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Scale-dependent effects of windthrow disturbance on forest arthropod communities

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Abstract The effect of disturbance on local communities may operate via a spatial landscape context. We examined the scale-dependent effects of windthrow disturbance caused by a large typhoon on three arthropod communities in a temperate forest of Japan. Canopy arthropods were collected by beating foliage, forest-floor arthropods were collected by sweeping the vegetation, and flying arthropods were collected in Malaise traps. To assess the "functional spatial scale" at which arthropods responded to tree-fall disturbance, the gap rate was quantified at different spatial scales by sequentially enlarging the radius of a circular landscape sector by 10 m from 10 to 500 m. We then analyzed the responses of order richness and abundance to the gap rate for each arthropod community. The spatial scale of the significant best-fitting model, which was selected from the models fitted to the gap rate at stepwise spatial scales, was regarded as the arthropod-specific functional spatial scale. Arthropod order richness was not dependent on the gap rate. In contrast, arthropod order abundance depended significantly on the gap rate in many orders, but varied in the response direction and functional spatial scale. These order-specific, scale-dependent responses to tree-fall gaps would complicate interactions among organisms, leading to complex community organization. An understanding of the spatial processes that link the use of space by organisms with the spatial scale at which ecological processes are experienced is required to elucidate the responses of populations, communities, and biotic interactions to disturbances in a spatial landscape context.

Keywords Arthropod diversity, Environmental heterogeneity, Functional spatial scale, Scale dependence, Tree-fall gap

Introduction

In recent years, the effects of spatial heterogeneity on population and community dynamics have been increasingly recognized (Kareiva 1990; Turner and Gardner 1991; Polis et al. 1997; Hutchings et al. 2000). In a heterogeneous environment, the landscape context, such as the area, spatial arrangement, and connectivity of habitats, potentially affects local species abundance, biotic interactions, and thus, community structure (Kareiva 1990; Kareiva and Wennergren 1995; Pickett and Cadenasso 1995; Roland and Taylor 1997; Gonzalez et al. 1998; Thies and Tscharntke 1999). Because organisms use various cues to locate favorable habitats and differ in their dispersal abilities, the habitat heterogeneity of a landscape may affect different species differently, resulting in spatial variation in community structure and species abundance via interactions among species with different habitat requirements (Holt 1996; With et al. 1999, 2002; Steffan-Dewenter et al. 2002; Thies et al. 2003, 2005).

Disturbances, such as fire and grazing in grasslands (e.g., Joern 2005), wave action in rocky intertidal zones (e.g., Smith and Witman 1999), and flooding in streams (e.g., Parsons et al. 2005), are the principal factors creating and maintaining habitat heterogeneity in a landscape. In forest ecosystems, windthrow disturbance, even if not catastrophic, is one of the major agents generating a mosaic of heterogeneous habitat patches at various spatial scales (Sinton et al. 2000; Kramer et al. 2001, 2004). Canopy gaps caused by windthrow disturbance can occur in a variety of sizes, from single fallen trees to large-scale blowdowns (Schowalter and Ganio 1999). Because such disturbance patches are located within a continuous broader landscape in a forest ecosystem, the occurrence and abundance of animals in these new habitat patches can be strongly affected by the location of patches within the surrounding forest mosaic (Steffan-Dewenter et al. 2002; Thies et al. 2003, 2005). Windthrow disturbance in forests should affect the inhabitants and their interactions in a spatial context (Pascual and Guichard 2005). Gaps created by windthrow disturbance can strongly influence the distribution and abundance of forest arthropods (Schowalter and Ganio 1999; see also Schowalter et al. 2005). A single fallen tree can degrade a habitat for some canopy arthropod species, whereas a gap created by multiple fallen trees can serve as a favorable patch for some grassland arthropod species. However, arthropods may live in a more fine-grained world in general; some herbivores select specific host-plant foliage, and the distributions of some flying insects can be affected by microhabitat light conditions.

We analyzed the variation in the order richness and abundance of three arthropod communities, i.e., canopy, forest-floor, and flying arthropods, in a northern deciduous forest to evaluate the scale-dependent effects of windthrow disturbance on these communities. Order richness and abundance were analyzed separately for the three arthropod communities because this taxonomic grouping, based on biological and ecological criteria, is suitable for detecting the sensitivity of species groups to forest gap creation. First, we evaluated the hypothesis that the spatial scale experienced by the arthropod communities and assemblages within each order depends on their ecological traits and trophic level, which create “functional spatial scales” (Thies et al. 2003, 2005) at which organisms respond to landscape patchiness. We then tested the significance of the response of order richness and abundance to the variation in forest gaps at the functional spatial scales.

Methods

Study site

The study was conducted in a temperate deciduous forest of the Tomakomai Experimental Forest (TOEF; 42°43' N, 141°36' E; ca. 30–90 m asl), Hokkaido, Japan. This cool–temperate forest received 1161 mm of precipitation annually and experienced an average annual temperature of 5.6°C. Oak (*Quercus crispula*), maple (*Acer mono*), and linden (*Tilia japonica*) dominated the forest. The canopy ranged from 15 to 25 m in height, and saplings of the dominant tree species grew on the forest floor. Deciduous trees broke bud in early to mid-May and shed leaves in late October.

