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Are there general laws in ecology?

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The dictionary definition of a law is: "Generalized formulation based on a series of events or processes observed to recur regularly under certain conditions; a widely observable tendency". I argue that ecology has numerous laws in this sense of the word, in the form of widespread, repeatable patterns in nature, but hardly any laws that are universally true. Typically, in other words, ecological patterns and the laws, rules and mechanisms that underpin them are contingent on the organisms involved, and their environment. This contingency is manageable at a relatively simple level of ecological organisation (for example the population dynamics of single and small numbers of species), and re-emerges also in a manageable form in large sets of species, over large spatial scales, or over long time periods, in the form of detail-free statistical patterns – recently called 'macroecology'. The contingency becomes overwhelmingly complicated at intermediate scales, characteristic of community ecology, where there are a large number of case histories, and very little other than weak, fuzzy generalisations. These arguments are illustrated by focusing on examples of typical studies in community ecology, and by way of contrast, on the macroecological relationship that emerges between local species richness and the size of the regional pool of species. The emergent pattern illustrated by local vs regional richness plots is extremely simple, despite the vast number of contingent processes and interactions involved in its generation. To discover general patterns, laws and rules in nature, ecology may need to pay less attention to the 'middle ground' of community ecology, relying less on reductionism and experimental manipulation, but increasing research efforts into macroecology.

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Introduction and definitions

Of course there are general laws in ecology. However, our science has rather few *universal* laws. My dictionary gives several different definitions of the word law. The most appropriate is: "Generalized formulation based on a series of events or processes observed to recur regularly under certain conditions; a widely observable tendency". Notice that there is nothing in this definition to say that a law has to be universally true; only that laws are usually true. In other words the title of this Minireview could have been: Are there laws in ecology?; the word "general" is redundant.

Parts of science, areas of physics for instance, have deep universal laws, and ecology is deeply envious because it does not. It has part ownership of a few universal laws, and I will say what they are in a moment. In this essay I particularly want to consider why ecology does not have many universal laws, and why the great majority, probably all, of our actual laws (in the sense of "widely observable tendencies") cannot simply be derived from first principles, building on the

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universal laws. Ecology, incidentally, is not alone in this position; it is shared by many other complex parts of the biological sciences, broadly defined, and by geology.

There are three deep universal laws that underpin all ecological systems, a set of general physical principles that can be grouped together to constitute a fourth set of laws, and one 'law' so simple that it is really no more than an observation. They are:

1. The first and second laws of thermodynamics.
2. The rules of stoichiometry, a particular application of the universal law that matter (in a non-nuclear world) cannot be created or destroyed, and the explanation for why alchemy is a dead profession.
3. Darwin's law of natural selection as an explanation for evolution.
4. The set of general physical principles governing diffusion and transport of gasses and liquids, the mechanical properties of skin and bone, aerodynamics and hydrodynamics, etc., that singly or in combination define limits to the performance of individual living organisms, and which underpin the study of plant and animal physiology.
5. The trivial, but important observation that organisms interact with one another (no species, anywhere in nature, lives in splendid isolation) and with their environment.

In deliberately simplified terms, it is 3–5 (and particularly 5) that make life difficult for ecologists seeking grand, unifying theories (GUTs), and which mean that we live on a wonderfully complicated biological planet. The universal laws do not allow us to predict the existence of kangaroos; they evolved (law 3), under the influence of myriads of interactions (5), constrained by laws 1, 2 and 4.

Without being too prescriptive, let me now define some terms. *Patterns* are regularities in what we observe in nature; that is, they are "widely observable tendencies". These emerge from the combined actions of laws 1–4 and observation 5; when we seek to understand patterns in ecology, a great deal of effort concentrates on trying to cut through the Gordian knots created by 3, 4 and 5. Although it is not actually consistent with the dictionary definition above, most ecologists think of *laws* and *rules* as the general principles that underpin and create the patterns, just as the laws (or rules) of sports and other games create rich patterns of human activity, but why we can tell quickly whether we are watching a hockey match or a football match. In many people's minds, laws are stronger, more fundamental and more general than rules. The most useful scientific laws yield deep insights into the workings of nature; rules are less grand. *Mechanisms* are weaker still; a mechanism or mechanisms can generate unique phenomena; but general rules require common mechanisms. *Generalisation* is a loose term, and implies something that usually happens, be it a pattern, or a rule. *Hypotheses* and *theories* are attempts to work out what the laws or rules are; hypotheses are more tentative than theories, and extremely well established theories eventually take on the mantle of laws and rules. *Models* are theories or hypotheses that codify laws or rules in mathematical form.

In ecology (and 1–5 above aside) our underlying laws and rules are not universal. Because environments are different, organisms are wonderfully different, and the laws, rules and mechanisms we end up with vary with the circumstances, that is they are *contingent*. Contingent means "only true under particular or stated circumstances". A contingent rule (or law) takes the form: if A and B hold, then X will happen, but if C and D hold, then Y will be the outcome. It follows that patterns will also be contingent, and so will theory. Some of the contingency may be 'historical accident' in its broadest sense, from the impact of meteorites, to the vagaries of chance mutations.

Notice that the same pattern can be generated by different rules (pattern does not imply process), and that the same underlying rules (for example a mathematical model) can generate different patterns, depending upon the contingent details.

Not everybody will agree with the terminology defined here. 'Cope's law', 'Bergman's rule' and 'Rapoport's rule' are, in my terminology, patterns not laws or rules, and not very regular patterns at that (e.g. Gaston et al. 1998a). Indeed they raise the vexing problem of how many exceptions to general patterns might exist before we would no longer regard them as patterns, or at least useful patterns. I have no answer to that, and basically propose to duck the issue, taking refuge in the common sense view that a pattern ought to be true at least in a majority of cases, and preferably much more often than this.

Having scrubbed and polished the semantic decks, we can now launch into the question. I will argue that ecology has plenty of (contingent) patterns, underpinned by laws and rules, but to discover useful generalisations we need to look at the correct scale. The most useful contingent theory, and the boldest contingent patterns, emerge both in relatively simple systems (e.g. populations), and in very large-scale systems (species-area relationships for instance). In contrast, community ecology is a mess, with so much contingency that useful generalisations are hard to find.

