

The dual nature of community variability

F. Micheli¹, K. L. Cottingham^{1,2}, J. Bascompte¹, O. N. Bjørnstad^{1,3}, G. L. Eckert⁴, J. M. Fischer⁵, T. H. Keitt¹, B. E. Kendall¹, J. L. Klug⁶ and J. A. Rusak⁷

¹National Center for Ecological Analysis and Synthesis, 735 State St., Suite 300, Santa Barbara, CA 93101-5504 (micheli@nceas.ucsb.edu). ²Present address: Dept of Biological Sciences, Dartmouth College, Hanover, NH 03755, USA. ³Univ. of Oslo, Div. of Zoology, Dept of Biology, Oslo, Norway. ⁴Dept of Ecology, Evolution, and Marine Biology, Univ. of California, Santa Barbara, CA 93106, USA. ⁵Section of Ecology and Systematics, Cornell Univ., Ithaca, NY 14853, USA. ⁶Dept of Zoology, Univ. of Wisconsin, Madison, WI 53706, USA.

⁷Dept of Biology, York Univ., Toronto, ON, Canada M3J 1P3.

Community variability has a dual nature. On the one hand, there is compositional variability, changes in the relative abundance of component species. On the other hand, there is aggregate variability, changes in summary properties such as total abundance, biomass, or production. Although these two aspects of variability have received much individual attention, few studies have explicitly related the compositional and aggregate variability of natural communities. In this paper, we show how simultaneous consideration of both aspects of community variability might advance our understanding of ecological communities.

We use the distinction between compositional and aggregate variability to develop an organizational framework for describing patterns of community variability. At their extremes, compositional and aggregate variability combine in four different ways: (1) stasis, low compositional and low aggregate variability; (2) synchrony, low compositional and high aggregate variability; (3) asynchrony, high compositional and high aggregate variability; and (4) compensation, high compositional and low aggregate variability. Each of these patterns has been observed in natural communities, and can be linked to a suite of abiotic and biotic mechanisms. We give examples of the potential relevance of variability patterns to applied ecology, and describe the methodological developments needed to make meaningful comparisons of aggregate and compositional variability across communities. Finally, we provide two numerical examples of how our approach can be applied to natural communities.

Ecological communities vary through time. Everyone, scientist and layman alike, is aware of this fact, and it is not surprising that community variability has been a focus of many theoretical and empirical studies (May 1974, McNaughton 1977, Connell and Sousa 1983, Pimm 1984, 1991). To date, ecologists have focused primarily on the causes and consequences of variability.

For example, studies have explored the environmental forces that drive biotic variability (Chesson 1990); changes in variability among taxa and across gradients of productivity, latitude, and elevation (Connell and Sousa 1983, Duarte 1989, Crowley and Johnson 1992); and the implications of variability for population and community persistence (Pimm 1991). However, ecologists have placed little emphasis on variability as a source of information about community dynamics; the challenge is to learn how to decipher that message. Therefore, we need conceptual models for describing patterns of variability and empirical approaches for relating these patterns to ecological mechanisms.

A starting point for learning from variability is to consider that there are two main dimensions of community variability. On the one hand, there is *compositional variability*, changes in the relative abundance of component species. It is clear that the species composition of some communities changes more through time than the species composition of others. For example, the community composition of annual herbs on a forest floor changes a great deal more from year to year than the community composition of the trees, though the different spatial and temporal scales of the community dynamics of herbs and trees are likely to confound this comparison (see Methodological issues). On the other hand, there is *aggregate variability*. Unlike compositional variability, aggregate variability is not concerned with individual species, but rather with changes in variables created by combining multiple species, such as total abundance, production, or biomass. Suppose that the densities of particular aphid species in a meadow vary widely from year to year, while the total density of

This paper was drafted during a collaborative working group at NCEAS. Editing and preparation for final submission were coordinated by the first two authors.

all aphids stays constant. If we were interested in the potential impact of aphids on plants, we might be tempted to claim that this community has low variability, since the number of aphids remains constant from year to year. However, if we were interested in the relative abundance of the component species, we might say that this community is highly variable. Thus, the same community may be classified as having either low or high variability, depending on whether the focus is on the dynamics of the constituent species or on the dynamics of aggregate properties that describe the community as a whole.

Explicitly distinguishing between compositional and aggregate variability may help to resolve some long-standing controversies in community ecology. For example, ecologists have long speculated on whether more diverse communities are more stable (Elton 1958, Goodman 1975, McNaughton 1977, Lawton and Brown 1993). May (1974) suggested that more species-rich communities tend to be less stable, while recent empirical studies have suggested the opposite (Tilman and Downing 1994, Tilman 1996, McGrady-Steed et al. 1997). These two viewpoints are not necessarily contradictory: May (1974) dealt with compositional variability, while these more recent studies have focused on aggregate variability. Thus, diversity may increase the stability of the aggregate (Doak et al. 1998, Tilman et al. 1998) without changing the stability of the components (Tilman 1996).

