

- 8 Kamil, A.C. (1989) in *Comparative Perspectives in Modern Psychology* (Leger, D.W., ed.), pp. 257–308, University of Nebraska Press
- 9 Wood-Gush, D.G.M., Dawkins, M.S. and Ewbank, R., eds (1981) *Self-awareness in Domesticated Animals*, The Universities Federation for Animal Welfare
- 10 Byrne, R. and Whiten, A., eds (1988) *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans*, Oxford University Press
- 11 Griffin, D.R. (1985) in *Leaders in the Study of Animal Behavior* (Dewsbury, D.A., ed.), pp. 121–142, Bucknell University Press
- 12 Bekoff, M. and Jamieson, D. *Perspect. Ethol.* (in press)
- 13 Nagel, T. (1974) *Philos. Rev.* 83, 435–450
- 14 Bernstein, I. (1981) *Behav. Brain Sci.* 4, 419–455
- 15 Tomback, D.F., Wachtel, M.A., Driscoll, J.W. and Bekoff, M. (1989) *Ethology* 82, 275–286
- 16 Hinde, R.A. (1987) *Individuals, Relationships and Culture: Links Between Ethology and the Social Sciences*, Cambridge University Press
- 17 Hinde, R.A. (1985) *Anim. Behav.* 33, 985–992
- 18 Byers, J.A. and Bekoff, M. (1986) *Ethology* 72, 342–345
- 19 Bateson, P. in *Interpretation and Explanation in the Study of Animal Behavior* (Bekoff, M. and Jamieson, D., eds), Westview Press (in press)
- 20 Eisenberg, J.F. (1981) *The Mammalian Radiations: An Analysis of Trends in Evolution, Adaptation, and Behavior*, University of Chicago Press
- 21 McNab, B.K. and Eisenberg, J.F. (1989) *Am. Nat.* 133, 157–167
- 22 Shea, B.T. (1987) *Int. J. Primatol.* 2, 139–156
- 23 Dupré, J. in *Interpretation and Explanation in the Study of Animal Behavior* (Bekoff, M. and Jamieson, D., eds), Westview Press (in press)
- 24 Wilder, H. in *Interpretation and Explanation in the Study of Animal Behavior* (Bekoff, M. and Jamieson, D., eds), Westview Press (in press)
- 25 Umiker-Sebeok, D.J. and Sebeok, T.A. (1980) in *Speaking of Apes: A Critical Anthology of Two-Way Communication with Man* (Sebeok, T.A. and Umiker-Sebeok, D.J., eds), pp. 1–59, Plenum Press
- 26 Savage-Rumbaugh, S. (1986) *Ape Language: From Conditioned Response to Symbol*, Columbia University Press
- 27 Kuhn, T.S. (1969) *The Structure of Scientific Revolutions*, University of Chicago Press
- 28 Stevenson, L. (1989) *Inquiry* 32, 213–222
- 29 Haraway, D. (1989) *Primate Visions: Gender, Race, and Nature in the World of Modern Science*, Routledge
- 30 Midgley, M. (1989) *Wisdom, Information, and Wonder: What is Knowledge For?* Routledge
- 31 Rollin, B. (1989) *Bioethics* 3, 211–225
- 32 Dawkins, M.S. *Behav. Brain Sci.* (in press)
- 33 Burley, N., Krantzberg, G. and Radman, P. (1982) *Anim. Behav.* 30, 444–455
- 34 Driscoll, J.W. and Bateson, P. (1988) *Anim. Behav.* 36, 1569–1574
- 35 Singer, P. (1975) *Animal Liberation: A New Ethics for our Treatment of Animals*, Avon
- 36 Finsen, S. in *Interpretation and Explanation in the Study of Animal Behavior* (Bekoff, M. and Jamieson, D., eds), Westview Press (in press)
- 37 Dunbar, R.I.M. (1989) *Anim. Behav.* 37, 699–700
- 38 Regan, T. (1985) *The Case for Animal Rights*, University of California Press
- 39 Callicott, J.B. (1980) *Environ. Ethics* 2, 311–338
- 40 Rachels, J. (1989) in *Animal Rights and Human Obligations* (Regan, T. and Singer, P., eds), pp. 95–103, Prentice-Hall
- 41 Ruse, M. (1989) in *What the Philosophy of Biology Is: Essays Dedicated to David Hull* (Ruse, M., ed.), pp. 1–15, Kluwer
- 42 Whiten, A. and Byrne, R.W. (1988) *Behav. Brain Sci.* 11, 233–273
- 43 Dennett, D.C. (1987) *The Intentional Stance*, MIT Press
- 44 Dennett, D.C. (1989) in *Goals, No-Goals and Own Goals* (Montefiore, A. and Noble, D., eds), pp. 101–116, Unwin
- 45 Sugden, A.M. (1989) *Trends Ecol. Evol.* 4, 256–257

Because of its unwieldy complexity, understanding organization at the community level has been an elusive, often frustrating enterprise. This survey concentrates on the assembly process itself, and examines whether there are mechanics to community assembly that provide the foundation for a general theory of organization at the community level.

