Species coexistence patterns in a mycophagous insect community inhabiting the wood-decaying bracket fungus *Cryptoporus volvatus* (Polyporaceae: Basidiomycota)

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Abstract. A study of the insect community inhabiting the wood-decaying bracket fungus, *Cryptoporus volvatus* was used to test two hypotheses proposed to account for the competitive coexistence of species in insect communities in patchy environments, niche partitioning and spatial mechanisms. A total of 8990 individuals belonging to 17 insect species emerged from 438 sporocarps (patches) collected from the field. Insect species richness increased and then declined with increase in the total insect biomass reared from a sporocarp, suggesting the potential importance of interspecific competition. Successional niche partitioning explained the spatial distribution of the four specialist species. The aggregation model of coexistence satisfactorily explained the stable coexistence of the species. The specialist species displayed higher population persistence than the generalists. Simulation studies suggest that restricted movements of adults could override patch-level larval aggregation. The effect of such restricted movements on stabilizing coexistence in fungus-insect communities has not been previously appreciated. These findings suggest that spatial mechanisms play a crucial role in the competitive coexistence of the species in the mycophagous insect communities inhabiting bracket fungi.

INTRODUCTION

Considerable effort has gone into studying the mechanisms underlying competitive coexistence in insect communities in patchy environments (Shorrocks et al., 1979; Ives, 1991; Toda et al., 1999; Wertheim et al., 2000; Takahashi et al., 2005b). Niche partitioning and spatial mechanisms are two commonly proposed explanations for competitive coexistence in patchy systems. The niche partitioning hypothesis posits that different insect species use different resources (resource partitioning, sensu Wertheim et al., 2000), or different developmental and/or life stages of a resource (successional niche partitioning; Guevara et al., 2000; Jonsell & Nordlander, 2004; etc.), or different organs and/or parts of a given resource (Matthewman & Pielou, 1971; Hackman & Meinander, 1979). The spatial mechanisms hypothesis posits that when different species are spatially aggregated in a number of patches (e.g., fungus-dwelling insects in individual sporocarps), this can by chance create spatial refuges for inferior competitors (the so-called aggregation model of coexistence; Atkinson & Shorrocks, 1981; Ives & May, 1985). Spatial refuges result from the under-exploitation of large-sized patches (Sevenster & Van Alphen, 1996; Toda et al., 1999). Also, the movements of insects are restricted at the scale of "clumps of patches" (hereafter superpatches), thereby increasing the number of patch-level spatial refuges for inferior competitors (Inouye, 1999).

Fungus-insect communities provide an excellent model system for testing the mechanisms leading to the coexistence of insect communities in patchy systems, because sporocarps constitute spatially subdivided habitats, where localized competitive interaction is expected to occur. Inherently, fungal sporocarps encompass a wide range of temporal variation in food and habitat quality for mycophagous insects (Hanski, 1989), including duration of a single sporocarp, seasonal occurrence (phenology) and year-to-year variation in sporocarp occurrence (Hanski, 1989). Ashe (1984) describes the contrasting extremes of the microhabitat characteristics of fungi for mycophagous insects: while Agaricales sporocarps are fragile and ephemeral, Polyporaceae sporocarps are physically tough and persist for several years. Thus, it is possible to use these two distinctive features to study how mycophagous insect communities are structured.

There is an abundance of evidence for exploitative competition in insect communities at one end of the "ephemeral mushroom" continuum (e.g. Atkinson & Shorrocks, 1981; Gilpin et al., 1986; Takahashi & Kimura, 2005). The niche partitioning hypothesis is supported by studies on *Drosophila* (Kimura, 1980; Grimaldi, 1985) but there is no experimental evidence for host specialization among *Drosophila* (Jaenike, 1978). Yamashita & Hijii (2007) found that developmental stages of sporocarps did not influence host utilization patterns by mycophagous flies and argued against successional niche partitioning. The importance of spatial mechanisms was demonstrated for a two-species *Droso-*

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phila community by Shorrocks et al. (1990), in which the superior competitor displaced the inferior competitor in undivided habitats, but the two species coexisted in spatially subdivided habitats. Sevenster & van Alphen (1996) developed an analytical tool for estimating intraspecific and interspecific association and coexistence in patches of various sizes, and then used it to explain the coexistence of several species of neotropical *Drosophila* inhabiting fallen fruit. Restricted movements of insects can promote coexistence of several species of *Drosophila* in rotten fruit (Inouye, 1999; Krijger & Sevenster, 2001). Inouye (1999) showed that spatial variation at the patch level may not be sufficient for coexistence, but the total variation at the patch and super-patch level allowed coexistence. Toda et al. (1999) and Wertheim et al. (2000), both carried out community-level studies, but differ in their conclusion as Wertheim et al. (2000) argue against resource partitioning. Takahashi et al. (2005b) suggest that the relative magnitude of the two mechanisms depends on the phylogenetic structure of the community and successfully resolved the opposing views.

