

LETTER

Stochastic and deterministic processes jointly structure tropical arthropod communities

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Abstract

The question of whether ecological assemblages are structured by stochastic and deterministic (e.g. interspecific competition) processes is controversial, but it is difficult to design sampling regimes and experiments that can dissect the relative importance of stochastic and deterministic processes in natural assemblages. Using null models, we tested communities of arthropod decomposers in tropical epiphytes for patterns of species co-occurrence, while controlling for habitat gradients, seasonal variations and ecological succession. When environmental conditions were controlled, our analysis showed that the communities were structured stochastically. However, analysing mixed sets of communities that were deliberately created either from two distinct heights or two successional stages revealed that communities were structured deterministically. These results confirm that habitat gradients and dispersal/competition trade-offs are capable of generating non-random patterns within decomposer arthropod communities, but reveal that when such effects are accounted for, species co-occurrence is fundamentally random.

Keywords

Rainforest arthropods, community structure, interspecific competition, niches, neutral theory, stochasticity.

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INTRODUCTION

The basic assumption of niche theory, that species differ in their traits and often show trade-offs that enable them to co-exist within communities for long periods of time (Chesson & Case 1986; Chesson 2000; Condit *et al.* 2006), contrasts with the assumptions of neutral theory, which emphasizes the importance of stochastic events such as dispersal, local extinction and speciation (Bell 2001; Hubbell 2001; Chave 2004). Empirical support for the neutral theory is equivocal, with studies both supporting (Condit *et al.* 2002; Novotny *et al.* 2002; Volkov *et al.* 2003; Hubbell 2005, 2006) and rejecting (McGill 2003; Gilbert & Lechowicz 2004; Volkov *et al.* 2005; Wootton 2005; Gilbert *et al.* 2006; Harpole & Tilman 2006; Thompson & Townsend 2006; Chu *et al.* 2007; Novotny *et al.* 2007) its predictions. Attempts are being made to incorporate elements of both niche and neutral theory into more general explanations for the structure of ecological communities (Uriarte & Reeve 2003; Tilman 2004; Gravel *et al.* 2006; Zhou & Zhang 2006; Adler *et al.* 2007).

However, a definitive answer to the central question of to what extent natural ecological communities are structured by stochastic or deterministic processes can be obtained only by coupling theoretical models with manipulative experiments and careful stratified sampling to test both the biological mechanisms and the resulting patterns in the structure of suitable real-life communities.

An effective way of testing for patterns of species co-occurrence is to use a null model (Gotelli 2000), which can be constrained according to one parameter (e.g. species co-occurrence) measured directly from the observed data. In this way *null* models contrast with *neutral* models which, because the relevant parameters are often difficult to quantify, may be of limited value as a null hypothesis for empirical tests (Gotelli & McGill 2006; Holyoak & Loreau 2006). Furthermore, neutral models are capable of producing non-neutral patterns that are consistent with Diamond's original assembly rules model (Diamond 1975; Ulrich 2004; Gotelli & McGill 2006). Instead of asking whether natural communities are structured according to particular assembly rules, we must establish whether non-random patterns are

the result of species interactions or stochastic drift processes and habitat heterogeneity (Ulrich 2004; Bell 2005).

Manipulative experiments are potentially very valuable in disentangling factors that shape natural communities (Ngai & Srivastava 2006; Chase 2007), but finding appropriate model systems is challenging. To be suitable for field experiments on species co-existence, ecological communities have to comply with rather exacting criteria: they should be limited to a single trophic level, so that biotic interactions are simplified to include only competition; they should be spatially discrete so that the entire community can be measured; they should contain a manageable number of species that can be readily identified and enumerated; and large numbers are needed for use as replicates in the experiments. Most importantly, the communities must occur in an ecosystem where our understanding of the relevant environmental variables is sufficient to enable us to control for them.

The epiphytic bird's nest fern (*Asplenium nidus* L.), common and widely distributed within the palaeotropics (Ozanne *et al.* 2003), satisfies these criteria. The ferns contain discrete animal communities based on the decomposition of trapped leaf litter (Ellwood *et al.* 2002; Ellwood & Foster 2004), and it is therefore feasible to focus on one trophic level – the arthropod decomposers. Moreover, the ferns occur as natural replicates and the successional stage of the fern communities can be controlled simply by ensuring that the ferns are of the same size. Finally, the ferns can be readily transplanted such that their spatial position within the forest can be precisely determined. In addition, it is possible to manipulate three biological processes that might have a major influence on the structure of the animal communities. First, by studying ferns either very high (> 40 m) or very low (< 4 m) within the canopy, it is possible to produce extremes of microclimate; second, by sampling ferns at different seasons, it is possible to study seasonal effects; and third, by removing all the animals from ferns and allowing them to be recolonized naturally, it is possible to study how the dispersal/competition trade-off influences community structure.

