

# The complexity and stability of ecosystems

Stuart L. Pimm

Department of Zoology and Graduate Program in Ecology, University of Tennessee, Knoxville, Tennessee 37996, USA

*Early studies suggested that simple ecosystems were less stable than complex ones, but later studies came to the opposite conclusion. Confusion arose because of the many different meanings of 'complexity' and 'stability'. Most of the possible questions about the relationship between stability-complexity have not been asked. Those that have yield a variety of answers.*

ELTON<sup>1</sup> noted the dangers of human simplification of the natural environment if ecosystems become less stable as they become more simple. The consequence may be increasingly unstable populations leading to extinctions, further simplification and even more instability. That there might be a single relationship between such gross variables as stability and complexity is intriguing theoretically, in a field where generalizations are scarce. The evidence on this topic is controversial. Early theoretical studies were logically simplistic, if appealing, in suggesting that complex systems were more stable. Later theoretical studies were more sophisticated and suggested exactly the opposite. Field studies are, superficially, ambiguous and contradictory. I shall try here to resolve some of this controversy by pointing to several different definitions of stability, of complexity and of various ecological variables of interest. Several score permutations of these definitions are possible and different ones will yield different results. The earlier theoretical treatments and field studies typically address different combinations from those of later studies; in the few cases where they treat the same combination, there is often good agreement. Most combinations, however, have not been explored and very few have been studied extensively by both theoreticians and field workers.

Early studies<sup>1–4</sup> argued that increased complexity enhanced ecosystem stability. This seemed so certain that the idea became a central feature of ecology texts. Watt<sup>5</sup> makes one of his core principles of ecology ‘...the accumulation of biological diversity... promotes population stability’. Later studies<sup>6–21</sup> typically came to the opposite conclusion. To see why early confidence was misplaced is easy with hindsight. The first of Elton’s six arguments was a theoretical one: simple population models are characterized by oscillations; more complex models were expected to fluctuate less. Another theoretical argument, that of MacArthur<sup>2</sup>, was that the more pathways for energy to reach a consumer, the less severe would be the failure of any one pathway. Perhaps because it represents conventional wisdom ('don't put all your eggs in one basket'), the argument was not given a formal mathematical treatment. The conflict between this argument and the diametrically opposite one from later studies is one I shall try to resolve.

One of Elton’s lines of evidence involved the increased chance of pest outbreaks in agricultural systems, another the absence of pest outbreaks in tropical (but not temperate) forests and the prevalence of population cycles in the Arctic and, finally, the ease with which species can invade small, remote (and hence species-poor) oceanic islands. Elton’s data were few: the absence of pest outbreaks in the tropics was based on a casual conversation with three tropical foresters<sup>1</sup>. Furthermore, man’s impacts on agricultural systems are many and varied: simplification may not be the only, or even the main cause of their instability.

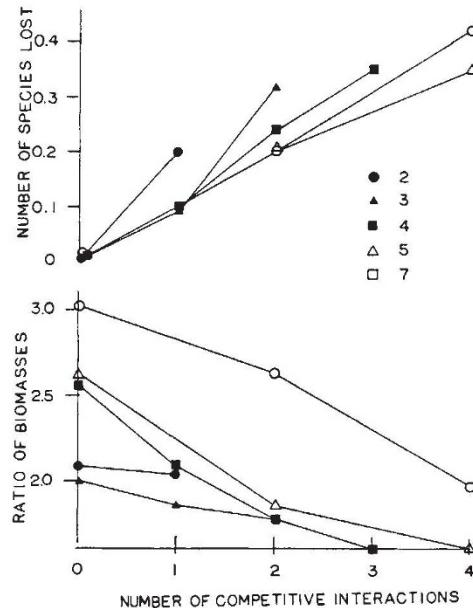
Simply, the early theoretical arguments and field studies were heterogeneous and ‘incomplete’<sup>22</sup>. Yet this heterogeneity only points to the fact that there are many questions to be answered

in the discussion of stability-complexity relationships. No single question has logical supremacy.

## Definitions

Table 1 lists definitions I shall use to build an array of complexity-stability questions. This set of definitions is not exhaustive<sup>23–26</sup>; I have included those definitions that have been most studied or which promise to be amenable to both theoretical and field studies. One can create ‘complexity-stability’ questions by taking the possible combinations of measures of complexity, stability and variables of interest. Looking at all the possible combinations suggests some features that should be discussed before answers are sought.

(1) The definitions of stability imply different kinds of comparisons. If a system is not stable (in the strict sense of Table 1), we will probably not observe it except in transition to a new equilibrium<sup>27</sup>. Rather special dynamics are required to permit



**Fig. 1** An illustration of the diametrically opposite effects of increasing complexity on two different measures of stability. Results are from model systems where the single herbivore is removed from a system of possibly competing plants. As the number of competitive interactions between plants increases (abscissa), the system is more likely to lose plant species (upper graph) but change biomass less (lower graph) when the herbivore is removed. In the lower graph, the ratio of biomass plotted is the total biomass of plants without herbivore/total biomass of plants with herbivore. Numbers indicate numbers of plant species in the system.

