humpty dumpty effect in which communities can not be reconstructed by "sequential" invasions (i.e. single species invasions separated by long intervals of time) and (2) cycling between sub-communities. To better understand the mechanisms underlying these phenomena, we analyze a system consisting of two predators and two prey competing for a shared resource. We show how simple dominance rules (i.e. R^* and P^* rules) lead to cycling between sub-communities consisting of predator–prey pairs; predator and prey invasions alternatively lead to prey displacement via apparent competition and predator displacement via exploitative competition. We also show that these cycles are often dynamically unstable in the population phase space. More specifically, while for too slow invasion rates (i.e. "sequential" invasions) the system cycles indefinitely, faster invasion rates lead to coexistence of all species. In the later case, the assembly dynamics exhibit transient cycling between predator-prey subcommunities and the length of these transients decreases with the invasion rate and increases with habitat productivity.

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Understanding rules and patterns of community assembly is a central theme in community ecology (Belyea and Lancaster 1999). Theoretical approaches to understanding community assembly divide roughly into two camps. the in-depth analysis of simple systems and Monte-Carlo simulations of complex systems. An ecological system may be classified as simple because either it consists only of a few interacting species (Holt 1977, Tilman 1980, Polis and Holt 1992, Holt and Lawton 1994, Holt et al. 1994, Holt and Polis 1997) or it involves a high number of species few of which interact (Hsu et al. 1978, Wolkowicz 1989 and Grover 1994). By studying these simpler systems, theoretical ecologists often uncover rules that govern the community assembly processes (Belyea and Lancaster 1999). On the other hand, simulation studies aid our understanding of more complex communities by monitoring how attributes such as species richness, invasion resistance, and predator-prey ratios change over time and by uncovering statistical relationships between assembly outcomes and source pool attributes (Post and Pimm 1983, Yodzis 1986, Case 1990, Drake 1990, Law and Blackford 1992, Luh and Pimm 1993, Law and Morton 1993, 1996, Lockwood et al. 1997, Hewitt and Huxel 2002).

A fundamental question addressed by both theoretical approaches is what are the possible end points of the assembly process? Two types of ending are possible; either a sequence of invasions terminates in a community that resists all invasion attempts or the community cycles endlessly between a finite set of subcommunities. Studies of simple communities with exploitative competition, apparent competition and intraguild predation shown that assembly invariably leads to an invasion resistant state (Hsu et al. 1977, Wolkowicz 1989, Polis and Holt 1992, Grover 1994, Holt et al. 1994, Holt and Polis 1997). In simulations of high dimensional

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Lotka-Volterra competitive communities, Yodzis (1986) showed that cycles are extremely common especially when the probability of pair wise competition leading to competitive exclusion is high. Alternatively, Law and Morton (1996) observed no cyclic endings when randomly assembling communities from source pools consisting of 5 to 15 basal species and 20 to 60 consumers with relatively low efficiencies of conversion of prey to predators. However, often end states consisted of "curiously fragile" communities that can not be rebuilt sequentially from their constituent species.

In this article, we investigate the linkages between "curiously fragile" communities and cycling with a simple model. Motivated by Kirlinger's study (1989) on cycling in linked predator-prey systems, we extend a model of Holt et al. (1994) to include a resource, two consumer species, and two predator species. For this model, we determine under what conditions cycling between predator-prey sub-systems occurs and under what conditions these cycles are dynamically unstable. We proceed to illustrate that while at slow invasion rates (e.g. sequential assembly) assembly can cycle indefinitely, faster invasion rates result in transient cycling culminating in the coexistence of all species. We conclude by examining how the length of these transients vary as a function of invasion rates and habitat productivity.

The model

Consider a system consisting of an abiotic resource R, two prey species with densities N_1 and N_2 that consume the resource, and two predator species with densities P_1 and P_2 . The assumptions underlying this model are the same as made by Holt et al. (1994). Namely, the system is closed and that the total amount of resource, summed over all available forms including nutrient bound in organisms (both predator and prey), is fixed at S. Predator i's per-capita rate of increase is determined by a linear functional response, with attack rates a_{ii} and conversion efficiency b_{ij} for prey j, minus densityindependent mortality rate m_i. Prey i's per-capita rate of increase is given by a linear uptake of nutrient (with affinities α_i and yield coefficients β_i), minus a density independent mortality rate μ_i and losses to predation. Under these assumptions, the dynamics of the predators, the prey, and the resource are given by

