The effect of landscape structure on community self-organization and critical biodiversity

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Abstract

Critical biodiversity has been defined as the level of species richness at which communities are most susceptible to disturbance, where even small perturbations resulting from the introduction or extinction of a single species may trigger a mass extinction event. Beyond this threshold, it has been hypothesized that ordered communities with well-defined spatial structure will spontaneously form; these ordered communities are predicted to be resilient to small perturbations such that mass extinctions will no longer occur. We adopted a complex systems approach to explore how landscape pattern affected the critical biodiversity threshold (S_c) and the ability of communities to self-organize in heterogeneous random and fractal landscapes representing a gradient of spatial contagion. Communities that evolved in random and clumped fractal ($H = 1.0$) landscapes attained nearly the same average species richness (random $S = 22$, fractal $S = 20.5$), but the range of variation in community species richness was $3\times$ greater in random landscapes (random CV = 66%, fractal CV = 21%). Some communities that formed on random landscapes collapsed completely and never recovered, whereas complete system collapse never occurred on landscapes with a high degree of spatial contagion (clumped fractal). Nevertheless, spatial contagion initially enhanced the susceptibility of communities to mass extinction, and thus the critical biodiversity threshold was higher in landscapes with high spatial contagion (random $S_c = 15$; clumped fractal $S_c = 20$). In other words, a greater number of species was ultimately required to buffer communities from the small perturbations that occasionally triggered mass extinctions on these highly ordered landscapes. The likelihood of attaining this critical biodiversity was also affected by landscape structure. Communities on clumped fractal landscapes evolved to (or got stuck at) the critical biodiversity threshold, whereas communities with an intermediate degree of order ($H = 0.5$) generally evolved beyond this point and attained a high level of species richness. Spatial structure is not a prerequisite for the emergence of community structure, but organized communities are inevitable in highly structured (ordered) landscapes. Order begets order and this order ultimately enhances system stability and the susceptibility of the system to mass extinction.
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1. Introduction

Biological systems as diverse as the human brain, termite colonies, and tropical rainforests all undergo a similar process of self-assembly resulting from localized interactions among a diverse array of compo-

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nents, which ultimately give rise to organization and complexity at higher levels (Solé and Manrubia, 1995; Bak, 1996; O'Toole et al., 1999). Despite the obvious differences among these systems, Levin (1998, 1999) distilled four properties common to all complex systems: (1) diversity among system components, which provides variability upon which selection can act; (2) nonlinear interactions among those components, which leads to (3) aggregation and hierarchical system organization, which is further reinforced by (4) flows among the emergent structures of the organized system. Communities (Drake et al., 1999), ecosystems (Plotnick and McKinney, 1993; Jørgensen et al., 1998; Levin, 1998; Bradbury et al., 2000) and landscapes (Perez-Trejo, 1993; Bak, 1996; Milne, 1998; Bolliger et al., 2003) are canonical examples of self-organized systems. Approaching the study of these ecological systems as complex adaptive systems (CAS) provides new insights into how large-scale organization arises and is maintained by local processes operating at finer scales of organization (Hartvigsen et al., 1998). The study of ecological systems as CAS can address some of the most fundamental questions regarding how biodiversity originates and is maintained, how ecological systems become assembled, and how ecosystem structure relates to function and affects the stability of such systems (Levin, 1998).

Some minimal level of species richness may be necessary for self-organization to occur in ecological systems (Drake et al., 1999). *Critical biodiversity* (*sensu* Kaufman et al., 1998) is the threshold level of species richness at which communities spontaneously self-organize. Communities are most susceptible to local perturbations (e.g., extinction) at the critical biodiversity threshold (S_c), where even a small disturbance (the loss or addition of a single species) can trigger a mass extinction event. Although the extinction of a single species has a negligible impact on the system most of the time, such small effects occasionally have large consequences owing to nonlinear dynamics that are characteristic of CAS. For example, the loss of a keystone species may trigger a cascade of species extinctions and alter the structure and dynamics of the system. It has been proposed that self-organizing systems have an inherent tendency to evolve to this critical point (self-organized criticality or SOC, Bak et al., 1988), where though maximally unstable (the "edge of chaos"), the system also pos-

sesses maximum potential for adaptation (Kauffman, 1993).

If communities naturally evolve to this critical point, then a power-law distribution in the size of extinction events (the number of species going extinct in a given time period) is expected. Power (or scaling) laws represent a fractal signature that is supposedly indicative of SOC, in which the system lacks a characteristic length scale but exhibits spatial or temporal structure that is statistically self-similar across a range of scales (Solé et al., 1999). As a consequence, the system possesses long-range correlations, where local disturbances can propagate globally. Evidence for SOC has supposedly been found in the fossil record for patterns of Phanerozoic extinctions (Sneppen et al., 1995; Bak, 1996; Solé et al., 1997), but this has been contested by some (Kirchener and Weil, 1998; Plotnick and Sepkoski, 2001). More convincingly, Keitt and Marquet (1996) have demonstrated how the introduction of exotic bird species to the Hawaiian Islands over the past 130 years led to a cascade of extinctions among these introduced species once a critical number ($S_c = 8$) became established. Beyond this point, extinction rates generally increased as more species were added, and the distribution of extinction event sizes exhibited a power law indicative of critical scaling ($\beta = -0.91$), as did the persistence times (time to extinction) of introduced species ($\beta = -1.16$). Given that most of these exotic species were introduced into disturbed areas from which native species had already been extirpated, the introduced Hawaiian avifauna demonstrate how communities can self-organize to a critical state.

If ecological systems invariably organized to a critical state, however, they would always be on the verge of collapse even in the absence of external drivers or global perturbations (Levin, 1999). Such a view of system behavior is not consistent with the notion of ecological resiliency, in which species diversity buffers the system against environmental or anthropogenic disturbances (Tilman and Downing, 1994; Peterson et al., 1998). Instead, ecological systems should ideally evolve to a point just beyond the critical state in which diversity and adaptability (system flexibility) have been maximized, but where the system is able to achieve dynamic stability (Kauffman, 1995; Drake et al., 1999). Beyond the critical biodiversity threshold, communities are predicted to become ordered, that is,

to exhibit organization (compartmentalization) which enhances system stability by preventing local perturbations from propagating globally and triggering mass extinction events (Kaufman et al., 1998; Plotnick and McKinney, 1993). For model ecosystems on landscape mosaics with random habitat distributions, Kaufman et al. (1998) found that the critical biodiversity threshold was not the ultimate point of attraction for the system, as the system eventually evolved beyond this to an ordered state. The system spent much of its time at the critical biodiversity threshold, however, because this posed a "kinetic barrier" to evolution. That is, it took progressively longer for the system to evolve past S_c owing to the extreme sensitivity of the system at the critical point where it is subject to mass extinctions that repeatedly pushed it back to a lower diversity (S). A system "stuck" in this state might be mistaken for SOC (Kaufman et al., 1998; see also Tainaka and Itoh, 1996 for discussion of apparent SOC).

Communities and ecosystems are themselves embedded within a larger self-organized system—the landscape. Landscape structure produces environmental or spatial heterogeneity (a form of "symmetry breaking" necessary for self-organization; Rohani et al., 1997), which may act as a template in generating complexity at other levels of ecological organization (e.g., Bonabeau, 1998). By ameliorating species interactions such as competition or predation, heterogeneity invariably leads to increased coexistence (higher diversity) and thus has the potential to affect the complexity and stability of ecological systems. Using fractal landscapes, Palmer (1992) explored how spatial contagion—the clumping of habitat or resources—affected coexistence in a simulated community of ten annual plants that varied in their performance (competitive or reproductive success) along an environmental gradient. Local species richness (at a given "microsite" or cell of the landscape grid) was enhanced when landscape patterns lacked spatial dependence ($D = 3.0$, where $D = 3 - H$, and H is the degree of spatial contagion or autocorrelation of the pattern), but overall species richness at the landscape scale increased with increasing spatial dependence ($D = 2.0$, $H = 1.0$). The effect of spatial pattern on species coexistence thus changes as a function of scale. Landscape complexity slowed competitive exclusion, such that communities were less likely to exist in a state of equilibrium on landscapes with low

spatial dependence ($D = 3.0$). Communities on landscapes with a higher degree of spatial contagion ($D = 2.0$) were thus more stable.