Biomes, climate, big pictures, messy details, and contingent theory

Figure 4.10 on page 167 of the second edition of *Communities and Ecosystems* (Whittaker 1975) shows the main types of terrestrial world biomes in relation to two simple environmental variables, mean annual pre-

cipitation and mean annual temperature. The diagram has been reproduced many times, and yet seems just as often forgotten by those who claim that there are no useful generalisations in ecology. There are, and this diagram is an example. Tundra, desert, temperate forest, tropical forest, savanna, and so on all lie in a characteristic portion of this simple environmental space. As Whittaker points out: "Boundaries between types cannot be located exactly", for example because climate is not solely responsible for determining where biomes occur; soil and fire also play a role. But as a good first approximation, the mechanisms underpinning this simple bold pattern in nature are well understood, and as a way of organising nature it is as good as anything the astronomers have in their attempts to classify stars (Keddy 1994).

The patterns revealed by Whittaker's diagram are bold and obvious because he avoided getting bogged down in detail. Locally, at smaller scales, nature will create endless variety, and generalisations disappear, or at least become much more difficult to see. But the patterns recognised by Whittaker are inevitably contingent. Rainfall and temperature are the main determinants of the world's terrestrial biomes, but their impacts are to a degree contingent on soil, fire, other climatic details (coastal versus continental influences for instance), and evolutionary history (eucalypts break the rules in Australia). It is this contingency that makes it difficult, indeed virtually impossible, to find patterns that are universally true in ecology. This, plus an almost suicidal tendency for many ecologists to celebrate complexity and detail at the expense of bold, first-order phenomena. Of course the details matter. But we should concentrate on trying to see where the woods are, and why, before worrying about the individual trees.

I want to explore the problem of contingent rules in more detail, before returning at the end of the review to big bold patterns. I will illustrate my case by discussing population dynamics (where the contingency appears manageable), and community ecology (where it does not).

Population dynamics and contingent theory

Overview

The tension between pattern seekers, those who believe there are some rules out there, and those who believe that nature is infinitely wonderful and complex is nicely illustrated by population dynamics. How many kinds of population dynamics do you imagine there are in the real world? Does every species have different dynamics? There may be ten million species of plants and animals on earth; are there really ten million kinds of population dynamics (Lawton 1992)?

At one level, the answer to this questions is clearly 'yes'. Indeed it is worse than 'yes', because different populations of the same species can also show markedly different dynamics (e.g. Murdoch and McCauley 1985). At quite another level, the answer is a resounding 'no'. There are not ten million kinds of population dynamics; rather there are a multitude of essentially trivial variations on a few common themes. How few remains to be seen, but it is not many. One key role of population dynamics theory is to elucidate and define these classes of population and metapopulation behaviour, and to specify the sorts of biological conditions, species interactions and environments (the laws, rules and mechanisms) likely to give rise to each kind, for example stable equilibria, limit cycles, chaos, or persistent but random fluctuations (Hassell et al. 1976, May 1981, Hanski et al. 1991, 1993a). The key contingent variables here include species intrinsic rates of increase, and the complexity of the food web in which they are embedded. A second class of generalisations, based on contingent theory, might be to predict the responses of different kinds of populations to moderate or major perturbations. In relatively simple systems, islands in the Bahamas, population theory accurately predicted four responses of spider and lizard populations to a hurricane (Spiller et al. 1998). Responses were contingent on the severity of the storm, body size and dispersal ability.

In other words, the theory of population dynamics, the search for ecological rules, is contingent on the organism and its environment. It is doubtful that this theory will ever be genuinely predictive, in the sense that given a species name, or type of organism, and where it lives, ecologists could, with any degree of certainty, specify the kind(s) of population dynamics it will display without actually having seen a time series, or knowing anything else about its biology. But all the evidence suggests that the contingent theory is not so complex and multidimensional as to make the range of population dynamics shown by organisms perfectly understandable in terms of a set of well-defined rules and mechanisms (Sinclair 1989).

Turning general, contingent theory into management tools

The difficulties start when the rules and mechanisms become enmeshed with the every-day, practical problems that confront population managers, the ecologists at the sharp end who have to control pests, sustain fisheries or rescue endangered species. Less thoughtful critics point out that since current theoretical models do not provide immediate, practical solutions to particular problems, ecology is a soft science, and worse, that the theory is pointless because it lacks predictive ability (Lawton 1992, 1996a). Put bluntly, as far as these

critics are concerned, there are no rules to provide immediate answers to pressing problems. But this simplistic, not to say naive, criticism fails to confront the equally obvious fact that theoretical astronomy cannot (and does not try to) predict the position, size and temperature of every star in the heavens, or physical chemistry the exact size and shape of the next snowflake. Nobody can accuse astronomy or physical chemistry of being soft sciences.

If we need, or want, to predict in detail the population dynamics of a particular species in a particular habitat, then there is no alternative but to study that species in detail, in the place(s) or habitat(s) of interest. Some progress might be made at an intermediate level by drawing on knowledge of the dynamics of similar species (taxonomic relatives with a similar body size and trophic position for instance) (Pimm 1991), but detailed predictions require detailed knowledge. That is, we will have to build species- and location-specific models, and painstakingly measure the appropriate parameters. We may also need a good weather forecast to boot.

Incidentally, the fact that some populations may show chaotic dynamics obviously means that like weather forecasts, we will be unable to predict exact trajectories very far ahead. But chaotic fluctuations are bounded on the surface of an attractor, and thus (like climate, rather than weather) they have predictable properties. Chaotic dynamics do not make nature inherently unpredictable, but we have to be careful what it is we are trying to predict.