$$\begin{split} \dot{P}_1 &= P_1(a_{11}b_{11}N_1 + a_{21}b_{21}N_2 - m_1) \\ \dot{P}_2 &= P_2(a_{12}b_{12}N_1 + a_{22}b_{22}N_2 - m_2) \\ \dot{N}_1 &= N_1(\alpha_1\beta_1R - \mu_1 - a_{11}P_1 - a_{12}P_2) \quad \text{where } \bullet = \frac{d}{dt} \end{split} \tag{1}$$

$$\dot{N}_2 &= N_2(\alpha_2\beta_2R - \mu_2 - a_{21}P_1 - a_{22}P_2) \end{split}$$

with the mass balance constraint (MBC)

$$\mathbf{R} = \mathbf{S} - \frac{\mathbf{N}_1}{\beta_1} - \frac{\mathbf{N}_2}{\beta_2} - \frac{\mathbf{P}_1}{\mathbf{r}_1} - \frac{\mathbf{P}_2}{\mathbf{r}_2}$$
(2)

Since the parameters β_i determine the number of prey produced per unit of consumed resource, the inverse of this quantity is the amount of resource produced per unit of dead prey. In a similar manner, the parameters 1/ r_i determine the amount of resource produced per unit of dead predator.

The analysis

Assembly with simple dominance rules

When two species engage in exploitative competition for a single resource, the species that depresses the resource to the lower equilibrium density displaces all other species (Hsu et al. 1978, Tilman 1990). Let R_i^{*} denote the resource equilibrium density when prey i is the only species in the system. For the remainder of this article, we assume that $R_1^* \leq R_2^*$. In other words, prey 2 never dominates in resource exploitation. A similar rule also applies to the predator when they compete for a single prey (Wolkowicz 1989, Grover 1994). Let N_{ij}^{**} with i,j =1,2 denote the prey equilibrium density when only prey i and predator j are in the system. If both predators compete for prey i, then the predator that suppresses the prey to the lower equilibrium density dominates. We assume that $N_{11}^{**} < N_{12}^{**}$ and $N_{22}^{**} < N_{21}^{**}$ (i.e. predator i is dominant with respect to prey i for i = 1,2).

Holt et al. (1994) analyzed (1) when there is a single predator species. Assume predator j with j = 1 or 2 is the only predator in the system. Holt et al. reduced the analysis of this four dimensional system to an analysis in the resource-predator j plane. In this plane, the nullcline for prey i consists of resource and predator densities at which the prey has a zero per-capita growth rate (i.e. $\alpha_i\beta_iR - \mu_i - a_{ij}P_j = 0$). For resource and predator densities a negative (resp. positive) per-capita growth rate. If prey i is at the equilibrium determined by predator j, the MBC equation Eq. 2 determines a line

$$\mathbf{R} = \mathbf{S} - \frac{\mathbf{N}_{ij}^{**}}{\beta_i} - \frac{\mathbf{P}_j}{\mathbf{r}_j}$$

in the resource-predator j plane. The relative position of the MBC lines and prey nullclines determine whether a prey can invade an equilibrium determined by the remaining species. For instance, if the MBC line and nullcline for prey 1 intersect at a point above prey 2's nullcline, then prey 2 can not invade the equilibrium determined by predator 1 and prey 1 (Fig. 1a). The relative positions of MBC lines determine four possible outcomes: prey displacement, coexistence, or a priority effect. Prey displacement occurs in two ways. First, if the

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Fig. 1. Prey nullclines and mass balance constraint (MBC) lines in the resource-predator j plane. The dashed lines correspond to MBC lines, the solid lines correspond to prey nullclines, and the solid circles represent an equilibrium in which only one prey species is present. In (a) and (b) prey 1 dominates, (c) predator j reverses prey dominance.

prey nullclines do not intersect (Fig. 1a) or the prey nullclines do intersect and both MBC lines cross the nullclines below the intersection point (Fig. 1b), then the prey 1 displaces prey 2 (Fig. 3c with j = 2). Second, if the prey nullclines intersect and both MBC lines cross the nullclines above the intersection point (Fig. 1c), then the predator reverses prey dominance (Fig. 3a with j = 1). The predator either mediates coexistence or creates a priority effect when one MBC line crosses below and one crosses above an intersection point of the prey nullcline. These latter possibilities do not occur when the system is sufficiently enriched (i.e. S is large) or the predator is effective at limiting its prey (i.e. larger values for a_{ii}b_{ii}) as increasing S shifts the MBC lines to the right without effecting the prey nullclines and increasing a_{ii}b_{ii} brings the MBC lines closer together.

