



Habitat fragmentation resulting in overgrazing by herbivores

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Received 30 September 2002; received in revised form 22 April 2003; accepted 18 July 2003

Abstract

Habitat fragmentation sometimes results in outbreaks of herbivorous insect and causes an enormous loss of primary production. It is hypothesized that the driving force behind such herbivore outbreaks is disruption of natural enemy attack that releases herbivores from top-down control. To test this hypothesis I studied how trophic community structure changes along a gradient of habitat fragmentation level using spatially implicit and explicit models of a tri-trophic (plant, herbivore and natural enemy) food chain. While in spatially implicit model number of trophic levels gradually decreases with increasing fragmentation, in spatially explicit model a relatively low level of habitat fragmentation leads to overgrazing by herbivore to result in extinction of the plant population followed by a total system collapse. This provides a theoretical support to the hypothesis that habitat fragmentation can lead to overgrazing by herbivores and suggests a central role of spatial structure in the influence of habitat fragmentation on trophic communities. Further, the spatially explicit model shows (i) that the total system collapse by the overgrazing can occur only if herbivore colonization rate is high; (ii) that with increasing natural enemy colonization rate, the fragmentation level that leads to the system collapse becomes higher, and the frequency of the collapse is lowered.

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Keywords: Herbivore's outbreak; Habitat fragmentation; Overgrazing; Cellular automaton; Tri-trophic systems

1. Introduction

Spatial landscape patterns determine biological interaction (Kareiva, 1990; Taylor, 1990; Hastings, 1990; Nee et al., 1997) and community structure (Reeve, 1988; Kareiva and Wennergren, 1995; Thies and Tscharnkte, 1999). One of the more general ways in which landscapes change spatially is by habitat fragmentation. Ecological studies have shown how habitat fragmentation alters the species composition of communities. It increases the probability of stochastic extinction of minor species (e.g. Menges, 1998), leads dispersal-limited species to deterministic extinction (Tilman et al., 1994). Moreover, effects of fragmentation can be transmitted to other species through interspecific interactions (May, 1994; Kareiva and Wennergren, 1995; Wennergren et al., 1995; Nee et al., 1997; Bascompte and Solé, 1998). Consequently, it alters the structure of

competitive (Nee and May, 1992; Tilman et al., 1994; Dytham, 1995a, b; Moilanen and Hanski, 1995; Stone, 1995) or trophic (May, 1994; Kareiva and Wennergren, 1995; Wennergren et al., 1995; Nee et al., 1997; Bascompte and Solé, 1998) communities.

Habitat fragmentation has been hypothesized to enhance a herbivore outbreak (Kareiva, 1987; Kruess and Tscharnkte, 1994). Empirical studies have shown that longevity and frequency of herbivore outbreaks are positively correlated with the degree of fragmentation (Kareiva, 1987; Roland, 1993; Roland and Taylor, 1997; Cappuccino and Martin, 1997; Rothman and Roland, 1998; Cappuccino et al., 1998). The disruption of trophic interaction is believed to be responsible for this trend (Roland, 1993; Zabel and Tscharnkte, 1998); natural enemies regulating herbivore population (Hawkins and Gross, 1992; Hawkins et al., 1993) are suppressed by fragmentation releasing herbivores from the top-down control. This, in turn, leads to a herbivore outbreak (Roland, 1993; Kruess and Tscharnkte, 1994; Zabel and Tscharnkte, 1998).

Among possible mechanisms (Zabel and Tscharnkte, 1998) of habitat fragmentation having stronger impact

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on natural enemy than on herbivore, one arises from higher dependence of higher trophic levels on colonization. Since colonization of species at higher trophic levels depends on successful establishment of prey populations (i.e. lower trophic levels), they tend to have less available resource patches than those at lower trophic levels. Consequently, natural enemy is supposed to be more disadvantaged by habitat fragmentation, which inhibits colonization processes, than herbivore (Zabel and Tscharrnke, 1998; Holt, 1996). However, this process is only about a process at a local spatial scale of a single habitat fragment, and there is a gap between this small-scaled process and herbivore outbreaks that take place at a larger spatial scale. To bridge over this gap it is essential to consider metapopulation processes (local extinction and re-colonization between multiple habitat fragments) that connect multiple habitat fragments at larger spatial scales.

