Darwin's "Circles of Complexity": Assembling Ecological Communities

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Darwin frequently rhapsodized about "how plants and animals, most remote in the scale of nature, are bound together by a web of complex relations"[1]. He relished figuring out how if "certain insectivorous birds were to increase in Paraguay," a species of flies would decrease; and how—since these flies parasitize newborn calves—this decrease would cause cattle to become abundant; which "would certainly greatly alter the vegetation." And he went on to show "how this again would largely affect the insects; and this again the insectivorous birds...and so onwards *in ever-increasing circles of complexity*." Yet, Darwin adds, "our ignorance is so profound...that we marvel when we hear of the extinction of an organic being; and as we do not see the cause, we invoke cataclysms to desolate the world, or invent laws on the duration of the forms of life!"

Today, we certainly no longer marvel when we hear of an extinction event. Confidence in a stable world has gone the way of many other Victorian oddities. Laws on the "duration of the forms of life" are out of fashion, too. On the other hand, cataclysms have come back—quite literally with a bang. "Mass extinction," writes David Raup, "is box-office" [2]. But it makes up for less than 5% of all extinctions. There is a steady background level of less spectacular extinctions due to internal and external stresses. Every ecosystem is continuously restructured by some species invading and others fading out.

All biological communities are transient, but some are more so. They collapse right away, without having to wait for the construction of a river dam, the mutation of a parasitic strain, or a series of harsh winters. They are doomed in their

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own right: they are *unsustainable*—that is, impossible in the long run. They do occur in nature, but it is hard to make them out before they are replaced by less fleeting configurations. Ecologists who wish to understand what happened have no time for a leisurely *post mortem*. Yet they must know why communities fail if they want to learn about those that persist.

J. F. Gause was the first to construct impossible ecocommunities in his lab; this led him to the *competitive exclusion principle* [3]. For obvious reasons, such artificial communities do rarely amount to more than a few strains of protozoa in a test-tube. To come any closer to real food webs—sustainable and otherwise—one has to simulate them on computers.

The stability of biocommunities is to a large extent, therefore, the domain of *mathematical ecologists*. However, their efforts were initially marred by a misunderstanding: They used a notion of stability inherited from engineering and physics. A *stable* steering device, for instance, is one that resumes its equilibrium after every small perturbation. But field ecologists would never expect to find, out there in the wild, the static, well-controlled state of affairs implied by such a stability notion. For those ecologists unspoiled by physics, the proverbial lynx-hare cycle—whose undamped oscillations have been recorded for two hundred years—epitomizes stability. They little care whether the population numbers converge or oscillate in a regular or chaotic fashion. For them, stability means that those numbers do not vanish—that the species making up the ecosystem do subsist. Not equilibrium, but *survival* is what counts (see [4-6]).

PERMANENCE: THE REPELLING SIDE OF STABILITY

The ecosystem at time t is described by the frequencies $x_1(t)$ to $x_n(t)$ of the populations making it up. It is stable *in an ecological sense* if for a long time none of these numbers drops to 0. If we denote the state of the system by a vector **x** in n-space—

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or, more precisely, in the positive orthant R_+^n—we have to watch whether it approaches the boundary of that orthant (where some x_i are zero) or not.

So far, so trivial. But next, we have to define the *dynamics* governing the evolution of the population frequencies x_1 to x_n, and that's where we are faced with a great many choices. For simplicity, let us stick with the most commonly used approach and model population growth by a differential equation

$$\dot{x}_i = x_i f_i(x_1, \ldots, x_n) \qquad (1)$$

$(i = 1, \ldots, n)$, where f_i, the per capita rate of increase of the i-th population, depends on the current frequencies of all populations: it becomes smaller, for instance, if there are more predators, and larger if there are more prey, and so on. If the f_i are linear, i.e., if $f_i(x_1, \ldots, x_n) = r_i a_{i1} x_1 + \ldots + a_{in} x_n$, where the interaction terms a_{ij} can be positive or negative, this yields the classical Lotka-Volterra equations (for a survey, see [7]).

If $x_i(t) = 0$ at some time t, then it remains so for all times. The boundary of the state space, where one or several of the populations are missing, is, therefore, invariant: this means that the evolution of the ecosystem, as modeled by (1), does not allow for the introduction of missing species "out of the blue." On the other hand, (1) is obviously just an idealization of the internal dynamics. In reality, some external, contingent factor—a migration, for instance—may well introduce a small amount of a species that had not been present before. The interior of the state space—where all x_i are strictly positive—is also invariant under (1), which means that under the internal dynamics, no population number can reach 0. But, of course, extinctions can happen, either when a random fluctuation superimposed on (1) wipes out a small population or when $x_i(t)$ becomes smaller than 1.

