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REPORT

Habitat subdivision causes changes in food web structure

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Abstract

Theory suggests that the response of communities to habitat subdivision depends on both species' characteristics and the extent to which species interact. For species with dynamics that are independent of other species, subdivision is expected to promote regional extinction as populations become small and isolated. By contrast, intermediate levels of subdivision can facilitate persistence of strongly interacting species. Consistent with this prediction, experimental subdivision lengthened persistence of some species, altering the extent of food web collapse through extinction. Extended persistence was associated with immigration rescuing a basal prey species from local extinction. As predicted by food web theory, habitat subdivision reduced population density of a top predator. Removal of this top predator from undivided microcosms increased the abundance of two other predator species, and these changes paralleled those produced by habitat subdivision. These results show that species interactions structured this community, and illustrate the need for investigations of other communities.

Keywords

Fragmentation, habitat subdivision, interaction strength, metacommunity, metapopulation, omnivory, persistence, Protista, rescue effect.

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INTRODUCTION

The subdivision of habitats into smaller and more isolated patches is expected to have various effects on both individual species and food webs. Small populations are subject to extinction through a variety of stochastic processes that may be alleviated by movement of individuals between populations, creating metapopulations (Levins 1969; Brown & Kodric-Brown 1977). Metapopulation theory may also help us to understand the effects of habitat subdivision on food webs. In theory, although single, or non-interacting, species can persist in sufficiently large areas of habitat, they are driven to extinction by habitat subdivision, starting with the least mobile species (Harrison & Taylor 1997). In contrast with single species, metapopulation models for species interactions show that intermediate degrees of habitat subdivision may promote persistence of species that interact strongly enough with other species that they would be driven to extinction within undivided habitats (Kareiva 1990; Harrison & Taylor 1997). At low degrees of subdivision, one species could drive another to extinction, but higher amounts of subdivision could provide spatial refuges for the species that would otherwise be driven to extinction (Hastings 1980; Tilman *et al.* 1994). Like single species, interacting species are expected to become regionally extinct at high levels of subdivision because rates of patch extinction exceed rates of patch colonization (Kareiva 1990; Holyoak & Lawler 1996a). In theory, these effects of fragmentation could extend to entire communities of interacting species, or "metacommunities" (Cousins 1990).

A variety of food web theory is also relevant to understanding the responses of ecological communities to habitat subdivision. Greatly restricted movement between patches within subdivided habitats may reduce the relevant area of habitat. Schoener (1989) proposed that the number of trophic levels is limited by the amount of "productive space" (productivity × area or volume) required for critical component populations to persist with high probability. Productive space influences the amount of energy reaching higher trophic levels and also population size of individual species. The greater energy and space requirements of species at higher trophic levels may make top predators more likely to become extinct than species at lower trophic levels. Consistent with this, Lawton (1995) suggested that large body size (related to

energy requirements) and diet specialization make species rare and susceptible to extinction; this suggestion is in agreement with modelling of food chains (Sterner *et al.* 1997), and omnivory (feeding on more than one species), which may also allow species at higher trophic levels to persist (McCann & Hastings 1997). Species at higher trophic levels may also be more prone to extinction for other reasons. In patch networks where species experience extinctions from local patches, top predators may also remain absent for long periods because of their slow recovery from low densities at colonization (Pimm 1991). Probabilistic models for linear food chains also suggest that top predators are most likely to be absent from patches because of the requirement that prey species are present for all species below them in food chains (Holt 1993); the probability becomes increasingly compounded for species at higher trophic levels, making it more likely that top predators are absent.

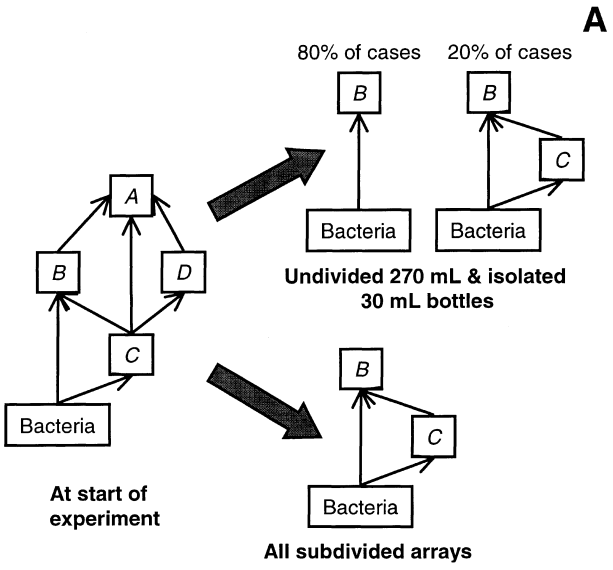
While the effects of habitat subdivision have been studied for pairs of interacting species (e.g. Holyoak & Lawler 1996b) and for biodiversity as a whole (Frank & Amarasekare 1998; Gonzalez *et al.* 1998), there have been few, if any attempts, to study the effects of subdivision on the structure of food webs. Presented herein are experiments using a microbial community consisting of bacteria and four species of freshwater protists to investigate the effect of subdivision on food web structure.