Despite theoretical studies (Kareiva and Wennergren, 1995; Wennergren et al., 1995; Bascompte and Solé, 1998) developed to examine the effect of habitat fragmentation on trophic communities at larger spatial scales, there are few studies that investigate the full trophic level impacts of fragmentation (but see Bascompte and Solé, 1998). An exceptional study by Bascompte and Solé (1998) demonstrated that habitat fragmentation increases the abundance of herbivores (i.e. prey) while decreasing natural enemy (predator) abundance. Such a model, dealing only with two-trophic systems (herbivore and natural enemy populations), cannot in principle incorporate plant–herbivore interactions. Consequently, their model is less applicable to cases where herbivore's overgrazing has a strong impact on basal plant species, as is the case in herbivore outbreaks, or higher trophic levels are strongly influenced by dynamics of resource plant species. Further, these models do not incorporate the recent developments in studies of herbivore outbreaks (e.g. Brodmann et al., 1997; Hastings et al., 1997; Wilson et al., 1999; Maron and Harrison, 1997; Maron et al., 2001) that herbivore population is regulated by top-down and bottom-up controls acting on heterogeneously in space.

Here, I present mathematical models of tri-trophic systems to show that habitat fragmentation can lead to plant extinction due to overgrazing and report that spatial structure resulting from local dispersal and local interaction can play a central role in this phenomenon. To explore the role of spatial structure in determining the impact of habitat fragmentation on tri-trophic communities, I compare spatially explicit model and mean-field model of a tri-trophic food chain consisting of plant, herbivore and natural enemy in a patchy environment. The mean-field model assumes spatially well-mixed individuals, while a spatially explicit model assumes spatially structured environment.

2. Models and results

Consider the habitat space envisaged as a plane composed of a large number of patches, where metapopulations of plant, herbivore and natural enemy are maintained through inter-patch colonization via dispersal and intra-patch extinction. In the metapopulation models of tri-trophic communities within-patch population dynamics is not explicitly incorporated; instead, it is approximated by making the following assumptions: (i) respective species only successfully colonize a patch when it is occupied by their resource but not by their consumer species; (ii) consumer's colonization quickly lowers reproductive rate of the resource species to very low levels; (iii) once colonized by its consumer, the resource species in that patch is consumed to extinction. These conditions represent a situation where consumers have very strong negative effects on their resource species and any resource-consumer systems are not stable at the local scale. (The assumption that consumer species can cause local extinction of resource species is required to generate extinction due to over-consumption at a larger spatial scale.)

Habitat fragmentation occurs by a proportion D of randomly chosen patches being permanently destroyed. No plant can colonize any fraction of destroyed patches $[D]$, and neither herbivore nor natural enemy occupies the destroyed patches. A patch that is not destroyed is characterized by the species that reproduce within the patch: that is, no species (E), plant (P), herbivore (H), natural enemy (N), or both plant and natural enemy (P/N). The metapopulation models describe the dynamics of the frequency of patches in each state (P , H , N and $P/N(=Q)$); global density of plant, herbivore and natural enemy are $(P+Q)$, H and $(N+Q)$, respectively. Assume that reproducing plant, herbivore and natural enemy disperse to other patches with constant stochastic rates, c_p , c_h and c_n , respectively. By the above assumptions (i) and (iii), plant dispersal succeeds only when it is to a patch occupied by neither plant nor herbivore. This reaction is represented as follows: $[P] + [E] \rightarrow [P] + [P]$ or $[P] + [N] \rightarrow [P] + [P/N]$. Colonization of herbivore and natural enemy only succeeds when dispersal occurs to a patch occupied by its resource (P for H , H for N) but not by its consumer (N for H). The possible reactions are: $[H] + [P] \rightarrow [H] + [H]$ for herbivore, $[N] + [H] \rightarrow [N] + [N]$ or $[P/N] + [H] \rightarrow [P/N] + [N]$ for natural enemy. Colonization rates of natural enemies (c_n) would be related to top-down force; that is, strong predation pressure is represented by a high natural enemy colonization rate (Feeny, 1976). Plant, herbivore and natural enemy within a patch become extinct by natural death or extinction of their resources with constant rates, m_p , m_h and m_n , respectively ($[P] \rightarrow [E]$ or $[P/N] \rightarrow [N]$ for plant extinction;

$[H] \rightarrow [E]$ for herbivore extinction; $[N] \rightarrow [E]$ or $[P/N] \rightarrow [P]$ for natural enemy extinction).