At the opposite end of the continuum there are the "persistent, bracket fungi", the studies of which have focused on trophic patterns (Komonen, 2001; Komonen et al., 2003) or the colonization abilities of mycophagous beetles (Jonsell et al., 2003; Jonsson, 2003), rather than on interspecific competition. Nonetheless, niche partitioning occurs in ciid (Ciidae) beetle communities. Guevara et al. (2000) report successional niche partitioning by two ciid beetles, demonstrating that age-related changes in the chemical composition (odour) of sporocarps may allow two competitive species to discriminate among the sporocarps of host fungi. Circumstantial evidence for successional niche partitioning is provided by Jonsell & Nordlander (2004) who show that polyphagous insects tend to use decaying sporocarps and so avoid the chemical defences of fungi. Using cross-dataset comparison and cluster analyses Orledge & Reynolds (2005) confirmed that the resource partitioning is determined by the ciid beetles' specific response to the age dependent characteristic volatile emissions of their fungal hosts (see also references therein). Spatial mechanisms greatly influence species occurrence patterns (Jonsell et al., 1999; Jonsson, 2003; Komonen, 2003a, 2008; Komonen & Kouki, 2005), but have never been explicitly linked with species coexistence. Komonen (2003a) documents both intraspecific and interspecific aggregation of two congeneric ciid beetles. The flight willingness and duration of a common and threatened tenebrionid species in the laboratory differ (Jonsson, 2003). The colonization patterns of polypore sporocarps by mycophagous beetles is affected not only by interpatch distance and habitat matrix characteristics (Jonsell et al., 1999), but also by the microhabitat preferences of the beetles (Komonen & Kouki, 2005; Komonen, 2008). That the movement of adults of *Bolitophagus cornutus* (Panzer) across super-patches (logs) is restricted was confirmed by a mark-and-recapture study (Heatwole & Heatwole, 1968). The frequent short-distance movements and infrequent long-distance dis-

persal of adults of *B. reticulatus* (L.) occur in only a few weeks in summer (Jonsell et al., 2003).

Current evidence indicates that in ephemeral mushroom systems, spatial mechanisms play a crucial role, whereas there is no evidence for niche partitioning. In contrast, in bracket fungi, resource partitioning and successional niche partitioning occur, whereas spatial mechanisms have not been studied. Remarkably, the evidence for interspecific competition, as a prerequisite for examining coexistence mechanisms, has not been assessed by previous authors. Evidence for interspecific competition can be sought at two different levels: strong evidence in terms of mortality induced by resource depletion and/or weak evidence in terms of a decrease in body size of emergent adults and the resultant decrease in fecundity (Hanski, 1989). One basic test would be to search for the relationship between species richness and biomass of insects at the patch scale. In the absence of interspecific competition, patch-level total insect biomass would linearly increase with increase in insect species richness. In contrast, if there is interspecific competition then the relationship would be unimodal with the patch-level biomass peaking at a certain level of species richness due to resource depletion (Abrams, 1988).

If the presence of interspecific competition is supported, then two potential coexistence mechanisms are examined. In the presence of successional niche partitioning, species respond differently to the different developmental stages of a sporocarp. One can test this by comparing models that explain patch-level insect species abundance with and without an interaction between insect species and the developmental stages of a sporocarp. The aggregation model of coexistence developed by Sevenster (1996) has been used to quantify the effects of spatial mechanisms (Toda et al., 1999; Wertheim et al., 2000; Takahashi et al., 2005b). This model assumes that the stability of the coexistence depends on the relative intensity of intraspecific and interspecific competition in different sized patches. Characteristically, sporocarps of bracket fungi occur solitarily on host trees, and constitute a spatial hierarchy of a patch (sporocarp) and super-patch (host tree) (following the terminology of Inouye, 1999). In the aggregation model, however, explanations for a spatially aggregated distribution do not distinguish between patch and super-patch level aggregation, yet these two spatial aggregations may involve quite different processes: larval (or egg) aggregation at the patch level and/or restricted movements of adults at the super-patch level. Therefore, it remains uncertain whether coexistence depends on aggregation at the patch or super-patch level.

In the present paper the coexistence patterns of mycophagous insects inhabiting the wood-decaying bracket fungus *Cryptoporus volvatus* (Peck) Shear are reported. *C. volvatus* is a suitable fungus for studies on the species coexistence patterns of mycophagous insects, because (1) it produces sporocarps each year (Harrington, 1980), which (2) are inhabited by a diverse insect community (Sestuda, 1993, 1995) and (3) the sporocarps are arranged in a spatial hierarchy (i.e., patch and super-patches) in

TABLE 1. Summary of the studies on insect communities inhabiting fungi, plus some of those associated with rotten fruit. Supporting evidence is shown in bold. This list is not exhaustive and includes indirect evidence or studies with useful implications, which are in square brackets. For definitions of resource portioning, successional niche portioning and feeding mode see text.

	Ephemeral mushrooms	Persistent bracket fungi
Evidence for competition	**Yes, e.g. Atkinson & Shorrocks (1981); Gilpin et al. (1986); Takahashi & Kimura (2005)**	?
Niche partitioning		
resource partitioning	Jaenike (1978); **Grimaldi (1985); Toda et al. (1999);** Wertheim et al. (2000); Yamashita & Hijii (2007)	**Lawrence (1973); Orledge & Reynolds (2005)**
successional niche	**Yamashita & Hijii (2007)**	**Guevara et al. (2000);** [Thunes et al. (2000); Jonsell & Nordlander (2004)]
feeding mode	**Hackman & Meinander (1979)**	**Matthewman & Pielou (1971)**
Spatial mechanisms		
patch-level aggregation	**Toda et al. (1999); Wertheim et al. (2000); Takahashi et al. (2005b)**	[Komonen (2003a)]
super-patch-level aggregation	**Inouye (1999); Krijger & Sevenster (2001)**	[Heatwole & Heatwole (1968); Rukke & Midtgaard (1998); Jonsell et al. (1999)]
spatial heterogeneity in sporocarp size	**Toda et al. (1999)**	None

forests. Sporocarps of *C. volvatus* persist for nearly three or four months from early spring to summer (Setsuda, 1995). Such temporal persistence of *C. volvatus* sporocarps may occupy an intermediate position in the continuum between ephemeral mushrooms and persistent bracket fungi. I first test for the occurrence of interspecific competition among the mycophagous insects inhabiting *C. volvatus* by examining the correlation between insect biomass and species richness at the patch-level. To test for successional niche partitioning, I determined whether mycophagous insect species increase in population density differently in different developmental stages of the sporocarps. The hypothesis that patch level spatial aggregation results in stable coexistence in the *C. volvatus* system was also tested. Lastly, the effect that super-patch level aggregation and it in combination with patch level aggregation have on the stability of coexistence were studied in a simulation model, which incorporated a data-driven statistical approach based on the results of the field study.