On 8 September 2004, about a year before the survey period, a destructive typhoon (no. 18, "Songda") hit Hokkaido Island, Japan, causing widespread tree damage. Based on a part of aerial survey conducted in the TOEF, the damage was mapped to roughly 20% of the total area, and the creation of many canopy gaps 10–100 m in diameter was noted (Fig. 1). Typhoon events at this scale are relatively rare, occurring in Hokkaido only once or twice a century. Therefore, the 2004 typhoon provided a unique opportunity to examine the effects of typhoon damage on forest ecosystems and wildlife communities.

Quantifying windthrow disturbance

A remotely sensed vegetation index was used to assess the magnitude of windthrow disturbance. The normalized difference vegetation index (NDVI) is a measure of greenness calculated from the reflectance of near-infrared and red portions of the electromagnetic spectrum. This index is positively correlated with total green biomass (cf., Pettorelli et al. 2005). We used aerial photographs taken during 20–22 September 2004, just after the typhoon, but before leaf fall, to calculate the NDVI/m^2 in the TOEF. Apart from the calculation of NDVI, the total gap area within the TOEF was roughly estimated at 20% using parts of optical-wavelength aerial photographs. The 20% quantile in the distribution of calculated NDVIs was defined as the threshold for the gap band, i.e., unit squares with NDVI less than the threshold were regarded as gaps. Thirty points were chosen along the whole gradient of disturbance rate assessed using NDVI (Fig. 1a) for secondary broad-leaved forests in the TOEF.

To determine the functional spatial scale for each group of arthropods, the effect of windthrow disturbance on order richness and abundance in arthropod communities was analyzed at nested spatial scales (Fig. 1b). The disturbance rate was calculated as the percentage of gap area within a given radius, which was increased successively by 10 m from 10 to 500 m from the center of each survey plot. The disturbance rate around each point varied greatly at relatively small spatial scales, ranging from approximately 0 to 80% at radii of 10 to 100 m. These values were similar to the gap sizes in the forest. When the radius was increased successively to 500 m, the disturbance rate converged to approximately 20%, which corresponded to the average disturbance rate within the forest (Fig. 2). Calculations to quantify windthrow disturbance were performed using the Geographical Information System software Arc GIS 9.0 (Environmental System Research Institute, Redlands, California, USA, 2004) and ERDAS Imagine8.7 (Leica Geosystems GIS & Mapping, Atlanta, Georgia, USA, 2004).

Arthropod sampling

Arthropods were sampled at 30 plots (Fig. 1a) using three different collection methods. Canopy arthropods were sampled by beating the foliage, arthropods in the forest-floor vegetation were sampled by sweeping, and flying arthropods were sampled using Malaise traps. Beating and sweeping were conducted in a 20-m^2 quadrat placed in the center of an area where the canopy and understory vegetation was relatively uniform. Beating was carried out at each plot once during 22–31 July 2005, on the foliage of randomly selected trees (<3 m in height) as many as possible for 20 min in each plot. Sweeping was conducted on the same dates as beating. The all-around forest floor in each plot was swept using a 0.5-mm mesh insect net for 20 min. Malaise traps were set 1 m above the ground on one corner of each quadrat. The traps were open simultaneously at all plots for 3 days from 16 to 18 July 2005. All arthropod samples were stored in 70% ethanol and sorted to order.

Statistical analysis

The effects of windthrow disturbance on order richness and abundance for the three arthropod communities were analyzed using generalized linear models (GLM; McCullagh and Nelder 1989) and the log link function, assuming a Poisson error structure in richness and a negative-binomial error structure in abundance. To assess the order-specific spatial scale at which each arthropod order responded to windthrow disturbance, the best-fitting model was selected from the models fitted to disturbance rate data at stepwise spatial scales based on the Akaike information criterion (AIC). The spatial scale (the radius from each survey plot) was increased stepwise from 10 to 500 m at 10-m intervals. Scales <10 m in radius were not considered in the analysis because arthropods were sampled within a 10-m radius area. The likelihood ratio between the null model (response is independent of disturbance), and the best-fitting model was tested to determine the significance of the disturbance effect. Arthropod orders with less than five individuals in total were excluded from the abundance analyses. All analyses were performed in the R environment for statistical computing (R Development Core Team 2005).

Results

In total, 3129 individuals from 15 orders were collected by beating, 18,652 individuals from 15 orders by sweeping, and 5329 individuals from 14 orders in Malaise traps. For arthropod order richness, the best-fitting model was selected at a spatial scale of 80 m in radius for communities sampled by sweeping and with Malaise traps, but only 10 m in radius for that sampled by beating (Fig. 3). However, the likelihood-ratio test revealed no significant dependence of arthropod order richness on disturbance rate for any community (P = 0.416 for beating, P = 0.318 for sweeping, and P = 0.409 for Malaise trap).