2.1. Mean-field model

Mean-field model assumes that an organism can potentially interact with every individual in the habitat space; in other words, total mixing occurs. Patches are occupied by plant $[P]$, herbivore $[H]$, natural enemy $[N]$ or both plant and natural enemy $[P/N]$. Plants can only colonize empty patches that have not been destroyed and are occupied by neither plant nor herbivore. When plants colonize natural enemy patches, the natural enemy patches become patches occupied by both plant and natural enemy $[P/N]$. Plants disappear because of natural extinction and colonization by herbivore. Herbivores colonize plant patches that are not occupied by natural enemy, and disappear because of natural extinction and colonization by natural enemy. Natural enemies only colonize herbivore patches and disappear due to natural extinction. Assuming an infinite number of patches, the frequency of respective patches is given by following equations:

$$dP/dt = c_p P(1 - D - P - H - N - Q) - m_p P - c_h PH + m_n Q, \tag{1a}$$

$$dH/dt = c_h PH - m_h H - c_n H(N + Q), \tag{1b}$$

$$dN/dt = c_n H(N + Q) - m_n N + m_p Q - c_p PN, \tag{1c}$$

$$dQ/dt = c_p PN - (m_n + m_p)Q, \tag{1d}$$

where P, H, N and Q are the frequencies of patch occupation by plant $[P]$, herbivore $[H]$, natural enemy $[N]$ and both plant and natural enemy $[P/N]$, respectively; c_i is the colonization rate, which represents per capita colonization rate of plant ($i = p$), herbivore (h) or natural enemy (n), m_i is the natural extinction rates of plant ($i = p$), herbivore (h) and natural enemy (n); D is the fraction of destroyed patches. $(m_n Q)$ in Eqs. (1a) and (1d) represents that a patch occupied by plant and natural enemy becomes to be a plant patch due to extinction of natural enemy. $(m_p Q)$ in Eqs. (1c) and (1d) represents that a patch occupied by plant and natural enemy becomes to be a natural enemy patch due to plant's extinction.

By setting the right-hand side of Eqs. (1a)–(1d) to zero, the possible equilibria are obtained as follows (Fig. 1):

- (I) If D is sufficiently small (to hold that $D < 1 - m_p/c_p - m_h/c_h - (m_n/c_n)(1 + c_h/c_p)$), plant, herbivore and natural enemy coexist ($P^* + Q^* > 0, H^* > 0, N^* + Q^* > 0$; see Appendix A for the detailed analysis).
- (II) If D is larger ($1 - m_p/c_p - m_h/c_h - (m_n/c_n)(1 + c_h/c_p) < D < 1 - m_p/c_p - m_h/c_h$), plant and

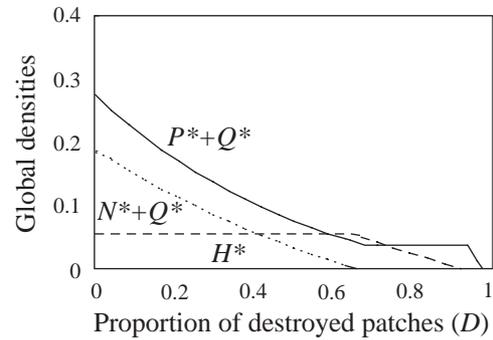


Fig. 1. The effects of habitat fragmentation on the density of plant (solid line; $P^* + Q^*$), herbivore (broken line; H^*) and natural enemy (dotted line; $N^* + Q^*$) in mean-field model. To make this figure, parameters $(m_p, m_h, m_n, c_p, c_h, c_n) = (0.01, 0.0667, 0.0667, 0.4, 1.6, 1.2)$ are used.

- herbivore coexist: $(P^*, H^*, N^*, Q^*) = (m_h/c_h, \{c_p(1 - D - P^*) - m_p\}/(c_p + c_h), 0, 0)$.
- (III) If D is much larger ($1 - m_p/c_p - m_h/c_h < D < 1 - m_p/c_p$), plant population alone persists: $(P^*, H^*, N^*, Q^*) = (1 - D - (m_p/c_p), 0, 0, 0)$.
- (IV) If D is extremely large ($D > 1 - m_p/c_p$), no species persist: $(P^*, H^*, N^*, Q^*) = (0, 0, 0, 0)$.

Chain length monotonously decreases with increasing fragmentation level. In odd-length food chain, plant and natural enemy (if exist) decrease with increasing fragmentation level (as confirmed by $d(P^* + Q^*)/dD = d\{1 - D - (m_p/c_p)\}/dD = -1 < 0$ in case III; see Appendix A for case I), while herbivore abundance remains constant ($dH^*/dD = d(m_n/c_n)/dD = 0$ in case I; Appendix A). In contrast, in even-length food chain, plant abundance is kept constant ($d(P^* + Q^*)/dD = d(m_h/c_h)/dD = 0$ in case II), while herbivore density decreases ($dH^*/dD = d[\{c_p(1 - D - P^*) - m_p\}/(c_p + c_h)]/dD = -c_p/(c_p + c_h) < 0$ in case II) with an increase in fragmentation levels, D .