Using an individual-based food web model, in which species interacted according to a predetermined set of interaction coefficients (a_{ij}), Keitt (1997) demonstrated that landscapes with a high degree of spatial contagion ($H = 1.0$) attained greater diversity (assessed as species richness, S) than those lacking spatial autocorrelation ($H = 0.0$). This is consistent with Palmer's (1992) study. Diversity is thus greater in landscapes with a higher degree of spatial contagion or order. Diverse communities were not the most complex, however, as species richness (S) was found to decrease with increased connectance (C, the fraction of non-zero interactions among species, $a_{ij} > 0$). This inverse relationship between diversity and connectance parallels that of May's (1972) stability criterion, in which communities with high connectance are less stable because extinctions can propagate more readily throughout the food web.

Landscape structure thus affects species coexistence, but how does it affect the evolution of biodiversity, the ability of ecological systems to self-organize, and the emergence of system properties such as complexity and stability? Neither Palmer's (1992) or Keitt's (1997) models were adaptive, in that species and their interactions did not evolve in these systems. For example, in Keitt's model, landscapes were seeded with a number of species ($S = 254$) and their interactions were specifically constructed so as to provide different levels of community connectance. Complexity is thus preprogrammed and stability is assessed in terms of the ability of the community to retain its original complement of species. Conversely, other ecosystem models that were adaptive (Hraber and Milne, 1997; Kaufman et al., 1998) have not examined the effect of landscape structure on community assembly. We therefore explored how landscape structure affects the evolution of diversity and community assembly for model ecosystems, and how this in turn relates to complexity and system stability. We addressed the following questions.

(1) How does landscape structure affect evolutionary trajectories? In other words, how does biodiversity

(assessed as species richness) originate on landscapes that differ in spatial complexity?

(2) How do extinction events scale as a function of landscape structure? Is there evidence for self-organized criticality?

(3) How does landscape structure affect the critical biodiversity threshold?

(4) Are communities driven to (or do they get stuck at) the critical biodiversity threshold, or do they evolve beyond this?

(5) Does order beget order? That is, are ecological systems more likely to become organized (ordered) on landscapes that themselves exhibit a high degree of order (spatial contagion)?

(6) Are communities more diverse, complex and stable above the critical biodiversity threshold?

(7) How does landscape structure affect the relationship between diversity and stability? Are diverse communities more complex? Are complex systems more stable?

2. Methods

2.1. Ecosystem model

The ecosystem model was developed within the context of complex systems theory, in which simple rules and localized interactions among species are capable of generating complexity in system structure at broader scales (Kaufman et al., 1998). The essential features of the model and its implementation are: (1) landscape is initially seeded with a single individual of a single species within a given habitat type (i.e., cell on landscape); (2) individuals have the potential to mutate, which has one of two consequences. Mutation results in either an increased competitive ability for a particular niche (enhanced fitness resulting from an increase in the adaptive weight for that niche) or a niche shift, which permits the exploitation of a new habitat or resource (i.e., speciation). The mutation rate per competition event (see (3)) per species varies dynamically as $R = [(0.75/L) \times (1/N)]$, where L is the length of the landscape and N is the size of the population. The goal of the model is to introduce small local perturbations (speciation events), and this calibration ensures that the mutation rate is always small relative to the rate at which species can spread across

the landscape, thus avoiding the problem of building an arbitrary length scale into the model (e.g., how far the species can spread before speciation occurs). (3) Species is able to spread to neighboring cells if the appropriate habitat or niche is available. Each generation (time step), an individual must compete for its current location as well as neighboring suitable sites (the four adjacent cells). Species with higher adaptive weights (i.e., fitness) for a particular niche are more likely to win the competition for space, but are not guaranteed to do so. Species in turn may provide the ecological niche for other species (e.g., species C can colonize a site if species B is present); and (4) ecological dependencies evolve through time and are not built into the model. The dependencies are one-way; this is not a consumer–resource or predator–prey model in which individuals at lower levels of the hierarchy are being consumed or depleted. Species at lower levels provide the environmental niche required by higher-order species, however, which creates a chain or web of ecological dependencies. Note that this model does not assume a hierarchical organization of species interactions involving trade-offs, such as between competition and colonization or between colonization and extinction, which are a feature of some other community assembly models (e.g., Tilman et al., 1994; Solé et al., 2004).

In summary, this model incorporates several important processes requisite to complex systems: continual generation of novelty through mutation, selection among that variation based on competition for niche space, localized interactions among species that affect competition for space and spread across the landscape, flows among structural components of the landscape and emerging community structure as species evolve and spread, and feedbacks that affect the evolution of ecological dependencies (see Kaufman et al., 1998 for how evolution of new species affects previous ones). Each simulation was run for 100,000 iterations (time steps or "generations"). Simulations were terminated at 100,000 generations because this is the point at which self-organization in community structure first emerged on random landscapes, and because system properties (e.g., critical biodiversity) were qualitatively similar when the model ran twice as long for 200,000 generations (Kaufman et al., 1998).
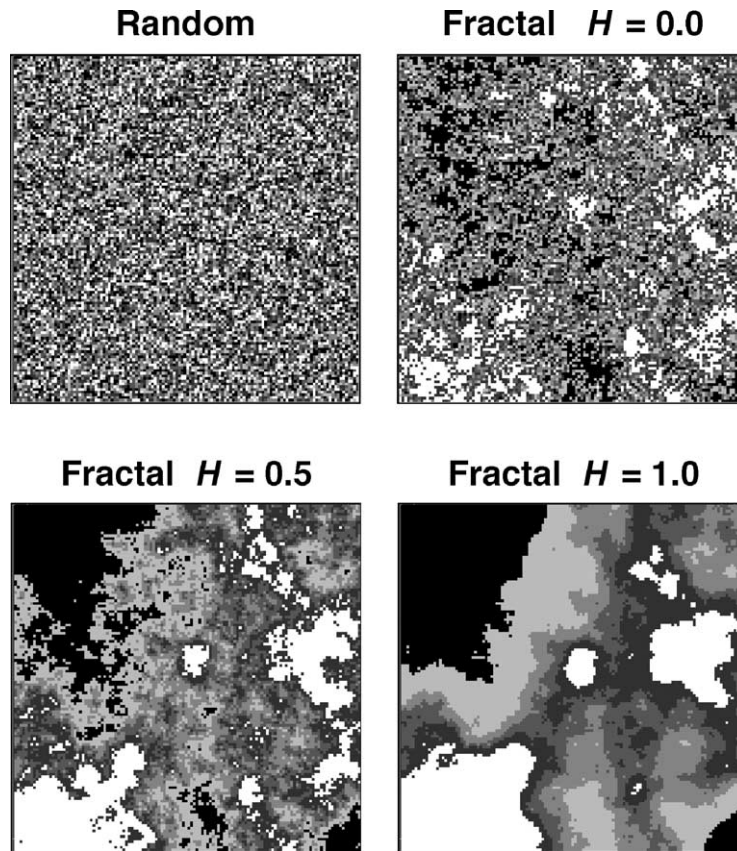
Fig. 1. Heterogeneous neutral landscapes consisting of either a random or fractal distribution of six habitat types. All habitat types have the same abundance on the landscape (∼17%). Fractal landscapes additionally vary in the degree of spatial contagion of habitat (H).

2.2. Generation of complex heterogeneous landscapes

We used neutral landscape models (Gardner et al., 1987; With, 1997; With and King, 1997) to create spatially complex landscape patterns (Fig. 1). All landscape maps had dimensions of 128 × 128 (16,384) cells. The model was implemented on replicate landscapes ($n = 15$) for each of the following scenarios, except for the single replicate required for the homogeneous landscape (total $n = 61$ landscape maps).

2.2.1. Homogeneous landscape

To get a baseline of what community patterns would be expected in the absence of landscape structure and heterogeneity, we initially ran the model on a simple landscape consisting of a single habitat or environ-

mental niche. Only a single run is presented as multiple runs gave identical results.