Table 1 Definitions of variables

	Complexity
Species richness	The no. of species in a system.
Connectance	The no. of actual interspecific interactions divided by the number of possible interspecific interactions.
Interaction strength	The mean magnitude of interspecific interaction: the size of the effect of one species' density on the growth rate of another species.
Evenness	The second moment (variance) of the species abundance distribution measures how uneven are the abundances. (Diversity indices are measures that combine the evenness of the species' abundances (equitability) and species richness. The relative weighting of these two components varies from index to index. One member of this family is the information theoretic index, $H$ .)
	Stability
Stable (units nondimensional and binary: 0 unstable, 1 stable)	A system is deemed stable if and only if the variables all return to the initial equilibrium following their being perturbed from it. A system is locally stable if this return is known to apply only certainly for small perturbations and globally stable if the system returns from all possible perturbations. The set of all values of the variables from which the system returns to a particular equilibrium is known as the domain of attraction. How fast the variables return towards their equilibrium following a perturbation. Resilience is not, therefore, defined for unstable systems.
Resilience (units of time; characteristic return time is time taken for a perturbation to return to $1/e$ ( $\sim 37\%$ ) of initial value.)	The time a variable lasts before it is changed to a new value. Turnover is the reciprocal of persistence.
Persistence (units of time)	The degree to which a variable is changed, following a perturbation.
Resistance (units nondimensional and continuous)	The variance of population densities over time, or allied measures such as the standard deviation of population densities, or the coefficient of variation (standard deviation divided by the mean density c.v.).
Variability (the units are those of animals squared per unit area (variance), animals per unit area (s.d.) dimensionless (c.v.))	
	Variables of interest
Individual species abundances	The densities of all the species in the system.
Species composition	The list of all the species in the system.
Trophic level abundance	The total density (or biomass) of all the species in a particular trophic level (or for comparable definitions, for some other interesting set of species).

species to persist with population densities which do not return to an equilibrium, but instead, cycle indefinitely. Such dynamics are theoretically fascinating but seem to characterize only a few populations<sup>28</sup>, such as lemmings and lynx. Thus, when we investigate the chances of stability of systems with different complexities we are implicitly comparing existing with hypothetical systems. For the other measures of stability, however, we could ask whether existing systems are more or less resilient, resistant, persistent or variable. (Although if they are not resilient, resistant or persistent enough or too variable, then, indeed, we may not observe them for long.)

(2) There are many kinds of perturbations to natural systems. Detailed answers to specific complexity-stability questions may depend on what is perturbed, when, and by how much. Some perturbations may involve changes in species abundances (like the English winter of 1962–63 which temporarily depressed bird populations<sup>29</sup>); others may involve the removal of some or all of the species (as in secondary plant succession) and thus involve recoveries of a much longer duration. Consequently, the definitions of resilience, persistence and resistance pose problems of scale when we attempt to measure them in the field<sup>30</sup>. It is obvious that large perturbations will disappear more slowly than small ones. The time taken for a perturbation to diminish to a given percentage of its initial value, however, may be relatively independent of the size of the perturbation. Such a statistic thus avoids the complication of the initial size of the perturbation, which will depend not only on the size of the disturbance but also on the system's resistance. The notion of persistence is more difficult to deal with. How long a system persists will not only depend on the system, but also on the properties of the disturbances. Defining comparable disturbances for different systems may often be difficult or impossible. But for some cases to be discussed, the differences in persistence clearly can be seen

to depend on the intrinsic differences between systems and not on the disturbances.

It is also obvious that long-lived organisms (say, trees) will be less resilient and more persistent in numbers than short-lived organisms (say, annual plants) on a time scale measured in years<sup>30</sup>. Why some systems are dominated by organisms with short or long life histories may be the answer to some questions about resilience and resistance. For others, we may wish to scale resilience or persistence further by correcting for the generation times of the species involved.

Perturbations also need to be defined spatially. Disturbing  $1 \text{ m}^2$  is not merely a smaller perturbation than disturbing  $1 \text{ km}^2$ : in the latter, the boundary is smaller relative to the total area, so immigration and emigration are likely to be relatively less important than birth and death processes.

In short, because of the problems of spatial and temporal scales, it may be impossible to compare widely different ecosystems. Yet for similar systems, contrasts of resilience, resistance, persistence and variability should be possible. Indeed, the field studies I shall discuss confirm this.

