

The emergence of diversity in plant communities

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Abstract – The diversity of functional forms and strategies in plant communities is essential to the maintenance of the services that ecosystems provide humanity, and ultimately to the homeostasis of the biosphere. This diversity emerges from evolutionary forces operating at lower levels; these exploit the opportunities for specialization presented by exogenous and endogenous spatial and temporal heterogeneity. Two major theoretical approaches have been taken to understand how strategies arise and are maintained: optimization models, which consider the fitnesses of types in isolation, and game-theoretic methods, which take frequency dependence into account. The game-theoretic approach is more powerful, but also more challenging to apply. For some relatively simple problems in the study of biodiversity, we show how the game-theoretic formulation can be translated into an equivalent problem in optimization. More generally, however, new techniques will be needed to explore the dynamics of multiple coexisting types and strategies. © 2000 Académie des sciences/Éditions scientifiques et médicales Elsevier SAS

biodiversity / evolutionary stable strategy / heterogeneity / life history / dispersal / seed size

Résumé – Émergence de la diversité dans les communautés de plantes. La diversité des formes fonctionnelles et des stratégies dans les communautés de plantes est essentielle au maintien des services rendus à l'humanité par les systèmes écologiques, et en dernier lieu à l'homostasie de la biosphère. Cette diversité émerge des forces de l'évolution opérant aux niveaux inférieurs ; celles-ci exploitent les opportunités de spécialisation présentées par l'hétérogénéité spatiale et temporelle exogène et endogène. Deux approches théoriques majeures ont été utilisées pour comprendre comment les stratégies naissent et comment elles perdurent : les méthodes d'optimisation qui considèrent la valeur adaptative des espèces en isolation et les méthodes de la théorie des jeux qui considèrent les interactions dépendant de la fréquence. Les méthodes de la théorie des jeux sont plus puissantes mais plus difficiles à appliquer. Nous démontrons comment une formulation utilisant la théorie des jeux peut être traduite en un problème équivalent d'optimisation pour certains problèmes simples dans l'étude de la biodiversité. Plus généralement, pourtant, nous démontrons que des techniques nouvelles seront nécessaires pour explorer les dynamiques des espèces et stratégies multiples coexistantes. © 2000 Académie des sciences/Éditions scientifiques et médicales Elsevier SAS

biodiversité / hétérogénéité / histoire de la vie / dispersion

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Version abrégée

Il y a peu de doutes sur le fait que la diversité des organismes biologiques est cruciale pour le maintien de l'atmosphère et du climat et que les forces de l'évolution ont joué un rôle fondamental en façonnant ces effets. Ce qui est en question, cependant, concerne le degré avec lequel les boucles de rétroaction exercées par le climat et l'atmosphère ont permis de guider l'évolution se déroulant dans les niveaux inférieurs. Du point de vue de l'évolution, la terre n'est pas une unité dont les propriétés ont été façonnées par la sélection naturelle parce qu'elles procurent simplement une meilleure valeur adaptative que tous les autres assemblages possibles. Il s'agit plutôt d'un système adaptatif complexe dont les propriétés émergent et sont maintenues par des forces sélectives opérant dans des niveaux d'organisation inférieurs. Sans doute, des boucles de rétroaction exercées par les niveaux supérieurs influencent l'évolution dans les niveaux inférieurs ; mais la question est simplement de comprendre de quelle manière de telles forces peuvent agir quand les interactions sont diffuses et les boucles de rétroaction faibles.

La clé pour comprendre l'évolution et le développement de la biosphère, tout comme l'évolution de tout autre système adaptatif complexe, réside dans l'explication de l'émergence des structures au niveau du système à partir de la sélection naturelle opérant dans un spectre de niveaux inférieurs. Cela demande une approche permettant d'intégrer la dynamique d'un système dans ces différents niveaux d'organisation, en construisant à partir des unités individuelles une mécanique statistique décrivant les populations et les communautés auxquelles ils appartiennent.

L'hétérogénéité est un élément essentiel de la biodiversité. L'hétérogénéité peut se manifester dans l'espace, dans le temps, ou d'autres manières encore. Ce n'est pas un phénomène exclusivement abiotique ou exogène. Il peut être et est le plus souvent au moins en partie endogène – généré par les organismes eux-mêmes par les différences dans leurs effets sur l'environnement, et par l'unicité de leurs distributions et de leurs structures.

La diversité des adaptations des espèces est reflétée par la diversité similaire des traits des habitats qui permettent la coexistence ; la dualité évidente apporte une approche complémentaire pour classer les mécanismes responsables de la genèse et du maintien de la diversité. L'hétérogénéité de l'environnement que nous mesurons est pertinente pour comprendre la coexistence et comment l'évolution a seulement permis aux espèces de l'exploiter, la flore constituant le filtre le plus utile pour caractériser l'hétérogénéité environnementale.

