HETEROCLINIC CYCLES IN THE RAIN FOREST: INSIGHTS FROM COMPLEX DYNAMICS

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Abstract

One of the persistent paradoxes of ecology has been the existence of megadiverse ecosystems such as tropical rain forests and coral reefs. A long tradition of applying ecological theory to this problem has not been completely satisfactory to most practitioners. Recent advances in the theory of population interactions involving non-linear complications may shed light on this classic question. Using data from a 15 year study of post hurricane succession in a forest in eastern Nicaragua, data are presented consistent with the hypothesis that alternative basins exist in the dynamics of this particular rain forest, suggesting that some form of complicated nonlinear dynamics might be partially responsible for the maintenance of species diversity. In particular the existence of unstable heteroclinic cycles driven by the enemies hypothesis could, in theory, allow for the coexistence of many species that, in the context of classical theory, should competitively exclude one another.

The idea of community structure in history: Darwin and Wallace traveled the world and marveled at its rich patterns of biodiversity, independently arriving at an elegant solution to the general problem of where it all came from. However, another problem they recognized has proven to be far more recalcitrant. While evolution through natural selection explains the origin of biodiversity as elegantly as gravity explains the motion of the planets, the ecological dynamics of that biodiversity remains as elusive as dark energy. Darwin's use of detailed natural history observations to elaborate the nature of the "force of selection," as he called it, could be considered as the first modern attempt at elaborating the ecological dynamics that determined whether a particular spot on earth contains one or one hundred species. The giants on whose shoulders we sit have pondered this question ever since. Probably every generation of ecologists feels that, perched on those shoulders, the nature of our metaphorical dark energy is very close to being illuminated. The current generation is no different, to be sure.

The formulation of frameworks that might help make sense of this fundamental problem has long been a major activity in the field of ecology. Of the more mathematical representations, the framework of Yodzis (1978) can be viewed as summarizing much of the earlier literature, at least in a very general way. Yodzis focused on "competitive" communities and broadly categorized them into two general types -- those characterized by a relatively large degree of interspecific competition and those characterized by a small degree of the same. Since the first type, large competition coefficients, would mean that the species that arrived in an area first would dominate the area, he termed this type "founder-controlled communities," to be contrasted to the second type, small competition coefficients, in which the species that had the largest competitive advantage would likely dominate, which he termed "dominance-controlled communities." Taking the classical Lotka-Volterra competition equations as a starting point, founder-controlled communities are those in which the competition coefficients are all greater than 1.0, and dominance-controlled communities as those in which the competition coefficients are all less than 1.0.

Yodzis' framework is certainly useful in categorizing theoretical models of competitive communities. It may also be useful in viewing the intellectual history of the subject. As the descriptive natural historical approach to ecology gave way to a more quantitative approach with the elaborations of Lotka and Volterra in the 1920s, followed by the influential experiments by Gause a decade later, competition became a focus. A milestone, in several ways, was the special meeting of the British Ecological Society in 1944 in which some of the world's most famous ecologists discussed the proposition that Gause's principle of competitive exclusion be taken as the foundation of community ecology (Anonymous, 1944). The implicit conclusion of that meeting was that yes, such an adoption would be a good thing, elevating the competitive exclusion principle to a foundational standard, implicitly on par with natural selection. Such a conclusion was not unanimous, with insect ecologist Diver cautioning that nature's complexity mitigated against the universal operation of such a simple principle and the ever insightful Haldane wondering about the effects of parasites that attack more than a single species. We shall return to Haldane's insights later. This historical meeting to some extent set the stage for ecologists to think more in terms of dominance-controlled communities.

If that meeting of the British Ecological Society was a culmination of the first century of post-Darwin thought on ecology, a couple of insights of Hutchinson would prove to usher in the next half century. One was in the deceptively titled "Concluding Ramarks" (1957) and the other was the "Paradox of the Plankton" (1961). "Concluding Remarks," the last chapter in the Cold Spring Harbor's 1957 symposium on quantitative biology, formulated the venerable idea of the ecological niche as a formal hypervolume and, more importantly, coupled the idea of niche overlap with the idea of competition. The importance of this work can hardly be overemphasized. Indeed, as noted by Lewontin (2000), the idea of the niche coupled with Darwinian adaptation, provides an incredibly powerful general theory of biodiversity – organisms adapt to fit into niches. While such a framework is largely incorrect (Lewontin, 2000; Olding-Smee et al., 2003), the idea of niche hypervolume and the overlap between the niches of two species being related to the interspecific competition between the two, remains an important theoretical grounding for at least one school of thought in community ecology.

But it is the other Hutchinson paper, the paradox of the plankton, that is most important for the present discussion.. It would appear that organisms that do nothing more than float passively in a liquid medium and photosynthesize (i.e., phytoplankton) are all in the same niche, which means that they are likely, according to the basic idea of

Gause's principle, to exclude one another until all but one species remains in the community. That is, they seem to be a classic example of a founder-controlled community. The fact that hundreds of species of plankton all coexist in the same medium is thus paradoxical.

The final chapter in this brief historical review was written by MacArthur (1960) when he recognized that there seem to be two classes of communities. On the one hand, there are those composed of populations that are effectively density independent, more or less following the pattern thought to be so common by the Australian school led by Andrewartha and Birch (1954). MacArthur noted that these communities are effectively populated with fugitive-like or opportunistic species, growing exponentially for some period of time before a density independent force drove them to lower densities from where they once again grew exponentially. He noted that such a pattern would likely result in a lognormal distribution, as had, by that time, been noted for many species of organisms (Preston, 1948; Patrick, 1954). These are the communities that would, after some additional modifications of the theory, correspond to Hutchinson's paradox of the plankton. Furthermore, as explained below, they correspond in principle to Yodzis' founder-controlled communities.

On the other hand, MacArthur recognized communities in which individual species fit into specific niches, more or less corresponding to the sort of structure that Hairston, Smith and Slobodkin (1960) imagined when they emphasized the importance of density dependence in maintaining community structure, and certainly what MacArthur and Levins (1968) had in mind when they introduced the idea of species packing. The enormous literature examining the details of food web structure and direct and indirect interactions can be thought of as the offspring of this view (e.g., Spiller and Schoener, 1988; 1990;, Werner, 1991; Werner and Anholt, 1996; Polis and Holt, 1992; Yodzis, 2000). For the present chapter it is only important to note that MacArthur recognized this sort of community as a type, the type in which niches were in fact important.

MacArthur’s original distinction was based on the idea of density independence which is, formally, quite distinct from what Yodzis’ classification implied. However, the spirit of MacArthur’s classificatory scheme was that the density-independent pattern could account for the ultimate coexistence of species even though their interactions with one another would imply exclusion over the long term. If all niches were separate, from the point of view of biodiversity, it would not matter whether density independence or density dependence were predominant, all species would be maintained in the system. It is only when niches are equal or, even more problematical, when species were especially antagonistic towards one another such that interspecific effects were greater than intraspecific ones, that density independence is especially important. Indeed, the intermediate disturbance hypothesis, simultaneously invented by Connell (1978) and Huston (1979), implicitly assumes density-independent dynamics in a founder-controlled community, periodically interrupted by some disturbance.

There is a certain utility in adopting Yodzis' classificatory scheme. Founder-controlled versus dominance-controlled can be thought of as defining a continuum, with MacArthur's categories positioned at either end. Virtually the same concepts were recognized in Connell's (1978) non-equilibrium versus equilibrium communities, or Wills et al. (1997) in their non-niche versus niche communities. However, rather than think of alternative structures, Yodzis' classification allows us to think of any particular community as occupying some position along this continuum, probably an important advance over debates about which of the community types actually represent the natural world (e.g., Hairston et al., 1960; Slobodkin et al., 1967; Erlich and Birch, 1967; Murdoch, 1966).

Despite the intellectually satisfying effect of acknowledging a diversity of community types and the likelihood of a world populated by many of those types along the Yodzis gradient, most of the basic questions asked about any of them remain unresolved. In particular, the fundamental question posed by Hutchinson about founder-controlled communities remains significant, and in my view, unresolved. As argued in the following section, many tropical ecologists have come to think of tropical rain forests as mainly founder-controlled, with the paradox of Hutchinson looming overhead.

Community structure and tropical rain forests: There have been numerous schema to explain the coexistence of large numbers of tree species in tropical forests. Connell (1978) suggested that most theories could be categorized in a dichotomous fashion, equilibrium-based theories and non-equilibrium-based theories, a position reiterated more recently (Zagt and Werger, 1998), and more-or-less corresponding to the two ends of the Yodzis continuum (equilibrium-based = dominance-controlled; non-equilibrium-based = founder-controlled). Dominance-controlled communities, which involve niche differences among species, include gap partitioning models (e.g. Orians, 1982; Brokaw, 1985; Denslow, 1987) and models of compensatory mortality (Janzen, 1970; Connell, 1971; Wills, 1996). Although these ideas are clear only when species are divided into pioneers and non-pioneers (or perhaps pioneers, intermediates and primary forest species), proponents of niche-based theory would argue that the division into pioneers and non-pioneers is only an initial rough cut and that finer divisions are not only possible, but also explain much of species coexistence, even if they are difficult to convincingly demonstrate in nature.

