



| | |
|------------------|---|
| Title | Patch size determines the strength of edge effects on carabid beetle assemblages in urban remnant forests |
| Author(s) | Soga, Masashi; Kanno, Nozomi; Yamaura, Yuichi; Koike, Shinsuke |
| Citation | Journal of Insect Conservation, 17(2), 421-428 https://doi.org/10.1007/s10841-012-9524-x |
| Issue Date | 2013-04 |
| Doc URL | http://hdl.handle.net/2115/55282 |
| Type | article (author version) |
| File Information | soga_et_al_2013_j_insect_conserv-1.pdf |



[Instructions for use](#)

Patch size determines the strength of edge effects on carabid beetle assemblages in urban remnant forests

Masashi SOGA^a, Nozomi KANNO^a, Yuichi YAMAURA^b, Shinsuke KOIKE^a

^a Tokyo University of Agriculture and Technology, 3-5-8 Saiwai, Fuchu, Tokyo 183-8509, Japan

^b Division of Environmental Resources, Graduate School of Agriculture, Hokkaido University, Nishi 9, Kita 9, Kita-ku, Sapporo 080-8589, Japan

Corresponding author: Masashi Soga

Tokyo University of Agriculture and Technology, 3-5-8 Saiwai, Fuchu, Tokyo 183-8509, Japan .

E-mail address: [soga06154053\(a\)yahoo.co.jp](mailto:soga06154053(a)yahoo.co.jp)

Tel: +81-42-367-5630; Fax: +81-42-364-7812

ABSTRACT

Habitat fragmentation due to urbanization is increasing rapidly worldwide. Although patch area and edge effect are both important determinants of species diversity and the number of individuals in fragmented landscapes, studies that tested interaction between two effects were limited. Here we examined the interaction between area and edge effects on species richness and the number of individuals of carabids in highly urbanized forests in Tokyo, central Japan. We surveyed carabids in each of 26 forest patches (1.1–121.6 ha) using pitfall traps set in both edge and interior zones. First, we correlated the edge-to-interior differences of both species richness and the number of individuals with patch area. Second, we examined the interaction between patch area and distance to the edge on species richness and the number of individuals using generalized linear models. We found a significant decrease in carabid species richness and the number of individuals in edge zones. The edge-to-interior differences in both species richness and the number of individuals were positively correlated with patch area. Model selection revealed the evident interaction effects between patch area and distance to the edge: higher number of individuals was predicted in only large interior zones. Our results indicated that carabid beetle assemblages were influenced by the interaction between area and edge effects. Thus, in urban areas where small forest remnants dominate, circularizing the shape of the forest patches to maximize the core areas may be the most feasible and realistic means to preserve biodiversity.

Keywords: area effects, carabid beetles, edge effects, forest fragmentation, urban forests, urbanization

INTRODUCTION

Today, more than half of the world's human inhabitants live in cities, and this proportion will increase further in the next 50 years (Grimm et al. 2008), making this an 'urban century' (Gaston 2010). Global urbanization accelerates the mass production and consumption of natural resources (Millennium Ecosystem Assessment 2005; Bagliani et al. 2008), causing many types of land-use changes (Kareiva et al. 2007; Gaston 2010). Therefore, understanding the causes, processes, and ecological consequences of land-use and land-cover changes, including urbanization, is considered as a critical topic in landscape ecology (Wu and Hobbs 2002), and clarifying the effects of urbanization on regional biodiversity is crucial for future biodiversity conservation (Dearborn and Kark 2009). Among the large-scale landscape changes that may profoundly influence community dynamics, habitat fragmentation is considered to be one of the greatest threats to global biodiversity loss (Fahrig 2003) and consequently attracts much attention in landscape ecology and conservation biology (Tscharntke and Brandl 2004; Ewers and Didham 2006).

In fragmented landscapes, patch area and shape complexity are important factors determining species diversity within patches (Fahrig 2003; Fletcher et al. 2007; Yamaura et al. 2008). In particular, the positive relationship between patch area and species richness is one of the most general laws in ecology (Lomolino 1990; Peay et al. 2007). Compared with small patches, large patches are more likely to intercept potential colonists ('*target area effect*'; Lomolino 1990) and have lower extinction rates due to their greater population sizes (e.g., MacArthur and Wilson 1967; Russell et al. 2006). Moreover, large patches may have more habitat heterogeneity and are more complex, consequently promoting an increase in the number of species (e.g., Connor and McCoy 1979; Russell et al. 2006). Because patches with complex shapes have much higher proportions of edge habitat relative to core habitat than patches of the same size with simpler shapes (Laurance and Yensen 1991), the population densities of core-dwelling species are likely to decrease in such patches due to edge effects (Woodroffe et al. 1998; Ries et al. 2004; Yamaura et al. 2008).