Dorénavant, nous nous concentrerons sur la diversité des traits d'histoire de vie parmi les plantes. Ces traits concernent le mode de croissance ; l'âge et la taille à maturité, le nombre, la taille et les modes de dispersion des recrûs ; les investissements dans la reproduction dépendants de l'âge et de la taille et les schémas de mortalité. Les plantes possèdent une grande variété de manières pour tenir compte des variations de l'environnement. À partir du précédent préambule, ces variations peuvent être vues aussi bien comme des challenges que des opportunités – elles constituent des problèmes qui doivent être résolus, mais elles constituent également des opportunités actuelles et nombreuses pour un rayonnement en évolution. Face à un environnement imprédictible, l'évolution peut conduire à une variété de façons pour moyenniser l'incertitude et augmenter la représentation dans les générations futures. Par exemple, les modes de reproduction annuels peuvent être remplacés par la pérennité et l'itéroparité, au moyen desquelles la reproduction s'étend sur plusieurs années ; ou bien le mode annuel est maintenu, en moyennisant par la dormance ou la dispersion.

Hamilton et May ont proposé un premier examen de ces questions en construisant un modèle de l'évolution de la dispersion parmi les plantes dans des habitats stables. Ils ont montré avec une argumentation directe et élégante que, dans un environnement homogène, l'évolution va permettre à une espèce intermédiaire de s'établir, cette espèce libérant une fraction de ses graines localement et dispersant le reste au loin. Dans la terminologie de Maynard Smith, ce type est une stratégie évolutionnairement stable (SES) qui, une fois établie, résistera à l'invasion de tout autre type. Par la suite, les stratégies évolutionnairement stables ont été examinées au travers de schémas de compétition plus généraux, et pour des habitats plus complexes ; des approches similaires ont été appliquées aux cas de la dormance, de la taille des graines, et d'autres caractères.

Bien qu'il soit possible de formuler la recherche de stratégies évolutionnairement stables dans le langage de la théorie des jeux, il est en général impossible de caractériser la solution dans le cadre d'un problème d'optimisation sous contrainte. Il y a quelques exceptions et nous en discutons quelques unes. Il y a quelques exceptions puissantes à la difficulté de représenter l'évolution d'une communauté par un problème d'optimisation. Sans doute, la méthode d'optimisation propose une approche valable pour comprendre un grand nombre de problèmes en morphologie, en physiologie et en comportement lorsque les contraintes sont imposées ; par exemple, le design optimal des organismes pour résister aux contraintes environnementales, pour utiliser l'énergie solaire, pour exploiter

des ressources nécessite dans chaque cas une conception technique, contrainte par l'histoire et l'évolution passée et peut-être seulement de manière secondaire par la dépendance à la fréquence. Au-delà de ces exemples, cependant, se trouvent les cas impliquant de manière fondamentale les interactions interspécifiques comme les associations hôte–parasite. Par exemple, parce que différentes souches virales sont en compétition pour des hôtes communs (et s'excluent mutuellement à cause de leurs réactions croisées et des réponses immunitaires des hôtes), l'évolution va sélectionner parmi eux ceux qui possèdent à la fois une potentialité de grande vitesse d'invasion à partir d'hôtes infectés, et aussi une aptitude à conserver leurs hôtes vivants. Dans le cas d'une complète immunité croisée, par exemple, la stratégie du parasite évolutionnairement stable est celle qui maximise le produit du temps d'infection.

La reformulation d'un problème de SES en un problème de maximisation d'une fonction donnée est une simplification puissante, et peut être étendue à l'analyse de l'évolution de la taille des graines et des caractéristiques de dispersion parmi les plantes en compétition annuellement. Nous construisons un modèle d'Ezoe, explorant une simulation spatiale dans laquelle la taille de la graine détermine à la fois la distribution des distances de dispersion et la capacité relative compétitive de différents types. Le résultat du modèle dû à Ezoe peut se généraliser à des formes fonctionnelles beaucoup plus générales que celles qu'il considère, et reformuler comme un problème de maximisation.

Les méthodes d'optimisation pour expliquer les traits écologiques considèrent trop souvent l'individu isolé, ignorant le contexte de la population dans laquelle le

trait se manifeste. La notion de stratégie évolutionnairement stable nous libère de cette limitation, et permet l'étude de l'évolution dans le cadre d'interactions dépendant de la fréquence, qui doivent se produire parmi des populations d'organismes en compétition pour des ressources communes.

Mais que dire de la communauté, et de l'écosystème bâti à partir de cela ? Les communautés naturelles ne sont pas des sanctuaires d'espèces isolées, les vainqueurs d'une lutte tout ou rien. Elles sont plutôt des sites de grande diversité biologique – d'espèces qui ont su trouver la voie pour coexister en partageant les ressources, et en construisant à partir des opportunités qu'elles s'apportent mutuellement. Dans une association d'espèces, le problème du partage des ressources a été une question centrale dans la théorie des communautés, et occupera notre attention pour le reste de cet article. Cependant, pour comprendre l'émergence de la diversité, nous devons aller au-delà de cela et examiner les complexités du mutualisme et de l'exploitation qui définissent la structure de la communauté et sa dynamique.

Les écosystèmes et la biosphère sont, dans une large mesure, le résultat de forces évolutives opérant dans les niveaux d'organisation inférieurs. Les forces darwiniennes qui déterminent les réponses des organismes à l'environnement combinent le façonnement des structures que nous observons à la fois au niveau de la communauté et de l'écosystème ; et ces structures à leur tour influencent par rétroaction l'évolution dans les niveaux inférieurs. Le challenge fondamental de l'écologie actuelle est peut-être de comprendre ces liens, et comment l'évolution opérant au niveau de l'individu et des populations peut donner naissance à l'organisation des communautés.