Specific management models are not developed in a theoretical vacuum

Nobody starts to construct detailed population management models in a vacuum. They elaborate and draw upon basic (contingent) theoretical models, using the same general principles (Lawton 1996a). One particularly nice example from many I could choose is the model developed by Potts (1986) from the Game Conservancy Trust at Fordingbridge in southern England, as a management tool for the grey partridge, *Perdix perdix*. Grey partridges are important game birds, or were until recently when populations severely declined. Potts and his group developed their model as a management tool, both to understand the causes of the decline and to devise ways of reversing it. The model incorporates no new population dynamic principles, and predicts very simple dynamics, namely stable equilibria set, inter alia, by habitat, food availability and predation. That is, it predicts the sort of general dynamics with stabilising, density dependent feed-backs that are shown by thousands of other animal populations. As I said earlier, there are rather few really distinct classes of population dynamics, and partridges are easily assigned to one of these classes. But as a management tool this model also shows that there are a very large number of minor, albeit practically important, variations on the one theme. The partridge model successfully predicts different population levels under different farming and predator-control regimes in Britain, and with a knowledge of changes in appropriate parameters, appears to make a good job of predicting partridge numbers in continental Europe, and North America where these birds have been introduced. It is a good management tool, based on excellent applied science.

However, it is sobering to realise that however good our contingent theory becomes, it is almost inevitable that specific population management questions will most reliably be solved by site- and location-specific studies to parameterise and refine the general models for the task in hand. In reality this means that good answers to population management questions are unlikely to be quick answers. Sometimes, there may be no alternative to a quick and dirty answer in a crisis; better a quick and dirty answer based on sound theory than wild or ill-informed guesses, or no answer at all. However, where there is time, ecologists must demand resources to provide properly researched answers. To do so does not mean that every case is so special that there are no rules. The rules are contingent, and for real populations they can be challenging to work out (Hilborn and Mangel 1997). They also have a proven track record of working.

Communities

Communities are orders of magnitude more complicated

The widely held notion that there are no rules or laws in ecology is primarily, I believe, due to the overwhelming emphasis placed by many practitioners on 'community ecology' – the ecology of sets of coexisting species interacting at local scales – and an equally strong emphasis on carrying out manipulative field experiments to discover how such assemblages are structured. Give or take some details, for this area of ecology the perceptions are correct. There are painfully few fuzzy generalisations, let alone rules or laws, and the necessary contingent theory looks unworkably complicated. Let me take some time to provide the background for this provocative statement.

In what follows I use the term 'community' very loosely to mean large sets of interacting species, and wherever possible follow Fauth et al. (1996) in using the more precise terms 'local guild' and 'assemblage' (which are what ecologists actually study).

Bracken insects and other systems

For twenty years, I studied a local guild of insects feeding on a patch of bracken fern, *Pteridium aquil-*

inum, at Skipwith Common, Yorkshire, in northern England. Over the study period, this bracken patch held an average of just over 17 species each year, with a minimum of 15, and a maximum of 19. The work was very much mainstream 'community ecology' in the broad sense of the word, dealing with a set of local species, interacting with one another, and their environment. I learned a substantial amount about the structure of this little local guild of insects (e.g. Lawton 1984, Cornell, in press, Lawton et al. 1993, Rashbrook et al. 1992). The majority of species populations are regulated by density-dependent processes, and their abundances are influenced by a mixture of top-down and bottom-up forces. The result is a high degree of temporal predictability in the rank order of species abundances (the rare species stay rare, and the common species stay common), although this predictability decays slowly over time (rank abundances are more similar two years than twenty years apart). The kinds of species in the system (how and when they feed), but not their abundances, appear strongly constrained by the need to avoid ant predation. Interspecific competition plays no detectable role.

As a study in community ecology, the approaches I took on the Skipwith bracken patch (strongly reductionist, with an emphasis on picking apart species interactions), and the kinds of insights I gained, are about par for the course. Some ecologists have done much better than I did in unravelling the processes involved in their favourite systems (outstanding, primarily zoological, examples from a variety of taxa and habitats include Davidson et al. 1984, Shorrocks and Rosewell 1987, Bradshaw and Holzapfel 1992, Paine 1992, 1994, Wise 1993, Hawkins and Sheenan 1994, Roughgarden 1995, Schoener and Spiller 1996, Wilbur 1997, and Spiller and Schoener 1998). In all these, and many other cases (mine included) the aim was, or is, to determine how the local community is structured by interactions between species, and between species and their environment, looking for 'assembly rules' (Diamond 1975); trying to understand why some species are common, others rare, and why some are excluded altogether; trying to sort out the relative importance of competition and predation, of top-down and bottom-up forces, or of disturbance on component populations, and so on.

The insights do not come easily (it is sobering that I can summarise twenty years of work on bracken at Skipwith in a short paragraph), but despite the challenges, ecology has made great strides in building up a series of case histories on local community assembly. The basic conclusion is that the important processes and resulting community dynamics differ, often markedly, from system to system, as Hutchinson (1957) realised would be the case over forty years ago. (Both Colwell (1984) and Schoener (1986) point out that this was also very much Robert MacArthur's position, although many subsequent practitioners of the discipline seem to have forgotten it.) In other words, there are no universal rules. Rather, as will now be obvious, the theories of community ecology are contingent upon the organisms involved, and on their environment. Unfortunately, the rules are contingent in so many ways (as we shall see in a moment) as to make the search for patterns unworkable. This is a hard-won insight, and we should not lightly discard it. Paradoxically, it is, in fact, a useful generalisation! The natural world need not have been organised like this – all local species assemblages could have worked according to exactly the same rules. That they do not does, however, present community ecologists with a fundamental dilemma.

Too much contingency

Although we now have a good understanding of how several local sets of interacting species work in nature, the problem is that we have no means of predicting which processes will be important in which types of system. To that extent, work on communities is no different to work on population dynamics. The difference is in the mind-boggling degree of contingency involved in work on communities.

One way to deal with numerous, particular examples is to classify them, in an attempt to discern emerging patterns and their underpinning rules, that is, to identify and define the contingencies (Strong et al. 1984, Giller and Gee 1987, Cornell and Lawton 1992, Huston 1994). Schoener (1986) provides by far the most comprehensive attempt to develop a body of contingent theory for community ecology, based not on taxonomy (e.g. birds vs barnacles vs beetles) (see McIntosh 1995) but on what he refers to as the two 'primitive axes' of organismal biology, and the environment. It is an heroic effort to pigeon-hole communities into types, and hence figure out the rules of engagement for different biotas and habitats.

Schoener defines six primitive organismic axes (body size, mode of recruitment, generation time, etc.) and six environmental axes (severity of physical factors, nature of resource inputs, spatial fragmentation, etc.). Assuming no correlations between kinds of organisms and kinds of environments, that makes 12 key drivers that create the basic template, and a vast number of unique combinations at particular points in this n-dimensional space, within which species can play out the game of community assembly. It is little wonder that the processes structuring communities differ markedly from system to system.