Founder-controlled community models emphasize chance and historical effects (Hubbell and Foster, 1986; Chessen and Werner, 1981), and, most recently, incorporate the concept of recruitment limitation and space (Hurtt and Pacala, 1995; Hubbell et al., 1999; Durrett and Levin, 1994). These ideas certainly seem obvious with the pioneer/non-pioneer categorization. However, most proponents of founder-control theory would argue that it is within, not among, such guilds that neutrality applies, and since there are only a few guilds, some form of neutrality or founder control is likely to be a major force.

As an example of combining the two extremes of the Yodzis continuum, it has been suggested that founder-control operates mainly at the level of recruitment of new individuals into the community, while factors of dominance control, such as competitive exclusion, operate mainly as individuals sort themselves out within treefall gaps (Zagt and Werger, 1998). Chance processes are largely associated with founder-controlled communities while predictable processes are largely associated with dominance-controlled communities, in this context. Thus the interpretation of Zagt and Werger (1998) suggests that both founder-control and dominance-control may be at play, but operative at different stages of forest succession.

Most recently (Wills, 1996; Howe and Miriti, 2000) it has been suggested that a dynamic pattern of natural enemy attack could explain the hyperdiverse nature of tropical rain forests, thus incorporating elements of both a non-equilibrium and equilibrium approach. If all species in the forest are subjected to natural enemies in the form of herbivores, seed predators, or diseases, the so-called Janzen/Connell hypothesis (Janzen, 1970; Connell, 1971) could apply at a large scale, preventing competitive exclusion at a large scale, even while permitting its classical operation at a small scale. That is, locally abundant species would be especially vulnerable to natural enemies simply because of their locally high population density (in epidemiological terms, as a local population increases in size, it eventually exceeds the critical value that makes $Ro > 1$). Over the long run, a given unit area (the size occupied by the canopy of a large individual adult tree) would be occupied by a succession of species, not quite randomly chosen from the species pool. If an individual of species A is in a location marked by an excessive abundance of conspecifics, the probability of one of its seedlings taking over that spot in the canopy is lowered due to the higher probability of being attacked by a natural enemy, a result of its presence in a locally dense concentration of its conspecifics. Although it may not be obvious intuitively, there are consequences of the natural enemies' specialization patterns that make this viewpoint especially interesting, namely the possibility of heteroclinic cycles associated with intermediate levels of polyphagy (Vandermeer and Pascual, 2004; Vandermeer et al., 2005), as described in detail below.

Alternative basins in early rain forest succession:

In classic competition theory (e.g., Vandermeer and Goldberg, 2003), if the intensity of competition is too high, exclusion will occur, in which one of two species will drive the other to extinction. If the competitive effect is sufficiently symmetrical, the system will be bistable, in that either of the two species can dominate, and the factor determining which will dominate is the founding density of each of the species (consequently the label "founder-controlled"). A saddle point separates two basins of attraction, and if experiments are performed in which the initial densities are varied, the expectation is that sometimes the starting point falls in one basin and one species dominates, other times the starting point falls in the other basin and the other species dominates, as was shown in the classic experiments of Park (1962). This basic idea applies to a multispecies community as well, if the competition coefficients are relatively large, which is to say, if the community is founder-controlled. Much that is debated about the structure of tropical rain forest communities revolves around the question of whether the community is founder-controlled or dominance-controlled, usually summarized as non-equilibrium versus equilibrium, as discussed above. If, as some expect, it turns out that the tree community of a tropical rain forest is an example of a founder-controlled community, we expect, theoretically, that there will be multiple basins of attraction, just as in the case of the bistable Lotka Volterra competition equations, except that we expect a minimum of the same number of basins as there are species in the community.

A dynamic feature of the bistable situation is that the Euclidian distance (in the space of population densities) between trajectories emanating from distinct starting points will generally increase over time in the bistable (non-equilibrium) case. Consider, for example, two experiments, one initiated in the basin for which species A will eventually dominate, and one initiated in the basin for which species B will eventually dominate. Even though the initiation points are in distinct basins, they could be very close together (as two drops of water dropped almost exactly on the continental divide, one of which is a millimeter to the west the other a millimeter to the east). Yet as they approach their equilibrium state, the distance between them inevitably increases. In contrast, if the underlying competitive system is one of coexistence of the two competitors, there is a single basin of attraction and any two initiation points will approach the same equilibrium point, and thus the Euclidian distance between them will decrease.

To visualize the pattern expected under either an equilibrium or non-equilibrium situation, standard Lotka Volterra competition equations were set up with ten equal species, first with standard competition coefficients set at 1.1 (which insures that all but a single species will become extinct, and that the winner will be a consequence of the initial population densities), second with those coefficients set at 0.9 (which insures that all species will be maintained in an equilibrium state). Figure 1a displays sample calculations for the multidimensional Euclidean distance between separate runs (representing alternative starting points in the ten dimensional system). As expected, when the competition coefficients are set at .9, all initiation points result in an ultimate decline in the Euclidian distance, since all trajectories are approaching the same equilibrium point. Also, as expected, when the competition coefficients are equal to 1.1, the Euclidian distance tends to increase. However, in the latter case, there is also the possibility of a decrease, when the initiation points for two trajectories happen to fall in the same basin of attraction, which is why two of the distance patterns with competition 1.1 in figure 1a decrease with increasing time.

Calculating the rate at which the Euclidean distance changes between two trajectories is a standard method in stability analysis, and its application is routine in systems of differential equations. But similar computations from data in the natural world are rare. What is required is two or more replicated time series where the systems have begun at similar points such that their convergence or divergence can be observed. Ecological succession comes to mind as an obvious case in which such behavior could be observed. In tropical rainforest situations, natural succession occurs after natural perturbations such as would be caused by storms or even simple tree falls, but rarely in a nicely replicated form.

The study of succession in light gaps caused by tree falls has long been a common feature of forest ecology (e.g. Bauer, 1964; Denslow, 1987; Sipe and Bazzaz, 1995), most often associated with the potential for light gaps to act as a disturbance which drives either the equilibrium or non-equilibrium interpretation of species diversity. At a larger scale, periodic storms act to increase the extent and rate of tree falls, sometimes on a massive scale (Canham and Loucks, 1984; Boucher, 1990; Brokaw and Walker, 1991). Damage from a large and strong storm represents an exceptionally large light gap and is thus one end of a scale that begins with a single tree-fall. More importantly, such an event provides us with an unusual natural experiment. With a storm as large as Hurricane Joan in Nicaragua in 1988 (Yih et al., 1991; Vandermeer et al 1990), the forest was physically destroyed, yet, because of the recuperative abilities of almost all the tree species, a great deal of resprouting occurred just after the damage, effectively initiating a massive experiment in competition, where all species (approximately 200 in our study) were initiated at the same time point and we were able to follow them for the next 10 years (Vandermeer et al., 2001; 2004). Separate plots were established, near enough to one another to be independent regarding short term competitive interactions, but far enough from one another to be thought of as independent samples of the same community. Thus, this data set offers the possibility of asking whether the initial stages of competition follow the expectations of an equilibrium or non-equilibrium situation.

One signal that would help distinguish between these two possibilities (equilibrium/dominance-controlled versus non-equilibrium/founder-controlled) would be the observation of independent trajectories diverging (the drops of water falling on opposite sides of the basin divide). Since the study is in an area that is quite homogenous with respect to topography and soil type, and the hurricane was similarly devastating throughout the region, it is quite reasonable to assume that any difference between two plots is a consequence of either initial conditions or subsequent distinct successional pathways, and not of microsite differences. Because of the arrangement of the study sites (Vandermeer et al., 2001; 2004) there were six possible comparisons in the search for increasing multidimensional distance, the signal for a founder-controlled (non-equilibriujm) community and multiple basins.

The results of this study are illustrated in figure 1b (to be compared to figure 1a as a theoretical base, the details of which can be found in Vandermeer et al., 2004). There is a clear pattern in which only two trajectories are clearly declining, while the other four are increasing. We conclude, at least tentatively, that for this particular situation, there seems to be a pattern consistent with a founder-controlled community. It is certainly the case that if these plots were followed for 50 or 100 years, the presently observed pattern could turn out to be one of initial increase, followed by a decrease, and ultimately consistent with the dominance controlled community. However, as far as the plots have been followed so far, the pattern seems to be one of increasing Euclidian distance between plots, for some of the comparisons.