In addition to explicitly distinguishing between aggregate and compositional variability, exploring the relationship between these two facets of community variability could be quite informative. However, this is not something that is commonly done: to date, most ecological studies have not explicitly related aggregate and compositional variability. We reviewed 439 abstracts from *Ecology* as a subsample from the recent literature (1 Jan. 1985–14 Apr. 1998). Of the 70 studies which examined variability in community composition or aggregate parameters, most measured either compositional (53%) or aggregate (17%) variability. Twenty one studies measured both compositional and aggregate variability, but only two of these combined them explicitly (Silvertown et al. 1994, Tilman 1996). Below, we develop an organizational framework for describing patterns of community variability that may facilitate simultaneous consideration of both compositional and aggregate variability. Hanski (1990) proposed a similar classification of communities based on the average level of variability in the species and on the concordance of their temporal abundance changes.

Relating the two facets of community variability

To facilitate the explicit consideration of aggregate and compositional variability, we place communities in a

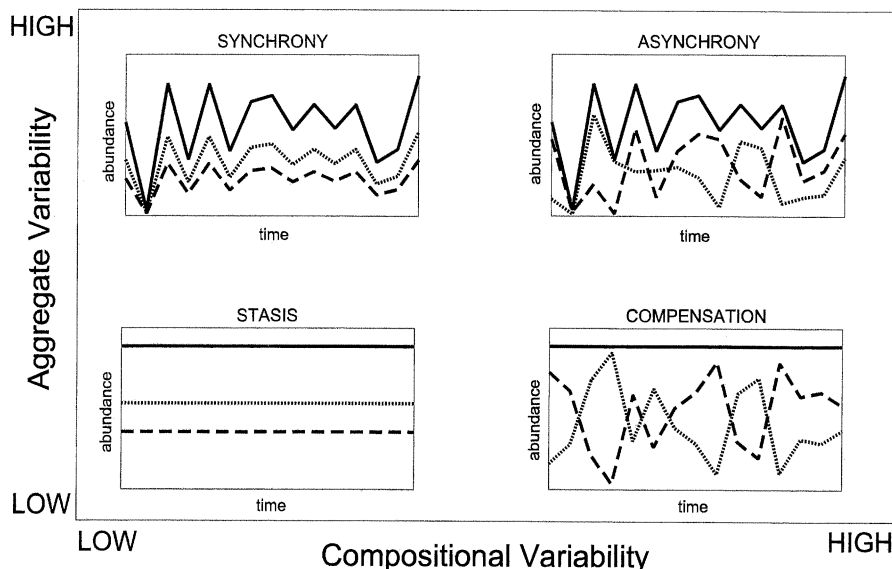


Fig. 1. A framework for explicitly considering the dual nature of community variability, where aggregate variability and compositional variability appear along independent axes of a two-dimensional space. The small sub-figures represent four idealized communities in which the dotted and dashed lines are time series for the abundance of two different species, and the solid line is the time series of the total abundance. The relative abundance of the two species is constant in the communities on the left (synchrony and stasis), and variable in those on the right (asynchrony and compensation). Total abundance is constant in the communities on the bottom (stasis and compensation) and variable in those on the top (synchrony and asynchrony). Of course, it is highly unlikely that either the aggregate or compositional variability of natural communities will ever be zero; thus, for natural communities, we think of the extremes as being “low variability” and “high variability”, rather than “constant” and “variable”.

Table 1. Scenarios and mechanisms that result in the variability patterns described in Fig. 1. Note that there is no one-to-one correspondence between mechanisms and patterns, or vice versa.

Pattern	Mechanism	Type	Example	Reference
Synchrony	Parallel responses to abiotic driver	Abiotic	Desert annuals and precipitation	Guo and Brown (1997)
	Consumers track resources with no time lags	Biotic	Raptors and rodents	Korpimäki (1994)
	Ecosystem engineering with parallel (either positive or negative) effects	Abiotic/Biotic	Marine polychaete and substrate	Woodin and Marinelli (1991)
Asynchrony	Species responding to different abiotic drivers	Abiotic	Freshwater phytoplankton and multiple limiting resources	Hutchinson (1961)
	Lotka-Volterra consumer-resource interactions	Biotic	Protozoan predator-prey system	Gause (1934)
	Species have opposite responses to abiotic drivers	Abiotic	Rocky intertidal invertebrates and temperature	Barry et al. (1995)
Compensation	Consumer-resource interactions with out-of-phase population cycles	Biotic	Adult azuki bean weevil and larval parasite	Utida (1957)
	Competitive release following abiotically driven decline in dominant competitor	Abiotic/Biotic	Freshwater zooplankton and lake acidification	Fischer (1997)
	Ecosystem engineering with differing (both positive and negative) effects	Abiotic/Biotic	Beaver impacts via changes in water level	Pollock et al. (1995)
	Lottery-type competition	Abiotic/Biotic	Tropical reef fish and settlement space	Sale (1977, 1978)
Stasis	Succession	Abiotic/Biotic	Temperate forests and limiting resources	Miles (1981)
	Consumer-resource interactions involving strong consumer self-limitation	Biotic	Red grouse and heather	Watson and Moss (1972)
	Strong competitive interactions in a Clementsian climax community	Biotic	Temperate forest	Clements (1916)

coordinate system defined by these two properties (Fig. 1). This framework is based on the hypothesis that community composition can vary independently of the aggregate properties. We identify four extreme patterns of community variability that occur at the corners of this two-dimensional space: (1) *stasis*, low compositional and low aggregate variability; (2) *synchrony*, low compositional and high aggregate variability; (3) *asynchrony*, high compositional and high aggregate variability; and (4) *compensation*, high compositional and low aggregate variability. Stasis and asynchrony occur when there is little covariance among constituent species, while synchrony and compensation result from strong positive and strong negative covariance among species, respectively.