(3) The definitions of stability are interrelated in complicated ways. Under some circumstances, resistant systems, because they change less under a given disturbance, will appear more persistent and less variable. For some populations, increasing resilience implies decreasing variability<sup>29</sup> and, as discussed above, resilience and resistance may or may not be confounded depending on how the former is scaled. I shall not discuss these relationships, in part because Harrison<sup>26</sup> has already done so. However, the principal reason is that despite the potential for the reverse, theoretical and even field results fall cleanly into the various definitions of stability; and even if the correlation between any two definitions is absolute, we will retain both when, under different circumstances, each variable becomes an

**Table 2** Theoretical and field studies on various combinations of measures of complexity, variables of interest and measures of stability

	THEORETICAL STUDIES		FIELD STUDIES	
	SPECIES RICHNESS	CONNECTANCE AND INTERACTION STRENGTH	SPECIES RICHNESS	CONNECTANCE AND INTERACTION STRENGTH
Individual species abundances	STABLE	<p>Local stability: with more species there is less chance of stability<sup>6-2</sup></p> <p>Modifications:</p> <ul style="list-style-type: none"> <li>(1) feasibility<sup>32</sup></li> <li>(2) structure<sup>10,11,31</sup></li> <li>(3) parameters<sup>10,11</sup></li> <li>(4) donor-control<sup>10</sup></li> <li>(5) succession, deletion and evolution<sup>33-36</sup></li> <li>(6) predator foraging patterns<sup>42,43</sup></li> </ul>	<p>Local stability: with more connectance and greater interaction there is less chance of stability<sup>6-9</sup></p> <p>1) <math>C_n \leq \text{constant}</math><sup>44-46</sup></p> <p>2) Food webs lack links that are particularly destabilizing<sup>2</sup>.</p> <p>3) Insect systems are more connected than vertebrate dominated ones<sup>50</sup></p>	
	RESILIENT	With more trophic levels there is less resilience <sup>53,54</sup>	With more species there is less resilience <sup>55</sup>	
	PERSISTENT	<p>1) Systems with more species are harder to invade<sup>36,56</sup></p> <p>2) With more species, it is less likely an invader will be a new species</p>	<p>With more interaction systems are harder to invade<sup>56,57</sup></p> <p>1) Succession: older systems with more species are more persistent<sup>58</sup></p> <p>2) Islands: those with fewer species are easier to invade<sup>1,59,60</sup></p>	
	RESISTANT			
	STABLE	Species deletion: with more species there is less chance of stability (except for donor-control where the reverse is true <sup>38,61</sup> )	Species deletion: with more connectance there is less chance of stability (except for donor-control where the reverse is true <sup>38,61</sup> )	Indirect evidence: most systems are changed considerably by predator removals and are thus not donor-controlled <sup>39</sup>
	RESILIENT			
	PERSISTENT			Geologically, systems with more species persist less <sup>63</sup>
	RESISTANT			
	RESILIENT		With more connectance there is possibly more resilience <sup>64,65</sup>	
	RESISTANT	With more species, there is usually less resistance <sup>66</sup>	With more connectance there is more resistance <sup>66</sup>	

easier or more appropriate measurement of stability.

(4) The variables of interest are hierachial in nature. If individual species abundances are maintained, then so are the number of species in the system, species composition and the total density or biomass of any subset of species. Yet species composition may remain the same while the densities of the species change, or vice versa.

(5) Connectance and interaction strength are closely related: their product measures how strongly all the species in the system interact. Theoretically, it is convenient to distinguish species pairs that interact from those that do not. Practically, we might expect a continuous gradation of interaction strengths from the strong to the weak and for these two measures to affect stability in comparable ways.

Table 2 compiles theoretical and field studies on some of the combinations of measures of complexity, variables of interest

and measures of stability. Later, I shall discuss evenness as a measure of complexity and variability as a measure of stability. I shall first summarize what results are available, then conclude by pointing to some questions which appear experimentally and theoretically tractable and yet which do not appear to have been answered.

### Individual species abundances

**Stability.** The majority of theoretical studies have examined local stability of species abundances. Initial results<sup>6-9</sup> found that increasing species richness, connectance or interaction strength decrease the chance that randomly assembled communities would be stable. Random assembly is an unreasonable assumption and other studies relaxed the assumptions on the structure and limits of the interaction parameters<sup>10,11,31,32</sup>. In addition,

models were allowed to develop through the successive additions or deletions of species<sup>33-36</sup>.