At the end of his book chapter, Schoener admits to being 'cautiously optimistic' that we will be able to develop a robust, contingent theory of community ecology by going down the route which he advocates. I am less certain. He is absolutely correct to draw attention to the complexity of the contingent constraints operating on community structure. As I have already pointed

out, ecologists should celebrate how far we have come in understanding this. But whether it is worth the effort of trying to shoe-horn every study into a point in n-dimensional space defined by combinations of at least 12 primitive axes, I have my doubts. That nobody has seriously attempted to use and test Schoener's model in the decade since it was published suggests that it may all be too complicated and too difficult to be useful.

The basic message is sobering. By painstakingly detailed studies of particular systems, we can broadly understand the local rules of engagement for interacting species at one place and time. But the Devil is in the contingent detail. Almost every place, time and species assemblage is sufficiently different to make more general patterns and rules almost impossible to find, and even if sometimes we can find weak generalisations, we will never be able to predict them from an a priori knowledge of six primitive organismic axes, and six primitive environmental axes (or any other, necessarily equally complex set of contingencies). Unlike population dynamics, I doubt that we could ever build a useful, practical model of an assemblage of even ten or twenty species (never mind hundreds of species) for management purposes. An alternative view, of course, is that I (and others) simply lack the imagination and courage to try.

Whole lake manipulations

One area in which these arguments certainly appear to be wrong is in limnology. The science of whole lake manipulations (for example adding or removing predatory fish at the top of the food chain to manipulate algal populations and hence water quality via a trophic cascade) is one of the triumphs of ecological science (Carpenter 1988, Carpenter and Kitchell 1993). Here there are certainly some relatively simple rules, contingent on a manageable number of variables. If it were not so, this technique of lake management would not work. And surely, lakes are complex ecosystems, with complex communities of organisms, involving hundreds of species? Yes they are, but for the purposes of the task in hand, they are not.

The trophic cascade in lakes involves relatively few key organisms, and (without doing too much violence to the biology) simple almost linear food chains (piscivorous fish → planktivorous fish → zooplankton → phytoplankton), each step with just one, or rather few species (except for the phytoplankton). Most of the diversity in the lake lies elsewhere, in the benthos and fringing reed margins. Hence the problem is basically one in population dynamics, not community ecology. There are important contingencies, even in this relatively simple system (see Kitchell 1992, Carpenter and Kitchell 1993 for detailed discussions), but not so many as to become unworkable. Similar remarks apply to work on terrestrial food chains on islands in the Bahamas (lizards → spiders → insects → plants), referred to above (Spiller and Schoener 1990, 1994, 1998). This is probably about as complicated and contingent as theoretical ecology can get at the moment. It clearly shows that there are general patterns, and useful rules underpinning them; but it also stakes out the boundaries of current progress.

Other types of generalisation

Before moving on, it is worth pointing out that generalisations of a quite different nature *have* emerged from the rummage-box of case histories in community ecology. We now know, for example, that several kinds of 'indirect interactions' (Bender et al. 1984, Kerfoot and Sih 1987, Polis and Holt 1992, Wootton 1994, Menge 1995, 1997) propagated through the food web (as opposed to direct trophic or competitive interactions) play an important role in determining local community membership and population abundances, and that surprisingly, indirect interactions do not take longer to reveal themselves than direct interactions in experimental manipulations of communities (Menge 1997). This is certainly not a law, but it is a useful generalisation. It warns us, for example, to expect unexpected changes in communities when they are manipulated or changed in some way; indirect interactions generate surprises.

Another set of generalisations that advance slowly, retreat, regroup and perhaps advance again are patterns in trophic webs. A decade ago, it really did look as though there were repeated patterns in food webs, and a theoretical framework to explain them (Pimm et al. 1991). Now, with much better empirical data, prompted by the earlier (some would say premature) generalisations, the whole thing looks much more uncertain, at least for some, if not all of the patterns of potential interest (Hall and Raffaelli 1993, 1997). I remain optimistic that there are patterns in, and rules governing, the structure of food webs, but have to confess that I could be wrong.

Other problems with trying to find rules for community ecology

In sum, ecologists quite rightly perceive that the huge research effort in community ecology, which is still ongoing, has not produced much in the way of patterns, or workable, contingent rules. There are also other reasons for this state of affairs. It is useful to bring them together briefly here, together with some of the problems I have already touched on, thereby cramming the essence of the arguments into a few short paragraphs:

1. Repeating myself to start off with, for most multispecies assemblages, with great effort we can work out some of the details of how the system is put together, but every system seems different, and we have no way of predicting what the local rules of

engagement are for a new, unstudied system. That is, we know theory is contingent but we find the contingency overwhelming.

2. Where hard-won insights have been gained about species interactions at one place and time, there is a worry that the important processes may change over time (Bengtsson et al. 1997, Maurer 1998a, b). By definition, they are bound to change in successional systems, and in the long run, reddened environmental noise (Halley 1996, Petchey et al. 1997) will destroy all nature's local handiwork. But if the local rules of engagement are transitory, it may be hard to use them to make predictions, even at the same locality, at some time in the future. It remains an open question whether key processes and interactions change and decay over time at different rates in different systems; presumably they do, not least because the generation times of dominant species are very different in different ecosystems.
3. What we have learned at great cost about species interactions within communities at one place may also not be readily transferable to broadly similar systems 'somewhere else'. This is a startling conclusion for those who believe, for example, that 'keystone species' exist. More likely, there are keystone interactions at one place, over a limited period of time; but the same species, in a different place may have much more feeble effects (Mills et al. 1993, Menge et al. 1994, Power et al. 1996). If you doubt this, recall that the impact of any species on its community depends upon its abundance, the environment, and the web of species interactions within which it is embedded. Since population abundances of all species vary throughout their range (often in systematic and interesting ways – Taylor and Taylor 1979, Gibbons et al. 1993, Maurer 1994, Lawton 1996b), and since no two locations on earth have exactly the same set of species and the same environment, it seems extremely unlikely that local rules of engagement in community ecology will easily generalise to 'somewhere else'.
4. Indirect effects, propagated through webs of species interactions, make predictions about the behaviour of even well studied systems to novel perturbations certainly very difficult, and probably unreliable. The best we can do is expect the unexpected. Actually this is better than nothing, because as a simple generalisation in its own right, it provides a useful policy tool if we wish to live with, and to manage uncertainty, rather than trying to control nature.
5. Paradoxically, perhaps *the* major weakness of traditional community ecology, and why it has so conspicuously failed to come up with many patterns, rules and workable contingent theory, is its overwhelming emphasis on localness. By assuming that most of the key drivers determining community structure happen internally, within the system, the discipline could be missing major parts of the action, at least for two important properties of local communities – the number of species involved, and their local abundances. I want to spend some time examining the first of these problems (the number of species), in the next section.