MATERIALS AND METHODS

Food web assembly and measurement

Standard culture techniques were used (Holyoak & Lawler 1996b) to establish a simple microbial food web supported on a plant-based nutrient medium in microcosms. The effects of habitat subdivision were investigated using three types of microcosm. Subdivided microcosms (arrays) consisted of groups of nine 30 mL plastic bottles with adjacent bottles linked by silicon rubber tubes (illustrated in Holyoak & Lawler 1996b). Microcosms containing all four protist species consisted of five arrays, five undivided microcosms of the same total volume (270 mL) to control for the effects of habitat size, and five isolated 30 mL bottles to test how long within-patch species interactions persisted. The undivided 270 mL volume was placed in a 1-L conical flask that gave the same depth and air: water surface area as the 30 mL bottles and arrays. To address the effects of species composition on persistence time and mean density there were also three replicates of isolated 30 mL bottles and three replicates of undivided 270 mL bottles containing every possible combination of up to three protist species (from the four species listed below). For brevity only selected results from microcosms with subsets of species are reported. The experiment was conducted at room temperature ($22 \pm 2\,^{\circ}C$).

The experiment began with nutrient solution bacterized with one bacterial loop per litre of the common freshwater bacteria species, *Bacillus subtilis* var. *niger*, *Enterobacter aerogenes*, *Escherichia coli* (K-12 strain) and *Serratia marcescens*. The food web is shown in Fig. 1A. Protist species were: *Amoeba proteus*, a predator that feeds on all



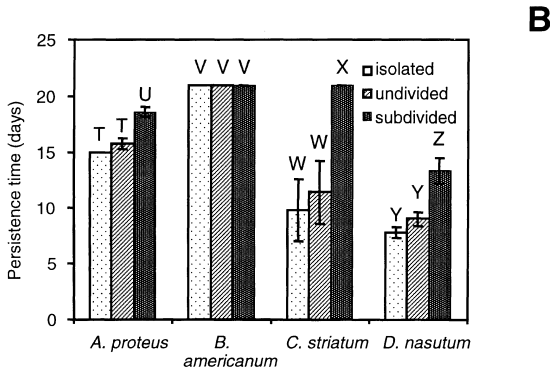


Figure 1 (A) Food webs with thin arrows drawn from prey to predator species. *A. proteus* (*A*), *B. americanum* (*B*), *C. striatum* (*C*) and *D. nasutum* (*D*). Links are based on known natural history and results from microcosms with different species combinations. The food web is shown both in its initial state and the collapsed state after 21 days in subdivided arrays or undivided 270 mL bottles and isolated 30 mL bottles; in both of the latter 80% of replicates collapsed to only bacteria and *B* and the remaining 20% of replicates to bacteria, *B* and *C*. (B) Persistence times of protist species in different microcosm types. Values are the mean $\pm$ 1 standard error. Bars represent isolated 30 mL bottles (stippled), undivided 270 mL bottles (cross-hatched) and subdivided 270 mL microcosms (black). For each species, bars beneath the same letter did not differ at $P < 0.05$ in Tukey's honest significant difference tests.