MATERIAL AND METHODS

Study system

The wood-decaying annual polypore *Cryptoporus volvatus* (Peck) Shear (Polyporaceae: Basidiomycota) in temperate forests in central Japan is inhabited by a species-rich insect community (Sestuda, 1993, 1995). The sporocarp of *C. volvatus* is morphologically distinct from that of other Polyporaceae. It has a subtending volva (volvoperidium), which encloses the hymenophore during early development. As the sporocarp matures a single elliptical ostiole develops at the base of the volva (Harrington, 1980; Gilbertson & Ryvarden, 1986). From early spring to summer, many sporocarps develop solitarily from bore holes made by bark beetles (Scotylidae) in the host tree of the fungus (Harrington, 1980). The Japanese red pine, *Pinus densiflora* Siebold & Zucc., is the only host in the study area and *C. volvatus* can only be found growing on recently dead, standing pine trees, mostly infested by the pine wilt dis-

ease nematode, *Bursaphelenchus xylophilus* (Steiner & Buhrer) Nickle. In Japan, the colonization of *C. volvatus* by mycophagous beetles is synchronized with the initiation of sporulation (Setsuda, 1995). The adults of *Parabolitophagus felix* Lewis and *Ischnodactylus loripes* Lewis (Tenebrionidae) breed inside the volval chambers and their larvae fed on the tissues of *C. volvatus* (Setsuda, 1995).

Study area

The study was carried out at two sites, Location A (Higashi- and Kita-yama area, 35°00–02′N, 135°48–49′E and 35°05–07′N, 135°45–49′E) and Location B (Nishi-yama area, 35°02–04′N, 135°36–39′E and 35°08′N, 135°31′E) in the suburbs of Kyoto, central Japan. These two sites are separated by at least 10 km and are different parts of a continuous secondary forest. At these locations there were old-growth pine trees, which were assumed to have a sufficiently high density of *C. volvatus* sporocarps for determining the composition and seasonal development of the local insect community inhabiting the sporocarps. A total of 62 trees were recorded (28 in Location A and 34 in Location B), with an average of 44.7 sporocarps ± 5.9 SE and a range of from 4 to 151 sporocarps per tree. Distances between trees were not recorded but were more than 10 m. The dominant forest type is a mixture of Japanese red pine, *Pinus densiflora*, and broadleaved deciduous oaks, *Quercus* spp., with patchy matrices of Japanese cedar, *Cryptomeria japonica* (L.f.) D.Don. Other common shrub species include *Castanopsis sieboldii* (Makino) Hatus., *Castanea crenata* Siebold & Zucc., *Ilex* spp. and *Acer* spp.

Sampling design

The field survey included three levels of spatial organization: (a) patch (a sporocarp), (b) super-patch (clumps of sporocarps on a dead tree) and (c) location. Every two weeks from mid-May to mid-July 2005 (total of seven samples), four trees were selected at each location (eight trees in total) and at least eight sporocarps growing at between 0 and 2.0 m were collected from each tree. In those cases where there were fewer than eight sporocarps, all the sporocarps were collected and another tree chosen for additional sampling of eight sporocarps. A total of 438 sporocarps (patches) were collected over the entire period. Data were pooled across locations by treating the total for each

location as a local community. Based on the results of Setsuda (1995) and a preliminary survey in 2004, the sampling period was set for mid-May to mid-July in order to include most of the seasonal variation in the mycophagous community.

Rearing

Sporocarps were individually wrapped in a piece of paper towel and brought back to the laboratory. Two measurements were recorded for each sporocarp: carrying capacity, which was estimated by cubing the width of each sporocarp (mm^3); the average width of the sporocarps was 2.83 cm ($\pm$ 1.7 SD). The developmental stage of each sporocarp was recorded using the four categories proposed by Setsuda (1995): (A) immature, (B) mature, (C) old and (D) very old. Stage A is the growing stage, when the sporocarps are fresh and immature and the hymenophore is covered by the volva. Stage B is the mature stage, when the sporocarp has an ostiole and emits a strong citrus-like odour. At Stage C the sporocarps start to decay and smell less than at Stage B, and at Stage D they are infested by mould or destroyed by mycophagous insect.

In order to obtain adults for identification all the insect larvae inhabiting each sporocarp were reared together in a plastic container (25 cm in diameter, 340 mL) containing a piece of paper towel, at 25°C and a photoperiod of 16L : 8D. To maintain an appropriate level of moisture in the containers, several small holes were made in the lid of each container and the sporocarps were sprayed with water every other day. Based on the results of the preliminary survey in 2004, the larvae of the three large-bodied species (>0.8 cm in body length) [*Amorophaga japonica*, Robinson (Tineidae), *Parabolitophagus felix* (Tenebrionidae) and *Ischnodactylus loripes*) (Tenebrionidae)] were easy to identify, so only the number of larvae of these three species were counted by carefully halving sporocarps. The other insect species were quantified by recording the number of adults of each species that emerged and were identified to species. The present study focused on the larvae feeding on the tissues of the sporocarp because it is during the sessile larval stage that competitive interactions are expected to occur. Other opportunistic visitors (e.g. detritivores, or predatory insects) were not documented. Note that this rearing method is not suitable for some Diptera, such as Cecidomyiidae or Mycetophildae, which pupate in the soil, but suitable for most Coleoptera and Lepidoptera, which pupate within a sporocarp.