A significant dependence of order abundance on disturbance rate was detected for several arthropod orders in the three communities. The abundance of 7 of 13 orders sampled by beating (Opiliones, Araneae, Isopoda, Lithobiomorpha, Collembola, Hymenoptera, and Coleoptera), 5 of 12 orders sampled by sweeping (Araneae, Psocoptera, Hemiptera, Hymenoptera, and Lepidoptera), and 4 of 10 orders sampled using Malaise traps (Araneae, Dermaptera, Hymenoptera, and Lepidoptera) significantly depended on the disturbance rate, but the direction of the effect of windthrow disturbance (i.e., positive or negative) was highly variable (Table 1). The most effective spatial scale for this dependence varied among orders and among communities (Table 1). For arthropods sampled by beating or sweeping, orders with significant responses showed negative responses to disturbance rate at small spatial scales, and positive responses at large scales. For arthropods sampled using Malaise traps, all orders with significant responses showed positive responses and to disturbance rate at an intermediate scale. In four dominant orders (Coleoptera, Diptera, Lepidoptera and Hymenoptera), the collected individuals were classified into four guilds based on the food habits and dispersal ability, and then the percentage abundance of each guild to total abundance of the order was calculated (Appendix).

Discussion

The responses of arthropod communities to the windthrow disturbance were unclear in terms of order richness, but were evident in the abundance of individuals within each order; a significant relationship was observed between order abundance and disturbance rate for some orders. However, the direction of the response and the spatial scale at which the abundance was best explained by the disturbance rate varied among orders and among the three communities, even for the same order.

Arthropods were sampled using three different methods, i.e., beating, sweeping, and Malaise traps, which targeted canopy dwelling, forest-floor-vegetation dwelling, and flying forest arthropod communities, respectively. Because the species composition of the same order should vary among the communities sampled using these three methods, the response of order abundance to the disturbance rate could be variable in direction and functional spatial scale. The responses to disturbance rate were positive in Hemiptera (sweeping), Coleoptera (beating), and Lepidoptera (sweeping and Malaise trap). These orders consist solely or largely of herbivores (see Appendix). An increase in their populations at sites disturbed by windthrow may be attributable to increased primary production caused by improved light conditions in tree-fall gaps. Although Schowalter and Ganio (1999) reported that the abundance of herbivores was reduced in severely disturbed forest (by hurricane) compared to intact forest, we found the opposite. This discrepancy may have occurred because the windthrow disturbance caused by the typhoon was not as catastrophic as that caused by the hurricane. In contrast, the abundance of individuals in carnivorous orders, i.e., Araneae (beating and sweeping), Hymenoptera (beating and sweeping), and Lithobiomorpha (beating), was negatively correlated with the disturbance rate. Because the Hymenoptera collected by beating and sweeping were mainly ants, these orders represent wingless arthropods with relatively sessile modes of life (see Appendix); Araneae and Lithobiomorpha are also wingless and relatively less mobile. The mobility of organisms is expected to affect the variation in their populations caused by habitat fragmentation (Ribas et al. 2005). The lower mobility of wingless versus winged organisms may cause a population size reduction in forest gaps because of low migration ability, although an alternative explanation that those wingless carnivores may prefer closed habitats such as fragmented forests to open one is possible. These opposing responses of herbivores and carnivores to windthrow disturbance, i.e., positive in the former, but negative in the latter, suggest the following consequences: herbivore populations would further increase under the relaxed predation pressure, and trophic interactions in the arthropod community would become unbalanced in strongly disturbed areas.

Araneae and Hymenoptera from Malaise traps responded positively to the disturbance rate. Araneae may have been attracted to the Malaise traps. However, the Hymenoptera specimens collected in Malaise traps were composed of highly mobile wasps or parasitoids (see Appendix), which may respond to changes in herbivore abundance. In all three arthropod communities, Araneae and Hymenoptera, as the two major predator orders, were most sensitively affected by disturbance in the spatial context. This also supports the general view that higher trophic levels should be more susceptible to disturbance (Kruess and Tscharntke 1994, 2000; Holt et al. 1999). Diptera consistently showed no significant response to windthrow disturbance in the three communities, suggesting that this taxon was too ubiquitous to vary in response to windthrow disturbance at the order level. The significant responses of detritivores, such as Opiliones (beating), Isopoda (beating), Collembola (beating), and Psocoptera (sweeping), were uninterpretable in terms of their direction, although Schowalter and Ganio (1999) reported that detritivores were less abundant in tree-fall gaps.

The defined functional spatial scale also varied among arthropod orders, partly reflecting their dispersal abilities according to the ecological traits of each order. The spatial scales for Araneae (beating, sweeping, and Malaise trap), Isopoda (beating), Lithobiomorpha (beating), and Hymenoptera (beating and sweeping; see Appendix) were <30 m in radius. These orders represent wingless arthropods. In contrast, the spatial scales were >50 m for flying arthropods such as Coleoptera (beating), Hemiptera (sweeping), Hymenoptera (Malaise trap; see Appendix), and Lepidoptera (Malaise trap). However, results on some wingless arthropods such as Opiliones (beating) and Collembola (beating) are unexplainable at the present, and therefore our explanations on the relationship between the functional spatial scale and dispersal ability are fractions of the possible ones.