MATERIAL AND METHODS

We compared the patterns of species co-occurrence among the decomposer communities (i.e. a set of ferns within the natural forest ecosystem) with statistical randomizations of the original species occurrence data. Using the computer program EcoSim (Gotelli & Entsminger 2008), we simulated 5000 random matrices for each analysis and tested the differences between these and the observed communities. We used the *C*-score (Stone & Roberts 1990), EcoSim's default co-occurrence index that measures the average number of checkerboard units between all possible pairs of

species in a co-occurrence matrix. The number of checkerboard units for each species pair is calculated as $CU = (r_i - S)(r_j - S)$, where *S* is the number of shared sites, that is sites containing both species, and r_i and r_j are the row totals for species *i* and *j*. The *C*-score is the average of all possible checkerboard pairs, calculated for species that occur at least once in the matrix. If a community is structured by competition, the *C*-score should be greater than expected by chance (Gotelli 2000). We used EcoSim's default randomization algorithm, which maintains fixed sums for row and column totals, so each matrix generated has the same number of species and number of samples as the original matrix (Connor & Simberloff 1979). This algorithm has a low chance of falsely rejecting the null hypothesis (Type I error), but has good power for detecting non-random patterns (Gotelli 2000).

Initially, we considered homogeneous sets of 30 communities (i.e. ferns) that we had made as similar as possible, by controlling for fern size, for season and for microhabitat. We then created sets of communities that were deliberately heterogeneous, by combining ferns that were known to differ in terms of microclimate (from high and low within the canopy), of season (May and December), and in terms of whether they consisted of recently (< 8 months) colonized or of stable, mature fern communities. This third element of heterogeneity that we introduced experimentally into the study was intended to reproduce the dispersal/competition trade-off, which is a common feature of natural communities. To do this, we collected ferns, removed the entire fauna from them, ensured that they were of standard size and reintroduced them to their original locations within the forest. We then sampled them again 8 months later, on the assumption that these ferns might provide a different niche more favourable to species that are selected to disperse readily. We measured the amount of species overlap (beta diversity) between the communities at different times and heights using the Chao–Jaccard abundance-based similarity index (corrected for unseen shared species) (Chao *et al.* 2005), as implemented in ESTIMATES (Colwell 2004).

To keep our power similar for both the homogeneous and heterogeneous samples, we created heterogeneous sets of 30 ferns by combining 15 ferns from each of two homogeneous sets, repeating the process 1000 times to get a representative sample of all possible combinations. As we expect 5% of these combinations to be significant by chance, we tested the observed number of significant deviations against this expectation with a one-tail binomial test. In both the homogeneous and heterogeneous sets of ferns, we tested for significant differences between the observed data and the statistical randomizations of the null model to establish whether species among the observed decomposer communities were distributed at random. All ferns were of a similar size (range 2.2–3.4 kg fresh weight).

We sampled only animals > 2 mm in length and counted, and identified to morphospecies, animals from the following phylogenetically distinct decomposer taxa: woodlice (Crustacea: Isopoda), millipedes (Myriapoda: Diplopoda), springtails (Hexapoda: Collembola), cockroaches (Insecta: Dictyoptera) and xylophagous/saprophagous beetles (Insecta: Coleoptera).

Fieldwork took place in undisturbed lowland dipterocarp forest in Danum Valley, Sabah, Borneo (4°58' N, 117°48' E). Ferns were placed in plastic bags to prevent the loss of animals or leaf-litter during collection. Before being removed from the bags, ferns were fogged with Pybuthrin® 33 insecticide (Ellwood & Foster 2002), left for 2 h, and shaken to remove superficial animals, loose soil and leaf-litter. Each fern was then placed in a detergent water bath, which had no detectable effect on the plant, but was effective at flushing the remaining animals from the soil and from among the roots. After rinsing the ferns, we microscopically examined both the roots and the soil washings, to ensure that all animals had been collected. Before being transplanted, each fern was standardized at a uniform size with sterilized organic material taken from other bird's nest ferns. We secured the transplanted ferns to branches with fishing nets and string. Tree crowns were accessed using climbing ropes (Ellwood & Foster 2001).

