



Title	Functional spatial scale of community composition change in response to windthrow disturbance in a deciduous temperate forest
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1 Title:

2 **Functional spatial scale of community composition change in response to**
3 **windthrow disturbance in a deciduous temperate forest**

4

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1 **Abstract** Community dynamics in local habitats are affected by landscape characteristics
2 such as the area and connectivity of surrounding habitats at a functional spatial scale
3 where the community responds to landscape structure. However, the functional spatial
4 scale at which community composition is affected by landscape structure has never been
5 explored. We assessed the functional spatial scales of composition change in birds and in
6 three types of arthropod communities (canopy, forest-floor and flying ones) with regard
7 to landscape heterogeneity resulting from a large typhoon in a temperate forest of Japan.
8 We examined the effects of tree-fall disturbance on the communities at various spatial
9 scales, with special attention to compositional evenness. The spatial scale of the
10 best-fitting model, which was selected from models fitted to the disturbance area at
11 stepwise spatial scales, was interpreted as the community-specific functional spatial scale.
12 The composition of all communities studied was all significantly dependent on gap area.
13 The functional spatial scale was highest in birds (370 m in radius), intermediate in flying
14 arthropods (90 m) and lowest in canopy and forest-floor arthropods (10 m). This result
15 may reflect typical dispersal ability and the spatial range of resource use in the
16 community. Compositional changes in each community were consistent with theory
17 regarding traits and responses of component taxa, although the enhancement of evenness
18 was observed only in the arthropod communities. These results imply that management
19 and reserve selection based on functional spatial scales can be effective in the
20 conservation of biodiversity and ecosystem services at the community level.

21

22 **Keywords** Arthropod communities, Bird community, Environmental heterogeneity,
23 Scale dependence, Tree-fall gap

1 **Introduction**

2

3 Most ecological processes such as population and community dynamics observed in a
4 local patch depend not only on the patch characteristics, but also on the characteristics of
5 the surrounding landscape (Wiens et al. 1993; Gustafson 1998; Turner et al. 2001).
6 Because organisms use various cues to locate favorable habitats and differ in dispersal
7 ability (Holt 1996), landscape characteristics such as the area, spatial arrangement, and
8 connectivity of habitats potentially affects local species abundance, biotic interactions,
9 and thus, community structure at specific spatial scales (Kareiva and Wennergren 1995;
10 Pickett and Cadenasso 1995; Roland and Taylor 1997). This specific scale can act as the
11 “functional spatial scale” (Thies et al. 2003, 2005) or “characteristic scale” (Holland et al.
12 2004) at which organisms respond to heterogeneity in a landscape.

13 Disturbances such as fire and grazing in grasslands (e.g., Joern 2005) and
14 flooding in streams (e.g., Parsons et al. 2005) are the principal factors creating and
15 maintaining spatial heterogeneity in a landscape, i.e., landscape patchiness. In forest
16 ecosystems, windthrow disturbance is one of the major agents generating a mosaic of
17 heterogeneous habitat patches at various spatial scales (Sinton et al. 2000; Kramer et al.
18 2001, 2004). Canopy gaps caused by windthrow disturbance can occur in a variety of
19 sizes, from single fallen trees to large-scale blowdowns (Schowalter and Ganio 1999;
20 Fuller 2000). The distributions of birds and arthropods, which are major components of
21 forest ecosystems, are strongly regulated by forest gaps (Schowalter and Ganio 1999;
22 Fuller 2000). A single fallen tree can create a favored nest site for some ground-nesting
23 birds, but degrade habitat for some canopy arthropods; a gap created by multiple fallen
24 trees can serve as a rich foraging patch for some grassland birds and as a desired habitat

1 patch for some grassland arthropods. Furthermore, arthropods respond to a more
2 fine-grained world than birds in general. For example, some herbivorous insects have
3 specific host-plant foliage, and the distributions of parasitic insects can be strongly
4 regulated by the distributions of their hosts (Esch et al. 2005). Thus, forest gaps should
5 have a scale-dependent effect on birds and arthropods because they have different
6 responses to grain size and environmental heterogeneity. Therefore, the functional spatial
7 scales at which organisms respond to habitat structure may vary among communities.

8 The functional spatial scale can be regarded as an emergent property
9 characterizing a population or community by the synergistic effects of dispersal ability,
10 spatial resource use, and so on; such effects are determined by the distinct relationships
11 between organisms and environmental parameters (Mitchell et al. 2001). Therefore, the
12 concept of functional spatial scale can provide valid spatial perspectives for conservation
13 planning for species and their biotic interactions (Tscharntke et al. 2005). In
14 agroecosystems, the concept of functional spatial scale at the population level offers
15 beneficial information for conservation practices in plant–pollinator systems
16 (Steffan-Dewenter et al. 2002) and in host–parasitoid systems related to biological
17 control (Thies et al. 2003, 2005). However, especially in the preservation of biodiversity
18 and ecosystem function, conservation planning and decision making at the community
19 level are frequently required (Schwartz 1999; Schwartz et al. 2000; Srivastava and
20 Vellend 2005). Tscharntke et al. (2005) pointed out the limitations of approaches
21 focusing solely on a particular target species. In reality, it is not desirable to restrict
22 management to preserve one species or one type of interaction because negative effects of
23 disturbances may be ongoing, even if the loss of one or few species is not immediately
24 visible (Tscharntke et al. 2005). Given these limitations, analyzing community

1 composition change in response to landscape context and then defining functional spatial
2 scales at the community level can be a promising approach for incorporating
3 considerations of spatial scale in the establishment of reserves and the development of
4 ecosystem management plans. Although a few empirical studies (e.g., Steffan-Dewenter
5 et al. 2002) have evaluated the functional spatial scale by examining species richness in
6 landscapes, the functional spatial scale with regard to community compositional change
7 has never been addressed.

8 Therefore, we analyzed the variation in species composition of a bird
9 community and that in taxonomic order composition of three arthropod communities, i.e.,
10 canopy, forest-floor, and flying arthropods, in a northern deciduous forest to evaluate the
11 scale-dependent effects of windthrow disturbance. The influence of the landscape
12 characteristic gap proportion (percentage) on these communities was sequentially
13 examined across multiple spatial scales to search for functional spatial scales at the
14 community level (following Wiegand et al. 1999; Holland et al. 2004). First, we
15 evaluated the hypothesis that the functional spatial scale experienced by the bird and
16 arthropod communities depends on the ecological traits characterizing focal communities
17 (see Holt 1996). We then tested the response of community composition to heterogeneity
18 in forest gaps at different functional spatial scales. Finally, we evaluated community
19 composition changes caused by the spatial heterogeneity of tree-fall gaps in light of the
20 changes in relative abundance of each species within communities (see Tokeshi 1999).