2.2. Spatially explicit model

To approximate spatially explicit version of the model I used a stochastic cellular automaton, where colonization is always restricted to the four nearest neighborhoods and the habitat is a torus composed of $n \times n$ sorted patches. Unit time step (T) consisted of $n \times n$ sets of the following steps:

Step 1: Choose two neighboring patches (Patches A and B) at random (the neighboring patches are the four adjacent cells). If Patch B (or A) can be colonized by species in Patch A (or B) (i.e. $[P]$ and $[E]$, $[P/N]$ and $[E]$, $[P]$ and $[N]$, $[H]$ and $[P]$, $[N]$ and $[H]$, or $[P/N]$ and $[H]$), proceed to Step 2. If either is impossible, proceed to Step 3.

Step 2: If Patch B (or A) is occupied by resource of species in Patch A (B), then the species in Patch A (B)

colonize the Patch B (A) with probability ($c_i/2$), where i ($= p, h, \text{ or } n$) is determined by the colonizing species. Then proceed to Step 3.

Step 3: A local extinction of either plant, herbivore or natural enemy may take place once out of three ‘unit time steps’. Choose a patch randomly. If the organism that may extinct in this step occupies this patch, it will become extinct with a probability, ($3m_i$) (≤ 1 ; $i = p, h$ and n , for plant, herbivore and natural enemy, respectively; we can deal with $m_i > \frac{1}{3}$ by multiplying Step 3 in unit time step, T).

Simulations were initiated with random distribution of the constant proportions of P , H and N ($P = 0.067$, $H = 0.022$, $N = 0.067$). I chose various parameter sets that with no habitat fragmentation ($D = 0$) allow the tri-trophic system to persist (in the present paper I provide examples for following parameters: (c_p, m_p, m_h, m_n) = (0.4, 0.01, 0.067, 0.067)). In order to examine the spatial distribution pattern of the organisms, the local density of each species is recorded during a simulation. Local density of species i (L_i) is defined as a probability with which a neighboring patch of a species i patch is occupied by the same species. It is expected that the ratio of local density to global density increases with increased clustering and should be 1.0 for randomly distributed individuals. If the local density, L_i , is higher than the corresponding global density, ($P + Q$), H , or ($N + Q$), then this implies that the species shows a clustered distribution.

In every run, populations showed stochastic fluctuations (Fig. 2). There is a general tendency that a local density of a higher trophic level is lower than that of a lower trophic level, and that habitat fragmentation decreases the local densities of all species (Fig. 2). Possible outcomes are plant–herbivore–natural-enemy coexistence ($P-H-N$), plant–herbivore coexistence ($P-H$), plant persistence (P) and total system collapse. To examine the probabilities of respective outcomes, I conducted 20 runs for each parameter set. Model analysis shows that the changes in food-chain length along a gradient of fragmentation level (D) depend on colonization rates of herbivore (c_h) and natural enemy (c_n) (Fig. 3), and can be expressed on a continuum ranging between two qualitatively different typical cases, Types I and II.

When c_h is low or c_n is high the food-chain length tends to decrease monotonously as fragmentation level increases (Type I; Figs. 3f and 4). At extremely low levels of fragmentation, plant, herbivore and natural enemy coexist. In tri-trophic systems the plant and natural-enemy densities decrease with increasing fragmentation level, but the density of herbivore patches can either increase or decrease (Fig. 4). When only a two-trophic interaction is considered, the global density of herbivore patches decreases whilst the density of plant patches increases with increased fragmentation level. With only the plant population, its global density