other protist species present; *Colpidium striatum*, a strict bacterivore; *Blepharisma americanum*, an omnivore that feeds on conspecifics (a cannibal), *C. striatum* and bacteria; and *Didinium nasutum*, a predator that feeds on *C. striatum*. Carolina Biological Supply Co. (Burlington, NC) supplied all organisms. Bacteria were introduced 1 day prior to *C. striatum*, and other protist species were introduced after a further 2 days. To produce uniform initial densities of all predator species in all treatments, species were added at a constant rate per unit volume into undivided bottles and into each array bottle. Replacement of 10% of nutrient medium per 2 days kept nutrient levels approximately constant. Patches were isolated prior to removal of medium, and the sample was used to count protists using a binocular microscope, giving density estimates for each species every 2 days. I counted protists in weighed subsamples that contained at least 10 cells per species or were 3 mL in volume. Subsample volumes ranged from 0.15 mL at high cell densities to 3 mL at low densities. Subsamples were diluted by weight when numbers were too high to count by eye. Bacteria were not censused on the assumption that their dynamics were rapid enough to be considered independent of the protist dynamics. The experiment continued for 21 days, by which time food webs in undivided 270 mL volumes had collapsed to just *C. striatum* and bacteria, or these species with *B. americanum*. These species combinations are capable of persisting for long periods, even in small undivided habitats (Holyoak & Lawler 1996b; Morin 1999; Holyoak *et al.* 2000).

The following statistics were looked at: (1) Persistence was the time until extinction of a species from entire microcosms. A Tukey's honest significant difference test tested for differences in ln-transformed persistence for each species in different kinds of microcosms with all species present. One-way ANOVAs tested for differences in ln-transformed persistence time between microcosms containing selected species combinations (see Results). (2) The outcome of dynamics was the percentage of microcosms in which *C. striatum* survived for the duration of the experiment. The proportion of replicates of different microcosm types with *C. striatum* surviving was logit-transformed and analysed in a generalized linear model; it was assumed that there was a binomial distribution of sampling error and that changes in deviance followed a χ^2-distribution. (3) Rescue effects occur when immigration raises the density of a species within patches, which forestalls extinction (Brown & Kodric-Brown 1977). If rescue effects were present, we would expect array patches that permit more dispersal (with more connecting tubes) to have a greater mean density, fewer recorded extinctions, and for species to remain absent for less time following an extinction. The statistics testing for these effects are given in Table 1. The interpretation of zero densities is complicated by the fact that zero density values from subsamples have a certain probability of representing a real extinction from an entire 30 mL bottle (a patch). In an earlier experiment, the probability of a single recorded zero density value representing a real extinction was 0.39, which was calculated by comparing subsamples with entire bottle contents (Holyoak, in press). For simplicity, the raw numbers of recorded zero densities for *C. striatum* (in Table 1) were used as an indicator of the frequency of actual extinction within array bottles and the duration of periods of absence. Tests of mean densities in patches with different numbers of connecting tubes were performed for other species, but these showed no significant results and (for brevity) are not reported. In these and other comparisons of mean densities below, only samples prior to extinction of any species in all microcosms being compared were used. (4) To test for effects of habitat subdivision on population densities, one-way ANOVAs were used to test for differences between undivided 270 mL volumes and average densities from entire arrays. Separate analyses were carried out for each species using ln(density + 1) to calculate means, and overall significance was tested across all four species using a MANOVA. (5) To test for an effect of interpatch movement on species' density, analyses were carried out similar to (4) but comparing isolated 30 mL bottles and average within-

Table 1 *C. striatum* dynamics in patches of subdivided microcosms

	Patch connectedness (tubes per bottle)				
	1 tube	2 tubes	4 tubes	$F_{2,12}$*	P*
Recorded extinctions†	1.80	1.35	1.00	5.24	0.041
Length of extinctions‡	3.52	2.72	1.90	5.50	0.020
Ln (density)§	3.06	3.32	3.46	9.02	0.011

*Results of 1-way ANOVA. †Mean number of recorded sequences of zero densities per bottle type per microcosm. ‡Mean number of consecutively recorded zero densities per bottle type per microcosm from samples at 2-day intervals. §Mean number of *C. striatum* per mL.

patch densities from arrays. (6) To test whether the presence of a species influenced the mean of ln(density + 1) of a species *x*, two-or three-way ANOVAs were carried out comparing mean densities of species *x* with and without each of the other species present. *Posthoc* least significant difference (l.s.d.) tests were used to identify which treatments differed, where each letter (A, B, C, D) represents the first letter of a protist genus. ANOVAs were used to test the effects of the presence of (i) B and D on mean density of A (C was present in all microcosms where A could be grown); (ii) A, C and D on the mean density of B; (iii) A, B and D on the mean density of C; and (iv) A and B on the mean density of D (C was present in all microcosms where D could be grown). These four ANOVAs were repeated for 30 mL and 270 mL bottles.