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22

23 **Methods**

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1 Study site

2

3 The study was conducted in a temperate deciduous forest of the Tomakomai
4 Experimental Forest (TOEF; 42°43' N, 141°36' E; ca. 90 m a.s.l.), Hokkaido, Japan. This
5 cool-temperate forest received 1161 mm of precipitation annually and had an average
6 annual temperature of 5.6°C. Oak (*Quercus crispula*), maple (*Acer mono*), and linden
7 (*Tilia japonica*) dominated the forest. The canopy ranged from 15 to 25 m in height, and
8 saplings of the dominant tree species grew on the forest floor. Deciduous trees broke bud
9 in early to mid-May and shed leaves in late October.

10 On 8 September 2004, a destructive typhoon, No. 18 ("Songda"), hit Hokkaido
11 Island, Japan, causing widespread damage to trees. Aerial surveys conducted in the TOEF
12 showed the creation of many canopy gaps 10–100 m in diameter (Fig. 1). TOEF is evenly
13 divided into natural forests, secondary ones and artificial ones. Before the typhoon, gap
14 rate in a permanent plot established in the natural forests was reported as 13.3% (Hiura et
15 al. 1998), and therefore whole gap rate in TOEF can be roughly estimated at 4.4%,
16 assuming that there were few gaps in secondary forests and artificial ones. Because
17 typhoon events at this scale are rare, and occur in TOEF only once or twice a century, the
18 2004 typhoon provided a unique opportunity to examine the effects of typhoon damage
19 on forest ecosystems and wildlife communities.

20

21 Quantifying windthrow disturbance

22

23 A remote-sensing vegetation index was used to assess the magnitude of windthrow
24 disturbance in the study area. The normalized difference vegetation index (NDVI) is a

1 measure of greenness, calculated from the reflectance of the near-infrared and red
2 portions of the electromagnetic spectrum (Pettorelli et al. 2005). This index is positively
3 correlated with total green biomass (but see Pettorelli et al. 2005). We used aerial
4 photographs taken on 20–22 September 2004, just after the typhoon but before leaf fall, to
5 calculate the NDVI/m². Apart from the calculation of NDVI, the total gap area within the
6 TOEF was approximately estimated at 20% using parts of optical-wavelength aerial
7 photographs. The 20% quantile in the distribution of calculated NDVIs was defined as the
8 threshold for the gap band, i.e., unit cells with NDVI less than the threshold were
9 regarded as gaps. For the survey of birds and arthropods, 32 observation points were
10 chosen along the whole gradient of disturbance rate assessed using NDVI (Fig. 1a) for
11 secondary broad-leaved forests in the TOEF.

12 To determine the functional spatial scale for bird and arthropod communities,
13 the effects of windthrow disturbance on the taxonomic composition of each community
14 were analyzed at nested spatial scales (Fig. 1b). The disturbance rate was calculated as the
15 percentage of gap area within a given radius, which was increased by 10 m from 10 to 500
16 m from the center of each survey plot. The disturbance rate around each point varied
17 greatly at relatively small spatial scales, ranging from approximately 0 to 80% among
18 radii from 10 to 100 m, which corresponded to gap sizes in the forest. When radii reached
19 500 m, the disturbance rate progressively converged to approximately 20%, which
20 corresponded to the average disturbance rate within the forest (Fig. 2). Calculations
21 quantifying windthrow disturbance were performed using the Geographical Information
22 System software Arc GIS 9.0 (Environmental System Research Institute, Redlands,
23 California, USA, 2004) and ERDAS Imagine8.7 (Leica Geosystems GIS & Mapping,
24 Atlanta, Georgia, USA, 2004).

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Bird observations

Bird communities were recorded using point-count bird observations for 30 min at each of the 30 survey plots (Fig. 1a). Observations were repeated four times in each point between 8 June and 20 July 2005. Bird calls and sightings were counted within a radius of 100 m at each observation point. Although we were careful not to repeatedly count the same individual, a bias toward overestimation of abundance cannot be ruled out. Observations were performed for 4 h after sunrise on days without strong wind, rain, or fog. To avoid bias caused by fixed observation times within a day, the order of point visits was randomized among the four observation dates.

Arthropod sampling

Sampling of arthropods was also performed at 30 plots, 28 of which were placed at the bird observation points; two other plots were used for arthropod sampling only (Fig. 1a). Three arthropod communities were collected at each plot using different methods. Arthropods living on tree foliage were sampled by beating the foliage (canopy community); those on forest-floor vegetation were sampled by sweeping the foliage (floor community); and flying arthropods were sampled using Malaise traps (flying community). Beating and sweeping were conducted in a 20-m square quadrat placed at each bird observation point where the canopy and understory vegetation was relatively uniform. Beating was carried out at each plot once during 22 to 31 July 2005, just after the final bird observation, on the foliage of randomly selected trees (~3 m tall) as many as

1 possible for 20 min in each plot. Sweeping was conducted at the same time as beating.
2 The all-around forest floor in each plot was swept using a 0.5-mm mesh insect net for 20
3 min. A half-sized Malaise trap (1 m high, 1 m long, 0.6 m wide; 0.5-mm mesh; see
4 Townes 1972) was set at 1 m above the ground on one corner of each 20-m square quadrat.
5 The traps were run simultaneously at all plots once for 3 days from 16 to 18 July 2005. All
6 arthropod samples were stored in 70% ethanol, and then sorted to order. Because the
7 taxonomic order is based on biological and phylogenetical criteria, this taxonomic
8 resolution is sufficient to detect the sensitivity of arthropod communities to forest gap
9 creation.

10

11 Statistical analysis

12

13 In our data, several changes in community composition in response to the windthrow
14 disturbance could have taken place among sampling locations. We defined the taxonomic
15 categories (species in the bird community and orders in the arthropod communities) as
16 the response y_i , recorded at the sampling location i , with $y_i = j$ for location i , $i = 1, \dots, n$.
17 The letter j denoted one of $1, \dots, J$ taxonomic categories. We assumed a multinomial
18 distribution for response y_i with class probabilities $\Pr(y_i = j)$. We estimated the taxonomic
19 occurrence probability $\Pr(y_i = j)$ as a function of disturbance rate (continuous explanatory
20 variable). The probability $\Pr(y_i = j)$ was estimated using a multinomial logit model
21 (Agresti 2002), which is a type of generalized linear model (GLM; McCullagh and
22 Nelder 1989). The model was expressed as follows:

23

1
$$\Pr(y_i = j) = \frac{\exp(X_i\beta_j)}{\sum_j \exp(X_i\beta_j)}$$

2

3 where y_i was the observed taxonomic categories, X was a vector of disturbance rate as a

4 explanatory variable, and β_j was a parameter vector. The linear predictor was given as

5 $\eta_j = X_i\beta_j$. Fitting the model involved maximizing the likelihood from a multinomial

6 distribution subject to the constraints of the aforementioned equation. Effects of

7 windthrow disturbance on the species composition of the bird community and the order

8 composition of the three arthropod communities (canopy, floor, and flying) were

9 analyzed using multinomial logit models. If the communities responded to the fraction of

10 disturbed area in the forest, scale-dependent changes in community composition by

11 windthrow disturbance could be inferred for bird and arthropod communities.