Close to the boundary of the state space, extinction looms. The community will be stable in an ecological sense, therefore, if the state vector $\mathbf{x}(t)$ keeps safely away from the boundary. There are several ways to make this precise: the notion which is best understood is that of *permanence*, first introduced by P. Schuster, K. Sigmund, and R. Wolff [8]. System (1) is said to be permanent if there exists a constant $k>0$ such that, whenever the x_i are initially all positive, then all $x_i(t)$ will be ultimately larger than k. This means that if all species are initially present (although possibly in very small quantities), they will have left, after some time, the zone where extinction threatens. In other words, the boundary of the state space is a *repellor*: if we start on the boundary and introduce some few members of the missing species, then (after a transient phase) extinction will threaten neither the newcomers nor the former inhabitants. Their numbers can—and often will—oscillate wildly, in a regular or irregular way; this does not matter as long as they keep well away from 0. Usually, one also assumes that they keep away from ∞. Clearly, every decent model ought to have this property, and we assume it from now on. In this case, permanence means that there exists a compact set in the interior of the state space R_+^n, where all orbits initiating from the interior end up. This compact set may contain one or several strange attractors. It must (as a consequence of Brouwer's fixed point theorem) also contain an equilibrium (see [9]), but this equilibrium need not be an attractor.

This shows again how different the "permanence" version of ecological stability is from the stability notion of engineers. The system would be stable in the latter's sense if it admitted an equilibrium $\hat{x}$ in the interior of the state space (all components strictly positive) that is asymptotically stable: every slight perturbation would be promptly cancelled. Such a condition is neither necessary nor sufficient for permanence (see, for example, the discussion in [7] or [10]).

If the system (1) is permanent, then no $x_i(t)$ can converge to 0, for $t \to +\infty$. But conversely, even if no $x_i(t)$ tends to 0, the system need not be permanent. There are essentially two reasons for this. The first is exemplified by the classical predator-prey equation of Lotka-Volterra:

$$\begin{aligned}\dot{x}_1 &= x_1(a - x_2) \\ \dot{x}_2 &= x_2(-b + x_1).\end{aligned} \qquad (2)$$

The equilibrium (a,b) is surrounded by periodic orbits. This system is *not* permanent. An orbit starting in the interior does not converge to the boundary—it cycles periodically. However, if it starts *very* close to the boundary, it keeps coming back, again and again, to where a small perturbation can send it to the boundary. Even if the system started near the equilibrium, a sequence of arbitrarily small and rare perturbations can send it closer and closer to the boundary. The internal dynamic does not work against this tendency. It does not send any population towards 0, but neither does it promote survival.

There is another, more interesting example that shows how things can go wrong. Its first (and simplest) form is due to May and Leonard [11]. Consider an "ecosystem" consisting of three competing species:

$$\begin{aligned}\dot{x}_1 &= x_1(r - x_1 - 2x_2 - \tfrac{1}{2}x_3) \\ \dot{x}_2 &= x_2(r - x_2 - 2x_3 - \tfrac{1}{2}x_1) \\ \dot{x}_3 &= x_3(r - x_3 - 2x_1 - \tfrac{1}{2}x_2).\end{aligned} \qquad (3)$$

Each species i by itself would converge to an equilibrium value E_i. Species 2 dominates 1 in the sense that it can invade a habitat containing only species 1 and drive species 1 to extinction. Likewise, species 3 dominates 2, and species 1, in turn, dominates 3. But what happens if all three species are initially

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present? This depends. For some interaction terms f_i, the boundary is a repeller and the system is permanent. For other f_i, however, the boundary *attracts* orbits from the interior. Such an orbit hovers for some time in the vicinity of E_1 (so that the habitat seems to contain mostly species 1); then, swiftly, it swings over to the vicinity of E_2 (where species 2 predominates) and lingers there for a much longer time, switches brusquely over to E_3, and so forth. The species supersede each other cyclically, but not periodically: the times between the revolutions grow exponentially, and the frequencies of the minority species become smaller and smaller. The lim inf x_i are 0, but the lim sup x_i are as large as the equilibrium densities E_i. This system, obviously, is not permanent; in fact, the distance between the $\mathbf{x}(t)$ and the boundary converges to 0. One of the species will eventually be wiped out by a random event, and whichever of the two remaining species dominates the other will prevail in the habitat. But its hegemony is not stable: if another random event (a migration from a nearby habitat, for instance) reintroduces the species that has been wiped out, this newcomer will take over.