RESULTS

Each bird's nest fern contained on average 12.2 ± 2.9 SD species of decomposers, with 8.1 ± 1.5 SD individuals per species. There were an average of 93 ± 12.1 SD ($n = 180$ ferns) individuals per fern, and 63 species sampled across all ferns. The Chao–Jaccard abundance-based similarity index reveals the substantial amount of species overlap between the different seasons, heights and colonization times (see Table S1). Compositional similarity was greater among the undisturbed ferns and those of the low canopy, compared with the ferns of the high canopy.

When we analysed the decomposer communities from 30 ferns all collected from the high canopy (> 40 m), we found no evidence of competition in terms of aggregated or segregated species co-occurrence: that is, there were no significant differences between the C -scores of the randomized communities simulated using the null model and the C -scores of the observed communities ($P = 0.408$, Fig. 1a). Similarly, co-occurrence between species among ferns collected from the low canopy (< 4 m) was also random ($P = 0.172$, Fig. 1b).

We then deliberately introduced environmental heterogeneity into the sample of ferns, by creating sets of samples consisting of 15 ferns from the high canopy and 15 from the low canopy, and found significant differences between the C -scores of the simulated and observed communities

[number of combinations significantly different (Sig. Diff.) = lower tail 4/1000, upper tail 75/1000, Binomial test against the expected 5% Type I error: $P < 0.001$, Fig. 1c]. We controlled for the effects of dispersal limitation by sampling ferns from trees (*Parashorea tomentella*: Dipterocarpaceae) that were at least 40 m apart. However, the importance of vertical stratification was highlighted in a canonical correspondence analysis (CCA), in which Monte Carlo randomizations confirmed the significance of the eigenvalues associated with height (0.322, $P = 0.012$), but not with season (0.031, $P = 0.505$) (Fig. 2).

To test the robustness of our initial results, we introduced seasonal heterogeneity into the co-occurrence analysis. Using ferns that were sampled 8 months after the initial collection, we again included 30 ferns from the high (> 40 m) canopy and 30 ferns from the low (< 4 m) canopy. As before, we found that the species within each of these communities were co-occurring at random ($P = 0.456$, Fig. 1d; $P = 0.538$, Fig. 1e). Moreover, when we created mixed sets of 30 ferns, consisting of 15 ferns from the initial samples at time zero, and 15 ferns sampled 8 months later, these sets of samples retained their random structure. This was true both for the high- and low-canopy samples analysed separately (high samples: number of Sig. Diff. = lower tail 10/1000, upper tail 5/1000, Binomial test $P = 1.0$, Fig. 1f; low samples: number of Sig. Diff. = lower tail 16/1000, upper tail 7/1000, Binomial test $P = 1.0$, Fig. 1g). This is a useful check on our methodology, since it shows that creating a mixed sample does not automatically create non-random patterns, even when such an effect might have been anticipated. However, when we deliberately introduced environmental heterogeneity into the 8-month samples (by combining both high and low ferns), as we did in the initial samples, the analysis showed again that the interactions between the species within the communities were significantly non-random (number of Sig. Diff. = lower tail 3/1000, upper tail 98/1000, Binomial test $P < 0.001$, Fig. 1h).

The third element of heterogeneity that we introduced experimentally was designed to explore tradeoffs between dispersal and competition, as shown in a CCA, which revealed that the recolonized communities were indeed different from the communities in the undisturbed ferns (Fig. 3). In this analysis, Monte Carlo randomizations confirmed the significance of the eigenvalues associated with time since recolonization (0.399, $P < 0.001$), as well as with height (0.217, $P < 0.001$). As in the original communities, there was no evidence that the recolonized communities were structured by a deterministic process such as competition when analysed separately, with species co-occurring at random in both the high and low canopy ($P = 0.096$, Fig. 4c; $P = 0.182$, Fig. 4d). Furthermore, as in the original experiment, these communities became