1. Introduction

The question of the sustainability of the biosphere as a life support system for humanity is increasingly attracting the efforts of scientists from all disciplines [1]. Such concerns have focused attention on the robustness of the biosphere as an integrated system, with stabilizing homeostatic mechanisms that maintain climate and biogeochemical cycles in a condition that can sustain life, and in particular on the role of biodiversity in maintaining critical services to humanity [2]. This attention has in turn added motivation to the quest to understand how the diversity of life forms present in the world originated and is maintained.

There is little doubt that the diversity of biological organisms is crucial to the maintenance of atmosphere and climate as we know it [3], and that evolution has played a fundamental role in shaping those influences.

What is debatable, however, is the degree to which feedbacks from the climate and atmosphere have served to guide evolution operating at lower levels [4, 5], a central tenet of the creed of Gaia [6]. The Earth is not an evolutionary unit, with properties shaped by natural selection because they impart a higher fitness compared to other possible assemblages. Rather, it is a complex adaptive system, whose features have emerged from, and are maintained by, selective forces operating at lower levels of organization [7]. Evolution operates with greatest force at the level of individual organisms and below; however, it can also operate at higher levels, rewarding reproductive units, such as colonies, whose characteristics lead to greater representation in future generations [8–10]. Certainly, there are feedbacks from higher levels that influence evolution at lower levels; but given that interactions are diffuse and feedback loops weak, the influence of these feedbacks is in general likely to be relatively small.

The key to understanding the evolutionary development of the biosphere, as for the development of any complex adaptive system, is to learn how patterns at the system level emerge from natural selection operating at a spectrum of lower levels. This focus, on the evolutionary dynamics of collectives, is analogous to efforts to understand the properties of economic systems in relation to the realization of the selfish agendas of the individual agents that comprise it. It requires an approach that can integrate the dynamics of systems at different levels of organization, building up from individual units to develop a statistical mechanics describing populations and communities of those agents.

In this paper, we assess progress towards developing such an approach to understanding the evolutionary dynamics of the diversity of strategies found in plant communities. Because all plants depend on essentially the same few resources – light, water and nutrients – the emergence and coexistence of diverse types in plant communities has long been of particular interest to ecologists. The presence of a diversity of functional types and of life history strategies in plant communities is also critical to the functioning of ecosystems and the provisioning of ecosystem services. In forests, for example, fast-growing, weedy plant species quickly cover soil and reduce erosion following disturbance, while slower-growing shade-tolerants follow later, and eventually sequester considerably more carbon in their tall canopies and dense wood than the early arrivals. Thus, the question of how the current diversity of plant strategies arose and is maintained is of both theoretical and applied interest.

2. Mechanisms enabling the evolution and maintenance of diversity

The fundamental force shaping plant diversity is natural selection, which in its simplest presentation acts through competition among types, and results in the exclusion of inferior ones. In the absence of variation in conditions (broadly defined), a single type – the type best suited for the particular combination of environmental conditions that occur – will in general be selected. This is the evolutionary equivalent of one of the central tenets of ecology, the competitive exclusion principle [11]. The reason for the centrality of this principle, however, is not the belief that similar species cannot coexist; there is, of course, abundant evidence of coexistence among competitors in diverse situations, from forests to grasslands to the oceans. The competitive exclusion principle is thus a null hypothesis, making clear the necessity of niche and habitat partitioning if stable coexistence is to be achieved. Indeed, the famous ecologist and limnologist, G. Evelyn Hutchinson, in a highly influential paper [12], posed the central challenge crisply by asking, in essence, how species manage to specialize their environmental niches so that they can coexist.

There is a diversity of mechanisms by which coexistence is enabled; the most direct is the exploitation of

different resources within a single habitat. Insects use different parts of the same plant; parasites exploit specific hosts; plants use different combinations of soil nutrients, and plankton do the same for dissolved nutrients. Early theoretical work showed that the number of coexisting species could not in general exceed the number of resources or limiting factors [13–15], although temporal variation could provide exceptions [12, 16]. The fundamental problem then became how to distinguish limiting factors – in particular, in heterogeneous environments, to determine how distinct habitats must be to represent unique resources.

Heterogeneity is thus an essential element of the evolution of diversity. Heterogeneity may present itself as in the potential for resource partitioning mentioned previously. It may occur in space – different microclimatic and soil conditions can provide diverse opportunities within even local habitats. Or heterogeneity may occur in time – through daily cycles, seasonal patterns or even the age of a patch of habitat, whereby different species become adapted to different stages of successional development following a treefall, windthrow, forest fire or lava flow. Given environmental variation, as well as tradeoffs that prevent any one type from dominating under all conditions and that lead types to differ in relative competitive ability under different conditions, evolution exploits the opportunities presented for specialization and differentiation, thereby leading to increased diversity.

