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The effect of urban form on biodiversity potential and the extinction of
experience: land sharing and land sparing compared

(都市の形状が生物多様性と自然体験の消失に及ぼす影響：土地の節約戦略と
共有戦略の比較)

北海道大学 大学院農学院

環境資源学専攻 博士後期課程

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SUMMARY

1. Conservation and restoration of urban biodiversity have increasingly become a significant consideration in city planning policies. From a conservation viewpoint, this is because urban area potentially harbors richer biological communities than those in rural areas. Nature in cities also provides opportunities for regular encounters by urban dwellers (i.e. averting the "extinction of experience").
2. As cities are typically designed by top-down policy-making, initial development schemes have a crucial role in determining the capacity to sustain regional biodiversity and ecosystem services. Currently, urban development forms are classified into two alternatives: urban land-sparing (intensive development in a small land) and urban land-sharing (extensive development in a greater land).
3. In this thesis, I investigated relative benefits of urban land-sharing and land-sparing for biodiversity conservation and promotion of people's nature experience.
4. As a result, I found that urban land-sparing is a better option for biodiversity conservation in general. Especially in areas that will become heavily urbanised, land-sparing shows a remarkable conservation benefit. On the other hand, I also found an advantage of urban land-sharing to promote human-nature interactions in urban areas: people living in urban land-sharing regions use urban greenspaces more frequently than those in land-sparing regions.
5. This thesis revealed a potential conflict in the design of cities between the urban form that is most desirable for the protection of regional biodiversity, and that which best promotes people's nature experiences. The challenge is thus to reconcile biodiversity conservation and promotion of people's nature experiences in urban landscapes.

INTRODUCTION

INTRODUCTION

Global trends in urban development

“Battle for life on earth will be won or lost in urban areas” (CBD 2007)

Cities expand drastically around the world, which is faster than increasing rates of other land use types (Foley et al. 2005). In 2008, for the first time the world's urban population exceeded that of rural areas (Grimm et al. 2008). In Japan, this turning point has already been experienced in the middle of the last century, and today more than 90 % of population lives in urban areas. By 2050, the world's urban population is expected to reach 6.3 billion, which corresponds to two thirds of total Earth's population (United Nations 2011). Whilst urban settlements cover only 4% of the total terrestrial lands, they sustain more than half of the world's population and utilise 75% of the total amount of natural resources consumed globally. Ecological footprint of urban areas (i.e., a measure of human demand on the Earth's ecosystems) is thus much greater than the area of other land cover types. In the light of sustainable development and resource management, cities have received increasingly attention (Wu 2010).

Impacts of urban development on biodiversity

Urbanisation has negative impacts on native biodiversity both at local, landscape, and regional-levels (Gaston 2010). At a local-level, urban development converts regional natural ecosystems into highly modified (artificial) systems, which makes urban ecosystems as “novel ecosystems” (Hobbs et al. 2009; Kowarik 2011). In urban ecosystems, both biotic (e.g., species interactions) and abiotic environmental features (e.g., temperature, wind direction, noise and light pollutions) are greatly different with those of other common ecosystems (Gaston 2010). Many previous researches

demonstrated that these drastic environmental changes degrade natural ecosystems and biological communities (see review by McKinney 2008). Although some generalist (common) species can adapt to such highly modified environments, other specialist (rare and native) species cannot survive (Sorace and Gustin 2009; Evans et al. 2011; Soga and Koike 2012a). In consequent, this compositional change of biodiversity at a local-scale urbanisation is considered as one of fundamental causes of global 'biotic homogenisation' (McKinney 2006; Devictor et al. 2007, 2008; Magura et al. 2010).

At a landscape-level, urban development causes habitat fragmentation (i.e. losses of primary habitat and artificial barriers between naturally connected habitats), which is a significant driver of global biodiversity loss (Fahrig 2003). As urban greenspaces are highly scattered and isolated (e.g., Tratalos et al. 2007; Fuller and Gaston 2009), urban flora and fauna are likely to be suffered from habitat fragmentation. Indeed, biodiversity decline and losses due to urban habitat fragmentation have previously been well-documented (e.g., plants: Porter et al. 2001, butterflies: Soga and Koike 2012a, beetles: Magura et al. 2004, bees: Zhanette et al. 2005, amphibians: Fuyuki et al. in press, birds: Morimoto et al. 2006, mammals: Mahan and O'Connell 2005).

Crucially, at a regional-scale, urbanised regions (areas with a higher number of population) are overlapped with ecologically valuable areas (i.e., warm and fertilize regions) (Balmford et al. 2001, Imhoff et al. 2004). Using a macro-ecological approach, Ricketts and Imhoff (2003) revealed that distribution of endemic plants and animals corresponds to lowland areas. Also, Yamaura et al. (2011) recently demonstrated that human-induced impacts on biodiversity are especially evident in warm and lowland areas. It is now widely acknowledged that the conservation and restoration of urban biodiversity greatly contributes to averting global biodiversity loss (McKinney 2002).

Reconnecting people and nature in cities: extinction of experience

Biodiversity decline in urban areas is also likely to accelerate the disconnection of people from nature (so called “extinction of experience”, Turner et al. 2004; Miller 2005). As a home to the majority of humanity, cities and towns accommodate more than half of population (United Nations 2011). It is therefore no doubt that urban greenspaces are one of few (or the only) areas in which people can daily and directly contact with nature (Miller 2005).

There is an increasing concern that the progress of extinction of experience brings negative and serious consequences both for human health and wellbeing (Nabhan and St Antoine 1993; Miller 2005; Keniger et al. 2013) (see Fig. 1). Evidence shows that people who do not regularly encounter nature are likely to lose substantial physical and psychological health benefits, which is linked to the long-term health problem, such as diabetes, circulatory and heart disease, and stroke (see review by Lee and Maheswaran 2011). Takano et al. (2002) also reported that the amount of urban greenspaces affects longevity of senior citizens. In the long run, failure to perceive health and wellbeing benefits from natural environments could have substantial health costs. Indeed, in UK, it had been calculated that the National Health Service could save £2.1bn a year if everyone had access to green spaces (National Health Service 2014).

Extinction of experience can also lead to the loss of public affinity to, interest in, and reliance on nature (Pyle 1993). Using a variety of methodologies and measures, researchers have shown that the frequency of contact with natural environments (especially in childhood) influences affinity to nature and biodiversity. For instance, Hinds and Sparks (2008) reported that people from rural childhoods reported stronger behavioural intentions and more positive attitudes to engage with the natural environment than participants living urban areas. Recent studies indicate that such a loss

of affinity to nature reduces motivations for biodiversity conservation. In Switzerland, Finger et al. (1994) has found that people who participated pro-environment behaviour (e.g. recycling) were likely to have frequently visited natural areas in their childhood stages. Nord et al. (1998) also reported that frequency of contact with natural environments is related to people's pro-environmental behaviours (e.g. willingness to pay for nature conservation). It is therefore urgently needed to reduce extinction of experience and reconnect nature and people in urban areas (Miller 2005).

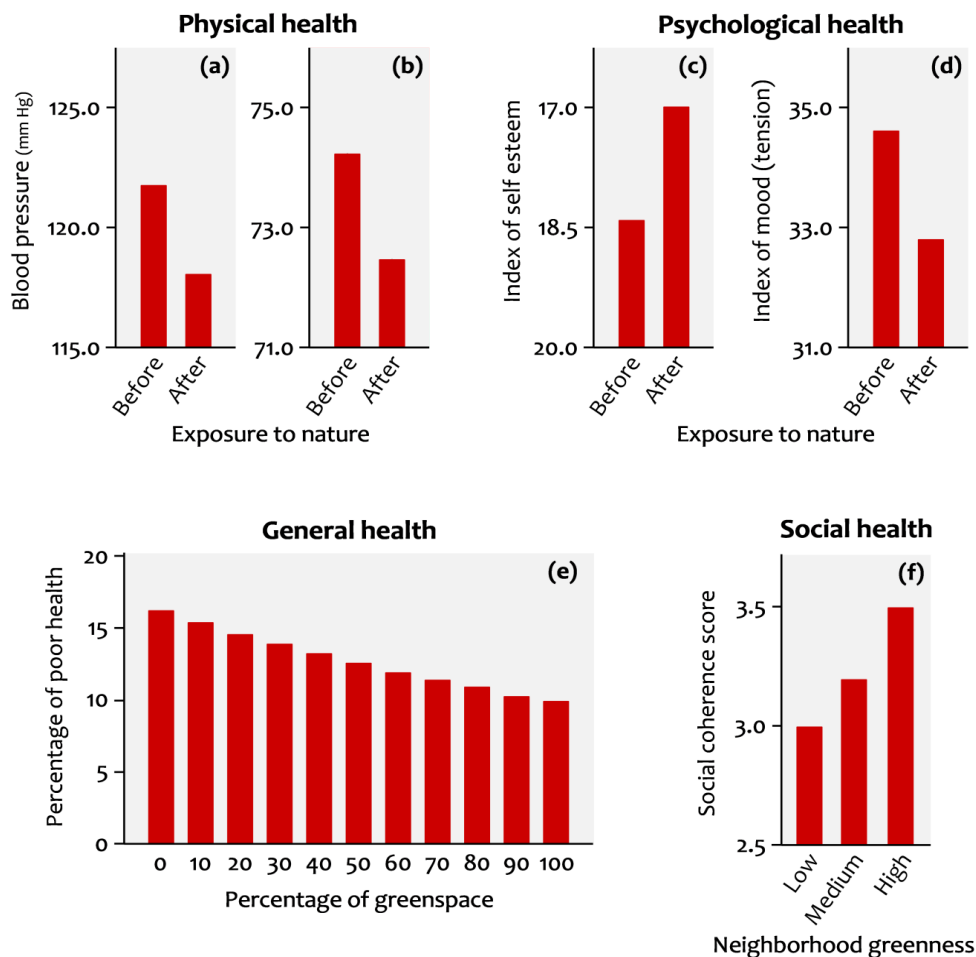


Fig. 1 Health changes due to extinction of experience. (a, b) Physical health ((a) systolic and (b) diastolic blood pressures) reported in Colchester, U.K. (Pretty et al. 2005). (c, d) Psychological health ((c) self-esteem and (d) tension levels) reported in the U.K. (Pretty et al. 2007). (e) General health (percentage stating survey respondents' health is less than good) reported in Netherlands (Maas et al. 2006). (f) Social health (social coherence scores) reported in Adelaide, Australia (Sugiyama et al. 2008). Exposure to nature was measured by (a, b, c, d) participation in exercise in natural environments and (e, f) levels of neighbourhood greenspace. Note that lower values of indices of self-esteem and mood (tension) indicate higher levels of self-esteem and lower tension, respectively. Higher scores of social coherence mean higher levels of emotional connectedness with neighborhood communities.

Challenges for urban biodiversity conservation

As previously mentioned, cities potentially have an important role both to protect global biodiversity and engage the majority of the people to the natural environments (Dearborn and Kark 2010). Urbanisation is not only the environmental problem itself, but also provides us a hint for sustainable development. In cities, we need to maintain multiple ecosystem services and goods (including biodiversity conservation) in a restricted area in order to enhance the quality of life of urban dwellers, which is arguably the greatest challenge facing humanity in this century. In short, cities offer a microcosm of global environmental issues. Nevertheless, the opportunities researches offer for urban biodiversity conservation have only recently been much debated. Conservation biologists have previously paid their attentions on wilderness nature (i.e. "virgin ecosystems") and these attentions on cities and towns have mostly been ignored (see review by Martin et al. 2012). However, in the last decade, this stereotypical view has gradually changed. Conservation biologists increasingly recognise the importance of urban biodiversity conservation (Gaston 2010; Kareiva and Marvier 2012).

At the beginning of urban ecological studies, most studies applied existing ecological paradigms to the urban areas (e.g., island biogeography theory: Fernandez-Juricic and Jokimaki 2001, disturbance gradient: Blair 1996; McDonnell and Hahs 2008). As research has proceeded, however, it has been revealed that socio and economic factors are important determinants of richness and composition of biological communities in urban areas (e.g. Hope et al. 2003; Davies et al. 2012). For instance, Hope et al. (2003) found that family incomes and housing age are associated with plant species richness across the city of Phoenix, central Arizona (called "luxury effects"). These studies indicate that people living in cities have an enormous influence on urban biodiversity (Fuller et al. 2008). It is therefore a substantial challenge to develop

interdisciplinary studies that use both ecological and social research approaches (e.g., Fuller et al. 2007).

Aims of this thesis

As cities are typically case designed by top-down policy-making (note: in many cases local citizens and communities also have an important role), initial development schemes have a crucial role in determining the capacity to sustain biodiversity and ecosystem services. Therefore, it is critically important to address how urban development forms influence on regional biodiversity and the provision of ecosystem services. Urban development forms are categorised into two contrasting strategies: intensive development over a small residential area (called "urban land-sparing") and extensive development over a large residential area (called "urban land-sharing") (Green et al. 2005; Fischer et al. 2008; Phalan et al. 2011). Urban land-sparing is one hand option which minimises the spatial extent of developed areas. In this option, residential areas are developed as intensively as possible, allowing the maintenance and persistence of relatively large-size greenspace (Fig. 2). Under urban land-sharing, on the other hand, urban development is more evenly, but less intensively, distributed. In this option, a larger land area is needed to accommodate a given number of houses, and greenspaces tend to be more fragmented but on average closer to residential areas (Fig. 2).

The main question of this thesis is that: *which urban development form (urban land-sharing vs. land-sparing) is better for biodiversity conservation and promotion of people's nature experiences?* To do so, I examined (1) whether revegetated habitats (established greenspaces) compensate for the loss of remnant habitats (Chapter 1); (2) which development form is better for biodiversity conservation between land-sharing and land-sparing (Chapter 2); and (3) which development form is better for promotion

of people's recreational uses in urban greenspaces between land-sharing and land-sparing (Chapter 3). In this study (Chapter 1 and 2), I use two exemplar insect taxa, butterflies and ground beetles they have been proven to be good indicators of environmental change and overall biodiversity (see Rainio and Niemelä 2003; Thomas 2005). To my knowledge, this thesis is the first opportunity to investigate relative benefits of urban land-sharing and land-sparing both for biodiversity conservation and promotion of people's recreational uses of urban greenspaces. Finally, I discuss and explore the possible solutions to reconcile urban development, biodiversity conservation, and people's nature uses in urban areas.

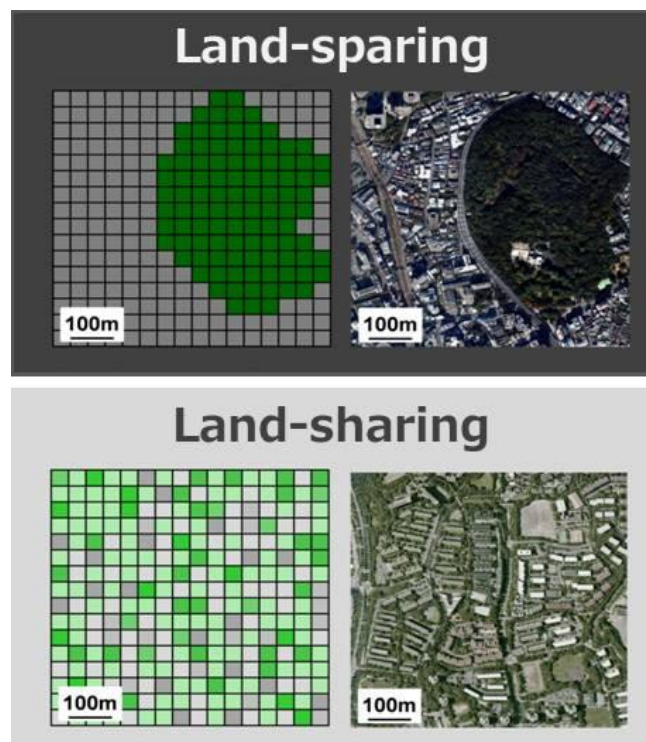


Fig. 2 Schematic illustrations and example images of urban land-sparing (upper panel) and land-sharing (lower panel). In schematic illustrations, green and gray meshes indicate vegetated and developed areas, respectively.

Chapter 1

Woodland remnants as an urban wildlife refuge:
a cross-taxonomic assessment

Abstract

Urban nature is crucial for the quality of human life both within cities and beyond. In many developed cities, the numbers of restoration-through-revegetation projects have rapidly increased over the decades. However, the extent to which revegetated habitats perform compensatory roles for remnant habitats is poorly understood. I compared butterfly and ground beetle assemblages among three park types (5 remnant parks, 4 newly established parks and 5 old established parks) and 7 built-up sites in Tokyo, central Japan. Butterflies were classified into woodland or open-land and into patch-dependent or matrix-dwelling species. For both taxa, remnant parks and built-up sites had the highest and lowest species richness and abundance, respectively. Although the richness and abundance of open-land and matrix-dwelling butterflies did not differ among the three park types, those of woodland and patch-dependent species were significantly highest in remnant parks. In short, after 50 years, established parks did not attain the same insect assemblages as those in remnant parks. These results illustrate that whilst revegetation is an effective and fast-acting conservation measure for generalist species (i.e., widely distributed species), this value is limited for specialists. In highly urbanised landscapes, therefore, even small remnant woodlands provide important refuges for urban wildlife. Remnant protection programs at the early stage of city development would decide the fate of urban biodiversity.

INTRODUCTION

For the first time in Earth's history, more than half of the human population lives in urban areas (United Nations 2011). Occupying only four percent of the land extent, these have served dramatically to aggregate people. For example, in Tokyo, one of the world's largest cities, 13.0 million people live in only 1400 square kilometers, at a density of approximately 9000 people/km² (Tokyo metropolitan government bureau of general affairs 2013, note: excluding marginal urban areas). Such extreme concentration of human population has radically degraded urban ecosystems. Despite such pressures, nature in cities fulfills important functions, including physical and psychological benefits (e.g., Fuller et al. 2007) and opportunities for regular encounters by urban dwellers (Brown and Grant 2005). Indeed, reconnecting urban dwellers with urban nature has been argued to be essential if the majority of people are to appreciate the consequences of global environmental change and biodiversity loss (Miller 2005). The conservation and restoration of urban biodiversity is thus crucial for the quality of life both within cities and beyond (Dearborn and Kark 2009).

To conserve and restore urban biodiversity, revegetation (e.g., greenspace establishment) is a straightforward approach because it can increase the population sizes of many species through the expansion of habitat extent and the enhancement of habitat connectivity (e.g. provision of 'stepping stones'; Fischer and Lindenmayer 2002). However, the question of whether revegetated habitats perform compensatory roles for remnant habitats, arguably one of the most fundamental issues in biodiversity conservation, has only recently been much debated (e.g., Munro et al. 2007). Although some species have been directly introduced into restored habitats ('reintroduction', Simberloff et al. 2005), in most cases they must arrive by their own abilities. Here, if significant dispersal limitation occurred, the assemblage compositions of revegetated

habitats would not approach those of remnants. Dispersal limitation seems to be affected by several factors. The potential dispersal ability of each species may be the most crucial (Woodcock et al. 2012). In addition, matrix-resistance will also play a role, because species have to cross the matrix unless revegetated patches are connected by greenways (Schtickzelle et al. 2006). Previous empirical studies have shown that matrix quality or species resistance to the matrix affect species movements (Ricketts 2001) and distributions (Haynes and Cronin 2003). In general, compared to habitat generalists (widely distributed species), specialists (patch-dependent species) are less likely to migrate among habitat patches (e.g., Ries and Debinski 2001; Soga and Koike 2013). For low-mobility and patch-dependent species the value of revegetation for their conservation would be limited.

Predicting species responses to revegetation helps restoration strategies to be implemented effectively. Nevertheless, there is a heavy taxonomic bias in this field of study and most previous work has focused on birds (see review by Munro et al. 2007). Because birds have relatively high dispersal abilities and are homoiothermic (Gill 2007), they often show high adaptabilities to human-altered environments (e.g., Evans et al. 2011). Therefore, generalisation based on birds would overestimate the performance of revegetation and may lead to incomplete or inappropriate conservation strategies (see also Pyšek et al. 2008 in the case of invasion ecology). To understand the conservation performance of revegetation more comprehensively, empirical studies using various taxonomic groups with different ecological traits are needed.

Here, I investigate the effect of long-term revegetation activities (urban park establishment) on butterfly and ground beetle assemblages in Tokyo, central Japan. In this city, many greenspaces of various types are preserved in the city planning scheme. I compare butterfly and ground beetle assemblages among remnant parks, newly

established parks and old established parks. The two species groups, butterflies and ground beetles, vary greatly in their typical life history characteristics. In general, butterflies have a predisposition in favor of early-successional environments (e.g., Makino et al. 2006), whereas ground beetles often need old-growth habitat elements, such as quantities of litter (Koivula et al. 1999) and decaying wood (Magura et al. 2004; Tikkanen et al. 2006). In this study, I test both taxonomic and functional-level hypotheses: Abundance and diversity of ground beetles, woodland and patch-dependent butterflies (species whose larval host plants are not planted in the urban matrix) in established parks are lower than those of remnants, but this is not the case for butterflies, and particularly open-land and matrix-dwelling butterflies (species whose larval host plants are planted in the matrix).