In the domain of the simple dominance rules (i.e. all three species sub-systems lead to displacement of one species), the addition of a single predator species results in four possible community assembly graphs (Fig. 2) whose vertices represent coexisting species and directed edges represent transitions from one community to another community due to single species invasions. If neither predator reverses prey dominance (i.e. Fig. 1a or 1b applies for j = 1, 2, then prey 1 always displaces prey 2 resulting in the eventual displacement of predator 2 by predator 1 (Fig. 2a). If both predators reverse prey dominance (i.e. Fig. 1c applies for j = 1,2), then community assembly always leads to an end state consisting of prey 2 and predator 2 (Fig. 2b). If predator 2 reverses prey dominance (i.e. Fig. 1a or 1b with j = 2) but predator 1 does not (i.e. Fig. 1c with j = 1), there is a priorty effect in which each predator i-prey i pair with i = 1,2 forms an uninvadable community (Fig. 2c). If predator 1 reverses prey dominance but predator 2 does not, then sequential invasions result in never ending cycling between the predator-prey sub-systems (Fig. 2d).

 $\{N_{1},P_{1}\} \xleftarrow{N_{1}} \{N_{2},P_{1}\} \{N_{1},P_{1}\} \xrightarrow{\mathbb{N}_{2}} \{N_{2},P_{1}\}$ $\downarrow P_{2} P_{1} \qquad \downarrow P_{2}$ $\{N_{1},P_{2}\} \xleftarrow{N_{1}} \{N_{2},P_{2}\} \{N_{1},P_{2}\} \xrightarrow{N_{2}} \{N_{2},P_{2}\}$ $(a) \qquad (b)$ $\{N_{1},P_{1}\} \xleftarrow{N_{1}} \{N_{2},P_{1}\} \{N_{1},P_{1}\} \xrightarrow{N_{2}} \{N_{2},P_{1}\}$

$$\begin{array}{c|c} P_1 & P_2 & P_1 \\ \hline P_1 & P_2 & P_1 \\ \hline P_2 & P_1 \\ \hline P_2 & P_1 \\ \hline P_2 & P_2 \\ \hline P_2 & P_1 \\ \hline P_2 & P_2 \\ \hline P_2 & P_1 \\ \hline P_2 & P_2 \\ \hline P_2 & P_1 \\ \hline P_2 & P_2 \\ \hline P_2 & P_1 \\ \hline P_2 & P_2 \\ \hline P_2 & P_1 \\ \hline P_2 & P_2 \\ \hline P_2 & P_1 \\ \hline P_2 & P_2 \\ \hline P_2 & P_1 \\ \hline P_2 & P_2 \\ \hline P_2 & P_1 \\ \hline P_2 & P_2 \\ \hline P_2 & P_1 \\ \hline P_2 & P_2 \\ \hline P_2 & P_2$$

Fig. 2. Community assembly graphs in which vertices represent predator-prey communities and edges represent transitions from one community to another due to single species invasions. In (a), neither predator reverses the exploitative dominance of prey 1. In (b), both predators reverse the dominance of the prey. In (c), predator 2 reverses prey dominance, but predator 1 does not. In (d), predator 1 reverses prey dominance, but predator 2 does not. In all figures, predator i with i = 1,2 is competitively dominant with respect to prey i.

Cycling occurs whenever the system is sufficiently enriched (i.e. S is sufficiently large) and the predators exhibit sufficiently strong preferences for different prey species (e.g. $a_{11} > a_{21}$, $a_{11} > a_{12}$, $a_{22} > a_{12}$ and $a_{22} > a_{21}$) due to differences in prey edibility (e.g. $b_{11} > b_{12}$ and $b_{22} > b_{21}$) or defenses (e.g. $b_{11} = b_{12}$ and $b_{22} = b_{21}$). The reason is as follows. When the predators exhibit sufficiently strong preferences for different prey species, the