As the example of succession illustrates, environmental heterogeneity need not be exclusively abiotic or exogenous. It can be and most often is at least in part endogenous – created by organisms themselves through differences in their effects upon the environment, and through their unique distributional patterns. Though it may have simple origins – for example, the chance landing of seeds on particular sites – heterogeneity feeds upon itself. Clumps of seedlings arise around adult plants of their own type, creating influences upon the landscape that can last for generations, in turn influencing the distributions of other species, of herbivores, and ultimately of the whole web of interactions. Janzen [17] and Connell [18] hypothesize that clumping of seed predators, pathogens and herbivores near parent trees and the resulting ‘death zones’ there constitute a major force structuring tropical tree communities and maintaining their high diversity. Spatiotemporal heterogeneity can also emerge from the habits of a keystone predator; the grazing of the starfish *Pisaster ochraceus*, for instance, continually opens up habitat for colonization by species that are competitively excluded in the absence of *Pisaster* [19, 20].

The diversity of habitat features that promote coexistence is mirrored by a similar diversity in species adaptations; the obvious duality provides a complementary approach to classifying mechanisms underlying the generation and maintenance of diversity. Measured environmental heterogeneity is relevant to the issue of coexistence only to the extent that evolution has enabled species to exploit it; the biota therefore provide the most relevant

filter for characterizing environmental heterogeneity. Species may differ in their environmental tolerances, their resource efficiencies, their life history traits or their interactions with other species. Interspecific differences in environmental tolerances or resource use efficiencies facilitate coexistence in environments that are heterogeneous in the corresponding environmental conditions (e.g. temperature) and resource concentrations (e.g. soil nitrogen). Interspecific differences in interactions with other species can take the form of differential resistance to the attacks of predators, herbivores or pathogens, or to differential benefits from mutualists; these can allow coexistence when there is spatial and/or temporal variation in the abundance of the other species, whether exogenous or endogenous. Finally, interspecific differences in life history traits also allow coexistence, contributing to the efficient exploitation of resources that would otherwise go unused. Ecological systems are in essence economic marketplaces, in which the invisible hand of Adam Smith can lead to patterns of resource use emergent from the selfish realization of individual evolutionary agendas [8–10].

On longer time scales, adaptive specialization of some types creates opportunities for others, fostering the emergence of patterns of diversity. Evolution is often thought of as an optimization process, proceeding to a single best type. Indeed, even the most influential mathematical theories – the dynamical representations of Fisher, Wright and Haldane, and Wright's evocative image of an adaptive landscape on which the ball of evolution seeks higher and higher levels – emphasize this aspect [21, 22]. But fitnesses are not static, and the evolutionary process is a highly nonlinear and historical one in which current evolutionary events change forever the landscape for future evolution. Instead of a fixed, constant landscape, we must think of one continually modified through frequency dependence and coevolution. Exploitation of a particular niche increases competition for that niche, reducing the fitness associated with it and elevating other options. This dramatically increases the potential for coexistence, creating new niches because others have become filled. Such a perspective should inform any investigation of how diversity emerges, and how diverse species manage to coexist within ecological communities, ostensibly competing for a small number of limiting resources.

3. Theoretical approaches to trait evolution

Given the almost limitless possible forms and strategies that plants can take, the problem of interest is to explain the emergence of the particular types and combinations of types that we see today. The theoretical approaches that have been taken to this problem fall into two general categories: constrained optimization approaches that attempt to predict which types do best in isolation, and game-theoretic approaches that focus on which types do best in competition.

Optimization arguments provide a valuable way to understand a variety of problems in morphology, physiology and behavior once constraints are imposed. The optimal design of organisms to withstand environmental stresses, to utilize the sun's energy or to forage for resources all involve issues of engineering design, constrained by physical limits and past evolutionary history, and perhaps only secondarily by frequency dependence. Thus, it can reasonably be assumed that evolution by natural selection will in the end produce the best-performing type, given constraints.

Optimization models have been constructed for numerous plant characters to provide insights into selective pressures and explain the adaptive significance of particular traits [23]. This research has led to quantitative predictions regarding how traits should change with environmental conditions and scale with other plant characters [23]. Some of these studies have quantified costs and benefits precisely from field and laboratory measurements, as in Givnish's study of optimal stomatal conductance and root allocation [24]. Others have examined questions of evolutionary optima on a more general level. For example, Niklas [25] investigated simulated phenotypic walks through multi-dimensional fitness landscapes, given selection on branching patterns for performance of one or more tasks, showing that the number and accessibility of phenotypic optima increase as the number of functional obligations contributing to total fitness increases.

Optimization approaches have also been used successfully in certain cases that fundamentally involve interspecific interactions, such as host–parasite associations. For example, because different viral strains compete for common hosts (and exclude one another because of their cross-reactivity and the immune responses of hosts), evolution will select among them based on both their potential for high rates of spread from infected hosts, and on their ability to keep their hosts alive. In the presence of complete cross-immunity, for instance, the evolutionarily stable parasitic strategy is one that maximizes the product of infectious time and transmission potential [26–28]. Because in essence the winning viral type is that which in isolation leaves the smallest possible population of susceptible individuals, the problem has a direct translation into the biology of resource use; susceptible individuals, indeed, comprise the resource for the pathogens. Thus, it is not surprising that this result has a direct parallel in the theory of resource use, and especially in Tilman's result that the winning type in resource competition is the type that reduces the resource to the lowest level [29].