Some basic natural history observations at these two sites also support the idea of a founder-controlled pattern. For example, at one of the sites one of the plots had an unusual abundance of one species (*Qualea parensis*) which survived the hurricane, even though experiencing a great deal of damage to each individual tree. One of the other plots at that site had experienced, seemingly because of a chance location of several seed trees nearby, an unusually high density of seedlings and saplings of another species (*Vochysia ferruginea*) in the understory before the hurricane and thus, even though all adults were killed by the hurricane, that plot experienced an unusual abundance of this species. So, one of the plots began growing with an unusual abundance of one species and the other with an unusual abundance of a different species, even though the two plots are only about 400 meters apart. The Euclidian distance between them thus increases as more of the *Vochysias* are recruited at one plot but not the other. In another example, one plot has an unusual abundance of *Hyronima alchorniodes* and *Dendropanax arborea*, while a nearby plot has few of these two species but an unusual abundance of *Pourouma bicolor*). This predominance has been increasing in the past 10 years, meaning that the two plots continue to increase their Euclidian distance. As mentioned previously, it could be that *Hyronima* or *Vochysia* or, for that matter, some other species or group of species will eventually come to dominate both sites and what we are now seeing is nothing more than transient behavior. But thus far, the data certainly seem remarkably consistent with a founder-controlled interpretation of the community structure of this forest.

Heteroclinic cycles in a founder-controlled community

The classic bistable case that results from the Lotka Volterra equations can become more complicated when multiple species are involved (a remarkable theorem for four or more competing species has, unfortunately, been mostly ignored by ecologists [Smale, 1976]). For example, May and Leonard (1975) provided an example in which each of three competing species approaches extinction in an oscillatory fashion. In the particular system they studied, the three species were related to one another in the typical rock, scissors, paper game, in which species A beats species B beats species C beats species A. The result is that species A begins dominating the system, thus reducing species B, which then releases C which increases only to put pressure on A which declines, thus reducing pressure on B which in turn begins to increase and put pressure on C, in a never ending cycle. For a particular parameter set one can calculate that an internal equilibrium point exists (i.,e. $A>0,B>0C>0$), but near that point the rock, scissors, paper cycle operates to form expanding oscillations that come ever closer to the "edges" of the space (i.e., where one or more of the species has a zero population density).

Thus there is an internal equilibrium point for which all three population densities are greater than zero, but it is an unstable point (also oscillatory), plus three saddle points, corresponding to the carrying capacities of each of the species along with the extinction of the other two (figure 2). Thus the three equilibrium points are P1 = (K,0,0), P2 = (0,K,0), and P3 = (0,0,K). The system oscillates such that it successively approaches each of the three points, P1 to P2 to P3 to P1, etcetera. However, at each cycle the system becomes closer to each of the actual points ($A = P_1$, $B=P_3$ and $C=P_2$), never actually reaching them (except in the limit). This is a classic heteroclinic cycle (Hofbauer and Sigmund, 1989; 1998), in which the output from one saddle cycle is connected to the input of another saddle cycle.

It is important to realize that a heteroclinic cycle can be either stable or unstable, just as any other limit cycle. If it is stable, the system gradually approaches the saddle points involved, but if it is unstable, similar to an unstable limit cycle, the system oscillates away from it. The meaning of this basic structure with regard to rain forest communities will be discussed presently.

Recently there has been growing interest in the idea that natural enemies (seed predators, herbivores, diseases) play an important role in the dynamics of rain forest communities (Wills, 1996). The original ideas of Janzen (1970) and Connell (1971) have been resurrected in slightly modified and greatly generalized form to help account for the large number of species in the rain forest. The idea is deceptively simple. As a species becomes locally abundant, perhaps because it had gained an initial advantage over potential competitors, its local high population concentration makes it a target for natural enemies. Its brief competitive advantage is thus eliminated by its natural enemies, and some other species takes its place and becomes, at least temporarily, competitively dominant.

This qualitative idea can be framed in such a way that it appears remarkably similar to the heteroclinic cycles of May and Leonard, as illustrated in figure 3. Rather than a strict rock, scissors, paper game, a multi-species version can be imagined in which species 1 gains a temporary advantage over all others, but by virtue of the hypothesized dynamics, it is doomed because that very dominance exposes it to attack by natural enemies. It is intuitively obvious how such an arrangement could result in a heteroclinic cycle, as illustrated in figure 3.

However, there is an important complication involved. When natural enemies are involved, there is an inherent cycle (due to the predator/prey arrangement). A heteroclinic cycle, as noted above, occurs when the outflow from one saddle point is directly connected to the inflow of another saddle point, and vice versa. If the saddle point happens to be an oscillatory one, the underlying dynamics appear more complicated, but they are in principle no different than the simple cycle illustrated in figures 2 and 3. The basic form is illustrated in figure 4.

The enemies hypothesis.

Species that appear to be ecologically equivalent ought not coexist, an idea with a long history, as reviewed at the beginning of this chapter. Indeed this is the basic problem in founder-controlled communities, where competition coefficients are greater than unity (I note in passing that the situation of neutrality, with competition coefficients exactly equal to 1.0 is expected to result in the same long-term consequence as a founder-controlled community through random drift – consequently it is reasonable to treat a neutral community as if it were founder-controlled, as is done, implicitly, throughout this chapter). Among the proposed mechanisms to avoid the seeming necessity of competitive exclusion, predation has long been thought to be a leading candidate, beginning with Darwin's famous mowing eperiments. This hypothesis takes many forms, from observations of Darwin (1998; also see Van Valen, 1974), to an explicit statement by Hutchinson (1948), to the classic experiments that established the central idea of the keystone predator (Paine,1974), to experiments with herbivores in grasslands (Harper, 1969; Ryerson and Parmenter, 2001; Bakker and Olff, 2003), to the Janzen/Connell hypothesis (Janzen, 1970; Connell, 1971) to more recent work with more complicated food webs (Spiller and Schoener, 1990) and the implied top down effect of predators on a lower trophic level (e.g., Schmitz, 2003).

More mathematically based theory has also weighed in on the issue. Slobodkin (1961) demonstrated graphically how adding predators could transform competitive outcomes and many subsequent authors elaborated on his basic theoretical scheme (Parrish and Saila, 1970; Hsu, 1981; Hutson and Vickers, 1983; Kirlinger,1986; Yodzis, 1995; deRoos et al., 1991;1998; Vandermeer et al., 2002). These various theoretical formulations perhaps reached their final conclusion with the work of Schreiber (1997; 1998), demonstrating in a general mathematical form that first, a completely generalist predator could never sustain in perpetuity more than a single competitor species in a founder-controlled community, and second, a minimum of n specialist predators are necessary to sustain n competitors in a founder-controlled community. Schneider's results are general and seemingly close the book on the problem.

However, a new theoretical question seems to emerge from this solution. As a corollary to the fact that a minimum of n specialists are necessary to maintain n competitors, it is also true that if there are fewer than n predators, the number of competitors will be reduced to one. That is, a founder-controlled community will completely collapse if the number of specialist predators is n-1 or less. In other words, a founder-controlled community maintained in a high diversity state by a single specialist predator acting on each of the species in the community is "structurally unstable" in that if a random event of some sort results in the extinction of any one of the predators, the system collapses entirely. More troublesome is the fact that if a high diversity founder-controlled community has just one of the competitors being controlled by a single predator, that too will be structurally unstable (if that predator should suffer a random extinction, the competitor will drive all the other competitors in the system to zero and the entire system will collapse) (Vandermeer et al., 2005; Vandermeer and Lin, 2005).

Thus it would appear that predators cannot effectively deter the ultimate collapse of a founder-controlled community. It is, not surprisingly, possible to avoid this conundrum with more complicated formulations. For example, structured models, either in the sense of age structure or spatial structure (deRoos et al.1991; 1998; Pascual and Levin, 2001), or non-linear behavioral modification such as predator switching behavior, or stochastic forces (Levins, 1979), can indeed permit the species in founder-controlled communities to coexist in perpetuity. However, the question remains whether there is any reasonable formulation short of these complications that will permit the perpetual coexistence of the species in a founder-controlled community. There are two: intermediate polyphagy and multiple unique predators, the second of which provokes new conceptual difficulties, and leads to a conjecture concerning the "necessity of complexity" as discussed in a later section.

Intermediate polyphagy is explored in considerable detail in other work (Vandermeer, 2004; Vandermeer and Pascual, 2005; Vandermeer et al., 2005). Here I offer a simple example to illustrate the general point. Suppose that a system of ordinary differential equations describes a founder-controlled community of competitors with predators that specialize on a particular prey item (where the prey are in competition with one another), but also eat other prey items at some rate. The following system is an extension of MacArthur's basic consumer/resource system:

$$\dot{P}_i = a[(X_i + c\sum_{j\neq i} X_j)\theta_i - m]P_i \tag{1a}$$

$$\dot{X}_i = X_i[1 - X_i - \alpha\sum_{j\neq i} X_j) - a(P_i\theta_i + c\sum P_j\theta_j)] \tag{2a}$$

$$\theta_i = \frac{1}{1 + b(X_i + c\sum_{j\neq i} X_j} \tag{3c}$$

where α is the competition coefficient, a is the predation coefficient, b is the functional response coefficient, and c represents the degree of polyphagy. For the purpose at hand the competition coefficient is set equal to 1.1, thus insuring that, in the absence of predators, all but one of the competitors will be driven to extinction. Furthermore, any population with a density below 10^{-8} is taken to be extinct. Considering a system of four competitors, and four predators, we choose parameters such that neither a set of perfectly specialist nor a set of perfectly generalist predators will provide any respite from the inexorable tendency of one of the competitors to be driven to extinction, and calculate the number of surviving competitor species after 10,000 iterations.