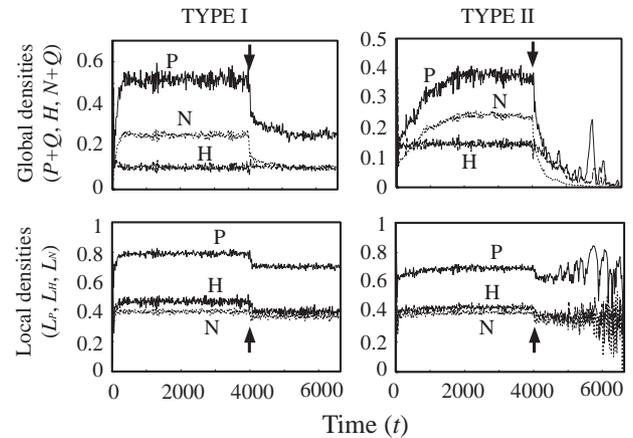


Fig. 2. The effects of habitat fragmentation on the global (upper panels) and local (lower panels) densities of plant (solid line), herbivore (broken line) and natural-enemy (dotted line) populations in spatially explicit model. The fragmentation ($D = 0.133$, that is, 3000 patches) is performed at time, $T = 4000$, as indicated by an arrow. The same level of habitat fragmentation results in a whole system collapse in Type II, but not in Type I. Parameters ($m_p, m_h, m_n, c_p, c_h, c_n$) = (a) (0.01, 0.0667, 0.0667, 0.4, 1.8, 0.8), and (b) (0.01, 0.0667, 0.0667, 0.4, 1.8, 1.2) are used.

generally decreases as fragmentation level increases. At extremely high levels of habitat fragmentation, the plant population cannot persist.

When c_h is high and c_n is low a strikingly different pattern (Type II) is observed. A relatively low level of habitat fragmentation, which allows plant population to persist if there is only plant population, can lead to the collapse of the whole system (Figs. 2, 3g, h, and 4) due to overgrazing by herbivores. In some cases, the level of fragmentation, that causes the system collapse in other simulation runs, results in a persistence of the plant population (Fig. 3g and h). This is due to the herbivore population becoming extinct before the extinction of the plant population. Under higher levels of habitat fragmentation, plant and herbivore populations coexist, and the number of trophic levels monotonously decreases as fragmentation level increases.

The frequency of the system collapses depends on c_h and c_n (Fig. 3f–h). When c_h is extremely high and c_n is very low (Fig. 3g), the total system collapses as a result of overgrazing (or persistence of plant because of the earlier extinction of herbivores). With increasing c_n or decreasing c_h , the fragmentation level that leads to the collapse is higher, and the frequency of the system collapse is lower (as depicted in Fig. 3h). When c_n is sufficiently high or c_h sufficiently low, the collapse is not observed (Fig. 3).

3. Discussion

The present models demonstrate how habitat fragmentation influences tri-trophic communities. The