RESULTS

The effects of habitat subdivision

The bacterivore *C. striatum* persisted for a mean of 97 generations in subdivided habitats compared to only 53 generations in undivided habitats of the same total volume (Fig. 1B; generation time = 5.18 h; Holyoak & Lawler 1996b). Strong evidence for rescue effects in *C. striatum* was provided by higher mean densities, fewer recorded extinctions, and periods of absence from patches being of shorter duration in bottles that had more connecting tubes (Table 1).

Subdivision extended persistence of *A. proteus* and *D. nasutum* by smaller amounts (Fig. 1B). This may have occurred because of the greater persistence of *C. striatum* on which they feed. There was no evidence for rescue effects in species other than *C. striatum*. Omnivorous *B. americanum* persisted for the duration of the experiment in all habitat types.

Spatial subdivision also altered the outcome of food web dynamics. The food web collapsed to only *B. americanum* and bacteria in 80% of undivided habitats and isolated patches, whereas *C. striatum* also persisted in all subdivided habitats ($\chi^2_1 = 8.6$, $P < 0.005$). Table 2 shows that relative to either isolated 30 mL bottles or undivided 270 mL habitats, there were substantial changes in mean densities of up to three protist species in subdivided habitats (Table 2). Compared with undivided 270 mL bottles, subdivided arrays contained 54% lower densities of *A. proteus*, and compared with isolated 30 mL bottles, arrays contained 33% lower densities of *A. proteus* (see Table 2 for statistics). By contrast to *A. proteus*, *D. nasutum* increased in mean density with subdivision; arrays contained 34% more *D. nasutum* than undivided 270 mL bottles, and 43% more than isolated 30 mL bottles (these differences were significant in ANOVAs and MANOVAs; Table 2). Densities of *B. americanum* were also 16% higher in subdivided arrays than in undivided 270 mL bottles, but isolated 30 mL bottles showed no significant difference from arrays (Table 2). Whilst these effects were transient (all species eventually went extinct), they suggest that habitat subdivision altered either conditions for protist growth or species interactions.

Dynamics in undivided and isolated microcosms with different species combinations

That subdivision had opposite effects on the densities of *A. proteus* and *D. nasutum* concords with comparisons of mean densities in undivided 270 mL microcosms containing different subsets of protist species. These results also

Table 2 Differences in mean ln-density during the time when species were present in all microcosms (the first 6 samples or 12 days) in univariate ANOVA's for each species. A comparison of 270 mL undivided habitats vs. subdivided arrays is given. Overall differences were significant in a MANOVA (Wilk's $\chi_{4,5} = 0.066$, $P < 0.005$). A comparison of isolated 30 mL bottles (without dispersal) with densities in subdivided arrays is then given. Differences were significant overall in a MANOVA (Wilk's $\chi_{4,5} = 0.071$, $P < 0.005$). Replicates were microcosms

Dependent variable	MS effect	MS error	$F_{1,8}$	P	Mean cells per mL	
Undivided 270 mL bottles vs. array					Array	270 mL
Amoeba	0.571	0.0347	16.5	0.004	1.07	2.33
Blepharisma	0.047	0.0032	14.4	0.005	9.36	8.04
Colpidium	0.013	0.0192	0.67	0.44	105.9	98.5
Didinium	0.140	0.0151	9.32	0.02	5.13	3.83
Isolated 30 mL bottles vs. array					Array	30 mL
Amoeba	0.199	0.037	5.38	0.049	1.07	1.59
Blepharisma	0.0002	0.050	0.005	0.95	9.36	10.02
Colpidium	0.0006	0.061	0.010	0.92	105.9	97.7
Didinium	0.211	0.033	6.40	0.035	5.13	3.59

