Community-level competition: Asymmetrical dominance

(faunal mixing/Lotka–Volterra competition/community assembly)

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ABSTRACT   Ecological competition between entire communities of species occurs only when geographic barriers are suddenly removed. Recent empirical analysis suggests that, following the disappearance of a barrier, one community may swamp a second community, causing most or all of its species to go extinct. I provide theoretical insight into this result by showing that two "naive" competition communities mix randomly following the removal of a barrier. However, if the two communities have been "assembled," or self-organized, through a history of competitive exclusion, the communities are likely to battle as coordinated armies, with one or the other side ultimately claiming the entire landscape.

The "struggle for existence" occurs at many levels in biology. Alleles struggle for accession at a genetic locus. Individuals of a species compete for resources, for living space, and for access to reproduction. Populations or full species compete by interference or depletion of resource levels. But is there such a thing as competition between full communities?

Direct interaction between previously isolated ecological communities is rare, occurring only when geographical barriers break down, either through natural geological events or, recently, through anthropogenic modifications of the landscape. Normally, isolated communities can only interact by sending "invasion propagules" between one another, a process that has been modeled by Roughgarden (1), Pimm (2), and Case (3), among others, all of whom have noted a buildup of the invasion resistance of a community with time. Using a military metaphor, such battle is waged between two separated and dug-in armies that send small sallies into the opposition's territory. Most such probes effect no permanent change. The case of the removal of a barrier is different; the armies are displaced from their defenses and are joined together in a grand battle reminiscent of the full infantry, cavalry, and artillery engagements of the 19th Century.

Fig. 1 contrasts the two types of possible community competition. Fig. 1A illustrates the case of community isolation. The letters represent different species in the two communities. The ovals represent the spatial location of the communities. Fig. 1B illustrates the case of interaction via reciprocally attempted species colonization. According to accepted theory, each of the two 5-species communities, whose species membership sets can be denoted as {A B C D E} and {V W X Y Z}, will likely be able to repel small invasions of a single species from the other community and will thus remain stable over time.

A second and quite different case occurs when two previously isolated communities merge, following the removal of a barrier. This process, possibly due to its relative rarity, has not hitherto been mathematically explored. Thus, it is not possible to prejudge what community structure might ultimately result following the faunal mixing. In Fig. 1C a possible instance of this mixing of two 5-species competition

communities is illustrated. The assumption is that the mixed set of 10 species will have to share the same resource base and that not all will be able to coexist in the newly connected system—that is, the system will collapse to one of fewer species. In this hypothetical example, a new 5-species system arises following competitive exclusion, whose membership set is {C D E V Z}, which represents a relatively even mixture of species from the two original communities.

Empirical Findings

Vermeij (4) has recently reviewed the empirical evidence concerning biotic interchanges or faunal mixing following the removal of isthmuses or the joining of land masses. His data from the last 20 million years are mainly from the fossil record of mammals and mollusks following sudden plate-tectonic-induced couplings of two previously separate "communities" (the ecology of these sets of species cannot be fully known from the fossils alone; thus, one must use the term community loosely). One striking pattern he finds is asymmetry: the movement of species following spatial coupling of the previously separated groups of species is decidedly one-sided—that is, one community dominates the other; its member species move across the breached barrier to supplant spatially the member species of the other, subordinate community. Using the language of Fig. 1C, Vermeij is finding that the post-mixing community will often be {A B C D E} or {V W X Y Z}. If the two original communities can be considered equal, that is, if each of the 10 species has one chance in two of being part of the ultimate mixed community, these two asymmetrical results—all from one side or the other side of the barrier—would each have a probability of 0.5^{10}, or 0.001. Such a discordance between the empirical findings and this simplistic theoretical prediction demands an explanation.

Community Versus Community: A Theoretical Model

I shall assume that all of the species under consideration are competitors, which is operationally defined as the condition that the increase in density or numbers of any of the species will be directly harmful, causing population decline, to any of the other species; this commonly results from population limitation due to a set of shared resources, or by direct interspecies interference.