Ecologists have previously recognized that each of these scenarios can occur (Strong et al. 1984, Hanski 1990), but have recently focused on the pattern we have called compensation because of its implications for the maintenance of ecosystem function despite changes in species abundance (Schindler 1990, Walker 1992, Lawton and Brown 1993, Frost et al. 1995, Walker 1995, Peterson et al. 1998). Alternative terms for compensation include ecological redundancy (Walker 1992),

functional redundancy (Walker 1995), and functional complementarity (Frost et al. 1995). Although there is clear evidence of compensation in some communities (Prins and Douglas-Hamilton 1990, Schindler 1990, Howarth 1991, Johnson and Mayeux 1992, Lawton 1994, Frost et al. 1995, Pratt and Cairns 1996, Fischer 1997), we have not yet determined the extent of compensatory dynamics in natural communities.

However, compensation is only one of the possible patterns of community variability (Fig. 1). We explicitly consider all possible combinations of low and high aggregate and compositional variability, as well as the mechanisms that might produce each scenario. Future studies should determine the frequency with which each pattern occurs in natural communities, as well as the conditions that tend to lead to a particular pattern.

Causal mechanisms

The four community variability scenarios, stasis, synchrony, asynchrony and compensation, can result from a variety of biological mechanisms (Table 1). For example, stasis can result from strong consumer self-limita-

tion (Lack 1954) or strong competitive interactions (Clements 1916), particularly in a relatively stable environment. Synchrony can occur when each species in a community responds similarly to seasonal or long-term changes in abiotic factors (Guo and Brown 1997) or when there are strong positive interactions among species. Asynchrony can result from complex species-specific responses to abiotic factors (Gleason 1926, Hutchinson 1961) or time lags in consumer-resource interactions (Gause 1934). Finally, compensation can occur when the dominant competitor in a community is negatively affected by some abiotic factor, allowing competitive inferiors to increase in abundance due to competitive release (Lawton and Brown 1993, Fischer 1997).

Below, we detail some specific examples of how particular abiotic and biotic mechanisms generate different patterns of variability. These examples highlight the tendency of certain mechanisms to push the pattern of community variability towards one of the four corners in Fig. 1.

Single abiotic and biotic mechanisms

Rainfall patterns are a powerful abiotic force that appears to cause seasonal synchrony in desert annual plant communities in the Chihuahuan Desert. Guo and Brown (1997) show that winter annuals germinate in response to autumn rains, and a non-overlapping set of summer annuals germinates in response to summer rains. Overall interannual variability in community composition is low because all species are synchronized to germinate in one of two seasons, whereas aggregate variability is high because of interannual variation in rainfall (see Fig. 3 in Guo and Brown 1997).

Consumer-resource interactions provide interesting case studies for biotic mechanisms because the time lag between the consumer and the resource will determine the observed pattern of community variability. With no time lag, the community may be synchronous, as exemplified by a Scandinavian raptor-rodent community in which a local increase in rodent abundance is followed by a nearly instantaneous increase in raptor abundance (Korpimäki 1994). However, there is usually a time delay between consumers and their resource. In a Lotka-Volterra model, for example, a time lag may result in compensatory dynamics if the lag leads to fluctuations that are perfectly out-of-phase. Interactions between the adult azuki bean weevil and its larval parasite appear to lead to this pattern of compensation (Utida 1957). In contrast, both compositional and aggregate variability are likely to be high in systems with an intermediate time lag because the components will fluctuate slightly out-of-phase. The predator-prey relationship between the protozoans *Paramecium* and *Didinium* is a classic example of this asynchrony (Gause 1934).

Combinations of biotic and abiotic mechanisms

Variability patterns of real communities are likely to be affected by both biotic and abiotic factors. For example, multiple abiotic factors appear to combine with biotic interactions to determine community structure in the 90-yr Park Grass Experiment (Silvertown et al. 1994). Although rainfall was a major determinant of total plant biomass in this experiment, asymmetric competition magnified the effect of rainfall and altered species composition. Overall, species composition was considerably more variable than total biomass (Silvertown et al. 1994, Dodd et al. 1995). Succession in terrestrial forests is another example of a combination of biotic and abiotic mechanisms. In hardwood forests, initial colonists are often shaded by later-arriving hardwood species. Hardwoods in turn may change the soil environment, favoring one group of species and inhibiting another (Miles 1981, 1987). Thus, in communities undergoing succession, aggregate variability might be low while the community composition varies strongly. In both of these examples, the interplay of biotic and abiotic processes leads to compensation; however, in other communities, abiotic and biotic factors might combine differently (Table 1).