The many subtleties to this work are reviewed by May<sup>37</sup>, McDonald<sup>13</sup> and Pimm<sup>27</sup> and one feature seems capable of completely reversing the original result. In most models, increasing the density of the predator, decreases the population growth rate of the prey. Alternatively, predators may consume prey that are likely to die or have died from other causes—disease or starvation, for example. For these donor-controlled models, increasing connectance and species richness increases the chances of finding a locally stable model<sup>10</sup>. This result matches MacArthur's<sup>2</sup> idea that complexity buffers the consequences of density variations in one prey species. His argument is, however, incomplete: it fails to consider the variations in densities of species at higher trophic levels. For these, the opposite is true: variations propagate more widely the more connected the system. It is this latter effect that predominates in many models but, by definition, is absent in donor-controlled models. Donor-control dynamics predict that predator removal should have no effect on prey species densities and certainly not on the resultant community's species composition. Usually this is not the case<sup>38</sup>. With the rejection of donor-control dynamics goes one plausible model where increased stability comes from increased complexity.

In Lotka-Volterra models, resource limitation of species at the base of the food web helps to stabilize the system, and predator effects on prey density (absent in donor-controlled models) are destabilizing. However, the predator interactions, themselves, can be stabilizing. Typical examples of this involve some mechanisms for the prey to escape predation at low densities. Here, predators might not be able physically to attack the prey because the latter are hiding or, perhaps, because low densities cannot be profitably exploited. In these models there can be stable interactions with prey depressed to levels far below those set by resource limitation. Detailed case histories<sup>39</sup>, general arguments about the structure of herbivore communities<sup>40</sup>, or about herbivores in general<sup>41</sup> all suggest that many species may be limited primarily by predators rather than resources. For such cases Nunney<sup>42</sup> showed that increasing complexity and species richness could lead to an increased chance of local stability. The generality of Nunney's arguments have been questioned<sup>43</sup> but they also require the product of connectance ( $C$ ) and species richness ( $n$ ) to be sufficiently large ( $Cn > 6$ ) to reverse the usual decrease in stability. I shall return to this point presently.

Is there any field evidence for these theoretical results? As argued above, the nature of the definition of local stability makes it unlikely (though not impossible) that we will observe anything other than locally stable systems. Many models suggest that, if interaction strength ( $i$ ) is assumed to be relatively constant, then  $C$  should vary with  $1/n$  in order to maintain local stability. Data from published food webs<sup>27,44</sup> or from more detailed studies of lizard communities<sup>45</sup> show that  $C$  does decrease linearly with  $1/n$  or nearly so<sup>46</sup> with  $Cn = 3-4$ . These values, incidentally, seem too low for Nunney's argument, in the previous paragraph, to hold. Unfortunately, these results say nothing more than that each species interacts with a fixed number of other species as  $n$  increases—a result that seems reasonable without recourse to stability explanations<sup>47</sup>. There are, however, certain other patterns of species interactions (particularly those that involve species feeding on more than one trophic level<sup>48</sup>, and the grouping of species interactions within a community<sup>49</sup>) that are particularly destabilizing in models. Natural systems show a statistical scarcity of these patterns<sup>49,50</sup>. Although interaction strength is hard to measure, it is likely to be less between an insect and its comparably sized insect parasitoid than between a large vertebrate predator and its small prey. Thus, stability should permit insect-parasitoid systems to be substantially more connected than vertebrate-dominated systems<sup>48</sup>. They are<sup>50</sup>. (With the exception just noted, most multi-species models do not consider parasitoid or parasite systems. Yet their distinctive features<sup>51</sup> and ecological importance<sup>52</sup>, plus their greater poten-

tial complexity, suggest that other results from local stability analyses may not be simply transferable to them.)

In sum, most theoretical studies of local stability are best interpreted by saying that the systems we observe should not be too complex. Field evidence suggests this is correct; indeed, patterns of species interactions that are particularly destabilizing in models are also rare in nature.

**Resilience.** In models, systems with more trophic levels (one way of adding species) are less resilient<sup>53,54</sup> and, for a given number of trophic levels, stable systems will often<sup>11,27</sup>, but not always<sup>43</sup>, be more resilient the more complex they are. Resilience is amenable to field determination<sup>29</sup> and unlike stability, permits comparisons of existing natural systems. However, I know of only one such study<sup>5</sup>. It found that plants in a species-poor system recovered more quickly from an unusual drought than those in a nearby species-rich field.

**Persistence.** How long should species densities continue to return to a given equilibrium and not to some other equilibrium involving the same or some different set of species? One long-term question is whether constantly simple systems persist longer than complex ones (for example, are the species abundances of species-poor desert communities more persistent than those of species-rich tropical forests?). I shall consider this topic below. A second, relatively short-term view, posits changes in both composition and individual abundances, effected, perhaps, by the addition of a species to the system. This presumes that the community has fewer species than the set of those capable of reaching the community (this set is called the species pool). This topic is particularly relevant to islands (either typically oceanic ones or abstract islands of isolated habitat which may lack a full complement of species) or communities which, following a major disturbance, may also lack species.