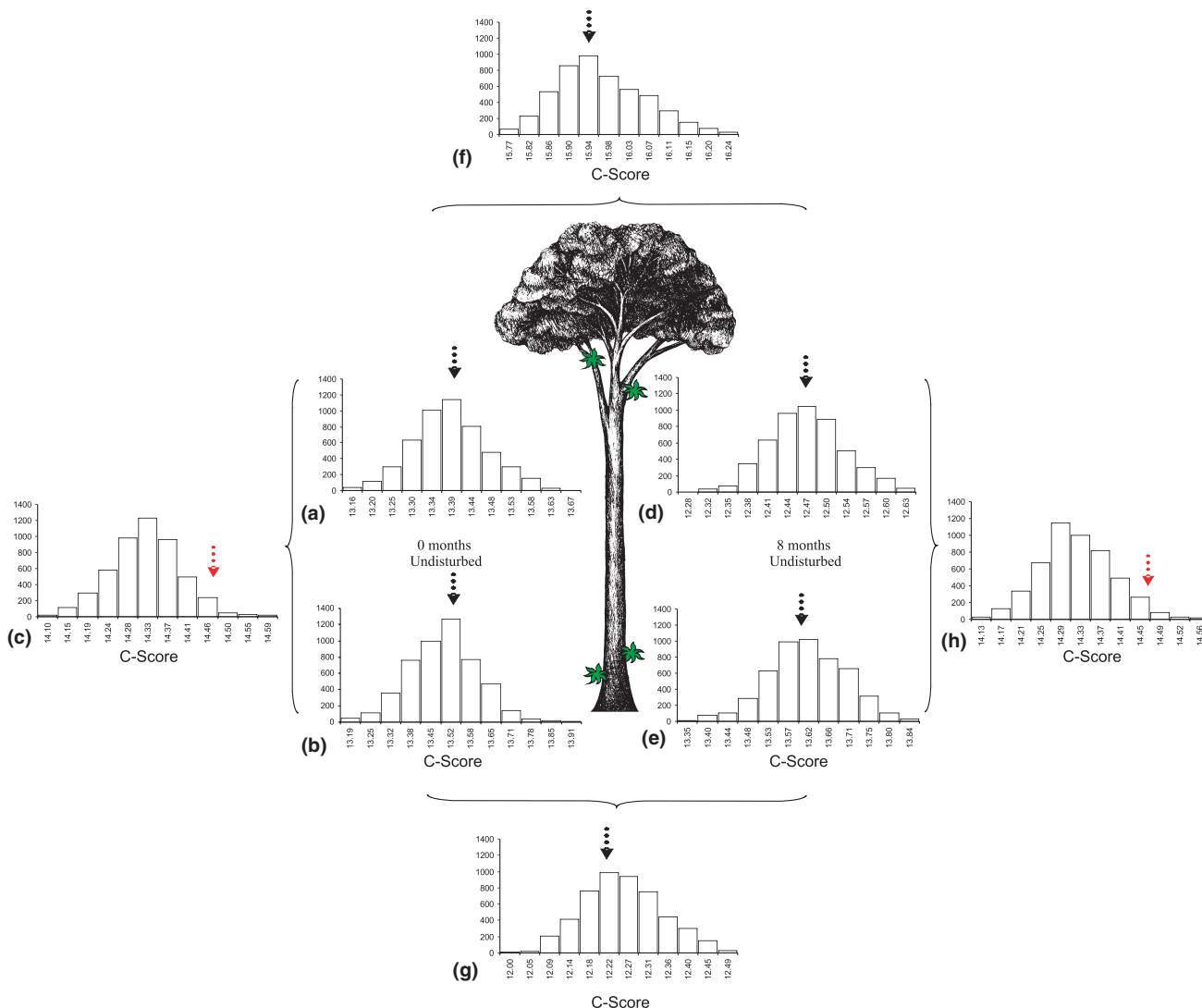


Figure 1 Histogram of C -scores from 5000 simulated random communities, each based on the co-occurrence of arthropod species among 30 ferns, with the placement of the observed C -scores shown as arrows. (a) Homogeneous set at time zero (all 30 ferns undisturbed and located above 40 m), Obs > Sim, $P = 0.408$. (b) Homogeneous set at time zero (all 30 ferns undisturbed and located below 4 m), Obs > Sim, $P = 0.172$. (c) Heterogeneous set at time zero (15 high + 15 low ferns), Obs > Sim, $P = 0.03$. (d) Homogeneous set after 8 months (all 30 ferns undisturbed and located above 40 m), Obs > Sim, $P = 0.456$ (also Fig. 4a). (e) Homogeneous set after 8 months (all 30 ferns undisturbed and located below 4 m), Obs > Sim, $P = 0.538$ (also Fig. 4b). (f) Heterogeneous set above 40 m (15 time zero + 15 after 8 months), Obs > Sim, $P = 0.561$. (g) Heterogeneous set below 4 m (15 time zero + 15 after 8 months), Obs > Sim, $P = 0.695$. (h) Heterogeneous set after 8 months (15 high + 15 low ferns), Obs > Sim, $P = 0.027$.