12 Furthermore, to assess the functional spatial scale at which each community

13 responded to windthrow disturbance, the best-fitting model was selected from the models

14 fitted to disturbance rate at stepwise spatial scales based on the Akaike information

15 criterion (AIC). The spatial scale (the radius from each observation point) was increased

16 from 10 to 500 m. The smallest scales (<100 m in radius) were excluded from the

17 analyses of bird communities because the area of bird observation was a 100-m radius.

18 For each community, the likelihood ratio between the null model, where the effect of

19 disturbance was not considered, and the best-fitting model was tested for significance of

20 disturbance effects. Finally, relative abundance distributions at the minimum and

21 maximum observed gap rate, which were calculated from an area under the selected

22 functional spatial scale, were derived from the estimated model for each community. The

23 estimated relative abundance of each species in birds or each order in arthropods was

1 plotted against the taxonomic rank. We then calculated the evenness (E) in each relative
2 abundance distribution as: $E = H'/\ln S$, where $H' = -\sum p_i \ln p_i$, p_i is the proportion of
3 individuals of the i th species, and S is the number of species in the assemblage (Magurran,
4 1988). $E = 1.0$ when all species are equally abundant. All analyses were performed in the
5 R environment for statistical computing (R Development Core Team 2006) with its
6 associated package nnet (Venables and Ripley 2002).

7

8

9 **Results**

10

11 In total, 3203 individuals of 40 bird species were observed (Appendix 1), and 3129
12 individuals of 15 arthropod orders were collected by beating (mainly
13 tree-foliage-dwelling arthropods, see Appendix 2), 18,652 individuals of 15 arthropod
14 orders by sweeping (mainly floor-vegetation-dwelling arthropods, see Appendix 2), and
15 5329 individuals of 14 arthropod orders using Malaise traps (mainly flying arthropods,
16 see Appendix 2).

17 Responses of community composition change to disturbance rate were detected
18 for all four communities, but the most effective spatial scale for this dependence varied
19 among communities (Fig. 3). For the bird community, the spatial scale of the best-fitting
20 model selected was for an area 370 m in radius (Fig. 3a), with a significant response of
21 species composition to disturbance rate (likelihood-ratio test, $P < 0.001$; change in
22 deviance of 120.88 and d.f. = 39). For the flying arthropod community dominantly
23 composed of Diptera and Hymenoptera, the selected spatial scale was an area 90 m in
24 radius (Fig. 3d), at which compositional change by windthrow disturbance was

1 significant ($P < 0.001$; change in deviance of 129.24 and d.f. = 13). The functional spatial
2 scale in both canopy and floor arthropod communities which were mainly comprised of
3 Araneae, Diptera, Hymenoptera, Coleoptera and Lepidoptera was an area 10 m in radius
4 (Fig. 3b, c), where both responses were significant ($P < 0.001$; change in deviance of
5 158.46 and d.f. = 14 for canopy arthropods, 256.56 and d.f. = 14 for floor arthropods). For
6 all communities, AIC values changed sharply around the functional spatial scales where
7 AIC indicated the lowest response (Fig. 3).

8 Clear responses of community composition changes to windthrow disturbance
9 were observed at certain spatial scales (Fig. 4). Bird communities exposed to tree-fall
10 disturbance in an area 370 m in radius showed complex species turnover (Fig. 4a), but
11 Narcissus Flycatcher (*Ficedula narcissina*; NF in Fig. 4a) and Brown-eared Bulbul
12 (*Hypsipetes amaurotis*; BEB in Fig. 4a) markedly increased, and Oriental Cuckoo
13 (*Cuculus saturatus*; OC in Fig. 4a) and Black-faced Bunting (*Emberiza spodocephala*;
14 BB in Fig. 4a) notably decreased with disturbance rate. The compositional changes in
15 arthropod communities were more distinct than in birds. In canopy (Fig. 4b) and floor
16 (Fig. 4c) arthropod communities with an area 10 m in radius, Coleoptera (O in Fig. 4b, c)
17 and Lepidoptera (P in Fig. 4b, c) were increased, but Hymenoptera (N in Fig. 4b, c) was
18 decreased with disturbance in particular. In flying (Fig. 4d) arthropod community with an
19 area 90 m in radius, the increase of Hymenoptera (N in Fig. 4d) and the decrease of
20 Diptera (M in Fig. 4d) with disturbance were especially obvious.

21 In all three arthropod communities, the evenness of community composition
22 increased with disturbance rate. Relative abundance distributions at sites with minimum
23 and maximum observed disturbance rate, which were derived from the estimated models,
24 demonstrated clear trends in evenness (Fig. 5). For all three arthropod communities at

1 their functional spatial scales, evenness indices at the site of maximum disturbance (0.691
2 in canopy arthropod community, 0.603 in floor one and 0.401 in flying one) were higher
3 than at the minimum disturbance (0.673 in canopy arthropod community, 0.500 in floor
4 one and 0.206 in flying one; see also Fig. 5b–d). However, bird communities show
5 substantial decrease of the evenness index from a site with minimum disturbance (0.838)
6 to a site with maximum one (0.783; see also Fig. 5a).

7

8

9 **Discussion**

10

11 The functional spatial scale at which the effect of disturbance rate on compositional
12 change is strongest varies according to the community. The functional scale appeared to
13 increase from canopy and floor arthropods (10 m in radius), to flying arthropods (90 m in
14 radius), and to birds (370 m in radius). The defined functional spatial scale for each
15 community may reflect its typical dispersal ability and spatial resource use according to
16 ecological traits of the communities. Canopy and floor arthropods are mainly wingless
17 (ants, caterpillars, and spiders; see Hirao et al. in press) or flight-limited (beetles and
18 midges; see Hirao et al. in press) and specialize in local habitat patch use. Thus, narrow
19 functional spatial scales (10 m in radius) are expected. In contrast, flying arthropods are
20 more mobile (flies and parasitoids; see Hirao et al. in press) and disperse to multiple
21 habitat patches; they exhibit intermediate functional spatial scales (90 m in radius). Birds
22 are much more mobile and can use many habitat patches at broader scales than arthropods.
23 The functional spatial scale of community composition change appears to reflect, and
24 may serve as a measure of, the typical dispersal ability of organisms in a focal

1 community.

2 Our observations on functional spatial scales at the community level are
3 consistent with the hypothesis of Holt (1996). According to this hypothesis, the density of
4 species at higher trophic levels is determined at larger spatial scales than that of species at
5 lower trophic levels. Specifically, herbivores should be confined to local habitat patches,
6 whereas the spatial distribution of predators should encompass several prey populations,
7 and thus, many habitat patches. Canopy and floor arthropod communities operating at
8 narrow spatial scales certainly contain many herbivorous taxa, whereas flying arthropods
9 operating at broader scales contain many predatory taxa (see Hirao et al. in press). Body
10 size can be also an alternative predictor of how organisms acquire resources in space
11 (Peters 1983; Ritchie and Olff 1999). For example, a correlation exists between the body
12 size of avian predators or mammalian seed dispersers and the spatial scale of their
13 landscape-wide resource use (Peterson et al. 1998). Forest fragmentation affects four
14 parasitoids of the forest tent caterpillar at different spatial scales depending on their body
15 sizes (Roland and Taylor 1997). Feeding strategy (e.g., specialist or generalist) also can
16 affect the functional spatial scale of organisms (Tscharntke et al. 2005). Generalist
17 predators are prone to be affected by the landscape context at broad spatial scales
18 (Symondson et al. 2002) in comparison to specialists having relatively small dispersal
19 ranges (Kruess and Tscharntke 1994, 2000). Along with environmental factors (i.e.,
20 landscape contexts), synergistic effects of these traits characterizing the component
21 organisms may regulate the functional spatial scale of community composition change,
22 which can be regarded as an emergent property.