Whether ecological communities are patterned structures, populations that respond independently to environmental gradients, or idiosyncratic, random collections of species has long been a central issue of ecology^{1–9}. Arguably, such distinctions form the most fundamental aspects of ecological thought and knowledge. Yet, despite considerable attention and a variety of approaches^{10–13}, neither an empirical nor a theoretical framework has emerged that adequately describes phenomenology at the community level. Reasons abound

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Communities As Assembled Structures: Do Rules Govern Pattern?

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for this lack of progress, ranging from the sheer complexity of ecological systems^{14,15}, to the belief that there are insufficient grounds for thinking that harmonious processes occur at the community level. Here I discuss the phenomenon of community assembly and evaluate whether the mechanics of assembly might provide the desired framework. I explore the evidence for the existence of community assembly rules, for example rules that govern the dynamics – or produce an ‘apparent’ lack of dynamics – of community change between states.

Before one can begin to ask whether rules of assembly exist – and by extension whether general principles exist – one must first have an adequate community definition. This is a seemingly simple task. However, a perusal of the ecological literature shows that insect, lizard,

plant or bird communities exist, or that the species comprising a guild (e.g. frugivorous birds) or inhabiting a location (e.g. benthos, parasites) have been considered as communities. However, it is clear that such diverse entities cannot simultaneously satisfy a community definition based on phenomenology (Box 1).

This is not simply a semantic problem. Inconsistent usage is risky in at least two ways. First, many of these ‘communities’ do not possess even a hint of community properties or, at best, possess only a portion of these properties. For example, if a few species (e.g. bacteria, birds or beetles) vary in abundance through time while the vast majority of the species and community biomass (e.g. vegetation) remains approximately constant, does the system tend towards equilibrium dynamics

Box 1. A community definition

For the purposes of this survey, a community is defined as the ensemble of species in some area whose limits are determined by the practical extent of energy flow¹⁶⁻¹⁹. What is the practical extent of energy flow? Paine¹⁶ showed that in the rocky intertidal system, predators often have very weak or spurious links to numerous prey species, while their diet is composed of only a few primary prey. If the population dynamics of the consumer and prey species are not influenced by the incidental predation events, such trophic links can properly be ignored. Clearly, the identification of spurious links is not a simple task. The key to determining community limits is to identify boundaries, manifest as interspecific interactions broadly defined, by documenting where the population dynamics of species in an ensemble (including indirect and cascading effects) are unaffected by each other.

This definition is based on observable phenomenology rather than arbitrary criteria. Such a definition may include a large number of species, so much so that critics might plead unwieldy complexity. However, nature proceeds without regard to human logistical and analytical sophistication. For example, soil arthropod activity can lead to an increase in above-ground primary productivity. Such effects can cascade throughout the entire system. Properties and processes must be used to delineate this level of organization. Measures of organization such as relative abundance, stability, diversity, topology, food web pattern and productivity are ensemble properties, not properties of community 'pieces' in isolation. While investigation of community components is an appropriate first step in community analysis, such studies provide insight into only part of the story – insight that may be misleading. It must be remembered that the behavior of isolated pieces (e.g. a population, guild or taxonomic association) may not reflect the dynamics of the whole. A reductionistic approach is a valuable tool, yet it has limited power here.

or not? This is a critical question, and serves to illustrate the scale problems inherent in whole-community analyses^{14,15}. If our 'community' is composed of only birds or insects, we might conclude a lack of equilibrium dynamics^{20,21}. If our view of the community includes all species, we may decide that the system is stable overall with some variation among minor components. This is a crucial distinction, but which view is correct? While organisms operating at disparate levels of scale (e.g. soil bacteria versus forest trees) may appear dynamically uncoupled, they are clearly not, and strong functional relationships exist regardless of vast differences in generation time.

Second, given that various community components (e.g. species, guilds, locations) are all studied under the guise of 'communities', it is not surprising that general prin-

ciples – if indeed they do exist – have gone largely undetected. This is not to say that all communities and their components are governed by the same processes and rules; simply, that comparative analyses using such data are of limited value. The analysis of community components can yield valuable insight into ecological structure. Clearly, much can be learned by concentrating on intra-guild interactions. To date, however, the search for generality among widely differing levels of organization has done little to suggest general principles. If further progress is to be made in understanding communities, *communities* must be studied rather than their components.