significantly non-random when mixed sets of samples from the high and low canopy were created (number of Sig. Diff. = lower tail 0/1000, upper tail 791/1000, Binomial test $P < 0.001$, figure not illustrated). Most importantly, however, when we created mixed sets of ferns, half of which were undisturbed ferns, and half of which were recolonized ferns, the pattern of co-occurrence between the species of arthropods became significantly non-random (high samples: number of Sig. Diff. = lower tail 0/1000, upper tail 692/1000, Binomial test $P < 0.001$, Fig. 4e; low samples:

number of Sig. Diff. = lower tail 1/1000, upper tail 200/1000, Binomial test $P < 0.001$, Fig. 4f). This is clearly not because of any seasonal effect over the 8-month experimental period, as we had controlled for this in the second set of experiments.

DISCUSSION

These results show that the organization of natural assemblages of animals can exhibit both random and

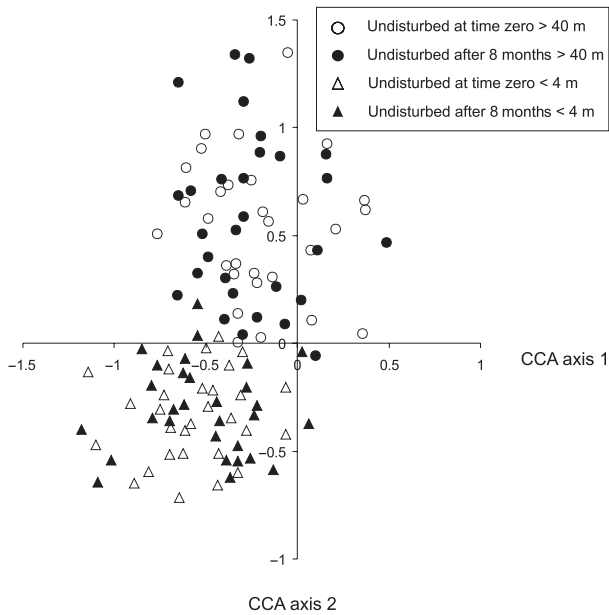


Figure 2 CCA of arthropod communities in bird's nest ferns. Intra-set correlation coefficients associated time with the first canonical axis ($r = 0.158$, X -axis) and height with the second canonical axis ($r = 0.373$, Y -axis). There is no temporal separation (undisturbed ferns at time zero shown with open symbols, undisturbed ferns after 8 months shown with closed symbols). There is, however, clear spatial separation [low ferns (< 4 m) shown with triangles, high ferns (> 40 m) shown with circles].

predictable patterns. In these communities of decomposer animals in tropical epiphytes, when we controlled for major environmental variables (by sampling at specific heights within the canopy) and for ecological succession, we were able to reveal that the species were co-occurring essentially at random. It should be remembered that among the undisturbed ferns, just as for the experimental ferns, we were also controlling for variables such as microclimate and trade-offs between dispersal and competition, by carefully sampling ferns of the same size and within a limited area of forest. This demonstration of stochasticity in the decomposer communities is remarkably robust as we, in effect, carried it out independently eight times: for the high and low ferns, at two different seasons, at two stages of succession and in combined sets of ferns from two seasons. This is a startling result and challenges our current understanding of the organization of natural assemblages of animals. It suggests that arthropod decomposers may be demographically equivalent, despite being superficially quite different (e.g. a cockroach vs. a millipede), a fundamental tenet of neutral theory (Bell 2001; Hubbell 2001). Furthermore, our results support the predictions of the continuum hypothesis (Gravel *et al.* 2006), which asserts that diversity and abundance patterns along environmental gradients are the