METHODS

Study region and parks sampled

All fieldwork was conducted from April to September 2012 within the western region (ward and city area, excluding marginal urban areas) of Tokyo (Fig. 1). Here, remnant woodlands, established parks, roadside amenity plantings and domestic gardens contribute much to urban greening and biodiversity. Butterfly and beetle survey sites were distributed amongst three park types within this region; remnant parks, old (> 50years) established parks, and newly (< 50 years) established parks (see details in Fig. 1). Remnant parks consist mainly two oaks, *Quercus serrata* and *Q. acutissima*; evergreen oaks, *Q. glauca* and *Q. acuta* are also present. Remnant parks are parts of predominantly broad-leaved secondary forests. Old and newly established parks are established parks that contain *Zelkova serrata*, *Prunus yedoensis* Matsumura, *Cinnamomum camphora*, *Ginkgo biloba*, and several oaks (e.g., *Quercus serrata* and *Q. acutissima*), and other ornamental plant species. Unlike remnant parks, established

parks were formerly used as other land-use types (e.g., factories and airfields), the large part of vegetation in established parks was therefore artificially planted. Established parks therefore have a wider range of vegetation structures compared to those of remnant parks. In addition, although remnant parks are mainly covered by woods, established parks are covered by a wider range of environments (e.g. artificially managed grasslands or artificial structures). As reference comparisons, I also surveyed built-up sites, mostly covered by built-up housing or roadside areas. The main habitat for butterflies and ground beetles in built-up sites is roadside amenity plants or small domestic gardens. Several butterfly species use these planted plants in built-up sites as larval hosts.

Butterflies and ground beetles were surveyed in fourteen parks (five remnant parks, five old established parks and four newly established parks) and seven built-up sites. Study parks were separated by > 2 km from each other and widely distributed (see Fig. 1). My preliminary analysis revealed no evidence of spatial autocorrelation in the data across the 21 sampling sites. In the later analyses, therefore, I treated the data from each site as a spatially independent sample. Park size ranged between 6.5 and 43.9 ha (mean = $18.8 \text{ ha} \pm 11.71 \text{ SD}$), and did not differ among the three park types (ANOVA, $F_{(2, 11)} = 0.27$, $P = 0.77$).

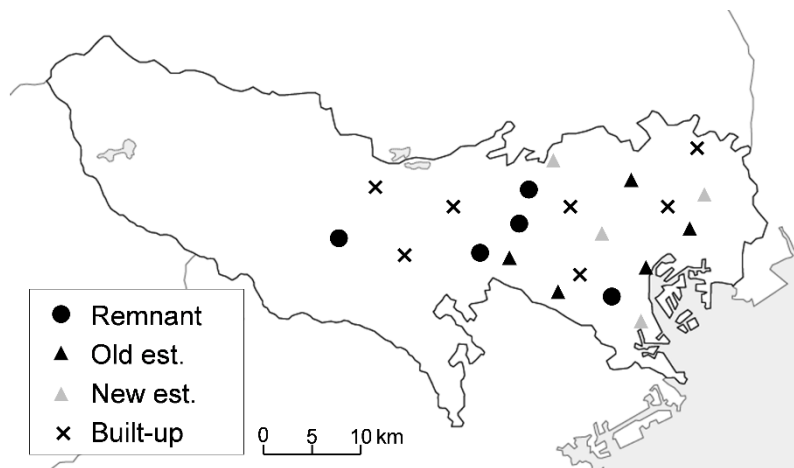


Fig. 1 Study area (Tokyo city) and fourteen parks sampled and seven built-up sites.

Field surveys and species classifications

Butterfly surveys

Butterflies were monitored using the line transect method (Pollard 1977). One 500 m transect was established in each study site, and counts were conducted once every month between 08:45 and 16:15 during the adult flight season (early April to early October 2012) under appropriate flying conditions. No surveys were conducted in August because several butterfly species have been reported to aestivate during this month. Butterflies within a 10 m radius of a position along each transect were recorded while walking at a steady pace (10 m/min). Individuals that could not be identified to species by sight were caught using nets, identified, and released.

All butterfly species observed in the field were classified into woodland or open-land and into patch-dependent or matrix-dwelling species (Table 1). Classification as woodland or open-land species was based on Tanaka (1988). Classification as patch-dependent or matrix-dwelling species depended on whether their larval host plants were planted in the matrix or not, following Soga and Koike (2012a) and unpublished field observations.

Ground beetle sampling

Ground beetles were sampled using pitfall traps. In each study site, trapping was conducted in July 2012. I placed 20 pitfall traps within each site, separated by at least 10 m from each other, using cups of 10 cm in diameter and 12 cm in depth and containing approximately 100 ml of propylene glycol as a preservative. Traps were collected after one week and individuals caught were dried, mounted, and identified to species in the laboratory. Due to the limited sampling periods, the capture rates of beetles in each trap were quite low. I therefore combined all 20 traps within a site and

used this value as the unit of species richness and abundance of ground beetles in the later analyses (see also the species accumulation curves of ground beetles in Fig. 2).

All ground beetles observed in the field were classified into woodland or open-land species, based on their main habitats (cf. Tóthmérész et al. 2011). Species that principally use woods or forests were classified as woodland species. Species that usually inhabit open-lands or grasslands and do not need woody conditions were classified as open-land species. In this study, however, only a few open-land ground beetles were observed (Table 1). We thus did not analyse woodland and open-land species separately.

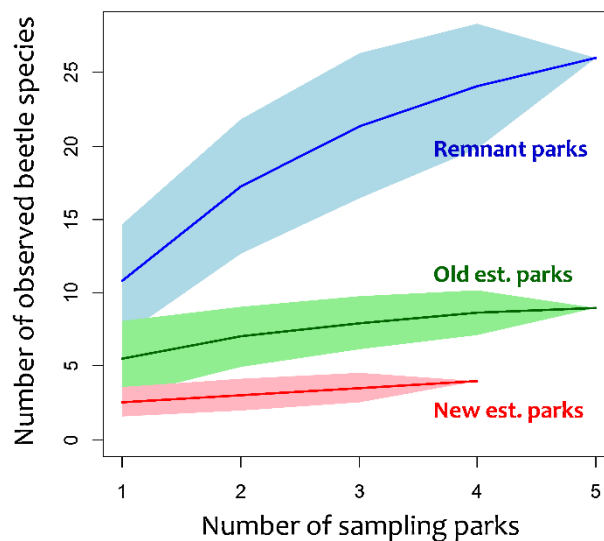


Fig. 2 Species accumulation curves of ground beetles in remnant parks (blue line), old established parks (green line) and newly established parks (red line). Pale colored polygons are 95% CIs.

Table 1 All butterfly and ground beetle species observed at 21 sampling sites (5 remnant parks, 5 old established parks, 4 newly established parks, and 7 built-up sites) and their main habitat types.

Species	Study sites																	Habitat types						
	Remnant					Old est.					New est.				Built-up							Woodland/ Open-land	Patch-dependent/ Matrix-dwelling	
	Fuchu-1	Hachioji-1	Mitaka-1	Hachioji-2	Hachioji-3	Setagaya-1	Chofu-1	Chuo-1	Koto-1	Kita-1	Shinagawa-1	Shinjuku-1	Sumida-1	Nerima-1	Built-up_1	Built-up_2	Built-up_3	Built-up_4	Built-up_5	Built-up_6	Built-up_7			
Butterflies																								
<i>Parnassius citrinarius</i>	-	-	-	-	●	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	open	patch
<i>Byasa alcinous</i>	●	●	-	-	●	●	-	-	-	●	-	-	-	●	-	-	-	-	-	-	-	-	wood	patch
<i>Graphium sarpedon</i>	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	wood	matrix
<i>Papilio machaon</i>	●	●	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	open	matrix
<i>Papilio xuthus</i>	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	wood	matrix
<i>Papilio helenus</i>	-	●	-	●	●	●	-	-	-	●	-	●	-	-	-	-	-	-	-	-	-	-	wood	matrix
<i>Papilio protenor</i>	●	●	●	●	●	●	●	●	-	●	●	●	●	●	-	-	-	-	-	-	-	-	wood	matrix
<i>Papilio memnon</i>	●	●	●	-	-	●	●	●	-	●	-	●	-	●	-	-	-	-	-	-	-	-	wood	matrix
<i>Papilio maclintus</i>	-	-	-	-	●	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	wood	matrix
<i>Papilio bianor</i>	●	●	-	●	●	-	●	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	wood	matrix
<i>Colias erate</i>	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	-	-	●	-	-	open	matrix
<i>Eurema hecabe</i>	●	●	●	●	●	●	●	-	●	●	-	●	●	●	-	-	-	-	-	-	-	-	wood	matrix
<i>Pieris spp.</i>	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	-	open	matrix
<i>Anthocharis scolymus</i>	●	●	-	●	●	-	●	-	-	●	-	-	-	●	-	-	-	-	-	-	-	-	open	matrix
<i>Parantica sita</i>	●	●	-	-	●	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	wood	patch
<i>Argyreus hyperbius</i>	●	●	●	●	●	●	●	●	●	●	●	●	●	●	-	-	●	-	●	●	-	-	open	matrix
<i>Limnitis camilla</i>	-	-	-	-	●	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	wood	patch
<i>Neptis sappho</i>	●	●	●	●	●	●	●	-	-	●	-	-	-	●	-	-	-	-	-	-	-	-	wood	matrix
<i>Polygonia c-aureum</i>	●	●	●	●	●	●	●	●	●	●	-	●	-	●	-	-	-	-	-	●	-	-	open	patch
<i>Nymphalis xanthomelas</i>	-	●	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	wood	patch
<i>Vanessa cardui</i>	●	-	●	-	●	●	●	●	●	●	●	●	●	●	-	-	-	-	-	-	-	-	open	patch
<i>Vanessa indica</i>	●	●	●	●	-	●	-	●	-	-	●	●	●	-	-	-	-	-	-	-	-	-	open	patch
<i>Kaniska canace</i>	●	●	-	●	-	●	●	-	-	-	-	●	-	●	-	-	-	-	-	-	-	-	wood	patch
<i>Hestina persimilis japonica</i>	●	-	-	-	●	-	●	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	wood	patch
<i>Hestina assimilis</i>	●	●	●	●	●	●	●	-	-	●	-	-	-	●	-	-	-	-	-	-	-	-	wood	patch
<i>Libythea celtis</i>	●	●	-	-	●	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	wood	patch
<i>Narathura japonica</i>	●	●	●	●	●	-	-	●	-	-	-	-	-	●	-	-	-	-	-	-	-	-	wood	matrix
<i>Narathura bazalus</i>	●	-	●	●	-	-	●	-	-	●	-	-	-	●	-	-	-	-	-	-	-	-	wood	matrix
<i>Japonica lutea</i>	●	●	-	-	●	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	wood	patch
<i>Japonica saepestriata</i>	-	●	-	-	●	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	wood	patch
<i>Antigius attilia</i>	●	●	-	●	●	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	wood	patch
<i>Rapala arata</i>	-	-	-	-	●	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	wood	matrix
<i>Callophrys ferrea</i>	-	●	-	-	●	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	wood	patch
<i>Lycaena phlaeas</i>	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	-	-	-	●	●	-	open	patch
<i>Lampides boeticus</i>	-	-	-	●	-	-	-	-	-	●	-	●	-	-	-	-	-	-	-	-	-	-	open	matrix
<i>Pseudozizeeria maha</i>	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	open	patch
<i>Celastrina argiolus</i>	●	●	●	●	●	●	●	●	●	●	●	●	●	●	-	-	-	-	●	●	-	-	wood	matrix
<i>Everes argiades</i>	●	●	-	-	-	●	-	-	-	-	●	-	-	-	-	-	-	-	-	-	-	-	open	matrix
<i>Curetis acuta paracuta</i>	●	●	●	-	●	●	●	-	-	●	-	-	-	-	-	-	-	-	-	-	-	-	wood	matrix
<i>Ypthima argus</i>	●	●	-	●	●	●	●	-	-	●	-	-	-	-	-	-	-	-	-	-	-	-	wood	patch
<i>Minois dryas</i>	-	●	-	●	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	open	patch
<i>Lethe diana</i>	●	●	-	●	●	-	●	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	wood	patch
<i>Lethe sicelis</i>	-	●	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	wood	patch
<i>Neope goschkevitschii</i>	●	●	●	●	●	●	●	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	wood	patch
<i>Erynnis montanus</i>	-	●	-	●	●	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	wood	patch
<i>Daimio tethys</i>	●	●	●	●	●	●	●	-	●	-	-	-	-	●	-	-	-	-	-	-	-	-	wood	patch
<i>Isoteinon lamprospilus</i>	●	●	-	-	●	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	wood	patch
<i>Potanthus flavum</i>	-	-	-	●	●	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	open	patch
<i>Parnara guttata</i>	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	-	-	-	●	●	-	open	matrix

Species	Study sites																	Habitat types						
	Remnant					Old est.					New est.				Built-up							Woodland/ Open-land	Patch-dependent/ Matrix-dwelling	
	Fuchu-1	Hachioji-1	Mitaka-1	Hachioji-2	Hachioji-3	Setagaya-1	Chofu-1	Chuo-1	Koto-1	Kita-1	Shinagawa-1	Shinjuku-1	Sumida-1	Nerima-1	Built-up_1	Built-up_2	Built-up_3	Built-up_4	Built-up_5	Built-up_6	Built-up_7			
Ground beetles																								
<i>Asaphidion semilucidum</i>	-	-	-	-	●	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	open	-
<i>Carabus albrecthi esakianus</i>	-	-	●	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	wood	-
<i>Carabus insulicola</i>	●	●	●	●	●	●	●	●	●	●	●	●	●	●	-	-	-	-	-	-	-	-	wood	-
<i>Carabus procerulus</i> Chaudoir	-	-	●	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	wood	-
<i>Myas cuprescens cuprescens</i>	●	●	-	●	●	●	●	-	-	●	-	-	-	-	-	-	-	-	-	-	-	-	wood	-
<i>Lesticus magnus</i>	-	-	●	-	-	-	-	-	-	-	-	-	-	●	-	-	-	-	-	-	-	-	wood	-
<i>Trigonotoma lewisii</i>	-	-	●	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	wood	-
<i>Pterostichus yoritomus</i>	●	-	-	●	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	wood	-
<i>Pterostichus prolongatus</i>	●	-	-	●	-	●	●	●	●	●	-	-	-	-	-	-	-	-	-	-	-	-	open	-
<i>Pterostichus takaosanus</i>	-	-	●	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	wood	-
<i>Pristosia aeneola</i>	-	-	●	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	wood	-
<i>Synuchus nitidus</i>	-	●	●	-	●	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	wood	-
<i>Synuchus cycloderus</i>	●	●	-	●	-	-	-	-	-	-	-	●	-	-	-	-	-	-	-	-	-	-	wood	-
<i>Amara chalcites</i>	-	●	-	●	●	-	●	●	-	●	-	-	-	-	-	-	-	-	-	-	-	-	wood	-
<i>Amara simplicidens</i>	●	●	-	-	●	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	open	-
<i>Amara macronota ovalipennis</i>	●	-	-	-	-	-	●	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	open	-
<i>Harpalus tridens</i>	-	●	-	●	-	●	-	●	-	-	-	-	-	-	-	-	-	-	-	-	-	-	open	-
<i>Diplocheila zeelandica</i>	●	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	open	-
<i>Haplochlaenius costiger</i>	-	●	●	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	wood	-
<i>Chlaenius abstersus</i>	●	●	-	●	-	-	●	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	open	-
<i>Chlaenius virgulifer</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	open	-
<i>Chlaenius micans</i>	-	●	-	●	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	open	-
<i>Chlaenius naeviger</i>	-	-	-	●	●	●	-	-	-	●	-	-	-	-	-	-	-	-	-	-	-	-	wood	-
<i>Chlaenius posticalis</i>	-	●	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	open	-
<i>Planetes puncticeps</i>	-	●	●	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	wood	-
<i>Necrophila japonica</i>	●	●	●	●	●	●	●	●	●	●	●	●	●	●	-	-	-	-	-	-	-	-	wood	-
<i>Nicrophorus quadripunctatus</i>	-	●	●	●	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	wood	-

Data analysis

Species richness and abundance

I investigated the effect of habitat type (remnant parks, old established parks, newly established parks, and built-up sites) on the species richness and abundance of butterflies and ground beetles. Since species richness and abundance are count data, they were modeled as Poisson-distributed variables with a log link. Here, I used generalised linear mixed-effect models (GLMMs) implemented within the ‘lme4’ package (ver. 0.999999.0) (Bates et al. 2012) in R software (ver. 2.15.0) (R Development Core Team 2012). In GLMMs, species richness and abundance and habitat type (as a categorical variable) were used as the response and explanatory variables, respectively. In the field there are several un-modeled factors that could affect insect assemblages but their effects would not be fully explained by habitat types (e.g., park size and vegetation structure). In this case, if I do not consider the effects of these factors in the Poisson regression models, I may overestimate the precision of parameter estimates. In order to overcome such problems (so-called ‘over-dispersion problem’), I considered site id as a random effect in GLMMs. I first analysed the summed counts of all butterfly and ground beetle species. Then, the subset of woodland or open-land and patch-dependent or matrix-dwelling butterflies were analysed (see Table 2). If the coefficients of habitat types reflected significant effects, I interpreted species richness and abundance as being significantly different between habitat types. In GLMMs, I used old established parks as reference comparisons (i.e., intercepts of models). I did not find ground beetles in the built-up study sites, which hinders the fitting of my data using GLMMs. Thus, I excluded seven built-up sites in this analysis.

Species composition

To determine how species composition differed among the four habitat types, I examined species-abundance matrices using the ‘vegan’ package (ver. 2.0.5) (Oksanen et al. 2012) in R software. Ordination of sites according to species similarity (Bray-Curtis index) was achieved using nonmetric multi-dimensional scaling (NMDS), allowing sites with more similar species composition to be placed closer together in reduced dimensional space. To test for differences among park types in species composition, I then used an Analysis of Similarity (ANOSIM), which is a nonparametric permutation test.

Species-level population responses

To reveal the population responses to different park types at a species-level, I again used GLMMs with Poisson error and a log link (see the details in the section 2.3.1). The purpose of this analysis is to investigate whether each species decreased in its population size in newly or old established parks compared to remnant parks. I therefore excluded built-up sites in this analysis and used three park types as explanatory variables (here I used remnant parks as reference comparisons). Abundance and park types were used as the response and explanatory variables, respectively. Site ID was also used as a random effect. If the coefficients of park types reflected significant effects, I interpreted the abundance of such a species to be significantly different between different park types. As the number of individuals of each ground beetle species was low (Table S1), I did not use the ground beetle data in this analysis. Six butterfly species were also removed in this analysis due to data limitations.

RESULTS

I recorded a total of 49 butterfly species (33 woodland and 16 open-land butterflies, and 27 patch-dependent and 22 matrix-dwelling butterflies) and 26 ground beetle species (Table 1). In park sites, there was an average of 23.9 ($\pm$ 9.5 SD) butterfly and 6.6 ($\pm$ 4.0 SD) ground beetle species for each site. In the built-up sites, on the contrary, I observed 4.6 ($\pm$ 2.6 SD) butterfly species and did not catch any ground beetles.

Species richness and abundance

For butterflies, species richness and total abundance were significantly higher in remnant parks than other habitat types, but differences were not found between old and newly established parks (Table 2, Figs. 3, 4). Especially, remnant parks had significantly higher species richness and abundance of woodland and patch-dependent species than other habitat types, but these differences were not found between old and newly established parks (Table 2). On the other hand, abundance and richness of open-land and matrix-dwelling species were not significantly different among remnant, old established, and newly established parks (Table 2).

For ground beetles, species richness and total abundance were significantly higher in remnant parks than other habitat types (Table 2, Figs. 3, 4). In contrast to butterflies, differences in species richness and abundance were also found between old and newly established parks (Table 2).

Table 2 Parameters of fixed effects (four habitat types) and standard deviations of random effects (site id) in GLMMs. Poisson models have a log link, so parameters are in units of log scale. Coefficients of old developed parks mean intercepts of models.