The detection of pattern and historical relics

The first step in determining whether rules of assembly exist is to demonstrate that a community exhibits pattern in excess of that expected by chance. There has already been considerable discourse on the construction of null models used to detect a departure from a random expectation^{7,22,23}. This issue remains unresolved. For example, several studies have shown that the detection or denial of pattern can be complicated by historical variation in the manner in which the community was assembled²⁴⁻³⁶ (Fig. 1). Alternative states are commonly observed among communities, and such states are likely to be the rule rather than the exception²⁴⁻³⁶. Comparison of patterns observed among some set of extant communities, and a null model of that community, cannot partition historical from contemporary effects.

Because communities are historically derived entities, an analysis of extant community properties alone may be unable to discern among: (1) pattern generated by processes that no longer operate – the 'ghost of processes past'^{37,38}; (2) pattern produced by currently functioning mechanisms; (3) an apparent lack of pattern, which is nonetheless deterministically produced (e.g. chaos); and (4) true randomness. Essentially, any past ecological process, such as a species invasion or extinction, or environmental perturbation, may have had a strong effect on subsequent community organiz-

ation. Without a knowledge of those events, it may not be possible to attribute mechanism to pattern²⁴.

Unfortunately, community assembly or *whole-community* succession has rarely (e.g. Krakatoa) been documented in nature. As a result, the impact of historical events often remains unseen. While such events may be unseen, it is not because they did not have an impact on the community. In many cases, it is simply impossible to infer cause and effect with data that represent, essentially, a thin slice of ecological time. In these terms, a community must be thought of as a continuous sequence or trajectory of states through time. These states may not be independent – that is, it may be impossible to understand current community conditions without information about previous states. If the current state is to be understood, it is essential to ask how the community arrived at that state. Are there multiple assembly routes to a single state, or can that state be reached only through a specific set of events? In the final analysis, the mechanisms that are currently functioning may actually have little to do with the pattern at hand.

Several controlled laboratory studies – studies using artificial habitats in nature, long-term field studies, and studies based on observed patterns of distribution – have shown that altering the order of species introduction used to assemble communities can produce communities containing different sets of species^{24-34,36}. This result holds – theoretically and empirically – despite equal access by all species to the assembling community^{24,39}. What are the implications of such dynamics? Communities assembled from the same species source pool can vary considerably and appear, by any measure (statistical, topological or otherwise), idiosyncratic upon comparison. Without historical information, one may rightly conclude that a given community lacks an identifiable and general pattern. However, with historical information about how the systems were assembled, it is clear that in many cases powerful mechanisms and process are operating. Is there anything in the mechanics of community assembly that might provide

a framework for understanding communities in general?

Assembly-rule mechanics: constructing a puzzle

The term 'assembly rule' has been used to describe the mechanics of how the species of a community fit together^{24,25,31,32,34,40-42}. In this sense, assembly is much like fitting together the pieces of a puzzle, where the rules of assembly are implicit in the relative shapes of the pieces (Fig. 2). In ecological terms, 'fit' has a variety of meanings, ranging from trophic accommodation and topological considerations⁴², to competitive relationships with other community members. In evolutionary terms, however, the relative shapes of the pieces and the rates of exchange between adjacent pieces are likely to change. New species may also be added as a result of speciation or invasion. These events serve to create, adjust or eliminate community assembly rules and subsequent emergent properties.

The analogy between a puzzle and a community lacks an essential and vitally instructive feature. A puzzle has but one picture regardless of the order in which the pieces are fitted together. A community may possess alternative states, replete with mutually exclusive sets of species and patterns of abundance. This has been well documented in nature, and provides us with a tool to explore community phenomena.

The mechanisms and processes behind the production of alternative states are the devices of assembly rules. These rules, in various forms, produce communities that are differentially vulnerable to invasion²⁴⁻³⁴. Certain species ensembles resist invasion by some species better than others. In such cases, competitive dominance hierarchies have little or no predictive value²⁴. This may not be because competition, for example, is strong enough to preclude invasion in one system but so diffuse in another system that the invader is successful. The ensemble itself can possess emergent properties that determine invasibility^{24,42}. Emergent properties may be thought of as the *expression of the set of assembly rules* that operates given a particular species composition and historical context.