Recently, the rates of species loss and population declines in small patches were reported to accelerate as a result of synergistic effects between area loss and edge effects (Ewers and Didham 2007; Ewers et al. 2007). Ewers et al. (2007) and Banks-Leite et al. (2010) demonstrated that differences in species richness and community composition between edge and core zones are distinct only in large patches; differences in small patches are obscured because they have high perimeter/area ratios and their centers are consequently affected by multiple edges (Malcolm 1994). Because all areas within small patches are subject to edge

effects, forest-dependent species would be expected to disappear. Ewers and Didham (2007) also demonstrated that the effects of shape complexity on population density and size are altered by patch size, indicating that area and edge effects interact. Because habitat fragmentation and perimeter/area ratios simultaneously decrease as patch size increases (Fahrig 2003; Ewers and Didham 2006; Laurance 2008), the interaction between patch area and edge effects is considered to be universal in terrestrial landscapes and one of the most important processes that degrade biodiversity (Fletcher et al. 2007).

From a conservation viewpoint, such an interaction suggests that the core zone is more important for the diversity and the number of individuals of core-dwelling species than the edge zone. Consequently, single large-circular reserves are most desirable (e.g. Diamond 1975). However, especially in urban areas, preserving or restoring large reserve areas is often difficult because of the high costs associated with their protection (Franklin 1993). Therefore, urban planners and conservation agencies need to evaluate whether increasing the circularization of patches can compensate for the inherent disadvantages of small urban forests. Urban forests offer wildlife habitat and improve human health and well-being (Gaston 2010), thus detecting interactions between patch area and shape and increasing patch quality by circularizing small patches are crucial for habitat management and restoration in fragmented landscapes (Ewers et al. 2007). If this interaction will degrade biodiversity in small patches in urban areas, clarifying the mechanism of the interaction will be crucial for conserving urban biodiversity in the future.

Here, we examined the relative importance of area and edge effects and their interaction for carabid beetle assemblages in Tokyo, central Japan, a '*hyper city*' or '*megacity*' of more than 20 million inhabitants (United Nations 2008). In western Tokyo, deciduous forests were once maintained as part of the traditional agricultural system and were widespread. However, since 1970, many of these deciduous forests have been entirely lost due to one of the most drastic urbanizations in Japan, the '*Tama Newtown Development*'. The remaining forest patches, which vary in size and shape, provide an excellent model system to examine area and edge effects in an urban area (Appendix 1). In Japan, most carabid species depend on forest environments for foraging, egg-laying, and hibernation (Sota 2002) and are consequently sensitive to forest fragmentation (e.g., Rainio and Niemelä 2003; Fujita et al. 2008). In this study, we tested the prediction that edge effects would interact with patch area such that the magnitude of edge-to-interior differences in species richness and the number of individuals of carabid beetles would increase with patch size.

METHODS

Study area and sampling sites

The study site (approximately 150 km²) is located in the Tama area, southwestern Tokyo, central Japan (Appendix 1). The western boundary of the study area was formed by a mountain range dominated by Mount Takao (599 m a.s.l.). The forest patches were dominated by deciduous forests of two oak species, *Quercus serrata* and *Q. acutissima*, with *Pinus densiflora*, *Abies firma*, and the evergreen oaks *Q. glauca* and *Q. acuta* also present. In this region, such deciduous forests were mostly maintained as part of the traditional agricultural system. Past aerial photographs show that such deciduous forests were once widespread in the study area until 1970. However, approximately from 1970 to 1980, many of these deciduous forests have been lost and fragmented rapidly due to the Tama New Town Development. These data suggest that the origin of forest patches in this region is the same, and they have relatively similar fragmentation history. Now, the remaining forest patches are small and isolated within a matrix of mainly residential areas, traffic roads, and office buildings. A total of 26 forest patches that ranged in area from 1.1 to 121.6 ha were selected for this study. We classified the patches into three size categories: small (1–5 ha, n = 9), medium (5.1–10 ha, n = 8), and large (>10.1 ha, n = 9) (Appendix 1). We defined the forest edge zone as a strip 20-m wide extending from the border of each patch into the forest and the forest interior zone as the remaining core area, because it is reported that woody plant species composition changes drastically in the border of 15 – 30-m from the forest edge in Japanese lowland forests (Iwasaki and Ishii 2005). Therefore, in this study, we sampled two habitat types (i.e. edge and interior habitat) from sites of three different sizes: large-interior (LI), large-edge (LE), medium-interior (MI), medium-edge (ME), small-interior (SI), and small-edge (SE) sites (Appendix 1).

Other authors have stressed the strong influence of other patch factors such as shape complexity (Laurence 1991) and connectivity (Vos and Stumpel 1995) on the number of species in fragmented landscapes. For carabids, 3- dimensional patch factors (e.g. orientation and slope) are also considered as important drivers determining the species distribution (Sota 2002). Therefore, we measured the shape index (Laurence and Yensen 1991) and connectivity (i.e. isolation index) (Hanski 1994) and average slope and orientation of each forest patch using ArcGIS (ESRI, Redlands, CA) and a 10-m solution digital elevation model. However, in this study, all these geographic factors had no significant effects on both species richness and the number of individuals (Soga unpublished data), so we removed these five factors from later analysis. Our main purpose is whether strength of edge effect on carabid

beetle assemblages can be explained by only patch size (Ewers et al. 2007).