show the effects of one species on densities of other species in the food web. An ANOVA showed that during the first six samples, the presence of *A. proteus* caused decline in the abundance of *D. nasutum* by an average of 33% (comparing mean ln[1 + *D. nasutum* per mL] in treatments CD and BCD vs. ACD and ABCD, $F_{1,10} = 9.36$, $P < 0.02$). This effect was not symmetrical, as the presence of *D. nasutum* did not influence the mean density of *A. proteus*; $F_{1,10} = 0.02$, $P = 0.9$ in an ANOVA comparing ln[1 + *A. proteus* per mL] in AC and ABC vs. ACD and ABCD. Similarly, persistence of *D. nasutum* was reduced by the presence of *A. proteus* ($F_{1,10} = 77.1$, $P < 0.001$ in an ANOVA comparing *D. nasutum* persistence in CD and BCD vs. ACD and ABCD); in 270 mL bottles with CD, *D. nasutum* persisted for 21 days, but only 9 days in ACD with *A. proteus* present ($P = 0.001$ in an l.s.d. test). However, there was no difference in persistence with and without *A. proteus* present when *B. americanum* was also present (treatments ABCD vs. BCD, $P > 0.9$ from an l.s.d. test). Again this effect was not symmetrical, because in 270 mL bottles there was no significant effect of the presence of *D. nasutum* on persistence of *A. proteus* ($F_{1,10} = 0.17$, $P = 0.3$ in an ANOVA comparing *A. proteus* persistence in AC and ABC vs. ACD and ABCD). Results for isolated 30 mL bottles with different species combinations were very similar to findings from the undivided 270 mL bottles, and for brevity are not reported.

The largest change with subdivision was the reduction in densities of *A. proteus*. Comparison of microcosms with all four protist species present vs. those lacking *A. proteus* showed that removal of *A. proteus* increased densities of *B. americanum*; for isolated 30 mL bottles this difference was significant in an l.s.d. test (treatment ABCD vs. BCD, $P = 0.008$) and *B. americanum* density increased by 106%, whilst for undivided 270 mL bottles the difference was not significant ($P = 0.16$) and mean density increased by only 16%. This could have been caused by either direct or indirect effects, and the difference in significance between 30 mL and 270 mL bottles might result from low statistical power (a power test indicated only modest power).

The presence of *A. proteus* did not influence mean *C. striatum* density in either 30 mL or 270 mL bottles (treatments C, BC, CD and BCD vs. AC, ABC, ACD and ABCD; in ANOVAs, $F_{1,16} = 3.0$, $P = 0.10$ for 30 mL and $F_{1,16} = 2.4$, $P = 0.15$ for 270 mL). However, the presence of *D. nasutum* caused significant reductions in *C. striatum* density (treatments C, BC, AC and ABC vs. CD, BCD, ACD and ABCD; $F_{1,16} = 44.9$, $P < 0.001$ for 30 mL and $F_{1,16} = 21.0$, $P < 0.001$ for 270 mL). The presence of *B. americanum* also reduced *C. striatum* densities significantly (and by similar amounts to *D. nasutum*; treatments C, CD, AC and ACD vs. BC, BCD, ABC and ABCD; $F_{1,16} = 20.1$, $P < 0.001$ for 30 mL and $F_{1,16} = 21.6$, $P < 0.001$ for 270 mL). For mean *C. striatum* density, there was a significant interaction between B and D ($F_{1,16} = 18.1$, $P < 0.001$ for 30 mL and $F_{1,16} = 18.2$, $P < 0.001$ for 270 mL). *C. striatum* density with both B and D was substantially lower than would be expected from the combination of the effects of B and D when alone on either an arithmetic or multiplicative (log-additive) scale; for example, in isolated 30 mL bottles, mean ln[1 + *C. striatum* per mL] values were 5.84 without B or D, 5.51 with B, 5.31 with D, and 4.53 with B and D.

DISCUSSION

The results show that the subdivision of habitat can radically alter both the persistence and the population densities of food web members. Gonzalez *et al.* (1998) also found that, relative to small isolated fragments, persistence of a terrestrial community was increased by habitat subdivision, but persistence was not prolonged relative to an undivided habitat of the same total area. Their results suggest effects of habitat subdivision on persistence through population size, rather than through spatial dynamics such as extinction–colonization dynamics (Levins 1969) or rescue effects (Brown & Kodric-Brown 1977). In contrast, three of the species used here showed extended persistence above that found in large undivided habitats. The pattern of habitat subdivision prolonging persistence of some species is expected in species whose persistence is determined by their interactions with other species (Kareiva 1990; Holyoak & Lawler 1996a, b), rather than having independent dynamics (Harrison & Taylor 1997). This is not surprising given the simplicity of habitats within patches and the lack of dormant propagules (Caceres 1997). It is possible that other communities will have some species with dynamics that are relatively independent of other community members (Lawton 1982), and these may respond differently to habitat subdivision.