To model the competitive mixing of two communities, I assume that the depressing per capita effect of species j on the growth of species i is linear and governed by a rate parameter α_{ij}. In the absence of interspecies interaction, each species reaches a carrying capacity, K_i, which, for the purposes to follow, can be normalized to unity. Without loss of generality, species per capita growth rates can also be normalized. This leads to the time-honored Lotka–Volterra model of community interaction, which is embodied in the differential equation $dn/dt = n(1 - An)$, where n is a nonnegative vector of normalized species densities and A is the matrix of interaction coefficients (the αs) with 1s on the main diagonal. Note that everything about the dynamics of these systems is

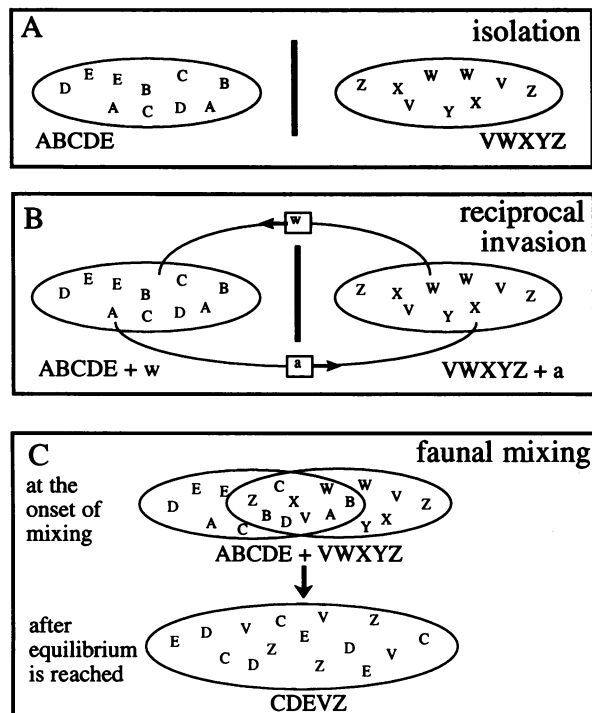Ecology: Gilpin

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FIG. 1. Schematic illustration of the manner by which two communities of species can interact. The letters A, . . ., Z represent species. The ovals represent communities. Each community initially contains five species. (*A*) Community isolation; the barrier prevents exchange of individuals. (*B*) Small invasion propagules disperse from one community to the other; these are likely to be repelled. (*C*) The two systems are geographically merged, which results in some competitive exclusions; in this case five species go extinct, A and B from the first community and W, X, and Y from the second community, leaving {C D E V Z} as the resulting community.

incorporated into the A matrix. Instances of this model can be constructed following statistical procedures on a computer and then, assuming some starting densities for the elements of the vector **n**, numerically integrated to determine the eventual fate of the system (3, 5, 6). For this study, the off-diagonal elements of A are uniformly distributed between 0 and 1, with a mean of 0.5, which implies that the per capita effect of interspecific competition is on average half the effect of intraspecific competition. In the study reported below α_{ij} is uncorrelated with α_{ji}.

I have constructed two sets of 20 five-species competition communities, specified completely by their individual interaction matrix, A$_i$. Member communities of the *assembled set* are created through a process in which a larger 10-species community is constructed from the random interspecific competition coefficients just described. Such systems typically have too much interspecific competition and many species are likely to be driven extinct, causing the system to collapse until it reaches a stable configuration. I chose only those that collapsed to a final 5-species configuration (roughly a third of the original systems). Such communities have structure due to interspecies competition experienced during their formation—that is, they are assembled through species selection under interspecies competition. The *random set* is obtained by simply creating 20 five-species systems that do not suffer the competitive exclusion of any member species.