2.2.2. Random heterogeneous landscapes

In the absence of landscape structure, how does habitat heterogeneity (landscape diversity) affect community self-organization and critical biodiversity? Heterogeneity is considered to be essential for the emergence and maintenance of self-organization (Rohani et al., 1997; Watts, 2002), and thus heterogeneous landscapes consisting of a random distribution of six habitat types (environmental niches) were created (Fig. 1). All habitat types had the same abundance on the landscape (∼17%). Six habitat types were used in simulating heterogeneous landscapes to permit direct comparisons with the results of Kaufman et al. (1998), who settled on six habitat types because it was unlikely that any one habitat

type would percolate across the entire landscape at this level (Appendix A). We thus sought to duplicate Kaufman et al.'s (1998) results with this series of simulations and provide a baseline for comparison with heterogeneous fractal landscapes.

2.2.3. Fractal heterogeneous landscapes

Fractal landscapes were generated using the midpoint displacement algorithm of Saupe (1988) as described in With (1997) and With et al. (1997). Briefly, the three-dimensional fractal surfaces created by the midpoint displacement algorithm were sectioned at the appropriate "elevation" to create two-dimensional landscape maps with the requisite amount of habitat (~17%) for each of the six types. In addition, the spatial contagion (clumping) of habitat (H) was varied at three levels ($H = 0.0, 0.5,$ and 1.0) to create landscape patterns representing a gradient of fragmentation severity (high, medium and low fragmentation, respectively; Fig. 1, Appendix A). Percolation of one or more habitat types was possible, particularly in clumped fractal landscapes ($H = 1.0$; Appendix A). These landscape scenarios allowed us to determine the effect of landscape structure (at a fixed level of habitat abundance and heterogeneity) on patterns of community self-organization and on critical biodiversity thresholds.

3. Results

3.1. Effect of landscape structure on evolutionary trajectories

Despite an early explosion of species richness ($S = 30$ at gen 50) on the homogeneous landscape, the system quickly settled into a dynamic equilibrium in which biodiversity fluctuated very little among generations around an average of seven species [$\bar{X} = 7.4 \pm 1.95$ (S.D.), $n = 99,990$ gen; Table 1]. In contrast, considerable variation (CV = 66%) existed among evolutionary trajectories on random heterogeneous landscapes. Although high levels of diversity (>60 species) were attained in some simulations, there was also the possibility ($1/15 = 0.07$) that the system would collapse completely and never recover. Unlike the homogeneous landscape, there was no early explosion of diversity, just a gradual accumulation of species. Evolutionary trajectories on fragmented ($H = 0.0$) fractal landscapes were less variable (CV = 49%) than on random landscapes, but there was still the possibility ($1/15 = 0.07$) that the system would collapse. Some simulations ($4/15 = 0.27$) did show an early explosion of diversity (10–25 species by gen 50), however. The main effects of increasing spatial contagion ($H = 0.5, 1.0$) were to increase the proportion of runs that exhibited a diversification

Table 1
Descriptors of community structure and patterns of extinction on homogeneous and heterogeneous landscapes

Parameter[a]	Homogeneous	Random	Fractal ($H = 0.0$)	Fractal ($H = 0.5$)	Fractal ($H = 1.0$)
S	8	22.0 (3.74) AB	16.5 (2.07) B	26.1 (1.93) A	20.5 (1.12) AB
CV (%)	na	66	49	29	21
Local S	1	6.4 (0.72)	6.4 (0.69)	7.8 (1.06)	7.2 (0.66)
H'	1.68	1.70 (0.203) A	2.06 (0.168) AB	2.55 (0.112) B	2.52 (0.069) B
E	0.76	0.57 (0.07) A	0.72 (0.06) AB	0.78 (0.02) B	0.83 (0.02) B
I_m	0.94	1.03 (0.019) A	1.09 (0.029) AC	1.29 (0.066) B	1.21 (0.040) BC
C	0.11	0.26 (0.061)	0.21 (0.033)	0.15 (0.008)	0.18 (0.011)
H_t	0.65	0.57 (0.005) A	0.59 (0.010) A	0.62 (0.009) B	0.63 (0.008) B
S_c	11	15	17	20	20

Where indicated, values represent the mean (± 1 S.E.) of 15 runs (run = 100,000 generations), except for the homogeneous landscape where only a single run was performed. In a comparison of communities on heterogeneous landscapes, means with the same letters are not significantly different ($P > 0.05$) based on Tukey tests.

[a] S, average species richness among runs (S assessed at end of run); CV, coefficient of variation in species richness among runs; local S, average species richness within individual grid cell of landscape; H', Shannon–Weiner diversity index; E, evenness (proportion of maximum diversity attained by community); I_m, Morisita's index (measure of species clumping in space); C, connectance (proportion of possible connections—ecological dependencies–among species); H_t, degree of correlated extinctions through time; S_c, critical biodiversity threshold (cf. Fig. 3).

peak by gen 50 ($H = 0.5$: $9/15 = 0.60$; $H = 1.0$: $10/15 = 0.67$), to increase the height of this early diversification peak ($H = 0.5$: $S = 40$; $H = 1.0$: $S = 52$), and to decrease variation among simulations ($H = 0.5$: CV = 29%; $H = 1.0$: CV = 21%) such that evolutionary trajectories appeared to converge on a particular level of diversity by gen 100,000.

3.2. Effect of landscape structure on biodiversity

The resulting species richness (S) was lowest on homogeneous landscapes ($S = 8$), and highest on fractal landscapes with an intermediate degree of spatial contagion ($H = 0.5$; $S = 26$; Table 1). There were significant differences in the level of biodiversity that evolved on heterogeneous landscapes ($F = 3.32$, d.f. $= 3, 55$, $P = 0.027$; ANOVA), which is reflected primarily in the contrast in species richness between fragmented ($H = 0.0$) fractal landscapes and those with an intermediate degree ($H = 0.5$) of spatial contagion ($P < 0.05$, Tukey test; Table 1). Although this same trend in species richness was also reflected at the local level (within individual grid cells of the landscape), these differences were not significant at this scale (Table 1). Evenness (E) was significantly higher in landscapes that had the greatest degree of spatial contagion ($H = 0.5, 1.0$; Table 1). [Evenness (E) is a standardized measure of diversity based on the Shannon–Weiner index (H') as $E = H'/\ln S$ (Magurran, 1988)]. Thus, diversity was significantly greater on heterogeneous fractal landscapes (i.e., ordered landscapes) than on random landscapes ($F = 5.06$, d.f. $= 3, 55$, $P = 0.004$; ANOVA, using an arcsine transformation based on the square-root of E to achieve normalization; Zar, 1999, p. 278).

3.3. Effect of landscape structure on susceptibility to extinction

The level of species richness attained on a landscape reflects a dynamic trade-off between speciation and extinction. Thus far, only patterns of speciation have been considered. To what extent does landscape structure affect extinction dynamics, in terms of whether extinctions propagate through time (does a single extinction event trigger other extinctions?) and space (does spatial contagion enhance a community's susceptibility to species extinction?). We performed a

Hurst analysis (Russ, 1994) to assess correlated extinctions through time (i.e., a rescaled range analysis). Extinctions were more correlated (more likely to propagate through time) in landscapes with a high degree of spatial contagion (i.e., fractal landscapes, $H = 0.5$, 1.0; Table 1). Note that extinctions had the greatest temporal correlation on homogeneous landscapes ($H_t = 0.65$), which lacked order. Extinctions were basically random through time ($H_t \to 0.5$) on random and fragmented ($H = 0.0$) fractal landscapes. The extinction dynamics within these two landscape types were significantly different from those in the more ordered fractal landscapes ($H = 0.5, 1.0$) ($F_{3,56} = 13.26$, $P = 0.0001$; ANOVA, using an arcsine transformation based on the square-root of H_t to achieve normalization; Zar, 1999, p. 278).

Although the vast majority of extinctions on these landscapes were of a single species, mass extinctions (>10 species/gen) occasionally occurred on landscapes with high spatial contagion ($H = 0.5, 1.0$), but not on random landscapes. The early diversification peak characteristic of these landscapes produced an explosion of diversity that was not sustained, but resulted in a cascade of species extinctions. Mass extinction events were not restricted to just the first 100 gen on these landscapes, however ($H = 0.5, 1.0$ in Fig. 2). The scaling of extinction events within the first 100 gen bears a fractal signature (i.e., a power-law distribution of extinction event sizes, in which exponent $\beta \to 1.0$), but the fit is not as good (based on R^2) as for longer time periods (>100 gen), especially in fragmented fractal ($H = 0.0$) landscapes (Table 2).