Linking mechanisms to variability patterns

Understanding the mechanisms that underlie the dynamics of multi-species communities is one of the biggest challenges in ecology. Because most ecological communities contain many interacting species, each of which may be affected by multiple biotic and abiotic factors, there are likely to be many ways in which we can attribute mechanisms to patterns of variability. There is no simple one-to-one relationship between patterns of variability and underlying mechanisms (Table 1). In natural communities with multiple and possibly diffuse interactions, experimental manipulations of species assemblages are needed to link mechanisms with different variability patterns. Simulation studies may also be a means of elucidating the relationship between mechanisms and patterns of variability; see Doak et al. (1998) for an example of how simulation might be used to elucidate the effects of different mechanisms on aggregate variability.

Implications for applied ecology

Explicit consideration of compositional and aggregate variability may be useful to species conservation, ecosystem management and restoration, and environmental monitoring. For example, changes in patterns of community variability may be used to classify different kinds of perturbations. Odum (1985) suggested that

perturbations increase the variability of ecological systems, but did not specify in what way variability might change. However, there is evidence to suggest that different perturbations may cause community variability to change in different ways. In lakes, for example, acidification appears to alter the variability of zooplankton community composition but not the variability of total zooplankton biomass (Schindler 1990, Frost et al. 1995, Fischer 1997), while eutrophication tends to alter the variability of total phytoplankton biomass without increasing phytoplankton compositional variability (Cottingham and Carpenter 1998).

To effectively manage ecosystems, we need to be able to distinguish between contrasting patterns of community variability (Cairns 1992). Specifically, it would be useful to know whether to expect changes in aggregate variability, compositional variability, both, or neither. For example, anticipating fluctuations in aggregate variates may allow managers to set quotas on how much plant or animal biomass can be harvested, whereas variability in relative community composition may influence extinction risk and determine what species should be made available for harvest. We believe that extensive cross-system comparisons of responses to different perturbations might aid in developing general expectations for how perturbations affect community variability. However, there are several important issues that need to be considered in order to ensure that the variability patterns of different communities are compared in meaningful ways.

Methodological issues

Although in principle it is possible to evaluate the compositional and aggregate variability of any assemblage, in reality the location of a particular community in variability space will be sensitive to the particular methodological criteria used to quantify variability. In this section, we show how variability patterns may be affected by how the community is delineated, the temporal and spatial scale of sampling, and the metric used to quantify variability.

Delineating a community

The concept of a "community" has been defined in many different ways in the ecological literature (Underwood 1986, Paine 1994). Examples include the members of a guild, multiple functional groups, a trophic pyramid, and other arbitrarily defined groups of taxa. Choice of a particular assemblage is likely to determine what kind of biological interactions, and thus what mechanisms, underlie the observed pattern of variability. For example, assemblages that are

structured by vertical trophic chains vs horizontal competitive interactions are likely to exhibit different patterns of variability. A community with predator-prey interactions could have near-perfect synchrony if variation at the bottom of the trophic chain cascades upward such that each species changes in lock-step (Table 1). On the other hand, a community with largely competitive species interactions might show compensation if changes in the abundance of some species are offset by changes in other species (Table 1). Whether the set of species included in a study is dominated by vertical trophic chains or horizontal competitive interactions will depend on how the researcher chooses to delineate the community. Therefore it will be important to use a consistent definition of community when making cross-system comparisons.

Scale issues: space and time

Effective cross-system comparisons will also require attention to differences that occur simply because variability is quantified over different spatial or temporal scales (Frost et al. 1988, Levin 1992). For example, increases in spatial scale can increase sample extent, which may reduce sampling error (Bascompte and Solé 1998). However, increasing the temporal extent of sampling may have the opposite effect, since longer time series appear to have higher variability than shorter time series (Gaston and McArdle 1994). Temporal scale can also be a complication when the communities to be compared have very different generation times; for example, approaches for comparing the dynamics of annual plants to the dynamics of long-lived trees need to be developed. In addition, sampling over a broad spatial or temporal scale might lead to the inclusion of two or more dynamically independent assemblages, obfuscating the variability patterns of each assemblage. Clearly, accurate cross-system comparisons will require advances in our understanding of how variability patterns change with scale.

Variability metrics

Another issue in the exploration of community variability is deciding on appropriate metrics to quantify compositional and aggregate variability from data on natural communities. For aggregate variability, there are a few obvious choices because the univariate measures developed for individual populations (Gaston and McArdle 1994) may be suitable metrics. Examples include the standard deviation (possibly after log-transformation) and coefficient of variation (standard

deviation/mean) of time series for total biomass, abundance or productivity (Gaston and McArdle 1994). For compositional variability, there is a whole suite of metrics for quantifying differences in species composition, including rank concordance, similarity/distance indices, and summary statistics from ordination and cluster analysis. Although comprehensive reviews of these measures exist (Legendre and Legendre 1983, Washington 1984, Gower and Legendre 1986, Rahel 1990), none as yet has evaluated what metrics work best for temporal data. Thus, development and testing of metrics for compositional variability should be a central focus of future research.