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Fig. 3. Population phase space (i.e. the axes correspond to population densities) for all three species sub-systems when a cycle is present. Dashed and solid curves represent population trajectories, and solid circles represent equilibria. Starting from (a) and moving to (d), the four dashed population trajectories and the associated equilibria determine the hetereoclinic cycle.

prey nullcines intersect in the resource-predator 1 plane (Fig. 1c with j = 1), but do not intersect in the resourcepredator 2 plane (Fig. 1c with j = 2). Thus, when this system is sufficiently enriched, the MBC lines in the resource-predator 1 plane cross the prey nullclines above their point of intersection (Fig. 1c with j = 1) and predator 1 reverses prey dominance. However, as the prey nullclines do not intersect in the resource-predator 2 plane, predator 2 does not reverse prey dominance.

Attracting versus repelling cycles

In reality the community assembly process is not sequential. Natural invasion rates vary between rare and frequent events. While the slightest deviation from extremely rare invasions (i.e. sequential invasions) does not effect the long-term assembly process in systems without cycles, it is not obvious how such deviations affect systems with cycles.

In past two decades, there have been mathematical developments that permit us to understand the dynamical behavior of cycles (Hofbauer 1981, 1994, Kirlinger 1989, Krupa 1997). In the mathematical literature, cycles are known as heteroclinic cycles: stable equilibria for the predator-prey sub-systems are connected in a cyclic way by population trajectories corresponding to invasions by missing species. These connecting trajectories in each of

the three species sub-systems of (1) are illustrated as dashed curves in Fig. 3. A simplified representation of this heteroclinic cycle is a square whose vertices represent predator-prey equilibria and whose directed edges represent the connecting trajectories (the boundary of Fig. 4a). A basic question about such cycles is whether they are attracting (resp. stable) or repelling (resp. unstable). If the cycle is repelling, then population trajectories supporting all four species and starting near the cycle move away from the cycle (4a, c). In fact when the cycle is repelling, the four species system is permanent: if all species are present initially, then their densities remain uniformly bounded away from extinction for all time. Alternatively, if the cycle is attracting, then population trajectories supporting all four species and starting near the cycle approach the cycle asymptotically (Fig. 4b, d). In this case, the population trajectory spends long periods of time near each of the predatorprey equilibria followed by quick transitions between these equilibria. After each transition, the population trajectory moves closer and closer to the heteroclinic cycle. Since every point on the heteroclinic cycle only supports three species, eventually a predator-prey pair reaches such a low density that demographic stochasticity would drive a species to extinction.

While there exist a variety of other methods (Brannath 1994, Krupa and Melbourne 1995), we illustrate how average Lyapunov functions (Hofbauer 1981, 1994)



Fig. 4. The left hand figures correspond to repelling cycles and the right hand side correspond to attracting cycles. Figure (a) and (b) are caricatures of the actual dynamics with solid circles representing predator-prey equilibria and directed curves representing population trajectories. Figure (c) and (d) correspond to numerical simulations of (1) when there are attracting and repelling cycles. Predator and prey densities as functions of time are represented as dashed and solid curves, respectively. In (c), all four species move away from extinction while in (d) predator-prey pairs exhibit oscillations that ultimately lead to the extinction of one predator-prey pair.

$$\begin{split} L(N_1, N_2, P_1, P_2) &= N_1^{h_1} N_2^{h_2} P_1^{h_3} P_2^{h_4} \\ \text{for some choice of } h_i &> 0 \end{split}$$

can be used to determine whether a heteroclinic cycle is attracting or repelling. The derivative of L with respect time is given by

$$\dot{\mathbf{L}} = \mathbf{L} \sum_{i=1}^{4} \mathbf{h}_{i} \mathbf{f}_{i}$$
(3)

where the fi are per-capita growth rates

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$$f_1 = \frac{\dot{N}_1}{N_1} f_2 = \frac{\dot{N}_2}{N_2} f_3 = \frac{\dot{P}_1}{P_1} f_4 = \frac{\dot{P}_2}{P_2}$$

If there exist $h_i > 0$ such that $\dot{L} > 0$ at all four of the predator-prey equilibria, then the heteroclinic cycle is repelling. This can be explained intuitively as follows. A population trajectory supporting all four species starting near the heteroclinic cycle initially spends most of its time near the predator-prey equilibria. Consequently, if $\dot{L} > 0$ at these equilibria, L is on average increasing and the population trajectory moves further away from extinction. Alternatively, if there exist $h_i > 0$ such that $\dot{L} < 0$ at all predator-prey equilibria, then L is on

average decreasing for a population trajectory initiated near the heteroclinic cycle and the population trajectory moves closer to the heteroclinic cycle.