Running this model seven times with random initiation points for all eight species, the average number of competitor species surviving as a function of the degree of polyphagy is shown in figure 5. The pattern is perhaps a bit complicated, but the overall qualitative result is clear and can be repeated for much larger systems (Vandermeer and Pascual, 2005). Intermediate levels of polyphagy reduce the likelihood of competitive exclusion. In particular, for this model situation, degrees of polyphagy between about 10 and 30 percent are capable of preserving most, sometimes all, of the competing species. To a great degree the precise result depends on the starting conditions. For example, with polyphagy at 0.27, all four competitor species are maintained in the system for almost all initiation points. However it is possible to find initiation points for which one or more of the species goes extinct (this usually happens in the transient phase at the beginning of a run). Furthermore, there are other situations in which the entire system collapses (i.e. all four species are lost) mainly because of erratic oscillations in the transient phase), for example, when polyphagy is above 90 percent. Furthermore, the general result is somewhat complicated if the assumption of pure symmetry is relaxed. These and other complications are explored in detail elsewhere (Vandermeer and Pascual, 2005; Vandermeer et al., 2005). Here I only wish to note the qualitative result that an intermediate level of polyphagy solves the problem of competitive exclusion in a predator-controlled founder-controlled community, as articulated above. As detailed by Schreiber (1997; 1998), on the one hand a completely generalist predator is unable to deter the exclusion process in a founder-controlled community, yet, on the other hand, controlling such a community with exactly the same number of specialists as there are competitors would be structurally unstable, thus allowing us to conclude that completely specialist predators also are unable to deter the exclusion process (at least not in the long run). Allowing for intermediate levels of polyphagy is one way of resolving this problem.

This result suggests a somewhat modified goal for field research. Since the original formulation of the enemies hypothesis for rain forests (e.g., Janzen, 1970; Connell, 1971), there has been a large number of studies focusing on the issue, in terms of seed predation (Boucher, 1981; Janzen, 1971), herbivores (Sullivan, 2003; Barone, 2000), and diseases (Gilbert, 2002; Gilbert et al., 1994.). The majority of these studies have assumed that the natural enemies under study were specialists. That may be true, but it would seem that a new question should be considered, that of the breadth of the niche of the natural enemies. Does the bruchid beetle that attacks the palm seeds in Costa Rica (Wilson and Janzen, 1972) also attack other plant species? Seemingly not, but there has never, to my knowledge, been a complete search for other species that this species of bruchid will attack. Haldane's apparent observation that shared natural enemies could have important consequences for competitive exclusion takes on new significance in light of these theoretical patterns.

Heteroclinic cycles and the enemies hypothesis.

The pattern illustrated in figure 5a derives from some simple mathematical structures, in particular, from chaos and heteroclinic cycles. First, as noted in recent work (Huisman and Weising 1999; 2001a; 2001b; Passage and Huisman 2002), coexistence of competitors in a chaotic pattern is likely when non-linearities are involved. Indeed, for the most part, the dynamical behavior of the system at high species diversity (i.e., within the 10 – 20% window of polyphagy in figure 5) is chaotic, as illustrated in figure 6a.

An additional dynamic feature is necessary to understand, at least qualitatively, the pattern shown in figure 5a. At relatively high values of polyphagy (above about 30% for the parameter settings that result in figure 5), the system generates a complicated heteroclinic cycle. The way the heteroclinic cycle creates the pattern of figure 5a can be seen in figure 5b, where the local minima of the log of the variable X_1 is plotted for the range of values of degree of polyphagy (parameter c in equations 1). For values between about 0.05 and 0.3, the minima are small, but do not always transcend the critical value of 10^{-8} to be judged extinct. At a critical value of about 0.3, the heteroclinic cycle becomes visible, which means the variable cycles ever closer to zero (and its logarithm cycles ever closer to minus infinity). Thus, there is a critical point at which the system is likely to have its diversity dramatically reduced, due to the generation of a heteroclinic cycle, the point that can be seen in figure 5a at about 0.3.

A remnant of that cycle can be visualized in a reduced dimensionality of system 1. Setting P3 = P 4 = X3 = X4 = 0, the system is reduced to the two competitor two predator model. For certain parameter settings the system can be forced into a mode of four alternative repellors, each of which is an oscillatory saddle system (oscillations approach a point, but deviate from that point when near it, such that there are effectively repeated oscillatory flybys). Under such circumstances the four dimensional system can be viewed in two dimensions by defining the following variables:

$\Delta x = X1-X2$

$\Delta P = P1 - P2$

and studying the system in ΔX,ΔP space (referred to here as delta space). In figure 6b a remnant of a heteroclinic cycle based on four oscillatory saddles is illustrated in this delta space.

The reversal of stability of a heteroclinic cycle can explain the results obtained for intermediate polyphagy, as show diagrammatically in figure 7. In figure 7a, there is a chaotic region bounded by an unstable heteroclinic cycle that pushes trajectories away from the edges toward the center, and an unstable oscillatory point that pushes trajectories away from the center. The resulting chaotic region eventually transcends the extinction limit of the prey species. Figure 7b shows an intermediate level of polyphagy in which the chaotic zone has become narrower, such that the extinction limit is no longer violated. Finally, at higher levels of polyphagy the heteroclinic cycle reverses its instability and attracts all trajectories toward the edges, eventually transcending the extinction limit for the prey.

The necessity of complexity in founder-controlled communities:

Finally we return to a point made earlier. Since it has been rigorously shown that a minimum of n specialist predators are required to stabilize a founder-controlled community of n competitors, it is evident that , even though n such predators could provide that control, such an arrangement would be structurally unstable, since the chance extinction of a single predator would cause the collapse of the entire system. As argued above, one way around this problem is with intermediate levels of polyphagy. However, another way is to have multiple predators controlling each competitor. For example if there are three competitors in a founder-controlled community and each has a single specialized predator controlling it, if the chance of random extinction of a predator in Δt time is p, the probability of system collapse is p. However if each competitor has two predators associated with it, the probability of system collapse is p(1/6)(1/5) (the probability that both predators of a given species will become extinct in Δt. Naturally with even more specialist predators associated with each prey species, the probability of system collapse due to a random predator extinction becomes very small. Thus, structural stability of a founder controlled community of competitors can be insured by multiple specialist predators associated with each competitor.

The theoretical problem with this solution derives from the same competitive exclusion principle. The multiple predators must coexist on a single resource. While this requirement is in violation of classic ideas of competitive exclusion, such a violation is avoided either by the inclusion of critical nonlinearities in the model formation (Armstrong and McGehee, 1980) and/or stochasticity (Levins, 1979). Either of these additions can be thought of as adding complexity to the basic formation, which, as can be seen, is a necessity to avoid critical structural instability (Vandermeer and Lin, 2005).

Discussion

The forests of lowland humid tropical regions have long been known for their rich diversity. The question addressed by Darwin and Wallace had to do mainly with the origin of this diversity, and the answer was a complex equation (made especially complex at the time because of a misunderstanding of genetics) of adaptation and ecological niches (Lewontin, 2000). Modern ecology has reformulated much of Darwin's original foray into the problem of ecological niches. Today this problem is sometimes dichotomized when recognizing the two ends of a continuum. At one end of the continuum is the idea that, much as ecological theory predicts when species occupy distinct niches, tree species in a tropical rain forest are sufficiently distinct from one another that they effectively occupy distinct niches. If this be so, the expectation is that they all will form an equilibrium state in which all species will be buffered against local extinction over the long run. This end of the continuum contains, as a complex intellectual heritage, ideas of density dependence, dynamic equilibrium, minimum niche overlap resulting from a limit on ecological similarity, etc... It is the Yodzis category of dominance-control.

At the other end of the continuum is the idea that, much as common sense suggests, the basic biology of trees predicts that they all occupy the same (or very similar) niche. If this be so, the expectation is that they will form a non-equilibrium state (more accurately referred to as a multi-stable state) in which population densities of all but a single species will decline to zero. This end of the continuum contains as an equally complex intellectual heritage, ideas of density independence, non-equilibrium dynamics, maximum niche overlap resulting from ecological similarity, etc ... It is the Yodzis category of founder-control.

Most practitioners today would argue that the nature of the tropical world is somewhere between these two continua, thus relegating the interesting intellectual debate to a liberal resolution of a little bit of this side and a little bit of that. Indeed, the most ardent proponent of the founder-controlled community would admit that some trees are undoubtedly pioneers and others undoubtedly characteristic of old-growth forest. Nevertheless, they hold that it is within the category of old-growth habit that hyperdiversity cannot be explained by distinct niches. Similarly, the most ardent proponents of the dominance-controlled community would admit that probably some groups of species occupy very similar niches in the context of the old-growth forest. Nevertheless, they hold that the pioneer/old-growth dichotomy is just the first rough cut in recognizing what must be important niche differences among all species. So the debate actually boils down to a question of whether the forest is "mainly" dominance-controlled or "mainly" founder-controlled.