In sum, community ecology may have the worst of all worlds. It is more complicated than population dynamics, so contingent theory does not work, or rather, the contingency is itself too complicated to be useful. But paradoxically, community ecology is not big and bold enough to break out of the overwhelming complexity within which it appears to be enmeshed. All this begs the question of why ecologists continue to devote so much time and effort to traditional studies in community ecology. In my view, the time has come to move on. One solution may well be to increase the scale of the endeavour even more, to the point at which all the special details 'average out', and life once again becomes organised around a few relatively simple underlying rules. Whittaker's biomes are a model example.

Macroecology

Overview

Macroecology is a blend of ecology, biogeography, and evolution and seeks to get above the mind-boggling details of local community assembly to find a bigger picture, whereby a kind of statistical order emerges from the scrum (Brown and Maurer 1989, Brown 1995, Blackburn and Gaston 1998, Maurer 1998b, Gaston and Blackburn 1999). Macroecology is the search for major, statistical patterns in the types, distributions, abundances, and richness of species, from local to global scales, and the development and testing of underlying theoretical explanations for these patterns. By identifying macroecology as an emerging ecological discipline, and giving it a name, Jim Brown and Brian Maurer have done our science an enormous favour. The main emphasis to date in this emerging discipline has been on patterns at the species level, but I see no logical reason why the approach cannot embrace higher units of biological organisation, from Whittaker's analysis of the distribution of biomes, to major patterns and regularities in the structure and function of ecosystems.

Individuals have been doing macroecology for decades, without giving it a special name. The canonical log normal distribution of population abundances (Preston 1962), the theory of island biogeography (MacArthur and Wilson 1967), tropical-temperate diversity gradients (Pianka 1966), and attempts to explain why the number of insect species attacking different kinds of plants within a geographic region varies by at least two orders of magnitude (Strong et al. 1984) are

four examples. In principle, each of these phenomena might have been revealed by detailed, reductionist studies of all the species involved, by studying their life histories, enemies, competitors, other interactions, migration rates, and so on. But actually, put like that, the task is clearly hopeless! The patterns only emerge by ignoring the details. (See Gaston and Blackburn (in press) for further discussion.) Let me give a contemporary example.

The relationship between local species richness and the size of the regional species pool

To see where we are heading, consider one of the simplest questions one could ask about a local guild, or an assemblage. What determines the number of species it contains (Lawton 1996c)? As pointed out earlier, I observed an average of about 17 species of herbivorous insects feeding on bracken at Skipwith each year. Why 17? In crude order-of-magnitude terms, why not 2, or 170? This most basic of all aspects of community structure may have surprisingly little to do with the local processes that dominate so much of traditional thinking in community ecology. Nor can the question necessarily be answered by doing any number of small-scale manipulative experiments. To answer it, we need to take a macroecological approach.

The main environmental filters

Assembling communities, local guilds, etc., is a multi-stage, multi-layered process. It starts with a regional pool of species, exactly as MacArthur and Wilson (1967) recognised over 30 years ago. The pool exists within a biogeographic region, extending over spatial scales many orders of magnitude larger than those of the local community. Understanding the origins of the pool requires a knowledge of the evolutionary history of the biota, of geology, of plate tectonics and so on. Most ecologists simply accept the pool as a given, and ignore its importance. Ricklefs has argued forcefully that such myopia is unwise (Ricklefs 1987, 1989, Ricklefs and Schluter 1993).

Local communities assemble themselves from this pool through a series of filters, or stages (two decades of thinking about these filters, and a huge literature, are encapsulated between Roughgarden and Diamond (1986) on the one hand and Zobel (1997) on the other). The filters themselves work on different spatial and temporal scales, and overlap. But broadly they are these. First, species have to arrive and establish populations. Distance, isolation from the pool, excludes many (as MacArthur and Wilson knew). Others get there but find the habitat unsuitable. Strong environmental filters work on all communities (e.g. Rørslett 1991, Keddy 1992). More subtle processes operate at the landscape scale, somewhere between the regional pool and the local community – what Holt (1993) calls 'ecology at the mesoscale'. We are all familiar with species-area relationships, but as well as the effects of area, differences in the number, shape and spatial arrangement of habitat patches can mean the difference between population persistence and local extinction (e.g. Robinson et al. 1992, Holt 1993, 1996, Wiens et al. 1993, Kruess and Tscharntke 1994, Hanski and Gilpin 1997, Collinge and Forman 1998, Davies and Margules 1998, Gonzalez et al. 1998, Lei and Hanski 1998), and will further filter and mould local assemblages. Only at the lowest level do the core concerns of traditional community ecology come into play – the role of species interactions in winnowing out the survivors who made it through all the other big filters. Viewed in this way, traditional community ecology is actually about second-, possibly even third-order processes (Lawton 1996c).

Of course, this series of large-scale hierarchical filters itself constitutes a set of contingent theoretical constraints. But out of this contingency emerges some rather simple patterns.