Statistical analysis

Population-level analysis

The population-level analysis explored what kind of factors can affect the number of individuals (species abundance) at the patch level. The factors considered were (a) sporocarp size, (b) developmental stage of sporocarp and (c) insect species. Only the four dominant species present over the whole sampling season were included in this study: *Amorophaga japonica Parabolitophagus felix*, *Ischnodactylus loripes*, and *Dorcatoma polypori* N. Hayashi (Anobiidae). The developmental stages of the sporocarps were converted into an ordinal variable (integers of from 1 to 4 for the developmental stages A–D). Beforehand, the correlations between sporocarp size, developmental stage and seasonality were checked: sporocarp development ceased at various sporocarp sizes (Kendall's correlation $\tau = 0.039$, $z = 1.06$, $P = 0.288$, n.s.) and is not correlated with seasonality (Kendall's correlation $\tau = 0.023$, $z = 0.671$, $P = 0.502$, n.s.). Because developmental stage reflected seasonality (Kendall's correlation $\tau = 0.385$, $z = 9.81$, $P < 0.001$) the latter was not incorporated into the model as it was already present in terms of the developmental stages of the sporocarps.

The distributions of insect abundance variables were highly skewed and included many zeros, therefore traditional analyses, which assume normality of errors, were inapplicable. The significance of the empty patches (or zero patches) is discussed in recent papers on mycophagous insect communities (e.g. Takahashi et al., 2005a) because classifying zero patches as either inhospitable or opportunistically empty can greatly affect estimates of spatial distribution and co-occurrence. One way of coping with zero-inflation and overdispersion is to compare the results of the analysis of the original dataset and that of the dataset excluding the zero patches (Takahashi et al., 2005a). Here, instead of excluding zero patches, a mixture model was used to accomodate zero-inflation and overdispersion.

The zero-inflated generalized Poisson model (hereafter, ZIGP) not only extends the Poisson generalized linear models to include zero-inflation and overdispersion, but also allows for regression on these parameters (Czado et al., 2007). Explanatory variables were designated by their mean, overdispersion and zero-inflation. Two working models were constructed. Model 1 and Model 2 differed in whether they took into account successional niche partitioning or not in explaining species abundance patterns. For Model 1, the mean matrix was modelled using three factors: sporocarp size (continuous variable), developmental stage (ordinal variable 1–4) and insect species (categorical, four levels). The overdispersion matrix included an insect species variable that expressed the different levels of overdispersion among the four species. The zero-inflation matrix contained a 1/0 variable, representing either the developmental stage A or not, given that the absence of insects (zero patches) might be due to inhospitable sporocarps. In contrast, Model 2 additionally included a term for the interaction between the developmental stage of a sporocarp and insect species, which represents the preference of the different insects for different developmental stages of sporocarps. A baseline constraint was set to *A. japonica* in both models. The most parsimonious model in terms of Akaike's Information Criterion (AIC) was selected from these two models.

Community-level analysis

(1) Evidence for patch-level competition: The unimodal relationship between species richness and biomass of the insect community was graphically assessed. The total patch-level insect biomass was calculated as the sum of the body mass (cube of body size, mm^3) of each insect species multiplied by the abundance of that species (Table 2). The body sizes of 10 randomly selected individuals, or all of the individuals when less than 10 adults emerged, were measured to the nearest 0.1 mm using calipers.

(2) Impact of spatial aggregation on competitive coexistence: The "aggregation model of coexistence" (Sevenster, 1996) was used to quantify three measures of spatial distribution: intraspecific aggregation (J), association between species (C_{xy}) and the relative effect of competitor aggregation (T_{xy}). The strength of intraspecific aggregation was measured by J, which takes into account differences in patch size:

$$J = \left\{ \frac{\sum e_i}{N^2} \cdot \sum \frac{n_i(n_i-1)}{e_i} \right\} - 1 \qquad (1)$$

where N is the total number of individuals, n_i is the number of adult individuals in patch i, e_i is the size of the patch measured by cubing sporocarp breadth (mm^3). Positive values of J indicate an aggregated distribution, negative values a uniform distribution and zero a random distribution. The interspecific association C_{xy} indicates the proportional increase in the average density of heterospecific competitors over that indicated by the Poisson distribution:

$$C_{xy} = \left\{ \frac{\sum e_i}{N_x N_y} \cdot \sum \frac{n_{xi} n_{yi}}{e_i} \right\} - 1 \qquad (2)$$

where subscripts x and y indicate species. N_x and N_y indicate total number of individuals of species x and y, respectively. The values of C_{xy}, ranging from minus unity to infinity, indicate whether competitive species co-occur in patches more or less frequently than expected if the distribution between patches is random. Combining J and C_{xy}, the relative effect of competitor aggregation (Sevenster, 1996) can be shown:

$$T_{xy} = \frac{1 + C_{xy}}{1 + J_y} \qquad (3)$$

$T_{xy} < 1$ is a necessary and sufficient condition for the persistence of species x in the presence of species y. Following previous studies (Wertheim et al., 2000; Krijger & Sevenster, 2001; Takahashi et al., 2005b), the "super-species approach" was adopted, where, relative to the focal species, clumping of the other competitors can simultaneously express multi-species competition, not pairwise competition (Sevenster, 1996). J, $C_{x,-x}$ and $T_{x,-x}$ were calculated for species x against all other species and indicated by subscript $-x$ (Krijger & Sevenster, 2001). Similarly a value of $T_{x,-x}$ of less than unity indicates stable population persistence of species x in the community.

$$T_{geom} = \exp\left[\frac{1}{S} \sum_{x=1}^{S} \log(T_{x,-x}) \right] \qquad (4)$$

The geometric mean of $T_{x,-x}$s, denoted by T_{geom}, indicates the stability index for the whole community. Since an aggregation model was available for snapshot datasets, the whole dataset was conventionally divided into three snapshot sections as follows: S1 mid-May to early-June; S2 early-June to late June; and S3 late-June to mid-July. Note that one sampling period in all three seasonal sections overlaps. The coexistence stability was calculated separately for each season. Zero patches were included in the analyses. While *Aphenpolia pseudosoronia* Reitter (Nitidulidae) is a spore-feeder (Setsuda, 1995), all the other species feed on the internal tissues of the fungus. For simplicity, the two different feeding habits were not distinguished. Two species, *Physoronia explanata* Reitter (Nitidulidae) and

Nemapogon sp. (Tineidae), of which only single specimens were recorded, were excluded from analysis because their coexistence stability could not be calculated.