Examples: effects of perturbations on community variability

In this final section, we provide examples of how aggregate and compositional variability may be compared in real communities. Example 1 (Fig. 2A, B) represents annual harvest data for four species of small game from Gävleborg County, central Sweden (Small et al. 1993). These species, the European hare and three species of birds, are central prey items for the red fox, which is known to regulate their numbers (Lindström et al. 1994). A disease greatly decreased the abundance of foxes in the late 1970's through most of 1980's. We quantified the inter-annual pattern of community variability in this assemblage of prey species eight years before (1971–1978) and eight years after (1981–1988) the reduction in fox abundance. Although there is a visible increase in interannual variability in total prey abundance after the decline in foxes (Fig. 2A), the relative proportions of the different species remained remarkably constant (Fig. 2B).

Example 2 (Fig. 2C, D) uses data from a zooplankton assemblage in a lake that was invaded by an exotic planktivorous cladoceran (*Bythotrephes cederstroemi*) around 1993 (Yan and Pawson 1997). We quantified the pattern of community variability in the three summers before (1990–1992) and three summers after (1993–1995) the invasion using abundance data from eight functional groups created by pooling species of similar sizes and trophic modes. Zooplankton community composition, particularly of subdominant groups, changed markedly after the invasion (Fig. 2D), while zooplankton total abundance changed much less (Fig. 2C).

We calculated compositional and aggregate variability for these two examples, then compared them using the framework developed in Fig. 1. We measured aggregate variability using the coefficient of variation of abundance calculated over all censuses. We measured compositional variability using the

mean Euclidean distance between sequential observations, where the distance was calculated by comparing the relative abundance of each species in successive samples, then summing across species. These measures were chosen from a long list of possible metrics for demonstration purposes, and may not be the most suitable metrics.

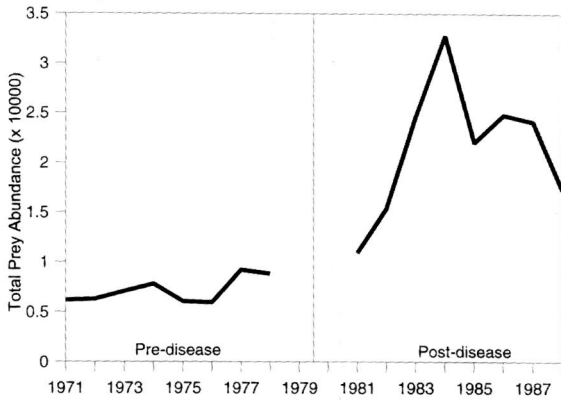
Patterns of variability were different before vs after perturbation in both communities (Fig. 2E). Both predator decline and exotic invasion tended to increase aggregate variability, although increases in variability due to the invasion were quite small. Interestingly, these perturbations appeared to have opposite effects on compositional variability such that the predator decline decreased compositional variability, while the exotic invasion increased it. These examples illustrate that compositional and aggregate variability can show contrasting responses to the same perturbation, and that different perturbations can change community variability in different ways. As noted above in Implications for applied ecology, widescale comparisons of many perturbations could generate expectations for how particular perturbations affect patterns of community variability.

Summary

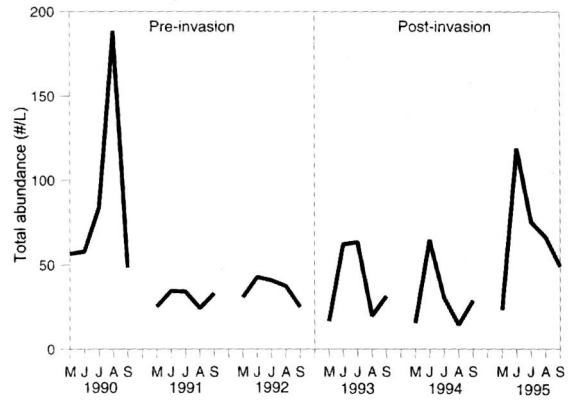
In this paper, we advocate a comprehensive representation of community variability that involves the simultaneous consideration of both compositional and aggregate variability, and suggest that relating these two aspects of community variability is a first step towards learning from community variability. We propose that using both aggregate and compositional variability as response variables in experiments, simulation studies, and cross-system comparisons will increase our basic understanding of ecological communities and make valuable contributions to resource management.