In numerous field and laboratory studies, the existence of alternative community states is a recurring phenomenon²⁴⁻³³. Are there any common features among community types that exhibit alternative states? Alternative states have been found in widely disparate community types. What are the rules that generate and maintain alternative states? That is, are there specific mechanisms, say competition, that always lead to alternative states? The answer appears to be no. Are there particular community 'architectures' or topologies that produce alternative states^{24,39,42}? The answer is still equivocal, and much work needs to be done in this area. Nevertheless, current evidence does suggest that alternative states (whether stable or not) do exist, as a direct function of assembly mechanics.

Consider a simple model of competitive intransitivity^{24,28,32,43} involving three species: A, B and C. In this scenario, species A competitively excludes or suppresses species B, which in turn suppresses species C. Species C, however, is capable of excluding species A. No state is stable when the third species colonizes, and the sequence of invasion as well as relative invasion rates determine the frequency of occurrence of each species and perhaps the community type. Using the same species, but in the absence of a temporal component to assembly, an immutable competitive hierarchy (A beats both B and C, and B beats C) can exist^{24,28}.

Given this intransitivity, operating within a guild embedded in a community, indirect effects initiated by the intransitivity may have numerous further effects. Species composition may act as a switch, turning the intransitivity 'on' or 'off', and affect the period of various states. Subsequently, the intransitivity may define much of the species composition of the community. One must ask whether it is the competitive interaction or the emergent property, manifest as an intransitivity, that is responsible for pattern at any given time. The mechanism of interaction alone (competition in this case) is clearly insufficient to explain the dynamics of the community. This argument can be extended to many kinds of ecological phenomenon. Hence,

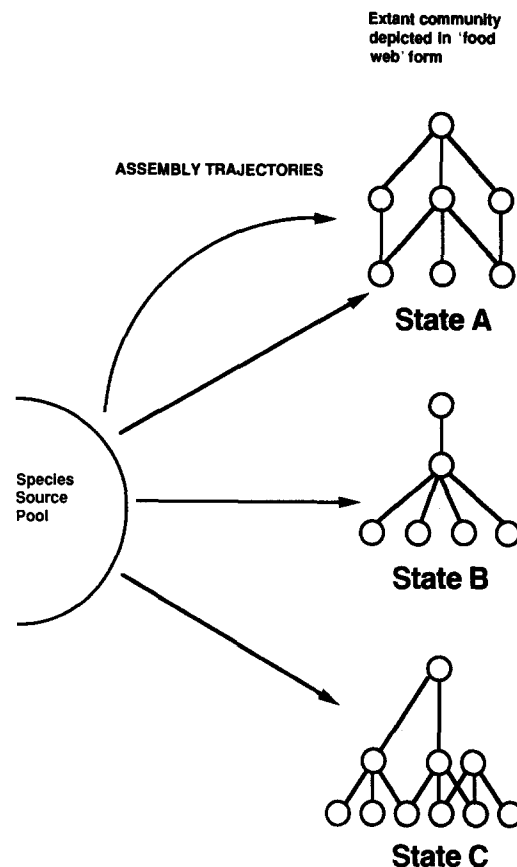


Fig. 1. Differences in extant community configurations (states A, B, C) that result from variation in assembly history (e.g. order of species invasion). Despite equal access by all species to all communities, alternative states arise as a direct result of assembly history. Here, four trajectories are depicted: two converge to the same extant community, and two reach other states. That variation in an assembly trajectory can lead to alternative states suggests that ecologists must understand the trajectory producing the state if that state is to be understood.

there are mechanics to assembly that add considerable variation to the kinds of patterns seen. *The mechanism behind the variation is the assembly rule.*

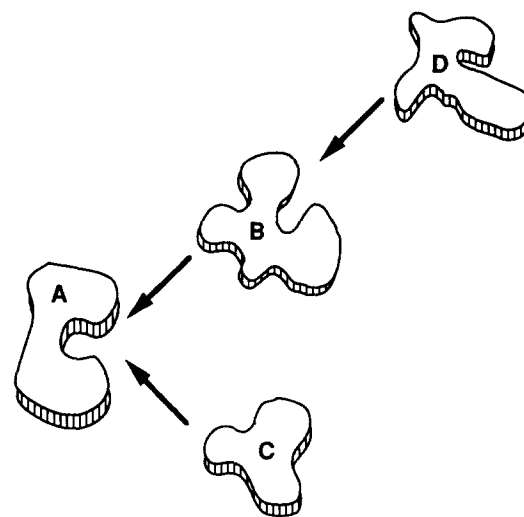


Fig. 2. Depiction of the 'puzzle' analogy for community assembly. If species A colonizes first, then either species B or species C can colonize – competition is assumed. Depending on whether B or C is successful, species D is either a potential colonist or finds the community resistant to invasion.