23 In the bird community, tree-fall disturbance at an area of 370 m in radius
24 increased the fraction of canopy insectivore species such as Narcissus Flycatcher and

1 edge-dependent species such as Brown-eared Bulbul. In contrast, Cuculiformes such as
2 Oriental Cuckoo and ground bush foragers such as Black-faced Bunting decreased with
3 disturbance. This compositional change is related to the availability of habitat area
4 required for each taxon. The compositional changes in arthropod communities were even
5 more distinct. In canopy and floor arthropod communities with an area 10 m in radius, the
6 fractions of herbivores such as Coleoptera and Lepidoptera increased with disturbance,
7 whereas those of carnivores such as Hymenoptera (mainly composed of ants) decreased
8 (see Hirao et al. in press). An increase in the abundance of herbivores at disturbed sites
9 may be attributed to increased primary production caused by light conditions in tree-fall
10 gaps, although decreases in herbivore abundance have been reported under severe
11 disturbance (Schowalter and Ganio 1999). Decreased carnivore abundance in disturbed
12 canopy and floor communities may reflect their low migration ability (Ribas et al. 2005).
13 In the flying arthropod community at an area 90 m in radius, the fraction of carnivores
14 such as Hymenoptera (mainly composed of highly mobile wasps and parasitoids; see
15 Hirao et al. in press) increased with disturbance. This may reflect changes in herbivore
16 abundance, although the decrease of Diptera with disturbance is unexplainable at present.
17 In all three arthropod communities, the major predator order, Hymenoptera, was most
18 sensitively affected by disturbance at the landscape level. This also supports the general
19 view that higher trophic levels should be more susceptible to disturbance because of the
20 variability in their populations (Kruess and Tschardtke 1994, 2000; Holt et al. 1999).

21 Windthrow disturbance resulted in the enhancement of compositional evenness;
22 the fraction of dominant taxa decreased overall, whereas that of rare taxa increased (Fig.
23 4). Relative abundance distributions indicate evenness in the community composition
24 (Tokeshi 1999). Although a shift in evenness with gap rate was unclear in the bird

1 community, shifts were evident in the three arthropod communities; relative abundance
2 distributions became more even at maximal disturbance. The enhancement of evenness in
3 community composition by moderate disturbance is well known (Mackey and Currie
4 2001). For example, Joern (2005) demonstrated that fire and grazing disturbances can
5 facilitate evenness in the insect herbivore community of a tallgrass prairie.

6 Landscape characteristics other than gap rate were not taken into account in this
7 study. However, tree species composition, ecotone, forest edge, and streams, may also
8 affect the community compositions of birds and arthropods (Schowalter and Ganio 1999).
9 Community responses to disturbance may also differ between simple and complex
10 landscapes (Tscharntke et al. 2005); a complex landscape can harbor larger source pools
11 for recolonization than a simple landscape, so that communities experiencing diverse
12 habitats in a complex landscape may be more resilient and persistent than ones using a
13 specific habitat in a simple landscape. Measures of habitat diversity in the landscape
14 (Weibull et al. 2000; Kruess 2003), such as forest type and ecotone area, may be
15 potentially valuable for future research.

16 The concept of the functional spatial scale of community composition change
17 provides useful information for biodiversity conservation. Tscharntke et al. (2005)
18 pointed out that high dispersal ability and large home ranges are life-history traits that
19 confer better survival in dynamic and disturbed landscapes because they have the
20 consequences of increased spatial flexibility and recolonization ability, resource
21 acquisition at large spatial scales, and low spatial turnover. High dispersal ability renders
22 the community less susceptible to compositional change in disturbed landscapes. The
23 capability of rapid recolonization and escape from disturbance by the component
24 organisms ensures the spatial flexibility of the community (Holt et al. 1999; Tscharntke et

1 al. 2005). Communities using large landscape scales may also be less sensitive to local
2 changes in resource availability than those specializing within local patches (Tscharntke
3 et al. 2005). Furthermore, communities with limited spatial use may result in a high
4 spatial turnover in community composition because of spatial isolation and low
5 connectivity (Leibold et al. 2004; Tscharntke et al. 2005). In general, communities
6 experiencing the landscape context at broad spatial scales can persist through small-scale
7 disturbances, whereas those organized at small scales are more sensitive to local
8 disturbances. The observation that compositional evenness was enhanced in arthropod
9 communities may imply higher susceptibility of arthropods to disturbance than bird
10 communities, which have broader functional spatial scales.

11 However, the relationship between the susceptibility and dispersal ability or
12 functional spatial scale in this system may depend on the dimension of disturbance itself.
13 The disturbance rate around each sampling point varied greatly at relatively small spatial
14 scales, ranging from ~0 to 80% at scales of 10 to 100 m in radius, corresponding to the
15 functional spatial scales for arthropod communities, whereas the disturbance rate
16 progressively converged to ~20% up to the maximum scale of 500 m in radius,
17 corresponding to the functional spatial scale of the bird community (Fig. 2). The narrower
18 range in variation of the disturbance rate at 500 m in radius may explain the weak
19 response of bird community evenness to disturbance. If the disturbance stemmed from the
20 typhoon is more severe and variable at 500 m in radius, the bird community may result in
21 more susceptible. This demonstrates another difficulty in approaches dealing with the
22 spatial aspects of natural systems.

23 Quantifying the reserve area required to conserve biodiversity and ecosystem
24 services at the community level is an important issue that involves spatial processes at the

1 landscape level (for reviews see Schwartz 1999; Tschamntke et al. 2005). Planning and
2 decision making for the preservation of biodiversity and ecosystem services based on the
3 functional spatial scale of community composition dynamics is pragmatic. Our results
4 demonstrate that different types of communities have different functional spatial scales at
5 which they respond to habitat structure, presumably according to the typical dispersal
6 ability of each community. We think that our approach of applying the concept of
7 functional spatial scale at the community level can aid in conservation. Effective plans for
8 the conservation of biodiversity and ecosystem services should be based on the
9 understanding of scale-dependent processes such as dispersal in community dynamics
10 across landscapes (Wiens et al. 1993). Few studies, however, have demonstrated
11 scale-dependent effects of landscape structure on local community structure (Roland and
12 Taylor 1997; Thies et al. 2003). Spatially explicit perspectives that consider space use by
13 organisms at the spatial scale of ecological processes are required to resolve the responses
14 of communities to disturbance and landscape structure.