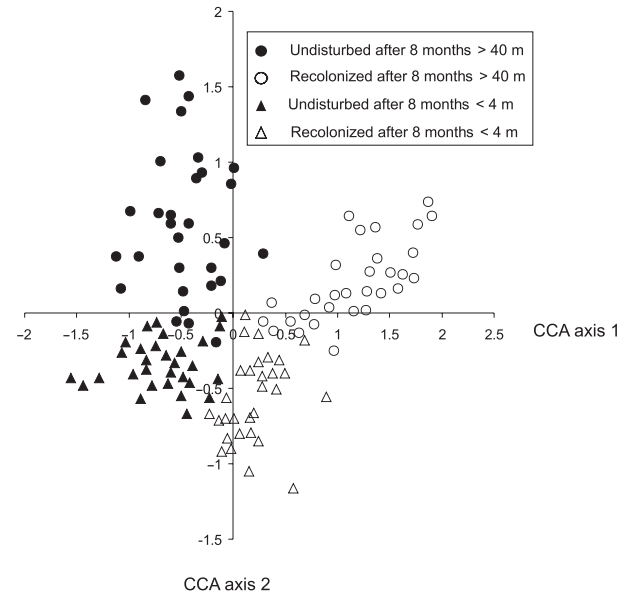


Figure 3 CCA of arthropod communities in bird's nest ferns. Intra-set correlation coefficients associated time with the first canonical axis ($r = 0.551$, X -axis) and height with the second canonical axis ($r = 0.411$, Y -axis). Clear separation is apparent both as a result of recolonization (undisturbed ferns after 8 months shown with closed symbols, recolonized ferns after 8 months shown with open symbols) and spatial location [low ferns (< 4 m) shown with triangles, high ferns (> 40 m) shown with circles].

consequence of the balance between stochastic processes and competitive exclusion.

From a more practical perspective, this study provides unique evidence that the scale at which we sample has strong implications on our perception of the forces that structure communities. While communities from ferns of the same size collected from the same canopy level seem to be purely stochastically assembled, samples not so narrowly collected show significant species segregation. This result is most likely to be related to changes in the local environment, or the different resource requirements associated with ecological succession and niche partitioning (Tokeshi 1986, 1999). The CCA analysis, which is based on species abundance, revealed clear differences in the composition of the communities at different heights and at different stages of succession (Figs 2 and 3). However, the Chao–Jaccard abundance-based similarity index (Chao *et al.* 2005; see Table S1) confirmed that the decomposer communities, particularly those of the undisturbed ferns and among those ferns in the low canopy, shared many of the same species. These results validate our assumption that all ferns used in this study had species in common: ferns at different heights and times did not represent segregated habitats. The overlap in species ranged from 35% (lowest) to 85% (highest),