Table 1. Some cases where assembly rules or assembly-rule phenomena have been documented^a

System	Mechanism or effect	Refs
Birds	Forbidden combinations or species co-occurrences, character displacement	5,7,8,11,12, 22,23,44
Amphibians	Priority effects, predator reversal of competitive effects	26
Marine invertebrates	Alternative states, invasion resistance	29,33
Ants	Alternative states	32
Aquatic microcosms	Alternative states that were sequence-driven	24–26,31
Diptera	Alternative states and multiple domains of attraction, priority effects	22
Lizards	Alternative states	45
Trees	Alternative states and multiple assembly pathways	27,37,43
Algae	Multiple stable states	24
Reef fishes	Competitive lottery	30
Small mammals	Invasion success as a function of species functional group	41
Insects	Multiple assembly/successional pathways, priority effects	46–48

^aMost of these studies illustrate rules for only a portion of the community. In several of the laboratory studies, species composition was completely known. The table is by no means exhaustive.

Species ensembles and higher-order pattern

Lawton⁴⁰ offered an evaluation of how the direction or trajectory of succession, defined as the change in species composition through time, may be influenced by 'pair-wise' interactions. He concluded that rules for assembly indeed exist, and that any number of mechanisms form the basis for such rules. A growing set of studies provides support for this conclusion (Table 1). At this point, the question is whether or not there are any common features that offer insight into the mechanics behind community assembly. If there are, what are these features, and do they form a viable framework from which to approach community questions?

Diamond's study^{34,49,50} of patterns of species coexistence among a portion of a community in New Guinea provides intriguing insight into assembly mechanisms. He concluded that competition was the force driving species distributions in the avifauna component. These results have been variously challenged and defended^{22,23}, but regardless of one's perspective, the mechanics suggested by Diamond and others for producing pattern do provide insight. Others have found similar examples where assembly mechanics produce alternative

states. Roughgarden⁴⁵ showed that lizard species composition between islands in the Lesser Antilles could be explained by the ecological separations created by the tectonic movements of the islands. Other workers, including Drake²⁴, Robinson and Dickerson²⁵, Wilbur and Alford²⁶, McCune and Allen²⁷, Gilpin *et al.*²⁸, Barkai and McQuaid²⁹ and Sutherland³³, have observed strong historical and sequence effects – effects strong enough to reverse normally deterministic outcomes. Cole³² found alternative stable combinations of ant species under different assembly scenarios. Barkai and McQuaid²⁹ have shown effects as dramatic as functional reversals in predator–prey relationships. Such phenomena continue to be uncovered, and they offer our best hope for the development of a theoretical understanding of communities in general.

In concert, these studies provide a conceptual framework for the mechanics of how communities assemble (Table 1). The pivotal element in each of these studies is not a specific mechanism, regardless of the mechanism involved (e.g. competition, predation, mutualism, parasitism). The consequence of the mechanism (coexistence, extinction, variation in ensemble properties and configurations) appears to

be strongly dependent on historical context. While specific events during community assembly may have a stochastic element (e.g. which species colonizes when), the result of assembly history can define which rules operate and which do not. For example, several experimental studies have shown that communities assembled with different sequences of invasion produced communities that contained different species^{24–26,28,31,32}. In my own work, I found that a species that is a good colonist and competitive dominant under one set of circumstances may find itself unable to survive given a slightly different assembly scenario. The point is simply that assembly rules have a strong historical component, which means that such rules are patently dependent on context.

In addition to the physical environment, including effects at local, regional and global scales, other variables can be examined for commonality, species composition, persistence, distribution and relative abundance, and any other community metric. The critical variables are (1) the context and history of how the system was assembled, and (2) the immediate or real time effect of interactions and ensemble effects. Both variables are important; one is a reflection of where the community has been and the other offers a glimpse of potential future states. It is very difficult to understand the reasons behind observed patterns, or lack of pattern, with only information about the community at hand.

In many cases we must rely on inference to understand observed community patterns. If we understand the events that directed community succession and can compare the dynamics of different situations (the assembly of communities with different sequences of species invasion – assembly mechanical differences), we should be able to detect assembly rules. By associating specific patterns with assembly scenarios capable of producing those patterns, we may be able to understand the reasons for variations among communities – even when no historical information is available. Further theoretical and empirical studies will be required before any such inferential base will be useful.

This must be done using an ap-

proach based on context rather than through the single-minded pursuit of some fashionable mechanism. We still do not understand enough about community assembly to produce a catalogue of patterns and assembly routes to those patterns. Whether such a rule base will be specific, say to aquatic systems, or generalizable to all systems is unknown. Careful laboratory and field work is still needed.