In this chapter I have argued that, first, some data from a post-hurricane forest in Nicaragua, supports (albeit perhaps only weakly) the founder-controlled end of the continuum. This support stems from the notion that if a community is founder-controlled, some trajectories ought to be located in different basins of attraction than other trajectories. In the forest damaged by Hurricane Joan in Nicaragua, a natural yet catastrophic event, early forest succession, not dominated by pioneers, suggests that some of the sample plots are located in distinct basins of attraction from one another, a signal expected from a founder-controlled community.

Among the most popular ideas of rain forest dynamices, not necessarily associated with either end of the dominance versus founder controlled continuum, is what has come to be called the "enemies hypothesis." Originating with some early ideas of Janzen (1970) and Connell (1971), it has become a centerpiece of thinking about rainforest dynamics. The idea is a simple one in principle. If an individual tree (seed, seedling, sapling or adult) is located in a high density clump of conspecifics, it will be an obvious target for natural enemies (seed predators, herbivores, diseases), especially specialist natural enemies. This enemies hypothesis leads logically to a theoretical structure that is not yet universally recognized. Well-known by theoretical ecologists, it has to with heteroclinic cycles, and leads to some interesting constraints on how communities can be organized via this mechanism.

The idea of a heteroclinic cycle is well known in theoretical ecology (Hofbauer and Sigmund, 1989; Kirlinger, 1986; Huisman and Weissing, 2001a; 2001b; Vandermeer and Pascual, 2004). Its mathematical form is quite obvious. The output from a saddle point is connected to the input of another saddle point and visa versa. The basic idea is evident in May and Leonard's classic (1975) analysis of a three species competitive system where there are three saddle points (1,0,0; 0,1,0; and 0,0,1). As the system approaches the equilibrium 1,0,0 (say) it approaches near the inset of that saddle point, yet it ultimately flies by that saddle point as it comes under the influence of the outset of that same point. It then approaches the second point, 0,1,0, but does the same thing, thus being thrown into an approach to the third point, 0,0,1. In this way the trajectories move from approaching point 1 to approaching point 2 to approaching point 3, to approaching point 1, and so forth.

Heteroclinic cycles can be stable or unstable. In a stable heteroclinic cycle the trajectories approach ever closer to their defining saddle points. If a zero population density is one of the values of one of the populations at the saddle point, this means that that population becomes ever closer to zero as the cycle progresses. This point was emphasized by May and Leonard (1975), where they emphasized the ultimate biological outcome of such a cycle is extinction, even though the mathematics predicts "persistence" (Kirlinger, 1986) (i.e., since the population becomes arbitrarily close to zero, it must be biologically extinct even though it is mathmatically persistant). On the other hand, a stable heteroclinic cycle defines a region within which the system cannot escape, and can thus be thought of as a basin boundary or separatrix. Here, the reverse dynamics is apparent. Using the same example as above, if the three species system is set near point 1 (1,0,0), say about (0.99999999, 0.000000001, 0.0000000001) each subsequent time around the cycle, it moves away from that point. Thus, the cycle formed by the output of point 1 connecting to the input of point 2 and the output of point 2 connecting to the input of point 3 and the input of point 3 connecting to the output of point 1, cannot be breached. It is as if the trajectory is on the edge of the rim of a bowl, and corresponds to the basic idea expressed long ago by Lewontin (1969) of "stability away from the edges".

Heteroclinic cycles can become visually complicated when the system involves natural enemies. Natural enemy systems are inherently oscillatory and thus the saddle points associated with them are frequently saddle cycles rather than points. However, the qualitative nature of the underlying dynamics remains the same, with the added complexity that as a fixed point is approached, the approach itself is oscillatory. This results in oscillations that seemingly are damped, but suddenly veer off and begin an approach to some other saddle point (which also could be oscillatory). This structure was pictured in figure 4 and 6b.

Given the reality of heteroclinic cycles in many ecological models, and the fact that their existence is more likely as systems become larger (Hofbaur and Sigmund, 1998), the basic structure, proposed by many authors, of natural enemy control over founder-controlled communities would seem inevitably to involve heteroclinic cycles. Indeed, some basic patterns involving heteroclinic cycles arise logically from what is known about the dynamic behavior of founder-controlled communities constrained by natural enemies (as I note is a popular theme amongst tropical ecologists), as argued graphically in figure 3.

Part of the logical structure that emerges derives from the extensive literature on "control from above" when applied to founder-controlled communities. That is, authors from Darwin to contemporary sages, note that there is some likelihood that natural enemies of some sort may distort the underlying inevitability of competitive exclusion in founder-controlled communities (see literature reviewed in the introduction). However, it is a general rule (under the assumption of classical dynamics) that 1) generalist natural enemies cannot change the qualitative outcome expected from founder-controlled communities, and 2) a minimum of n specialist natural enemies is necessary to counter competitive exclusion in a founder-controlled community of n competitors (Schreiber, 1997; 1998). To appreciate this latter point it is important to add that if, in a founder-controlled community, a single competitor species lacks any natural enemy control, the entire community, all competitors save the dominant, and all their natural enemies will go extinct. In this sense, a community in which a single competitor species has only a single specialist predator can be thought of as "structurally unstable" since a stochastic extinction of its predator would result in collapse of the entire system.

Thus, the theoretical literature on the enemies hypothesis suggests that neither complete generalist nor complete specialist predators can create conditions for which a founder-controlled community will not collapse. There appear to be two solutions to this theoretical conundrum: 1) nature is far more complicated and if we add things like population structure, storage, space, stochasticity and more non-linearities, the underlying problem disappears and 2) intermediate levels of polyphagy can result in structurally stable maintenance of a founder-controlled community. The first of these solutions is, of course, a hodgepodge of issues that are not included in the most elementary models and that may very well represent the final answer to the original question of maintenance in a founder-controlled community. However, this "retreat into complexity", begs the question. Is it, with the classical formulation of the models, absolutely necessary to add such complexities to solve the problem. One issue that remains within the simplicity of the classical modeling approach is that of intermediate polyphagy (Vandermeer and Pascual, 2005), recalling the queries made by Haldane in 1944 (see introduction).

Empirically, it is not difficult to construct models in which intermediate levels of polyphagy will allow for coexistence in a system in which both fully generalist and fully specialist predators are not capable of deterring the inevitability of competitive exclusion. One such example was presented in figure 5. In such examples, it is frequently the case (perhaps always the case) that there is a bifurcation point at some critical level of polyphagy at which a critical heteroclinic cycle transforms from a stable cycle (in which most species go extinct) to an unstable cycle (in which the cycle contains a portion of space, maintaining the system within that space), as explained qualitatively in figure 7. Such a structure may or may not be associated with a chaotic attractor also.

There are certainly practical consequences to these theoretical results. If tropical rain forests are in fact basically founder-controlled, any force that limits the natural enemies associated with them may result in the loss of polyphagous control, thus ultimately resulting in the collapse of the community due to competitive exclusion. One could speculate that perhaps some of the still enigmatic "monodominant" tropical forests could be examples of this phenomenon. For example, the palm *Raphia taedigera* occurs in almost monodominant stands in isolated pockets of swamps in the Neotropics (Urquhart, 1999). There are sites in Costa Rica in which it occurs in small isolated swamps, but not in other isolated swamps that appear perfectly suitable for it. It is likely that its absence in these latter swamps is due to dispersal limitation (Hartshorn, personal communication), since it has no known dispersal mechanism. Where it does occur, it dominates the forest, which is thus not very diverse. Where it does not occur, a relatively high diversity forest emerges. Is this a case in which a particular species, *Raphia taedigera*, lacks natural enemies (which does, in fact, seem to be the case) and the potential community of hundreds of species of trees has "collapsed?" Other similar examples could be cited (e.g., Torti et al, 2001, but see also Gross et al, 2000).

There is also a practical side to this issue. Much as small pockets of swamps may or may not contain a particular species, as the lowland tropics becomes fragmented, each small fragment may be subjected to random extinctions, not of the trees themselves (which, of course, could also occur) but of the all-important natural enemies. Might it be the case that only highly generalist natural enemies are capable of avoiding the stochastic extinctions that are inevitable in smaller patches of habitat? If this were the case, we might expect higher levels of extinction in the long term, than would be expected from a metapopulation-type model that incorporated only purely stochastic extinctions in its dynamics. Stochastic extinction at the level of natural enemies could have the effect of switching the overall level of polyphagy such that what was an unstable heteroclinic cycle becomes stable, and the system collapses to a very low biodiversity. This is, of course, purely conjecture, but may be added to the variety of other possible mechanisms of sudden extinction (McCann and Yodzis, 1994; Nee and May, 1992) previously proposed.