Species groups	Variables	Estimates	SE	p-values
Butterflies				
All species richness (SD of random effects: 0.12)	Old est. parks	3.02	0.11	$p < 0.001$
	Built-up sites	-1.51	0.21	$p < 0.001$
	New est. parks	-0.24	0.18	0.15
	Remnant parks	0.48	0.15	0.01
All abundance (SD of random effects: 0.26)	Old est. parks	4.32	0.13	$p < 0.001$
	Built-up sites	-2.31	0.21	$p < 0.001$
	New est. parks	-0.28	0.19	0.18
	Remnant parks	0.45	0.18	$p < 0.001$
Open-land species richness (SD of random effects: 0.00)	Old est. parks	2.22	0.15	$p < 0.001$
	Built-up sites	-0.91	0.25	$p < 0.001$
	New est. parks	-0.02	0.22	0.92
	Remnant parks	0.30	0.19	0.13
Open-land abundance (SD of random effects: 0.12)	Old est. parks	3.86	0.08	$p < 0.001$
	Built-up sites	-1.98	0.18	$p < 0.001$
	New est. parks	-0.18	0.13	0.16
	Remnant parks	0.07	0.12	0.53
Woodland species richness (SD of random effects: 0.26)	Old est. parks	2.40	0.18	$p < 0.001$
	Built-up sites	-2.58	0.46	$p < 0.001$
	New est. parks	-0.45	0.29	0.12
	Remnant parks	0.62	0.24	0.01
Woodland abundance (SD of random effects: 0.42)	Old est. parks	3.31	0.21	$p < 0.001$
	Built-up sites	-3.27	0.45	$p < 0.001$
	New est. parks	-0.46	0.32	0.15
	Remnant parks	0.87	0.28	0.02
Patch-dependent species richness (SD of random effects: 0.13)	Old est. parks	2.07	0.17	$p < 0.001$
	Built-up sites	-1.63	0.35	$p < 0.001$
	New est. parks	-0.42	0.28	0.14
	Remnant parks	0.74	0.21	$p < 0.001$
Patch-dependent abundance (SD of random effects: 0.28)	Old est. parks	3.23	0.15	$p < 0.001$
	Built-up sites	-2.38	0.31	$p < 0.001$
	New est. parks	-0.23	0.24	0.34
	Remnant parks	0.76	0.21	$p < 0.001$
Matrix-dwelling species richness (SD of random effects: 0.00)	Old est. parks	2.53	0.13	$p < 0.001$
	Built-up sites	-1.44	0.25	$p < 0.001$
	New est. parks	-0.14	0.20	0.49
	Remnant parks	0.28	0.17	0.10
Matrix-dwelling abundance (SD of random effects: 0.21)	Old est. parks	3.91	0.11	$p < 0.001$
	Built-up sites	-2.28	0.22	$p < 0.001$
	New est. parks	-0.31	0.18	0.08
	Remnant parks	0.23	0.16	0.15
Ground beetles				
All species richness (SD of random effects: 0.00)	Old est. parks	1.69	0.19	$p < 0.001$
	New est. parks	-0.77	0.37	0.002
	Remnant parks	0.73	0.23	0.00
All abundance (SD of random effects: 0.16)	Old est. parks	3.26	0.11	$p < 0.001$
	New est. parks	-0.57	0.19	0.003
	Remnant parks	1.02	0.14	$p < 0.001$

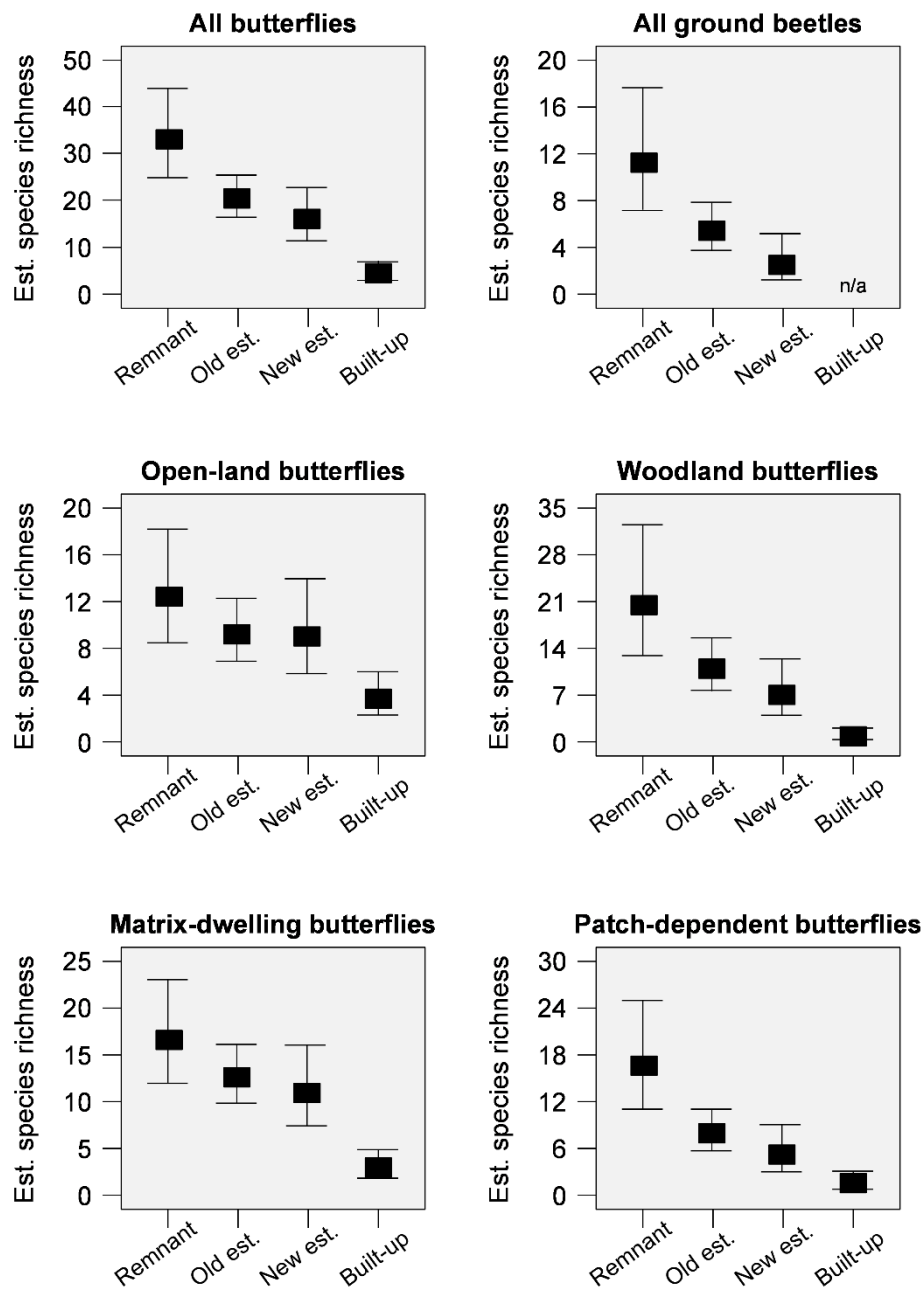


Fig. 3 Species richness of butterflies and ground beetles in four habitat types estimated by GLMMs; remnant parks (Remnant), old established parks (Old est.), newly established parks (New est.), and built-up sites (Built-up), respectively. Estimates are shown using the mean values (black squares) and associated 95% CIs (vertical bars). Because I used old established parks as a reference category, the estimate of each habitat type was calculated by the sum of intercepts of old parks and slope of each habitat type (see Table 2). Note that each estimated value on the panels is shown after exponential transformation (the log-scale estimated values of GLMMs were shown in Table 2). Because in this study ground beetles were not found in the built-up sites, I removed these sites from the panels for ground beetles.

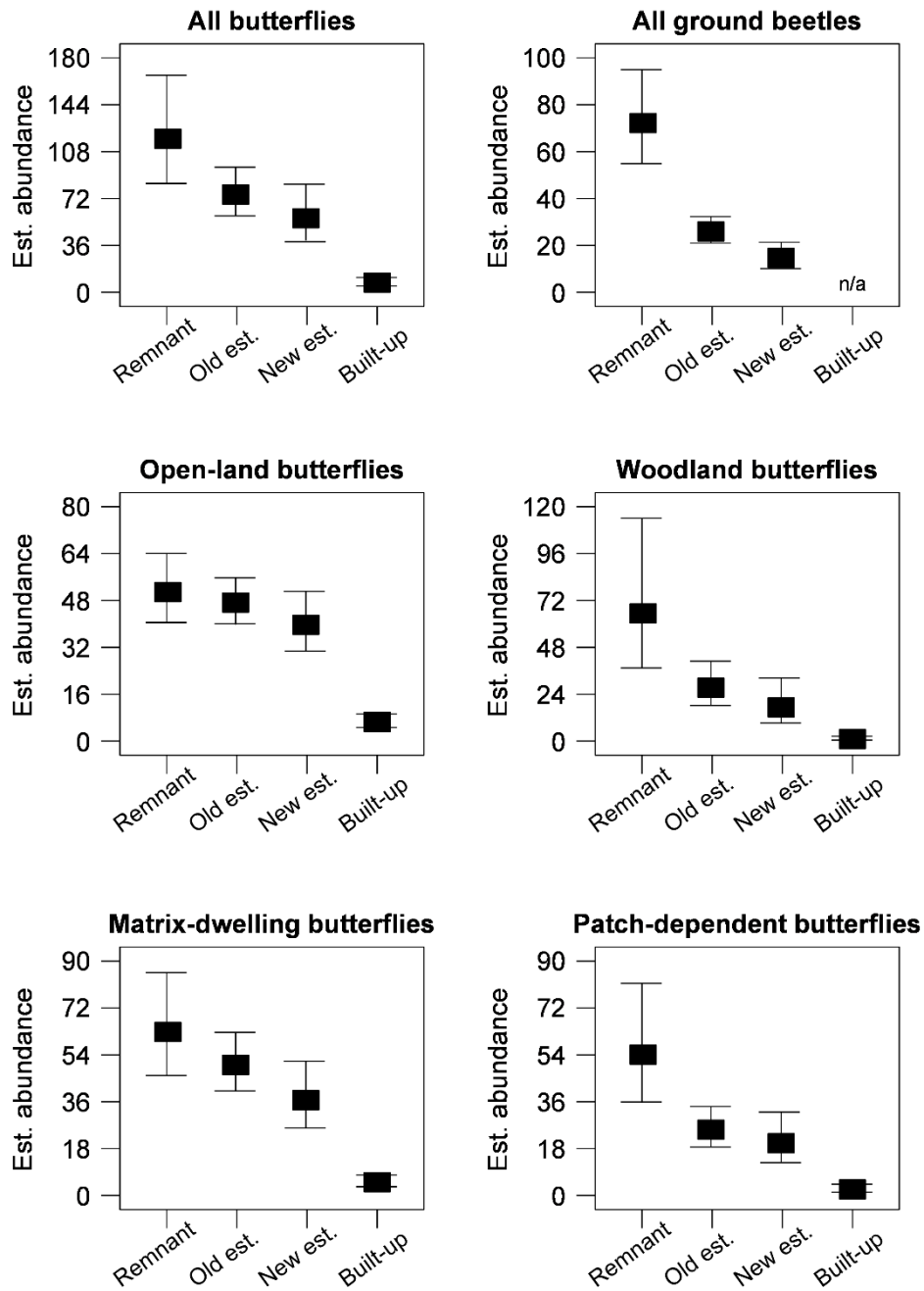


Fig. 4 Abundance of butterflies and ground beetles in four habitat types estimated by GLMMs. Details were shown in Fig. 3.

Species composition

Species composition differed among the habitat types for both butterflies (Fig. 5, ANOSIM, $R = 0.50$, $P = 0.001$) and ground beetles ($R = 0.36$, $P = 0.011$). For both groups, species assemblages in old established parks were different from those in remnant parks (butterflies: $R = 0.51$, $P = 0.02$, ground beetles: $R = 0.48$, $P = 0.03$). Although butterfly assemblages were not significantly different between old and newly established parks ($R = 0.05$, $P = 0.26$), those of ground beetles were significantly different ($R = 0.48$, $P = 0.03$).

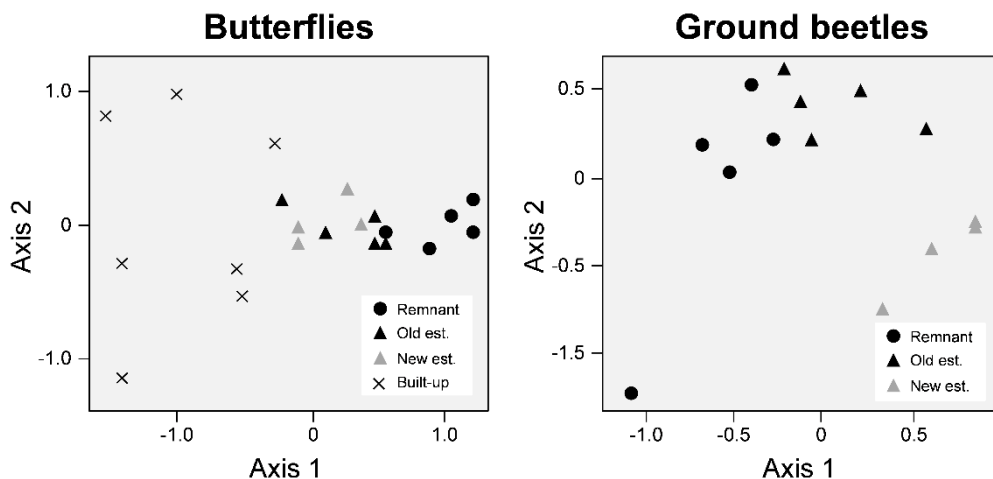


Fig. 5 Non-metric multidimensional scaling (NMDS) ordination of the butterfly and ground beetle assemblages in each park type. Symbols indicate remnant (black circles), old established (black triangles), newly established parks (gray triangles), and built-up sites (black crosses), respectively. Because none were not caught in the built-up sites, I removed these for ground beetles.

Species-level population responses

More than half of woodland and patch-dependent butterfly species significantly decreased their abundances in established parks (Fig. 6). However, despite population decline, over 70 percent of open-land and matrix-dwelling butterfly species were found within established parks (Fig. 6). In general trends, the ratio of species whose abundance significantly declined compared to remnant parks (black and dark gray bars in Fig. 6) was higher in newly established parks than in old established parks.

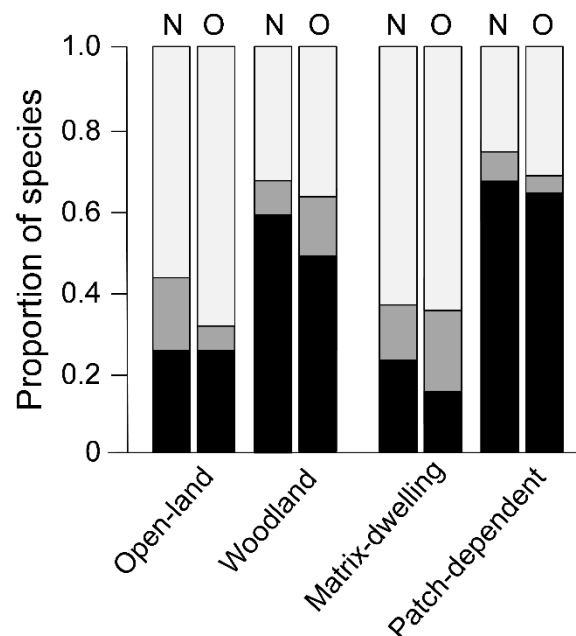


Fig. 6 Species-level responses of butterflies in two types of established parks (old (O) and newly established parks (N)) compared to remnant parks. Bars indicate the percentage of species recorded in remnant parks that were not found (black), significantly declined (dark grey), and did not change (light grey) in old and newly established parks. There was no species that significantly increased its population in both old and newly established parks compared to remnant parks.

Discussion

Revegetation has several benefits for promoting biodiversity in urban areas (Alvey 2006). First, and most importantly, in highly urbanised landscapes even small greenspaces can provide valuable habitats for wildlife (e.g. Thompson et al. 2003; Gaston et al. 2005; Carbó-Ramírez and Zuria 2011). In my study area of Tokyo, built-up areas (the highly urbanised matrix) support few insect species. Therefore, there is no doubt that greenspaces of any kind are essential elements in conserving urban biodiversity (and often called ‘biodiversity hotspots’, Croci et al. 2008). Second, it is also notable that revegetated areas often support similar assemblages to remnants. In my study area, even newly established parks supported as abundant and diverse assemblages of open-land and matrix-dwelling butterflies as did remnant parks. Therefore, for these species, we can restore habitats relatively quickly by a simple revegetation technique.

Despite the benefits involved in urban revegetation, the results presented here also demonstrate several challenges for the urban biodiversity restoration. After 50 years, old established parks did not attain the same insect assemblages as remnant parks (Fig. 5), and many species were not found in established parks (Fig. 6). As I hypothesized, for ground beetles and woodland and patch-dependent butterflies, abundance and diversity of established patches did not approach those of remnants. These results illustrate that, for these species, revegetation using only tree planting cannot perform compensatory roles for remnant parks and does not provide immediate benefit (Hobbs et al. 2003; Cunningham et al. 2005). Indeed, in this study several butterfly species were not observed in established parks even if their host plants were there in quantity (Soga unpubl. data). Based on these facts, urban biodiversity restoration through revegetation would at least need much longer times than previously expected.

I did not measure habitat quality variables, such as vegetation structure (Wettstein and Schmid 1999), micro-habitat conditions (Magura et al. 2005), and the amount of food resources available for my focal taxa (Soga and Koike 2012b). Indeed, as ground beetles often need old-growth habitat elements for their survival, their low diversity and abundance in established parks would be partly explained by the scarcity of such resources in established parks (cf. Magura et al. 2008). Nevertheless, the fact remains that, by the current restoration program, it takes more than 50 years before established parks are capable of supporting similar insect assemblages to those of remnants.

In summary, greenspace establishment is an effective and fast-acting conservation measure for highly-mobile and habitat generalist species, but this value is limited for low-mobility and specialist species. For the success of urban biodiversity conservation, it is therefore key to conserve and restore these specialist species in established greenspaces. In this case, both promoting species migration and improving the habitat quality would be straightforward approaches. To promote species dispersal in fragmented landscapes, establishing corridors and improving matrix quality are valuable (Beier and Noss 2008; Vasas et al. 2009). Also, revegetated habitats should be created near the remnant habitats because remnants often act as ‘seeds’ for biodiversity restoration (cf. Soga et al. 2013b). On the other hand, improving habitat quality (including habitat matrix surrounding focal patches) is also essential to assist species’ colonisation into revegetated habitats (e.g., Woodcock et al. 2010). Indeed, the restoration method that aims to create structurally and floristically diverse and thick vegetation (e.g., ‘ecological restoration plantings’) typically supports higher faunal diversity than simple tree planting (e.g., Kanowski et al. 2005). A combined approach that integrates the above conservation options would bring the greatest outcomes for the conservation and restoration of urban biodiversity.

Finally, I conclude that there is a need to recognise the value of small ‘remnants’ even in highly urbanised landscapes. Especially at the early stage of city developments, remnant conservation programs should be the core of urban planning and greening schemes. As the abundance of butterflies and ground beetles in established parks was significantly lower than in remnant parks in this study, established parks would require much larger areas than remnants to support the same level of abundance. This is critical in urban landscape planning, because the cost of land acquisition for conservation in cities is typically high. Moreover, restoration projects often require human intensive and long-term investment in public resources to maintain their expected level of performance (Simenstad et al. 2006). Remnant habitats therefore have a critical role to maintain biodiversity cost-effectively. As woodland remnants provide the ‘refugia’ for urban wildlife, whether some coverage by remnants will be left within cities would decide the fate of urban biodiversity.

Chapter 2

Land sharing vs. land sparing: does the compact city reconcile urban development and biodiversity conservation?

ABSTRACT

As cities around the world rapidly expand, there is an urgent need to implement the best development form to minimise the negative impacts of urbanisation on native biodiversity. Two divergent forms for the expansion of cities are land-sharing and land-sparing developments. To date their relative benefits for biodiversity conservation are poorly understood. I quantified the relative conservation benefits of cities under land-sharing and land-sparing developments for butterflies and ground beetles in Tokyo, central Japan. For each insect species I determined which approach resulted in a larger total population size. At a higher level of urbanisation (higher number of buildings in a landscape), land-sparing rather than land-sharing resulted in a higher total population size for the majority species of both taxa. However, at a lower level of urbanisation, butterflies and ground beetles showed different responses to city development forms. Ground beetles had their highest total population sizes under land-sparing, whereas for butterflies, especially open-land and matrix-dwelling species, this was achieved under land-sharing. I have shown that the negative impacts of urbanisation on biodiversity differ greatly between land-sharing and land-sparing development forms. I also revealed that the relative conservation benefits of land-sharing and land-sparing depend on the levels of urbanisation. Based on my results, in areas that will be heavily urbanised in the future, city planners and policy makers should adopt approaches that follow a land-sparing strategy, and that protect large blocks of greenspace free from development. Where possible (most likely in creating new cities or urbanising substantial extents), as land-sharing was suggested to be the better strategy for many butterfly species at lower levels of urbanisation, a matrix approach could be adopted that integrated areas of land-sharing and of land-sparing, which might have the additional benefit of enhancing the delivery of some other ecosystem services by bringing nature and people closer together in some areas.

INTRODUCTION

Towns and cities are now home to the majority of humanity. Indeed, the proportion of urban dwellers continues to grow at an unprecedented pace, and by 2050 over two-thirds of the Earth's population will be living in urban areas (United Nations 2011). Given this scale of urbanisation, it is critically important to reconcile urban development and biodiversity conservation. There are several main reasons. First, cities are commonly built on areas previously occupied by highly productive ecosystems (e.g. lowland woodlands and grasslands, Imhoff et al. 2004), and thus such developments are, relative to their extent, disproportionately threatening processes. Second, nature in cities is essential for the maintenance and improvement of human health and wellbeing, with diverse impacts from physiology to social behavior (e.g. Fuller et al. 2007; Dallimer et al. 2012; Irvine et al. 2013; Keniger et al. 2013). Third, exposure to nature in cities plays a key role in reducing the extinction of experience and disengagement of people from natural environments, which may have broader consequences for the support for conservation action, and thus for the future of biodiversity (Miller 2005). In recognition of these concerns, conservation and restoration of urban biodiversity have increasingly become a significant consideration in city planning policies and schemes.

Halting, and ultimately reversing, biodiversity loss due to urbanisation constitutes a major challenge for city governance and planning, raising the crucial question of which city development forms best protect biodiversity. To address this challenge, Lin and Fuller (2013) recently highlighted the usefulness of applying the land-sharing vs. land-sparing paradigm in urban areas. Previously focused on issues of balancing food production and biodiversity conservation, this paradigm compares the relative conservation performances of two alternative options (Green et al. 2005; Fischer et al. 2008; Phalan et al. 2011). On the one hand, in the urban context, land-sparing minimises

the spatial extent of developed areas, such that residential areas (the primary component of urbanisation) are developed as intensively as possible, enabling the maintenance and persistence of consolidated blocks of greenspace (Fig. 1). On the other hand, under land-sharing development is more evenly, but less intensively, distributed, such that, a larger land area is needed to accommodate a given number of houses, and greenspaces tend to be more fragmented but on average closer to residential areas (Fig. 1). Whilst under land-sparing biodiversity is essentially concentrated into one or a few large greenspaces, under land-sharing it is distributed across the whole of a landscape but in a large number of smaller, fragmented, greenspaces (so-called ‘soft matrix’; Fischer et al. 2005).