(3) Spatial aggregation at two different spatial scales: The relative effect on coexistence of larval aggregation at the patch level versus restricted movements by adults at the super-patch level was evaluated by simulation. The original dataset was manipulated to generate species abundance matrices for varying combinations of fixed/random procedures at (a) the patch level and (b) super-patch level. Four types (R1–R4) of simulated matrices were created 500 times respectively, and for each simulation the coexistence criterion T_{geom} was computed. Four types of matrices (R1–R4) were generated as follows:

(R1) Completely random, with the total number of individuals fixed.

(R2) Patch-level aggregation fixed (only larval aggregation at the patch level).

(R3) Super-patch-level aggregation fixed (only limited movement of adults across super-patches).

(R4) Patch- and super-patch-level aggregations fixed (both larval aggregation at the patch level and limited movement of adults at the super-patch level).

In R1, the total number of individuals of each species was redistributed randomly to each patch. To generate such random matrices, each individual was randomly allocated to a habitat (patches and/or super-patches), instead of using the Poisson distribution. In R2, all the patch-level "cells" were swapped for each species, fixing the number of individuals over patches. Note that, in R2, the degree of super-patch-level aggregation can vary. In R3, the number of individuals per super-patch was randomized over super-patches for each species and the total number of individuals in each super-patch was then redistributed within each super-patch. The combined simulation, R4, shuffled patch-level cells only within each super-patch independently for each species. The simulations were conducted only for the four common species *A. japonica*, *P. felix*, *I. loripes* and *D. polypori*, as in the population-level analysis above. The

TABLE 2. Insects collected: taxonomy, body size (mm), abundance and patch occupancy by the mycophagous insects inhabiting the bracket fungus *Cryptoporus volvatus*. For convenience, each species is given a three-letter code (Abbr.). Patch occupancy is the number of patches occupied expressed as a percentage of the total number ($n = 438$) of patches over the period mid-May to mid-July 2005.

Order	Family	Species	Abbr.	Body size (mm)	Abundance	Occupancy (%)
Lepidoptera	Tineidae	*Amorophaga japonica* Robinson	AMO	10.11	207	77
		Nemapogon sp.	NEM	5.39	145	70
		Erechthiinae gen. sp.	ERE	10.02	33	24
Coleoptera	Cryptophagidae	*Cryptophagus enormis* Hisamatsu	CRY	3.59	457	72
	Nitidulidae	*Aphenolia pseudosoronia* Reitter	APH	5.97	60	28
	Tenebrionidae	*Parabolitophagus felix* Lewis	PAB	7.83	245	114
		Ischnodactylus loripes Lewis	ISC	7.96	595	86
		Platydema subfascia Walker	PSU	3.73	208	32
		Platydema recticorne Lewis	PRC	3.85	5	4
		Platydema pallidicole Lewis	PPA	3.08	3	2
	Anobiidae	*Dorcatoma polypori* N.Hayashi	DOR	1.87	5422	202
	Mycetophagidae	*Mycetophagus pustulotus* Reitter	MYP	3.59	115	32
		Mycetophagus antennatus Reitter	MYA	3.84	73	29
	Ciidae	*Neoennearthron bicarinatum* Miyatake	NET	1.54	1402	19
Diptera	Drosophilidae	*Mycodrosophila gratiosa* Okada	MCD	2.10	9	4
		Scaptodrosophila coracina Kikkawa et Peng	SCP	1.40	6	1
		Leucophenga atrinervis Okada	LEU	2.58	3	2

TABLE 3. Maximum likelihood estimates of zero-inflated generalized Poisson model parameters. Species codes: AMO = *Amorophaga japonica*; PAB = *Parabolitophagus felix*; ISC = *Ischnodactylus loripes*, DOR= *Dorcatoma polypori*; Developmental stages = the four development stages of a sporocarp.

Model 1

		Estimate	SE	Z	P
Intercept		0.627	0.215	2.912	<0.05
Species	AMO	0	0	0	
	PAB	0.0247	0.154	0.161	n.s.
	ISC	0.988	0.229	4.320	<0.001
	DOR	3.034	0.155	19.63	<0.001
Developmental stages		−0.2510	0.0678	−3.706	<0.001
Sporocarp size		0.0068	0.00082	8.298	<0.001
Overdispersion					
Species	AMO	0	0	0	
	PAB	−2.658	1.004	−2.636	<0.01
	ISC	1.221	0.2233	5.467	<0.001
	DOR	1.556	0.1200	12.97	<0.001
Zero-inflation					
Developmental stage	Immature	0.773	0.3799	2.034	<0.05
Log Likelihood		−2300.6			
Pearson Chi Squared		1412			
AIC		4621			

Model 2

Variable		Estimate	SE	Z	P
Intercept		2.434	0.559	4.378	<0.001
Species	AMO	0	0	0	
	PAB	−1.332	0.665	−2.000	<0.05
	ISC	−3.110	0.738	−4.212	<0.001
	DOR	0.968	0.595	1.627	n.s.
Developmental stages		−1.237	0.252	−4.903	<0.001
Dev × Species	AMO	0	0	0	
	PAB	0.676	0.298	2.277	<0.05
	ISC	1.778	0.300	5.928	<0.001
	DOR	1.058	0.266	3.974	<0.001
Sporocarp size		0.0079	0.00085	9.328	<0.001
Overdispersion					
Species	AMO	0	0	0	
	PAB	−1.285	0.317	−4.048	<0.001
	ISC	1.362	0.239	5.699	<0.001
	DOR	1.562	0.109	14.37	<0.001
Zero-inflation					
Developmental stage	Immature	1.890	0.308	6.138	<0.001
Log Likelihood		−2273.3			
Pearson Chi Squared		1555			
AIC		4573			

median test was used for significance testing. The sequential Bonferroni adjustment was applied before ascribing significance assuming an experimental error rate of $\alpha = 0.001$. The analyses were carried out separately in each section.