15
16

17 **Acknowledgments**

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1 Figure legends

2

3 **Fig. 1** Map of the study site at Tomakomai Experimental Forest, Hokkaido, northern
4 Japan. White cell shows the canopy gap and grey one shows living foliages. (a) Locations
5 of 32 survey plots (28 common plots for bird and arthropod surveys; 4 plots for only bird
6 [B] or arthropod [A] surveys) and the distribution of large gaps created by windthrow
7 disturbance from typhoon No.18 in September 2004. (b) Two example plots with high
8 and low disturbance rates; five nested circular sectors ranging from 100 to 500 m in
9 radius are indicated around each survey plot. In the analysis, we used circular sectors at
10 10-m intervals.

11

12 **Fig. 2** Trajectories of the disturbance rate evaluated within nested circular sectors
13 increasing in radius from 10 to 500 m at 30 survey plots for (a) birds and (b) arthropods.
14

15 **Fig. 3** Scale-dependent responses of community composition change to windthrow
16 disturbance in (a) bird, (b) canopy arthropod, (c) floor arthropod and (d) flying arthropod
17 communities. The AIC value for each model is plotted against the spatial scale (radius of
18 the survey plot) at which the disturbance rates are evaluated. The model with the lowest
19 AIC (indicated with an asterisk) is the best-fitting model, and the corresponding scale is
20 regarded as the functional spatial scale. The solid line indicates the AIC value for the null
21 model independent of disturbance rate as an explanatory factor.

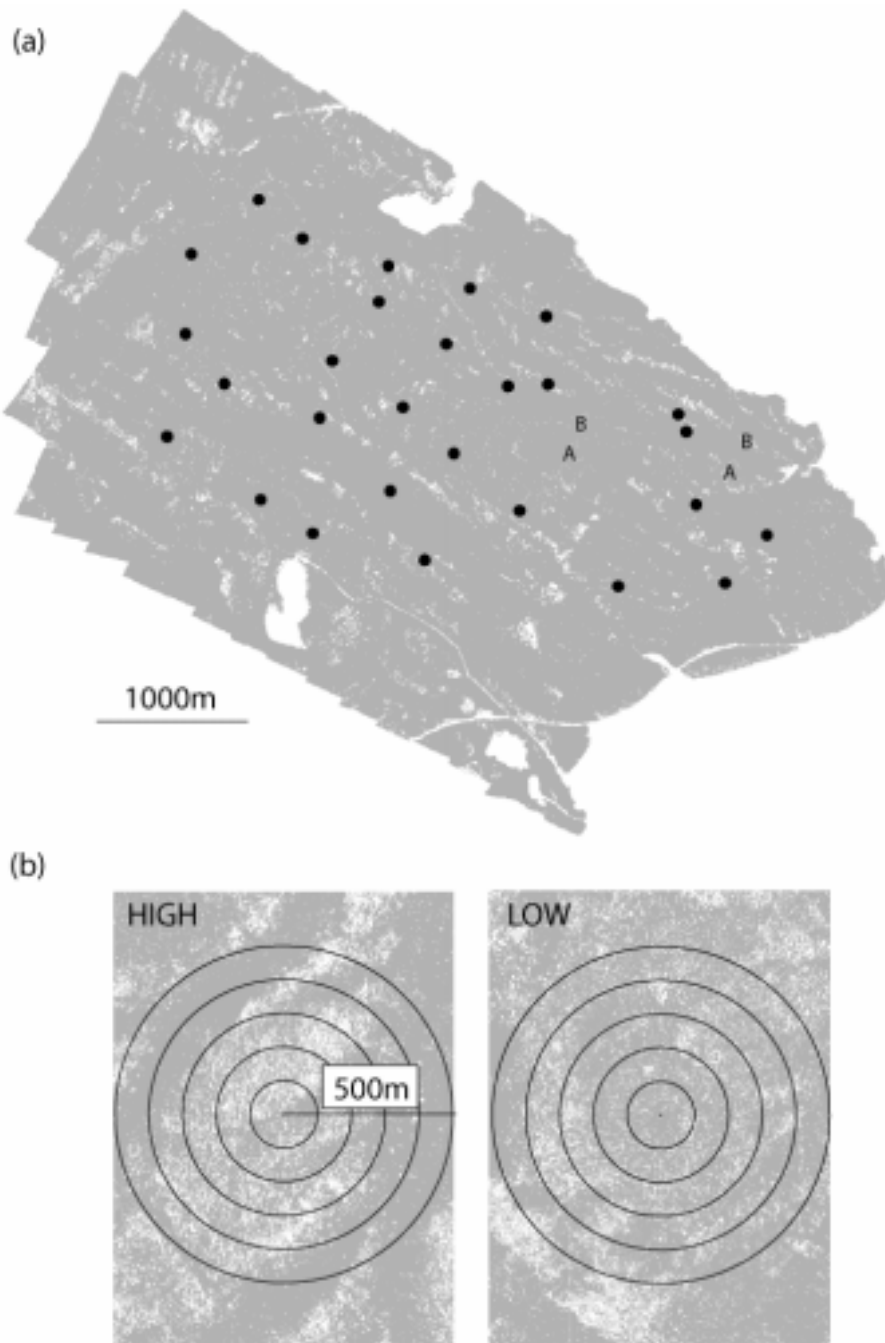
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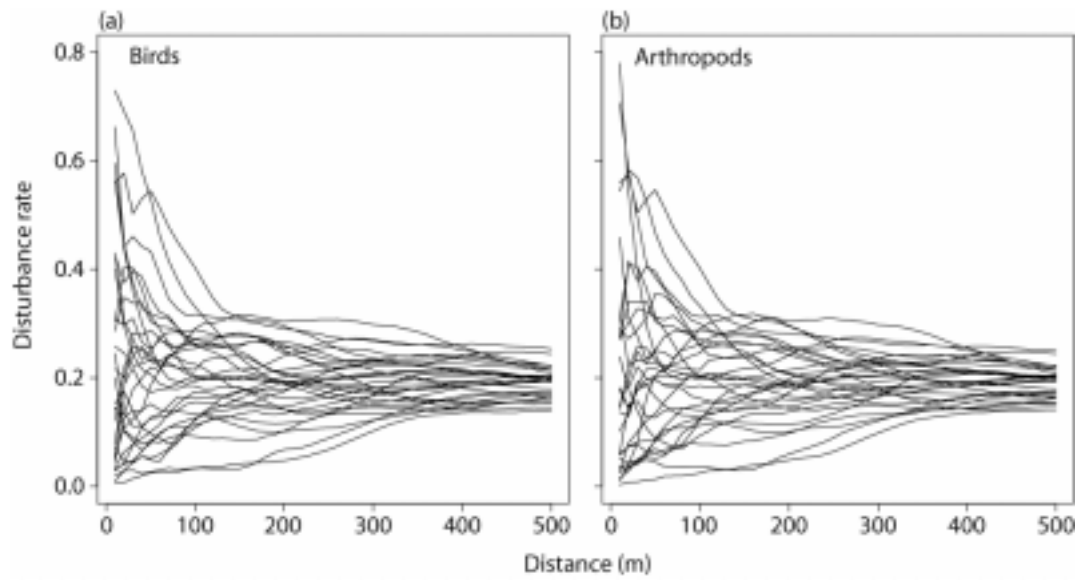
23 **Fig. 4** Estimated compositional change in response to windthrow disturbance in (a) bird,
24 (b) canopy arthropod, (c) floor arthropod and (d) flying arthropod communities. The