Carabid beetles sampling

We sampled carabid beetles using pitfall traps. In each patch, trapping was conducted in early summer (May–June) and autumn (September) of 2010. In both sampling seasons, we placed 40 pitfall traps within each patch, with 20 traps in the interior zone and 20 traps in the edge zone. The traps were 10 cm in diameter and 12 cm in depth and contained approximately 100 mL of propylene glycol as a preservative (Lemieux and Lindgren 1999). Traps were collected after two days. Individuals caught in each trap during the trapping period were dried, mounted, and identified to species, and data were pooled (i.e. mixing summer and autumn samples) for analyses. In this study, we classified all 23 carabid beetle species that were observed in the field surveys as either ‘forest species’ or ‘non-forest species’ based on Lake Biwa Museum (2012) and unpublished field experiences of the first author (M. Soga). Species that use woods or forests as their main habitat were classified as ‘forest species’. On the other hand, species that usually inhabit openlands or grasslands and do not need woody conditions were classified as non-forest species. In general, forest species are more sensitive to habitat fragmentation (e.g. Bender and Fahrig 2005; Devictor et al. 2008). Therefore, we excluded non-forest species (6 species and 6 individuals) and used only forest species (17 species and 1497 individuals) in latter analyses.

Statistical analysis

Patch edge versus interior

We sampled carabid beetles in two habitat type from sites of three different sizes (i.e., LI, LE, MI, ME, SI, and SE sites). To estimate the strength of edge effects on carabid assemblages in each patch, we calculated the differences in species richness and number of individuals between the edge and interior zones (i.e. species richness and individuals of interior zone minus species richness of edge zone). Then, we related these differences to log-transformed patch area using correlation coefficients and simple regression models.

Interaction between area and edge effects

Second, we examined the effect of distance to the forest border on carabid species richness and number of individuals. To examine the interactions between area and edge effects, we used generalized linear models (GLMs) with a Poisson distribution and a log-link function. The number of carabid species and the number of individuals in each sampling area

was used as a response variable, and patch area, distance to edge (in meters), and their interaction (area effect \times edge effect) were used as explanatory variables. To select the best of the five possible combination models (i.e. full model, null model, model containing only patch area, model containing only distance to edge and model containing both patch area and distance to edge, see also Table 1), we used the small-sample corrected version of Akaike's Information Criterion (AIC_c , Burnham and Anderson 2002). The AIC_c for each model quantifies its parsimony (based on the trade-off between the model fit and the number of parameters) relative to other models considered. All of the models were ranked by ΔAIC_c ($\Delta AIC_c = AIC_c - AIC_{c_{min}}$; where AIC_c and $AIC_{c_{min}}$ represented the i^{th} model and the best model in the model subset, respectively), such that the model with the minimum AIC_c had a value of 0. Models for which $\Delta AIC_c \leq 2$ were considered to have substantial support (Burnham & Anderson 2002). The plausibility of each model was quantified by its relative likelihood, which was proportional to the exponent of $-0.5 \times \Delta AIC_c$ given our data. For each candidate model, we divided this likelihood by sum of the all models, and compiled the Akaike weights (w_i). We conducted these analyses using the 'dredge' function in the 'MuMIn' package (ver. 1.0.0) (Barton 2009). All analyses were conducted using R software package (R Development Core Team 2003).

RESULTS

Patch edge versus interior

We recorded a total of 1,503 individuals belonging to 23 species in the 26 patches (Appendix 2). The samples were numerically dominated by *Eusilpha japonica* (496 individuals), *Pterostichus prolongatus* (340), *Carabus insulicola* (297), and *Carabus albrechti esakianus* (134). In total, we captured 22 (95.6 %) species in the interior zones and 11 (47.8 %) in the edge zones. Thirteen species were captured exclusively in interior zones, while only *Lesticus magnus* was captured exclusively in edge zones (1 individual). We found a significant decrease in the richness and the number of individuals of carabid species in edge zones (Mann-Whitney test, $n = 26$, $U = 184.5$, $p < 0.01$).

Interaction between area and edge effects

The strength of edge effects on species richness and the number of individuals was dependent on patch size: the edge-to-interior differences in species richness and the number of individuals were larger in large patches than in small patches (Fig. 2). The differences in species richness and the number of individuals between edge and interior zones were positively correlated to patch area (species richness: $r = 0.60$, $p = 0.001$; the number of individuals: $r = 0.43$, $p = 0.03$) (Fig. 2). By excluding one potential outlier in the number of individuals analysis (Fig. 2), a strong positive correlation was found ($r = 0.62$, $p < 0.001$).

Model selection based on AIC_c showed that full models (containing all three explanatory variables) were best supported for the number of individuals analyses (Tables 1, 2), suggesting that patch area and edge effect interacted. The full models (Tables 1, 2) predicted that interior zones in large patches had the highest number of individuals (Fig. 3). However, the interaction between patch area and edge effects was weak and model containing distance to edge was best supported in the species-richness analysis (Tables 1, 2).