All the statistical analyses were done using R version 2.7.1 (R Development Core Team, 2008) and package ZIGP for developing zero-inflated models (Czado et al., 2007).

RESULTS

Overview

A total of 8990 individuals of 17 insect species, consisting of 11 species of Coleoptera ($n = 8586$ individuals), three species of Lepidoptera ($n = 386$), and three species of Diptera ($n = 18$) (Table 2), were reared from sporocarps between mid-May and mid-July 2005. The commonest and the most widespread species was *Dorcatoma polypori* ($n = 5422$), which peaked in abundance in mid-summer. Although *Neoennearthron bicarinatum* Miyatake was the second most abundant species ($n = 1402$), it peculiarly only occurred in a small number of patches. Three tenebrionid species, *Parabolitophagus felix*, *Ischnodactylus loripes* and *Platydema subfascia* Walker, were also moderately abundant, while the other *Platydema* species, *P. recticorne* Lewis and *P. pallidicole* Lewis, occurred infrequently. Two coleopteran species,
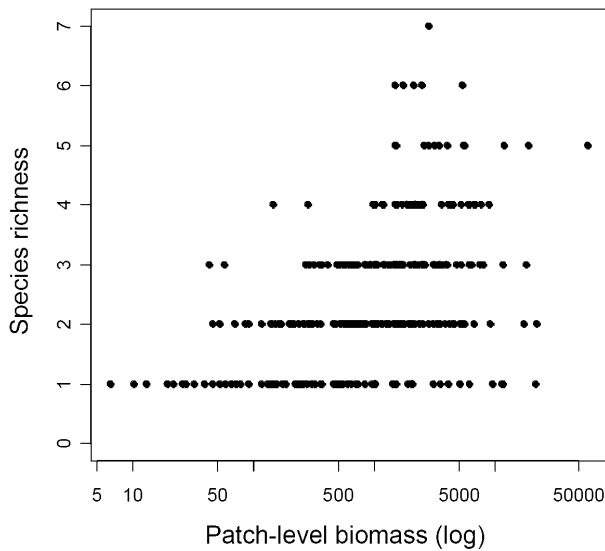
Fig. 1. Patch-level relationship between insect species richness and insect biomass. Patch-level biomass was estimated using the body size and abundance of the insects in each patch (see Table 2) and then logarithmically transformed.

Mycetophagus pustulotus Reitter and *M. antennatus* Reitter, belonging to the Mycetophagidae, were uncommon.

Population-level analysis

In a comparison of the performance of the two models in terms of AIC, Model 2 outperformed Model 1 (Table 3), supporting the hypothesis that successional niche partitioning plays a significant role in explaining spatial distribution at the patch level. For example, *A. japonica* tended to use younger sporocarps than *I. loripes* and *D. polypori*. The two models revealed four common patterns in the parameter estimates (Table 3). Large sporocarps contained more insects than small sporocarps and old sporocarps fewer insects than young sporocarps. Both models indicated that the different insect species showed different levels of over-dispersion at the patch level. *P. felix* was less over-dispersed than *A. japonica*, while the other two species (*I. loripes* and *D. polypori*) were more over-dispersed. Immature stages of sporocarps significantly contributed to zero-inflation in both models.

Community-level analysis

(1) Evidence for resource depletion and interspecific competition

The total biomass of the mycophagous insect community increased as the number of species increased at the patch level (Fig. 1). In contrast, when the biovolume reached ca. 1000–5000 mm^3 species richness rapidly declined. Accordingly, the relationship between patch-level species richness and biovolume exhibited a unimodal relationship, suggesting the potential for interspecific competition.

(2) Stability of populations predicted by the aggregation model

The aggregation model of coexistence satisfactorily predicted the stable coexistence of the species in the mycophagous insect community and indicated that the coexistence was facilitated by spatial aggregation. The community-level stability was consistently very stable

TABLE 4. Characterization of the stability of coexistence of the species inhabiting the bracket fungus *Cryptoporus volvatus*. Population persistence $T_{x,-x}$ and abundance are shown for all the community members, and the values of T_{geom} for each section at the bottom of the table. The three-letter codes for the species are those listed in Table 2. Note that species occurred at different times during the year so the number of species differed between seasons.