Upon examining the relationship between trophic level and spatial distribution, Holt (1996) hypothesized that the density of species of higher trophic levels is determined at larger spatial scales than that of species in lower trophic levels. Accordingly, herbivores would be confined to local habitat patches, whereas the spatial distribution of predators should encompass several prey populations, and thus, many habitat patches. However, we found no evidence to support this hypothesis, except for parasitoid wasps of the Hymenoptera. The principal reason for this lack of support is that the relationship between body size and trophic level was confounded because we analyzed the relationship at the order level (see also Thies et al. 2003). Body size is a valid predictor of how organisms acquire resources in space (Roland and Taylor 1997; Ritchie and Olff 1999).

We did not consider landscape characteristics other than gap rate. Tree species composition, ecotone, forest edge, and rivers or streams, may function as sources of species diversity (Schowalter and Ganio 1999). Attempts to quantify habitat diversity (Weibull et al. 2000; Kruess 2003), such as forest type and ecotone area, in the landscape context and evaluate the contribution of the interaction between disturbance rate and habitat diversity to species diversity are potentially valuable for future research. We focused on the variation in taxon richness at the community level and abundance at the order level; as a consequence, we detected no scale-dependent responses to windthrow disturbance at the community level. However, the analysis of changes in community composition in response to disturbance using multivariate models and defining the spatial scale at a community level may be promising approaches.

Our study is informative for the conservation of forest entomofauna. It is necessary to quantify the amount of area required to conserve biodiversity in a landscape context, but current approaches to examining the relationship between biodiversity and ecosystem services are mostly unconcerned with spatial processes (for reviews see Schwartz 1999; Tscharntke et al. 2005). Our results provide evidence that different groups of organisms have different functional spatial scales at which they specifically respond to habitat structure. Some arthropod taxa showed statistically significant positive or negative responses to windthrow disturbance at order-specific spatial scales, reflecting their typical modes of life. Therefore, conservation plans based on the census or monitoring of only a portion of the taxa will be problematic in conserving biodiversity and ecosystem function at the landscape level. Effective plans for the conservation of biodiversity and ecosystem services should be based on the understanding of spatial-scale-dependent processes in community dynamics and interactions among different organisms and environmental elements under a spatial landscape mosaic pattern (Wiens et al. 1993; Wiegand et al. 1999; Holland et al. 2004).

The direction of the response to windthrow disturbance and the spatial scale of the landscape context determining the variation in abundance were fairly consistent with the ecological traits and trophic levels of each order. This implies that interactions among different groups of organisms should vary under the spatial context of the landscape mosaic. For example, habitat selection by predators at the spatial scales of their search area should be affected by the response of their prey to tree-fall gap dynamics. A prey–predator community would be assembled through complicated spatial processes (e.g., Holt 1996). Community organization at the landscape level would vary spatially through the various scale-dependent responses of and interactions among component organisms. This suggests that the concept of community assembly (Chase 2003) in a spatial context should be applied to understand ecosystem structure and function at the landscape level; few studies, however, have demonstrated the effects of landscape contexts on local community structure (Roland and Taylor 1997; Thies and Tscharntke 1999; Thies et al. 2003). Spatially explicit perspectives that link the specific use of space by organisms at the spatial scale the ecological process is experienced are required to resolve the responses of populations, communities, and biotic interactions in the landscape context.

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References

Chase JM (2003) Community assembly: when should history matter? Oecologia 136:489–498

Gonzalez A, Lawton JH, Gilbert FS, Blackburn TM, Evans-Freke I (1998) Metapopulation dynamics, abundance, and distribution in a microecosystem. Science 281:2045–2047

Holland JD, Bert DG, Fahrig L (2004) Determining the spatial scale of species' response to habitat. BioScience 54:227–233

Holt RD (1996) Food webs in space: an island biogeographic perspective. In: Polis GA, Winemiller KO (eds) Food webs: integration of patterns and dynamics. Chapman & Hall, New York, pp 313–323

Holt RD, Lawton JH, Polis GA, Martinez ND (1999) Trophic rank and the species–area relationship. Ecology 80:1495–1504

Hutchings MJ, John EA, Stewart AJA (2000) The ecological consequences of environmental heterogeneity. Cambridge University Press, Cambridge

Joern A (2005) Disturbance by fire frequency and bison grazing modulate grasshopper assemblages in tallgrass prairie. Ecology 86:861–873

Kareiva P (1990) Population-dynamics in spatially complex environments—theory and data. Philos Trans R Soc Lond Biol 330:175–190

Kareiva P, Wennergren U (1995) Connecting landscape patterns to ecosystem and population processes. Nature 373:299–302

Kramer MG, Hansen AJ, Taper ML, Kissinger EJ (2001) Abiotic controls on long-term windthrow disturbance and temperate rain forest dynamics in southeast Alaska. Ecology 82:2749–2768

Kramer MG, Sollins P, Sletten RS (2004) Soil carbon dynamics across a windthrow disturbance sequence in southeast Alaska. Ecology 85:2230–2244