Type I and Type II systems

Consider the relationship between regional species richness (the pool) and local species richness (the community, local guild, assemblage, etc.) (Cornell and Lawton 1992, Cornell 1993, in press, Cornell and Karlson 1997, Srivastava 1998). Plot the richness of regional pools on the x-axis, and the richness of local assemblage(s) appropriate for each pool on the y-axis. Because every species cannot live everywhere, and chance or isolation excludes others, with a few notable exceptions (e.g. Dawah et al. 1995), we do not expect every species in the regional pool to occur in every community (Zobel 1992). The simplest model of the relationship between regional and local species richness is then one of 'proportional sampling' (Type I), with local richness directly proportional to, but less than, regional richness. Basically, this model says that knowledge of local species interactions (interspecific competition, predation, parasitism, disease, apparent competition, intra-guild predation, and the other emerging games played out in complex local assemblages and guilds) is not sufficient to understand local species richness. Local richness is directly proportional to the size of the regional species pool.

On the other hand, if species interactions are important in structuring communities, and specifically if they set hard limits to the number of species able to coexist locally, then (other things being equal) the graph of local vs regional richness will be a negatively accelerating curve to a plateau (Type II). Biologically realistic models of interacting species assembled from a regional pool produce nicely saturating curves (Caswell and Cohen 1993, Morton and Law 1997). Real sets of species could lie anywhere between a Type I and a Type II system, as species interactions become more and more important in con-

straining local species richness. But notice that at this level, the possible outcomes have simplified. We are no longer overwhelmed by detail. Theory defines just two extreme outcomes, plus intermediates. Patterns emerge once more.

There are, inevitably, some (contingent) theoretical complications. Modest levels of environmental disturbance that knock out patches of species within the community can generate linear (Type I) local-regional richness plots, even if interspecific competition is strong enough to create Type II curves in the absence of disturbance (Caswell and Cohen 1993). Alternatively, models that simulate sampling from a regional pool of species, with abundances conforming to the widely observed canonical log normal distribution, can generate 'pseudo-saturated' Type II curves with low sampling efficiency, but a complete absence of species interactions (Caley and Schluter 1997). In other words, pattern alone does *not* define mechanism. I return to this problem later. But whatever the underlying mechanism(s), the question of where real ecological assemblages lie on the continuum from Type I to Type II systems has major implications for community ecology, and the search for patterns and rules in nature.

If Type II systems are common, or the norm, with hard and consistent limits to local richness set by species interactions, the concerns of traditional community ecology are vindicated; local processes dominate over regional ones. Under these circumstances, an agenda for community ecology focusing on small-scale local manipulation experiments, designed to unravel the rules of community assembly, would be entirely justified, and we are in for a long haul. But if Type I systems, or weakly curvilinear, intermediate systems are the norm, this is no longer true. To understand the most basic fact about a local assemblage – how many species does it contain, and all that must flow from this – the traditional agenda of community ecology looks unnecessarily complicated (Lawton 1996c).

Are most real systems Type I or Type II? Technical concerns

On present evidence, the answer to the question 'are most real systems Type I or Type II?' is 'in the majority of cases, they are Type I'. One of my students, Diane Srivastava, has done a thorough job of reviewing the literature; this summary draws heavily on her thesis (Srivastava 1997) (see also Srivastava 1998), and on an independent review by Cornell and Karlson (1997). First we need to think about some technical problems.

Srivastava makes the point that there is confusion in the literature on the types of data that are appropriate for testing where real systems lie in this model framework. For instance, data mixing up different habitats in the same region, involving different types of species, albeit broadly related ones (e.g. local and regional plant species richness in forests, grasslands, bogs and heaths in a single geographic area – Pärtel et al. 1996) will usually be inappropriate, because they can easily generate artefactual Type I relationships. The details are unimportant here, but mean we must focus on data involving similar taxa and habitats, derived from different regions, or (for parasites and plant-feeding insects) different host-species within one region.

Srivastava's second point is that formal statistical tests to distinguish between Type I (linear) and Type II (curvilinear, saturating) relationships are far from straightforward; for example local and regional species richness are not statistically independent (Cresswell et al. 1995, Zobel 1997), and data on local richness may be pseudoreplicated. Problems can also arise through, and artefactual relationships be created by, difficulties and errors in estimating what constitutes the regional pool (Cornell and Lawton 1992, Eriksson 1993, Zobel 1997) (overestimation of the pool size, for instance, can generate false Type II curves).

These kinds of difficulties are not unique to the relationship between local and regional richness. Similar problems are encountered throughout the emerging discipline of macroecology (Blackburn and Gaston 1998, Gaston and Blackburn 1999), where data are hard to get, and may often have been gathered originally for purposes other than the task in hand. The best way forward is not to be paralysed by technical details (Gaston et al. 1998b), but rather to proceed cautiously on two fronts. The first is to ask what the available data actually look like, despite the known problems, and to draw preliminary conclusions – tentative models of what the world seems to be like. The second is then to seek independent evidence for whichever model seems best to describe a particular system (e.g. Hawkins and Compton 1992). In the present case, we might seek experimental or statistical evidence for strong species interactions (interspecific competition for resources, apparent competition via shared enemies, etc.) in systems that appear to be Type II. The counter-prediction is obviously that equivalent, strong interactions will be absent from Type I, and from weakly curvilinear, intermediate systems; or (more subtly) that their effects are mitigated by overriding processes (see Cornell and Lawton 1992, Cornell and Karlson 1997, Srivastava 1998), for example disturbance (Caswell and Cohen 1993), or by strong spatial heterogeneity in species' distributions (e.g. Shorrocks and Rosewell 1987, Shorrocks and Sevenster 1995).

A review of examples

As I have already stated, a majority of ecological systems appear to be Type I. Examples include bracken insects (Lawton 1990) and other plant-feeding insects (Cornell 1985a, b, Zwölfer 1987, Lewinsohn 1991), wood-boring beetles (Stevens 1986), tiger beetles (Pearson and Juliano 1993), fig wasps and the parasitoids of fig wasps (Hawkins and Compton 1992), other para-

sitoids (Gaston and Gauld 1993, Dawah et al. 1995), helminth parasites of alien fish (Kennedy and Guégan 1994), corals (Cornell and Karlson 1996), fish (Westoby 1993, Hugueny and Paugy 1995, Oberdorff et al. 1995, 1998, Griffiths 1997, Hugueny et al. 1997), lizards (Westoby 1993), birds (Pearson 1977, Wiens 1989), a variety of vertebrate taxa (fish, reptiles, mammals and birds, each analysed separately) (Caley and Schluter 1997), and plants (Wisheu and Keddy 1996). Conservatively counting papers with data for more than one taxon only once, the list currently contains at least 23 examples. Other studies also suggest Type I relationships (e.g. *Phylloscopus* warblers, Richman 1996), but the data presented are not complete enough to be sure.