However, in general, the optimization approach is limited by its failure to account for frequency dependence and coevolution, both of which are ubiquitous in nature. Essentially, optimization assumes a fixed adaptive landscape, one not affected by the relative abundances of types. This may be appropriate in the case of artificial selection – in which the breeder imposes a fitness on each type, and hence a fitness landscape – but it does not

generally capture the dynamics of natural selection, in which fitnesses are frequency-dependent and the adaptive landscape is dynamic. This is especially true for evolution of life history traits among plants, upon which we will focus for the remainder of this paper. Such traits include growth pattern; age and size at maturity; number, size and dispersal patterns of offspring; and age- and size-specific reproductive investments and mortality schedules [30]. In ignoring frequency dependence, one is in effect finding the ‘co-operative optimum’ that would be achieved if selection were to act on populations, rather than the usually distinct competitive optimum that results from selection at the level of the individual [31].

Many, if not most, problems involving natural selection require a game-theoretic approach that asks which type will be selected in a mixture of other types, and which will be evolutionarily stable such that it resists invasion by mutant types. It is in this context that Maynard Smith and Price [32] introduced the concept of an evolutionarily stable strategy (ESS) – a strategy that, when common, has higher fitness than any other strategy and thereby resists invasion and displacement. However, this immunity to invasion once established does not insure that an ESS will actually become established during the course of evolution [33, 34]. An ESS will become established only if it is convergence stable, such that types closer to the ESS can always invade populations dominated by types farther than the ESS, thereby making the ESS essentially an evolutionary attractor [35, 36]. In a game-theoretic context in general, the problem becomes the identification of those types that are convergence stable and evolutionarily stable – that is, types that will come to dominate any assemblage of types; given the existence of some mechanism for continually generating variation in strategies, these types will eventually arise and come to dominate in it.

Hamilton and May [37] provided an early application of a game-theoretic approach to a problem in plant life history strategies, constructing a model for the evolution of dispersal among annual plants in stable habitats. Plants that disperse their seeds have an obvious advantage over those that do not, in that they will occasionally capture new sites presently held by nondispersers, but are at no risk of losing their own sites. The problem becomes more complicated, however, when two different dispersal strategies are considered – say, involving two types that risk different fractions of their seeds to dispersal beyond their natal site, and to the attendant increased possibility of mortality before germination. Hamilton and May show, through straightforward but elegant arguments, that in a homogeneous environment evolution will eventually settle upon a single intermediate type, which drops a fraction of its seeds locally and sends the rest far away. This type is an ESS, and further, it is convergence stable: it will increase in abundance in any environment in which it is in competition with other types, eventually displacing them and thereby establishing itself against invasion by mutants. The model is a deliberately simplistic one, and hence powerful in its illustrative power.

Evolutionarily stable strategies are not generally the same ones that would be considered best in an optimization framework. Hamilton and May [37], for example, show that in a version of their model in which sites can become vacant, the ESS migration fraction is always higher than the fraction that maximizes the proportion of sites occupied. Higher migration, while it may not be ‘best for the population’, results from selective pressure upon types to avoid intratype competition.

Following Hamilton and May, most theoretical work on the evolution of life history strategies has focused upon scenarios in which a single best strategy would evolve. Evolutionarily stable strategies for dispersal have been examined for more general competition schemes [38], and in more complex habitats [39–41] (see [42] for a review of dispersal models); similar approaches have been applied to the examination of dormancy [43–45], seed size [46], tree height [47–49] and other characters. Exact analytical results have proved achievable in some cases; in others, especially in spatially explicit models, answers have been obtained only or primarily through simulations.

ESSs may be pure strategies, or they may be expressed in terms of distributions – mixed strategies in which a single genotype may exhibit a variety of behaviors. Indeed, even in the Hamilton and May example, it is not possible to distinguish between a pure strategy that disperses a fixed fraction of its seeds, and a mixed strategy that probabilistically disperses a fraction of its seeds, with a given mean. Similarly, Iwasa and Levin [50] find such mixed ESSs apply to the timing of life-history events. Specifically, they examine the tradeoffs between risking the vicissitudes of harsh winter conditions, faced by those that emerge or breed too early, and the competitive penalties associated with late emergence. They find that if the benefit of the earlier start to breeding is given purely by the excess time for growth, and if offspring are pooled across many subpopulations with different disturbance times, then there is a single pure ESS for a synchronous start to breeding on a given date. However, if disturbance occurs synchronously over the whole population, then the ESS is a mixed strategy of asynchronous breeding in which individuals may start breeding on one of several different days, with the probability of starting on each day given by a probability distribution.

Under different conditions still, the ESS for onset of breeding found by Iwasa and Levin [50] may be an evolutionarily stable mixture [51]; that is, a mixture of pure strategies able to resist invasion by other types. In particular, if subpopulations experience different disturbance times and either early breeding leads to a competitive advantage or population regulation occurs within local subpopulations before offspring are mixed across subpopulations, then a mixed strategy, a mixture of pure strategies, or a combination of the two will evolve. The variation among sites in disturbance times essentially creates a number of ‘niches’ that are best satisfied by types differing in their time to start breeding. Local competitive

advantage or population regulation ensures that types do not simply experience the arithmetic average of their success in different environments, and the combination with site heterogeneity results in frequency dependence of fitnesses that stabilizes mixtures of pure types. In this way, habitat heterogeneity creates conditions for the emergence of a diversity of types.