| Category	Late spring			Early summer			Mid-summer		
	Species	n	$T_{x,-x}$	Species	n	$T_{x,-x}$	Species	n	$T_{x,-x}$
Very stable	CRY	433	0.047	DOR	3921	0.11	DOR	3032	0.12
(0.00–0.40)	ISC	189	0.29	ISC	267	0.27	ISC	283	0.33
	PAB	159	0.14	PAB	108	0.25	PSU	152	0.18
	AMO	104	0.14	AMO	88	0.13	AMO	96	0.078
	APH	60	0.11	PSU	61	0.27	PAB	55	0.40
				MYA	58	0.40	CRY	24	0.0056
				CRY	19	0.011	MCD	9	0.023
				APH	12	0.051	SCP	6	0.022
							PRC	5	0.064
							LEU	3	0.049
Moderadely stable	DOR	1186	0.45	NET	1368	0.51	NET	1164	0.56
(0.40–0.80)	PSU	29	0.50	NEM	115	0.57	MYP	86	0.66
	ERE	10	0.62	ERE	26	0.51	NEM	71	0.57
							MYA	51	0.44
							ERE	21	0.64
							PPA	3	0.57
Marginally stable	NEM	24	0.81	MYP	56	0.88			
(0.80–1.00)	MYP	18	0.91						
Unstable (>1.00)	NET	149	1.62						
Community-level stability T_{geom}			0.33			0.21			0.15
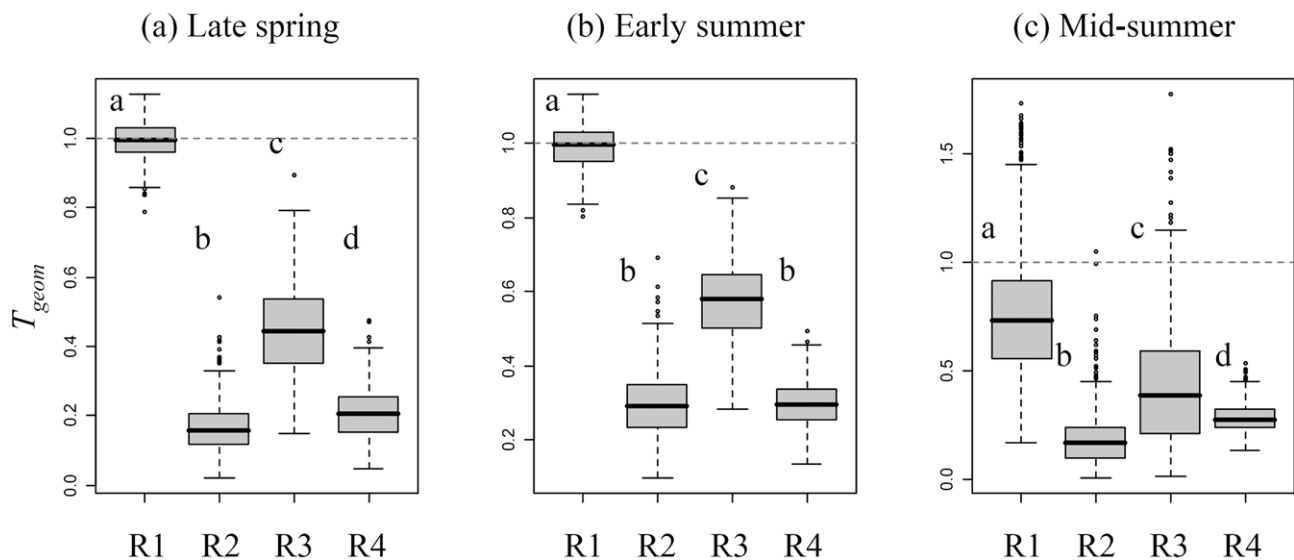
Fig. 2. Relative effects of patch-level and super-patch-level aggregation on the coexistence of four species of insects in each season. Geometric mean of coexistence stability, T_{geom} (A–C) for *Amorophaga japonica* (AMO), *Parabolitophagus felix* (PAB), *Ischnodactylus loripes* (ISC) and *Dorcatoma polypori* (DOR). Within each season, T_{geom} was computed 500 times and compared among four types of simulated species abundance matrices (R1–R4): R1 – completely random; R2 – patch-level aggregation; R3 – super-patch-level aggregation; R4 – both patch-level and super-patch-level aggregation. The horizontal dashed lines indicate thresholds of community-level extinction; if larger than unity (1.00), more than half of community membership was competitively excluded. Different letters indicate a significant difference using multiple comparisons and a sequential Bonferroni-adjusted error rate (experimental error $\alpha = 0.001$).

(0.15–0.35) (Table 4.). Overall, the populations of the specialist insects inhabiting *C. volvatus* tended to remain very stable or moderately stable over long periods of time, while those of some of the generalists, such as *Neoennearthron bicarinatum* and *Mycetophagus pustulotus,* were not. Community membership is classified under one of four categories of population persistence, T_{geom}, in Table 4.

(3) Multi-scale spatial aggregation

The four types of simulation differed in their predicted stability of coexistence (Fig. 2). The rank order from more to less stable is R2 > R4 >> R3 >> R1 for late spring to early summer, and R2 > R4 > R3 > R1 in midsummer. Every combination of the simulations (R1–R4) differed significantly ($P < 0.001$), except that between R2 and R4 in early summer ($P = 0.303$) (Fig. 2b).

Spatial aggregation at both patch and super-patch level enhanced coexistence, but their separate effects on coexistence were not consistent. From late spring to midsummer, super-patch level aggregation alone can account for stable coexistence. In contrast, in late summer, spatial aggregation at the patch level was the necessary condition for coexistence. The combined effects of patch- and super-patch-level aggregation did not result in greater stability.

DISCUSSION

The *Cryptoporus*–insect community was characterized by a high proportion of Coleoptera in terms of species richness, abundance and biomass. This predominance of Coleoptera is reported to occur in northern Europe

(Thunes et al., 2000; Komonen, 2001, 2003a), North-east China (Komonen et al., 2003), the United Kingdom (Paviour-Smith, 1960) and Canada (Pielou & Verma, 1968). This pattern might be a general one for bracket fungi, irrespective of the longevity of the sporocarps (e.g. annual or perennial). We confirmed the occurrence of the previously recorded monophagous species: *Aphenolia pseudosoronia, Dorcatoma polypori, Cryptophagus enormis* (Setsuda, 1993). Interestingly, these have counterparts in North America, for example, *Aphenolia monogama* (Crotch) (Nitidulidae), *Cryptophagus maximus* Blake (Cryptophagidae) and also a fungus moth, *Morophaga cryptophori* Clarke (Tineidae) (Lawrence, 1973). This supports the proposal of Komonen et al. (2003) that the taxonomic composition of mycophagous insect communities across boreal Eurasia is very similar.