In contrast, 15 papers describe curvilinear relationships. Only some of these appear to be strictly Type II, saturating curves; the rest are intermediate and weakly curvilinear (see Cornell and Karlson 1997 for examples). Classifying those cases where we can be reasonably confident that the relationships are either saturating '[strong]', or weakly curved '[weak]', (the remainder have too few data points, or other uncertainties to be sure), the non-linear set of examples includes marine crustaceans (Abele 1984), deep-sea gastropods (Stuart and Rex 1994 [weak]), tiger beetles (Pearson and Juliano 1993), fish and amphibian parasites (Aho 1990 [strong], Aho and Bush 1993 [strong], Kennedy and Guégan 1994 [strong]), fish (Bohnsack and Talbot 1980, Tonn et al. 1990), birds (Ricklefs 1987 [weak], Case 1996 [weak]), mammals (Van Valkenburgh and Janis 1993 [strong], Kelt et al. 1996 [strong]) and higher plants (Rørslett 1991 [strong], Westoby 1993, Richardson et al. 1995 [weak]).

Not all these examples were plotted and analysed by their original authors in the way I am proposing here. They are included where the results can be sensibly interpreted in the light of this model, or where re-analysis of the data produces linear or curvilinear fits (Wiens 1989, Cornell and Lawton 1992, Srivastava 1997, Cornell and Karlson 1997). There are also a small number of cases where the original authors, Srivastava, and Cornell and Karlson reach different conclusions. For instance Hawkins and Compton (1992) find that a curvilinear model provides a slightly better fit than a linear model for fig wasps, but point out that the improved fit is at the 'wrong end' (i.e. the low diversity end) of the local-regional diversity plot. Srivastava places this example firmly in Type I, because there is no evidence of curvilinearity in moderate to high diversity systems. Cornell and Karlson included this example in their weakly curvilinear category.

This head-count of papers is not in any way definitive. Many of them suffer from one or more of the statistical and methodological problems outlined earlier, whilst some of the studies supporting the Type II model are based on just two data points, showing equal local richness despite big differences in regional pool sizes. They have been included here, and taken on their face value, but we cannot rule out the possibility that the systems they represent are actually Type I, with two randomly drawn points that happen to have the same local richness.

Taking all these caveats into account, the tentative conclusion is that Type I systems, and weakly curvilinear, intermediate systems have been reported at least twice as frequently in the real world as saturating Type II systems. Indeed if we simply add up the numbers, and ignore the 'don't knows', Type I and weakly curvilinear systems could be about four times commoner than Type II systems. We can, if you like, treat this as our current working hypothesis. Given all the complexities of community ecology, what emerges is a rather simple picture – emerging patterns and rules that set the bounds on two possible extremes of behaviour for one of the most fundamental problems that ecologists might want to answer: what determines the number of species in my chosen study system? By getting above the details, macroecology simplifies what we need to know, and measures and reveals things that all the small-scale, detailed, reductionist experiments in the world will not reveal (Gaston and Blackburn 1999).

Are these conclusions supported by other evidence?

As Cornell and Karlson (1997) point out, in part these data are broadly in line with what one might expect on other grounds. For instance, interspecific competition is not generally a strong or pervasive force in bracken-feeding insects (Lawton 1984, in press), nor in other local guilds of phytophagous insects (Strong et al. 1984), consistent with the fact that available studies with this group all conform to Type I. (This is not to say that some phytophagous insects do not compete some of the time. They do. It only says that interspecific competition is not all pervasive in this group.) But there are also some puzzles, reminding us that the similar patterns can be generated by more than one process. Parasite assemblages on amphibia and fish appear to saturate strongly, yet at least one expert on fish parasites has argued that these systems are very far from being saturated with species (Rohde 1998). It is also hard to see many other taxonomic or habitat-related patterns in the data, echoing the difficulties encountered in attempts to identify and classify different types of communities discussed earlier. Some of the same taxa appear in both camps, but when this appears to be related to habitat (e.g. Pearson and Juliano 1993), it is not at all clear why. We are therefore stuck back with the problem of not having any a priori way of knowing whether a potential study system is Type I, Type II, or somewhere in between. I currently see no route out of this dilemma – macroecology is not a magic bullet. But I prefer the simplicity of the basic pattern between local and regional species richness, to the full-blown complexity of life before we had this simple model.

Conclusions

In a clear majority of studies, possibly the great majority, the main driver of local species richness appears to be the size of the regional species pool, with local richness linearly, or weakly curvilinearly, related to regional richness. Data consistent with hard limits to local richness exist, but they are not a majority. Strong dependence of local richness on regional richness may arise because species interactions – the stuff of traditional community ecology – are weak; or species interactions are strong but do not constrain species richness (for example strong 'top-down' impacts of specialist enemies); or they are strong but their effects are overridden by other processes (Cornell and Lawton 1992, Cornell and Karlson 1997), for example disturbance (Caswell and Cohen 1993), or spatial heterogeneity (e.g. Shorrocks and Rosewell 1987, Shorrocks and Sevenster 1995). The rules are contingent, but not so contingent as to be impossible to understand. And whatever the contingent rules, in all these circumstances, to answer the most basic questions about a community – how many species does it contain, and why? – community ecologists have to lift their heads above the parapet, and become macroecologists. When you do, the questions change, but the patterns become both simpler and clearer, and with that comes the possibility of discovering some simple, albeit still contingent, underlying rules.

Other macroecological patterns and conclusions

Macroecology is not a panacea in the search for patterns and rules in ecology. But like the relationship between temperature, rainfall and biomes, or local species richness and the size of the regional pool of species, sufficient other examples exist to convince me that standing back to get the bigger picture will reveal far more general ecological patterns and rules than will the arch reductionism that currently grips our subject (Gaston and Blackburn 1999). The rules and patterns will be contingent, as I hope I have made plain. They will not be universal laws. But, on present evidence, manageable contingency emerges at macroecological scales.