Acknowledgements – We thank P. Kareiva for his support and constructive criticism throughout this project. Our ideas about variability have been shaped by conversations with W. Fagan, T. Frost, M. Holyoak, A. Ives, P. Kareiva, A. Liebhold, W. Murdoch, G. Russell, E. Seabloom, K. Somers, J. Thompson, N. Yan, and the NCEAS Community Dynamics Working Group. Data for our real-world examples were graciously provided by N. Yan and T. Willebrand. Reviews of the manuscript were provided by T. Frost, A. Ives, P. Kareiva, W. Murdoch, E. Seabloom, J. Thompson, E. Borer, R. Bolser, V. Boucher, R. Burton, L. Goldwasser, W. Gram, S. Harpole, I. Hanski, C. Parmesan, G. Russell, and F. Wagner. Finally, and quite importantly, our synthetic efforts were made possible by the creative environment and the financial support of the National Center for Ecological Analysis and Synthesis, a center funded jointly by the National Science Foundation, the State of California, and the Univ. of California at Santa Barbara.

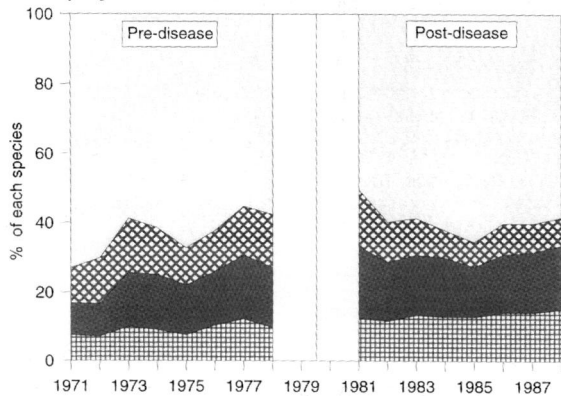
A. Fox prey: total abundance



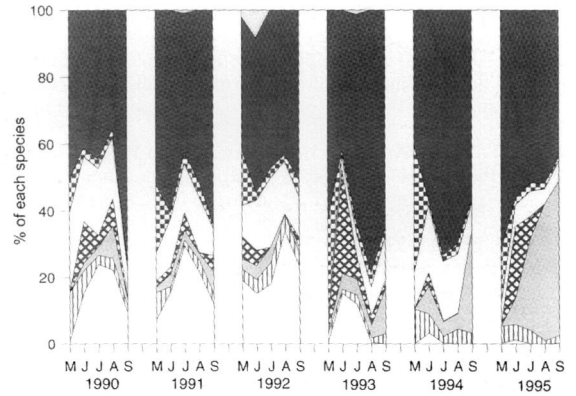
C. Crustacean zooplankton: total abundance



B. Fox prey: relative abundance



D. Crustacean zooplankton: relative abundance



E. Fox prey & crustacean zooplankton in variability space

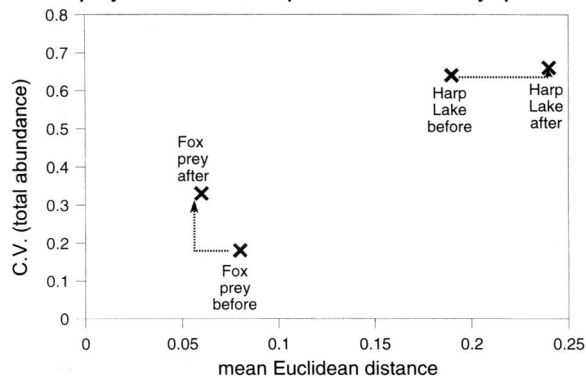


Fig. 2. Examples of changes in community variability with perturbation. A. Total abundance of fox prey, contrasted before and after a disease severely impacted fox abundances. Data for 1979 and 1980 are not included because the fox abundance was intermediate during this period. B. Relative abundance of four fox prey through time; each shading pattern indicates a different prey species. C. Total abundance of crustacean zooplankton from Harp Lake, contrasted before and after the invasion of an exotic zooplanktivore, *Bythotrephes cederstroemi*, in May–September of each year. D. Relative abundance of eight functional groups of crustacean zooplankton; as in B, each shading pattern indicates a different functional group. E. Aggregate and compositional variability of the fox prey and crustacean zooplankton before vs after perturbation.

References

Barry, J. P., Baxter, C. H., Sagarin, R. D. and Gilman, S. E. 1995. Climate-related, long-term faunal changes in a California rocky intertidal community. – *Science* 267: 672–675.
 Bascompte, J. and Solé, R. V. (eds) 1998. Modeling spatiotemporal dynamics in ecology. – Springer-Verlag, Berlin.
 Cairns, J. 1992. Monitoring for global change. – In: Cairns, J.,

Jr., Niederlehner, B. R. and Orvos, D. R. (eds), Predicting ecosystem risk. Princeton Scientific, Princeton, NJ, pp. 63–75.
 Chesson, P. L. 1990. Geometry, heterogeneity and competition in variable environments. – *Philos. Trans. R. Soc. Lond. B* 330: 165–173.
 Clements, F. E. 1916. Plant succession: analysis of the development of vegetation. – *Carnegie Inst. Wash. Publ.* 242: 1–512.