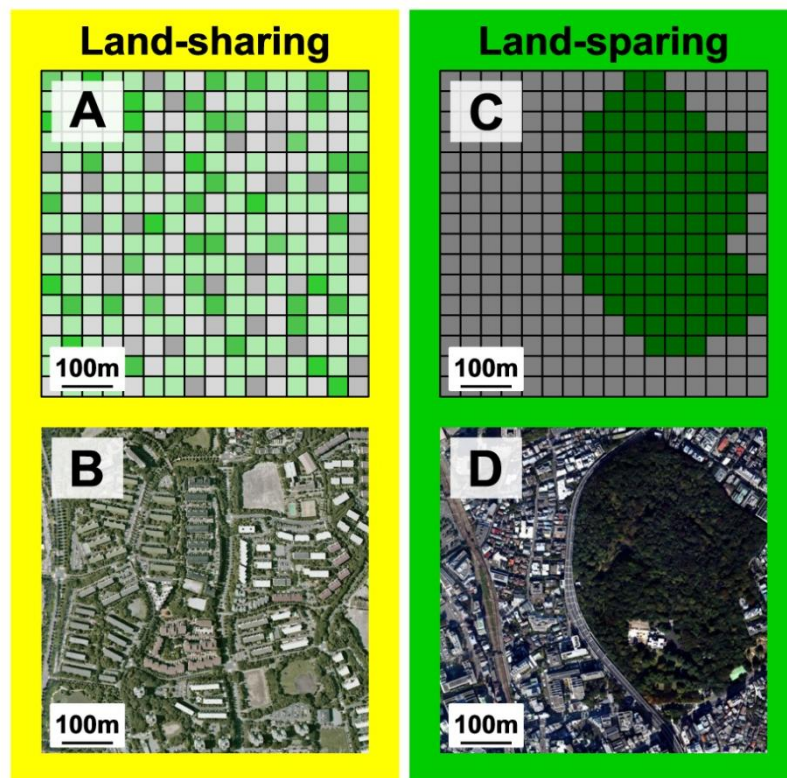


Fig. 1 Schematic illustrations and examples of land-sharing (panels A and B) and land-sparing developments (panels C and D). Under land-sharing development, all lands are developed at the same intensity. Land-sparing development consists of maximally urbanised and non-urbanised (“set-aside”) areas. Green and grey cells indicate vegetation (e.g. trees and grass) and urbanised areas.

Although undoubtedly a substantial simplification, understanding how urban land-sharing and land-sparing respectively influence levels and patterns of biodiversity is helpful to illustrate the potential consequences of adopting different planning options. This is particularly so given that, as cities are typically designed by top-down policy-making, initial development schemes have a crucial role in determining the capacity to sustain regional biodiversity. Notwithstanding, to date few studies have systematically compared the biodiversity benefits from urban land-sharing and land-sparing, and they focused on single taxonomic groups (Gagné and Fahrig 2010a; Sushinsky et al. 2013). Because species with different ecological traits show different responses to urbanisation (McKinney 2008), a more general conclusion requires further investigations.

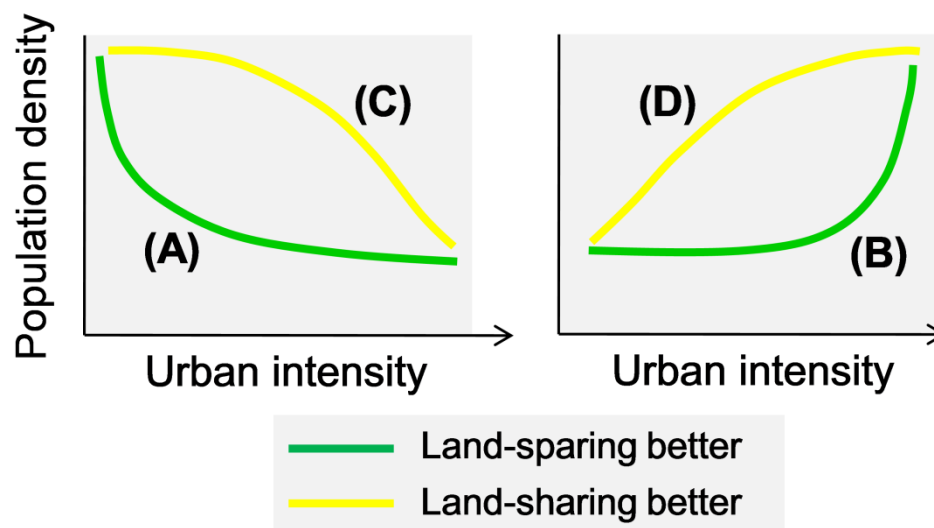


Fig. 2 Examples of different functional relationships between urban intensity and species' population densities. If the population density of a species declines sharply at a low level of urban intensity or increases only at a high urban intensity level (green lines), land-sparing is better. If, on the other hand, population density declines at high levels of urban intensity or increases at a low urban intensity level (yellow lines), land-sharing is better.

A major challenge in landscape ecology lies in estimating the total population sizes of species at landscape rather than patch scales (Wiens 1995; Gaston 2003). If the functional relationship can be determined between population density and an index of urban development intensity, then whether land-sharing or land-sparing forms of city development achieve larger total population sizes of a given species (which we assume is key for their conservation) can be estimated (Green et al. 2005; Phalan et al. 2011). Species' functional responses to urban development intensity can be broadly classified into four types (see Fig. 2). If the population density of a species declines sharply at low levels of urban development intensity (e.g. density of housing) or increases only at high intensity levels (forms A and B in Fig. 2), land-sparing is better than land-sharing for its conservation. For species with functional form A (urban sensitive species), as even low levels of habitat modification (i.e. fragmentation) result in a drastic decline of population size, a large consolidated greenspace (land-sparing) is thus a better option to protect these species (Diamond 1975). If, on the other hand, species' population density declines at high levels of urban development intensity or increases at low intensity levels (form C and D in Fig. 2), land-sharing is better (see more details in Green et al. 2005).

Here, I present a rare attempt to quantify the relative conservation benefits of land-sharing and land-sparing development forms in cities. As a case study I use two exemplar insect taxa, butterflies and ground beetles, and the city of Tokyo, central Japan. Compared with butterflies, ground beetles are less likely to adapt to patchy landscapes (i.e. land-sharing) because this taxon is sensitive to a higher density of public roadways (Keller and Largiader 2003) and alteration of microhabitat conditions due to habitat fragmentation (Magura et al. 2008; Soga et al. 2013a). I therefore predict that ground beetles, and woodland and patch-dependent butterflies (species whose larval host plants

are not planted in the matrix), will have higher total population sizes in land-sparing development, whereas the total population sizes of open-land and matrix-dwelling butterflies (species whose host plants are planted in the matrix) will be higher in land-sharing development. As species' responses to urbanisation depend on the levels of urban development intensity (McKinney 2008), I also investigate how the relative conservation benefits of the two development forms change with the levels of urbanisation.

METHODS

Study area

Fieldwork was conducted in Tokyo, central Japan. I used 1×1 km squares (1 km grid) as the unit scale of this study, because populations of butterflies and ground beetles are typically influenced by landscape structure at such a resolution (e.g. Vanbergen et al. 2005; Öckinger et al. 2009). Following previous studies (Gagné and Fahrig 2010a; Sushinsky et al. 2013), I used building density (the number of houses and other buildings) as an index of urbanisation intensity (Fig. 3). The map of buildings in the study area was derived from the Geospatial Information Authority of Japan (2013). Across Tokyo, I selected thirty-five 1 km^2 study squares, covering as wide a range of building density as possible (minimum: 0, maximum: $5,404/\text{km}^2$). The percentage of forest area within a square ranged from 0 to 100 % (mean = $25.5 \% \pm 39.2 \text{ SD}$). To reduce non-independence of study squares, each was separated from the others by more than 2 km.

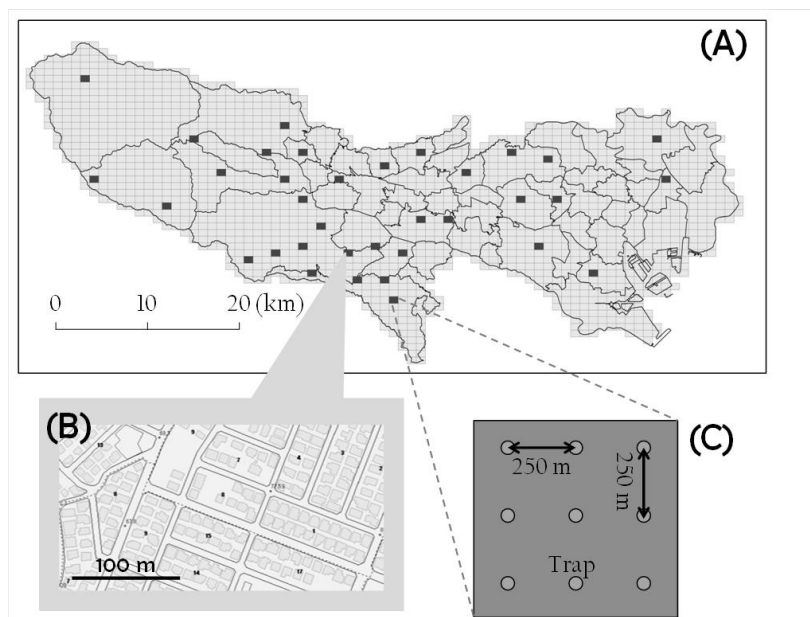


Fig. 3 35 sampling squares (A), an example of distribution map of building structures (B), and the planned location of traps for ground beetle sampling (C).

Field surveys and species classifications

I monitored butterflies using the line transect method. Three 500 m transects were randomly established along streets in each study square. Although the transect routes often crossed public parks, they did not cross private lands and gardens. I counted butterflies once every month between 08:45 and 16:15 during the adult flight season under appropriate flying conditions. To cover the flight periods of all butterfly species, monitoring was conducted from early April to early October 2012. However, no surveys were conducted in August because several butterfly species have been reported to aestivate then. Individuals within 5 m either side of a position along each transect were recorded while walking at a steady pace (10 m/min). To avoid double counting, I walked each transect only in one direction. Individuals that could not be identified to species by sight were caught using nets, identified, and released.

I sampled ground beetles using pitfall traps. To cover the adult stage of as wide a range of species as possible, sampling was conducted in July 2012. In each study square I placed 9 pitfall traps in woodland remnants, public green spaces, and roadside verges, separated by 250 m from each other (see Fig. 3). I buried black-colored plastic boxes of 20 cm in diameter and 27 cm in depth and containing approximately 200 ml of propylene glycol as a preservative. If it was not possible to bury traps at the intended location due to obstacles (e.g. roots, stones, concrete surfaces, or private lands), they were moved to as close as possible. Traps were established for the whole month and individuals collected after each week. Individuals caught were dried, mounted, and identified to species in the laboratory.

All butterfly species observed in the field were classified into either woodland or open-land and either patch-dependent or matrix-dwelling. Classification as woodland or open-land species was based on Tanaka (1988). Classification as patch-dependent or

matrix-dwelling species depended on whether the larval hosts were planted in the matrix or not, using the methodology of Soga et al. (2014). For ground beetles, our preliminary surveys revealed that in this region there were no matrix-dwelling species, so they were categorised only as either woodland or open-land species. Classification was based on their main habitats (Soga et al. 2014). Species whose habitat is restricted to woody environments, including secondary, coniferous and mature forests, were classified as woodland species. Species that usually (or sometimes) inhabit open-land environments (e.g. grasslands, pasture lands, farmlands, riverbeds, and sandy lands) and do not need woody conditions were classified as open-land species. In this study, however, open-land ground beetles comprised only 3.6% of individuals (172/ 4,779 individuals, see Table 1). I thus removed these from the later analyses.

Data analyses

Modeling species density and building density relationships

To determine whether land-sharing or land-sparing development is better for conservation, I estimated each species' total population size under two hypothetical landscapes and compared them. To do so, I first modeled the relationship between population density and building density for each species. Then, based on these functional relationships, I calculated each species' total population size under land-sharing and land-sparing development. All statistical analyses were performed with the R software (version 3.0.0, R Core Team 2013).

To model each species' population density versus building density relationship I used generalised linear mixed models (GLMMs), using the 'lme4' package and the 'glmer' function (ver. 0.999999.0; Bates et al. 2012). In GLMMs, population density (the number of observed individuals/ 1 km² square) and building density were used as

dependent and independent variables, respectively. Because the number of individuals are count data and do not take negative values, GLMMs with Poisson-distributed variables and a log link function were fitted for each species. To deal with un-modeled site-specific factors, I also used site id as a random effect.

Table 1 A list of butterflies and ground beetles observed in the field and the best fitted models (GLMMs).

Scientific name	Number of individuals observed	AIC values in each model			Coefficients						Classifications	
		First order	Second order	Null	Intercept	(SE)	Building density	(SE)	Building ² density	(SE)	Habitat	Matrix
Butterflies												
<i>Parnassius citrinarius</i>	50	92.9	94.1	118.6	1.08	0.45	-0.0014	0.0004			Open	Patch
<i>Byasa alcinous</i>	17	70.7	65.2	69.1	-2.67	1.03	0.0022	0.0010	-4.684E-07	2.0672E-07	Wood	Patch
<i>Graphium sarpedon</i>	36	105.1	106.7	103.2	-0.39	0.25					Wood	Matrix
<i>Papilio machaon</i>	16	67.4	62.4	65.5	-2.75	1.18	0.0025	0.0013	-6.746E-07	3.3502E-07	Open	Matrix
<i>Papilio machaon</i>	92	148.5	141.4	147.7	0.21	0.29	0.0009	0.0003	-1.733E-07	5.883E-08	Wood	Matrix
<i>Papilio helenus</i>	21	65.8	67.5	76.6	0.24	0.41	-0.0010	0.0004			Wood	Matrix
<i>Papilio protenor</i>	36	100.5	90.3	99.0	-0.69	0.44	0.0014	0.0005	-3.728E-07	1.2431E-07	Wood	Matrix
<i>Papilio memnon</i>	29	86.6	77.8	92.5	-0.36	0.45	0.0020	0.0009	-1.009E-06	4.1539E-07	Wood	Matrix
<i>Papilio macilentus</i>	81	59.0	60.2	107.1	2.42	0.14	-0.0041	0.0008			Wood	Matrix
<i>Papilio bianor</i>	77	115.2	112.9	138.2	1.20	0.39	0.0006	0.0010	-7.33E-07	4.7187E-07	Wood	Matrix
<i>Papilio maackii</i>	49	-	-	-	-	-	-	-	-	-	Wood	Patch
<i>Colias erate</i>	147	185.5	179.3	183.5	0.53	0.35	0.0010	0.0004	-2.308E-07	7.668E-08	Open	Matrix
<i>Eurema hecabe</i>	160	169.6	165.0	190.6	1.72	0.30	0.0004	0.0005	-3.486E-07	1.4473E-07	Wood	Matrix
<i>Pieris spp.</i>	569	263.4	252.3	262.7	2.28	0.21	0.0007	0.0002	-1.845E-07	4.6862E-08	Open	Matrix
<i>Anthocharis scolymus</i>	19	64.7	57.3	63.4	-4.48	2.42	0.0064	0.0037	-2.403E-06	1.3671E-06	Open	Matrix
<i>Parantica sita</i>	30	78.2	74.3	93.8	0.36	0.34	0.0011	0.0009	-9.15E-07	5.0377E-07	Wood	Patch
<i>Argynnis paphia</i>	13	-	-	-	-	-	-	-	-	-	Wood	Matrix
<i>Nephargynnis anadyomene</i>	22	-	-	-	-	-	-	-	-	-	Wood	Matrix
<i>Argyreus hyperbius</i>	129	157.5	157.4	167.9	1.56	0.20	0.0000	0.0002	-9.337E-08	6.1951E-08	Open	Matrix
<i>Limnitis camilla</i>	26	68.9	68.4	82.9	0.32	0.44	0.0009	0.0017	-1.25E-06	1.0387E-06	Wood	Patch
<i>Neptis sappho</i>	146	167.3	151.5	183.8	1.07	0.36	0.0019	0.0007	-9.278E-07	2.8052E-07	Wood	Matrix
<i>Araschnia burejana</i>	56	-	-	-	-	-	-	-	-	-	Wood	Patch
<i>Polygonia c-aureum</i>	57	116.4	101.3	120.4	0.25	0.29	0.0011	0.0004	-4.087E-07	1.1803E-07	Open	Patch
<i>Polygonia c -album</i>	1	-	-	-	-	-	-	-	-	-	Wood	Patch
<i>Nymphalis vaualbum</i>	1	-	-	-	-	-	-	-	-	-	Wood	Patch
<i>Nymphalis antiopa</i>	3	-	-	-	-	-	-	-	-	-	Wood	Patch
<i>Nymphalis xanthomelas</i>	6	-	-	-	-	-	-	-	-	-	Wood	Patch
<i>Cynthia cardui</i>	26	85.9	74.4	85.3	0.00	0.00	0.0000	0.0000	0.3894	0.2185	Open	Patch
<i>Vanessa indica</i>	15	58.8	55.1	60.8	0.00	0.00	0.0000	0.0000	-0.4004	0.2582	Open	Patch
<i>Kaniska canace</i>	48	97.0	89.3	119.2	0.00	0.00	0.0000	0.0000	-0.8473	0.2161	Wood	Patch
<i>Dichorragia nesimachus</i>	7	-	-	-	-	-	-	-	-	-	Wood	Patch
<i>Hestina persimilis japonica</i>	20	69.1	68.2	74.7	0.00	0.00	0.0000	0.0000	-0.0166	0.2384	Wood	Patch
<i>Hestina assimilis</i>	45	109.7	94.8	115.4	0.00	0.00	0.0000	0.0000	-0.6257	0.2183	Wood	Patch
<i>Sasakia charonda</i>	1	-	-	-	-	-	-	-	-	-	Wood	Patch
<i>Libythea celtis</i>	61	106.4	103.2	129.4	0.00	0.00	0.0000	0.0000	-0.0742	0.2198	Wood	Patch
<i>Narathura japonica</i>	36	91.4	77.0	102.1	0.00	0.00	0.0000	0.0000	0.1150	0.2055	Wood	Matrix
<i>Narathura bazalus</i>	15	61.0	56.0	64.1	0.00	0.00	0.0000	0.0000	-0.1552	0.3487	Wood	Matrix
<i>Artopoetes pryri</i>	12	-	-	-	-	-	-	-	-	-	Wood	Patch
<i>Japonica lutea</i>	44	94.4	93.1	103.0	0.00	0.00	0.0000	0.0000	-1.3230	0.5449	Wood	Patch
<i>Japonica saepestriata</i>	74	118.6	110.2	126.6	0.00	0.00	0.0000	0.0000	-1.7511	0.6388	Wood	Patch
<i>Antigius attilia</i>	135	147.8	137.0	167.1	0.00	0.00	0.0000	0.0000	-1.8267	0.4689	Wood	Patch
<i>Favonius orientalis</i>	20	60.1	61.6	65.4	-0.55	0.79	-0.0014	0.0008			Wood	Patch
<i>Rapala arata</i>	15	62.9	55.2	64.6	-1.59	0.76	0.0032	0.0015	-1.491E-06	6.7339E-07	Wood	Matrix
<i>Callophrys ferrea</i>	22	60.1	59.7	79.9	0.45	0.30		0.0003				
<i>Lycaena phlaeas</i>	157	184.9	177.5	185.4	1.13	0.25	0.0007	0.0003	-2.141E-07	6.6494E-08	Open	Patch
<i>Lampides boeticus</i>	27	78.2	63.2	80.9	-2.00	0.91	0.0063	0.0022	-3.295E-06	1.1891E-06	Open	Matrix
<i>Pseudozizeeria maha</i>	230	191.7	186.7	191.3	1.30	0.21	0.0006	0.0002	-1.132E-07	4.2297E-08	Open	Patch
<i>Celastrina sugitanii</i>	59	-	-	-	-	-	-	-	-	-	Wood	Patch
<i>Celastrina argiolus</i>	384	214.4	198.0	251.2	2.70	0.14	0.0004	0.0002	-2.928E-07	6.3979E-08	Wood	Matrix
<i>Everes argiades</i>	16	63.5	46.2	65.6	-2.05	0.88	0.0061	0.0019	-3.291E-06	1.0582E-06	Open	Matrix
<i>Curetis acuta</i>	38	85.0	76.3	106.6	0.65	0.26	0.0013	0.0007	-1.055E-06	4.1827E-07	Wood	Matrix
<i>Ypthima argus</i>	90	143.1	132.6	155.8	0.93	0.29	0.0009	0.0004	-4.534E-07	1.5176E-07	Wood	Patch
<i>Minois dryas</i>	52	80.2	78.6	121.4	1.46	0.18	-0.0001	0.0007	-7.037E-07	4.5194E-07	Open	Patch
<i>Lethe diana</i>	219	163.5	153.9	202.1	2.42	0.28	0.0010	0.0007	-1.031E-06	3.5867E-07	Wood	Patch
<i>Lethe sicelis</i>	64	108.8	104.0	135.3	1.21	0.26	0.0006	0.0007	-6.303E-07	3.1748E-07	Wood	Patch
<i>Neope goschkevitschii</i>	116	138.8	129.3	158.6	1.10	0.47	0.0027	0.0013	-1.795E-06	6.7866E-07	Wood	Patch
<i>Erynnis montanus</i>	131	110.9	112.4	169.5	2.54	0.10	-0.0014	0.0001			Wood	Patch
<i>Daimio tethys</i>	38	105.7	95.6	106.4	-0.54	0.45	0.0016	0.0006	-5.641E-07	1.95E-07	Wood	Patch
<i>Choaspes benjamini</i>	16	46.5	48.5	59.8	0.23	0.45	-0.0020	0.0008			Wood	Patch
<i>Isoteinon lamprospilus</i>	13	54.4	53.2	58.7	-0.91	0.63	0.0017	0.0018	-1.204E-06	9.5413E-07	Wood	Patch
<i>Potanthus flavum</i>	22	73.6	64.6	78.9	-0.89	0.58	0.0031	0.0014	-1.704E-06	7.3235E-07	Open	Patch
<i>Parnara quittata</i>	253	203.9	204.7	211.6	2.27	0.18	-0.0003	0.0001			Open	Matrix