It is therefore interesting to ask: what is the evidence that species influenced the dynamics (persistence or mean density) of other species? This could also be reworded as: Do species respond directly to habitat subdivision, or do they show changes in dynamics that are more likely to be caused by interactions with other species (which showed direct responses to habitat fragmentation)? The extended persistence of *C. striatum*, *A. proteus* and *D. nasutum* in subdivided habitats (compared with undivided habitats) may have resulted from the rescue effects in *C. striatum* (Table 1), which is fed on by *A. proteus* and *D. nasutum*.

The dynamics within subdivided microcosms did not provide any evidence as to why the top predator, *A. proteus*, had lower mean densities relative to the undivided microcosms or isolated patches. However, food web

theory is replete with explanations as to why top predators should be particularly vulnerable to extinction, thereby suggesting direct effects of habitat subdivision on this species. Explanations include: (1) energetic requirements (Schoener 1989); (2) long times to recover from low densities (Pimm 1991); (3) low densities of top predators because of large body size or diet specialization (Lawton 1995); and (5) the requirement for all species lower in the food chain to be present (Holt 1993). Densities of *A. proteus* were lower in all microcosms than other food web members (e.g. Table 2), which fits in with hypotheses (1)–(3). The population doubling time for *A. proteus* is also longer than for the other protist species present and they are larger bodied, which fits with both (2) and (3). Unlike one aspect of (3), the diet of *A. proteus* was actually less specialized than that of *D. nasutum* (Fig. 1A), and *D. nasutum* increased in abundance from subdivision (Table 2). Clearly there are elements of all of the first three of these hypotheses that hold for *A. proteus*, they are not mutually exclusive, and they suggest direct effects of habitat subdivision on *A. proteus*. Hypothesis (4) deals with the case where species are present in only some patches and is not relevant during the early stages of this experiment where all species were present in all patches. However, this hypothesis might contribute to food web collapse once species start to go locally extinct.

All of the changes in species density that occurred in the subdivided habitats relative to the undivided habitats could have resulted from the decline in density of *A. proteus* caused by subdivision; this indicates that species interactions structured the food web. Comparison of different species combinations in undivided habitats or isolated patches showed that *D. nasutum* was more abundant when *A. proteus* was absent than when it was present. Comparison of treatments with all four species present vs. those lacking *A. proteus* also showed that *B. americanum* also increased in density when *A. proteus* was absent. Observed changes in average densities of *D. nasutum* and *B. americanum* during habitat subdivision were qualitatively consistent with those caused by removal of *A. proteus* in undivided microcosms.

It is possible that the eventual decline to extinction of *D. nasutum* might also follow once *A. proteus* declined to low densities. Again, the undivided habitats with different species combinations show a possible mechanism by which *D. nasutum* might be excluded by *B. americanum*. In undivided bottles the presence of both *B. americanum* and *D. nasutum* depressed *C. striatum* densities substantially when either *B. americanum* or *D. nasutum* was present alone. At low *C. striatum* densities, *B. americanum* has a competitive advantage over *D. nasutum* because *B. americanum* can also feed and survive on bacteria (Holyoak & Sachdev 1998; Morin 1999). The dynamics (intraguild predation) of *C. striatum*, *B. americanum* and bacteria have been extensively studied by Morin (1999). A simple model of competition between specialists and generalists in patchy environments also shows that generalists are more likely to be able to persist in local communities, whereas specialists are frequently driven extinct locally (Frank & Amarasekare 1998). Here, the species that did best despite habitat fragmentation was an omnivore, a trophic generalist.

The results show that habitat subdivision can cause large changes in species persistence and that unpredicted changes in food web structure may follow. However, we need to be careful when assuming that all changes in food web structure are directly caused by subdivision. Complex indirect effects of removal of one species may influence the species remaining in food webs, and the extent to which species in communities are independently regulated vs. interactive is expected to be important in this regard. In general, we know little about the kinds of species that will become important in the structure and functioning of fragmented food webs. Various traits that might enhance the ability of species to survive in patchy habitats have been found (Diamond 1975; Didham *et al.* 1998; Davies *et al.* 2000), and this paper has discussed various food web characteristics in this context. However, more experimental tests are badly needed. During field studies we should also be alert for changes in the structure and functioning of food webs and ecosystems caused by habitat subdivision and other aspects of fragmentation.

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BIOSKETCH

Marcel Holyoak's research programme focuses on the spatial dynamics of populations and communities. He uses microcosm experiments and field studies to test and develop ecological theory. His interests span population biology, community ecology, conservation, biostatistics and modelling.

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