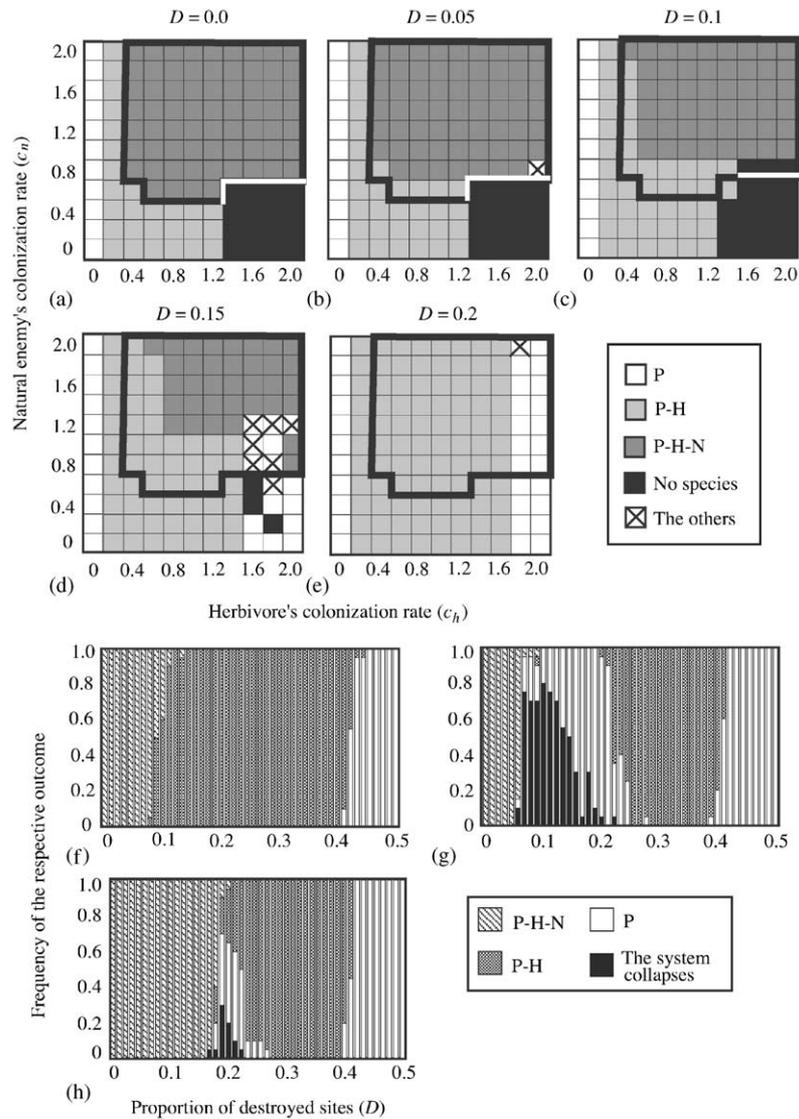


Fig. 3. The effects of habitat fragmentation ($D = 0.0-0.2$) on the food-chain length in spatially explicit model (a–e). Twenty simulations are conducted for each parameter set of (c_h, c_n) . Each color represents community composition that is frequently observed (more than 10 simulations): plant alone ($P^* + Q^* > 0, H^* = 0, N^* + Q^* = 0$) for white, plant and herbivore ($P^* + Q^* > 0, H^* > 0, N^* + Q^* = 0$) for light gray, plant, herbivore and natural enemy ($P^* + Q^* > 0, H^* > 0, N^* + Q^* > 0$) for dark gray, no species ($P^* + Q^* = 0, H^* = 0, N^* + Q^* = 0$) for black, square with a cross for the other compositions. Long-time average ($T = 3000-4000$) of the species abundance (global density) is calculated to judge community composition of a simulation. Plant, herbivore and natural enemy coexist without habitat destruction ($D = 0.0$) in the region surrounded by thick line. The frequency of each outcome, tri-trophic ($P-H-N$), two-trophic ($P-H$), one-trophic (P) system and the total system collapse, for sets of (c_h, c_n) in spatially explicit model (f–h). Long-time average ($T = 3000-4000$) of the species abundance (global density) is calculated after the system reaches a quasi-stable state. The parameters are $(c_h, c_n) =$ (f) (1.2, 0.8), (g) (1.8, 0.8), and (h) (1.8, 1.6). The other parameters are the same as used in Fig. 2.

changes in respective populations along a gradient of habitat fragmentation level depend on the number of trophic levels (food-chain length) and their position within the food chain. Further, there are some differences between spatially explicit and mean-field models, suggesting a role of spatial structure in the impact of habitat fragmentation on trophic communities.

Mean-field model predicts a step type of the pattern in the abundances of organisms along a gradient of habitat fragmentation (Fig. 1). Habitat fragmentation only

influences the odd-number trophic levels from the top. This is explained by considering what controls the abundances of trophic levels. The equilibrium densities of the odd-number trophic levels are controlled by top-down forces, and those of the even-number trophic levels are controlled by bottom-up forces (Oksanen et al., 1981). Therefore, habitat fragmentation, which is a bottom-up force by definition, influences only even-number trophic levels. In this model the top-positioned species (natural enemy if a tri-trophic system, herbivore if a two-trophic system) always goes extinct by