Scientific name	Number of individuals observed	AIC values in each model			Coefficients						Classifications	
		First order	Second order	Null	Intercept	(SE)	Building density	(SE)	Building ² density	(SE)	Habitat	Matrix
Ground beetles												
<i>Asaphidion semilucidum</i>	3	-	-	-	-	-	-	-	-	-	Open	-
<i>Carabus albrechti esakianus</i>	440	119.08	120.92	129.24	2.65488	1.25337	-0.005044	0.0020857	-	-	Wood	-
<i>Carabus insulicola</i>	995	217.52	207.55	222.12	-0.7105	1.31942	0.0074721	0.0027251	-3.351E-06	1.1617E-06	Wood	-
<i>Carabus procerulus</i>	74	93.286	95.177	118.14	1.75233	0.4679	-0.002137	0.0005177	-	-	Wood	-
<i>Myas cuprescens cuprescens</i>	15	43.733	45.675	64.552	0.47295	0.28996	-0.001696	0.0005249	-	-	Wood	-
<i>Trigonotoma lewisii</i>	8	37.526	35.911	44.437	-0.7257	0.53622	0.0030182	0.0024854	-3.051E-06	2.0516E-06	Wood	-
<i>Pterostichus yoritomus</i>	102	94.876	96.856	119.61	2.21489	0.45501	-0.002699	0.0006083	-	-	Wood	-
<i>Pterostichus prolongatus</i>	68	-	-	-	-	-	-	-	-	-	Open	-
<i>Pterostichus takaosanus</i>	14	40.446	42.305	55.619	0.55254	0.29371	-0.002602	0.0009335	-	-	Wood	-
<i>Synuchus nitidus</i>	15	-	-	-	-	-	-	-	-	-	Wood	-
<i>Synuchus cycloderus</i>	952	207.82	207.07	256.94	4.36986	0.43971	-0.000715	0.0010746	-7.296E-07	5.0818E-07	Wood	-
<i>Amara chalcites</i>	116	128.1	120.54	148.51	0.97317	0.50141	0.0030028	0.0015143	-2.154E-06	8.527E-07	Wood	-
<i>Amara simplicidens</i>	25	-	-	-	-	-	-	-	-	-	Open	-
<i>Amara macronota ovalipennis</i>	14	-	-	-	-	-	-	-	-	-	Open	-
<i>Harpalus tridens</i>	9	-	-	-	-	-	-	-	-	-	Open	-
<i>Diplocheila zeelandica</i>	1	-	-	-	-	-	-	-	-	-	Open	-
<i>Haplochaenius costiger</i>	10	-	-	-	-	-	-	-	-	-	Wood	-
<i>Chlaenius abstersus</i>	13	-	-	-	-	-	-	-	-	-	Open	-
<i>Chlaenius virgulifer</i>	10	-	-	-	-	-	-	-	-	-	Open	-
<i>Chlaenius micans</i>	11	-	-	-	-	-	-	-	-	-	Open	-
<i>Chlaenius naeviger</i>	33	70.527	72.037	97.379	1.12914	0.20258	-0.001274	0.000267	-	-	Wood	-
<i>Chlaenius posticalis</i>	2	-	-	-	-	-	-	-	-	-	Open	-
<i>Odacanthinae spp.</i>	5	-	-	-	-	-	-	-	-	-	Open	-
<i>Planetes puncticeps</i>	10	-	-	-	-	-	-	-	-	-	Wood	-
<i>Brachinus scotomedes</i>	10	63.4	64.505	85.346	0.80103	0.23594	-0.001153	0.0002817	-	-	Wood	-
<i>Synuchus dulcigradus</i>	42	77.676	77.154	100.4	0.78611	0.4739	0.0009843	0.0020663	-1.655E-06	1.4327E-06	Wood	-
<i>Galerita orientalis</i>	10	43.302	43.584	51.212	-0.1951	0.38116	-0.000989	0.0003962	-	-	Wood	-
<i>Pterostichus microcephalus</i>	11	-	-	-	-	-	-	-	-	-	Open	-
<i>Eusilpha japonica</i>	1736	281.65	282.57	318.38	4.98601	0.45966	-0.001704	0.0002499	-	-	Wood	-
<i>Nicrophorus quadripunctatus</i>	25	37.415	38.445	50.964	0.06509	0.35535	-0.001687	0.0006389	-	-	Wood	-

Because preliminary analyses showed that there were no species for which scatter plots followed an extreme concave-up shaped pattern, I fitted first- and second-order polynomial regressions. These two types of GLMM can describe a wide variety of functional forms (see examples in Fig. 4). In these models, if a functional relationship for a species is best fitted by first-order regression, land-sparing is better than land-sharing at all levels of urbanisation. If a species' functional relationship is best fitted by second-order regression, land-sharing is sometimes (or always) better than land-sparing. In order to rank three candidate models (first-order, second-order, and null models), I used Akaike's information criterion (AIC). Models with the smallest AIC were considered as the best. As a result of model construction and selection, for most species either first- or second-order terms of best models had significant effects on population density. One butterfly species (*Graphium sarpedon*) whose best model was the null was removed in the later analyses. I also removed species with lesser than 10 individuals and 5 observed sites to avoid biasing our conclusions.

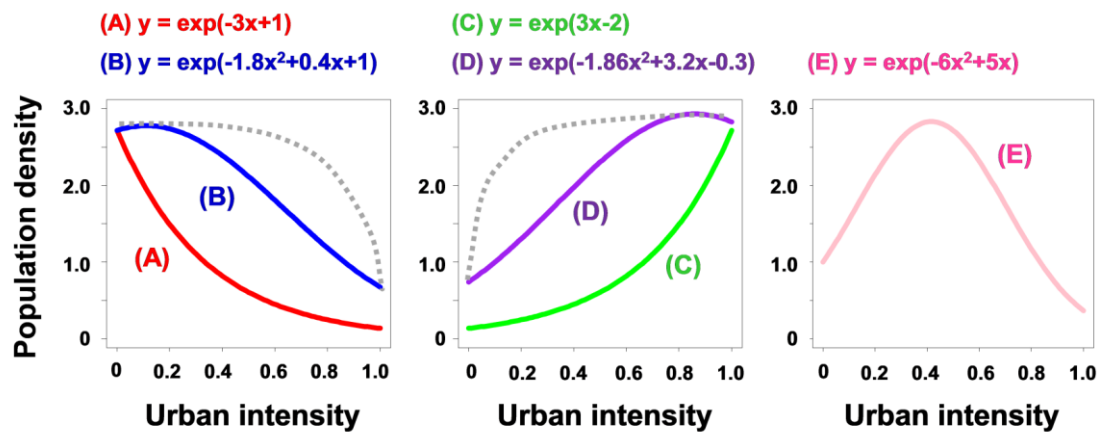


Fig. 4 Examples of the shape of function between species' population density and urbanisation intensity. In this study, I fitted first- and second-order polynomial regressions. These two types of GLMM can describe a wide variety of functional forms

Estimating the total population size under land-sharing and land-sparing strategies

Based on the above GLMMs, I calculated each species' total population size under land-sharing and land-sparing developments. Under land-sharing, all landscape areas are assumed to be developed equally for residential purposes (Fig. 1). The total population size of a species under land-sharing is therefore calculated simply as the product of the population density in residential areas (the number of individuals/ km²) and its size (1 km²). To estimate the population density in residential areas I used the functional relationships for that species between population density and building density (above GLMMs).

Under a land-sparing development form, residential areas are assumed to be developed as intensively as possible, whereas remaining areas are not developed (Fig. 1). Hence, the total population size of a species is estimated as the sum of its population in residential areas (maximally urbanised areas, 5,404 buildings/ km²) and its population in remaining areas (non-urbanised areas, no buildings). The total population sizes in residential and non-urbanised areas are calculated as the product of the size (km²) and population density (number of individuals/ km²) of the respective land types. To estimate the population density of each species both in maximally and non-urbanised areas, I again used the above GLMMs. Under land-sparing development, the size of residential areas is obtained by dividing the total number of buildings within a 1 km² landscape by the maximum number of buildings within a 1 km² landscape (5,404 buildings). Hence, the size of non-urbanised areas is the size of a hypothetical landscape (1.0 km²) minus the size of residential areas. For example, with the total number of 1,351 buildings per km², land-sparing development needs one quarter of a square for residential purposes (1,351 buildings/ (5,404 buildings/ km²) = 0.25 km²). Hence, the

size of non-urbanised areas is 0.75 km^2 . Under both land-sharing and land-sparing development forms, the total population size of each species was calculated for all levels of urbanisation (the possible range of total number of buildings/ km^2 , from 0 to 5,404).

RESULTS

In the field surveys I observed 62 butterfly species (4,410 individuals) and caught 30 ground beetle species (4,779 individuals). Although the species richness and population density of open-land and matrix-dependent butterflies were highest in areas with intermediate building density, those of woodland and patch-dependent butterflies and ground beetles decreased as building density increased (Fig. 5). Model selection of GLMMs also revealed contrasting responses of butterflies and ground beetles to increasing building density (Table 1). For butterflies, second-order regression was supported as the best model for most species (85.7 %), first-order regression was the best model for only 14.3 % of species. For ground beetles, on the other hand, first-order regression provided the best model for 66.7 % of species, and second-order regression for the remainder.

Species responses to city development forms differed among taxonomic groups. For ground beetles, the expected total population size of the majority of species was higher in land-sparing than land-sharing forms at all urbanisation levels (Fig. 6). In the case of butterflies, the number of species with higher total population size from land-sharing increased with decreasing urbanisation levels (Fig. 6). Especially for open-land and matrix-development butterflies, the number of species for which a land-sharing development form was better was larger than that for land-sparing at a medium or low level of urbanisation (Fig. 6). Although the same patterns were also shown by woodland and patch-dependent butterflies, the number of species whose better development form was land-sharing was less than that for which it was land-sparing (Fig. 6). At a high level of urbanisation, however, land-sparing resulted in a higher total population size for the majority of species regardless of species groups (Fig. 6).

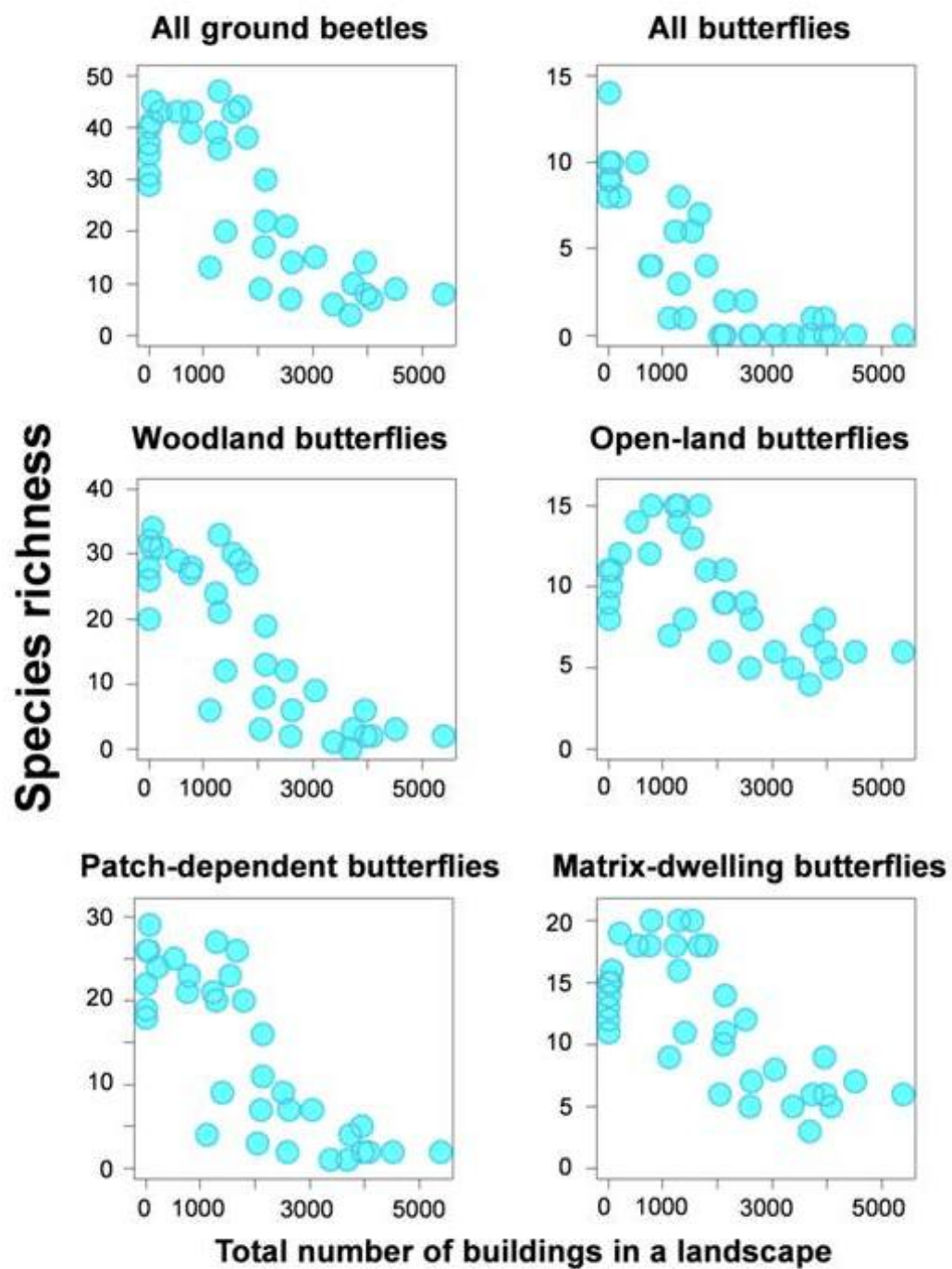


Fig. 5 Relationships between building density and species richness (blue circles), and population density (pink circles).

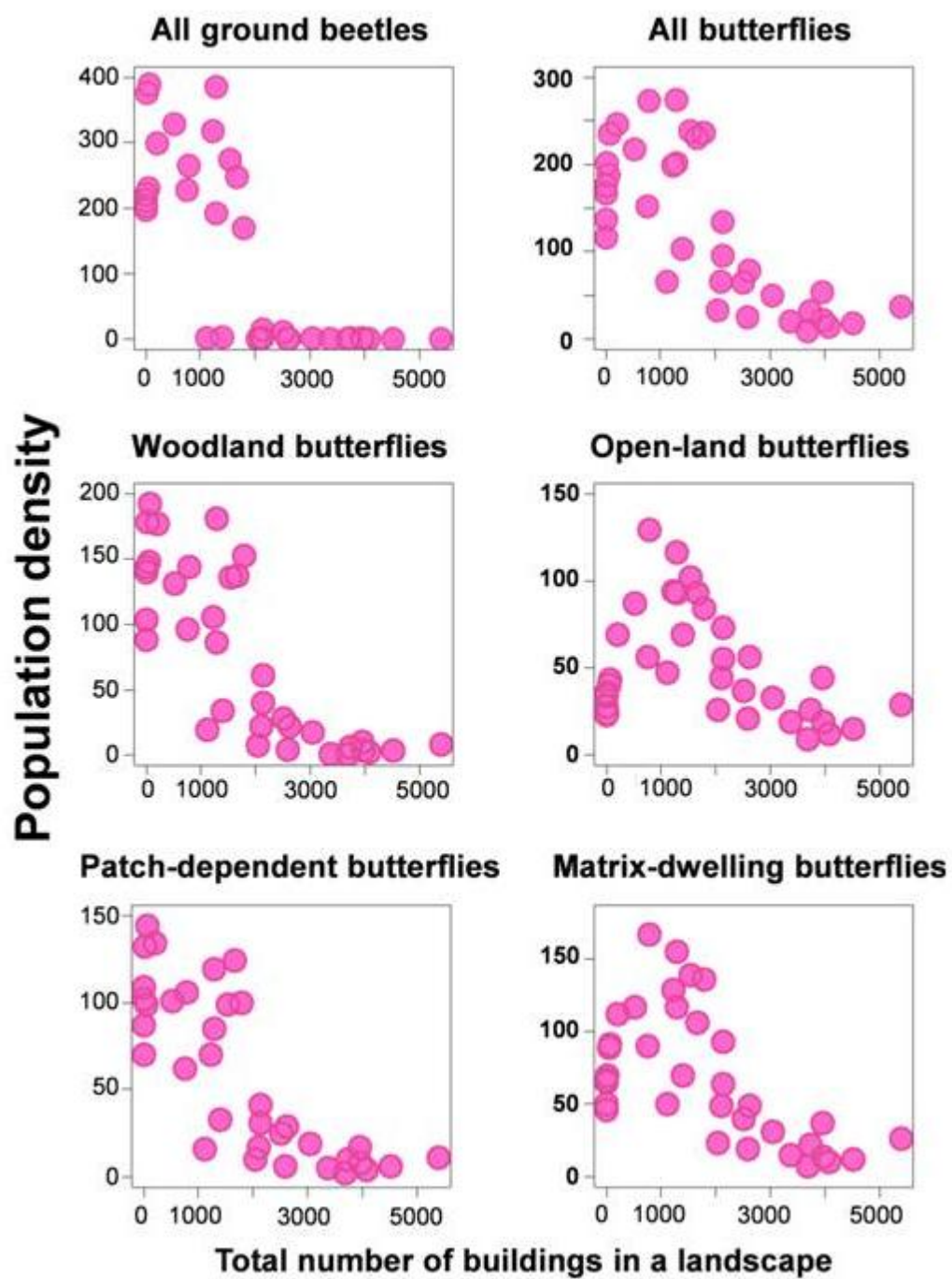


Fig. 5 Continued.

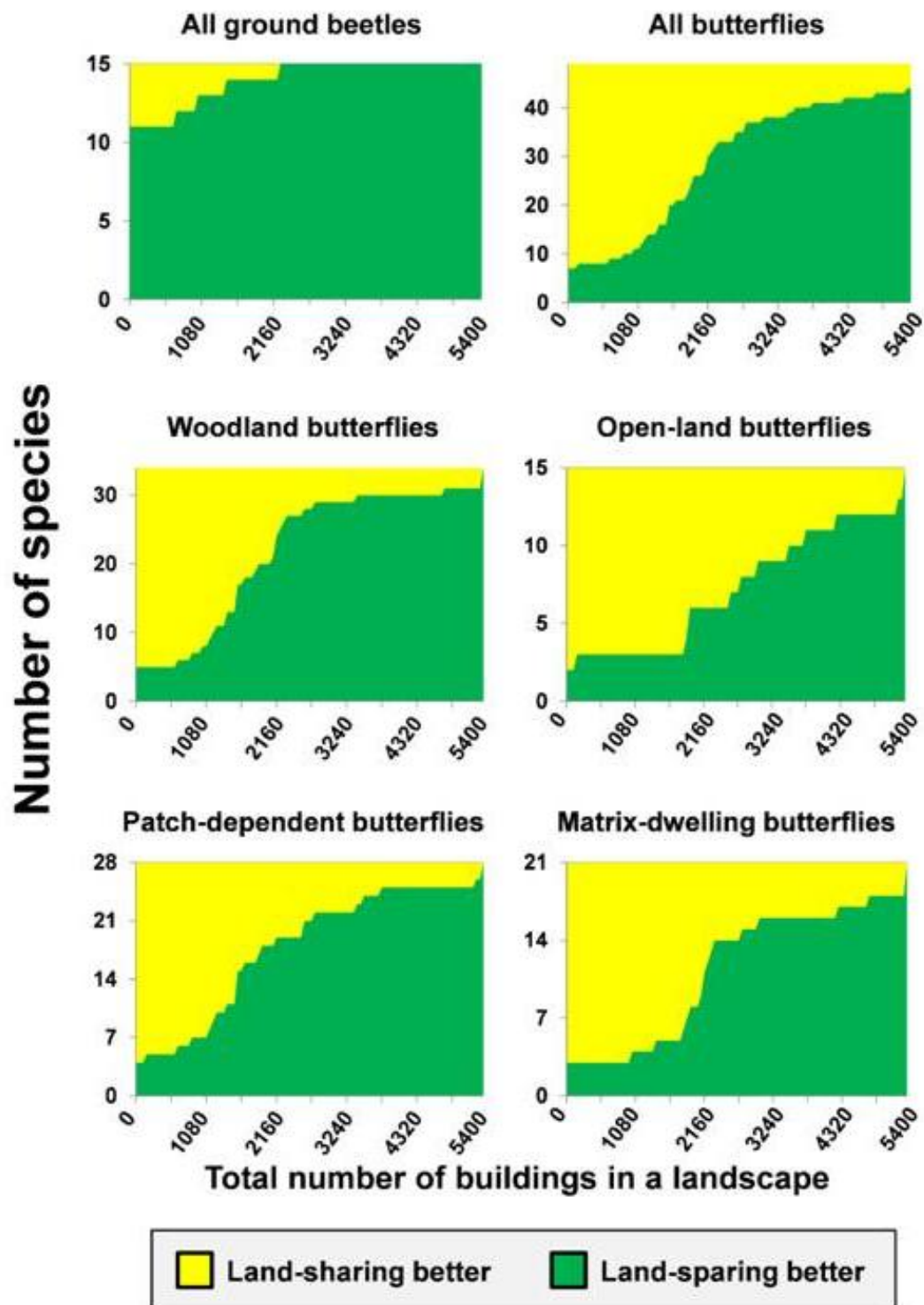


Fig. 6 Numbers of species whose total population size is higher under land-sparing (green) or land-sharing (yellow), in relation to the levels of urbanisation (the total number of buildings in a 1 km² square).