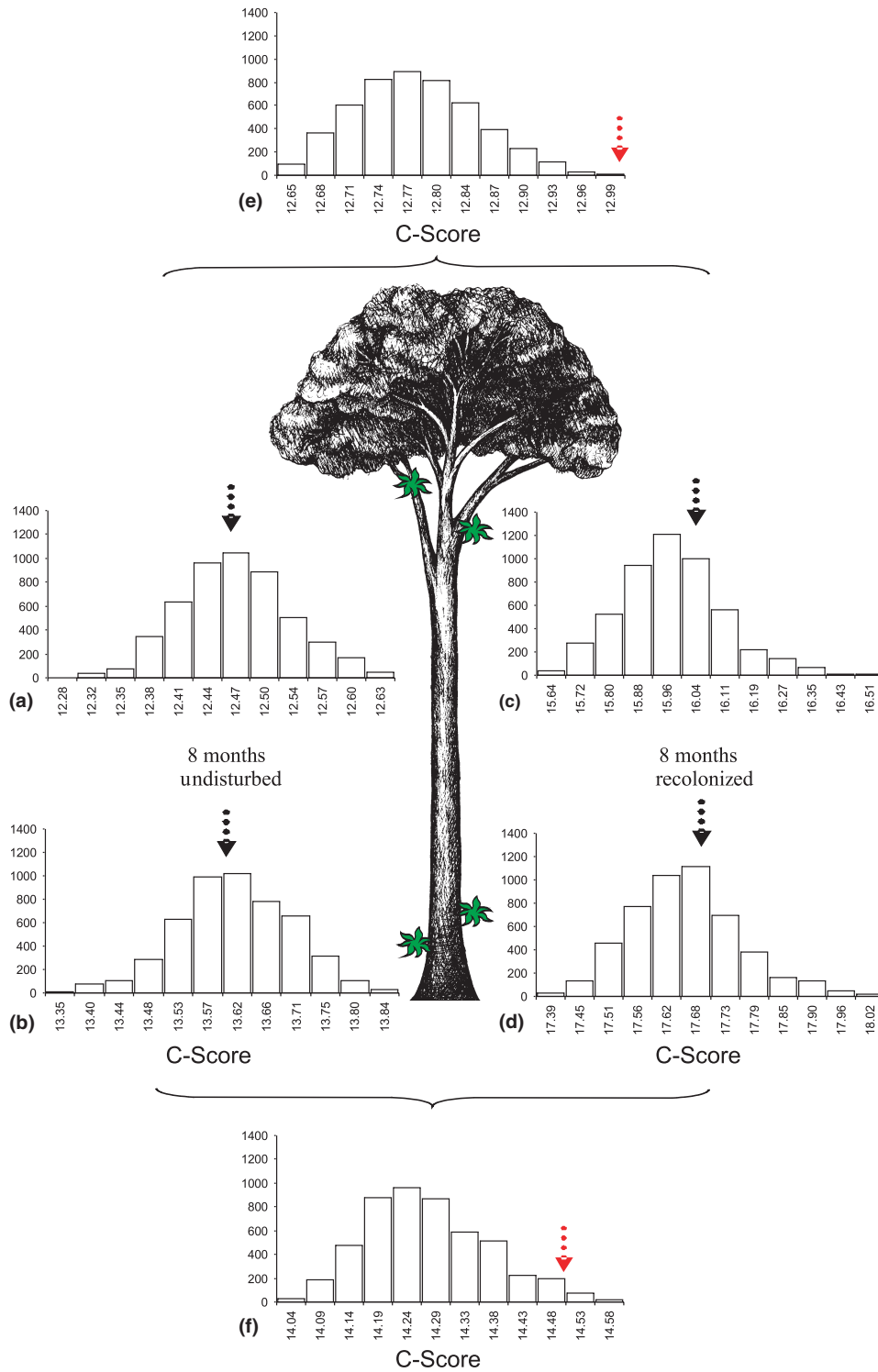


Figure 4 Histogram of *C*-scores from 5000 simulated random communities, each based on the co-occurrence of arthropod species among 30 ferns, with the placement of the observed *C*-scores shown as arrows. (a) From Fig. 1d. (b) From Fig. 1e. (c) Homogeneous set after removal of all animals and 8 months of recolonization (all 30 ferns recolonized and located above 40 m), Obs > Sim, $P = 0.096$. (d) Homogeneous set after removal of all animals and 8 months of recolonization (all 30 ferns recolonized and located below 4 m), Obs > Sim, $P = 0.182$. (e) Heterogeneous set above 40 m (15 undisturbed ferns after 8 months + 15 recolonized ferns after 8 months), Obs > Sim, $P < 0.001$. (f) Heterogeneous set below 4 m (15 undisturbed ferns after 8 months + 15 recolonized ferns after 8 months), Obs > Sim, $P = 0.021$.

which strengthens the reasoning behind our sampling regime and justifies our experimental manipulations. We have shown elsewhere that arthropods distribute themselves according to canopy structure and microclimate (Dial *et al.* 2006). Our work, together with many other studies of resource partitioning among rainforest arthropods (e.g. Basset *et al.* 2001; Grimbacher & Stork 2007), provides a robust demonstration of how local environmental conditions, and hence the niches and the animal communities that occupy them, change throughout the canopy. Tropical rainforests in particular should be sampled with the utmost care, because it is here that large numbers of rare species make the elucidation of community structure especially difficult (Novotny & Basset 2000), and where studies investigating the diversity and distribution of species often use mass-collecting techniques. Such techniques make functional interpretations difficult, even when improved methods are used (e.g. Floren & Linsenmair 2000).

Differentiating between random and predictable patterns in natural assemblages is not straightforward. If we were to sample arthropod communities from ferns in a way that took no account of their environment and history, then the communities would appear to be structured in accordance with niche theory (Chesson & Case 1986; Condit *et al.* 2006). On the other hand, if we were to take a sample of similarly sized ferns from a narrow area, we would probably conclude that it supports neutral theory (Bell 2001; Hubbell 2001). This not only confounds attempts to conceptualize the structure of natural assemblages, it also misleads functional interpretations of the nature of species within communities, and of the ecological guilds that make up the communities themselves. Only detailed knowledge of the local environment and the history of the arthropod communities allowed us to define the spatial and temporal resolution at which to test for competitive interactions between species, a fundamental step if we are effectively to sample natural communities and develop universal models to explain species assemblages.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1 Chao–Jaccard index of species overlap between ferns.

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