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Figure captions

Figure 1. Euclidean distance in the space of population densities between alternative trajectores over time. a. Theoretical expectations shown for six comparisons of either dominance-controlled communtiies (□=0.9) or founder-controlled communtiies (□=1.1). b. Actual euclidean distances for six comparisons of post-hurricane rain forest plots in Nicaragua (after Vandermeer et al., 2004).

Figure 2. Diagrammatic representation of the heteroclinic cycle resulting from the rock-scissors-paper arrangement of competitors studied by May and Leonard (1975).

Figure 3. Diagrammatic representation of the heteroclinic cycle resulting from the operation of the enemies hypothesis on a founder-controlled community (compare to figure 2).

Figure 4. Illustration of a heteroclinic cycle in which the saddle points are oscillatory.

Figure 5. a. Average number of species surviving after 6000 iterations as a function of the degree of polyphagy in the system (average of 7 independent simulations with random starting points), based on equations 1. Parameter values are a = 10, a = 1.1, m = 1, b = 2. b. Local minima for the same range of "degree of polyphagy" for the logarithm of the variable X_1.

Figure 6. Heteroclinic cycles in the four dimensional system. a. the space of predator (P) versus competitor (x). b. The delta space (the difference between the density of the two predators versus the difference between the density of the two competitors), where the four unstable oscillatory situations are clear.

Figure 7. Diagrammatic representation of the basic bifurcation between stable and unstable heteroclinic cycle, illustrating the chaotic dynamics (shaded area) that may result from an unstable heteroclinic cycle.

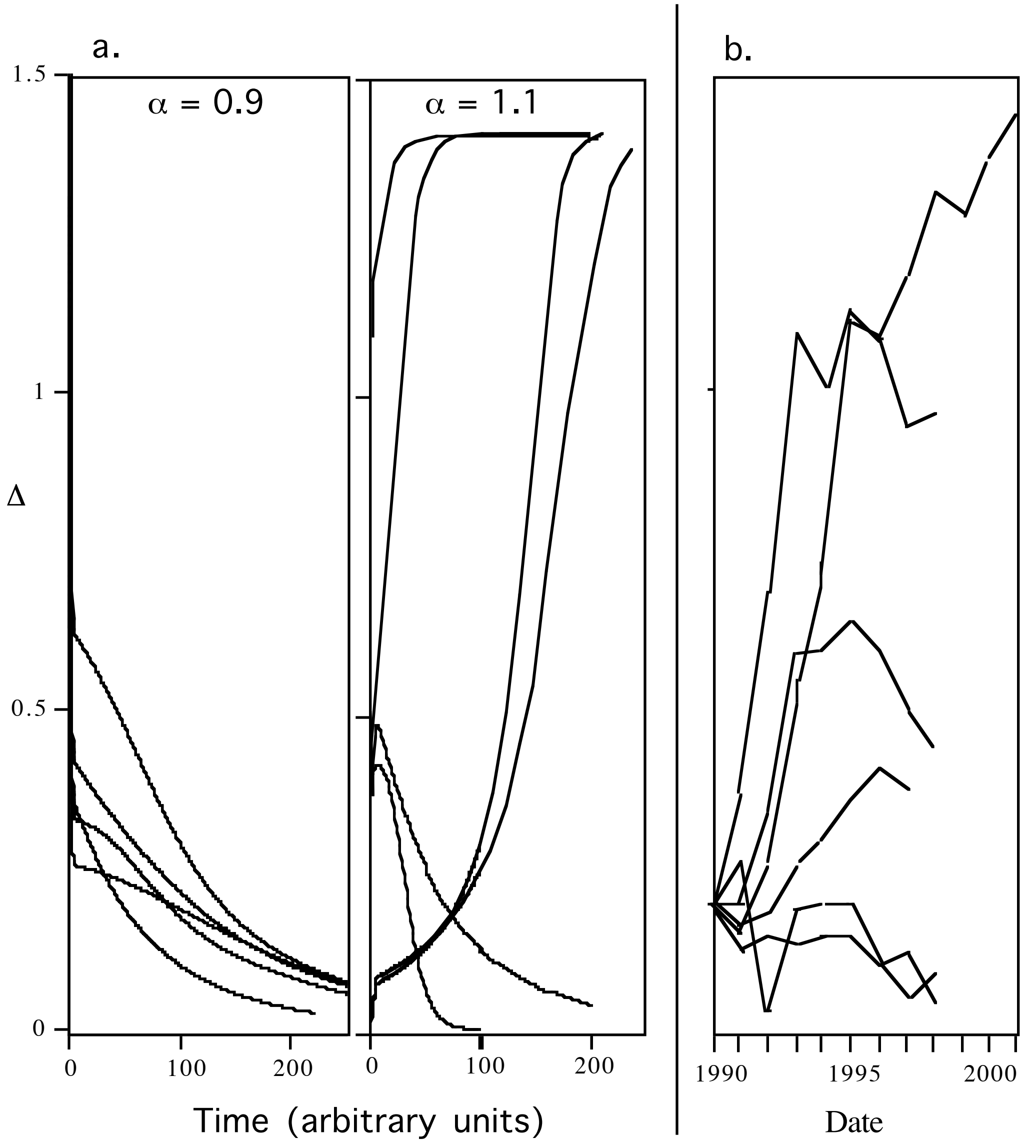


fig 1

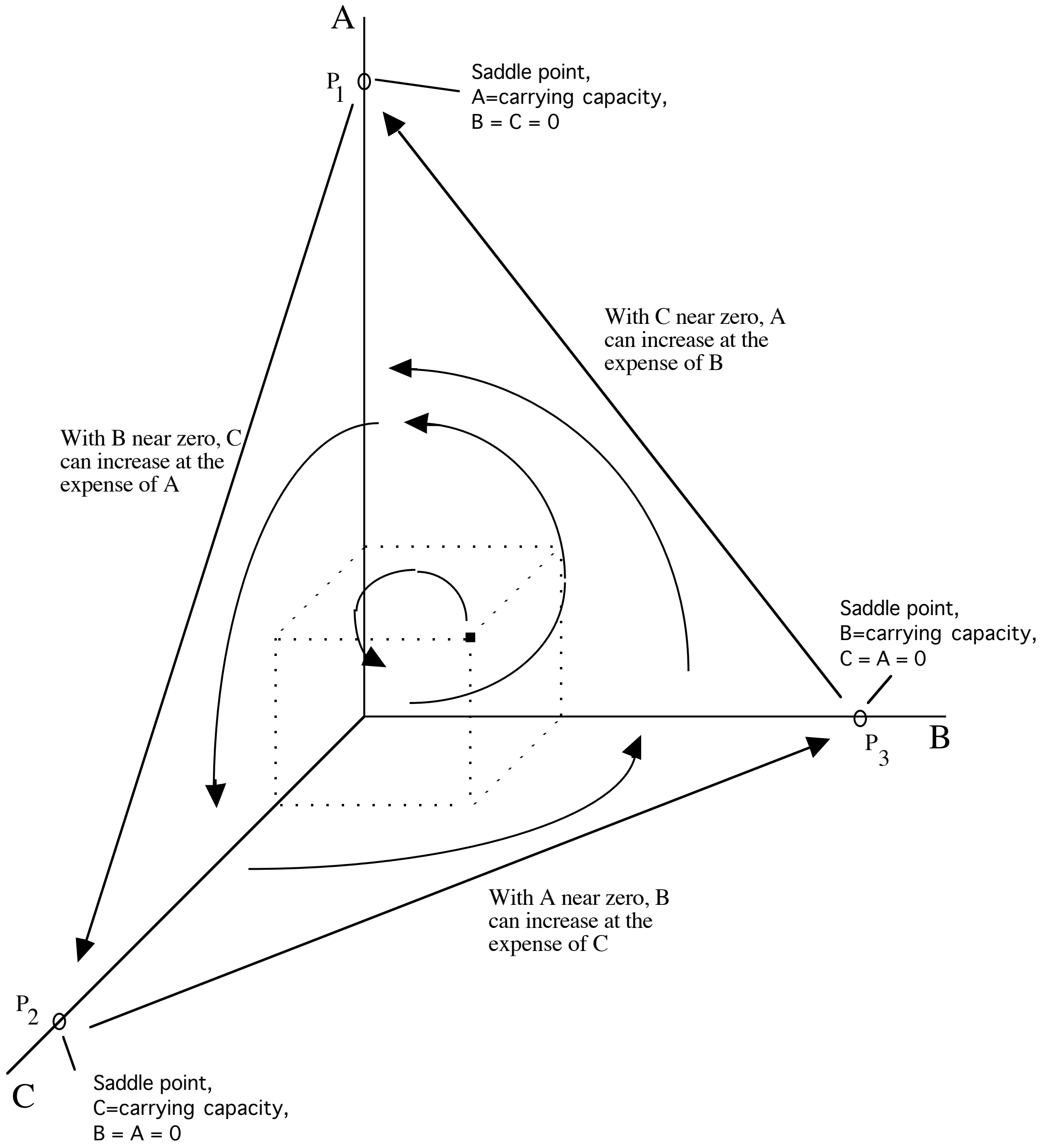

A
P_1
Saddle point,
A=carrying capacity,
B = C = 0
With C near zero, A can increase at the expense of B
With B near zero, C can increase at the expense of A
Saddle point,
B=carrying capacity,
C = A = 0
P_3
B
With A near zero, B can increase at the expense of C
P_2
C
Saddle point,
C=carrying capacity,
B = A = 0