I also calculated the ratio of total population size for land-sparing to that for land-sharing. For ground beetles, mean predicted total population size in land-sparing was larger than in land-sharing at all urbanisation levels (Fig. 7). On the contrary, for butterflies mean predicted total population size in land-sparing was not always larger than in land-sharing: at a low level of urbanisation land-sharing was the better development form (Fig. 7). Moreover, compared with woodland and patch-dependent butterflies, open-land and matrix-development butterflies were more likely to have higher total population sizes under land-sharing (Fig. 7).

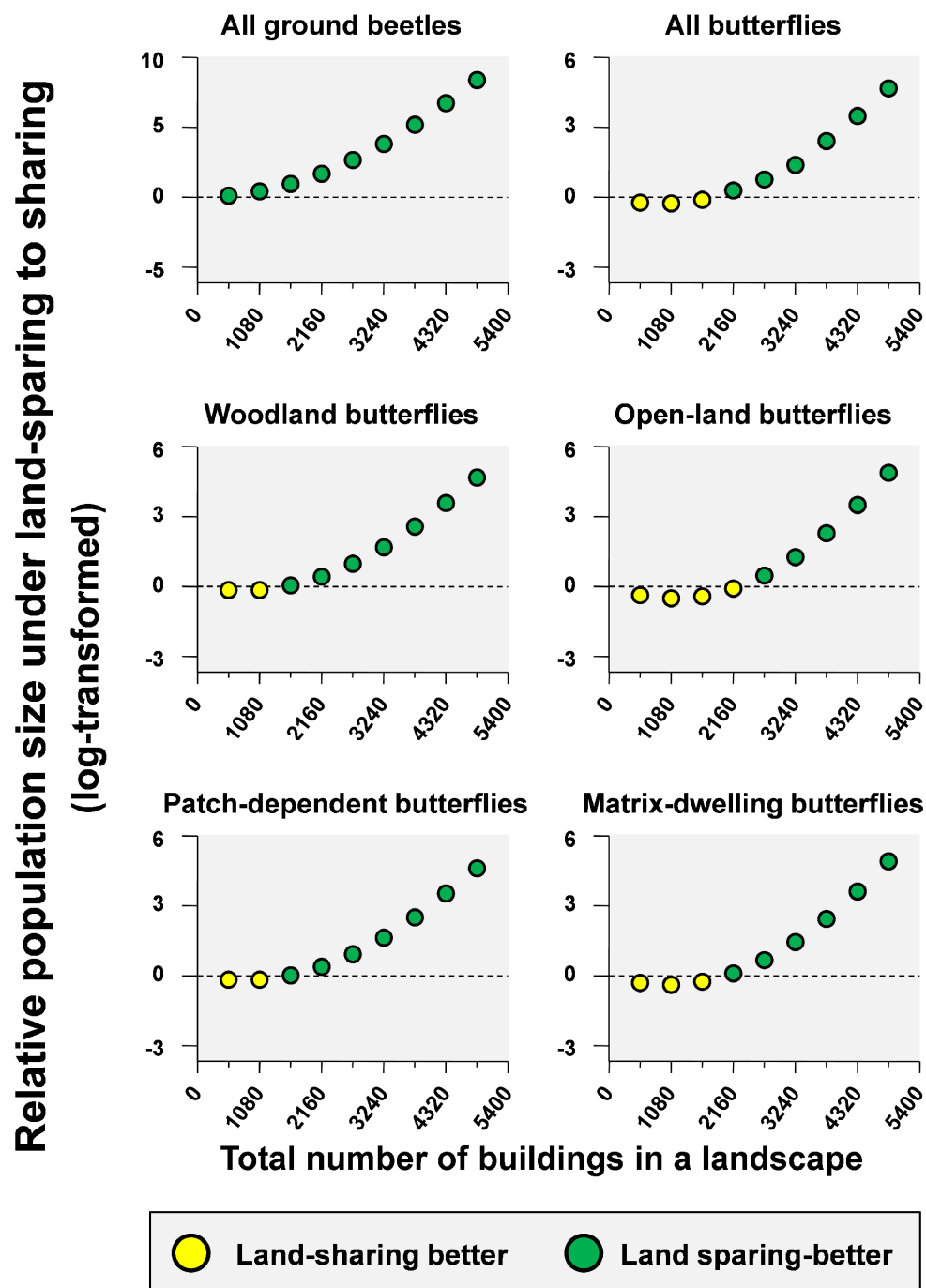


Fig. 7 Mean total population size under land-sparing relative to under land-sharing, in relation to the level of urbanisation (total number of buildings in a 1 km² square). Each species' relative total population size was calculated by dividing total population size for land-sparing by that for land-sharing, and these values were then log transformed and averaged for each species group. Broken horizontal lines indicate log [relative population size] = 0 (i.e. no difference between two development forms), and green and yellow circles mean land-sparing or land-sharing is better, respectively.

DISCUSSION

As cities expand rapidly around the world there is an urgent need to establish the best development form to minimise the negative impacts of urbanisation on native biodiversity. Thus, studies examining the consequences for biodiversity of urban land-sharing and land-sparing provide many practical implications for city planners and governments. This paper demonstrates that although most butterfly and ground beetle species decreased in population density with increasing building density, negative impacts of urbanisation differed between the two contrasting city development forms. With well-planned development schemes, therefore, the negative ecological consequences of global city expansion can be reduced. This is significant because, as the restoration of biological communities after city development is time consuming and costly (Soga et al. 2014), initial development schemes have a crucial role in determining the fate of urban biodiversity (Sharpe et al. 1986).

In line with my predictions, urban land-sparing showed a marked benefit for ground beetles. At all urbanisation levels, the negative impacts were lower under land-sparing development for this taxon (Figs. 6, 7). It is therefore quite important to develop cities with a land-sparing form, especially for species groups that have been reported to show sensitive responses to urbanisation or habitat fragmentation (McKinney 2008). With increasing urban sprawl, therefore, biological communities will increasingly be dominated by generalist or urban adapted species (so called ‘biotic homogenisation’; McKinney 1999). Such a rapid decline of biodiversity due to urbanisation would have other serious consequences, such as the loss of function and resilience of ecosystems, and of ecosystem goods and services (Fischer et al. 2006; Gaston and Fuller 2008; Gaston et al. 2013).

For butterflies, on the other hand, higher population size was sometimes achieved

in land-sharing rather than land-sparing development (Figs. 6, 7). Whilst for a large proportion of ground beetles relationships between the density of individuals of the species and building density were best explained by first-order regression models, for most butterflies second-order regression models were better. These contrasting patterns of response to urbanisation between butterflies and ground beetles may be caused by their different adaptabilities to urbanised environments. Unlike ground beetles, resources for butterflies (e.g. nectar producing flowers or larval host plants) are often abundant in the urbanised environments as amenity plants in roadside verges (Henriksen and Langer 2013) and private gardens (Smith et al. 2006). Indeed, the amounts of such resources often exhibit strong influences on the distribution of butterflies (e.g. Steffan-Dewenter and Tscharntke 2004; Soga and Koike 2012b, 2013). Thus, the high number of butterflies under land-sharing development could be explained by resource complementarity (Haynes et al. 2007). Notably, I observed that matrix-dwelling butterflies showed a relatively higher ability to tolerate the progress of urbanisation, albeit there are variations among species. This result raises the potential that biodiversity decline due to urbanisation is partly reduced by the improvement of matrix environments (cf. Soga and Koike 2012a). In areas where substantial extents of urban sprawl already occur (e.g. Tratalos et al. 2007; Fuller and Gaston, 2009), therefore, matrix management would have a substantial role in conserving and restoring biological communities.

Surprisingly, for most butterflies the better city development form changed with the level of urbanisation (the total number of buildings in a 1km² square). A large proportion of butterfly species did better with land-sharing at a lower level of urbanisation, whereas at a higher urbanisation level they did better with land-sparing (Fig. 6). This result suggests that, although many butterflies in our study area can to

some extent survive in developed landscapes, there is likely to be a threshold of building density above which population sizes change greatly (extinction threshold; Fahrig et al. 2002). For example, for many butterfly species the best development form changed at a density of 2,000 buildings/ km² (Fig. 6). However, as these thresholds will vary among regions and species, applying those derived in our study area to conservation planning in other regions involves substantial uncertainties (Rhodes et al. 2008). Nevertheless, our findings highlight an important implication for future urban development: the recommended development forms for biodiversity conservation depend on the levels of urbanisation.

Policy implications for future urban development

The results of this study have several implications for city planning and policy making for the protection of native biodiversity from ongoing urban expansion. They show a remarkable conservation benefit of land-sparing at high levels of urbanisation. In areas that will become highly urbanised in the near future (e.g. emerging countries in Africa and Asian), therefore, policies should aim to protect relatively large consolidated greenspaces free from development. These areas would be the last refuges for much wildlife (Soga et al. 2014). Conversely, in areas that are to be urbanised but not at high intensity (e.g. marginal urban areas), land-sparing would not necessarily be needed or may not be recommended for several reasons. First, as butterflies and ground beetles show contrasting responses to development forms, there is a risk that the adoption of a form that is more appropriate for some species groups will have negative consequences for others. Indeed, Gabriel et al. (2013) argued that as the best development form depends on the target species (or higher taxon) and region, there is no single solution to debate around the relevant benefits of land-sharing versus land-sparing. Second, at a low or medium level of urbanisation, I did not find a predominant benefit of urban

land-sparing to protect biodiversity. In this case, policy makers could pay more attention to other factors than biodiversity conservation in their development schemes. Recent studies suggest that extreme segregation of natural environments and components from residential areas reduces the provision of several key ecosystem services (e.g. health and well-being benefits: Barbosa et al. 2007; micro-climate regulation: Gaitani et al. 2011). Also, the establishment and maintenance of large greenspaces within cities will engender enormous financial costs (Naidoo et al. 2006). Except in highly urbanised situations, therefore, a more flexible development approach that integrates both advantages of urban land-sharing and land-sparing would provide a better outcome not only for nature but also for humans (more specific implications were shown in the final chapter).

Chapter 3

Land sharing reduces extinction of experience of nature in cities

ABSTRACT

Halting the ‘extinction of experience’, the progressive disengagement of people with the natural world, is vital to human wellbeing and to public support for global biological conservation. Home to the majority of humanity, urban areas are the key for engaging people with nature, raising the crucial question of how cities should best be designed to facilitate these experiences. For the purposes of maintaining species richness and composition, intensive development within a small area (urban land-sparing) has been shown to be better than extensive development over a large area (urban land-sharing). Here, I investigated for the first time how different city forms affect people's experience of nature, measured in terms of their use of greenspaces. I selected five pairs of land-sharing and land-sparing study regions with different coverage of greenspaces within the city of Tokyo, central Japan and used a questionnaire survey to determine the use residents made of these spaces. Results showed that urban land-sharing promotes the frequency of people's recreational use of urban greenspaces. Moreover, satisfaction with local green environments is also enhanced by land-sharing. This suggests a potential conflict in the design of cities between the urban form that is most desirable for the direct protection of regional biodiversity, and that which best promotes people's nature experiences and the support for its wider protection. A strong emphasis on the advantages of urban land-sparing may increase the separation of humans from nature, and further reduce public interest in, and awareness of, biodiversity and its benefits.

INTRODUCTION

The strong historical personal experience, and associated awareness, of nature is dramatically weakening as the majority of people today settle in urban areas (Turner et al. 2004; Miller 2005). As has been well-documented, those who do not regularly directly encounter nature are likely to lose substantial health and wellbeing advantages (Ulrich et al. 1991; Takano et al. 2002; Keniger et al. 2013), are less likely to perceive the value of nature and the benefits that it brings (Bixler et al. 2002; Wells and Lekies 2006), and are less motivated to want to protect it (Finger et al. 1994; Kals et al. 1999). This ongoing separation of people from nature, the ‘extinction of experience’ (Pyle 1978; Nabhan and St Antoine 1993), is thus considered both a major public health issue (‘nature deficit-disorder’; Louv 2005) and one of the most fundamental obstacles to halting and reversing the global biodiversity crisis (Pyle 1993). A reconnection of the large majority of people with nature is urgently needed (Pyle 2002; Miller 2006).

Vital to redressing the extinction of experience is the active engagement of city dwellers, the majority of the global population, with the natural environments that occur in their locale (Pyle 1993; Miller 2005, 2006). In particular, this typically requires their recreational use of urban greenspaces (Johnson and Hurley 2002; Lin et al. 2014). A key question then becomes what urban forms best promote this use, and should therefore be favored in redevelopment and new development schemes. Two extreme forms are commonly distinguished, extensive development over a large area (dispersed development) and intensive development within a small area (compact development) (Green et al. 2005; Fischer et al. 2008; Lin and Fuller 2013). The first constitutes a form of urban land-sharing, in which development intensification per unit area is relatively low, but a greater area of development is required to accommodate a given number of people, number of houses etc (Lin and Fuller 2013). The second constitutes a form of

urban land-sparing, in which larger amounts of natural area are better separated from developed ones, but the latter are developed as intensively as possible. Although urban land-sparing rather than land-sharing is known typically to be better for the protection of regional biological diversity (e.g. Gagné and Fahrig 2010a, 2010b; Sushinsky et al. 2013; but see Lenth et al. 2006), the implications of the two divergent approaches for reducing the extinction of experience remain unknown.

Here, I use five pairs of land-sharing and land-sparing study regions with different amounts of greenspace within the city of Tokyo, central Japan (Fig. 1), and a questionnaire survey, to determine the level of human-nature interactions measured as the use residents make of these spaces.

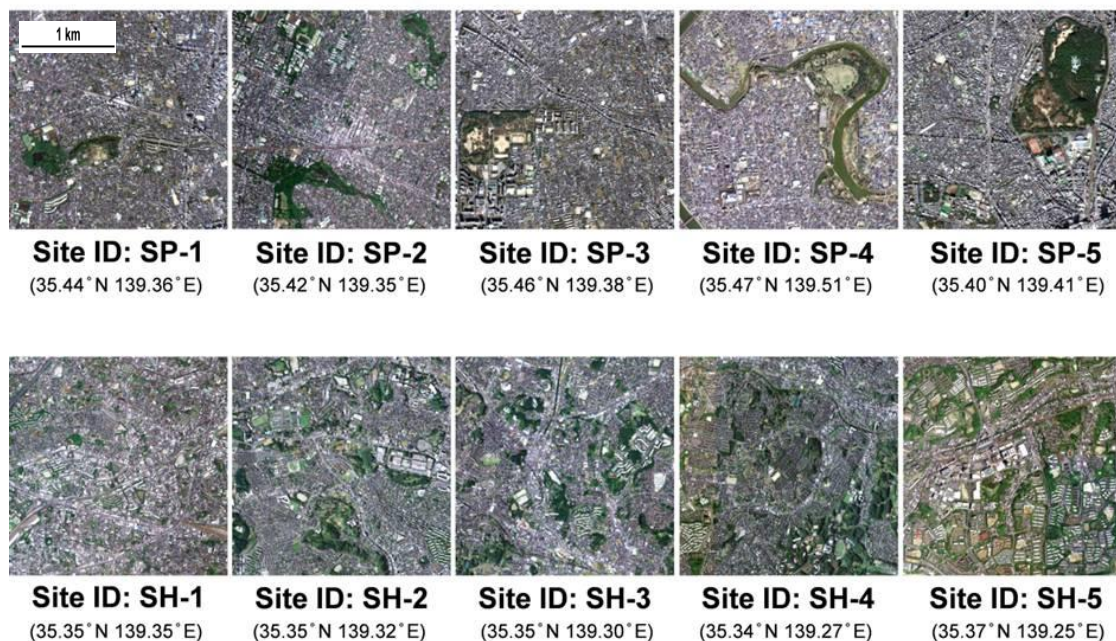


Fig. 1 Aerial photographs of my study regions (five land-sharing and land-sparing regions). The location (latitude/ longitude of the central point) of each study region is also shown. A land-sparing and a land-sharing region were, respectively, defined as one in which more than 85% of urban greenspace was comprised of a single contiguous area and one in which the largest urban greenspace occupied less than 25 % of the total area of greenspace.

METHODS

Study sites

The study was conducted in the city of Tokyo and Kawasaki city, central Japan. To investigate the effects of urban form (land-sharing or sparing) on people's recreational use of urban greenspace, I selected five pairs of land-sharing and land-sparing study regions ($2.5 \times 2.5 \text{ km}^2$). In these study regions, the greenspace areas were the same for each pair, but they are different between pairs (see five pairs of land-sharing and land-sparing study regions in Fig. 1). Greenspaces were extracted from the aerial images and these areas were not different between land-sharing and land-sparing regions (ANOVA, $F_{(1, 8)} = 0.15$, $P = 0.71$). I defined a land-sparing region as one in which more than 85% of urban greenspace was comprised of a single contiguous area: one study region did not meet this constraint (SP-2), but analysis revealed that this does not influence the results reported. A land-sharing region was defined as one in which the largest urban greenspace occupied less than 25 % of the total area of greenspace.

Questionnaire design

I conducted data collection by questionnaire to assess whether the difference in city form influenced people's recreational use of urban greenspace. A four-page postal questionnaire was sent to 10,000 residents in August 2013 (1,000 residents in each study region). Respondents were selected randomly. In each study region, we chose 25 plots (approximately 150 m radius) and dispensed 40 questionnaires in each. After three months, 1,644 people (16.4 %) returned the questionnaire (note: including six blank returns).

Table 1 The full survey questionnaires used in this study.

Q.1	How often do you visit greenspaces?
	1. Less than 1 or 2 times/ year
	2. 1 or 2 times/ few months
	3. 1 or 2 times/ month
	4. 1 or 2 times/ week
	5. 3 or 4 times/ week
	6. More than 5 times/ week
Q.2	How long do you spend in greenspaces (per visit)?
	1. Less than 10 minutes
	2. 11 to 30 minutes
	3. 31 to 60 minutes
	4. 1 to 2 hours
	5. More than 2 hours
Q.3	How far do you travel to reach greenspaces?
	1. Less than 100 meters
	2. 100 to 500 meters
	3. 500 to 1,000 meters
	4. More than 1,000 meters
Q.4	How do you reach greenspaces?
	1. Walk
	2. Bicycles
	3. Owned cars
	4. Public transports
Q.5	How long do you spend visiting greenspaces?
	() minutes

Q.6 What is the purpose of the visit to greenspaces?

1. A walk
2. Walk dog
3. Run
4. Physical relax
5. Enjoy the view
6. Read books
7. Photography
8. Think something
9. Observe plants and animals
10. Meet friends
11. A picnic
12. Play with children
13. Participate local events
14. Watch sports
15. Others

Q.7 How satisfied are you with the accessibility to greenspaces?

1. Very dissatisfied
2. Dissatisfied
3. Neither satisfied nor dissatisfied
4. Satisfied
5. Very satisfied
- (6. I do not know)

Q.8 Would you increase your use of greenspaces if they were closer?

1. I strongly disagree
2. I disagree
3. Neither agree nor disagree
4. I agree
5. I strongly agree
- (6. I do not know)

Q.9-1 How satisfied are you with local green environments for "walking"?

1. Very dissatisfied
2. Dissatisfied
3. Neither satisfied nor dissatisfied
4. Satisfied
5. Very satisfied

Q.9-2 How satisfied are you with local green environments for "playing"?

1. Very dissatisfied
2. Dissatisfied
3. Neither satisfied nor dissatisfied
4. Satisfied
5. Very satisfied

Q.9-3 How satisfied are you with local green environments for "relaxing"?

1. Very dissatisfied
2. Dissatisfied
3. Neither satisfied nor dissatisfied
4. Satisfied
5. Very satisfied

Q.9-4 How satisfied are you with local green environments for "observing nature"?

1. Very dissatisfied
2. Dissatisfied
3. Neither satisfied nor dissatisfied
4. Satisfied
5. Very satisfied

Q.9-5 How satisfied are you with local green environments for "contact with local communities"?