Cohen and Levin [41] also investigate the effects of habitat heterogeneity upon evolutionarily stable strategies, and specifically upon whether or not there is a single such strategy. They consider dispersal strategies in environments that are temporally correlated and spatially heterogeneous in site quality, with site quality expressed as a limit upon the total number of offspring that can be produced there. Previous work by Levin et al. [38] showed that in an environment composed of sites in which the environmental quality varies in a random and uncorrelated manner between patches, there is a single pure ESS for the fraction of offspring that disperse beyond their natal patch. Cohen and Levin [41] find that a single ESS also emerges when the patch environments are positively correlated in time. However, when there is negative temporal correlation, there is no single ESS. They do find what they term an evolutionarily compatible strategy – one that can invade any other nearby type individually but can also be invaded by every other nearby type. Further, they posit the existence of coalitions of different strategies that could resist invasion – that is, an ESS that is a mixture of pure strategies.

Ludwig and Levin [52] extend the results of Cohen and Levin [41] to elucidate the evolutionarily stable coalitions that emerge in the above model. They find that under conditions of negative temporal correlation in the environment and intermediate mortality of dispersing propagules, there exist evolutionarily stable combinations of two pure strategies that together can resist invasion by other types. These types will also come to dominate in any mixture of other types.

Mixed strategies and evolutionary stable combinations begin to give an inkling about how diversity can be maintained. Where mixed strategies are stable against invasion, so too are mixtures of types, at least neutrally so. Such diversity can arise in any life-history dimension that supports genotypic variance – dispersal characteristics, dormancy, reproductive allocation, etc.

4. Translation of an ESS problem into an optimization problem: an example

While the advantages of the game-theoretic approach over the optimization approach in finding winning strategies are clear, the game-theoretic approach is usually computationally and mathematically more difficult. Fortunately, there are cases in which an ESS problem can be transformed into one of maximizing a given function; this is a powerful simplification. We present an example of such a translation here, building on a model of Ezoe [46],

who explores a spatial simulation in which seed size determines both the distribution of dispersal distances and the relative competitive ability of types. Ezoe's result can be generalized to much more general functional forms than he treats, and restated as a maximization problem, from which the result of Hamilton and May, among others, is included as a special case. So far, however, this approach cannot be extended beyond the most straightforward situations, leaving numerous open challenges.

Ezoe considers an essentially infinite landscape, with individual sites that can be occupied by a single annual plant. He assumes that the population is at equilibrium at density D per unit area; without loss of generality, we rescale the spatial measure so that $D = 1$. Plant genotypes are designated by a value w . For Ezoe, w denotes seed weight (though more generally, as in the work of Hamilton and May, w may be any continuous index of genotype). Associated with w are a function $n(w)$, indicating the number of seeds a type w plant produces, a second function $a(w)$ denoting competitive advantage and a third function $\delta(w, r)$ that specifies the probability that a seed will be dispersed to a particular site a distance r from its origin. Ezoe considers space to be a continuum; we modify his treatment by regarding space to be divided into cells that can house one plant each. In this way, $\delta(w, r)$ can be interpreted as a probability rather than as a density function.

It is a considerable simplification and restriction to assume that competitive advantage, $a(w)$, is a property of one type alone, independent of its competitors. As formulated, this competitive advantage can be thought of as a germination probability, converting a number of seeds arriving at a site to a number of seedlings, or of effective competitors. More general models are clearly needed. This simplification, however, allows $a(w)$ and $n(w)$ to be collapsed into a single function

$$\rho(w) = a(w) n(w) \quad (1)$$

the overall measure of competitive success. This function essentially gives the total number of competitors in the next generation produced by a single parent plant.

To determine the ESS, Ezoe frames the problem in terms of rates of invasion of mutant types w in an environment initially dominated by \bar{w} . The number of second generation plants emergent from an individual mutant w is then

$$f(w|\bar{w}) = \sum_{\Omega} \frac{\rho\delta}{\rho\delta + \bar{\rho}(1 - \bar{\delta})} \quad (2)$$

where the summation is taken over the entire Ω . For such a continuous fitness function, at the ESS \bar{w} we must have

$$\left. \frac{\partial f}{\partial w} \right|_{w = \bar{w}} = 0 \quad (3)$$

[51]. Thus, Ezoë's approach allows one to show that an evolutionarily stable strategy is a type for which the summation

$$\sum_{\Omega} (1 - \delta) \frac{d(\rho\delta)}{dw} \quad (4)$$

vanishes. By computing the expected number of second generation plants emergent from an individual mutant w in this way (essentially mimicking the technique used in the epidemic problem discussed earlier), Ezoë suppresses the uncertainties associated with the stochastic nature of invasion. While this approach ignores possible complications due to clustering, it is a reasonable place to begin, and numerical simulations corroborate Ezoë's findings.

Ezoë assumes particular functional forms for ρ and δ ; but more generally, it can be shown that, because δ always integrates to 1, (4) is equivalent to the condition

$$\frac{d}{dw} \left\{ \rho^2 \left[1 - \sum_{\Omega} \delta^2 \right] \right\} = 0 \quad (5)$$

(Levin and Muller-Landau, in prep.). Indeed, it can further be shown that convergence stable evolutionarily stable strategies, if they exist, correspond to maxima of the function

$$F(w) = \rho^2 \left(1 - \sum_{\Omega} \delta^2 \right) \quad (6)$$

This requires examining the full invasion dynamics and not simply condition (5). More generally, (6) may have multiple critical points, including possible multiple ESSs.