The susceptibility to extinction, $\chi(S)$, is the average extinction size as a function of diversity (S) and was assessed as:

$$\chi(S) \equiv \frac{1}{S} \int_{t_0}^{\infty} E(t, S'(t)) \theta(S', S) \, dt \qquad \begin{cases} \theta = 0 : S' \geq S \\ \theta = 1 : S' < S \end{cases}$$
$$S'(t_0) > S$$
(1)

where E is the sum total of extinctions integrated over a range of species S' (Kaufman et al., 1998). The level of species richness (S) at which the susceptibility to extinction, $\chi(S)$, is greatest defines the critical biodiversity threshold (S_c). Among heterogeneous landscapes, critical biodiversity increased with increasing spatial contagion, ranging from $S_c = 15$ for random
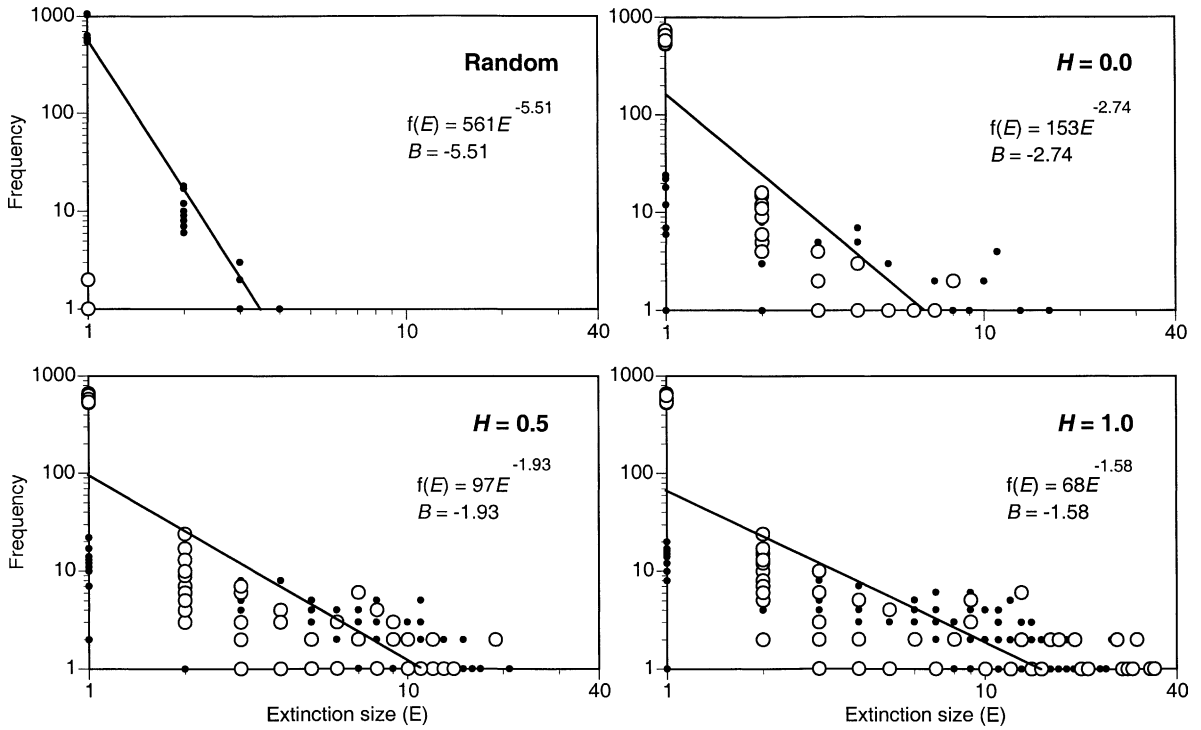
Fig. 2. Frequency of extinction events of different sizes on heterogeneous random and fractal landscapes. Line is fitted using least-squares regression of the log-transformed data over the entire run (100,000 gen) for all 15 maps. Extinction events that occurred during the first 100 gen (○) and for the remainder of the run (●) are also indicated.
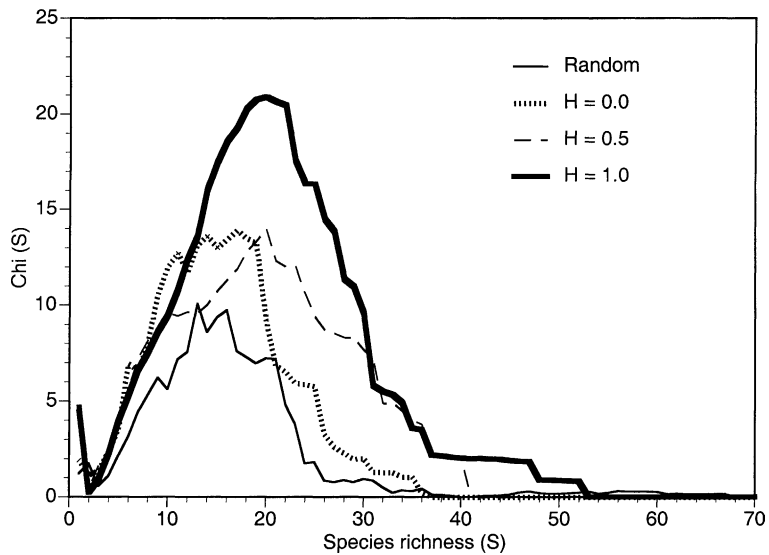

Fig. 3. Susceptibility to extinction as a function of species richness, $\chi(S)$, for communities that evolved on random or fractal landscapes (H). The critical biodiversity threshold is defined as the level of species richness at which the susceptibility to extinction is greatest.

Table 2
Scaling of extinction event sizes on homogeneous and heterogeneous landscapes

Landscape Time period	β	R^2	F	d.f.	P-value
Homogeneous[a]	−1.59	0.668	24.17	1, 12	0.004
≤100 gen	−0.75	0.612	18.89	1, 12	0.001
Random[b]	−5.51	0.973	1358.39	1, 38	0.0001
Fractal ($H = 0.0$)	−2.74	0.733	181.03	1, 66	0.0001
≤100 gen	−0.71	0.340	17.51	1, 34	0.0002
>100 gen	−3.89	0.838	243.32	1, 47	0.0001
Fractal ($H = 0.5$)	−1.93	0.721	361.59	1, 140	0.0001
≤100 gen	−0.80	0.573	136.74	1, 102	0.0001
>100 gen	−2.25	0.649	120.29	1, 65	0.0001
Fractal ($H = 1.0$)	−1.58	0.665	357.56	1, 180	0.0001
≤100 gen	−0.73	0.562	177.24	1, 138	0.0001
>100 gen	−1.63	0.631	119.81	1, 70	0.0001

Analysis based on least-squares regression of log-transformed extinction events occurring across all runs (run = 100,000 gen) for a given landscape type. Separate analyses were conducted for the first 100 gen to capture the early diversification peak present in some landscapes and for the remainder of the run (>100 gen) to examine shifts in the scaling coefficient (β).

[a] Analysis not broken down by time period for >100 gen because the system was in a dynamic steady state in which only one or two species went extinct at a time (i.e., there were only two extinction event sizes).

[b] Analysis not broken down by time period for random landscapes because there was no early diversification peak and no extinctions occurred within the first 100 generations.

landscapes to $S_c = 20$ in clumped fractal landscapes ($H = 0.5, 1.0$; Fig. 3). The critical biodiversity threshold in homogeneous landscapes was $S_c = 11$ (not displayed in Fig. 3). Extinctions were thus more likely to propagate in space and time on fractal landscapes with high spatial contagion ($H = 0.5, 1.0$), such that a higher level of species richness was required to overcome the critical biodiversity threshold.

3.4. Consequences of critical biodiversity for community order and ecological complexity

Past the critical biodiversity threshold (S_c), we hypothesized that communities should exhibit a high degree of (1) diversity (assessed by evenness, E); (2) organization (i.e., a non-random distribution of species across the landscape); and (3) complexity (level of connectance among species within the community).