Kruess A (2003) Effects of landscape structure and habitat type on a plant–herbivore–parasitoid community. Ecography 26:283–290

Kruess A, Tscharntke T (1994) Habitat fragmentation, species loss, and biological control. Science 264:1581–1584

Kruess A, Tscharntke T (2000) Species richness and parasitism in a fragmented landscape: experiments and field studies with insects on *Vicia sepium*. Oecologia 122:129–137

McCullagh P, Nelder JA (1989) Generalized linear models. Chapman & Hall, London

Parsons M, McLoughlin CA, Kotschy KA, Rogers KH, Rountree MW (2005) The effects of extreme floods on the biophysical heterogeneity of river landscapes. Front Ecol Environ 3:487–494

Pascual M, Guichard F (2005) Criticality and disturbance in spatial ecological systems. Trends Ecol Evol 20:88–95

Pettorelli N, Vik JO, Mysterud A, Gaillard JM, Tucker CJ, Stenseth NC (2005) Using the satellite-derived NDVI to assess ecological responses to environmental change. Trends Ecol Evol 20:503–510

Pickett STA, Cadenasso ML (1995) Landscape ecology—spatial heterogeneity in ecological systems. Science 269:331–334

Polis GA, Anderson WB, Holt RD (1997) Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annu Rev Ecol Syst 28:289–316

R Development Core Team (2005) A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Ribas CR, Sobrinho TG, Schoereder JH, Sperber CF, Lopes-Andrade C, Soares SM (2005) How large is large enough for insects? Forest fragmentation effects at three spatial scales. Acta Oecol/Int J Ecol 27:31–41

Ritchie ME, Olff H (1999) Spatial scaling laws yield a synthetic theory of biodiversity. Nature 400:557–560

Roland J, Taylor PD (1997) Insect parasitoid species respond to forest structure at different spatial scales. Nature 386:710–713

Schowalter TD, Ganio LM (1999) Invertebrate communities in a tropical rain forest canopy in Puerto Rico following Hurricane Hugo. Ecol Entomol 24:191–201

Schowalter TD, Zhang YL, Progar RA (2005) Canopy arthropod response to density and distribution of green trees retained after partial harvest. Ecol Appl 15:1594–1603

Schwartz MW (1999) Choosing the appropriate scale of reserves for conservation. Annu Rev Ecol Syst 30:83–108

Sinton DS, Jones JA, Ohmann JL, Swanson FJ (2000) Windthrow disturbance, forest composition, and structure in the Bull Run basin, Oregon. Ecology 81:2539–2556

Smith F, Witman JD (1999) Species diversity in subtidal landscapes: maintenance by physical processes and larval recruitment. Ecology 80:51–69

Steffan-Dewenter I, Munzenberg U, Burger C, Thies C, Tscharntke T (2002) Scale-dependent effects of landscape context on three pollinator guilds. Ecology 83:1421–1432

Thies C, Roschewitz I, Tscharntke T (2005) The landscape context of cereal aphid–parasitoid interactions. Proc R Soc Lond B Biol Sci 272:203–210

Thies C, Steffan-Dewenter I, Tscharntke T (2003) Effects of landscape context on herbivory and parasitism at different spatial scales. Oikos 101:18–25

Thies C, Tscharntke T (1999) Landscape structure and biological control in agroecosystems. Science 285:893–895

Tscharntke T, Klein AM, Kruess A, Steffan-Dewenter I, Thies C (2005) Landscape perspectives on agricultural intensification and biodiversity—ecosystem service management. Ecol Lett 8:857–874

Turner MG, Gardner RH (1991) Quantitative methods in landscape ecology: the analysis and interpretation of landscape heterogeneity. Springer–Verlag, New York

Weibull AC, Bengtsson J, Nohlgren E (2000) Diversity of butterflies in the agricultural landscape: the role of farming system and landscape heterogeneity. Ecography 23:743–750

Wiegand T, Moloney KA, Naves J, Knauer F (1999) Finding the missing link between landscape structure and population dynamics: a spatially explicit perspective. Am Nat 154:605–627

Wiens JA, Stenseth NC, Vanhorne B, Ims RA (1993) Ecological mechanisms and landscape ecology. Oikos 66:369–380

With KA, Cadaret SJ, Davis C (1999) Movement responses to patch structure in experimental fractal landscapes. Ecology 80:1340–1353

With KA, Pavuk DM, Worchuck JL, Oates RK, Fisher JL (2002) Threshold effects of landscape structure on biological control in agroecosystems. Ecol Appl 12:52–65

Figure Legends

Fig. 1 Map of the study site, the Tomakomai Experimental Forest, Hokkaido, northern Japan. White cell shows the canopy gap and grey one shows living foliages. (a) Location of 30 survey plots (solid circle) and the distribution of large gaps (white area) created by windthrow disturbance from typhoon no. 18 in September 2004. (b) Two example plots with high and low disturbance rates; five nested circular sectors ranging from 100 to 500 m in radius are indicated around each survey plot.