The role of disturbance and stochastic effects

That stochastic effects or periodic but drastic seasonal shifts in climate may regulate community pattern has been known for some time. This is an important component of assembly-rule processes. Clearly, some systems exist under highly variable conditions. The frequency and magnitude of disturbance, coupled with the generation times of community members and topological response, defines the role that disturbance plays in assembly processes. The role of disturbance, and the frequency of its occurrence in relation to species composition, may well be pivotal points in community assembly.

Sale³⁰, Chesson⁵¹, Chesson and Case⁵² and others have stressed that stochastic effects can eliminate or reduce competition (or any other process) to the point where the process has no effect on community organization. How do such effects influence community assembly and assembly processes? These may very well be the only cases where a null model comparison would hold up. Here, the characteristics of the disturbance determine what ecological outcomes or assembly rules are possible. The frequency of the disturbance can be vital in determining the overall effect of the disturbance. If the frequency of perturbation is greater than the survival time of the propagule (or propagule source), will variation in species composition increase, decrease or be unaffected? This question, and how the resulting rules of assembly are changed, remains largely unexplored.

Conclusions

There is enough evidence to conclude that assembly rules can govern community patterns. While beyond the scope of this article, a

growing body of theoretical studies also supports these conclusions. Admittedly, assembly rules are difficult to uncover in natural communities because of our inability to view past events. Inference is often disconcerting. Pattern may not be the result of contemporary ecological processes but of events that occurred sometime during community assembly. Given our current level of analytical sophistication, it may not be possible to understand pattern in many communities. This is indeed a disturbing conclusion, but all is not lost. 'Bundles' or genera of assembly rules appear likely to exist within specific community types (e.g. Mediterranean-type grasslands), and to produce specific patterns regardless of the nature of the community. Before such a conclusion can be drawn, additional work at the whole-community level must be done. This work must be focused on community assembly mechanics and the specific mechanisms involved.

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References

- 1 Clements, F.E. (1916) *Plant Succession: An Analysis of the Development of Vegetation*, Carnegie Institution of Washington (No. 242)
- 2 Gleason, H.A. (1926) *Bull. Torrey Bot. Club* 53, 7–26
- 3 Forbes, S.A. (1880) *Ill. Nat. Hist. Surv.* 3
- 4 Camerano, L. (1880) *Atti. Accad. Torino* 15, 393–414
- 5 Simberloff, D. (1981) in *Biotic Crises in Ecological and Evolutionary Time* (Nitecki, M.H., ed.), pp. 53–81, Academic Press
- 6 Lindemann, R. (1942) *Ecology* 23, 399–417
- 7 Grant, P.R. and Abbott, I. (1980) *Evolution* 34, 332–341
- 8 Connor, E.F. and Simberloff, D. (1979) *Ecology* 60, 1132–1140
- 9 Andrewartha, H.G. and Birch, L.C. (1954) *The Distribution and Abundance of Animals*, University of Chicago Press
- 10 Cody, M.L. and Diamond, J.M., eds (1975) *Ecology and Evolution of Communities*, Harvard University Press
- 11 Diamond, J. and Case, T.J., eds (1986) *Community Ecology*, Harper & Row
- 12 Strong, D.R., Simberloff, D., Abele, L.G. and Thistle, A.B., eds (1984) *Ecological Communities*, Princeton University Press
- 13 Gray, A., Crawley, M.J. and Edwards, P.J., eds (1987) *Colonization, Succession and Stability*, Blackwell
- 14 Allen, T.F.H. and Starr, T.B. (1982)