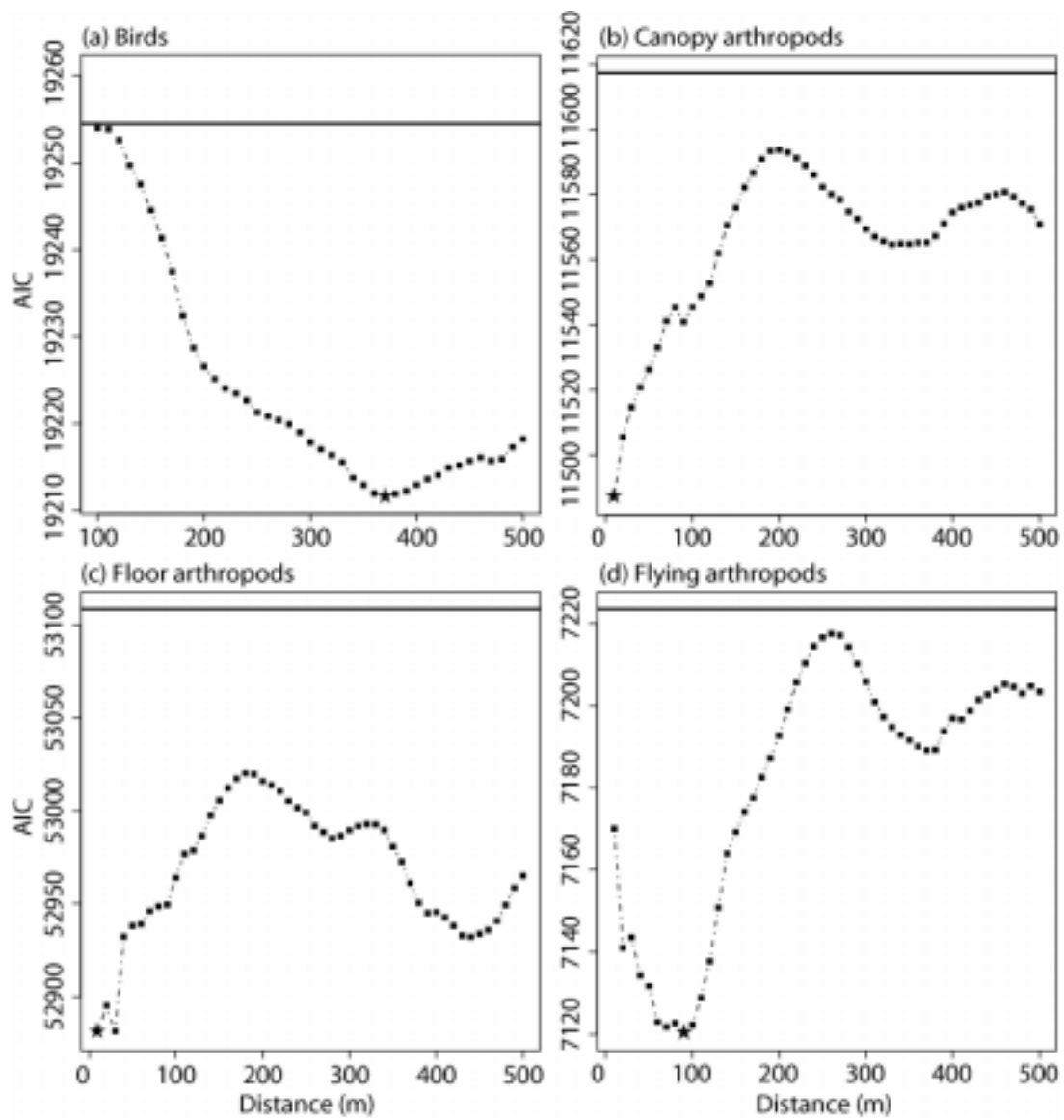
1 occurrence probability of each taxon is plotted against the disturbance rate computed
2 from area of the selected functional spatial scale (370 m in radius for birds, 10 m for
3 canopy and floor arthropods, and 90 m for flying arthropods). The position of each
4 taxonomic code (see Appendices 1, 2) on the right side of each plot corresponds to the
5 order of occurrence probability for each taxon at the maximum disturbance rate observed
6 within the focal area.

7

8 **Fig. 5** Relative abundance distributions at minimum and maximum observed disturbance
9 rates derived from the estimated models in (a) bird, (b) canopy arthropod, (c) floor
10 arthropod and (d) flying arthropod communities. The estimated relative abundance of
11 each species in birds or each order in arthropods is plotted against the taxonomic rank by
12 abundance at minimum (broken line) and maximum (solid line) disturbance rates
13 respectively, which were calculated from the area of the selected functional spatial scale
14 (370 m in radius for birds, 10 m for canopy and floor arthropods, and 90 m for flying
15 arthropods).