I do not propose to produce an exhaustive list of current macroecological patterns, nor some of the criticisms that have been levelled at them. The reader should look in Brown and Maurer (1989), Gaston (1994), Brown (1995), Blackburn and Gaston (1998), Maurer (1998a, b) and Gaston and Blackburn (1999). All the patterns admit of some exceptions, because the driving processes are contingent. But the generalisations are considerably more numerous and robust than the few, and often weak conclusions to emerge from traditional community ecology. For some there are arguments about the details, but these arguments are largely about second-order phenomena, interesting and important as these may be for understanding the underlying processes.

I have deliberately chosen a range of different types of examples, including some ecosystem-level patterns, to illustrate the breadth of the approach, as well as highlighting some obvious advantages and disadvantages. Some of the patterns will be familiar to almost everybody. I present them to make the case that there are plenty of patterns in ecology, underpinned by well-studied rules and mechanisms, albeit that a widespread pattern does not have to be generated by the same processes everywhere; arguably, the most robust patterns are those for which there are several alternative theoretical explanations, and which can hence be generated by several different mechanisms (good examples are provided by 4–7 below) (Lawton 1996c, Gaston and Blackburn 1999). The patterns are:

1. Truncated, roughly log normal distributions in the frequency of species abundances within animal assemblages (Preston 1962, Nee et al. 1991), and approximately log normal frequency distributions in the size of species geographic ranges (Gaston 1994). Intriguingly, with high-quality data, both patterns may display significant left skew; that is compared with a log normal distribution there are too many species with tiny populations and very small ranges (Gaston and Blackburn 1997, Gaston 1998). The significance of these 'tails' is unclear, although a left skewed frequency distribution of population abundances can be generated by a simple model of the way in which species divide up resources (Sugihara 1980, 1989, Nee et al. 1991) (once again getting above the messy detail of traditional work in this area). But the model remains contentious. Theoreticians have only recently started to address the left-skewed distribution of range sizes (J. Harte, A. Kinzig and J. Green unpubl.). In other words, analyses at this scale can point to important research questions, as well as identifying broad patterns in nature.
2. Truncated log normal patterns in the number of animal species, locally and globally, within different body-size classes (May 1978, Morse et al. 1988, Blackburn and Gaston 1996a, Siemann et al. 1996, Fenchel et al. 1997, Lawton 1998).
3. Intriguing 3- and 4-way relationships between species richness, population abundance, size of geographic range, and body size (Gaston and Lawton 1988a, b, Morse et al. 1988). It is currently unclear where cause and effect lies in these higher dimensional patterns.
4. Species-area relationships, predominantly (but not always) linear on double log axes, with interesting differences between local, regional and continental scales (Connor and McCoy 1979, Rosenzweig 1995).

5. An almost universal positive interspecific correlation between local population abundances, and the size of species geographic ranges (Brown 1984, Hanski et al. 1993b, Gaston et al. 1997, Gonzalez et al. 1998), and a more poorly studied, but emerging intraspecific correlation of the same form (Gaston et al. 1997, Donald and Fuller 1998). (Notice that given the interspecific relationship, the same species ought to be involved in the tails of the left-skewed frequency distributions of both range sizes and population abundances (1, above), but there have been no tests of this prediction.) Patterns (4) and (5) can be united by a single theoretical model (Hanski and Gyllenberg 1997).
6. Very familiar relationships between latitude and species richness (Rosenzweig 1995), but with many intriguing departures from the broad pattern (see Gaston 1996 for a short review). For example, in marine prosobranch gastropods (Roy et al. 1998), peak diversity lies about 10° N of the equator; in parasitoid wasps it lies even further north (Quicke and Kruft 1995, Sime and Brower 1998), and in some taxa the pattern is reversed (Rabenold 1979, Kouki et al. 1994). For so well known a broad pattern, there is absolutely no consensus about the rules and mechanism(s) underpinning it (Rosenzweig 1995, Blackburn and Gaston 1996b, Rosenzweig and Sandlin 1997, Rohde 1997, 1998 and references therein), nor about whether the anomalies and exceptions share common features.
7. Related, but distinct, patterns between energy inputs to ecosystems and species richness (Wright 1983, Currie 1991, Wright et al. 1993, Francis and Currie 1998). Again, the mechanism(s) are not well understood (Srivastava and Lawton 1998), although in the broad patterns we begin to see the merger of ecosystem processes with studies of species richness.
8. In what is typically regarded as the heartland of ecosystem science, there are also big bold patterns galore. Although they have been developed by a quite different group of scientists, for quite different reasons, they have all the hallmarks of macroecology, not least a scant regard for the myriad of detailed species interactions within them. The patterns emerge well above that level, for example linking net primary production with net consumer biomass and rates of consumption (McNaughton et al. 1989, Cyr and Pace 1993), revealing fascinating differences in these patterns between terrestrial and aquatic ecosystems.
9. Quite different perspectives on ecological processes are provided by the fossil record. As with large-scale patterns in space, long time horizons filter out the details to reveal unsuspected regularities in nature. For example, at very large time scales in the fossil record (10^8 years) we see the emergence of 'evolutionary faunas and floras'. In the marine environment there are three – the Cambrian, Palaeozoic, and Modern (Jablonski and Sepkoski 1996). Each marine evolutionary fauna appears to have its own characteristic level of diversity, increasing in stepwise succession from oldest to youngest. One hypothesis might be that these characteristic levels of diversity arise as a strong signal from the myriads of weak, fuzzy interactions that community ecologists study in contemporary time.

Concluding remarks

I could go on, but these are quite sufficient. These, and other macroecological patterns, set the boundary conditions within which the overwhelming details of ecological interactions take place. The patterns suggest a framework of contingent laws and rules for ecology. The patterns themselves emerge from four truly universal laws that govern our discipline. From the interplay of these four universal laws, nature has created a glorious diversity of life, that is fun to study, and never-ending in its surprises. General ecological patterns emerge most clearly from this glorious diversity when systems are not too complicated, that is when the contingencies are manageable (as in the population dynamics of single species, or very small numbers of interacting species), and at very large scales, when a kind of statistical order emerges from the scrum. The middle ground is a mess. It is fascinating to study, and rich in wonderful biology. But by studying it, do not expect universal rules, even simple contingent general rules, to emerge. If and when they do, treasure them.

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