Fig. 2 Disturbance-rate trajectories evaluated within nested circular sectors increasing in radius from 10 to 500 m around 30 survey plots.

Fig. 3 Scale-dependent responses of arthropod order richness to windthrow disturbance in communities sampled by (a) beating canopy vegetation, (b) sweeping forest-floor vegetation, and (c) using Malaise traps. The Akaike information criterion (AIC) for each model was plotted against the spatial scale (radius of the survey plot) at which the disturbance rate was evaluated. The model with the lowest AIC (indicated by an asterisk) was selected as the best-fitting model, and the corresponding scale was regarded as the "functional spatial scale." The solid line indicates the AIC for the null model independent of disturbance rate as an explanatory factor.

Table 1 The selected model that best explains the variation in abundance across the 30 survey plots by windthrow disturbance rate (DR), with the results of likelihood-ratio tests and the "functional spatial scale" for each arthropod order, shown separately for communities sampled by beating canopy vegetation, sweeping forest-floor vegetation, and using Malaise traps. For Orthoptera, no values are given for any sampling, because the number of individuals captured through all sampling was less than five.

Order	Beating							Sweeping				
	Intercept	DR Coefficient	Likelihood-ratio test			Response direction	Spatial scale (m)	Intercept	DR Coefficient	Likelihood-ratio test		
			Null deviance (df =29)	Residual deviance (df =28)	P (χ^2)					Null deviance (df =29)	Residual deviance (df =28)	P (χ^2)
Opiliones	1.7821	-3.9907	39.483	33.738	0.017*	negative	130	3.2103	-1.0209	34.205	31.556	0.104
Araneae	3.3957	-0.7381	35.715	30.956	0.029*	negative	10	4.0491	-0.7293	37.460	30.480	0.008**
Isopoda	0.2367	-47.854	18.891	8.190	0.001**	negative	10	-5.2642	18.605	8.866	8.335	0.466
Lithobiomorpha	0.3054	-14.402	32.802	18.842	<0.001***	negative	10	-	-	-	-	-
Collembola	-8.9743	29.969	23.714	11.589	<0.001***	positive	150	-	-	-	-	-
Dermaptera	1.3335	-1.0309	34.728	33.232	0.221	-	-	1.1241	-1.4310	35.486	34.727	0.384
Orthoptera	-	-	-	-	-	-	-	-	-	-	-	-
Psocoptera	0.4495	1.4279	35.835	34.893	0.332	-	-	-1.8583	7.8362	33.056	27.363	0.017*
Hemiptera	1.6057	1.0837	32.549	31.634	0.339	-	-	1.9759	2.7689	37.730	31.287	0.011*
Mecoptera	-	-	-	-	-	-	-	-4.1529	9.3121	16.118	13.949	0.141

Neuroptera	-0.7388	-3.0768	19.623	18.911	0.399	-	-	-0.0625	0.6802	31.760	31.291	0.493
Trichoptera	-	-	-	-	-	-	-	-	-	-	-	-
Diptera	0.4783	2.2326	37.094	33.846	0.071	-	-	4.6789	4.3297	33.731	31.851	0.170
Hymenoptera	3.9151	-3.3854	45.669	32.443	<0.001***	negative	10	5.7530	-1.5151	36.889	31.252	0.018*
Coleoptera	2.4001	3.7609	36.309	30.382	0.015*	positive	290	2.6036	3.2363	33.028	30.372	0.103
Lepidoptera	1.9066	1.2838	35.912	34.251	0.198	-	-	2.6662	1.5341	40.524	31.589	0.003**