1. Very dissatisfied
2. Dissatisfied
3. Neither satisfied nor dissatisfied
4. Satisfied
5. Very satisfied

Age

1. 15 - 24 years of age
2. 25 - 49 years of age
3. 50 - 64 years of age
4. 65 - 79 years of age
5. Over 80 years of age

Gender

1. Male
2. Female

Employment status

1. Regular
2. Irregular
3. Housewife
4. Student
5. Retiree
6. Others

Can you identify the following six species (2 plants, 2 butterflies, and 2 birds)?

Plants



(Yes , No)



(Yes , No)

Butterflies



(Yes , No)



(Yes , No)

Birds



(Yes , No)



(Yes , No)

The questionnaire consisted of four parts (Table 1). The first part explained its purpose. To avoid confusion, I clearly defined the term ‘urban greenspace’ (as all publicly accessible open greenspace with some vegetation cover (e.g. parks, woodlands, and greenways) within 2.5 km around the houses (maximally 25 minutes to walk)) and provided several sample pictures. Urban greenspace usage was broadly defined as any type of visitation, including for physical, psychological, and social activities (see Ques. 6 in Table 1). However, I excluded the passage through greenspaces by commuters.

In the second part, respondents were asked six questions to investigate patterns of urban greenspace usage, such as visit frequency, distance traveled and means to reach urban greenspace, time to reach urban greenspace and stay in urban greenspace, and the purposes of a visit. Respondents who never visited greenspace were permitted to skip all of these questions, and such responses were removed from later analyses. Except with regard to the purposes of a visit, respondents were permitted to choose one answer to each question. Time to reach urban greenspace was described as a specific time (minutes) and finally categorised as five classes. For the main purposes for visiting urban greenspace, respondents were permitted to choose more than one purpose. Following Irvine et al. (2013), these purposes were finally classified into six groups: physical, space qualities, children, cognitive, social, and others.

In the third part, respondents were asked to examine their level of satisfaction with the accessibility to urban greenspace and their local green environment. Satisfaction with the accessibility to urban greenspace was measured by two questions. First, respondents were asked their satisfaction with the distance to urban greenspace that they daily use. Second, respondents were asked how much they would increase urban greenspace usage, if urban greenspace were closer. Satisfaction with their local green environments was measured by five questions. Respondents were asked how

satisfied they were with local green environments to meet five purposes of visits, to walk; to play; to relax; to observe nature; and to contact local communities. In this part, if respondents could not judge their satisfaction levels, they were permitted to select "*I don't know*", which was excluded from later analyses (Ques. 7 ($n = 13$) and Ques. 8 ($n = 161$)).

Finally, in the fourth part, I asked the respondent's personal questions, such as age, gender, and employment status. To increase return rates, I did not include any questions concerning economic factors (e.g., household incomes). Under employment status employees with intermittent or irregular were classified as irregular employment that is different with regular employment. In this part, I also asked respondent's knowledge (identification skills) of wildlife (Table 1). Respondents were asked to identify six wildlife species (2 plants, 2 butterflies, and 2 birds). All these six species are very common in our study area.

Statistical analyses

I analysed the quantitative interview data to detect whether urban form, greenspace area, and personal status affected respondents' recreational activities in urban greenspace. Here, I used ordinal logit regression models to analyse questionnaire responses, because it allows analysis of ordered categorical data (i.e., Likert scale data). To fit these models I used the "clmm" function within the "ordinal" package (ver. 2013.9-30, Christensen 2013) in R (ver. 3.0.1, R Core Team 2013). I used a proportional odds logit link function (default), and the ID of each study region as a random effect. In these models, the answer to each question was used as a response variable (all categorical answers were ordered), and urban greenspace area (log-transformed), urban form, age category, sex, and employment status were used as explanatory variables. In the above categorical explanatory variables, land-sparing (urban form), 50-64 (age

category), male (gender), and regular employment (employment status) were used as reference categories. Thus, the effect sizes of all other categories were interpreted as the comparison to these reference categories. In all of these analyses, blank answers and the answer '*I do not know*' were all removed.

RESULTS AND DISCUSSION

Of the 10,000 questionnaires distributed equally across the ten study regions, 1,644 (16.4 %) were returned. Characteristics of the sample respondents are summarised in Fig. 2 and Table 2. 50.8 % of the respondents visited urban greenspaces at least once a week, 12.3 % did so almost every day (more than 5 times/ week), and 10.8 % almost never visited an urban greenspace (less than 1 or 2 times/ year). Most respondents (79.1 %) visited urban greenspaces by walking. The main purpose of a greenspace visit was for physical activities (50.6 %).

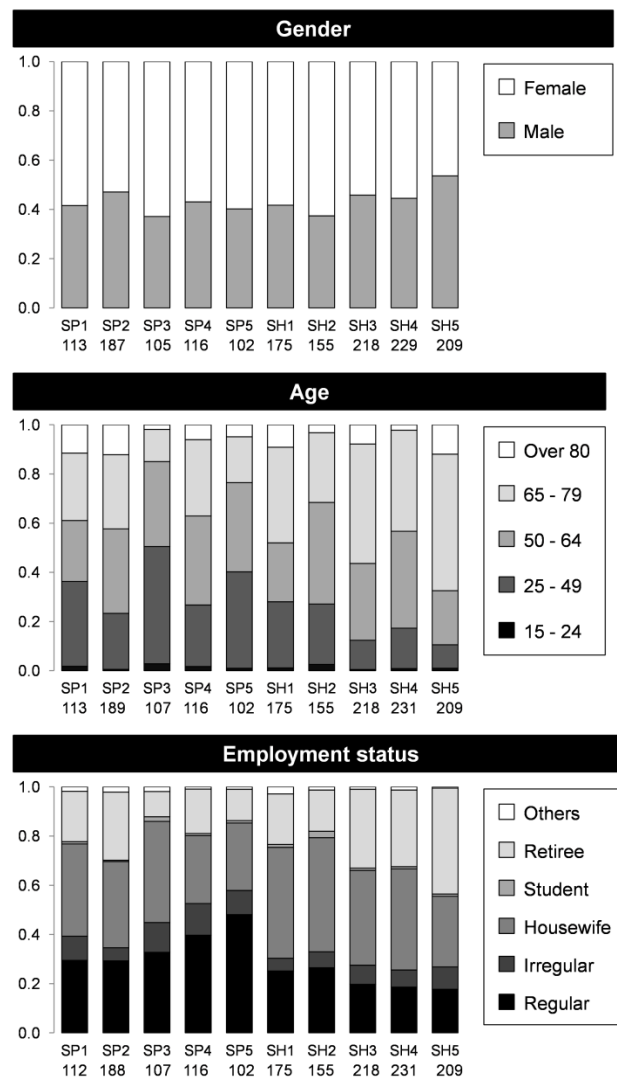


Fig. 2 Individual characteristics (age, gender, and employment status) of the study sample. The number for each bar indicates the total number of respondents.

Table 2 Individual characteristics (age, gender, and employment status) of the study sample.

Characteristics	Land-sparing regions		Land-sharing regions	
	Number	%	Number	%
Age				
15 - 24 years of age	9	1.4	11	1.1
25 - 49 years of age	202	31.7	169	16.9
50 - 64 years of age	209	32.8	311	31.1
65 - 79 years of age	157	24.6	429	42.9
Over 80 years of age	50	7.8	68	6.8
(No answer)	11	1.7	12	1.2
Gender				
Male	265	41.5	445	44.5
Female	358	56.1	541	54.1
(No answer)	15	2.4	14	1.4
Employment status				
Regular	218	34.2	208	20.8
Irregular	59	9.2	71	7.1
Housewife	212	33.2	390	39
Student	6	0.9	12	1.2
Retiree	120	18.8	294	29.4
Others	10	1.6	13	1.3
(No answer)	13	2	12	1.2

The patterns of people's urban greenspace visits were significantly different between the two urban forms (Figs. 3, 4, 5; Table 3). A land-sharing form and a greater area of greenspace, had similar significant positive effects on the frequency of urban greenspace visits ($P < 0.001$, Fig. 5). This suggests that critical to reducing the extinction of experience and increasing people's interactions with nature is simply increasing the opportunities for such interactions by embedding people's lives in urban environments with closer proximity to nature (Miller 2006).

The importance of the proximity of nature to the frequency of people's interactions with nature is supported by the finding that respondents in land-sharing regions (and, to a lesser extent, regions with larger amounts of urban greenspace) traveled significantly shorter distances ($P < 0.001$) and took shorter times ($P < 0.001$) to reach urban greenspaces (Fig. 5). Indeed, the frequency of urban greenspace visits was negatively correlated to the distance to them (*Spearman's* $r = -0.40$, $P < 0.001$) and to the time to reach them ($r = -0.43$, $P < 0.001$). This is consistent with previous studies showing that the likelihood or frequency of use of greenspaces was associated with their ease of access (e.g. Coombes et al. 2010). In addition, the proportion of people who visited urban greenspaces by walking rather than by other modes of transport (vehicles) tended to be higher in land-sharing regions (Fig. 4), suggesting that this urban form also served further to promote physical exercise and exposure to outdoor environments.

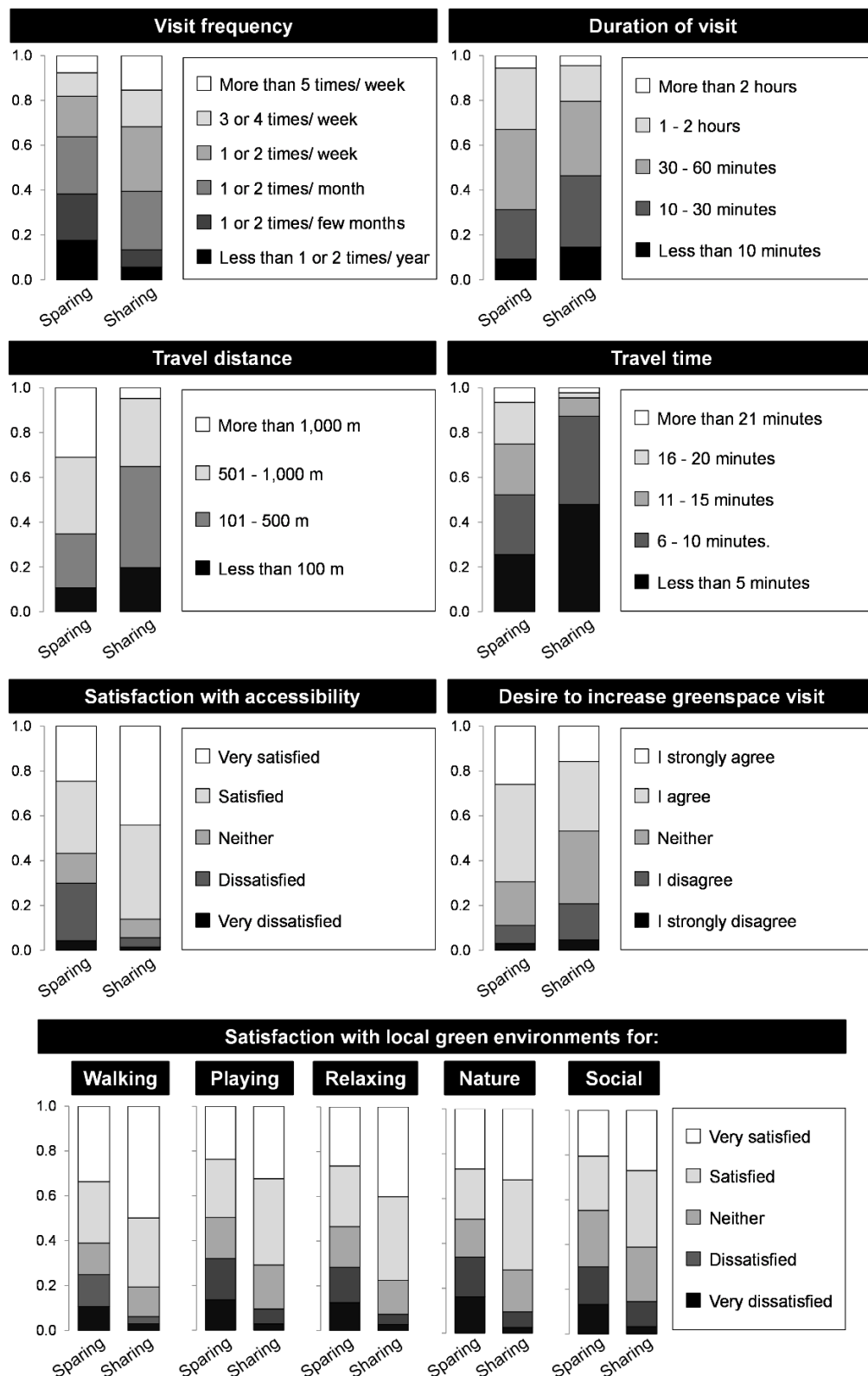


Fig. 3 Differences in patterns of urban greenspace usage and satisfaction with the accessibility to urban greenspace and local green environments between two urban forms. The data for five land-sharing and land-sparing regions were summed, respectively (see more detailed results in Fig 4).

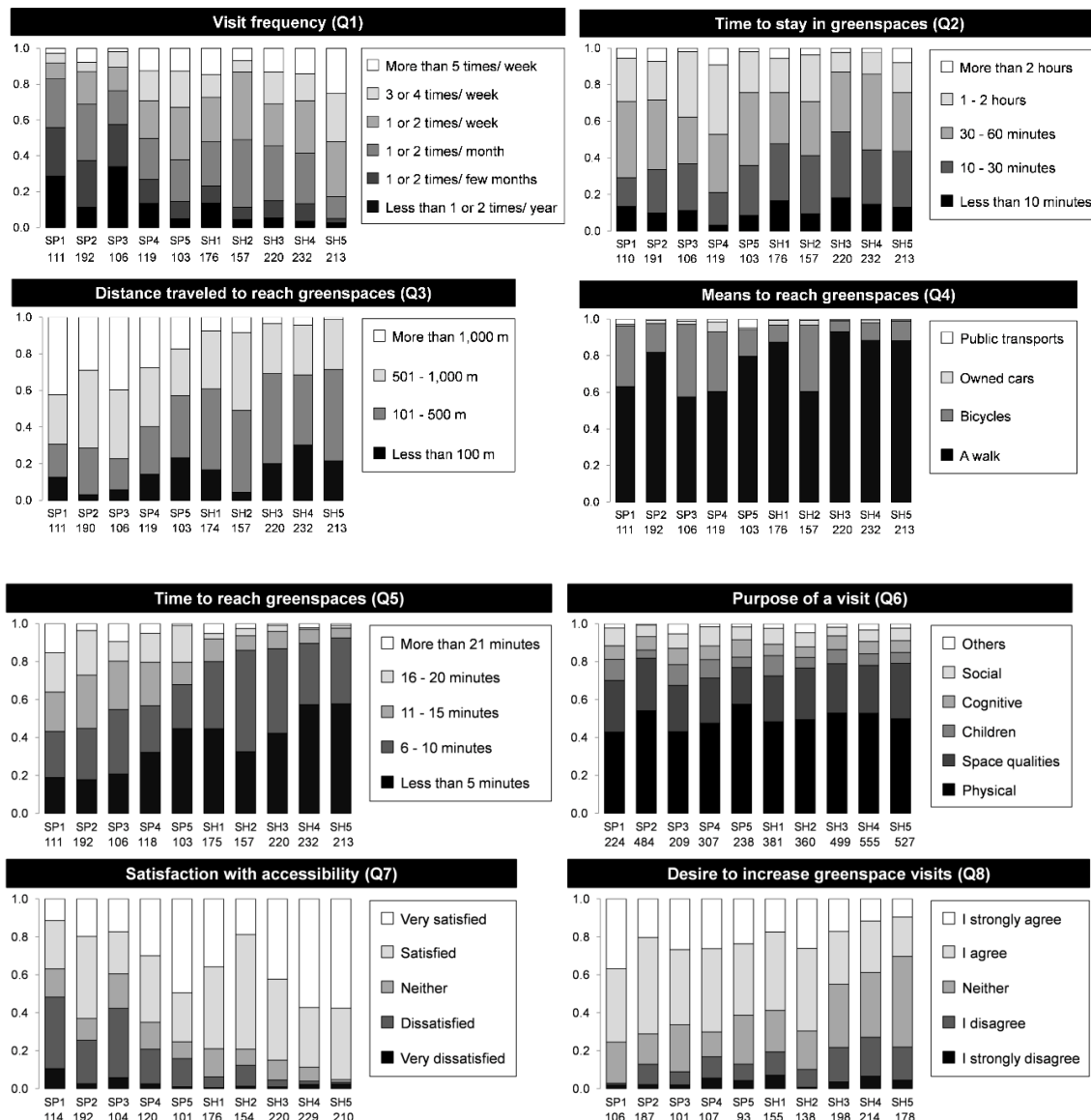


Fig. 4 The results of respondents' answers to all questions. The number for each bar indicates the total number of respondents (in Ques. 6, the total number of purposes was shown). SH and SP indicate land-sharing and land-sparing regions, respectively.

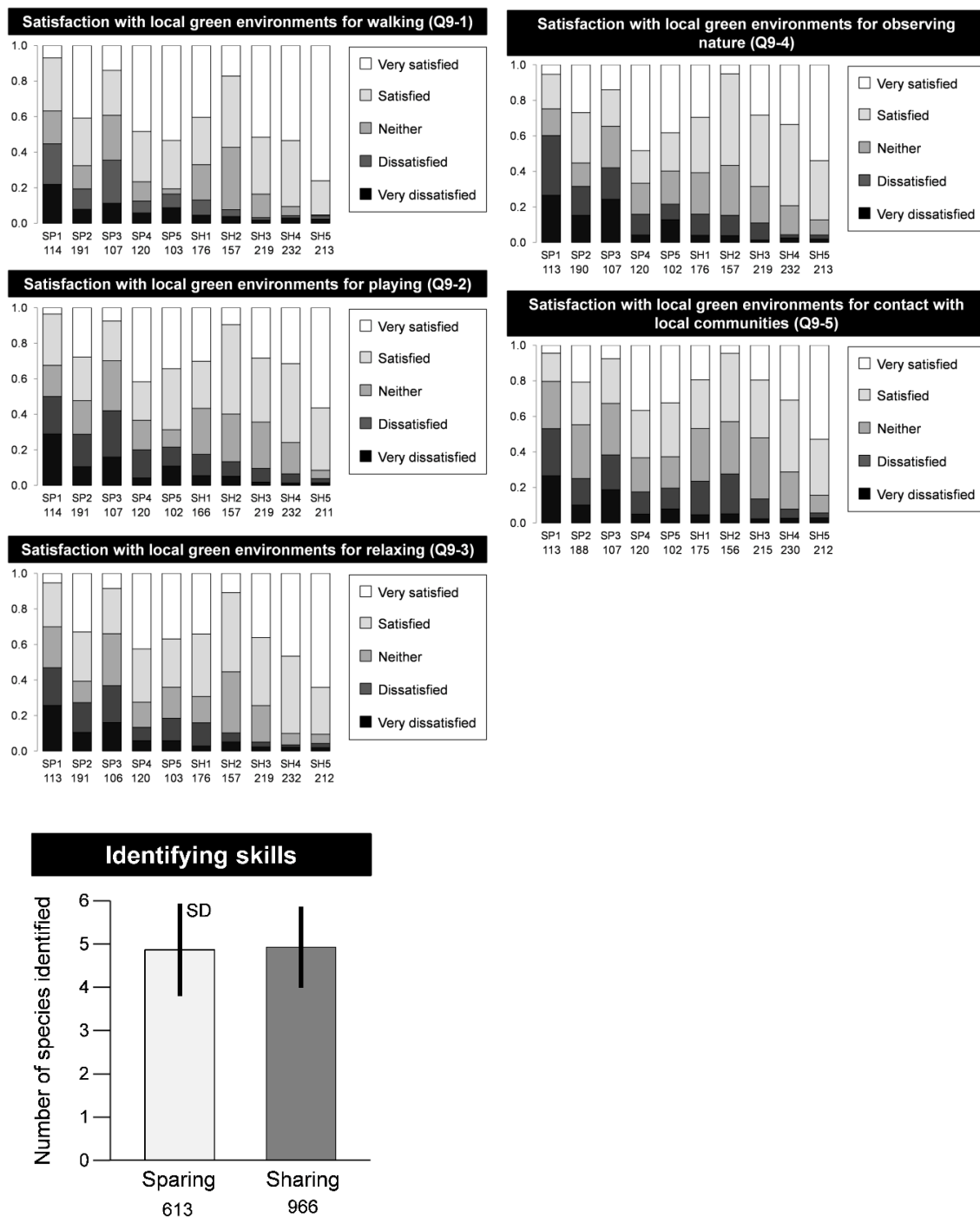


Fig. 4 Continued.