Fig 2

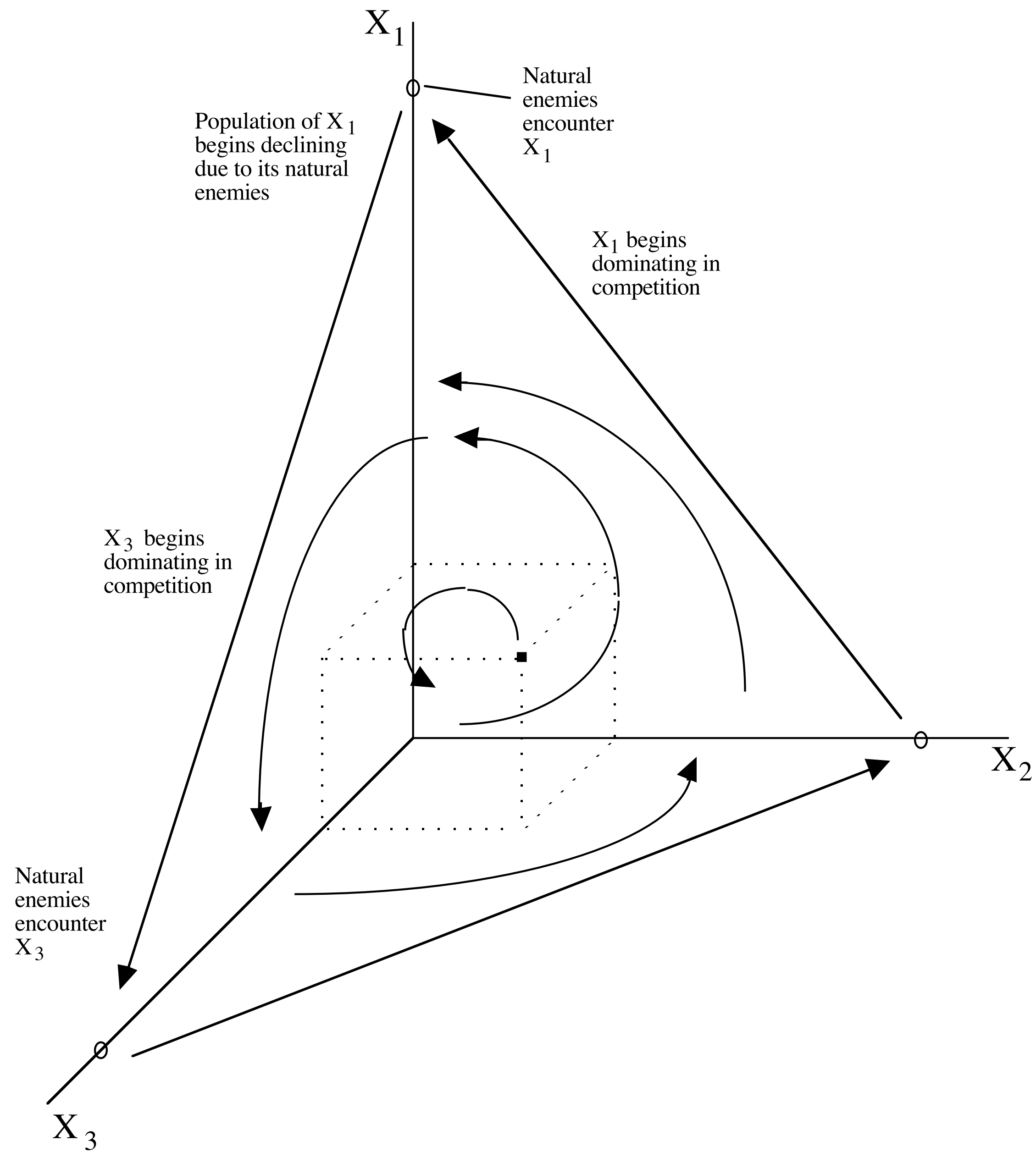

X_1
Natural enemies encounter X_1
Population of X_1 begins declining due to its natural enemies
X_1 begins dominating in competition
X_3 begins dominating in competition
X_2
Natural enemies encounter X_3
X_3