Equation 3 and our discussion implies that if there exists $h_i > 0$ such that $\sum_{i=1}^{4} h_i f_i > 0$ at all of the predatorprey equilibria, then the heteroclinic cycle is repelling. By the definition of an equilibrium, the per-capita growth rate of any species supported by the equilibrium is zero. Consequently, at each predator-prey equilibrium, the sum $\sum_{i=1}^{4} h_i f_i$ has exactly two non-zero terms. One of these terms corresponds to the negative per-capita growth rate (NGR) of the species that can not invade the predator-prey equilibrium and the other term corresponds to the positive per-capita growth rate (PGR) of the species that can invade. For instance, at the predator 1-prey 1 equilibrium, f_2 is the PGR (Fig. 3a) and f_4 is the NGR (Fig. 3d). Solving the four inequalities $\sum_{i=1}^{4} h_i f_i > 0$ at all the predator-prey equilibria via back substitution reveals that there exists the desired choice of $h_i > 0$ if and only if the product of the four PGRs is greater than the product of the four NGRs. A similar round of reasoning shows that the heteroclinic cycle is attracting if the product of the four NGRs is greater than the product of the four PGRs.

While in general understanding the products of the NGRs and the product of the PGRs is quite complex, it is possible to understand it reasonably well in two special cases: the prey and predators exhibit a strong symmetry or the system is highly enriched. We discuss these special cases below.

Systems with symmetry

Consider the case in which the two predators attack their prey in a similar manner (i.e. $a_{11} = a_{22} > a_{12} = a_{21}$, $b_{11} = b_{22} = b_{12} = b_{21}$, $m_1 = m_2$) and in which both prey consume the resource in the same manner (i.e. $\alpha_1 = \alpha_2$, $\beta_1 = \beta_2$, $\mu_1 = \mu_2$). Provided that the system is sufficiently enriched to support a positive equilibrium for each predator-prey pair, the system exhibits a cycle. More specifically, whenever both predators compete for prey i (i = 1,2), predator i who has the higher searching efficiency with respect to prey i displaces the other predator. Whenever predator i consumes both prey species, prey i which is the preferred prey for predator i is displaced via apparent competition. In the appendix we show that this cycle is always repelling.

Highly enriched systems

For highly enriched systems, a cycle occurs whenever the prey nullclines do not intersect in the resource-predator 1 plane (Fig. 1a) and the prey nullclines do intersect in the resource-predator 2 plane (Fig. 1c). For highly enriched systems with a cycle, the ratio of the product of the NGRs to the product of the PGRs is given by

$$\frac{b_{12}b_{21}a_{12}a_{21}(a_{11}r_1+\alpha_1\beta_1)(a_{22}r_2+\alpha_2\beta_2)}{b_{11}b_{22}a_{11}a_{22}(a_{12}r_2+\alpha_1\beta_1)(a_{21}r_1+\alpha_2\beta_2)}$$

When this expression is less than one, the cycle is repelling. When this expression is greater than one, the cycle is attracting. In the Appendix we show that the presence of a cycle implies

$$\frac{a_{12}a_{21}(a_{11}r_1 + \alpha_1\beta_1)(a_{22}r_2 + \alpha_2\beta_2)}{a_{11}a_{22}(a_{12}r_2 + \alpha_1\beta_1)(a_{21}r_1 + \alpha_2\beta_2)} < 1$$

Thus, if $b_{11}b_{22} \ge b_{12}b_{21}$ (i.e. the predators convert their preferred prey at least as efficiently their less preferred prey), the cycle is repelling.