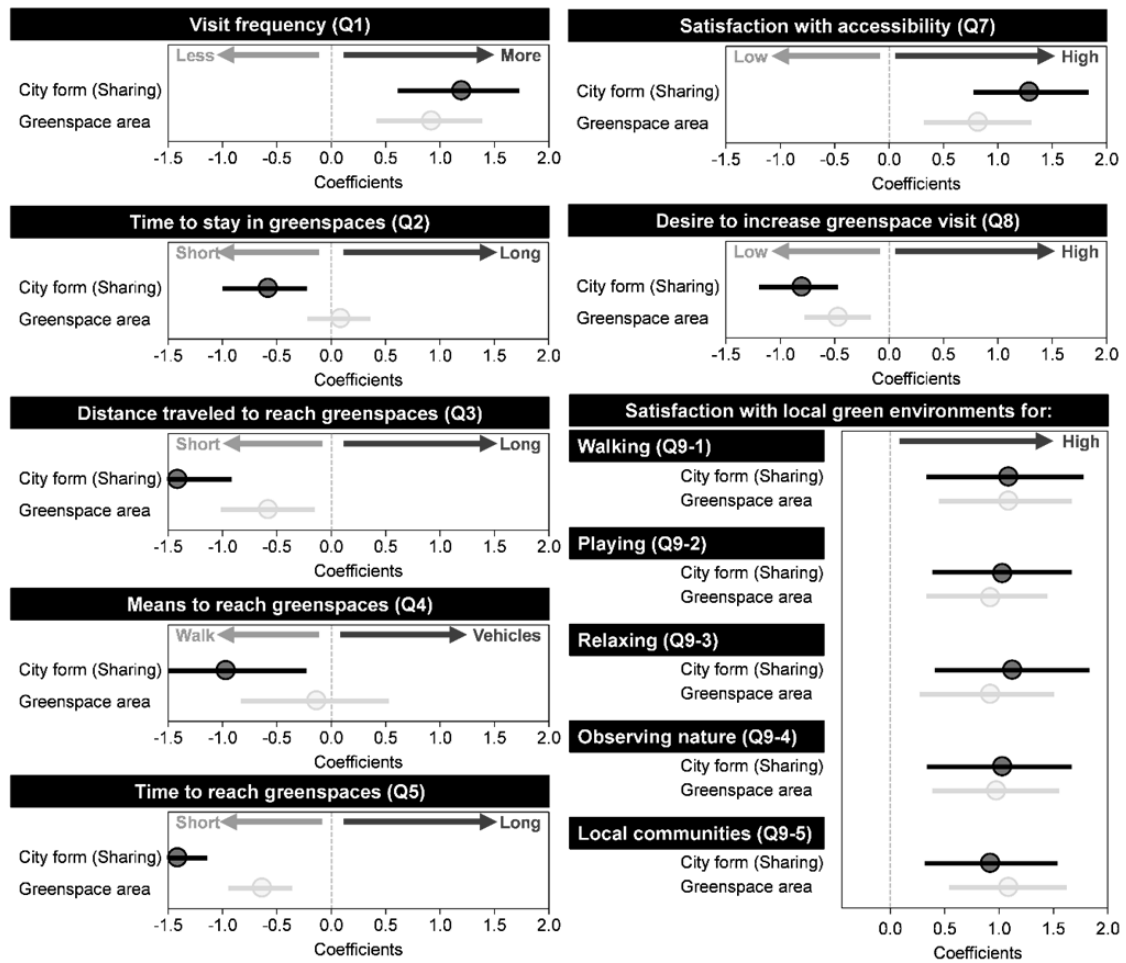


Fig. 5 Effect size of urban form (land-sharing city form) and greenspace area. Circles and bars indicate the mean values and 95 % confidence intervals of coefficient values, respectively (black: urban forms (land-sharing), gray: greenspace area). 95 % confidence intervals were calculated by mean values $\pm 1.96 * SE$ (see also Table 3).

Not only were levels of usage of urban greenspace influenced by its immediate availability, but so were people's levels of satisfaction with the accessibility to greenspace and local green environments (Figs. 3, 4, 5; Table 3). Respondents in land-sharing regions showed higher satisfaction with the accessibility to urban greenspace that they used daily than did those in land-sparing regions ($P < 0.001$, Fig. 5). More than 80 % of respondents in land-sharing regions were satisfied with the accessibility, and only 5 % of respondents were dissatisfied (Fig. 3). Conversely, in land-sparing regions, 30 % of respondents were dissatisfied with the accessibility to urban greenspace, and approximately 70 % desired to increase their usage of urban greenspace if it were closer (Fig. 3).

People may use urban greenspaces for a wide variety of purposes. For all of those recognised in the survey (walking, playing, relaxing, observing nature, and contacts with local communities) greater satisfaction was expressed with the availability of greenspaces in land-sharing urban forms and where greenspace coverage was greater ($P < 0.001$, Figs. 3, 4, 5; Table 3). Doubtless complex relationships exist between the use of greenspace for such purposes, the health and wellbeing benefits of greenspace per se, and the health and wellbeing benefits of these activities (Lee & Maheswaran 2011). Contact with nature in urban greenspaces delivers a wide range of valuable benefits to health and wellbeing (Dallimer *et al.* 2012; Irvine *et al.* 2013; Keniger *et al.* 2013), and people who visit urban greenspaces more frequently typically show improved health and wellbeing, as do those who take regular exercise and have better developed social lives (e.g. Coombes *et al.* 2010; Nutsford *et al.* 2013). Unpicking the mechanistic links in this nexus is a substantial research challenge.

The increased use made of, and the increased levels of satisfaction with the provision of, greenspace in land-sharing urban forms could arise in two different, but

not mutually exclusive, ways. First, they could simply reflect the importance of opportunity, with greater levels of interaction with nature occurring where this is more easily achieved. Second, people with stronger motivations to engage with natural environments may be more likely to choose to reside in land-sharing urban forms. In other words, the patterns we report herein could have components both of opportunity and orientation (cf. Lin et al. 2014). One potential indicator of people's emotional affinity to nature is their knowledge of it, such as their ability to recognise different common species of wildlife (Dallimer et al. 2012). There was no difference in this ability between land-sharing and land-sparing regions in this study (ANOVA, $F_{(1, 1577)} = 1.42$, $P = 0.23$; Fig. 4).

In contrast to the evident benefits of land-sharing as an urban form for human use and experiences of nature, land-sparing has been found to be more beneficial for the purposes of maintaining biodiversity in urban areas (e.g. Gagné and Fahrig 2010a, 2010b; Sushinsky et al. 2013). This is unsurprising in as much as, whilst some components of biodiversity do well in close proximity to human activities, others do not (McKinney 2006; Evans et al. 2011). There are two obvious approaches to dealing with this situation. First, one could take the view that because of the health and wellbeing benefits (Irvine et al. 2013; Keniger et al. 2013), and those for awareness of biodiversity, its benefits and its regional and global importance (Miller 2005), the green infrastructure of urban areas should principally be designed and maintained to maximise the ease with which people will make use of it. In other words, local biodiversity will not be maximised but to some extent sacrificed for direct local human benefit and wider biodiversity gain (Miller 2006). Second, one could employ a more hybrid strategy, in which one tried to develop green infrastructure in urban areas that comprised a mix of land-sharing and land-sparing forms to provide more of a mix of locally human-focused

and both local and regional/global biodiversity-focused benefits (cf. Yamaura et al. 2012). It is likely that by default the former option is the only practicable one in many existing urban areas, where opportunities to create substantial greenspaces are limited. In the design of new cities and areas of substantial urban expansion both options may be available.

Table 3 The results of ordinal logit regression models (standard deviation of random effects (study regions) and coefficients, standard errors, and P values of each explanatory variable) of all questions (except Q.6). In these models, land-sparing (urban form), 50-64 (age), male (gender), regular employment (employment status) were used as reference categories, thus the effect size of all other categories was interpreted as the comparisons to these reference categories.

Variables	Coefficients	SE	p-values
Q.1			
(*SD of Random effects = 0.42)			
Urban form(Land-sharing)	1.21	0.29	< 0.001
log(Greenspace size)	0.92	0.25	< 0.001
Age (15 - 24)	-0.95	0.76	0.21
Age (25 - 49)	0.09	0.12	0.48
Age (65 - 79)	0.34	0.12	< 0.01
Age (over 80)	-0.14	0.21	0.49
Sex (Male)	-0.06	0.14	0.67
Employment status (Irregular)	-0.01	0.18	0.94
Employment status (Housewife)	0.40	0.16	0.01
Employment status (Student)	0.91	0.81	0.26
Employment status (Retiree)	0.74	0.15	< 0.001
Employment status (Others)	2.01	0.47	< 0.001
Q.2			
(*SD of Random effects = 0.22)			
Urban form(Land-sharing)	-0.58	0.17	< 0.001
log(Greenspace size)	0.06	0.15	0.68
Age (15 - 24)	1.61	0.73	0.03
Age (25 - 49)	0.42	0.13	< 0.001
Age (65 - 79)	-0.05	0.12	0.69
Age (over 80)	-0.04	0.20	0.83
Sex (Male)	-0.19	0.13	0.15
Employment status (Irregular)	-0.18	0.19	0.33
Employment status (Housewife)	0.06	0.16	0.68
Employment status (Student)	-0.71	0.75	0.35
Employment status (Retiree)	0.36	0.15	0.02
Employment status (Others)	0.67	0.44	0.13

Q.3

(*SD of Random effects = 0.37)

Urban form(Land-sharing)	-1.45	0.27	< 0.001
log(Greenspace size)	-0.59	0.23	< 0.01
Age (15 - 24)	-0.29	0.85	0.73
Age (25 - 49)	-0.06	0.13	0.66
Age (65 - 79)	-0.02	0.13	0.87
Age (over 80)	-0.05	0.22	0.81
Sex (Male)	0.14	0.14	0.32
Employment status (Irregular)	0.03	0.19	0.89
Employment status (Housewife)	-0.51	0.16	< 0.01
Employment status (Student)	0.09	0.87	0.91
Employment status (Retiree)	-0.01	0.15	0.95
Employment status (Others)	0.57	0.46	0.22

Q.4

(*SD of Random effects = 0.57)

Urban form(Land-sharing)	-0.95	0.39	0.02
log(Greenspace size)	-0.14	0.34	0.68
Age (15 - 24)	0.90	0.97	0.35
Age (25 - 49)	0.30	0.17	0.07
Age (65 - 79)	-0.21	0.18	0.25
Age (over 80)	-0.26	0.32	0.41
Sex (Male)	-0.10	0.19	0.58
Employment status (Irregular)	0.16	0.25	0.53
Employment status (Housewife)	0.03	0.22	0.89
Employment status (Student)	0.19	1.05	0.86
Employment status (Retiree)	0.28	0.21	0.20
Employment status (Others)	1.35	0.56	0.02

Q.5

(*SD of Random effects = 0.20)

Urban form(Land-sharing)	-1.48	0.17	< 0.001
log(Greenspace size)	-0.61	0.14	< 0.001
Age (15 - 24)	-0.77	0.78	0.32
Age (25 - 49)	-0.04	0.13	0.75

Age (65 - 79)	0.08	0.13	0.54
Age (over 80)	0.18	0.22	0.41
Sex (Male)	0.14	0.14	0.32
Employment status (Irregular)	0.15	0.19	0.44
Employment status (Housewife)	-0.25	0.16	0.13
Employment status (Student)	0.70	0.80	0.38
Employment status (Retiree)	-0.06	0.15	0.71
Employment status (Others)	0.92	0.47	0.05

Q.7

(*SD of Random effects = 0.41)

Urban form(Land-sharing)	1.33	0.29	< 0.001
log(Greenspace size)	0.81	0.25	< 0.01
Age (15 - 24)	1.08	0.92	0.24
Age (25 - 49)	0.00	0.13	1.00
Age (65 - 79)	0.19	0.13	0.13
Age (over 80)	-0.14	0.22	0.53
Sex (Male)	0.05	0.14	0.73
Employment status (Irregular)	0.27	0.19	0.17
Employment status (Housewife)	0.25	0.16	0.13
Employment status (Student)	-1.11	0.91	0.22
Employment status (Retiree)	0.35	0.16	0.02
Employment status (Others)	-0.67	0.48	0.16

Q.8

(*SD of Random effects = 0.21)

Urban form(Land-sharing)	-0.82	0.17	< 0.001
log(Greenspace size)	-0.47	0.15	< 0.01
Age (15 - 24)	-0.53	0.84	0.53
Age (25 - 49)	0.14	0.13	0.30
Age (65 - 79)	-0.10	0.13	0.43
Age (over 80)	0.11	0.22	0.60
Sex (Male)	0.44	0.15	< 0.01
Employment status (Irregular)	0.01	0.19	0.97
Employment status (Housewife)	-0.25	0.17	0.14
Employment status (Student)	0.25	0.84	0.77

Employment status (Retiree)	0.06	0.16	0.69
Employment status (Others)	-1.57	0.55	< 0.01

Q.9-1

(*SD of Random effects = 0.54)

Urban form(Land-sharing)	1.13	0.37	< 0.01
log(Greenspace size)	1.13	0.32	< 0.001
Age (15 - 24)	1.53	0.80	0.06
Age (25 - 49)	-0.12	0.13	0.36
Age (65 - 79)	0.16	0.13	0.21
Age (over 80)	-0.05	0.24	0.82
Sex (Male)	0.00	0.14	0.98
Employment status (Irregular)	0.03	0.19	0.88
Employment status (Housewife)	0.45	0.17	< 0.01
Employment status (Student)	-2.13	0.82	< 0.01
Employment status (Retiree)	0.48	0.16	< 0.01
Employment status (Others)	-0.88	0.51	0.08

Q.9-2

(*SD of Random effects = 0.46)

Urban form(Land-sharing)	1.04	0.32	< 0.001
log(Greenspace size)	0.88	0.28	< 0.01
Age (15-24)	0.18	1.02	0.86
Age (25-49)	-0.18	0.13	0.16
Age (65-79)	0.01	0.12	0.92
Age (over 80)	-0.16	0.23	0.49
Sex (Male)	-0.05	0.14	0.72
Employment status (Irregular)	0.08	0.19	0.67
Employment status (Housewife)	0.32	0.16	0.05
Employment status (Student)	-0.79	1.03	0.44
Employment status (Retiree)	0.54	0.15	< 0.001
Employment status (Others)	-0.82	0.47	0.08

Q.9-3			
(*SD of Random effects = 0.52)			
Urban form(Land-sharing)	1.18	0.35	< 0.001
log(Greenspace size)	0.95	0.31	< 0.01
Age (15-24)	1.07	0.77	0.17
Age (25-49)	-0.12	0.13	0.35
Age (65-79)	0.07	0.13	0.59
Age (over 80)	-0.16	0.23	0.47
Sex (Male)	-0.14	0.14	0.33
Employment status (Irregular)	0.20	0.19	0.28
Employment status (Housewife)	0.40	0.16	0.01
Employment status (Student)	-1.17	0.78	0.13
Employment status (Retiree)	0.52	0.15	< 0.001
Employment status (Others)	-0.85	0.51	0.09

Q.9-4			
(*SD of Random effects = 0.51)			
Urban form(Land-sharing)	1.00	0.35	< 0.01
log(Greenspace size)	0.95	0.30	< 0.01
Age (15-24)	0.48	0.89	0.59
Age (25-49)	-0.15	0.13	0.22
Age (65-79)	0.09	0.12	0.49
Age (over 80)	0.15	0.23	0.52
Sex (Male)	-0.02	0.14	0.87
Employment status (Irregular)	0.26	0.19	0.16
Employment status (Housewife)	0.48	0.16	< 0.01
Employment status (Student)	-0.54	0.90	0.55
Employment status (Retiree)	0.46	0.15	< 0.01
Employment status (Others)	-0.27	0.55	0.62

Q.9-5			
(*SD of Random effects = 0.44)			
Urban form(Land-sharing)	0.92	0.30	< 0.01
log(Greenspace size)	1.13	0.26	< 0.001
Age (15-24)	0.64	0.73	0.38
Age (25-49)	0.07	0.12	0.55

Age (65-79)	0.15	0.12	0.24
Age (over 80)	-0.20	0.22	0.38
Sex (Male)	-0.01	0.14	0.96
Employment status (Irregular)	0.26	0.19	0.16
Employment status (Housewife)	0.42	0.16	< 0.01
Employment status (Student)	-1.30	0.75	0.09
Employment status (Retiree)	0.35	0.15	0.02
Employment status (Others)	-0.11	0.51	0.84

GENERAL DISCUSSION AND CONCLUSIONS

GENERAL DISCUSSION AND CONCLUTIONS

In the first chapter of my thesis, I revealed that the loss of remnant habitats cannot be compensated by revegetated habitats (Chapter 1). This suggests that initial development schemes have a crucial role in determining the capacity to sustain regional biodiversity. Then, how should we design cities both to maximise biodiversity potential and human-nature interactions? The answer to this question is not simple: the best urban form seems to be context-dependent. In the Chapter 2, I clarified that urban land-sparing is better development strategy for the conservation of regional biodiversity than land-sharing. Especially in areas that will become heavily urbanised in future, land-sparing shows a remarkable conservation benefit. However, in Chapter 3, I found that this urban land-sparing may reduce people's recreational use of urban greenspaces. It is therefore a substantial challenge to reconcile biodiversity conservation with people's nature uses in urban areas. In this section, I discuss the potential solution to deal with this conflict.

Importance of urban land-sparing for biodiversity conservation

It has been well-documented that establishing large greenspaces (i.e. urban land-sparing) is a better conservation option for biodiversity conservation than several small greenspace patches (i.e. urban land-sharing). Diamond (1975), one of pioneer researchers in this field, argued that nature reserves should be large and circular. After few decades, many researchers have supported his idea (e.g. Ewers and Didham 2008; Yamaura et al. 2008). As mentioned in the Chapter 2, land-sparing has enormous advantages to conserve biodiversity. Most importantly, land-sparing can maintain relatively large natural (undisturbed) habitats within landscapes (Fischer et al. 2008). It

is known that some wildlife species (especially large animals) require large-size habitats for their long-term survivals (e.g. Chapa-Vargas and Robinson 2013). In many cases, such species are also likely to sensitive to human-induced environmental changes such as urbanisation (Soga and Koike 2012a). Although I concluded that protecting large greenspaces is an essential task for the conservation of urban biodiversity (Chapter 2), this does not discount the conservation value of areas where urban sprawl has already occurred. In a real-world, it is not always achieved to maintain large greenspaces because this engenders enormous financial costs (Naidoo et al. 2006). In this case, protecting and managing small habitat remnants would be a substitute option for the conservation of urban biodiversity (Soga et al. 2013b; Soga et al. 2014).

Importance of urban land-sharing for people's nature experiences

From a perspective of human-nature interactions, urban land-sparing may not be a sustainable solution. In Chapter 3, I revealed that urban land-sharing rather than land-sparing enhances people's recreational uses of urban greenspaces. Several researchers (Wilson 1984; Kellert 2008) argued that, as human has for a long time spent their time in natural environments, they are considered to be developed a psychological dependency for the natural world. They also suggested that this dependency for nature is related to an innate affinity to, and reliance for nature. This means that, although living in highly altered urban environments, urban dwellers still have a desire to be contact with biodiversity (c.f. Fuller et al. 2007). In order to improve quality of life of urban dwellers, therefore, increasing people's opportunities to interact with nature has an important role (Irvine et al. 2013; Keniger et al. 2013). Nevertheless, urban dwellers become increasingly separated from the natural world, and are losing the affinity and

reliance to nature, and concern to environmental problem. This extinction of nature experiences is considered as the root cause of global biodiversity decline (Miller 2005).

Trade-offs between biodiversity conservation and nature use in cities

Unfortunately, this thesis suggests a potential conflict in the design of cities between the urban form that is most desirable for the protection of regional biodiversity (land-sparing), and that which best promotes people's nature experiences (land-sharing). The challenge is thus to reconcile biodiversity conservation and promotion of people's nature experiences in urban areas. Since greenspaces in cities potentially harbor richer biological communities than those in rural area (e.g. Knapp et al. 2008), protecting biodiversity in urban areas per se has an important role to achieve global biodiversity conservation (McKinney 2006). That being said, considering the small proportion of urban area to the Earth's surface, we could sacrifice some parts of local biodiversity (land-sharing form) to gain a broad public interest for global biodiversity conservation (Miller 2005). In the latter case, besides the amount and configuration of urban greenspaces (Lin et al. 2014), conservation educational programs would also be important to increase people's recreational activities and biodiversity knowledge (Bonney et al. 2009).

Reconciling urban development, biodiversity conservation, and nature use in cities

In the paradigm of urban land-sharing vs. land-sparing, the most straightforward way to reconcile different land-use purposes within a restricted space may be a hybrid system that integrates both land-sharing and land-sparing approaches (Yamaura et al. 2012). From a conservation viewpoint, Gabriel et al. (2013) also recommended such a

hybrid landscape approach. They argued that as the best development form depends on the target species (or higher taxon) and region, there is no single solution to debate around the relevant benefits of urban land-sharing versus land-sparing. That being said, in areas where urbanisation has already occurred, this approach would not be realistic because such areas typically have only few (or no) large greenspaces within landscapes (e.g. North America and Australia). Moreover, whether we can apply land-sharing or land-sparing depends strongly on situations. For example, in regions under high development pressures (e.g. city centre and commercial zone), land-sharing would not be easily achieved. Therefore, policy makers should flexibly apply land-sharing and land-sparing approaches, considering social, economic, and cultural backgrounds in focal regions (Fisher et al. 2008).

Another possible solution is to apply different urban development forms at different spatial scales. Urban land-sharing could be considered as small-scale urban land-sparing (c.f. Balmford et al. 2012). This suggests that we can apply land-sparing approach for some ecosystem services (e.g. biodiversity conservation), applying land-sharing approach for others (e.g. people's recreational uses). Indeed, Chandler et al. (2013) suggest that such a small-scale land-sparing could not only benefit from biodiversity conservation, but also provision of other ecosystem services (e.g. wind protection, erosion control, and pollination). In already developed landscapes, this approach may be easier and more cost-effective to apply. Although this approach cannot maximise biodiversity potential in cities, this may have the additional benefit of enhancing the delivery of some ecosystem services by bringing nature and people closer together in some areas. It is likely that by default the former option is the only practicable one in new or developing cities. In many existing urban areas, where

opportunities to create substantial greenspaces are limited, the latter option may be available.

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