DISCUSSION

Relative importance of edge and core zones in urban remnant forests

In this study, we captured 22 (1024 individuals) of 23 total carabid species in the interior zone, but only 11 species (479 individuals) in the edge zone (Appendix 2). These results indicate that the forest interior zone provided many carabid species with habitat indispensable to their persistence in our study area. In general, core areas are more stable, both abiotically and biotically (e.g., Murcia 1995); core areas within patches have been considered to be important determinants for forest-dependent species richness or the number of individuals (e.g., Ewers and Didham 2007; Yamaura et al. 2008).

In contrast to our results, in forest-grassland transects, carabid species richness in edge areas was typically highest, because edge areas harbored both forest-dependent and grassland (i.e. non-forest) species (Báldi and Kisbenedek 1994; Magura et al. 2001; Magura 2002). Also, in woodland-arable field transects, Bedford and Usher (1994) examined the distribution of carabids and reported that open habitats and forest edges had elevated species richness. Unlike these previous studies, however, we did not obtain high richness or the number of individuals of carabid species at the forest edges. One important difference between these previous studies and ours was that the matrix environments surrounding our patches were completely urbanized, whereas those in previous studies were mostly grasslands. Urbanization has substantial negative effects on carabids via high ground temperatures and low humidity (Magura et al. 2008). Traffic roads are also thought to have negative effects on the ability of carabids to migrate between patches (Koivula and Vermeulen 2005). Therefore, almost no species, including open-land species, would survive outside the remnant forest patches in our urbanized study area; consequently, species richness and the number of individuals of were both low in the edge zones. Although almost all grasslands in the matrix have been lost due to urbanization in this region, several small grasslands or openlands were left in forest patches. Therefore, in this study, 5 non-forest carabid beetle species would be found in interior zones.

Patch area as the driver of edge effect strength

In this study, large interior (LI) sites had the highest species richness and number of individuals, whereas those of other sites (i.e. LE, MI, ME, SI and SE) were low (Fig. 1). Consequently, the edge-to-interior differences in species richness and the number of individuals were especially clear in large patches, whereas those in small patches were not evident (Fig. 2). In this study, we found a five-fold increase in the strength of edge effects (i.e.

edge-to-interior differences in the number of individuals) when patch size increased by a factor of ten (e.g., a comparison between $10^{0.5}$ ha and $10^{1.5}$ ha) (Fig. 2). GLM analyses also supported that large interior sites had the highest number of individuals, whereas those of small patches were low even in the interior patches (Fig. 3). These results indicate that patch area not only had direct effects on carabid assemblages, but also indirect effects through edge effects (Ewers et al. 2007): i.e. there is an interaction between area and edge effects.

There are two main concepts of interactive effect between area and edge effects. First, Malcolm (1994) suggested that the total strength of the edge effect within patches is the sum of the edge effects from multiple edges (i.e., the ‘*additive model*’). Second, Ewers et al. (2007) demonstrated that there is a synergistic interaction between area and edge effects and that the strength of the edge effect increases exponentially with decreasing patch size (i.e., ‘*synergistic model*’). In either case, the models based on our results indicated that species losses and population declines associated with urbanization would be accelerated by both area and edge effects. Another reason why edge-to-interior differences were not evident in small patches may be that interior zones were not left in such small patches (i.e. small patches are composed of only edge zones).

Conservation and management implications for urban fragmented forests

Interactions between area and edge effects revealed by this study have particular relevance for the conservation and management of urban remnant forests. Based on our results, large interior habitats are most valuable for conserving diversity and populations of carabid species. In this study, we define the edge zone as a 20-m wide swath along the border of the forest patch following to Iwasaki and Ishii (2005). Theoretically, in this case, if a 1 ha circle were maintained, the edge area would not exceed the core area. This fact optimistically suggests that the maintenance of the forest interior is comparatively easy. However, in our study area, the edge area exceeded the core area even in 6 ha patches (Soga unpublished data) because patches in actual landscapes are not circular. Core area is rapidly lost as patch shape becomes increasingly irregular (Laurance and Yensen 1991). Furthermore, edge penetration distance depends on the abiotic environments (e.g. Magura 2002), so we might underestimate such distances in this study. From these reasons, species diversity in urban landscape, where most patches have complex shapes, may be more seriously impacted than formerly thought (Ewers and Didham 2008).

Based on these facts, the most effective strategy to conserve carabids in urbanized areas would be to establish large forest remnants with compact shapes (i.e. more circular shape). In

urban area, square shape may be more desirable for nature reserves than circular shape because cities are typically more likely to show linear designs. Therefore, to maintain populations that are able to resist local extinction, a single large nature preserve is more desirable than several small preserves of equal total area. However, in urban areas, forest patches are typically small and scattered. Therefore, instead of increasing patch area, simplifying the shapes of forest patches to minimize edge effects and to maximize the core areas may be the most feasible and realistic means of preserving biodiversity in urban woodlots (Yamaura et al. 2008). In fact, we observed high numbers of carabid individuals, even in small patches (Fig. 1). In this case, circularization of small forest patches, could compensate for their small population sizes. Therefore, (1) when large forest remnants remain, they should be preferentially preserved, and (2) when the small forest remnants dominate, their shapes should be circularized as an effective means of conserving forest-dependent species like carabids.

