Compensatory dynamics are rare in natural ecological communities

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In population ecology, there has been a fundamental controversy about the relative importance of competition-driven (density-dependent) population regulation vs. abiotic influences such as temperature and precipitation. The same issue arises at the community level; are population sizes driven primarily by changes in the abundances of cooccurring competitors (i.e., compensatory dynamics), or do most species have a common response to environmental factors? Competitive interactions have had a central place in ecological theory, dating back to Gleason, Volterra, Hutchison and MacArthur, and, more recently, Hubbell's influential unified neutral theory of biodiversity and biogeography. If competitive interactions are important in driving year-to-year fluctuations in abundance, then changes in the abundance of one species should generally be accompanied by compensatory changes in the abundances of others. Thus, one necessary consequence of strong compensatory forces is that, on average, species within communities will covary negatively. Here we use measures of community covariance to assess the prevalence of negative covariance in 41 natural communities comprising different taxa at a range of spatial scales. We found that species in natural communities tended to covary positively rather than negatively, the opposite of what would be expected if compensatory dynamics were important. These findings suggest that abiotic factors such as temperature and precipitation are more important than competitive interactions in driving year-to-year fluctuations in species abundance within communities.

biological interactions | community dynamics | negative covariance | neutral models | zero-sum

A foundational controversy in ecology has centered on the long-term stability of population and community abundance, sometimes called "the balance of nature" (1). Darwin's famous "struggle for existence" on the "entangled bank" poetically expressed Thomas Malthus' principal idea that species' capacity to reproduce greatly exceeds their resources (2). Hence, fierce competition should structure the species and assemblages we see today. Similarly, papers in the 1920s–1950s presented the view that population abundances fluctuate much less than their intrinsic rates of increase would allow (3–5). This observation suggested to early ecologists that populations were regulated by density-dependent factors, and that competition was the most plausible underlying mechanism. In contrast, other authors emphasized abiotic environmental factors as the primary drivers of population fluctuations, often largely in the absence of competition (6–9). Recurring debates about the relative importance of biotic regulation vs. abiotic forcing have been dubbed "ecology's 12-year cycle" (1, 10).

The same set of issues applies at the community level. Diamond (11), Tilman (12, 13), and Wisheu and Keddy (14), among others, have presented models of plant community structure based on the relative competitive abilities of community members. More recently, Hubbell's (15) unified neutral theory of biodiversity and biogeography similarly, ". . . rests on a key first principle, namely that the interspecific dynamics of ecological communities is a stochastic zero-sum game" (16). That is, the total number of individuals in a community is constant or at least only stochastically varying.

Yet, Cooper (1) points out that arguments about the balance of nature, "attempt to settle questions about what kinds of ecological factors are most important, as determinants of demographic behavior and/or community structure, from a largely *a priori* perspective, with at best a smattering of empirical cases sprinkled in for good measure." For example, in Hubbell's book (15), support for the zero-sum assumption comes in the form of: (*i*) an empirical linear relationship between the size of the sampling unit (SU) and the number of individual trees found on a 50-hectare plot on Barro Colorado Island, Panama; and (*ii*) logical arguments based on finite resources. The empirical relationship is unconvincing because, whereas a positive area–abundance relationship is necessary in a world where biological communities are saturated, it is certainly not sufficient. Hubbell's (15) logical arguments about communities resemble Lack's arguments about individual populations: "Limiting resource availability per unit area will ultimately impose a finite limit on the density of competing organisms within a given ecological community in a defined space". This argument works only if communities are assumed always to be at or near carrying capacity. Hubbell ends this discussion with the statement of a general principle, that "large landscapes are essentially always

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Abbreviation: SU, sampling unit.

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