How hard are communities to invade? Those that are hard to invade will be persistent and vice versa. Models that examine species competing for resources arranged along some gradient<sup>56</sup> and more general models of food web assembly<sup>36,57</sup> suggest that communities with more species are harder to invade. In addition, the smaller the fraction of the species pool present in a community, the more likely an invading individual will be of a new species. The more new species that invade per unit time, the more likely it is that one of them will be able to increase and so change the existing system's equilibrium. Simply, both effects mean that the fewer the species in the system, the less persistent that system will be. The effect of increased interaction between species is also to increase persistence<sup>56,57</sup>.

There are two kinds of field evidence for these effects. First, during succession, species that enter the community later (when there are usually more species) persist longer than those that enter earlier<sup>58</sup>. In part, this must be due to longer-lived organisms arriving later. The question of whether later-arriving organisms persist longer relative to their generation times has not been asked. Of course, that longer-lived organisms arrive later may simply be a reflection of the greater likely persistence of later successional stages. The second evidence avoids these difficulties, for even among species with similar generation times, species are more likely to colonize remote, species-poor islands successfully than species-rich continents<sup>1,59,60</sup>.

## Species composition

**Stability.** If individual species abundances remain fixed, then so does species composition; thus, much of the previous section applies to this one. It remains to ask, under what conditions does species composition remain unchanged, even though individual abundances change considerably? There are two kinds of studies. The first kind considers the effect of removing species on the composition of the remaining species ('species deletion stability'). Other studies consider whether, following changes in density, species abundances will return to their original equilibrium or move to some new equilibrium involving different abundances but the same composition.

Theoretically, species deletion stability decreases with increasing numbers of species and connectance<sup>61</sup>, but it also depends

critically on which species are selected for removal<sup>38</sup>. If model plants are removed, more species and greater connectance will lead to a lessened chance of losing more species: these results confirm MacArthur's<sup>2</sup> intuition. For model predators, however, the result is reversed. Of course, donor-controlled systems are not affected by predator removals and, for these, more complex systems will be more species deletion stable<sup>38</sup>. As noted above, donor-controlled dynamics do not predominate in nature<sup>38</sup>.

A second problem involves populations which appear to continue at one level for years, then shift to another one and remain there. Lotka-Volterra models do not have this property—more complex dynamics with more parameters are required<sup>62</sup>. In this special sense, systems with greater (dynamic) complexity may permit species composition to remain unchanged when comparable simple models would predict species losses.

**Resilience.** How fast species composition returns to equilibrium following, say, a major reduction in species, is a question central to the topic of ecological succession. Data are certainly available on how fast succession proceeds. However, I know of no synthesis that relates the rate at which disturbed systems approach their former composition to the various definitions of complexity.

**Persistence.** I have already noted that species composition should and does last longer when more species are present—at least when viewing the process of succession. But what about the non-successional differences among systems, the species richness of forests versus deserts, for example? In the long term, we might expect development of better prey or predators and changing environmental conditions to cause species losses. From the results on species deletions, we might expect systems with more species to last for shorter periods. The relationship of the persistence of species composition to species richness, therefore, may be dependent on the timescale considered. Boucot<sup>63</sup> finds that for marine fossil assemblages ‘trophically complex systems... are far more fragile and subject to extinctions’ than simpler systems and, hence, tend to last for shorter periods. As E. R. Pianka has observed (personal communication), excepting succession, species compositions of many systems are persistent over at least human life spans.

## Total density or biomass

The total density (or biomass) of all or some subset of the species in an ecosystem may correlate far more closely with our notions of what defines an ecosystem than the abundances or identities of particular species. For example, we readily recognize a deciduous forest. But consider, say, 1 km<sup>2</sup> plots of deciduous forest in eastern North America or western Europe. Within these plots there will be a wide range of tree species, an even greater variation in the abundance of individual tree species, but not, I suspect, a large variance in the total biomass of all tree species.

**Resilience.** Theoretically, densities of certain sets of species can be more resilient than those of their constituent species and, moreover, this resilience can increase with increasing connectance<sup>64,65</sup>. I know of no field study that relates biomass resilience during succession to complexity.

**Resistance.** There are both theoretical<sup>66,67</sup> and experimental<sup>55,68,69</sup> studies of the degree of change of biomass and density with the addition or removal of a species or resource. Two of these studies<sup>66,69</sup> focus on the effects of large mammalian grazers on plant biomass. Models with few plant species but more connectance (interactions between plants) have greater resistance<sup>66</sup>. The former result also holds for very complicated ecosystem models<sup>67</sup>. Greater evenness of prey abundances (a measure of complexity not yet discussed) correlates with greater resistance both theoretically<sup>66</sup> and in field studies of mammalian grazing<sup>69</sup>.

## Other variables

I have not discussed variability as a measure of stability because I believe there are difficulties in testing the various theoretical

ideas. How much populations vary will depend not only on intrinsic factors involving ecosystem complexity<sup>70-72</sup>, but on the extrinsic nature and frequency of the perturbations. In the species-rich tropics, populations do not vary less than in temperate systems<sup>22,72,73</sup>. Yet populations do vary more in climatically unpredictable systems than in predictable ones<sup>73</sup>, suggesting that extrinsic factors may govern variability more than intrinsic ones.