Fig 3

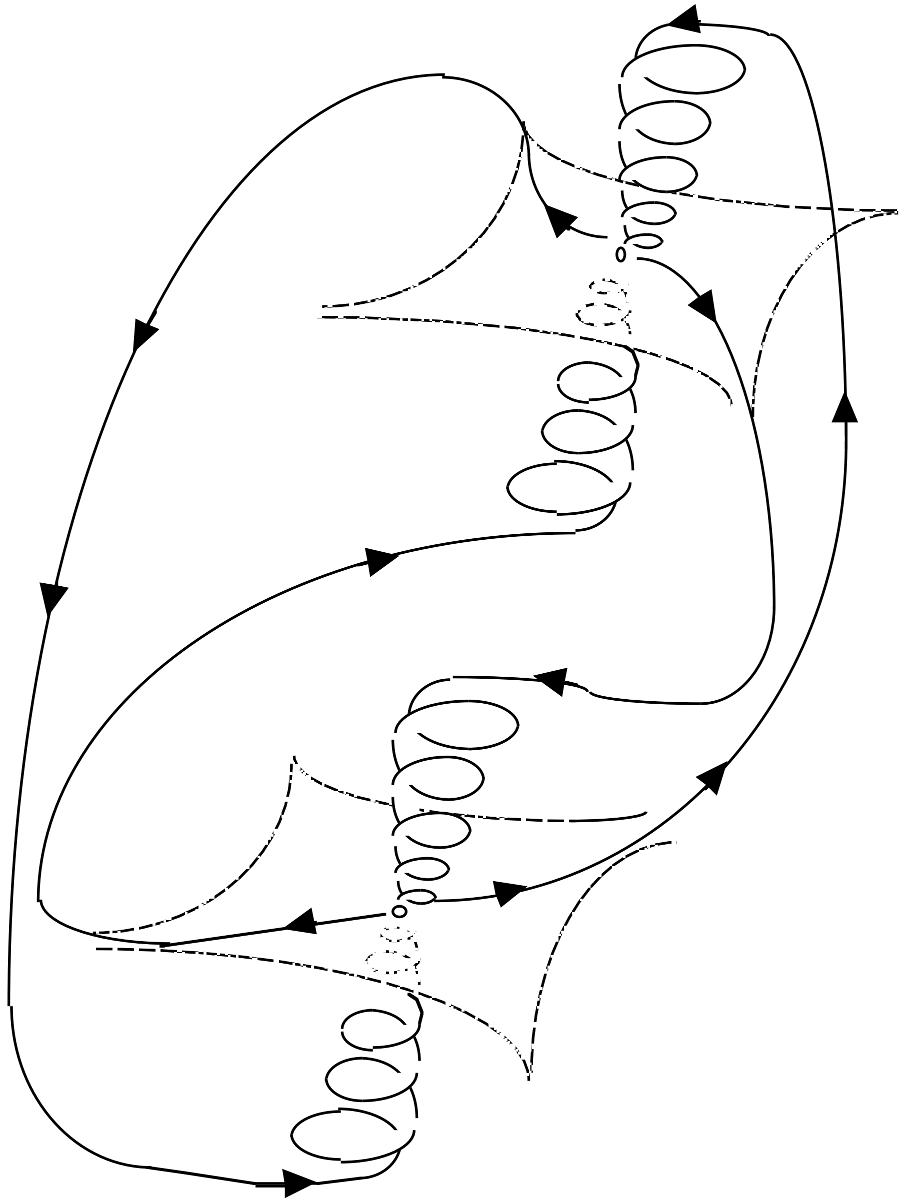


Fig 4

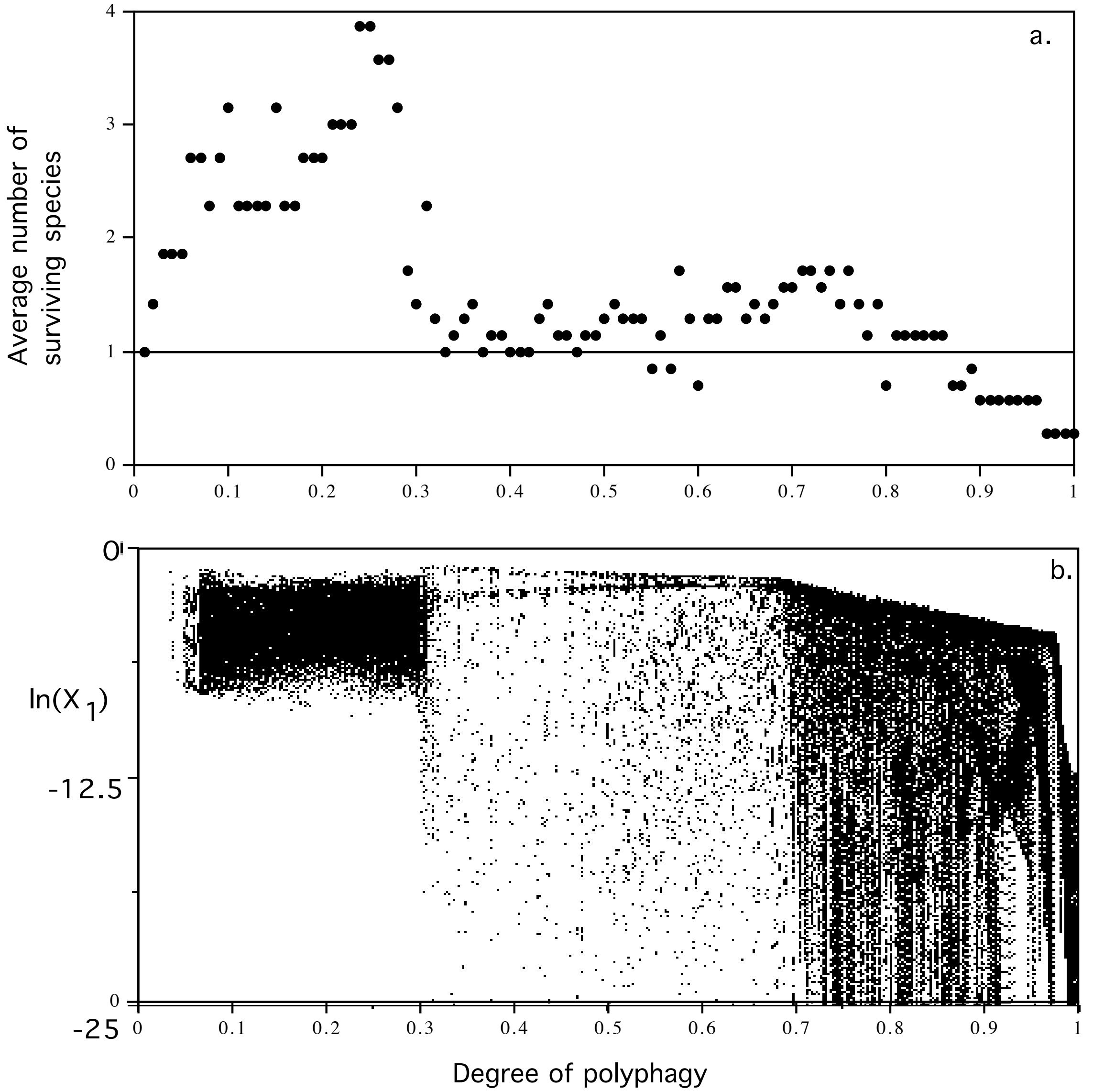

a.
Average number of surviving species
0
1
2
3
4
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
b.
ln(X 1)
0
-12.5
-25
0
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
Degree of polyphagy

Fig 5

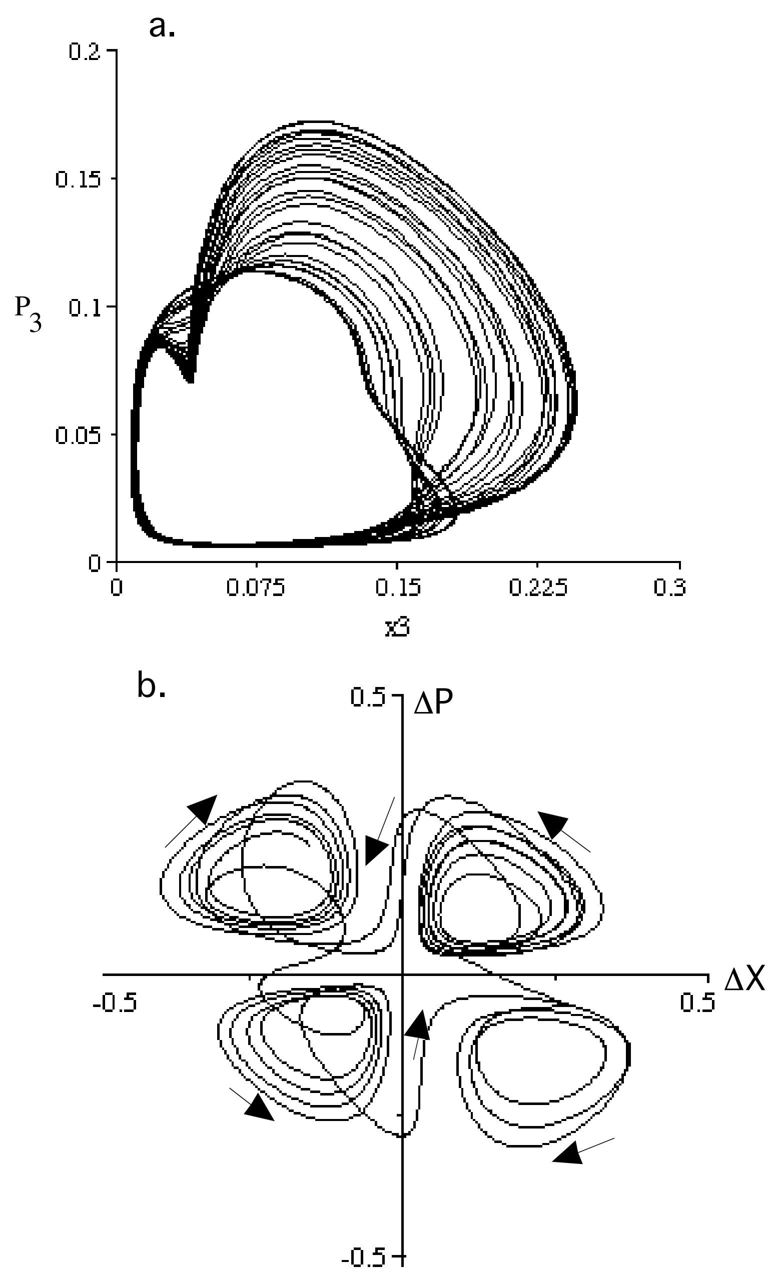
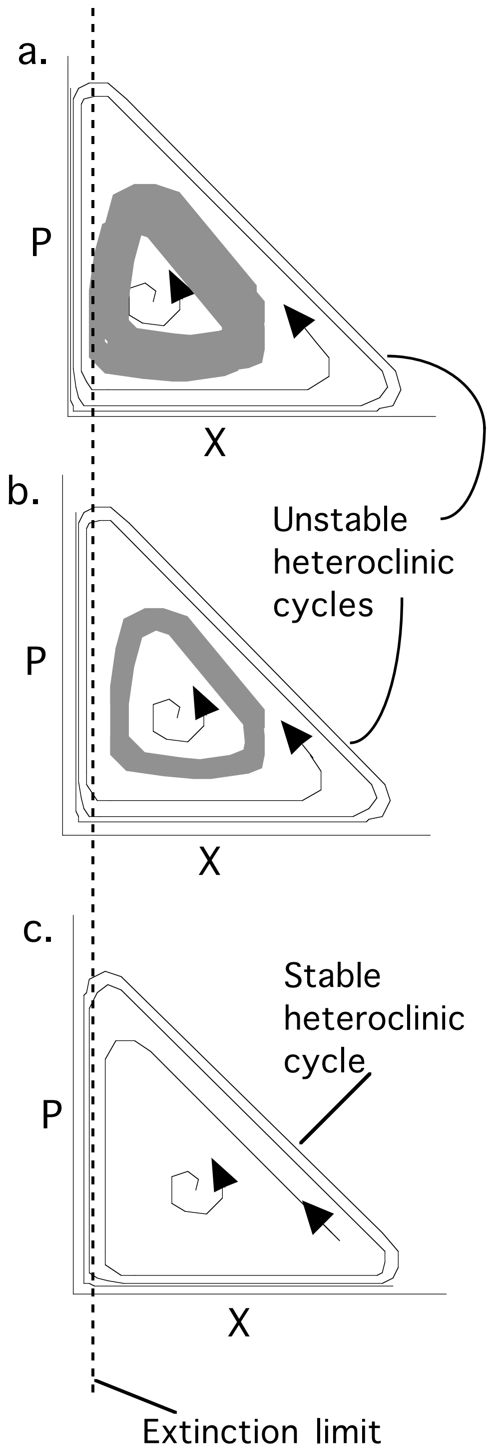


Fig 6.


a.
P
X
b.
P
X
Unstable heteroclinic cycles
c.
P
X
Stable heteroclinic cycle
Extinction limit