Invasions rates and repelling cycles

When a cycle is repelling, invasions rates can play an important role in the assembly process. To understand the effect of invasion rates, we numerically studied (1) for a set of parameters that correspond to a nearly symmetric system. In this numerical study, at discrete intervals of time of length T "days" species were chosen randomly (i.e. each of the four species was chosen with equal likelihood) and introduced at small densities (i.e. a density of 0.001). Each simulation was run for 50000 "days". During each simulation, populations falling below the invasion density were presumed to go extinct and reset at zero. Fig. 5a and 5b illustrate how predator and prey densities varied over time in typical simulations. For each simulation, we recorded the first time at which all species densities remained 100 times above the invasion density for the remainder of the simulation. We view this as the assembly time for the community. For example, in Fig. 5a, the assembly time occurs a little after 500 "days", while in Fig. 5b community establishment never occurs during the 50 000 "days". In this latter case, the assembly time is recorded as 50000 "days". To understand how time T between invasions and habitat productivity S influence the time to community establishment, for each value of S and T we ran 500 simulations. The means of these assembly times as a function of S and T are reported in Fig. 5c and 5d. These figures show that the mean assembly time increases as the time between invasion increases. This increase is initially gradual and exhibits a sharp jump around T =325 days. This sharp jump corresponds to the fact that for these large T values, the community fails to assemble by the end of the simulation. Alternatively, Fig. 5d shows that productivity has the largest affect on assembly times at the extremes. For a large interval of intermediate S values, the mean assembly time is approximately 2000 "days".

Fig. 5. Random assembly runs for communities with repelling cycles. At discrete intervals of time of length T, species are randomly chosen and introduced at low densities. Sample simulations corresponding to T = 50 and T = 350 are shown in (a) and (b), respectively, where prey and predator densities as functions of time are represented as solid and dashed curves, respectively. In (c) and (d), the mean assembly times of the simulations are plotted as function of the time T between introductions and the total amount S of resource in the system.



Discussion

While sequential assembly of a community exhibiting exclusively exploitative competition or apparent competition does not cycle indefinitely between subcommunities (Hsu et al. 1978, Wolkowicz 1989, Grover 1994, Holt and Lawton 1994, Holt et al. 1994), we have shown that sequential assembly of a community combining exploitative and apparent competition can. More specifically, for a community consisting of two prey species exploiting a resource and being exploited by two predator species, cycling occurs whenever two conditions are met. First, each predator has a preferred prey species that it can suppress to a lower equilibrium density than the other predator. Second, in the presence of each predator, the predator's preferred prey is excluded via exploitative or apparent competition. When these assumptions are met, alternating invasions of predators and prey lead to cycling between predator-prey subcommunities in which prey and predators are displaced via apparent and exploitative competition. These criteria are met whenever the system is sufficiently enriched and the predators exhibit sufficient preferences for different prey species due to differences in prey edibility or prey defenses.

We have proven that cycles in the aforementioned scenario are dynamically unstable and, consequently, the four species can coexist. If community assembly only occurs sequentially (i.e. single species invasions separated by very long intervals of time), then this community exhibits a "humpty dumpty" effect (Pimm 1991) in which a community of coexisting species can not be assembled by sequential invasions of its constituency. Law and Morton (1996) called such communities "curiously fragile" and in their simulation studies observed that 40% (i.e. 8 out 20 of the entries in their Table 3) of the assembly end points were curiously fragile. In fact, one of Law and Morton's end points is very similar to our system; "comprising of two basal species and two consumer species...[,t]his community lacks a three species subcommunity with an equilibrium point so there is no attractor with three species, and no way of getting from a two-species subcommunity to the full community by sequential invasions." We conjecture that many of these curiously fragile communities are the byproduct of dynamically unstable cycles.

Sequential assembly corresponds to the extreme of an "infinitesimal" invasion rate that ensures the system settles down to a limiting dynamical state prior to the invasion of the next species (Post and Pimm 1983, Drake 1990, 1991, Law and Blackford 1992, Law and Morton 1993, 1996, Morton et al. 1996). However, in nature invasion rates vary reflecting how often and how easily individuals are released as propagules by neighboring species (Lockwood et al. 1997). When cycles exist and are dynamically unstable, we found that there is a critical invasion rate below which the community cycles indefinitely and above which the community reaches an end state after some transient cycling. The existence of this critical invasion rate implies that the humpty-dumpty effect is sensitive to invasion rates (i.e. if all the king's horses and all the king's men worked sufficiently fast, they could have put humpty back together again). We also found that the length of the transient cycling decreases with invasion rates and increases initially gradually and then sharply with productivity. Hence, community assembly dynamics may partially explain the unimodel relationship between species richness and productivity (Ricklefs and Schulter 1993). More precisely, at low productivity there are insufficient resources to support many species and at high productivity community assembly becomes more difficult.