Nor have I discussed pest outbreaks. While it may be that pest species are the most variable<sup>74</sup>, it is more likely that they are simply those species whose densities are high relative to what humans require them to be. Pimental's<sup>75</sup> finding of lower densities of herbivorous insects with greater species richness might be explained by considerations of equilibrium densities rather than by the definitions of stability used here. The determinants of equilibrium densities<sup>76</sup> or human requirements<sup>77</sup> fall outside the scope of this review, but within its scope is the question of what determines how fast an insect population returns to an economically unacceptable equilibrium after being severely reduced by insecticides. I have already considered resilience a measure of stability. In contrast, for pest outbreaks, a resilient population might be considered unstable, while one that recovered slowly might be considered stable. Resilience might indicate stability or instability depending on one's viewpoint<sup>78</sup>. As noted above, with fewer species, resilience tends to increase: whether this is a general explanation of outbreaks is an intriguing possibility, but one clearly based on too few theoretical and field studies.

## Conclusions

Theoretically, the more species that are present in a community: (1) the less connected it should be, if it is to be stable. (2) the less resilient will be its populations, (3) the greater will be the change in composition and in biomass when a species is removed, (4) the longer the persistence of species composition in the absence of a species removal. The more connected a community: (1) the fewer species it must have if it is to be stable, (2) the more likely it is to lose other species if one is removed, but (3) the more resilient will be its populations, (4) the more persistent will be its composition and (5) the more resistant will be its biomass if a species is removed. Clearly, different complexity-stability questions yield different answers (Fig. 1). The fact that they do, often explains some of the earlier controversy generated, it is now obvious, by different authors addressing different questions.

Which questions have not been examined? Local stability is a clearly defined concept mathematically and the majority of theoretical studies examine it, alone<sup>26</sup>. Field studies have not usually addressed local stability because, I suspect, it involves a comparison of existing and hypothetical systems. What field studies have examined are questions that permit comparisons of existing systems and which involve more general views of a system than individual species' abundances. How fast does species composition or total biomass return to equilibrium, how long does composition remain unchanged and how much is composition or total biomass changed following, say, the addition of a species? These questions are as theoretically tractable as those of local stability. Similarly, some accessible theoretical ideas—like resilience—are rarely measured in the field, despite the potential to do so. Put simply, progress in our understanding of the complexity and stability of ecosystems will come from more theoretical and field studies, but is likely to be fastest when these studies consider which questions are both theoretically tractable and experimentally testable: I suggest the many gaps in Table 2 provide a guide to what these questions are.

I thank R. A. Armstrong, J. H. Lawton, R. M. May, S. J. McNaughton and E. R. Pianka for comments on earlier versions of this paper. This research was supported by the NSF's Ecosystems Studies Program under Interagency Agreement DEB 77-25781 with the US Department of Energy under contract W-7405-eng-26 with Union Carbide Corporation: Environmental Sciences, Oak Ridge National Laboratory.