- Connell, J. H. and Sousa, W. P. 1983. On the evidence needed to judge ecological stability or persistence. – *Am. Nat.* 121: 789–824.
- Cottingham, K. L. and Carpenter, S. R. 1998. Population, community, and ecosystem variates as ecological indicators: phytoplankton responses to whole-lake enrichment. – *Ecol. Appl.* 8: 508–530.
- Crowley, P. H. and Johnson, D. M. 1992. Variability and stability of a dragonfly assemblage. – *Oecologia* 90: 260–269.
- Doak, D. F., Bigger, D., Harding, E. K., Marvier, M. A., O'Malley, R. E. and Thomson, D. 1998. The statistical inevitability of stability-diversity relationships in community ecology. – *Am. Nat.* 151: 264–276.
- Dodd, M., Silvertown, J., McConway, K., Potts, J. and Crawley, M. 1995. Community stability: a 60-year record of trends and outbreaks in the occurrence of species in the Park Grass Experiment. – *J. Ecol.* 83: 277–285.
- Duarte, C. M. 1989. Temporal biomass variability and production/biomass relationships of seagrass communities. – *Mar. Ecol. Prog. Ser.* 51: 269–277.
- Elton, C. S. 1958. The ecology of invasions by animals and plants. – Chapman and Hall, New York.
- Fischer, J. M. 1997. Zooplankton community responses to acidification: the role of rapid evolution and compensatory dynamics. – Dissertation, Univ. of Wisconsin, Madison, WI.
- Frost, T. M., DeAngelis, D. L., Bartell, S. M., Hall, D. J. and Hurlbert, S. H. 1988. Scale in the design and interpretation of aquatic community research. – In: Carpenter, S. R. (ed.), *Complex interactions in lake communities*. Springer-Verlag, New York, pp. 229–258.
- Frost, T. M., Carpenter, S. R., Ives, A. R. and Kratz, T. K. 1995. Species compensation and complementarity in ecosystem function. – In: Jones, C. and Lawton, J. (eds), *Linking species and ecosystems*. Chapman and Hall, New York, pp. 224–239.
- Gaston, K. J. and McArdle, B. H. 1994. The temporal variability of animal abundances: measures, methods and patterns. – *Philos. Trans. R. Soc. Lond. B* 345: 335–358.
- Gause, G. F. 1934. The struggle for existence. – Williams and Wilkins, Baltimore, MD.
- Gleason, H. A. 1926. The individualistic concept of the plant association. – *Bull. Torrey Bot. Club.* 53: 7–26.
- Goodman, D. 1975. The theory of diversity-stability relationships in ecology. – *Q. Rev. Biol.* 50: 237–266.
- Gower, J. C. and Legendre, P. 1986. Metric and euclidean properties of dissimilarity coefficients. – *J. Classification* 3: 5–48.
- Guo, Q. and Brown, J. H. 1997. Interactions between winter and summer annuals in the Chihuahuan desert. – *Oecologia* 111: 123–128.
- Hanski, I. 1990. Density dependence, regulation and variability in animal populations. – *Philos. Trans. R. Soc. Lond. B* 330: 141–150.
- Howarth, R. W. 1991. Comparative responses of aquatic ecosystems to toxic chemical stress. – In: Cole, J. J., Lovett, G. and Findlay, S. (eds), *Comparative analyses of ecosystems: patterns, mechanisms, and theories*. Springer-Verlag, New York, pp. 169–195.
- Hutchinson, G. E. 1961. The paradox of the plankton. – *Am. Nat.* 95: 137–145.
- Johnson, H. B. and Mayeux, H. S. 1992. Viewpoint: a view on species additions and deletions and the balance of nature. – *J. Range Manage.* 45: 322–333.
- Korpimäki, E. 1994. Rapid or delayed tracking of multi-annual vole cycles by avian predators? – *J. Anim. Ecol.* 63: 619–628.
- Lack, D. L. 1954. The natural regulation of animal numbers. – Clarendon Press, Oxford.
- Lawton, J. H. 1994. What do species do in ecosystems? – *Oikos* 71: 367–374.
- Lawton, J. H. and Brown, V. K. 1993. Redundancy in ecosystems. – In: Schulze, E. D. and Mooney, H. A. (eds), *Biodiversity and ecosystem function*. Springer-Verlag, Berlin, pp. 255–270.
- Legendre, L. and Legendre, P. 1983. *Numerical Ecology*. – Elsevier, Amsterdam.
- Levin, S. A. 1992. The problem of pattern and scale in ecology. – *Ecology* 73: 1943–1967.
- Lindström, E. R., Andrén, H., Angelstam, P., Cederlund, G., Hörnfeldt, B., Jäderberg, L., Lemnell, P.-A., Martinsson, B., Sköld, K. and Swenson, J. E. 1994. Disease reveals the predator: sarcoptic mange, red fox predation, and prey populations. – *Ecology* 75: 1042–1049.
- May, R. M. 1974. *Stability and complexity in model ecosystems*. – Princeton Univ. Press, Princeton, NJ.
- McGrady-Steed, J., Harris, P. M. and Morin, P. J. 1997. Biodiversity regulates ecosystem predictability. – *Nature* 390: 162–165.
- McNaughton, S. J. 1977. Diversity and stability of ecological communities: a comment on the role of empiricism in ecology. – *Am. Nat.* 111: 515–525.
- Miles, J. 1981. *Effect of birch on moorlands*. – Institute of Terrestrial Ecology, London.
- Miles, J. 1987. Vegetation succession: past and present perceptions. – In: Gray, A. J., Crawley, M. J. and Edwards, P. J. (eds), *Colonization, succession, and stability*. Blackwell Scientific, Oxford, pp. 1–29.
- Odum, E. P. 1985. Trends expected in stressed ecosystems. – *BioScience* 35: 419–422.
- Paine, R. T. 1994. Marine rocky shores and community ecology: an experimentalist's perspective. – Ecology Institute, Oldendorf, Luhe.
- Peterson, G., Allen, C. R. and Holling, C. S. 1998. Ecological resilience, biodiversity, and scale. – *Ecosystems* 1: 6–18.
- Pimm, S. L. 1984. The complexity and stability of ecosystems. – *Nature* 307: 321–326.
- Pimm, 1991. *The balance of Nature*. – Univ. of Chicago Press, Chicago.
- Pollock, M. M., Naiman, R. J., Erickson, H. E., Johnston, C. A., Pastor, J. and Pinay, G. 1995. Beavers as engineers: influences on biotic and abiotic characteristics of drainage basins. – In: Jones, C. G. and Lawton, J. H. (eds), *Linking species and ecosystems*. Chapman and Hall, New York, pp. 117–126.
- Pratt, J. R. and Cairns, J. 1996. Ecotoxicology and the redundancy problem: understanding effects on community structure and function. – In: Newman, M. C. and Jagoe, C. H. (eds), *Ecotoxicology: a hierarchical approach*. CRC Lewis, Boca Raton, FL, pp. 347–370.
- Prins, H. H. T. and Douglas-Hamilton, I. 1990. Stability in a multi-species assemblage of large herbivores in East Africa. – *Oecologia* 83: 392–400.
- Rahel, F. J. 1990. The hierarchical nature of community persistence: a problem of scale. – *Am. Nat.* 136: 328–344.
- Sale, P. F. 1977. Maintenance of high diversity in coral reef fish communities. – *Am. Nat.* 111: 337–359.
- Sale, P. F. 1978. Coexistence of coral reef fishes – a lottery for living space. – *Environ. Biol. Fishes* 3: 85–102.
- Schindler, D. W. 1990. Experimental perturbations of whole lakes as tests of hypotheses concerning ecosystem structure and function. – *Oikos* 57: 25–41.
- Silvertown, J., Dodd, M. E., McConway, K., Potts, J. and Crawley, M. 1994. Rainfall, biomass variation, and community composition in the Park Grass Experiment. – *Ecology* 75: 2430–2437.
- Small, R. J., Marcström, V. and Willebrand, T. 1993. Synchronous and nonsynchronous population fluctuations of some predators and their prey in central Sweden. – *Ecography* 16: 360–364.
- Strong, D. R., Lawton, J. H. and Southwood, R. 1984. *Insects on plants. Community patterns and mechanisms*. – Blackwell Scientific, Oxford.
- Tilman, D. 1996. Biodiversity: population versus ecosystem stability. – *Ecology* 77: 350–363.