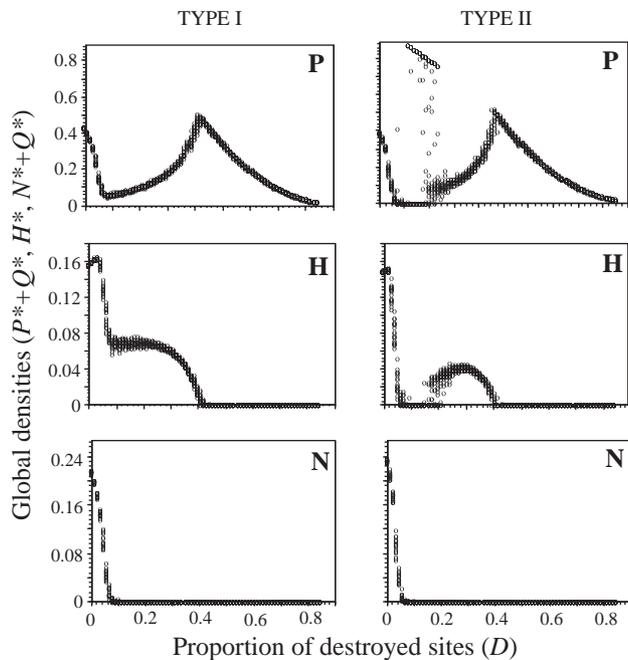


Fig. 4. Two typical patterns of the changes in plant (upper panel), herbivore (middle panel) and natural-enemy (lower panel) populations along a habitat fragmentation gradient in spatially explicit model; (a) Type I, and (b) Type II (see text). The equilibrium frequencies of patches occupied by respective populations (i.e. global density) derived from 20 runs are plotted against the fragmentation level. Long-time average ($T = 3000\text{--}4000$) of the each species global density is calculated after the system reaches a quasi-stable state. Parameters are $(m_p, m_h, m_n, c_p, c_h, c_n) = (0.01, 0.0667, 0.0667, 0.4, 1.6, 1.6)$ (Type I), and $(0.01, 0.0667, 0.0667, 0.4, 1.6, 0.8)$ (Type II).

fragmentation. Thus, with an increased proportion of destroyed patches, the system can change from a tri-trophic one to a two-trophic one, one-trophic system or even total collapse. A similar pattern has been reported by previous studies dealing with two-trophic systems (Bascompte and Solé, 1998).

A completely different pattern emerges in spatially explicit model (Fig. 4), that is, changes in trophic-chain length along a gradient of fragmentation levels depend on some characteristics of the species composition of the food chain (Fig. 3). When the herbivore colonization rate is low, the observed pattern is similar to that of spatially implicit model (i.e. a gradual decrease in food-chain length with increasing fragmentation). In contrast, when herbivore colonization rate is sufficiently high, and natural enemy colonization rate is sufficiently low, certain levels of habitat fragmentation can result in plant extinction and thus lead to the collapse of the whole system. In such cases the system can change from a tri-trophic one to total collapse (due to overgrazing), two-trophic one, one-trophic system and total collapse again (due to a low habitat availability) as fragmentation level increases. This provides a theoretical support to the hypothesis (Roland, 1993; Kruess and Tschardtke, 1994; Zabel and Tschardtke, 1998) that

habitat fragmentation can lead to overgrazing by herbivores.

Why do low fragmentation levels lead to the plant extinction in spatially explicit model? There are two possible mechanisms. First, through changes in plant colonization (direct effect). Habitat fragmentation decreases available habitat patches for plants, resulting in unsuccessful colonization. Second, through changes in trophic interactions (indirect effect). If habitat fragmentation increases grazing pressure by altering plant–herbivore or herbivore–natural enemy interaction, then it would decrease plant abundance. Although their relative contributions are unclear, the result that fragmentation has a completely different effect on plant abundance in the two- and tri-trophic systems suggests that trophic interactions hold the key to the effect of fragmentation on trophic communities. In two-trophic systems plant abundance increases with increasing habitat fragmentation (Fig. 4). This implies that habitat fragmentation has a potential to weaken the plant–herbivore interactions (herbivore colonization or grazing pressure) in two-trophic systems. This is supported by the fact that a herbivore population with a high colonization rate (c_h) and a plant population, that do not coexist at low fragmentation levels, can coexist in the absence of natural enemy when the fragmentation level is higher (Figs. 3 and 4). When the fragmentation level is lower, herbivore and plant cannot coexist, because the herbivore with a high colonization rate overexploits the plant population. On the other hand, a higher fragmentation level inhibits the herbivore colonization, and the two-trophic system of plant and herbivore can persist. In tri-trophic systems, in contrast, plant abundance increases with increasing habitat fragmentation (Fig. 4). This reversal of fragmentation impact on plant abundance in the two-trophic and tri-trophic systems would be explained if assuming that natural enemies (or herbivore–natural enemy interaction) are more vulnerable to habitat fragmentation than herbivores (or plant–herbivore interaction). In such a case grazing pressure can increase with increasing fragmentation in tri-trophic systems and thus can decrease plant abundance. This explanation does not contradict the two trends: first, natural enemy abundance generally decreases with increasing habitat fragmentation (Figs. 2 and 4); second, a high natural enemy colonization rate (c_n) can prevent the total system collapse (Fig. 3).

The high vulnerability of natural enemies to habitat fragmentation can emerge from the spatial distribution pattern of the three trophic levels. Every species tends to show a clustered distribution (as indicated by the fact that the local density of a species is always higher than its global density; see Fig. 2), as colonization is a local process in spatially explicit model. In such a distribution, once a consumer species (H or N) has invaded a

cluster of its resource species (P or H), the advance of the consumer species depends on the local density of the resource species: a clumped resource distribution enhances the advance of the consumer species. In such cases habitat fragmentation inhibits an advance of herbivores within a plant cluster by decreasing the local densities of plants (Fig. 2). An advance of natural enemy in a herbivore cluster is more suppressed by fragmentation than that of herbivores, since herbivores, which utilize a cluster of plants, tend to be less clumped than resource plants (Fig. 2). Therefore, natural enemies experience a resource (herbivore) cluster with more empty patches than herbivores—that is, a habitat is more fragmented for natural enemies than for herbivores. Then it follows that natural enemies are more vulnerable to habitat fragmentation than herbivores.