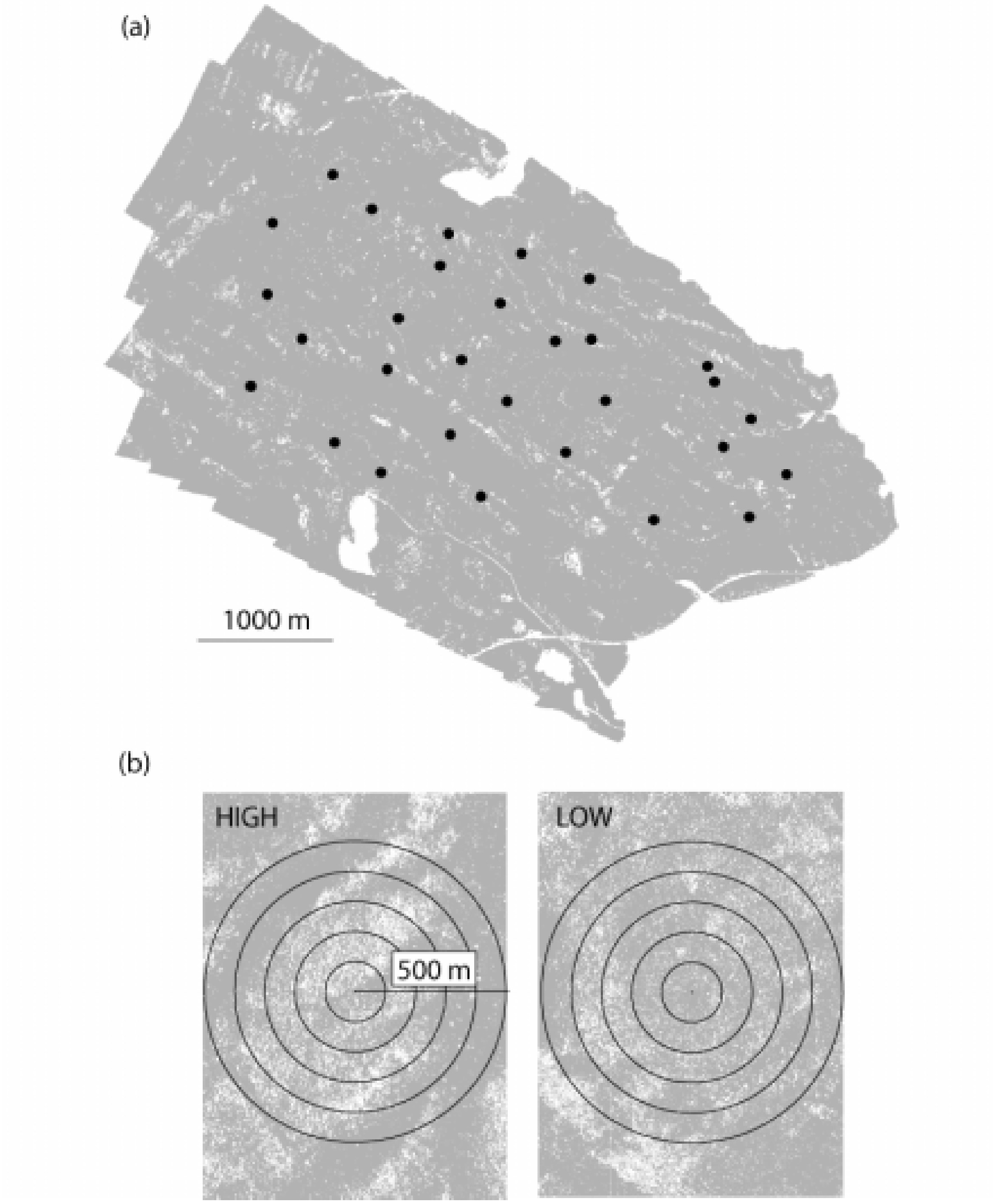
Table 1 (continued)

Sweeping		Malaise trap						
Response direction	Spatial scale (m)	Intercept	DR Coefficient	Likelihood-ratio test			Response direction	Spatial scale (m)
				Null deviance (df = 29)	Residual deviance (df = 28)	P (χ^2)		
-	-	-	-	-	-	-	-	-
Negative	10	-1.2430	3.4938	32.212	27.031	0.023*	positive	30
-	-	-	-	-	--	-	-	-
-	-	-	-	-	-	-	-	-
-	-	-0.0057	2.2404	34.420	33.621	0.371	-	-
-	-	-3.9400	5.8780	19.334	10.829	0.004**	positive	10
-	-	-	-	-	-	-	-	-
Positive	110	0.7481	-7.9969	26.947	26.400	0.460	-	-
Positive	90	0.1649	2.2608	36.920	34.816	0.147	-	-
-	-	-	-	-	-	-	-	-
-	-	2.8051	-26.384	16.118	14.084	0.154	-	-
-	-							
-	-	3.8981	5.7800	34.001	33.004	0.318	-	-
Negative	30	0.9511	4.5808	46.196	32.984	<0.001***	positive	70

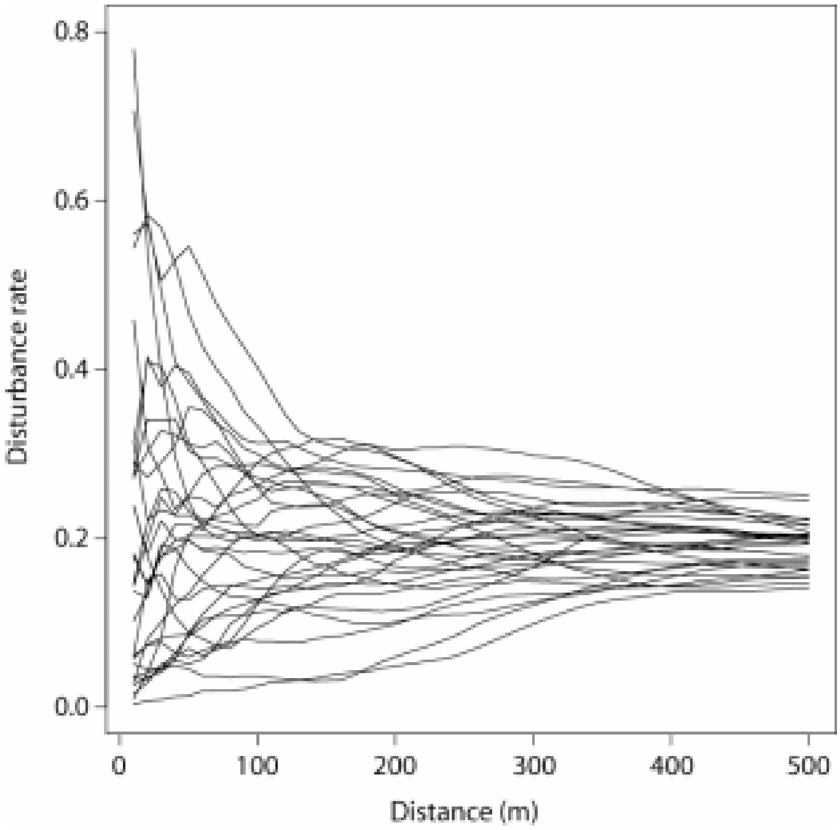
-	-	1.6623	1.2386	36.279	34.566	0.191	-	-
Positive	10	1.0841	3.2238	45.256	30.053	<0.001***	positive	50