- Tilman, D. and Downing, J. A. 1994. Biodiversity and stability in grasslands. – *Nature* 367: 363–365.
- Tilman, D., Lehman, C. L. and Bristow, C. E. 1998. Diversity-stability relationships: statistical inevitability or ecological consequence? – *Am. Nat.* 151: 277–282.
- Underwood, A. J. 1986. What is a community? – In: Raup, D. M. and Jablonski, D. (eds), *Patterns and processes in the history of life*. Springer-Verlag, Berlin, pp. 351–368.
- Utida, S. 1957. Population fluctuation, an experimental and theoretical approach. – *Cold Spring Harbor Symp. Quant. Biol.* 22: 139–151.
- Walker, B. H. 1992. Biodiversity and ecological redundancy. – *Conserv. Biol.* 6: 18–23.
- Walker, B. H. 1995. Conserving biological diversity through ecosystem resilience. – *Conserv. Biol.* 9: 747–752.
- Washington, H. G. 1984. Diversity, biotic and similarity indices: a review with special relevance to aquatic ecosystems. – *Water Res.* 18: 653–694.
- Watson, A. and Moss, R. 1972. A current model of population dynamics in red grouse. – In: Voous, K. H. (ed.), *Proceedings of the XVth International Ornithological Congress*, pp. 139–149.
- Woodin, S. A. and Marinelli, R. 1991. Biogenic habitat modification in marine sediments: the importance of species composition and activity. – In: Meadows, P. S. and Meadows, A. (eds), *The environmental impact of burrowing animals and animal burrows*. Oxford Univ. Press, Oxford, pp. 231–250.
- Yan, N. D. and Pawson, T. W. 1997. Changes in the crustacean zooplankton community of Harp Lake, Canada, following the invasion by *Bythotrephes cederstroemi*. – *Freshw. Biol.* 37: 409–425.