3.4.1. Are communities more diverse above the critical biodiversity threshold?

There was no indication that communities became more diverse (as assessed by evenness, E) above the critical biodiversity threshold (S_c; Fig. 4). In random

landscapes, the most species-rich community was also the least diverse (i.e., least evenly distributed). If we arbitrarily adopt $E = 0.7$ to represent communities with high diversity, then half of the communities that form on random landscapes ($8/15 = 0.53$) exhibit low diversity (evenness) whereas nearly all the communities on fractal landscapes (especially those with high contagion, $H = 1.0$) attain high levels of diversity, irrespective of the critical biodiversity threshold. Furthermore, it appears that communities on clumped ($H = 1.0$) fractal landscapes (i.e., highly ordered landscapes) are driven to (or get stuck at) the critical biodiversity threshold (Fig. 5). This was seen in the convergence of evolutionary trajectories, but the level of species richness at which these communities converge is the critical biodiversity threshold (S_c). Communities in fractal landscapes with an intermediate degree of spatial contagion or order ($H = 0.5$) generally evolve beyond the critical biodiversity threshold ($8/15 = 0.53$; Fig. 5). The same might also be said of communities on random landscapes, where $S > S_c$ for half of the communities ($8/15 = 0.53$), but some communities fail to reach the critical biodiversity threshold ($S < S_c$), resulting in a more variable response as was evidenced in the
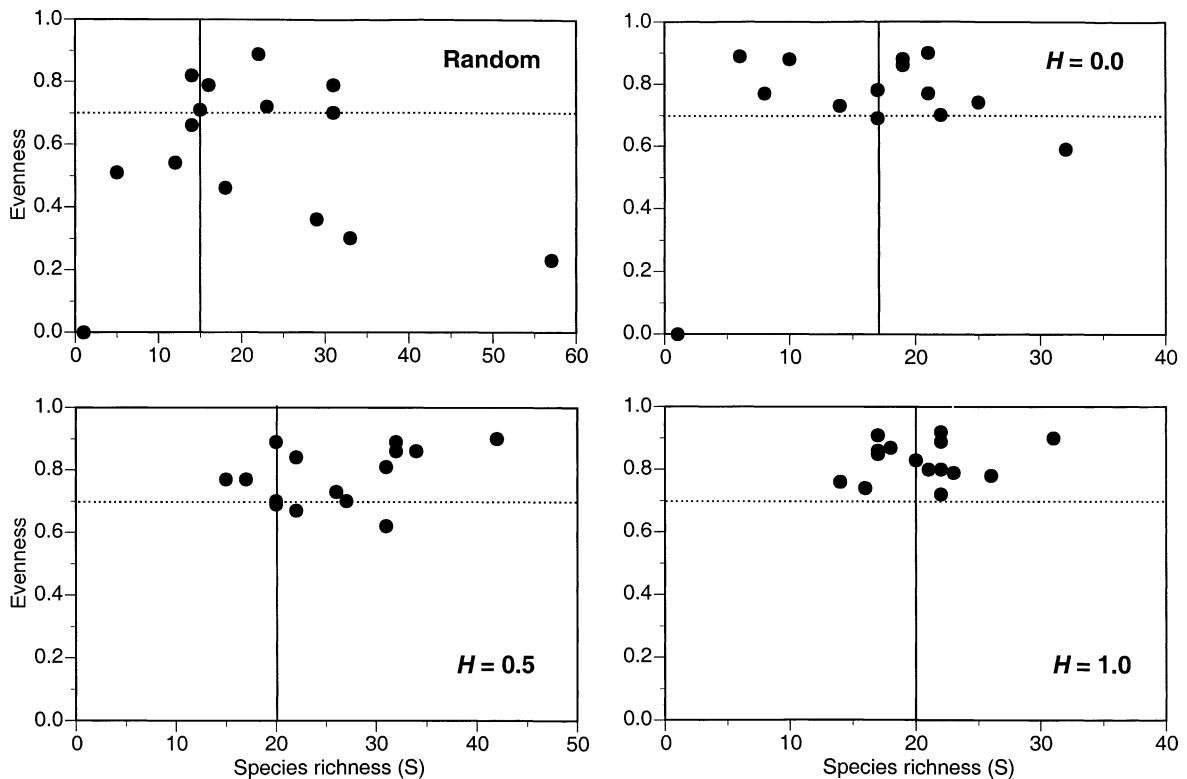
Fig. 4. Diversity (evenness, E) attained by communities evolving on different landscapes relative to the critical biodiversity threshold for each landscape type (solid vertical line). Horizontal line indicates an arbitrary level of high diversity ($E = 0.7$).

great variation among evolutionary trajectories on this landscape type. On average, then, species richness was less than the critical biodiversity threshold on random landscapes ($S < S_c$), converged on the critical biodiversity threshold on clumped ($H = 1.0$) fractal landscapes ($S = S_c$), and was greater than the critical biodiversity threshold on landscapes with an intermediate degree of spatial contagion ($H = 0.5$; $S > S_c$; Table 1).

3.4.2. Are communities more organized above the critical biodiversity threshold?

Community organization–a measure of order–was assessed by evaluating whether species exhibited a non-random distribution across the landscape, which was determined by Morisita's index (I_m). Morisita's index quantifies the probability that two species drawn at random will have come from the same cell on the landscape (Hurlbert, 1990; With et al., 1997). Morisita's index ranges from $I_m = 1.0$ for random distributions, to $I_m < 1.0$ for overdispersed patterns,

to $I_m > 1.0$ for clumped (ordered) distributions. The aggregation of species (I_m) can be assessed at different scales on a landscape (e.g., With et al., 1997), and thus we present the results of the analysis attained at a 4×4 resolution (i.e., a 16-cell block) because this was the scale at which community organization was most evident (based on the highest model R^2 attained from the analysis of I_m at different scales, which was $R^2 = 0.30$ at this scale and ranged 0.14–0.29 for the other six scales of analysis). In general, communities that evolved on homogeneous landscapes lacked order and were overdispersed ($I_m < 1.0$, Table 1). The degree to which communities became organized differed significantly among heterogeneous landscapes ($F_{3,55} = 7.63$, $P = 0.0002$; ANOVA). Communities on random landscapes generally did not organize beyond a random distribution, and thus exhibited the lowest degree of order among heterogeneous landscapes (Table 1). Surprisingly, the highest degree of order in community organization was not found in
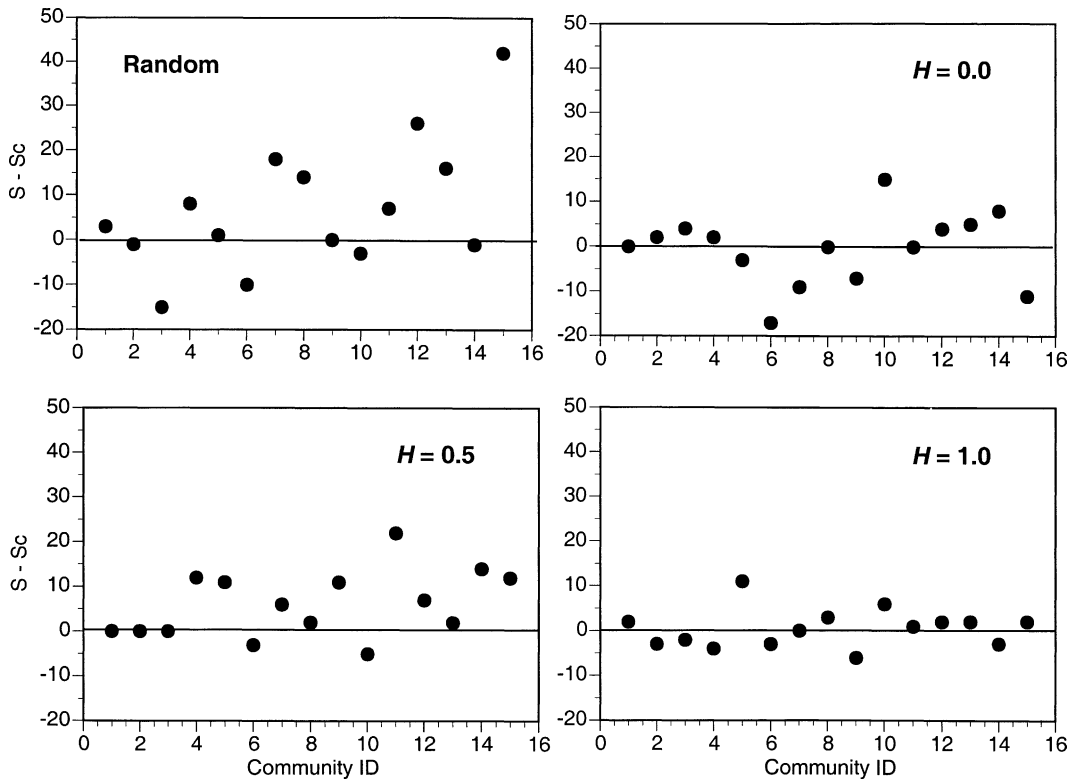
Fig. 5. Normalized diversity, the divergence from the critical biodiversity threshold ($S - S_c$), for communities evolving on different landscapes.