Admittedly, such a rock-scissors-paper cycle of three competitors has never been found in nature. We use it only as the simplest example of a *heteroclinic cycle*. But as soon as we come to more complex ecosystems (for instance, two prey species and two predators), the likelihood of similar cycles grows.

The general approach behind these arguments is that on top of the "internal dynamics" (1), we have to expect the influence of small, external perturbations. The "real ecosystem" will not follow one orbit of (1) but will occasionally jump from one orbit to another. This can increase the oscillations, as in Eq. (2), or it can allow a missing species to be reintroduced, as in Eq. (3). Such minor fluctuations can lead to extinction, but not if (1) is permanent.

We cannot exclude, of course, some major effect spoiling the system. This can destroy even permanent networks. The *top predator* is a case in point. Such a predator, who lives at the top of a food chain, is usually rare. What happens if it gets eliminated (say by human interference)? At first glance, one might think that the rest of the network will benefit from the removal of the top exploiter. But this is not necessarily so (see [12]). It can happen, for instance, that two prey and one predatory species form a permanent system, but that the two prey species, in the absence of the predator, are no longer permanent: one of them eliminates the other (see [9]). In this sense, a predator can "stabilize" (i.e., render permanent) a two-prey system which, by itself, is *not* permanent because one species dominates the other.

There is another case where a two-prey system is not permanent, namely, when none of the two species can invade the other (bistability). Such a system cannot be stabilized by the introduction of a suitable predator (see [9]). On the other hand, it can be stabilized by the introduction of two predatory species, each one specialized upon one of the prey (see [13]). Alternatively, it can be stabilized by the introduction of one competing species and one predatory species. Similarly, a nonpermanent system consisting of three competing species forming a rock-scissors-paper cycle can be rendered permanent by an additional competing species or by a predatory species with suitable parameters (see [14]). It follows that if, in the resulting four-species system, the predator is eliminated (by hunting, for instance), then the system collapses: only one of the three competitors will survive. Such a predator can be viewed as a keystone of the ecosystem.

Ecosystems with only three or four species don't exist in nature, of course, but such "toy communities" help us to understand more complex food webs. It ought to be stressed that their dynamics can be extremely complex: so far, not even the Lotka-Volterra equation describing three competing species is fully understood. But if one is interested just in the permanence of such a system, one can reach fairly comprehensive answers, in part because the problem is reduced to the dynamic behavior close to the boundary, i.e., one dimension down.

By now, there is a solid body of mathematical results on permanence for all kinds of population dynamics (see [15] for a comprehensive survey). Roughly speaking, one has two problems to solve in order to prove permanence: (a) find the invariant sets on the boundary which are candidates for attracting orbits from the interior, and (b) show that they don't. The best technique for (a) is given by the notion of chain-recurrent sets (see [16-18]); for (b), by the method of average Ljapunov functions (see [19-20]). The two methods have been neatly combined by J. Hofbauer [21]. For Lotka-Volterra equations, more explicit conditions are known. Thus the system is permanent if there exist strictly positive p_i such that

$$\sum p_i(r_i + a_{i1}z_1 + \ldots + a_{in}z_n) > 0$$

holds for all equilibrium points $\mathbf{z}$ on the boundary of R_+^n (see [22]), or, alternatively, if the convex hull of the boundary equilibria is disjoint from the set of all states $\mathbf{x}$ where no species increases (i.e., where $f_i \leq 0$ for all i) (see [21]). Both conditions can easily be checked by linear programming. Both, by the way, are not necessary for permanence if $n > 3$. But if the Lotka-Volterra equation is permanent, then there is a *unique*

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equilibrium $\hat{x}$ with all species present, and it is the limit of all time-averages of orbits in the interior of the state-space. If D is the Jacobian at $\hat{x}$, then $(-1)^n \det D > 0$, and $trace D < 0$. Furthermore, $(-1)^n \det A > 0$, where A is the matrix of the interaction terms a_{ij} (see [7]).

NOAH'S ASSEMBLY: ADRIFT ON THE GENE POOL

These results allow us to study the permanence question for multi-species Lotka-Volterra equations by numerical simulations, and hence to get a feeling for the likelihood of permanence in randomly assembled ecological networks. The first results (see [23]) were extremely negative: for higher-dimensional models (with $n=10$, say, or larger), the probability of permanence was vanishingly low. But Mother Nature, of course, does not assemble her networks by throwing n species together in one go. It makes more sense to assume that she adds one species after another through successive invasions.