In summary, the model suggests the possibility that relatively low levels of habitat fragmentation, which without higher trophic levels allow the persistence of the plant population, could have a dramatic impact on the whole trophic community. A tri-trophic community becomes extinct for a grazing pressure even in huge reserves before their habitat is fully fragmented. This is because even a low level of habitat fragmentation can destroy the critical ‘balance’ between top-down (natural enemy attack) and grazing pressure maintaining the tri-trophic systems. Also, the impact of fragmentation on the trophic community strongly depends on the characteristics of species composition of the community. This suggests that if we are to understand fully the effect of fragmentation on trophic communities, precise understanding of biological interaction with the community is essential.

Acknowledgements

I thank Yutaka Kobayashi and Gaku Takimoto for discussion, Hefin Jones, Norio Yamamura, Matthew Walker, Nanako Shigesada and an anonymous referee for valuable comments on a manuscript, and Masahiko Higashi for his encouragement and suggestions that inspired the present study.

Appendix A

A.1. Analysis of equilibrium point with $P^ > 0$, $H^* > 0$, $N^* > 0$ and $Q^* > 0$*

The equilibrium point (P^* , H^* , N^* , Q^*) is given by setting the right-hand sides of Eqs. (1a)–(1d):

$$c_p P^*(1 - D - P^* - H^* - N^* - Q^*) - m_p P^* - c_h P^* H^* + m_n Q^* = 0, \tag{A.1a}$$

$$c_h P^* H^* - m_h H^* - c_n H^*(N^* + Q^*) = 0, \tag{A.1b}$$

$$c_n H^*(N^* + Q^*) - m_n N^* + m_p Q^* - c_p P^* N^* = 0, \tag{A.1c}$$

$$c_p P^* N^* - (m_n + m_p) Q^* = 0. \tag{A.1d}$$

Eqs. (A.1c) and (A.1d) taken together make that $N^*(c_n H^* - m_n)\{1 + c_p P^*/(m_n + m_p)\} = 0$, suggesting that $H^* = (m_n/c_n)$ at a non-trivial equilibrium. This result and Eqs. (A.1a) and (A.1d) taken together make:

$$N^* = (m_p + m_n)(A - c_p P^*)/(m_p c_p + c_p P^{*2}). \tag{A.2}$$

Eqs. (A.1b) and (A.1d) taken together make:

$$N^* = (m_p + m_n)(c_h P^* - m_h)/\{c_n(m_p + m_n + c_p P^*)\}, \tag{A.3}$$

where $A = c_p\{1 - D - (m_n/c_n)\} - m_p - (c_h m_n/c_n)$. D should be smaller than $\{1 - m_p/c_p - m_h/c_h - (m_n/c_n)(1 + c_h/c_p)\}$ for non-trivial (P^* , N^*), an intersection of lines represented by Eqs. (A.2) and (A.3) in the region of $P^* > 0$ and $N^* > 0$, to exist. When it holds that $\{1 - m_p/c_p - m_h/c_h - (m_n/c_n)(1 + c_h/c_p)\} > D$, $A > 0$ and Eq. (A.2) represents that N^* is P^* 's decreasing function ($N^* = f(P^*)$) crossing $(P^*, N^*) = (0, A(m_n + m_p)/(m_p c_p))$ and going to $\{-(m_n + m_p)/c_p\} < 0$ at the infinite limit of P^* in the region $P^* > 0$ and $N^* > 0$. Eq. (A.3) represents that N^* increases with increasing P^* ($N^* = g(P^*)$) and $N^* = 0$ when $P^* = m_h/c_h$ in region, $P^* > 0$ and $N^* > 0$. Changing D does not alter the shape of $g(P^*)$ and decreases N^* for a given P^* in $f(P^*)$. Taken these together, it follows that P^* and N^* should decrease with increasing D . Noting that Q ($= c_p P^* N^*/(m_n + m_p)$) derived from Eq. (A.1d) is an increasing function of ($P^* N^*$), increasing D should decrease Q .

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