the most ordered ($H = 1.0$) landscapes, but in fractal landscapes with an intermediate degree of spatial contagion ($H = 0.5$), although this difference was not statistically significant. Nevertheless, communities tended to attain a significantly higher degree of order on ordered landscapes than on random landscapes.

There was no tendency for communities to become more organized beyond the critical biodiversity threshold (S_c), except perhaps in fractal landscapes with an intermediate degree of spatial contagion ($H = 0.5$; Fig. 6). The highest degree of order was also attained by communities in these landscapes (27% of runs had $I_m > 1.4$), all of which were above the critical biodiversity threshold (S_c).

3.4.3. Are communities more complex above the critical biodiversity threshold?

We assessed complexity in terms of the degree of ecological dependency that evolved among species within a community. Communities exhibiting a high degree of complexity have a high level of connectance (C) among species. Connectance is the fraction of possible connections (ecological dependencies) among species, which is obtained as $C = 2L/[N(N - 1)]$, where L is the proportion of possible links attained and N is the number of species. Although the most ordered communities were expected to be the most complex, communities on random landscapes (which had a low degree of order; Fig. 6) had the highest connectance (Table 1). In fact, the most ordered communities—those that evolved on landscapes with an intermediate degree of spatial contagion ($H = 0.5$)—were the least complex. These relationships were not statistically significant, but the trend is revealing.

Although it was expected that communities above the critical biodiversity threshold (S_c) would be more complex, they were actually less complex, at least for random and fragmented ($H = 0.0$) fractal landscapes (Fig. 7). Communities on clumped fractal
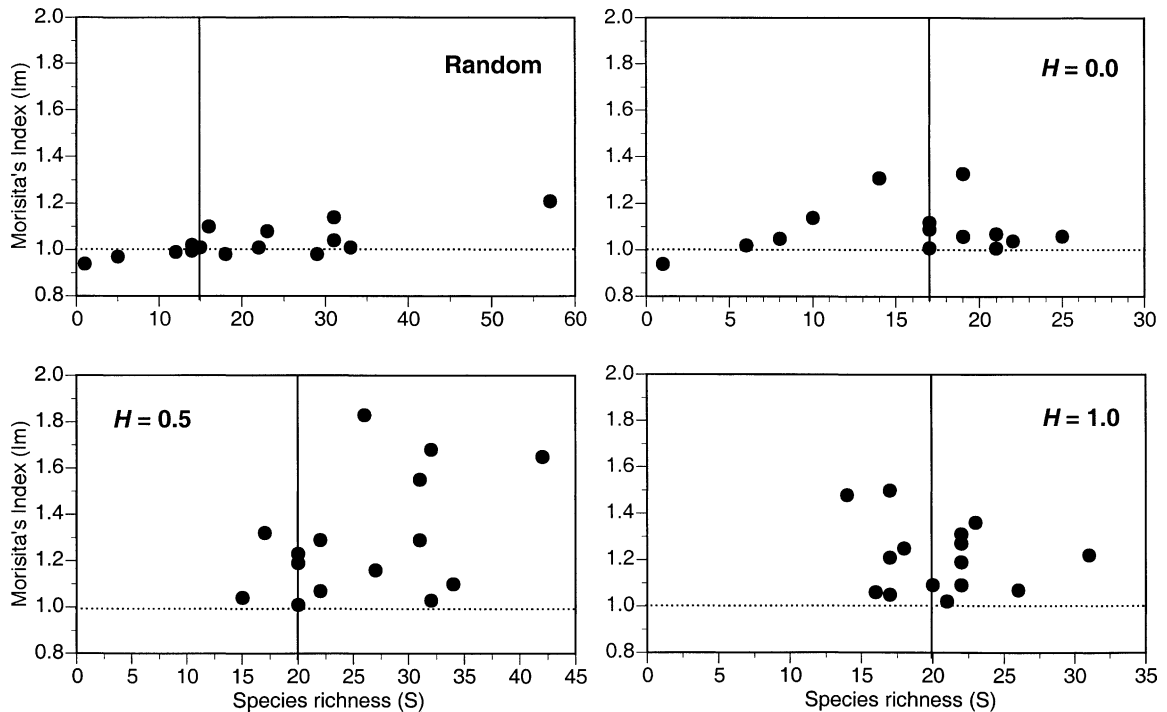
Fig. 6. Organization attained by communities evolving on different landscapes relative to the critical biodiversity threshold for each landscape type (solid vertical line). Horizontal line indicates a random distribution of species ($I_m = 1.0$); $I_m > 1.0$ indicates aggregation of species into communities (i.e., organization).

landscapes ($H = 0.5$, 1.0) converged on a particular level of connectance (i.e., there was little variation in C among communities), especially for landscapes with an intermediate degree of spatial contagion ($H = 0.5$). Communities on the latter landscapes all had about the same, low level of connectance, $C = 0.15$. To understand better what factors contributed to connectance, we undertook a stepwise multiple regression that included the effects of landscape type, species richness (S), local species richness (local S), diversity (E), and aggregation (I_m assessed at scales 1 and 3, a 1 × 1-cell and 4 × 4-cell block, respectively). Because landscape type was a significant descriptor of connectance (partial $R^2 = 0.13$, $F_{3,55} = 12.94$, $P = 0.0006$), we performed separate analyses for each of the heterogeneous landscape types. In random landscapes, connectance was positively associated with diversity (E partial $R^2 = 0.33$, $F_{2,12} = 21.94$, $P = 0.0005$), but negatively associated with aggregation at the finest scale (scale 1 partial $R^2 = 0.35$, $F_{2,12} = 13.24$, $P = 0.0034$). In fragmented fractal