1. Elton, C. S. *The Ecology of Invasions by Animals and Plants* (Chapman & Hall, London, 1958).
2. MacArthur, R. H. *Ecology* **36**, 533–536 (1955).
3. Hutchinson, G. E. *Am. Nat.* **93**, 145–159 (1959).
4. Margalef, R. *Perspectives in Ecological Theory* (University of Chicago Press, 1968).
5. Watt, K. E. F. *Principles of Environmental Science* (McGraw-Hill, New York, 1973).
6. Gardner, M. R. & Ashby, W. R. *Nature* **228**, 784 (1970).
7. May, R. M. *Stability and Complexity in Model Ecosystems* (Princeton University Press, 1973).
8. McMurtie, A. J. *J. theor. Biol.* **50**, 1–11 (1975).
9. Gilpin, M. E. *Nature* **254**, 137–139 (1975).
10. DeAngelis, D. L. *Ecology* **56**, 238–243 (1975).
11. Pimm, S. L. *Theor. Popul. Biol.* **16**, 144–158 (1979).
12. Siljak, D. *Nature* **249**, 280 (1974).
13. MacDonald, N. *Nature* **275**, 117–118 (1978).
14. Tuljapurkar, S. D. & Semura, J. S. *Nature* **275**, 388–389 (1975).
15. Jeffries, C. *Theor. Popul. Biol.* **7**, 149–166 (1975).
16. May, R. M. *Nature* **238**, 413–414 (1972).
17. Tansky, M. *Mém. Coll. Sci. Kyoto Univ. B7*, 87–94 (1978).
18. Webber, M. I. in *Ecological Stability* (eds Usher, M. B. & Williamson, M. W.) 165–178 (Chapman & Hall, London, 1974).
19. Kirkwood, R. S. M. & Lawton, J. H. *J. theor. Biol.* **93**, 225–237 (1981).
20. Goh, B. S. *Math. Biosci.* **40**, 157–166 (1978).
21. Kindlemann, P. & Rejmánek, M. *J. theor. Biol.* **94**, 989–993 (1982).
22. Goodman, D. Q. *Rev. Biol.* **50**, 237–266 (1975).
23. Botkin, D. B. & Sobel, M. J. in *Ecosystem Analysis and Prediction* (ed. Levin, S. A.) 144–150 (Society of Industrial and Applied Mathematics, Philadelphia, 1975).
24. Innis, G. in *Ecosystem Analysis and Prediction* (ed. Levin, S. A.) 131–139 (Society of Industrial and Applied Mathematics, Philadelphia, 1975).
25. Orians, G. H. in *Unifying Concepts in Ecology* (eds van Dobben, W. H. & Lowe-McConnell, R. H.) 139–150 (Junk, The Hague, 1975).
26. Harrison, G. W. *Am. Nat.* **113**, 659–669 (1979).
27. Pimm, S. L. *Food Webs* (Chapman & Hall, London, 1982).
28. Tanner, J. T. *Ecology* **47**, 733–745 (1966).
29. Pimm, S. L. in *Ecological Communities: Conceptual Issues and the Evidence* (eds Strong, D. R. Jr., Simberloff, D. S. & Abele, L. G.) (Princeton University Press, in press).
30. Connell, J. H. & Sousa, W. P. *Am. Nat.* **121**, 787–824 (1983).
31. Lawlor, L. R. *Am. Nat.* **112**, 445–447 (1978).
32. Roberts, A. *Nature* **251**, 607–608 (1974).
33. Tregonning, K. & Roberts, A. *Bull. math. Biol.* **40**, 513–524 (1978).
34. Tregonning, K. & Roberts, A. *Nature* **281**, 563–564 (1979).
35. Roberts, A. & Tregonning, K. *Nature* **288**, 265–266 (1981).
36. Post, W. M. & Pimm, S. L. *Math. Biosci.* **64**, 169–192 (1983).
37. May, R. M. in *Population Dynamics* (eds Anderson, R. M., Turner, B. R. & Taylor, L. R.) 385–407 (Blackwell, Oxford, 1979).
38. Pimm, S. L. *Oikos* **35**, 139–149 (1980).
39. Hassell, M. P. *J. Anim. Ecol.* **49**, 603–628 (1980).
40. Lawton, J. H. & Strong, D. R. Jr. *Am. Nat.* **118**, 317–338 (1981).
41. Hairston, N. G., Smith, F. E. & Slobodkin, L. B. *Am. Nat.* **84**, 421–425 (1960).
42. Nunney, L. *Am. Nat.* **115**, 639–649 (1980).
43. Abrams, P. A. & Taber, D. A. *Am. Nat.* **119**, 240–249 (1982).
44. Rejmánek, M. & Stary, P. *Nature* **280**, 311–313 (1979).
45. Pianka, E. R. in *Ecology and Evolution of Communities* (eds Cody, M. L. & Diamond, J. M.) 291–314 (Harvard University Press, 1975).
46. Yodzis, P. *Nature* **284**, 544–545 (1980).
47. Pimm, S. L. *Nature* **285**, 591 (1980).
48. Pimm, S. L. & Lawton, J. H. *Nature* **268**, 329–332 (1978).
49. Pimm, S. L. & Lawton, J. H. *J. Anim. Ecol.* **49**, 879–898 (1980).
50. Pimm, S. L. *Ecology* **61**, 219–225 (1980).
51. Dobson, A. P. in *Population Biology of Infectious Diseases* (eds Anderson, R. M. & May, R. M.) 1–25 (Springer, Berlin, 1982).
52. Anderson, R. M. *Population Dynamics of Infectious Diseases* (Chapman & Hall, London, 1982).
53. Pimm, S. L. & Lawton, J. H. *Nature* **268**, 329–331 (1977).
54. Vincent, L. L. & Anderson, L. R. *Theor. Popul. Biol.* **15**, 217–231 (1979).
55. Leps, J., Osbornova-Kosinova, J. & Rejmánek, M. *Vegetatio* **50**, 53–63 (1982).
56. May, R. M. & MacArthur, R. H. *Proc. natn. Acad. Sci. U.S.A.* **69**, 1109–1113 (1972).
57. Robinson, J. V. & Valentine, W. D. *J. theor. Biol.* **81**, 91–104 (1979).
58. Shugart, H. H. & Hett, J. M. *Science* **1279**–1281 (1973).
59. Long, J. L. *Introduced Birds of the World* (David & Charles, Newton Abbott, 1981).
60. Moulton, M. P. & Pimm, S. L. *Am. Nat.* **121**, 669–690 (1983).
61. Pimm, S. L. *Oikos* **33**, 351–357 (1977).
62. May, R. M. *Nature* **269**, 471–477 (1977).
63. Boucot, A. J. *J. Paleont.* **57**, 1–30 (1983).
64. Armstrong, R. A. *Am. Nat.* **120**, 391–402 (1982).
65. Armstrong, R. A. *Oak Ridge natn. Lab. Tech. Memo.* (in the press).
66. King, A. W. P. & Pimm, S. L. *Am. Nat.* **122**, 145–149 (1983).
67. Austin, M. P. & Cook, B. F. *J. theor. Biol.* **45**, 435–458 (1974).
68. Hurd, L. E., Mellinger, M. V., Wolf, L. L. & McNaughton, S. J. *Science* **173**, 1134–1136 (1971).
69. McNaughton, S. J. *Am. Nat.* **111**, 515–525 (1977).
70. DeAngelis, D. L. *Bull. math. Biol.* **37**, 291–299 (1975).
71. Saunders, P. T. & Bazin, M. J. *Nature* **256**, 120–121 (1975).
72. Leigh, E. F. in *Ecology and Evolution of Communities* (eds Cody, M. L. & Diamond, J. M.) 74–80 (Harvard University Press, 1975).
73. Wolda, H. *Am. Nat.* **112**, 1017–1045 (1978).
74. Watt, K. E. F. *Can. Ent.* **97**, 887–895 (1965).
75. Pimentel, D. *Ann. ent. Soc. Am.* **54**, 76–86 (1964).
76. Bedington, J. R., Free, C. A. & Lawton, J. H. *Nature* **273**, 513–519 (1978).
77. Conway, G. in *Theoretical Ecology* (ed. May, R. M.) 356–386 (Blackwell, Oxford, 1981).
78. Turelli, M. *Theor. Popul. Biol.* **13**, 244–267 (1978).