This approach has been used by Richard Law and co-workers in a remarkable series of papers [24-27]. In his computer simulations, Law starts out with a more or less judiciously chosen *species pool* consisting of primary producers and consumer species. He then assembles communities by an iterative procedure which mimics sequential invasion attempts: he randomly selects a species from the pool which is not present in the community and checks whether it can invade the community, i.e., whether it increases when rare. (For Lotka-Volterra equations, this is easy to do since one has only to check the invaders' growth rate at the equilibrium point of the invaded community, *even if this point is unstable.*) If the invasion attempt fails, the species goes back to the pool to try its luck another time. But if the invasion attempt is successful, a new community will be obtained. It may simply be the *augmented* community—i.e., the previous species and the invader—but the invader may also eliminate some of the indigenous species. In no case, apparently, will the invader itself be driven to extinction by having eliminated members of the previous community; i.e., it will not be a victim of the community collapse caused by its invasion (but it can, of course, be eliminated by later arrivals).

This iterative procedure yields a succession of permanent communities that frequently leads to an end state where no further species from the pool can invade. This *end state* need not be unique, but may depend on the (contingent) sequence of arrivals. But as Law notes in [26], the number of such end states is typically very small—history has an effect, but one that is rather limited; often a different order of arrivals does not lead to a different end point. No such end state can be a subset of another end state, by the way. It can also happen that there is no end species at all. In this case, the community structure is transient: some species undergo endless cycles of elimination and successful reinvasion. Another curious fact is that end states often lack reassembly paths; they cannot be arrived at through a sequence of stepwise increasing permanent subcommunities but instead need supplementary species that catalyze their construction and are eventually lost. In other words, one needs to know more than just the species present in order to understand how the community was assembled.

A growing number of ecologists believe that the method of community construction will lead to insights on the structure of multispecies communities, such as number of throphic levels, connectance, complexity, resistance to invasion and so on (see [28-30]). But previous studies were often too much focussed on stable equilibria and missed a substantial number of possible "succession chronicles" (see [31-33]). The permanence notion used by Law is more appropriate. As he writes, "the dynamics close to an interior equilibrium point are not the main issue for coexistence; what matters is whether the densities of rare species tend to increase."

On the other hand, it must be admitted that the permanence concept has its drawbacks. There can be permanent systems whose repelling "skin" covering the boundary is too thin to protect against extinction. There can also be systems in which a part of the boundary attracts orbits (hence, no permanence) while another part repels orbits so that they end up on an attractor in the interior, perfectly safe from extinction. In this sense, the notion of permanence is both too strong and too weak. One can easily think of other definitions which reflect more faithfully an ecologist's notion of a stable community, but these definitions seem mathematically intractable so far.

Some other aspects of the assembly approach to ecocommunities need qualification. It is by no means sure that invading species alight one at a time. If a land bridge forms, for instance (such as the Isthmus of Panama), then the habitat is subject to many simultaneous invasion attempts. Furthermore, the "species pool" from which all invaders are drawn is obviously a convenient abstraction. How large should it be, and how should one choose the interaction terms between the species? One can follow two complementary strategies: either draw on the very extensive level of expertise on real food webs found in nature or in experiments (see [34-40]) or else deliberately ignore it and study community assembly as a purely mathematical problem. P. J. Taylor, a pioneer in this approach, points out that if one restricts parameters in advance to realistic values, one loses the opportunity to find out whether they have been selected by the ecological dynamics [41]. Only in this way can one hope to explain, for instance, the rarity of feeding loops where species 1 eats 2, which eats 3, which eats 1 [42].

In reality, invading species do not come from a species pool, of course; they arise (occasionally) through speciation events and (much more frequently) through migration from other communities that are not randomly assembled but structured, in turn, by long histories of invasions and eliminations. This is somewhat analogous to the construction of new genomes, which arise (occasionally) through mutation and (much more frequently) through recombination of genomes which are themselves the products of a long history.

A *metapopulation* (i.e., a patchwork of communities linked by migration) tends to be much more stable than a single, well-mixed system (see [43-46]). In particular, V. Jansen has recently shown that even by linking only two (nonpermanent) predator-prey models of type (2), one obtains permanence [47]. Unfortunately, few useful conditions for permanence in spatially structured communities are known so far. But just as communities are assembled stepwise, through trial and elimination, so the ecologists who work on community assembly have to proceed stepwise, restructuring their models by repeatedly adding new facets in order to trace Darwin's "ever-increasing circles of complexity."

In the end, we may find, as P. J. Taylor suggested, that this ecological complexity "persists by virtue of the transience of any ecological system" [41]. Permanence is just a tool; transience is here to stay.

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