landscapes ($H = 0.0$), connectance was negatively associated with species richness (S partial $R^2 = 0.35$, $F_{3,11} = 22.75$, $P = 0.0006$), and positively associated with diversity (E partial $R^2 = 0.38$, $F_{3,11} = 38.93$, $P = 0.0001$) and aggregation at the broader scale (I_m partial $R^2 = 0.08$, $F_{3,11} = 4.67$, $P = 0.05$). Connectance on landscapes with an intermediate degree of spatial contagion ($H = 0.5$) was not significantly associated with any variable, as might be expected given the low level of variation among runs (i.e., convergence on $C = 0.15$; Fig. 7). Finally, connectance on clumped fractal landscapes ($H = 1.0$) declined with increasing species richness at the landscape (S partial $R^2 = 0.25$, $F_{3,11} = 20.27$, $P = 0.0009$) and local scales (local S partial $R^2 = 0.24$, $F_{3,11} = 9.95$, $P = 0.009$), and increased with increasing aggregation at the broadest scale (scale 3 partial $R^2 = 0.24$, $F_{3,11} = 15.97$, $P = 0.002$). Thus, diverse communities were complex only in random and highly fragmented fractal ($H = 0.0$) landscapes (i.e., landscapes with a low degree of order). In fractal landscapes, ordered com-
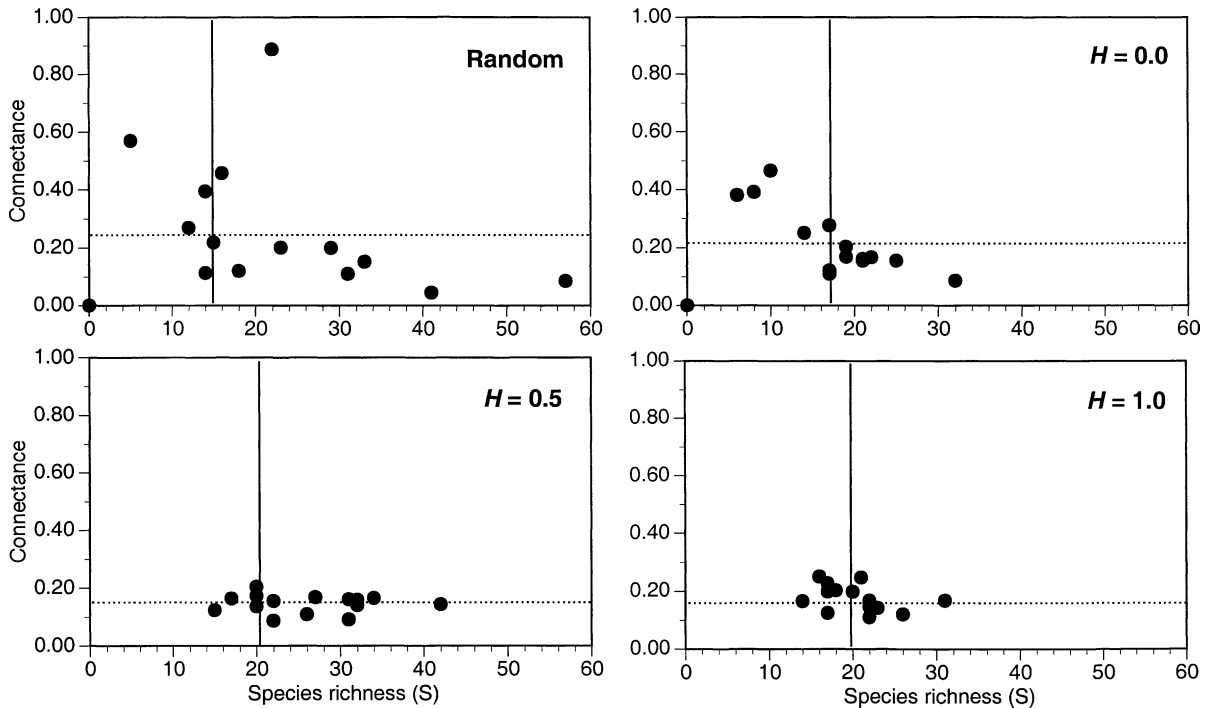
Fig. 7. Degree of connectance (proportion of interactions among species) attained by communities evolving on different landscapes relative to the critical biodiversity threshold for that landscape type (solid vertical line). Horizontal line is the average connectance attained by communities within a given landscape type.

munities were the most complex (at least for $H = 0.0$ and 1.0).

4. Discussion

Although random and highly ordered ($H = 1.0$) landscapes attained roughly the same level of species richness (S), evolution on random landscapes was highly variable and there was the possibility of complete system collapse even in the absence of external perturbations. Community self-organization was unlikely to occur in random landscapes within the timeframe we modeled, but apparently emerged eventually in longer runs on these landscapes (e.g., by 200,000 gen; Kaufman et al., 1998). In contrast, evolutionary trajectories converged on the critical biodiversity threshold (S_c) in highly ordered landscapes. This may be an attractor for the system, or it may be an example of kinetic inertia where the system gets "stuck" at the critical biodiversity threshold owing to

the extreme sensitivity of the system to local perturbations (extinction) in this region (Kaufman et al., 1998). Despite being poised at the critical biodiversity threshold, organized communities ($I_m > 1.0$) invariably formed on highly ordered landscapes. Order in landscape structure thus appears to beget order at other levels of ecological organization.

How could system order emerge in highly ordered landscapes if they are poised at the critical biodiversity threshold (the "edge of chaos")? Indeed, the organizing force of landscape structure was so strong that ordered communities developed in fractal landscapes regardless of where communities ended up with respect to the critical biodiversity threshold. This may be attributable to the early explosion of diversity that enabled these communities to get beyond the S_c hurdle (kinetic barrier) quickly, thus enabling communities to self-organize early in the evolution of these systems. Some evidence for this is apparent in the critical scaling of extinction events in the early evolution of these systems (<100 gen), but not after the diversification

peak. A diversification peak occurs in ordered (fractal) landscapes but not in random ones because the greater spatial contagion of fractal landscapes concentrates species within habitat patches, thereby increasing the rate of interactions among species (i.e., coevolutionary responses) leading to an explosion of diversity. Interestingly, this same phenomenon is also observed in the homogeneous landscape, which represents the ultimate in habitat contagion (i.e., the landscape is entirely connected). Patchiness (compartmentalization) may thus enhance evolutionary rates. Natural landscapes exhibit compartmentalization in the form of patchiness across a range of scales, such as in the distribution of landforms, soil types, habitat types or other resources. If the world were truly random, self-organization in community structure may eventually occur (e.g., Kaufman et al., 1998) but would take a very long time and is not guaranteed (i.e., complete system collapse is possible; this study). Thus, although landscape structure is not necessary for community self-organization, self-organization is inevitable in ordered landscapes ("order for free"; Kauffman, 1995).

This begs the question of whether there would be ecological communities or ecosystems in the real world if landscapes were not ordered? How much landscape order is sufficient for system self-organization to occur? Communities on landscapes with a low degree of order ($H = 0.0$) had the lowest species richness among heterogeneous landscapes (including random) and were susceptible to complete system collapse. Nevertheless, these communities could be as diverse (E) and as ordered (I_m) as communities that developed on highly ordered ($H = 1.0$) landscapes. At the other extreme, communities on highly ordered landscapes may achieve a high level of diversity and organization (I_m), but these systems are also poised at the critical biodiversity threshold (S_c), which is the region of maximum instability where local perturbations (extinctions) propagate through space and time. This was evident in (1) the high degree of correlated extinctions through time (H_t); (2) a higher critical biodiversity threshold (S_c); and (3) the frequency of mass extinction events (>10 species/gen) that continued to occur throughout the simulation run (>100 gen).

The ideal state of a CAS is just beyond the critical biodiversity threshold, where maximum diversity has been attained but the system has achieved dynamic stability and is no longer rocked by mass extinction events (Kauffman, 1995). In our adaptive systems, communities achieved the highest degree of order in landscapes with an intermediate degree of order ($H = 0.5$), and most communities evolved past the critical biodiversity threshold (S_c) into the ordered domain. Communities that evolved on these landscapes attained the highest species richness in addition to a high level of diversity. This is in contrast to Palmer's (1992) and Keitt's (1997) model ecosystems in which species richness increased linearly with increasing spatial contagion. Although half of the communities on random landscapes also appeared to reach a level of species richness that should place them in the ordered domain, they were not, in fact, ordered. This apparent paradox can be resolved by considering that such communities had probably not yet achieved a dynamic equilibrium given that self-organized communities do eventually form on random landscapes (>100,000 gen; Kaufman et al., 1998). Thus, self-organization is a protracted process in the absence of existing spatial structure. Spatial structure promotes rapid diversification early in the evolution of the system, which may enable it to more quickly and easily clear the S_c hurdle and achieve organization.

Thus, species richness by itself does not indicate whether a system is ordered or not. It also depends on where along the evolutionary trajectory the system is located, which means that knowing a system's history is necessary for understanding its current configuration and for being able to predict its future dynamics (e.g., Drake, 1991; Drake et al., 1999). Second, high species richness may not equate to system complexity. Species-rich communities on random landscapes and fractal landscapes with low spatial contagion ($H = 0.0$) were the least complex (C). This inverse relationship between richness and complexity is at least consistent with some previous studies of model ecosystems (e.g., May, 1972; Keitt, 1997). Interestingly, the communities on landscapes with an intermediate degree of order converged on a particular (albeit low) level of complexity which was maintained even at high species richness. Presumably, the high degree of community organization achieved on these landscapes further compartmentalizes species interactions, leading to this relatively low level of interconnectedness among species across the landscape. Thirdly, complexity appears to be inversely

related to stability. Although communities on ordered landscapes initially have the highest susceptibility to extinction owing to the propagation of extinctions in time and space (low stability), spatial contagion also enhances the evolution and maintenance of diversity and promotes self-organization. The occasional mass extinction events (>10 species/gen) that appeared after the initial burst of diversity on these landscapes (>100 gen) were restricted to individual habitat or community types on the landscape. Mass extinction events were virtually nonexistent near the end of the run (i.e., >85,000 gen). Community self-organization (compartmentalization) and low connectance thus buffer the system from widespread mass extinction, which contributes to greater global stability. Diversity thus emerges in ordered landscapes owing to enhanced stability. Diversity does not beget stability so much as stability begets diversity.