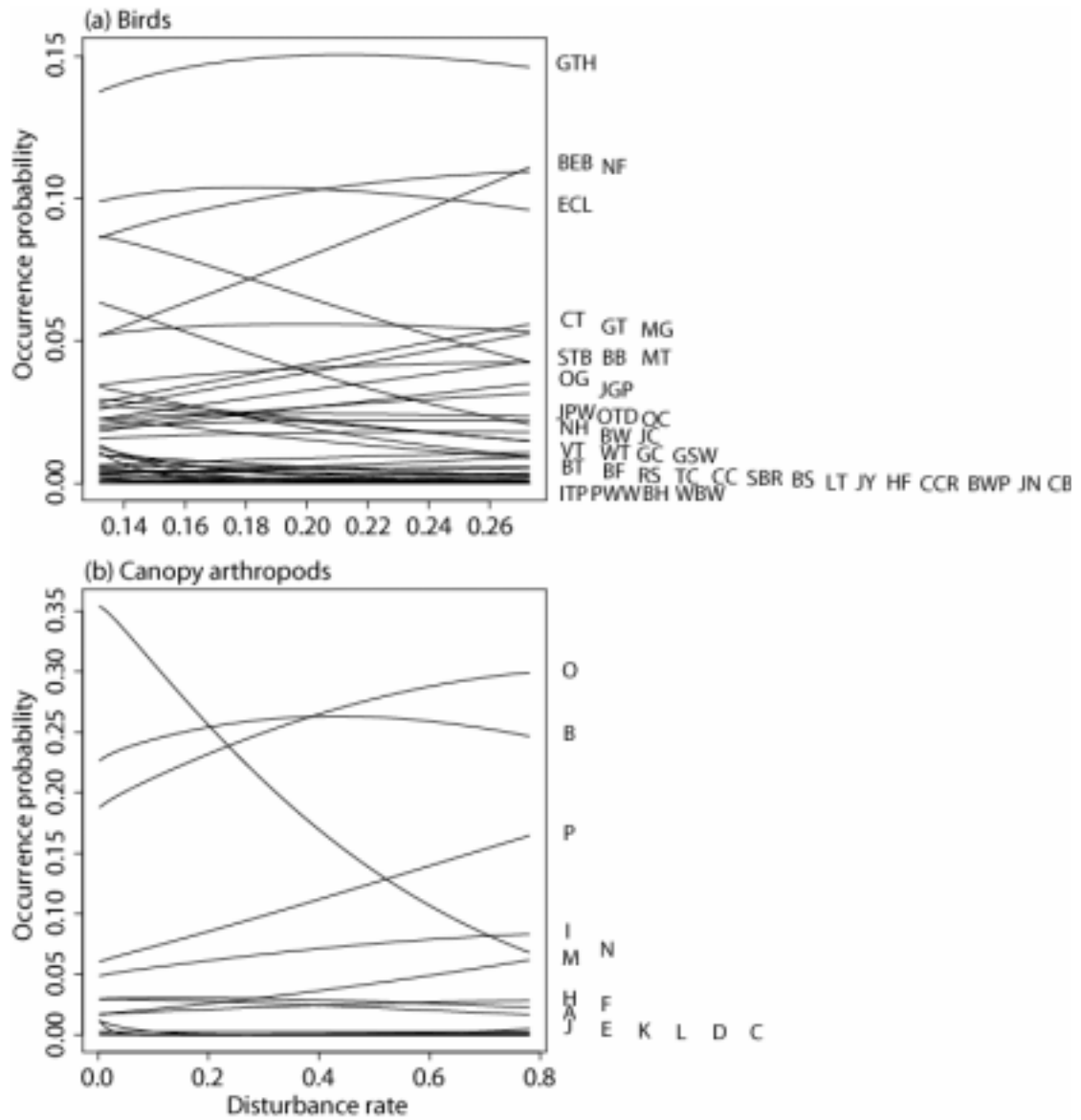






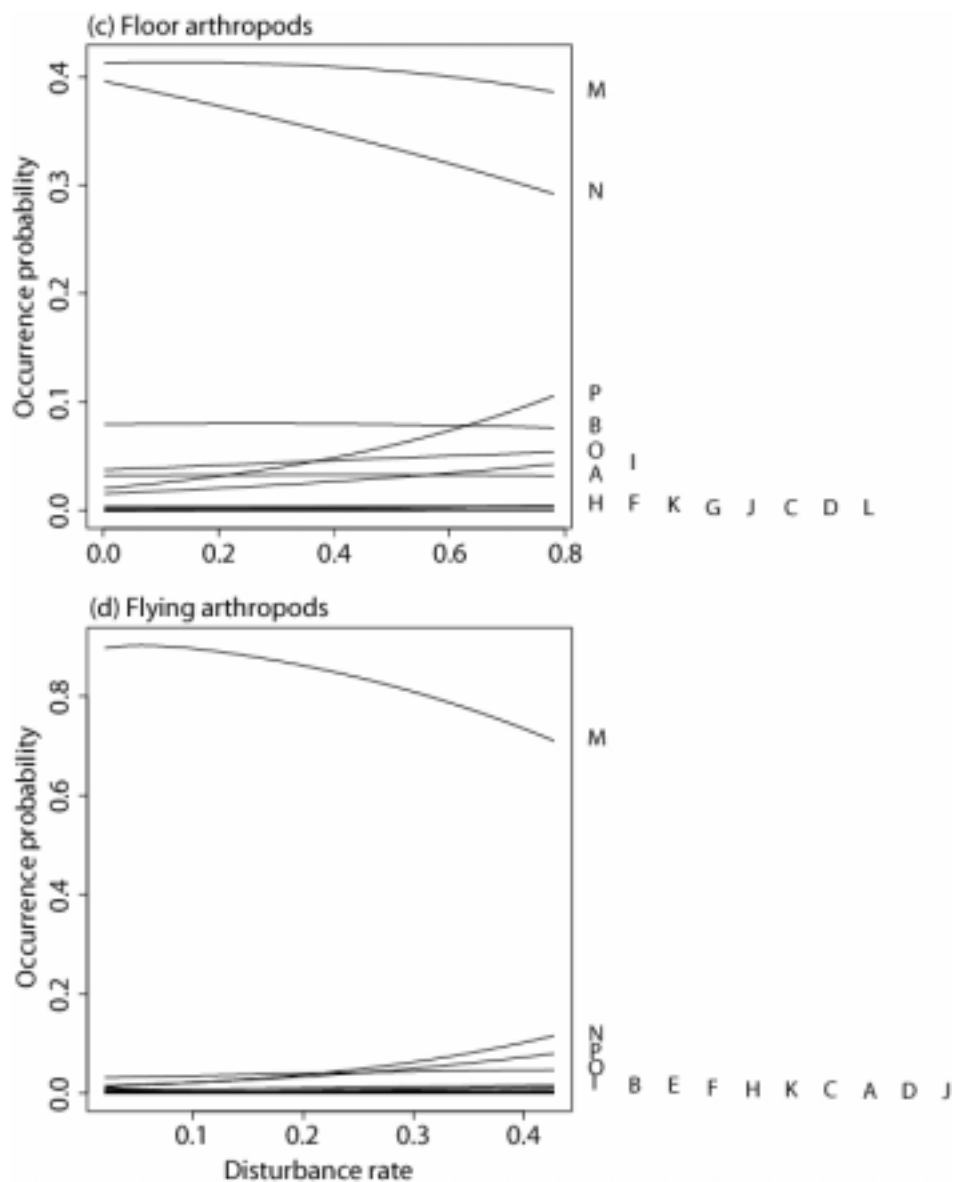
1 Fig. 4

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1 Fig. 4 (continued)

