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Effects of windthrow disturbance on a forest bird community depend on spatial scale

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Abstract

Community structure is expected to be affected by spatial heterogeneity in a landscape. We examined the spatial-scale-dependent effects of windthrow caused by a large typhoon on a forest bird community. Typhoon events of this magnitude are rare in Hokkaido, Japan, occurring only once or twice a century. To assess the "functional spatial scale" at which bird groups (community, species, body-size class, and foraging guild) specifically responded to landscape heterogeneity, the canopy gap rate (CGR, gap percentage) was evaluated at different spatial scales by varying the radius of a circular landscape sector from 100 to 500 m stepwise by 10 m. We then analysed bird community responses, in terms of species richness and abundance, to CGR. Bird species richness did not significantly depend on CGR. In contrast, abundance was significantly dependent on CGR in many groups (species, body-size class, and foraging guild). The guild-level response was clearer than the species-level response, which suggests that the integration and filtration of species traits by guild can reveal a clear response of bird abundance to the extent of canopy gaps. For example, the scale dependence of responses to disturbance clearly varied among body-size classes, where larger birds had larger functional spatial scales. These results reveal that different groups of organisms have different functional spatial scales at which they respond to habitat heterogeneity. Our results also suggest that monitoring only a small number of species could be misleading for conserving biodiversity at the landscape level.

Zusammenfassung

Die Struktur einer Gemeinschaft sollte durch die räumliche Heterogenität in der Landschaft beeinflusst werden. Wir untersuchten die von der Raumskala abhängigen Effekte des Windwurfs nach einem schweren Taifun auf die Waldvogelgemeinschaft. Um die "funktionale Raumskala" abzuschätzen, bei der Vogelgruppen (Gemeinschaft, Art, Körpergrößenklassen, Nahrungsgilde) spezifisch auf die Landschaftsheterogenität reagierten, wurde die Kronenlückenrate (KLR, prozentualer Lückenanteil) bestimmt, indem der Radius eines kreisförmigen Landschaftsausschnitts in Schritten von 10 m von 100 m bis 500 m variiert wurde. Wir analysierten dann die Reaktion der Vogelgemeinschaft (gemessen als Artenreichtum und Abundanz) auf KLR. Der Artenreichtum der Vögel hing nicht signifikant von KLR ab. Dagegen gab es einen signifikanten Zusammenhang bei vielen Gruppen (Art, Körpergrößengilde, Nahrungsgilde). Die Reaktion war auf der Gildenebene deutlicher als auf der Artebene, was nahelegt, daß die Integration und

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Filtration von Arteigenschaften durch die Gildenzuordnung eine klare Reaktion der Vogeldichte auf das Ausmaß der Kronenlücken erkennbar werden lassen kann. Beispielsweise variierte die Skalenabhängigkeit der Reaktion auf die Störung deutlich zwischen den Körpergrößenklassen, wo große Vögel größere funktionale Raumskalen aufwiesen. Diese Ergebnisse zeigen, dass unterschiedliche Gruppen von Organismen unterschiedliche funktionale Raumskalen besitzen, bei denen sie auf die Habitatheterogenität reagieren. Unsere Ergebnisse legen auch nahe, daß das Monitoring einer nur geringen Anzahl von Arten für den Schutz der Biodiversität auf der Landschaftsebene irreführend sein könnte.

Keywords: Bird guild; Body size; Canopy gap; Functional spatial scale; Habitat heterogeneity; Species richness; Typhoon

Introduction

Most landscapes are spatially heterogeneous. The area, spatial arrangement, and connectivity of habitats potentially affect local species abundance, biotic interactions, and community structure (Kareiva 1990; Pickett & White 1985; Thies & Tscharntke 1999; Turner & Gardner 1991; Wiegand, Moloney, Naves, & Knauer 1999). Because organisms use various cues to find favourable habitats, responses to landscape heterogeneity, including favourable microhabitats and their arrangement, can vary among organisms (see Thies, Steffan-Dewenter, & Tscharntke 2003). Thus, the heterogeneity of a landscape can cause spatial variation in community structure through the responses of species with different habitat requirements (With, Cadaret, & Davis 1999; With, Pavuk, Worchuck, Oates, & Fisher 2002).

Disturbance events can be destructive for natural communities by removing organisms inhabiting the sites (Pickett & White 1985; Sousa 1984). On the other hand, they can create heterogeneity in a landscape, which may promote the diversity of the communities (Brawn, Robinson, Thompson, & Frank 2001). Fire in grasslands (e.g., Bond & Midgley 2001), wave action in rocky intertidal zones (e.g., Sousa 1979), or flooding in streams (e.g., Matthaei, Uehlinger, & Frutiger 1997), are important factors creating habitat heterogeneity (Brawn et al. 2001; Sousa 1984). In forest ecosystems, windthrow disturbance is a major agent generating a mosaic of heterogeneous habitat patches at various scales (Kramer, Hansen, Taper, & Kissinger 2001; Kramer, Sollins, & Sletten 2004; Sinton, Jones, Ohmann, & Swanson 2000). Canopy gaps caused by windthrow vary in size, from single fallen trees to blow-downs covering several hectares (Fuller 2000). The occurrence and abundance of animals in habitat patches can be strongly affected by the size and location of patches in the surrounding mosaic (Thies et al. 2003). Therefore, any habitat disturbance should affect inhabitants and their interactions in a spatial context (Pascual & Guichard 2005).

Many studies have emphasised the importance of habitat heterogeneity to maintain the diversity of birds (reviewed by Askins 2000; Brawn et al. 2001; Hinsley, Bellamy, Newton, & Sparks 1995). For forest ecosystems, gaps created by disturbances can strongly affect the distribution and diversity of birds (Drapeau et al. 2000; Fuller 2000). For example, the avian diversity of riparian forests along the Colorado River is threatened by a decrease in forest heterogeneity created by flood disturbance due to water flow control by damming (Askins 2000). Forest heterogeneity can affect bird diversity both positively (Bollinger & Switzer 2002; O'Leary & Nyberg 2000) and negatively (Ford, Barrett, Saunders, & Recher 2001; Rolstad 1991; Walters, Ford, & Cooper 1999). The influx of energy from outside forest fragments and structural complexity at the forest edge can support a greater number of birds (Bollinger & Switzer 2002), whereas the risk of predation is much higher at the forest edge, which can lower diversity in fragments (Hinsley, Bellamy, & Moss 1995; Walters et al. 1999). Thus, variation in response to habitat heterogeneity should be examined to understand the importance of habitat heterogeneity in maintaining avian community diversity.

Species-level responses are also expected, and population-level analyses should be performed to access habitat suitability and species-specific response to heterogeneity. However, Pearman (2002) suggested that examination of the effect of vegetation structure on avian community structure at the level of guilds is an advantageous and feasible approach when most species within a community are rare (Karr, Robinson, Blake, & Bierregaard 1990), making population-level analyses ineffective in this situation. Furthermore, a species-level examination may not be effective for conservation measures at the community-level, because many traits, such as foraging range, resource specialisation, population-size, or trophic position, can vary among species (Tscharntke & Brandl 2004). This can cause difficulties in detecting the causal factor for the community-level response to habitat heterogeneity. On the other hand, the focus on guilds or functional groups is another way to examine the question (Golden & Crist 1999, 2000). At the guild level, more coherent differences in the response to forest gap creation can be expected, because species that