In this study, we demonstrated that carabid diversity was lowest in small patches due to a synergistic interaction between area and shape. However, the intrinsic value of small patches should not be overlooked, because such small patches could contribute to the persistence of regional populations by serving as stepping stones to larger patches (Urban and Keitt 2001). In fact, we observed several forest species in small forest patches. However, patterns of carabid beetle movement across patches are unclear in this study. Such metapopulation patterns merit further investigation using DNA and mark-recapture analyses.

REFERENCES

- Bagliani M, Galli A, Niccolucci V, Marchettini N (2008) Ecological footprint analysis applied to a sub-national area: The case of the Province of Siena (Italy). *J Environ Manag* 86: 354-364
- Báldi A, Kisbenedek T (1994) Comparative analysis of edge effect on bird and beetle communities. *Acta Zoologica* 40: 1-14
- Banks-Leite C, Ewers RM, Metzger JP (2010) Edge effects as the principal cause of area effects on birds in fragmented secondary forest. *Oikos* 119: 918-926
- Barton K (2009) MuMIn: multi-model inference. R package version 1. 0. 0.
- Bedford S, Usher M (1994) Distribution of arthropod species across the margins of farm woodlands. *Agri Ecosyst Environ* 48: 295-305
- Bender DJ, Fahrig L (2005) Matrix structure obscures the relationship between interpatch movement and patch size and isolation. *Ecology* 86: 1023-1033
- Burnham KP, Anderson DR (2002) Model selection and inference: a practical information-theoretic approach. Springer, New York
- Connor EF, McCoy ED (1979) The statistics and biology of the species-area relationship. *Amer Nat* 113: 791-833
- Dearborn DC, Kark S (2009) Motivations for conserving urban biodiversity. *Conserv Biol* 24: 432-440
- Devictor V, Julliard R, Jiguet F (2008) Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. *Oikos* 117: 507-514.
- Diamond JM (1975) The island dilemma: lessons of modern biogeographic studies for the design of natural reserves. *Biol Conserv* 7: 129-146
- ESRI. Inc., ArcView GIS ver. 3.2, ESRI Inc, Redlands, USA. (1999)
- Ewers RM, Didham RK (2006) Confounding factors in the detection of species responses to habitat fragmentation. *Biol Rev* 81: 117-142
- Ewers RM, Didham RK (2007) The effect of fragment shape and species' sensitivity to habitat edges on animal population size. *Conserv Biol* 21: 926-936
- Ewers RM, Didham RK (2008) Pervasive impact of large-scale edge effects on a beetle community. *Proc Nat Acad Sci USA* 105: 5426-5429
- Ewers RM, Thorpe S, Didham RK (2007) Synergistic interactions between edge and area effects in a heavily fragmented landscape. *Ecology* 88: 96-106
- Fahrig L (2003) Effects of habitat fragmentation on biodiversity. *Annu Rev Ecol Evol Syst* 34: 487-515

- Fletcher RJ, Ries L, Battin J, Chalfoun AD (2007) The role of habitat area and edge in fragmented landscapes: definitively distinct or inevitably intertwined? *Can J Zool* 85: 1017-1030
- Franklin JF (1993) Preserving biodiversity - species, ecosystems, or landscapes. *Ecol Appl* 3: 202-205
- Fujita A, Maeto K, Kagawa Y, Ito N (2008) Effects of forest fragmentation on species richness and composition of ground beetles (Coleoptera: Carabidae and Brachinidae) in urban landscapes. *Entomol Sci* 11: 39-48
- Gabriel D, Roschewitz I, Tschamntke T, Thies C (2006) Beta diversity at different spatial scales: plant communities in organic and conventional agriculture. *Ecol Appl* 16: 2011-2021
- Gauston KJ (2010) *Urban ecology*. Cambridge University Press, Cambridge
- Grimm NB, Faeth SH, Golubiewski NE, Redman CL, Wu JG, Bai XM, Briggs JM (2008) Global change and the ecology of cities. *Science* 319: 756-760
- Haila Y (2002) A conceptual genealogy of fragmentation research: From island biogeography to landscape ecology. *Ecol Appl* 12: 321-334
- Iwasaki A and Ishii H (2005) Vegetation structure of fragmented shrine/ temple forests in Southeastern Hyogo Prefecture –estimation of edge-effect distance and minimum conservation area–. *Hum Nat* 15: 29-41
- Kareiva P, Watts S, McDonald R, Boucher T (2007) Domesticated nature: shaping landscapes and ecosystems for human welfare. *Science* 316: 1866-1869
- Koivula MJ, Vermeulen HJW (2005) Highways and forest fragmentation - effects on carabid beetles (Coleoptera, Carabidae). *Landscape Ecol* 20: 911-926
- Kurosawa R, Askins RA (2003) Effects of habitat fragmentation on birds in deciduous forests in Japan. *Conserv Biol* 17: 695-707
- Lake Biwa Museum (2012)
http://www.lbm.go.jp/emuseum/zukan/gomimushi/kamei_list.html. Accessed Mar. 22, 2012.
- Laurance WF (1991) Edge effects in tropical forest fragments: application of a model for the design of nature reserves. *Biol Conserv* 57: 205–219
- Laurance WF (2008) Theory meets reality: how habitat fragmentation research has transcended island biogeographic theory. *Biol Conserv* 141: 1731-1744
- Laurance WF, Yensen E (1991) Predicting the impacts of edge effects in fragmented habitats. *Biol Conserv* 55: 77-92