From such sets of 20 five-species communities, two communities, A$_1$ and A$_2$, are chosen at random and competitively mixed in a way that gives each species of a community an equal chance against the members of the other set of five species. Such between-group competitive symmetry is required if one is looking for within-group properties that produce asymmet-

rical community dominance. A random interaction coefficient is drawn (according to the same uniform 0 to 1 probability distribution that produced off-diagonal elements of the original competition matrices) to join pairs of species from the two communities; this is done symmetrically, such that the per capita effect of the first species on the second is equal to the per capita effect of the second on the first. The total community matrix, A$_{full}$, for the resulting 10-by-10 system is

$$A_{full} = \begin{bmatrix} A_1 & C \\ C^T & A_2 \end{bmatrix},$$

where each of the above submatrices is 5 by 5, where A$_1$ and A$_2$ are the community matrices of the two randomly chosen assembled competition communities, where C is a matrix of random competition coefficients, and where the superscript T denotes the transpose operation. Since each species is now suffering competition from twice as many interspecies competitors for the implicitly limited resources, extinctions are again almost certain to occur, causing a post-mixing sequence of competitive exclusions that will produce an equilibrium with member species selected from each of the two initial communities of 5 species.

Results

Two thousand trial tournaments are run with the *assembled set* and the *random set* to compare the asymmetry of the final species comparison. At equilibrium, the resulting community can be characterized by the number of species from the first and second community—e.g., 2:3 stands for two from one community and three from the other. I consider outcomes of 5:0, 4:0, 5:1, and 4:1 to be asymmetrical and other combinations to be symmetrical. Table 1 shows the contingency table of the results ($x^2 > 400$, df $= 1$, and $P < 0.0001$). For the assembled set, 138 results are all five from one of the five-species communities, and zero from the other. In only 1 case of 2000 does this arise from the random set.

Discussion

Clearly, there are many different ways to perform such computer analyses. A more exhaustive investigation in which the sizes of the communities, the strengths of the interactions, the covariation of within-set α_{ij} values, and a number of other properties are varied will be reported elsewhere (M.G. and T. J. Case, unpublished data). However, all preliminary investigations underscore the robustness of this conclusion: Assembled communities have a cohesiveness that empowers them to "do battle" against other such communities as a "team," with the result that one or the other team may prevail completely.

There is thus a parallel between natural experiments deciphered from the fossil record and mathematical dynamics of competition systems. Abstract mathematics do not, of course, explain historical events. But the surprising concordance of these two very different realms of ecological investigation certainly calls for further investigations.

This result also warns us about the character of biodiversity loss we face from some kinds of landscape modification. To the extent we join the ecological system by building canals,

Table 1. Simulation results

Trial	Random	Assembled
Asymmetrical	141	587
Symmetrical	1859	1413

Shown are the number of trials out of 2000 that are characterized as asymmetrical (4 or 5 from one community and 0 or 1 from the other) or symmetrical (all other cases).

adding transportation corridors, cutting mountain passes, re-routing rivers, and the like, we risk extinctions that are not obvious from one-on-one competition but that are mediated through a network of community interactions in which indirect effects dominate. Once started, the consequences of faunal mixing will be hard to predict and harder to control.

1. Roughgarden, J. (1987) *Evolution* **41**, 1130–1134.
2. Pimm, S. L. (1985) in *Conservation of Island Birds: Studies for the Management of Threatened Species*, ed. Moors, P. J. (Cambridge Univ. Press, Cambridge, U.K.).
3. Case, T. J. (1990) *Proc. Natl. Acad. Sci. USA* **87**, 9610–9614.
4. Vermeij, G. J. (1991) *Science* **253**, 1099–1104.
5. May, R. M. (1973) *Stability and Complexity in Model Ecosystems* (Princeton Univ. Press, Princeton, NJ).
6. Gilpin, M. E. & Case, T. J. (1976) *Nature (London)* **261**, 40–42.