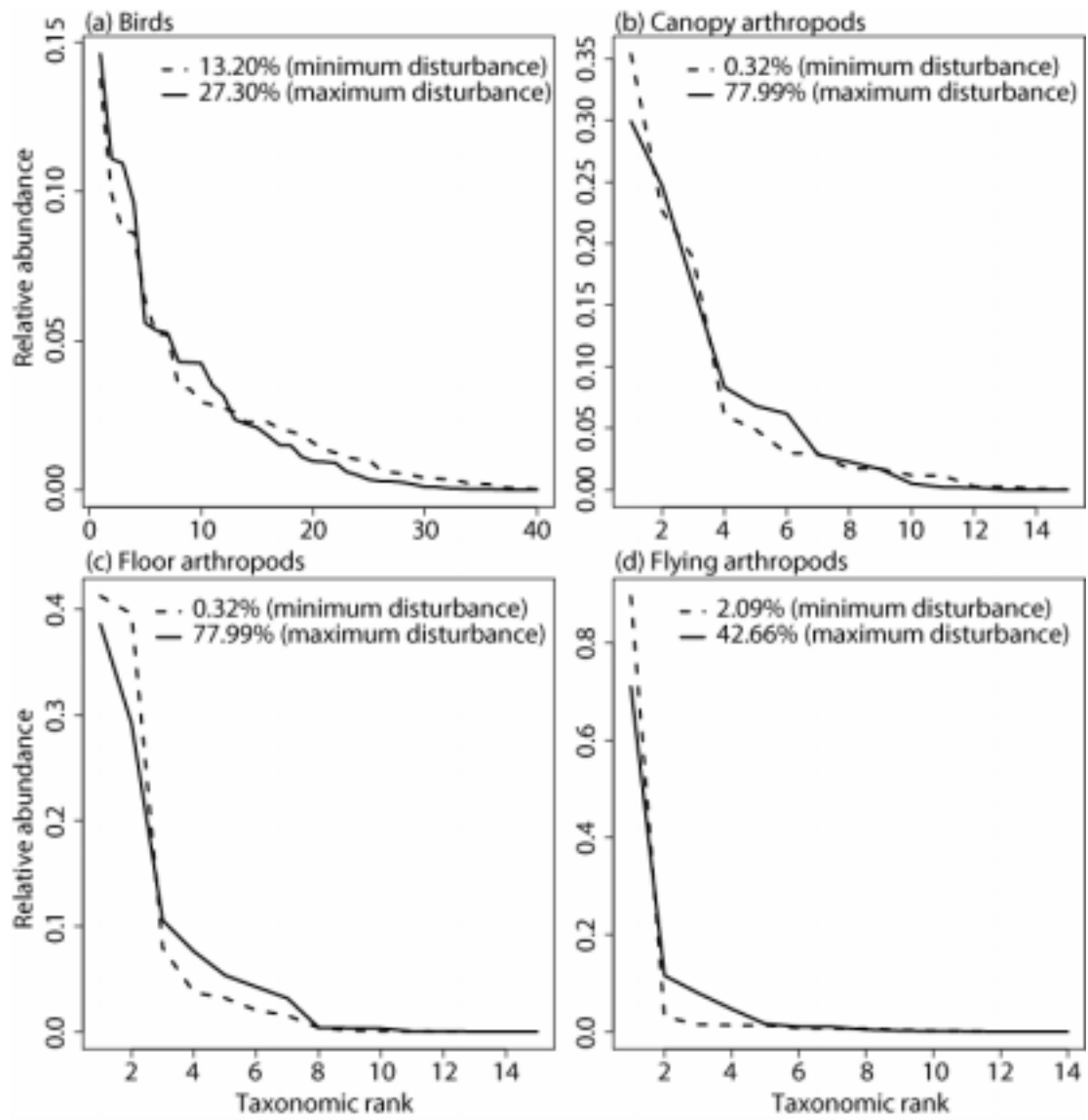
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1 Fig. 5

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2



- 1 **Appendix 1** List of codes, species names, and abundance in the community for birds
 2 recorded at 30 observation points in a deciduous temperate forest of Japan.

Code	Species	Abundance
CB	Common Buzzard (<i>Buteo buteo</i>)	1
BH	Brown Hawk-owl (<i>Ninox scutulata</i>)	1
OTD	Oriental Turtle Dove (<i>Streptopelia orientalis</i>)	69
JGP	Japanese Green Pigeon (<i>Sphenurus sieboldii</i>)	84
CC	Common Cuckoo (<i>Cuculus canorus</i>)	5
OC	Oriental Cuckoo (<i>Cuculus saturatus</i>)	133
JN	Jungle Nightjar (<i>Caprimulgus indicus</i>)	1
BWP	Black Woodpecker (<i>Dryocopus martius</i>)	6
WBW	White-backed Woodpecker (<i>Dendrocopos leucotos</i>)	1
GSW	Great Spotted Woodpecker (<i>Dendrocopos major</i>)	51
JPW	Japanese Pygmy Woodpecker (<i>Dendrocopos kizuki</i>)	77
ITP	Indian Tree Pipit (<i>Anthus hodgsoni</i>)	9
BEB	Brown-eared Bulbul (<i>Hypsipetes amaurotis</i>)	252
BS	Bull-headed Shrike (<i>Lanius bucephalus</i>)	2
SBR	Siberian Blue Robin (<i>Erithacus cyane</i>)	12
WT	White's Thrush (<i>Turdus dauma</i>)	67
BT	Brown Thrush (<i>Turdus chrysolaus</i>)	16
GTH	Grey Thrush (<i>Turdus cardis</i>)	472
BW	Bush Warbler (<i>Cettia diphone</i>)	70
STB	Short-tailed Bush Warbler (<i>Cettia squameiceps</i>)	103
GC	Gold Crest (<i>Regulus regulus</i>)	19
PWW	Pale-legged Willow Warbler (<i>Phylloscopus tenellipes</i>)	5
ECL	Eastern Crowned Leaf Warbler (<i>Phylloscopus occipitalis</i>)	326
NF	Narcissus Flycatcher (<i>Ficedula narcissina</i>)	322
BF	Blue-and-white Flycatcher (<i>Cyanoptila cyanomelana</i>)	18

MT	Marsh Tit (<i>Parus palustris</i>)	127
CT	Coal Tit (<i>Parus ater</i>)	132
GT	Great Tit (<i>Parus major</i>)	176
VT	Varied Tit (<i>Parus varius</i>)	28
LT	Long-tailed Tit (<i>Aegithalos caudatus</i>)	14
NH	Nuthatch (<i>Sitta europaea</i>)	56
TC	Tree Creeper (<i>Certhia familiaris</i>)	20
BB	Black-faced Bunting (<i>Emberiza spodocephala</i>)	213
OG	Oriental Greenfinch (<i>Carduelis sinica</i>)	84
MG	Japanese Grosbeak (<i>Eophona personata</i>)	123
HF	Hawfinch (<i>Coccothraustes coccothraustes</i>)	4
RS	Russet Sparrow (<i>Passer rutilans</i>)	12
JY	Jay (<i>Garrulus glandarius</i>)	6
JC	Jungle Crow (<i>Corvus macrorhynchos</i>)	73
CCR	Carrion Crow (<i>Corvus corone</i>)	13

1 **Appendix 2** List of codes, order names, and abundance in the community for canopy,
 2 forest-floor, and flying arthropods collected from 30 sampling points in a deciduous
 3 temperate forest of Japan.

Code	Order	Abundance		
		Canopy arthropods	Floor arthropods	Flying arthropods
A	Opiliones	86	602	3
B	Araneae	770	1483	22
C	Isopoda	4	7	1
D	Lithobiomorpha	11	3	3
E	Collembola	8	0	47
F	Dermaptera	93	70	6
G	Orthoptera	0	1	0
H	Psocoptera	64	27	14
I	Hemiptera	186	389	58
J	Mecoptera	1	4	1
K	Neuroptera	8	33	4
L	Trichoptera	1	1	0
M	Diptera	81	7661	4535
N	Hymenoptera	850	6956	229
O	Coleoptera	703	773	212
P	Lepidoptera	263	642	194

4