Landscapes with an intermediate degree of order thus afford the right amount of spatial contagion that balances the opposing forces of evolution and extinction (another manifestation of the "Goldilock's principle"). It is intriguing that natural landforms often exhibit an intermediate degree of spatial contagion (i.e., mid-range correlations in spatial heterogeneity; Godchild and Mark, 1987; Bolliger et al., 2003), although landscapes may exhibit different degrees of spatial dependence as a function of scale and degree of human alteration of landscape patterns (Krummel et al., 1987). Nevertheless, the complexity of many natural landscapes is close to the intermediately clumped landscapes of our study. It is tempting to speculate that the level of spatial dependence found in many natural landscapes is exactly the level that best promotes self-organization and dynamic stability in ecological systems. This remains a hypothesis to be tested through experimental or empirical investigations that study the effect of landscape structure on community assembly (e.g., Drake et al., 1993).

Critical biodiversity may be evident in studies that have documented a threshold effect of species richness on system stability or resilience (Scheffer et al., 2001). For example, productivity in a grassland system declined precipitously below a threshold number of species ($S = 9$; Tilman and Downing, 1994). Species-rich communities maintained productivity in the face of a severe drought, and were able to recover more fully after the drought than species-poor communi-

ties. Thus, ecological systems may be resilient to even broad-scale external perturbations, such as drought, above the critical biodiversity threshold. In this domain, the loss of a single species is unlikely to affect system stability because other species are present that are resistant to the perturbation (e.g., drought-tolerant plants) and can compensate for species that are lost from the system. Loss of biodiversity below the threshold is thus expected to affect system function, such as productivity, stability and sustainability. Complex systems theory suggests that the system is also more likely to retain its diversity in the region above the critical biodiversity threshold in the face of such perturbations, because the loss of a single species is unlikely to propagate across the system and trigger a mass extinction event. This provides additional incentive for preserving biodiversity and attempting to manage or restore systems beyond the critical state.

Our research on the effects of landscape structure on ecological assembly and critical biodiversity has some sobering implications for the biodiversity crisis. The wholesale destruction and fragmentation of habitat by humans has led to the mounting concern over the simplification of landscape structure and biological communities. Habitat loss and fragmentation may well precipitate a collapse in biodiversity past some critical level of habitat loss (Solé et al., 2004). Human land-use activities coupled with rampant species extinctions may be pushing ecological systems below the critical biodiversity threshold, thus compromising the inherent order and stability of these systems. For example, simple landscapes, such as agricultural or forest monocultures, are the least stable in which a single perturbation (pest outbreak) often causes complete system collapse (Levin, 1998). CAS theory may eventually contribute to better system management and more effective conservation and restoration efforts, by highlighting the importance of preserving the interconnections among species (the ecological dependencies) in addition to the species themselves. Local interactions among species is what ultimately gives rise to system complexity and global properties such as stability and resilience. Successful ecological restoration or rehabilitation of degraded ecosystems is not likely until a critical level of biodiversity has been attained and unless species are able to interact in ecologically meaningful ways. Finally, a complex systems approach reiterates the importance of

diversity (or heterogeneity more generally) for maintaining system stability or resilience in the face of external perturbations such as global climate change, invasive species, human land-use change and other environmental impacts. Evaluating the critical level of diversity required for the emergence and maintenance of complexity and stability within a given system remains a research challenge (Scheffer et al., 2001). This task is made all the more urgent by the prediction of critical thresholds in biodiversity, in which the loss of a single species can have disproportionate effects on system function, especially if this triggers a cascade of species extinctions that propagate throughout the ecosystem. From a restoration standpoint, the successful establishment of each successive species should have progressively greater impacts on system function up to the critical biodiversity threshold, although hysteresis may well occur, making it more difficult to recover a critical level of biodiversity then it was to lose it in the first place. Beyond this critical state, however, diversity may function to enhance system resilience to the types of external perturbations that now threaten most of the world's ecological systems.

Acknowledgements

Appendix A

Patch-based metrics for habitat types within heterogeneous random and fractal landscapes (cf. Fig. 1)

Landscape type	Habitat					
	1	2	3	4	5	6
Random						
Number of patches	1856.4 (29.25)	1853.4 (23.52)	1837.3 (23.88)	1833.8 (35.54)	1851.8 (17.71)	1838.0 (25.23)
Average patch size	2.1 (0.05)	2.1 (0.08)	2.2 (0.06)	2.2 (0.05)	2.1 (0.07)	2.2 (0.10)
Correlation length[a]	1.4 (0.05)	1.4 (0.06)	1.5 (0.07)	1.5 (0.04)	1.5 (0.06)	1.4 (0.07)
Largest patch size	9.3 (2.00)	10.3 (2.71)	12.1 (2.77)	10.4 (1.71)	10.6 (2.07)	10.2 (1.55)
Percolation frequency[b]	0.0	0.0	0.0	0.0	0.0	0.0
Fractal ($H = 0.0$)						
Number of patches	634.1 (72.55)	1347.2 (73.96)	1534 (79.39)	1539.1 (63.57)	1351.2 (92.31)	616.1 (94.45)
Average patch size	85.9 (45.72)	4.2 (0.60)	3.1 (0.31)	3.1 (0.29)	4.0 (0.57)	126.3 (74.38)
Correlation length	9.4 (3.09)	2.3 (0.20)	1.9 (0.12)	1.8 (0.11)	2.2 (0.20)	10.7 (2.92)
Largest patch size	320.4 (147.65)	21.3 (4.64)	16.0 (3.46)	15.0 (4.06)	20.1 (5.22)	426.3 (186.3)
Percolation frequency	0.0	0.0	0.0	0.0	0.0	0.0
Fractal ($H = 0.5$)						
Number of patches	118.6 (26.84)	263.7 (72.39)	416.6 (144.88)	393.5 (159.08)	267.8 (104.40)	105.7 (29.59)
Average patch size	1028.9 (586.74)	250.7 (363.29)	129.8 (246.75)	306.7 (664.33)	429.1 (728.93)	1137.8 (680.7)
Correlation length	19.8 (4.07)	13.1 (6.90)	9.1 (7.62)	12.0 (13.33)	14.4 (8.46)	19.3 (4.37)
Largest patch size	1493.7 (535.86)	518.8 (499.04)	280.0 (380.61)	465.9 (747.00)	675.6 (738.24)	1546.1 (610.43)
Percolation frequency	0.0	0.0	0.0	0.1	0.0	0.0
Fractal ($H = 1.0$)						
Number of patches	9.3 (5.81)	22.1 (8.40)	27.3 (8.69)	27.1 (16.61)	21.6 (12.16)	12.7 (9.44)
Average patch size	2010.9 (606.61)	1682.5 (601.41)	1749.4 (644.79)	2002.3 (595.58)	1929.6 (625.71)	1759.8 (644.37)
Correlation length	24.6 (4.01)	33.2 (7.14)	38.1 (7.33)	40.8 (5.80)	33.6 (7.68)	21.1 (3.45)
Largest patch size	2240.3 (464.23)	1981.9 (488.82)	1964.8 (608.39)	2242.6 (450.13)	2190.3 (490.68)	2036.2 (513.56)
Percolation frequency	0.0	0.1	0.5	0.4	0.1	0.0

Patches were defined by the "nearest neighbor rule", in which only adjacent habitat cells (in the four cardinal directions) were considered part of the patch. Values are averages (± 1 S.D.) for an independent sample of maps ($n = 10$).

[a] Correlation length is the average number of cells through which a species can spread in a given habitat.

[b] Percolation frequency is the proportion of maps in which a continuous cluster of habitat spanned the entire landscape.

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