- Lemieux J, Lindgren BS (1999) A pitfall trap for large-scale trapping of Carabidae: Comparison against conventional design, using two different preservatives. *Pedobiologia* 43: 245-253
- Lomolino MV (1990) The target area hypothesis – the influence of island area on immigration rates of non-volant mammals. *Oikos* 57: 297-300
- MacArthur RH, Wilson EO (1967) *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey
- Magura T, Tothmeresz B, Molnar T (2001) Forest edge and diversity: carabids along forest-grassland transects. *Biodivers Conserv* 10: 287-300
- Magura T (2002) Carabids and forest edge: spatial pattern and edge effect. *For Ecol Manag* 157: 23-37
- Magura T, Tothmeresz B, Molnar T (2008) A species-level comparison of occurrence patterns in carabids along an urbanisation gradient. *Landscape Urban Plann* 86: 134-140
- Malcolm JR (1994) Edge effects in central Amazonian forest fragments. *Ecology* 75: 2438-2445
- Millennium Ecosystem Assessment (2005) Washington, DC, USA.
- Murcia C (1995) Edge effects in fragmented forests: implications for conservation. *Trends Ecol Evol* 10: 58-62
- Peay KG, Bruns TD, Kennedy PG, Bergemann SE, Garbelotto M (2007) A strong species-area relationship for eukaryotic soil microbes: island size matters for ectomycorrhizal fungi. *Ecol Lett* 10: 470-480
- Rainio J, Niemelä J (2003) Ground beetles (Coleoptera: Carabidae) as bioindicators. *Biodivers Conserv* 12: 487-506
- R Development Core Team (2003) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, <http://www.R-project.org>.
- Ries L, Fletcher RJ, Battin J, Sisk TD (2004) Ecological responses to habitat edges: Mechanisms, models, and variability explained. *Annu Rev Ecol Evol Syst* 35: 491-522
- Russell GJ, Diamond JM, Reed TM, Pimm SL (2006) Breeding birds on small islands: island biogeography or optimal foraging? *J Anim Ecol* 75: 324-339
- Sota T (2002) *The Four Seasons of Carabid Beetles: The Evolution of Life History and the Species Diversity*. Ecological Library 8. Kyoto University Press, Kyoto.
- Tscharntke T, Brandl R (2004) Plant-insect interactions in fragmented landscapes. *Annu Rev Entomol* 49: 405-430
- United Nations (2008) *World Urbanization Prospects. The 2007 Revision*. New York:

United Nations

Urban D, Keitt T (2001) Landscape connectivity: a graph-theoretic perspective. *Ecology* 82: 1205-1218

Woodroffe R, Ginsberg JR (1998) Edge effects and the extinction of populations inside protected areas. *Science* 280: 2126-2128

Wu JG, Hobbs R (2002) Key issues and research priorities in landscape ecology: An idiosyncratic synthesis. *Landscape Ecol* 17: 355-365

Yamaura Y, Kawahara T, Iida S, Ozaki K (2008) Relative importance of the area and shape of patches to the diversity of multiple taxa. *Conserv Biol* 22: 1513-1522

Vos CC, Stumpel HP (1995) Comparison of habitat isolation parameters in relation to fragmented distribution patterns in the tree frog (*Hylea arborea*). *Landscape Ecol* 11: 203-214

FIGURE LEGENDS

Fig. 1

Carabid beetle species richness (left) and the number of individuals (right) in two habitat types from sites of three difference sizes (Appendix. 1). The horizontal bar in the boxplot indicates the median, the ends of the boxes indicate the interquartile range, and the whiskers indicate the 10th and 90th quantiles.

Fig. 2

Relationships between patch area and edge to the difference in species richness (left) and the number of individuals (right) between interior and edge habitats (i.e. species richness and individuals of interior zone minus species richness of edge zone). Lines indicate the fitted regression models. On the right, the white circle was a potential outlier that was not used to calculate the regression.

Fig. 3

Relationships between patch area and distance to forest edge and the number of individuals (right). Contour lines show carabid species richness predicted by the best model (full model) in Table 1.

SUPPLEMENTARY INFORMATION

Appendix 1

Map of forest cover in 2010 (gray) and 26 sampling patches (black) in the Tama Newtown Development, Tokyo, Japan, and depictions of two habitat types from sites of three different sizes (SE, small-edge; SI, small-interior; ME-medium-edge; MI, medium-interior; LE, large-edge; LI, large-interior).

Appendix 2

List of 23 carabid beetle species observed in this study.