- Hierarchy*, Chicago University Press
- 15 O'Neill, R.V., DeAngelis, D.L., Waide, J.B. and Allen, T.F.H. (1986) *A Hierarchical Concept of Ecosystems*, Princeton University Press
- 16 Paine, R.T. (1983) in *Current Trends in Food Web Theory* (DeAngelis, D., Post, W.M. and Sugihara, G., eds), pp. 11–16, Oak Ridge National Laboratory (TM-5983)
- 17 Schoener, T.W. (1986) in *Community Ecology* (Diamond, J. and Case, T.J., eds), pp. 467–479, Harper & Row
- 18 Yodzis, P. (1980) *Nature* 284, 544–545
- 19 Hutchinson, G.E. (1978) *An Introduction to Population Ecology*, Yale University Press
- 20 Wiens, J.A. (1977) *Am. Sci.* 65, 590–597
- 21 Pimm, S.L. and Redfern, A. (1988) *Nature* 334, 613–614
- 22 Gilpin, M.E. and Diamond, J.M. (1984) in *Ecological Communities* (Strong, D.R., Simberloff, D., Abele, L.G. and Thistle, A.B., eds), pp. 297–315, Princeton University Press
- 23 Connor, E.F. and Simberloff, D. (1984) in *Ecological Communities* (Strong, D.R., Simberloff, D., Abele, L.G. and Thistle, A.B., eds), pp. 316–331, Princeton University Press
- 24 Drake, J.A. *Am. Nat.* (in press)
- 25 Robinson, J.V. and Dickerson, J.E. (1987) *Ecology* 68, 587–595
- 26 Wilbur, H.M. and Alford, R.A. (1985) *Ecology* 66, 1106–1114
- 27 McCune, B. and Allen, T.F.H. (1985) *Can. J. Bot.* 63, 367–376
- 28 Gilpin, M.E., Carpenter, M.P. and Pomerantz, M. (1986) in *Community Ecology* (Diamond, J.M. and Case, T.J., eds), pp. 23–40, Harper & Row
- 29 Barkai, A. and McQuaid, C. (1988) *Science* 242, 62–64
- 30 Sale, P.F. (1978) *Environ. Biol. Fishes* 3, 85–102
- 31 Robinson, J.V. and Edgemon, M.A. (1988) *Ecology* 69, 1410–1417
- 32 Cole, B.J. (1983) *J. Anim. Ecol.* 52, 349–355
- 33 Sutherland, J.P. (1974) *Am. Nat.* 108, 859–873
- 34 Diamond, J.M. (1975) in *Ecology and Evolution of Communities* (Cody, M.L. and Diamond, J.M., eds), pp. 342–444, Harvard University Press
- 35 May, R.M. (1977) *Nature* 269, 471–477
- 36 Abrams, A.D., Sprugal, D.G. and Dickman, D.I. (1985) *For. Ecol. Manage.* 10, 31–48
- 37 Connell, J.H. (1980) *Oikos* 35, 131–138
- 38 Strong, D.R. (1984) in *Ecological Communities* (Strong, D.R., Simberloff, D., Abele, L.G. and Thistle, A.B., eds), pp. 28–41, Princeton University Press
- 39 Drake, J.A. (1988) in *Mathematical Ecology* (Hallam, T.G., Gross, L.J. and Levin, S.A., eds), pp. 585–604, World Press
- 40 Lawton, J.H. (1987) in *Colonization, Succession and Stability* (Gray, A.J., Crawley, M.J. and Edwards, P.J., eds), pp. 225–244, Blackwell
- 41 Fox, B.J. *J. Ecol.* (in press)
- 42 Sugihara, G. (1983) in *Current Trends in Food Web Theory* (DeAngelis, D., Post, W.M. and Sugihara, G., eds), pp. 25–36, Oak Ridge National Laboratory (TM-5983)
- 43 Buss, L.W. and Jackson, J.B.C. (1979) *Am. Nat.* 113, 223–224
- 44 Moulton, M.P. and Pimm, S.L. (1986) in *Community Ecology* (Diamond, J.M. and Case, T.J., eds), pp. 80–97, Harper & Row
- 45 Roughgarden, J. (1989) in *Perspectives in Ecological Theory* (Roughgarden, J., May, R.M. and Levin, S.A., eds), pp. 203–226,

Princeton University Press
 46 Brown, V.K. (1985) *Oikos* 44, 17–22
 47 Kneidel, K.A. (1983) *Ecol. Entomol.* 8, 163–169
 48 McBrien, H., Haramen, R. and Crowder, A.

(1983) *Ecology* 64, 1035–1039
 49 Diamond, J.M. (1982) *Proc. Natl Acad. Sci. USA* 79, 2420–2424
 50 Diamond, J.M. and Gilpin, M.E. (1982) *Oecologia* 52, 64–74

51 Chesson, P. (1985) *Theor. Popul. Biol.* 28, 263–287
 52 Chesson, P. and Case, T.J. (1986) in *Community Ecology* (Diamond, J.M. and Case, T.J., eds), pp. 229–239, Harper & Row

Evolution of Insecticide Resistance

In his recent review on the evolution of insecticide resistance, Mallet¹ made some interesting statements on which we would like to comment.