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Appendix

In this appendix, we derive the conclusions about the ratio of NGRs to PGRs as stated in the text. To determine the NGRs and PGRs, we begin by noting that the equilibrium supporting prey i and predator j with i, j = 1, 2 is given by

$$\begin{split} N_{ij}^{**} &= \frac{m_j}{a_{ij}b_{ij}} \\ P_{ij}^{**} &= \frac{a_{ij}b_{ij}r_jS\alpha_i\beta_i - m_jr_i\alpha_i - a_{ij}b_{ij}r_j\mu_i}{a_{ij}b_{ij}(a_{ij}r_i + \alpha_i\beta_i)} \end{split}$$

At this equilibrium, prey i and predator j have a zero per-capita growth rate. The per-capita growth rate of the missing predator $k \neq j$ is given by

$$a_{ik}b_{ik}N_{ij}^{**} - m_k = \frac{a_{ik}b_{ik}m_j}{a_{ij}b_{ij}} - m_k$$
(4)

and the per-capita growth rate of the missing prey $l \neq i$ is given by

$$\alpha_{l}\beta_{l}(S - N_{ij}^{**}/\beta_{i} - P_{ij}^{**}/r_{j}) - \mu_{l} - a_{lj}P_{ij}^{**}$$
(5)

Systems with symmetry

Assume that $a = a_{11} = a_{22}$, $b = b_{11} = b_{22} = b_{12} = b_{21}$, $\kappa = a_{12} = a_{21}, \ \mu = \mu_1 = \mu_2, \ \alpha = \alpha_1 = \alpha_2, \ \beta = \beta_1 = \beta_2, \ and$ $m = m_1 = m_2$. Assume that $a > \kappa$. This choice of coefficients ensures that there is cycling whenever S is sufficiently large to support all predator-prey pairs. The per-capita growth rates for the missing prey and missing predator at the prey I-predator i equilibrium i = 1,2 are given by

$$\frac{(a-\kappa)r(ab(S\alpha\beta-\mu)-m\alpha)}{ab(ar+\alpha\beta)} \quad \text{and} \quad \left(\frac{\kappa}{a}-1\right)m_{\alpha}$$

respectively. Alternatively, the per-capita growth rates for the missing prey and missing predator at the prey i-predator j equilibrium $i \neq j$ are given by

$$\frac{(a-\kappa)r(m\alpha+b\kappa(\mu-S\alpha\beta))}{b\kappa(\kappa r+\alpha\beta)} \quad \text{and} \quad \left(\frac{\kappa}{a}-1\right)m,$$

respectively. Using these expressions and simplifying, the ratio of the product of the four NGRs to the product of the four PGRs becomes

$$\frac{(ar + \alpha\beta)^2(m\alpha + b\kappa(\mu - S\alpha\beta))^2}{(\kappa r + \alpha\beta)^2(m\alpha + ab(\mu - S\alpha\beta))^2}$$
(6)

To show that this quantity is always strictly less than one, we will show that (6) is an increasing function of S and that value of (6) as S approaches ∞ is strictly less than one. Taking the derivative of (6) with respect to S, we get

$$\frac{2b(a - \kappa)m\alpha^{2}\beta(ar + \alpha\beta)^{2}(b\kappa(S\alpha\beta - \mu) - m\alpha)}{(\kappa r + \alpha\beta)^{2}(ab(S\alpha\beta - \mu) - m\alpha)^{3}}$$
(7)

We claim that (7) is positive. Since $a > \kappa$, it suffices to show that $b\kappa(S\alpha\beta - \mu) - m\alpha > 0$, and $ab(S\alpha\beta - \mu) - m\alpha > 0$. Since the equilibrium value of predator 1 in the predator 1-prey 1 sub-system is given by

$$r\bigg(\frac{ab(S\alpha\beta-\mu)-m\alpha}{ab(ar+\alpha\beta)}\bigg)$$

and assumed to be positive, we get that the numerator $ab(S\alpha\beta - \mu) - m\alpha$ must be positive. Since the equilibrium value of predator 1 in the predator 1-prey 2 subsystem is given by

$$r\left(\frac{b\kappa(Slphaeta-\mu)-mlpha}{b\kappa(\kappa r+lphaeta)}
ight)$$

and is assumed to be positive, we get that the numerator $b\kappa(S\alpha\beta - \mu) - m\alpha$ must be positive. Therefore, (7) is positive. Taking the limit of S to ∞ in (6) gives

$$\frac{\kappa^2(ar+\alpha\beta)^2}{a^2(\kappa r+\alpha\beta)^2}$$

Rewriting this expression as

$$\frac{\left(r + \alpha\beta/a\right)^2}{\left(r + \alpha\beta/\kappa\right)^2}$$

and recalling that $a > \kappa$ implies that the limit of (6) as $S \rightarrow \infty$ is strictly less than one. Thus, we have shown that (6) is always less than one. Equivalently, the product of the PGRs is greater than the product of NGRs.