Fig. 1

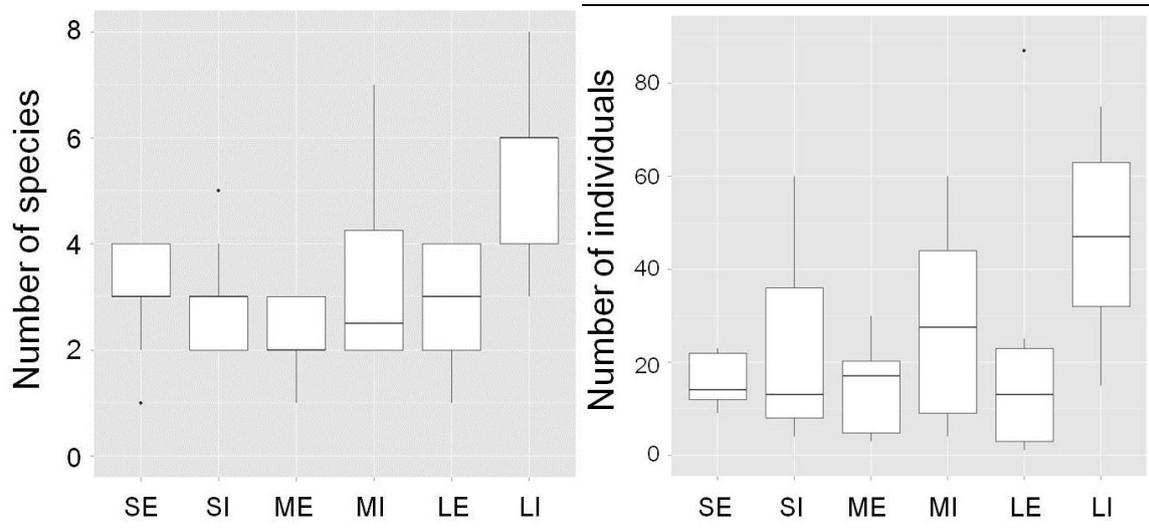


Fig. 2

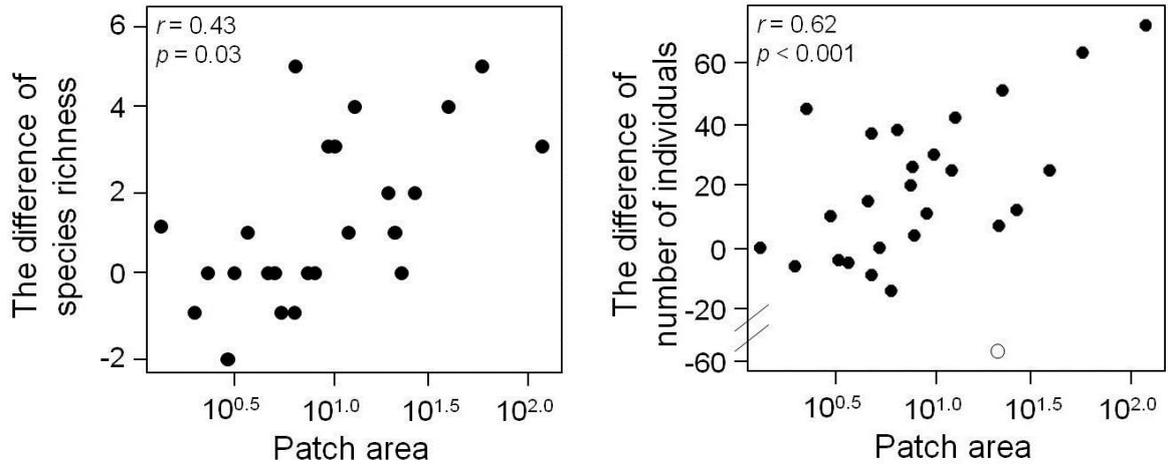


Fig. 3

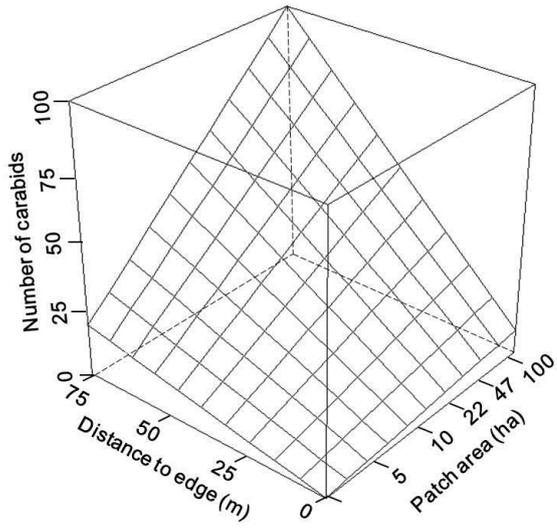


Table 1

Table 1. Results of model selection based on *Akaike information criterion*.