The idea that herbivores often develop insecticide resistance prior to their parasites and predators because of an inherently high activity of detoxifying enzymes for handling plant toxins is appealing. However, there are, to date, no data suggesting that the three principal systems of detoxifying enzymes (glutathione S-transferases, mixed-function oxidases and esterases) are more active or more abundant in herbivorous than in carnivorous insects. In fact, the results of an examination of the levels of mixed-function oxidase activity in numerous insect species showed that relatively high levels of these detoxification enzymes were found in omnivorous, carnivorous, phytophagous and nectar-feeding species². Furthermore, several species now resistant to a wide variety of insecticides have barely any contact with plant materials (e.g. the sheep blowfly *Lucilia cuprina*³), and we feel that it is unwise to extend the theory to encompass resistance in mosquitoes by suggesting that plant chemicals are leached into the larval habitat. However, we would agree that it is possible that a relationship exists between the ability to develop increased detoxification and the variability of the toxicity of the environment.

According to Mallet, a single major resistance gene is selected in field conditions (leading to a monogenic inheritance of resistance), whereas under laboratory selection several genes of small effect arise (giving a polygenic inheritance of resistance). It is questionable that selection is weaker in the laboratory than in the field since (1) the insecticide concentration used to select laboratory strains can be very high, sometimes reaching the limits of insecticide solubility, and (2) the strength of field selection is very difficult to determine accurately.

Polygenic inheritance has mainly been demonstrated in populations displaying a low level of resistance (below tenfold), i.e. in instances where inheritance is difficult to study using bioassay data^{4,5}. It is therefore

possible that polygenic inheritance is assumed because of the statistical difficulty in distinguishing a linear dose–mortality curve from one with a small inflexion at predicted mortalities in the F₂ or backcrosses. An alternative explanation to that of Mallet is that the genes conferring high levels of resistance may not be available in laboratory strains because of a low mutation rate and a reduction in genetic variability (since strains were maintained for many generations prior to selection). For instance, inbred greenhouse populations of *Tetranychus urticae* did not develop resistance to the insecticide Pentac, despite seven years of selection, until outcrossed to a wild strain⁶. We would like to see some references for Mallet's statement that 'Neodarwinian theory predicts that novel traits will evolve fastest when many loci, each of which has a small effect, determine the phenotype'.

Mallet's discussion of models on the evolution of resistance entails hypotheses used in population genetics at least since Fisher⁷. Hence these models were not new, even if 'insecticide resistance has its own quirks'. All the results concerning the fixation of resistance genes, whether recessive, codominant, dominant or with different initial frequencies, are directly derived from models in classical population genetics textbooks. The very valuable contribution of resistance models, however, was in the prediction of a quantitative result, for example in the comparison of the efficiency of insecticide rotations and mixtures^{8,9}.

Finally, as a comment on the ques-

tion raised by Mallet on 'the evolution of insecticide resistance: have the insects won?', we would like to mention the life/dinner principle of Dawkins¹⁰: 'the rabbit runs faster than the fox because the rabbit is running for his life while the fox is only running for his dinner'. Insect species are developing resistance to survive whereas Man is controlling insects to protect crops and reduce diseases. Has Man invested as much in control as insects have in resistance?

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References

- Mallet, J. (1989) *Trends Ecol. Evol.* 4, 336–340
- Brattsen, L.B. and Metcalf, R.L. (1970) *J. Econ. Entomol.* 63, 101–104
- McKenzie, J.A. and Whitten, M.J. (1980) *Experientia* 38, 84–85
- Crow, J.F. (1957) *Annu. Rev. Entomol.* 2, 227–246
- Wool, D., Noiman, S., Manheim, O. and Cohen, E. (1982) *Biochem. Genet.* 20, 621–633
- McEnroe, W.D. and Lakoy, A. (1969) *J. Econ. Entomol.* 62, 283–286
- Fisher, R.A. (1930) *The Genetical Theory of Selection*, Clarendon Press
- Mani, G.S. (1984) *Genetics* 109, 761–783
- Georghiou, G.P., Lagunes, A. and Baker, J.D. (1983) in *IUPAC Pesticide Chemistry, Human Welfare and the Environment* (Miyamoto, J. et al., eds), pp. 183–189, Pergamon Press
- Dawkins, R. (1982) *The Extended Phenotype*, Oxford University Press

Reply from J.L.B. Mallet

One of the most interesting questions about resistance evolution is: why do pests often become resistant before their natural enemies? Two major hypotheses have been put forward: first, pests are helped by having a greater initial ability to detoxify foreign chemicals, perhaps in part because plant chemicals induce defences; and second, insecticidal kills favour the population dynamics of

pests over those of their natural enemies. Neither hypothesis is based on hard evidence, and I did not intend to give an impression of certainty in my review. Tabashnik and Johnson¹ have recently reviewed these hypotheses, as well as other important possibilities such as bias in documentation and differences in genetic variability, and conclude that evidence for greater detoxification by