*$P < 0.5$, **$P < 0.01$, ***$P < 0.001$.

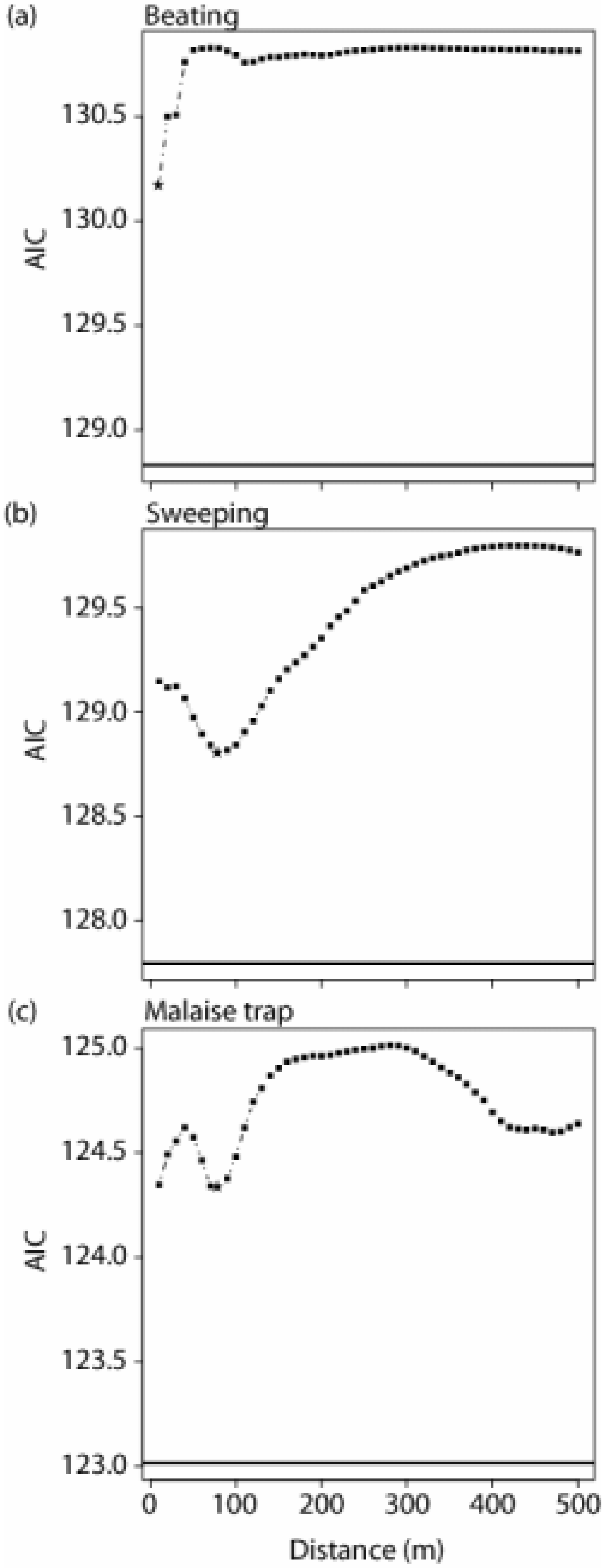
Hirao et al. Fig. 1



Hirao et al. Fig. 2



Hirao et al. Fig. 3



Appendix Percentage abundance of each guild in four dominant orders captured by beating, sweeping and Malaise trap.

	Herbivore	Detritivore*	Carnivore (winged)	Carnivore** (wingless)
Beating				
Coleoptera	71.8	22.4	5.8	0
Diptera	1.6	87.3	11.1	0
Lepidoptera	100	0	0	0
Hymenoptera	0	0	5.4	94.6
Sweeping				
Coleoptera	55.4	38.7	5.9	0
Diptera	0.2	98.4	1.4	0
Lepidoptera	100	0	0	0
Hymenoptera	0.2	0	63.4	36.4
Malaise trap				
Coleoptera	48.5	49.0	2.5	0
Diptera	30.8	68.1	1.1	0
Lepidoptera	100	0	0	0
Hymenoptera	0	0	98.6	1.4

*Detritivore includes xylophagous and fungivorous species.

**Wingless carnivore is comprised of ants.