At the patch level, the increase in insect biomass was possibly associated with the accumulation of insects at patches with a low species richness. This is the commonly proposed explanation for why more productive patches tend to include more individuals (Abrams, 1988) and consequently more species. In contrast, the decrease in biomass at species-rich patches means that a few species dominated at those patches with a disproportionately high biomass. As formulated by Abrams (1988), a unimodal relationship can constitute evidence for resource depletion and the potential importance of interspecific competition at the patch level. This is consistent with the observation that the sporocarps kept in the laboratory were often completely destroyed by the larvae when the adults emerged. However, such unimodal relationships can also result from successional change in the insect

community; if species prefer different developmental stages of sporocarps but overlap in time, then the mid-developmental stages of sporocarps may harbour the highest species richness. The weak correlation between size and the developmental stage of *C. volvatus* sporocarps indicates they stop growing at different sizes. If it is assumed that the successional change in the insect community is related to the developmental stage of sporocarps, then it is unlikely that the successional change in the insect community alone can create a uni-modal pattern. However, the results of this study do not exclude this possibility because it was impossible to disentangle two confounding factors, mortality due to resource depletion and emigration of freshly emerged adults. It should be noted that these two explanations differ in the time scale of the interspecific competition; resource depletion involves contemporary forces of inter-specific competition, whereas successional niche parti-tioning involves a "ghost of competition past" (Connell, 1980), which is a consequence of the former. Experi-mental studies are needed to rigorously test whether con-temporary forces of interspecific competition are important in structuring this insect community.

Large sporocarps are inhabited by more insect species than small sporocarps. This simply involves an accumula-tion of individuals that results from the increase in the number of eggs laid by females and/or the number of visits by ovipositing females (Hartley & Shorrocks, 2002). There was a decrease in the number of individuals in sporocarps in the late stages of development, either due to high mortality associated with the deterioration in the food supply for the mycophagous insects, and/or emigra-tion of the freshly emerged adults. Previous studies docu-ment an increase in the number of ciid beetles infesting the later developmental stages (e.g. Thunes et al., 2000), which did not occur at our study site. This is possibly because ciid beetles typically complete several genera-tions in the same sporocarp of perennial polypores, but not in those of annual polypores. The four specialist spe-cies showed different levels of overdispersion at the patch level, which may reflect different patch-selection behav-iour or mobility of the species. For example, adults of the two tenebrionid species walk to nearby sporocarps, while those of *D. polypori* often fly between sporocarps in the evenings (K. Kadowaki, unpublished).

The fact that Model 2 outperformed Model 1 supports successional niche partitioning. *A. japonica* tended to inhabit younger sporocarps than the other beetle species. Field observations indicate one plausible mechanism, the two tenebrionid species, *P. felix* and *I. loripes*, use the volval chambers of *C. volvatus* sporocarps as breeding sites (Setsuda, 1995), whereas *A. japonica* and *D. poly-pori* do not. In fact, the tenebrionids mate in the volval chambers of mature sporocarps and lay their eggs on the hymenophore (Kadowaki, in press). Thus, the morpho-logical development of *C. volvatus* sporocarps might partly result in successional niche partitioning. As dis-cussed by Wertheim et al. (2000), successional niche par-titioning can quantitatively reduce the intensity of competitive interaction but not to the level achieved by resource partitioning. The results indicate that succes-sional niche partitioning affected the direction of the competitive interaction, but did not result in coexistence.

The aggregation model of coexistence accurately pre-dicted the stable coexistence of the mycophagous insects. The populations of the specialist species in this commu-nity (Setsuda, 1995) persisted over long periods of time whereas those of the polyphagous species did not. This is not surprising because generalists feed on several species of fungi in addition to *C. volvatus*, or perhaps need to utilize them because *C. volvatus* alone could not support a generalist species. This is circumstantial evidence sup-ports resource partitioning operating across *C. volvatus* and other polypore species. Specialist and generalist neo-tropical *Drosophila* inhabiting fallen fruit show a similar pattern (Sevenster & Van Alphen, 1996).

The simulations indicated that not only patch-level larval aggregation but also the restricted movements of adults at the super-patch level facilitate coexistence. Remarkably, the restricted movements of adults can on its own account for the competitive coexistence in this mycophagous insect community. This implies that the restricted movements of adults at the super-patch level might be more important than the aggregation of larvae at the patch-level, although many studies on competitive coexistence do not include multiple spatial scales in the investigation (e.g. Toda et al., 1999; Wertheim et al., 2000). Empirical studies have demonstrated that restricted movements occur at much larger scales than a patch, but at a smaller scale than limitation by dispersal (Heatwole & Heatwole, 1968; Rukke & Midtgaard, 1998; Jonsell et al., 2003). Although the combined effect of patch- and super-patch-level aggregation did not increase stability, certain super-patches attracted more individuals and con-sequently more species of insects. This might be related to a difference in super-patch sizes (i.e., the total number of sporocarps per super-patch), or the number of years during which *C. volvatus* produced sporocarps on the same tree.

The aggregation model of coexistence provides an explanation of how the observed spatial aggregation greatly contributes to species coexistence, but unfortu-nately does not answer why insects are spatially aggre-gated. Van Teeffelen & Ovaskainen (2007) provide a practical means of identifying the many reasons for spa-tial aggregation, e.g. endogeneous factors (dispersal or pure spatial effects) versus exogenous factors (correlated environmental factors), by comparing the diagnostics indicated by three models. The causal mechanisms resulting in interspecific aggregation may be closely related to microhabitat preferences for specific types of resource and therefore niche partitioning. For example, Komonen (2003a) conjectured that the interspecific aggregation of two congeneric ciid beetles is determined by their preference for sporocarps of similar quality. Hence, spatial aggregation is not purely "spatial" aggre-gation, but is relevant to disentangling the effects of two

coexistence mechanisms, niche partitioning and purely spatial mechanisms.

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