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Highly enriched systems

From Eq. 4, we get that the per-capita growth rate of predator 2 at the prey 2-predator 1 equilibrium and the per-capita growth rate of predator 1 at the prey 1-predator 2 equilibrium are given by

$$\frac{a_{22}b_{22}m_1}{a_{21}b_{21}} - m_2 \tag{8}$$

$$\frac{a_{11}b_{11}m_2}{a_{12}b_{12}} - m_1 \tag{9}$$

Alternatively, Eq. 5 implies that the per-capita growth rates of prey 2 at the prey 1-predator 1 equilibrium and prey 1 at the prey 2-predator 2 equilibrium are given by

$$\frac{r_1 S(a_{11} \alpha_2 \beta_2 - a_{21} \alpha_1 \beta_1)}{a_{11} r_1 + \alpha_1 \beta_1} + C_1$$
(10)

$$\frac{r_2 S(a_{22}\alpha_1\beta_1 - a_{12}\alpha_2\beta_2)}{a_{22}r_2 + \alpha_2\beta_2} + C_2$$
(11)

where C_1 and C_2 are constants that are independent of S. Consequently, whenever S is sufficiently large, $a_{11}\alpha_2\beta_2 \neq a_{21}\alpha_1\beta_1$, and $a_{22}\alpha_1\beta_1 \neq a_{12}\alpha_2\beta_2$, the signs of these percapita growth rates can be determined by ignoring these constants C_1 and C_2 . To get a cycle, we need that all four of these per-capita growth rates are positive. Equations 8 and 9 are positive if and only if

$$\frac{\mathbf{m}_1}{\mathbf{a}_{21}\mathbf{b}_{21}} > \frac{\mathbf{m}_2}{\mathbf{a}_{22}\mathbf{b}_{22}} \tag{12}$$

and

$$\frac{m_2}{a_{12}b_{12}} > \frac{m_1}{a_{11}b_{11}}$$
(13)

These inequalities merely state the R^* rules for exploitative competition between the predators; $m_1/(a_{i1}b_{i1})$ and $m_2/(a_{i2}b_{i2})$ with i = 1,2 are the equilibrium densities of prey i when consumed exclusively by predator 1 and 2, respectively. Equations 10 and 11 are positive if and only if

$$\frac{\alpha_2\beta_2}{a_{21}} > \frac{\alpha_1\beta_1}{a_{11}}$$

and

$$\frac{\alpha_1\beta_1}{a_{12}} > \frac{\alpha_2\beta_2}{a_{22}}$$

These inequalities imply that

$$\frac{\left(\mathbf{r}_{1} + \frac{\alpha_{1}\beta_{1}}{a_{11}}\right)\left(\mathbf{r}_{2} + \frac{\alpha_{2}\beta_{2}}{a_{22}}\right)}{\left(\mathbf{r}_{1} + \frac{\alpha_{2}\beta_{2}}{a_{21}}\right)\left(\mathbf{r}_{2} + \frac{\alpha_{1}\beta_{1}}{a_{12}}\right)} < 1$$
(14)

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Alternatively, the ratio of the product of NGRs to the product of PGRs as $S\!\uparrow\!\infty$ can be shown using MAPLE to equal

Thus, Eq. 14 implies if $b_{11}b_{22} \ge b_{12}b_{21}$, then the product of the NGRs is less than the product of the PGRs and the cycle is repelling.

$$\frac{b_{12}b_{21}}{b_{11}b_{22}}\frac{\left(r_1+\frac{\alpha_1\beta_1}{a_{11}}\right)\left(r_2+\frac{\alpha_2\beta_2}{a_{22}}\right)}{\left(r_1+\frac{\alpha_2\beta_2}{a_{21}}\right)\left(r_2+\frac{\alpha_1\beta_1}{a_{12}}\right)}$$