For the special case considered by Ezoë, there is a unique, convergence stable ESS corresponding to the global maximum of (6). Similarly, the problem considered by Hamilton and May emerges as another special case having a unique ESS. In general, the most intriguing result is that one can determine convergence stable ESSs by searching for maxima of the function $F(w)$. Note that the term in parentheses in (6) has a compact biological interpretation: it is the probability that two seeds from a single plant will not land on the same site, hence, a measure of how widely plants disperse seeds. In general, the larger this is, the more successful the strategy, since sib–sib competition is thus avoided. Similarly, the larger is ρ , the more competitive is the strategy. Because larger seeds compete better but have more limited dispersal, there will be a tradeoff between these two measures; the optimal type is that which maximizes the product. This is in neat analogy to the results mentioned earlier for successful parasites.

The Hamilton–May and Ezoë models deal with homogeneous, saturated environments; in such environments, there is usually a single winning type. In natural communities, both variable abiotic conditions and the distributions of organisms themselves create extensive heterogeneity. As discussed earlier, such heterogeneity dramatically increases the possibilities for stable coexistence of different types. It remains an open question

whether the methods developed here for transforming this particular ESS problem into an optimization problem can be extended to cases in which the environment is heterogeneous.

5. Biodiversity emergent

The theoretical examples considered so far have all dealt with situations in which one or very few plant types emerge. Yet plant communities are not shrines to single species, the winners in all-or-nothing struggles. They are rather sites of high biological diversity, with species exhibiting a diversity of forms and strategies. We argued earlier that heterogeneity is essential to this biodiversity. Every theoretical case examined here in which the evolution and maintenance of multiple types was possible contained some sort of spatiotemporal heterogeneity. The representation of heterogeneity was relatively limited, however, and this is the principal reason that diversity remains low in the examples considered. To understand how the high diversity of types found in natural communities emerges, we must better incorporate heterogeneity into our models.

A number of studies has examined how spatial and/or temporal heterogeneity affects the number of types that can be maintained by a tradeoff between the ability of types to colonize new sites and their ability to take over sites from other types in the long run. Plant communities are comprised of species showing considerable variation in characters, such as seed size, that govern the competition–colonization tradeoff [53]. How do these different types emerge, and how can we understand this emergence and coexistence theoretically? The key to modeling this process is to provide a framework in which disturbance continually opens up sites for recolonization (exogenously imposed heterogeneity), and in which sites can differ in species composition (allowing endogenous heterogeneity to develop). Neither of these features is present in the saturated and homogeneous landscape considered by Ezoë. We do not treat these issues in detail in this paper; but a theory is emerging from extensions of the metapopulation framework introduced by Levins and used in a number of the theoretical examples discussed earlier [37, 38, 41, 52, 50].

The metapopulation approach divides space into discrete sites, which can differ in characteristics such as the timing of disturbance, as well as in which types are present. Essentially, populations are treated as metapopulations, structured into subpopulations at different sites, within which individuals mix freely and among which they move less often. Tilman [54], using this approach, considers a spectrum of species that vary in a single characteristic that affects both colonization ability and (inversely) competitive ability, and shows that a high diversity of (nonevolving) types differing in these characters can be maintained. Kinzig and her colleagues [55], building on this work and that of Hastings, use simulations and analytical approximations to understand the dynamics of types within this framework when new types continually

invade the system. They find that a power-law relationship (with exponent $-3/2$) emerges between abundance and fecundity (colonization ability). The specifics change when a broader class of tradeoffs is considered, but the fundamental point – that patterns at the community level emerge from individual competitive interactions – remains robust. Geritz [56] solves for the evolutionarily stable distribution of types in a very similar model, showing how it varies depending upon the specific assumptions made.

The work by Kinzig et al. [55] and Geritz [56] only begins to indicate the possibilities for the coexistence of multiple types. While the theoretical examples considered here always treat only one axis of differentiation at a time, real species are differentiated from one another in multiple characters – not only in competitive and colonization abilities, but also in other life history traits, in environmental tolerances and environmental effects, and in resistance to herbivores and pathogens. As multiple axes of differentiation among types are considered, the adaptive landscape becomes higher-dimensional, and the potential for stable coexistence increases. Furthermore, the metapopulation approach is limiting in its neglect of explicit space. Because all sites within a metapopulation framework are equally connected, there is only one scale at which heterogeneity can emerge. In contrast, a spatially explicit approach to this problem localizes feedbacks to a greater degree, and allows heterogeneity to develop at multiple scales; this enhances the potential for complexity.

