

A new look at the relationship between diversity and stability

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7.1 Introduction

The relationship between biodiversity and ecosystem functioning has emerged as one of the most exciting and controversial research areas in ecology over the last decade. Faced with the prospect of a massive, irreversible loss of biodiversity, ecologists have begun investigating the potential consequences of these dramatic changes in biodiversity for the functioning of natural and managed ecosystems. These investigations have been motivated by both the scientific challenge and the need to understand better the role biodiversity plays in providing sustainable ecological goods and services for human societies. An increasing amount of evidence suggests that changes in biodiversity can have adverse effects on the average rates of ecosystem processes such as primary production and nutrient retention in temperate grassland ecosystems (see chapters by Hector *et al.*, Chapter 4; Tilman *et al.*, Chapter 3; Wardle and van der Putten, Chapter 14). Most of this evidence, however, comes from relatively short-term experimental studies (see, however, Petchey *et al.*, Chapter 11) under controlled experimental conditions, which are little informative about sustainable functioning.

The temporal variability of natural environments over a broad spectrum of time scales from days to centuries (Halley 1996), as well as increasing anthropogenic pressures (Sala *et al.* 2000), inevitably generate temporal changes in both population sizes and ecosystem processes. It is therefore of considerable interest to understand how biodiversity loss will affect long-term temporal patterns in

ecosystem functioning. Will ecosystem functional properties and services become more variable and less predictable when species diversity is reduced? Are species-rich ecosystems more capable of buffering environmental variability and maintaining ecosystem processes within acceptable bounds than species-poor ecosystems?

To answer these questions appropriately and avoid 'reinventing the wheel', it is important to realize that they address in a new form a long-standing debate in ecology concerning the relationship between the complexity (loosely defined as a combination of species diversity and the number and strength of species interactions) and stability of ecological systems. The study of this relationship has had a long and controversial history (May 1974; Pimm 1984, 1991; McCann 2000). To delineate the differences between contemporary issues and the historical debate, we first briefly revisit the central components of this debate, and propose a new, integrated conceptual framework derived both from lessons from this debate and insights newly arising from current research on biodiversity and ecosystem functioning. We then examine, within this framework, how recent theoretical and experimental work provide new insights into the complexity–stability debate. Our treatment therefore complements some recent reviews of the topic (Loreau 2000a; McCann 2000; Schwartz *et al.* 2000; Cottingham *et al.* 2001) which have not used the framework we present. Finally, we discuss the need to develop new theoretical and methodological approaches and to strengthen

the link between theory and experiments in this area. We conclude with some implications for policy and management.

7.2 Historical and conceptual background

The early view that permeated ecology until the 1960s was that diversity (or complexity) begets stability. This view was formalized and theorized by people such as Odum (1953), MacArthur (1955) and Elton (1958) in the 1950s. Odum (1953) and Elton (1958) observed that simple communities are more easily upset than rich ones, i.e. they are more subject to destructive population oscillations and invasions. MacArthur (1955) proposed, using a heuristic model, that the more pathways there are for energy to reach a consumer, the less severe is the failure of any one pathway. These conclusions were based on either intuitive arguments or loose observations, but lacked a strong theoretical and experimental foundation. Probably because they represented the conventional wisdom ('don't put all your eggs in one basket') and the prevailing philosophical view of the 'balance of nature', they became almost universally accepted.

This 'conventional wisdom' was seriously challenged in the early 1970s by theorists such as Levins (1970), Gardner and Ashby (1970) and May (1972, 1974), who borrowed the formalism of deterministic autonomous dynamical systems from Newtonian physics and showed that, in these model systems, the more complex the system, the less likely it is to be stable. Stability here was defined qualitatively by the fact that the system returns to its equilibrium or steady state after a perturbation. The intuitive explanation for this destabilizing influence of complexity is that the more diversified and the more connected a system, the more numerous and the longer the pathways along which a perturbation can propagate within the system, leading to either its collapse or its explosion. This conclusion was further supported by analyses of one quantitative measure of stability, resilience (Table 7.1), in model food webs (Pimm and Lawton 1977; Pimm 1982). This theoretical work had a number of limitations. In particular, it

was based on randomly constructed model communities. More realistic food webs incorporating thermodynamic constraints and observed patterns of interaction strengths do not necessarily have the same properties (DeAngelis 1975; de Ruiter *et al.* 1990). Also, there have been few direct experimental tests of the theory, and many of the natural patterns that agree with theoretical predictions can be explained by more parsimonious hypotheses such as the trophic cascade model (Cohen and Newman 1985). Despite these limitations, the view that diversity and complexity beget instability, not stability, quickly became the new paradigm in the 1970s and 1980s because of the mathematical rigour of the theory.

There are other limitations in this theory which are critical for the questions that we address here. First, stability is really a meta-concept that covers a range of different properties or components. Summarizing the debate, Pimm (1984) recognized a number of these properties and concluded that the relationship between diversity and each of them need not be the same. In Table 7.1, we attempt a classification—albeit imperfect, as any classification—of the different components of stability, which includes more recent notions. Second, each of these stability properties can be applied to a number of variables of interest at different hierarchical levels, such as individual species abundance, community species composition, or ecosystem-level processes or properties (Table 7.1). Again, the relationship between diversity and any stability property may be different for different variables (Pimm 1984). This creates a large matrix of potential combinations of stability properties and variables of interest, of which the new theory concerned only a small part. Specifically, May's (1974) and Pimm's (1982) theory concerned the qualitative stability and resilience of communities as ensembles of populations, not ecosystem-level aggregate properties.

Third, the formalism of autonomous, deterministic dynamical systems, which describes a fixed set of variables with time-independent parameters, inherently excludes a number of phenomena that characterize biological and ecological systems. In particular, it does not allow for the fact that these systems are subject to continuous environmental changes at various temporal scales and have the