## ARTICLES

## The Hubble constant as derived from 21 cm linewidths

Allan Sandage & G. A. Tammann\*

Mount Wilson and Las Campanas Observatories, Carnegie Institution of Washington, 813 Santa Barbara Street, Pasadena, California 91101, USA

The IR 21 cm linewidth–absolute magnitude relation is calibrated by means of local galaxies with known distances, including new distance determinations of M33 and M81. The calibrated relation is applied to 17 Virgo cluster galaxies of type Sab to Sd and yields a cluster modulus of  $(m - M)_{\text{Virgo}}^0 = 31.47 \pm 0.34$ . Reliable relative distance indicators are used to extend the distance scale to the Coma cluster, for which a distance modulus is found of  $(m - M)_{\text{Coma}}^0 = 35.39 \pm 0.35$ . The blue 21 cm linewidth–absolute magnitude relation gives slightly larger distances. A combination of the two methods leads to a Hubble constant at the distance of the Coma cluster of  $H_0 = 55 \pm 9 \text{ km s}^{-1} \text{ Mpc}^{-1}$ . This value agrees with the global value of  $H_0 = 50 \pm 7 \text{ km s}^{-1} \text{ Mpc}^{-1}$ , giving a Hubble time of  $H_0^{-1} = 19.5 \times 10^3 \text{ Myr}$ , in agreement with the age of the chemical elements and with the age of our Galaxy, determined from globular clusters.

In a recent discussion of the Tully–Fisher relation<sup>1</sup> it was stated that the extragalactic distance scale and the value of the Hubble constant depend now only on the infall velocity towards Virgo, and on the distances of the galaxies in the neighbourhood of the Milky Way. Because the former is now well determined from an accurate measurement of the relative distance between the Virgo and Coma clusters<sup>2</sup>, and because new fundamental distances to two nearby calibrating galaxies, M33 and M81, have recently become available<sup>3–5</sup>, it seems justified to look into the consequences of these new developments.

\* Permanent address: Astronomisches Institut der Universität Basel, European Southern Observatory, Venusstrasse 7, CH-4102 Binningen, Switzerland.

The Tully–Fisher relation, that is the dependence of the luminosity of disk galaxies on their 21 cm linewidth, has been widely used to derive extragalactic distances, either by correlating the absorption-corrected blue B magnitude (ref. 6 and refs therein) or the nearly absorption-free IR H magnitude (ref. 1 and refs therein) of a disk galaxy with its inclination-corrected 21 cm linewidth  $\Delta v_{21}$ . So far the IR Tully–Fisher relation has consistently led to a surprisingly low Virgo cluster distance of only 16 Mpc, compared with 22 Mpc which follows from other distance indicators, which are insensitive to selection effects and statistical bias<sup>7,8</sup>. We investigate here this discrepancy, as well as the consequences for the Hubble constant  $H_0$ .