| <i>Rank</i> | <i>Variable (s)</i> | <i>K*</i> | <i>Deviation</i> | <i>AICc</i> | $\Delta AICc$ | w_i |
|------------------------------|-------------------------|-----------|------------------|-------------|---------------|-------|
| Species richness | | | | | | |
| Model 1 | Edge | 2 | -91.77 | 187.8 | 0.00 | 0.459 |
| Model 2 | Area + Edge | 3 | -91.21 | 188.9 | 1.14 | 0.260 |
| Model 3 | Area + Edge + Area×Edge | 4 | -90.15 | 189.2 | 1.38 | 0.230 |
| Model 4 | Area | 2 | -94.40 | 193.0 | 5.26 | 0.033 |
| Model 5 | null model | 1 | -96.04 | 194.2 | 6.38 | 0.019 |
| Number of individuals | | | | | | |
| Model 1 | Area + Edge + Area×Edge | 4 | -442.47 | 893.8 | 0.00 | 0.969 |
| Model 2 | Area + Edge | 3 | -447.10 | 900.7 | 6.90 | 0.031 |
| Model 3 | Edge | 2 | -460.05 | 924.4 | 30.55 | 0.000 |
| Model 4 | Area | 2 | -507.92 | 1020.1 | 126.27 | 0.000 |
| Model 5 | null model | 1 | -545.51 | 1093.1 | 199.29 | 0.000 |

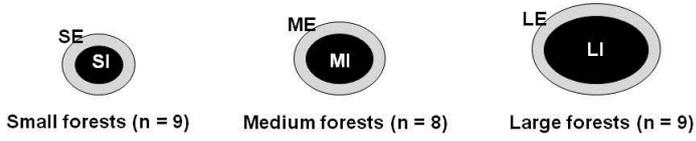
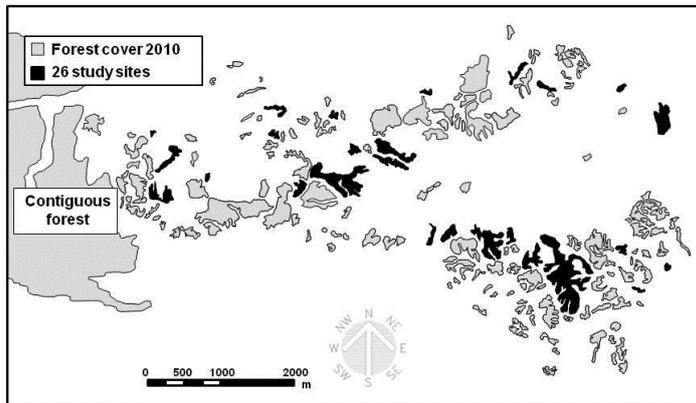
* Number of model parameters, $\Delta AICc$: *AICc* differences, w: Akaike weights (w_i).

Table 2

Table 2. Coefficients of best models (Model 1) in Table 1.

| <i>Coefficients</i> | <i>Estimate</i> | <i>SE</i> | <i>z-value</i> | <i>Pr(> z)</i> |
|-------------------------|-----------------|-----------|----------------|--------------------|
| Species richness | | | | |
| (intercept) | 1.49 | 0.86 | 5.92 | <0.0001 |
| Edge | 0.01 | 0.004 | 3.00 | 0.003 |
| Abundance | | | | |
| (intercept) | 2.77 | 0.13 | 20.99 | <0.0001 |
| Area | 0.03 | 0.11 | 0.31 | 0.76 |
| Edge | 0.00 | 0.004 | 0.92 | 0.36 |
| Area×Edge | 0.01 | 0.003 | 3.04 | 0.002 |

Appendix 1



Appendix 2

Appendix. List of 23 species observed in this study.

| Species | Interior | Edge | Total |
|------------------------------------|-----------------|-------------|--------------|
| <i>Carabus insulicola</i> | 186 | 111 | 297 |
| <i>Carabus albrechti esakianus</i> | 112 | 22 | 134 |
| <i>Leptocarabus procerulus</i> | 1 | 0 | 1 |
| <i>Trigonognatha cuprescens</i> | 1 | 0 | 1 |
| <i>Lesticus magnus</i> | 0 | 1 | 1 |
| <i>Pterostichus yoritomus</i> | 41 | 20 | 61 |
| <i>Pterostichus prolongatus</i> | 244 | 96 | 340 |
| <i>Pterostichus takaosanus</i> | 1 | 0 | 1 |
| <i>Synuchus nitidus</i> | 1 | 1 | 2 |
| <i>Synuchus cycloderus</i> | 41 | 5 | 46 |
| <i>Synuchus. ssp</i> | 30 | 12 | 42 |
| <i>Amara chalcites</i> | 12 | 22 | 34 |
| <i>Amara macronota ovalipennis</i> | 1 | 0 | 1 |
| <i>Harpalus tridens</i> | 1 | 0 | 1 |
| <i>Diplocheila zeelandica</i> | 1 | 0 | 1 |
| <i>Haplochlaenius costiger</i> | 3 | 0 | 3 |
| <i>Chlaenius abstersus</i> | 1 | 0 | 1 |
| <i>Chlaenius micans</i> | 9 | 0 | 9 |
| <i>Chlaenius naeviger</i> | 21 | 7 | 28 |
| <i>Chlaenius posticalis</i> | 1 | 0 | 1 |
| <i>Ophionea indica</i> | 1 | 0 | 1 |
| <i>Planetes puncticeps</i> | 1 | 0 | 1 |
| <i>Eusilpha japonica</i> | 314 | 182 | 496 |
| Species richness | 22 | 11 | 23 |
| Abundance | 1024 | 479 | 1503 |