Optimization arguments to explain ecological traits too often consider the individual in isolation, ignoring the population context in which traits must arise. The notion of the evolutionarily stable strategy frees us of that limitation, and allows the examination of evolution within the framework of frequency-dependent interactions that must exist among populations of organisms competing for common resources. Game-theoretic approaches, by incorporating the feedbacks of individuals upon the selective environment, essentially move the problem of trait evolution from a static adaptive landscape to a dynamic one continually modified by the other players in the game. But so far we have considered as players only other members of the same group of competing species – ignoring the impact upon their fitness landscapes of their herbivores, pathogens, mutualists, etc. The actions and reactions of these other species, in ecological and evolutionary time, add additional complexity and dynamism to adaptive landscapes, in large part through the heterogeneity they add to real landscapes. They constitute important selective forces modifying which types emerge in a given community, the relative abundances of these types, and the long-term stability or instability of the resulting assemblages in evolutionary time.

Some of the best-studied extra-guild influences upon plant community structure and diversity are those of herbivores, and in particular, of grazers upon grasslands. The presence of herbivores exerts selection pressure for faster-growing grasses, for shorter stature, for unpalatability, and

for physical defenses – such as spines – against herbivores [57, 58]. In experiments, herbivores have been shown to either increase or decrease diversity in ecological time, depending upon whether dominants are relatively more or less favored [59–62]. Over evolutionary time, herbivores almost certainly increase trait diversity, since defenses are costly [63]. Relative level of defense thus adds another axis of differentiation upon which selection can act, and spatiotemporal variability in herbivore pressure will favor different levels of defense in different places.

In addition to exerting general selective pressure for particular structural and strategic traits, herbivores and pathogens can enter into coevolutionary arms races with plants, distinguishing types that are otherwise ecologically equivalent through subtle differences in secondary chemistry and other species-specific defenses. This is considered one of the principal explanations for the high diversity of plant species in tropical forests [17, 18] and theoretical work has affirmed its potential to maintain high species diversity [64, 65]. The evolutionary dynamics of specialist herbivores and their hosts – or of hosts and pathogens more generally – have also been the subject of theoretical work, which essentially examines how hosts and pathogens continually modify each other's selective landscapes [66]. However, important as these processes may be for maintaining species diversity in general, our concern here is with functional diversity of types that are demonstrably not ecologically equivalent. Hence, we will not consider further either these equilibrium or complementary nonequilibrium [22, 67–69] explanations for diversity of competitive equivalents.

While theoretical work has incorporated the feedbacks of competing species upon each other's fitness landscapes, and of pathogens and hosts upon each other when hosts are otherwise competitively equivalent, the coevolutionary dynamics of herbivores and plants in the larger strategic landscape has received little attention. Herbivores, pathogens and the like affect not just the balance of species that are competitive equivalents in everything except their relationships to particular pathogens or mutualists, but also the dynamics of nonequivalent types; and these in turn feed back to the herbivores and pathogens themselves. What is needed is a theoretical framework for considering evolution on the adaptive landscapes of the plants and of their herbivores or pathogens simultaneously, in a framework in which the balance in each group affects the landscape of the other, as well as its own.

The subject of community and ecosystem organization is advancing rapidly, and raises a spectrum of fundamental questions in the theory of self-organizing systems. Most fascinating, perhaps, is the question of where the self-organizing tendencies of communities take them – to the stable and ordered world of Gaia, with homeostatic mechanisms regulating stability and higher-level ecosystem processes, or to the dizzying world of self-organized criticality, with high species turnover [70], or to some

world inbetween. It is this challenge that makes the study of ecosystem organization such an intellectually exciting one.

6. Conclusions

Anyone who studies natural systems cannot help but be awed by two features: the exquisite adaptations of organisms to their environments, and the integration of these independent elements into functioning wholes that maintain themselves, cycle nutrients, moderate weather, and seem almost to be superorganisms. Charles Darwin, who wondered at the same things, gave us a framework that allows us to understand how evolution has shaped the properties of organisms; it has been tempting for some to apply the same thinking to ecosystems and the biosphere.

Indeed, ecosystems and the biosphere are, to a large extent, the result of evolutionary forces operating at lower levels of organization. The Darwinian forces that craft the responses of organisms to their environments combine to shape the patterns that we see at the community and ecosystem level; and those patterns, in turn, feed back to influence evolution at lower levels, albeit diffusely.

Perhaps the fundamental challenge in ecology today is to understand these linkages, and how evolution operating at the level of individuals and populations can give rise to community organization. The questions are little different

for ecological communities than they are for economic communities, or for any self-organizing system. In this paper, we have attempted to raise some of the central issues, and to provide at least a hint of current work dedicated to addressing them. Our approach has been a self-organizing one, in which known forces at lower levels are examined first, and the community properties treated as emergent. As such, it should be viewed as complementary to efforts such as the family of Daisyworld models [71, 72] or to the investigations of Bak and others into self-organized criticality. Indeed, the issues are such that a diversity of complementary approaches are needed. Hopefully, a sequel to this paper a decade from now will be able to report that the pieces can now be assembled to provide a view of community evolution that is more complete than is available today. These are indeed exciting times to be addressing such issues.

Acknowledgements: This work was supported by the Andrew Mellon Foundation and National Science Foundation Grants INT-9725937 and DMS-9807755 to S. A. Levin; and a National Science Foundation Graduate Fellowship and a Smithsonian Tropical Research Institute Pre-doctoral Fellowship to H.C. Muller-Landau. E. Leigh and D. King provided helpful comments on earlier drafts of this manuscript. The authors thank P. Auger and P. Tortell for help with translations of the abstract and abridged version into French.

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