Doctoral dissertation

The effectiveness of urban wooded corridors: Can they increase bird species richness in urban patchy woodlots?

(都市の樹林性コリドーの有効性：

コリドーはパッチ状樹林地における鳥類多様性を高めるか)

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Abstract

Remnants of woodlands in urban areas providing urban residents with recreational and aesthetic values can still function as refuges for some species and need appropriate managements for biodiversity conservation. Vegetation corridors, such as street trees in urban areas, which connect patchy woodlands and mitigate habitat isolation, are expected to enhance the persistence of birds in urban landscapes. However, the effectiveness of urban corridors on birds remains equivocal because vegetation corridor is often managed for human use with little consideration of wildlife and is embedded in anthropogenic landscapes. Here I investigated the availability of urban wooded corridors for bird species in connected or neighboring patches, focusing on their vegetation structures.

In Chapter 2, I showed the relationship between bird species and vegetation structures in wooded corridors. Avian species observed in eight lines of corridors located in and around Tokyo were explained by their vegetation structures and forest coverage and agricultural field coverage in the surrounding matrix. These results suggest the distribution of bird species varied with vegetation structures in corridors and the species might be moved from the surroundings.

In Chapter 3, I showed the effectiveness of corridors on bird species in connected or

neighboring woodlots. I compared the effects of three major corridors of varying vegetation structures (trees with a dense understory, trees with a sparse understory, and grassy areas with sparse trees) on the species richness and abundance of birds in 21 wooded patches in the center of Tokyo, Japan, during wintering and breeding seasons. I found that the effectiveness of corridors depended on the tolerance of birds to urbanization. Urban avoider species, having low tolerance to urbanization, demonstrated lower species richness and abundance in patches close to the corridor with a sparsely vegetated understory as compared with patches close to the understory-richer corridors during winter, although such an effect disappeared during the breeding season. My results suggest that corridors with scarce understory vegetation may limit the persistence of birds avoiding urban areas.

In Chapter 4, according to these results, I recommend from the view of management of greenspaces, the maintenance of shrub or understory vegetation is encouraged not only in patches but also in corridors. However, this may be in conflict with safety and aesthetic values of the environments for humans in urban landscapes. One possible strategic approach is to differentially select and manage corridors for forest-dwelling bird species, particularly for urban avoiders. On the basis of my results, I suggest that the management practice of increasing vegetation in corridors will be better implemented in a landscape with numerous scattered greenspaces or that neighbor larger patches, whereas management for humans should be prioritized in a landscape with more artificial land use.

Chapter 1: General introduction

1.1 Importance of urban biodiversity conservation

Biodiversity conservation previously focused on setting large protected areas in primitive nature to exclude human pressure and disturbances, leading to less care of urban biodiversity (Stott et al. 2015), although urbanization is rapidly expanding worldwide and is a major threat to biodiversity (Grimm et al., 2008; McKinney, 2002). Urban biodiversity can provide variety of ecosystem services for human beings such as experience in nature (Soga et al. 2015; Miller 2005), improvement of psychological and physical health (Keniger et al 2013; Dallimer et al. 2012) as well as regulation and provisioning services (Edmondson et al. 2014; MA 2005). The remnants of woodlots in urban areas experience severe anthropogenic disturbances such as intensive modification or development of land into residential, commercial, and agricultural areas, leading to habitat fragmentation across the landscape (Grimm et al. 2008). However, they can still function as refuges for some species and thus require appropriate management for biodiversity conservation (Goddard et al., 2010; Hedblom and Söderström, 2008).

1.2 Habitat patches in urban areas

Conserving biodiversity, it is desired to assure amount of habitats and their vegetation types that meet the habitat requirement of species according to previous studies that found positive correlation between species richness and habitat patch area (Shanahan et al. 2011; Collier et al. 2006) and different responses of each species to vegetation types (Ikin et al. 2012; Heyman 2010; Katoh 1996). However, we face the severe fragmentation of habitats and the difficulty to create a lump of greenspaces because of financial costs or insufficient space in urban areas (Fuller and Gaston 2009). Also, vegetation in urban areas is likely to be managed for optimal human use. The common management practice of urban green infrastructures is the clearance of shrub or understory vegetation to enhance the recreational or aesthetic value (Heyman, 2010; Hedblom and Söderström, 2008). This practice can negatively affect some species that utilize shrub or understory vegetation as foods, refuges, and nesting sites (Heyman 2010; Katoh 1996). Then habitat patches in urban areas are in danger for wildlife.

1.3 Movement corridors

Corridors were defined as “narrow strips of land which differ from the matrix on either side” in Forman and Gordon (1986). They could connect remnant patches to mitigate isolation effects by working as “routes that facilitate movement of organisms between habitat fragments” (Hilty et al. 2006). The functions were expected to decrease in demographic stochasticity of populations and a chance of inbreeding depression, and provide pathways to necessary resources in surroundings of focal habitats (Haddad et al. 2003; Beier and Noss 1998; Simberloff et al. 1992). These functions of corridors will vary with their quality related to significant components of habitats for each target species such as the width, length and vegetation (Beier and Noss 1998; Harrison 1992). Since the early stage of the studies, previous studies have investigated that the effectiveness of corridors would vary with their vegetation as well as the others by varying their proximity to habitat patches (Tewksbury et al., 2002; Sutcliffe and Thomas, 1996; Haas, 1995) and their widths (King et al., 2009; Haddad, 1999; Andreassen et al., 1996). However, the studies evaluating the effectiveness of corridor vegetation were limited for small mammals (Bennet 1994; Ruefenacht and Knight 1994; Henein and Merriam 1990) or were investigated in an experimental study (Haddad and Tewksbury 2005 for butterflies). We can’t simply apply those obtained results to other organisms in urban areas because corridor requirements vary with species-specific characteristics including habitat preference, dispersal capacity, and area requirements (Vos et al. 2002; Beier and Noss 1998), and landscape characteristics such as different intensity of human landuse and degree of habitat fragmentation (Vos et al. 2002; Ricketts 2001). The effectiveness of urban corridors may depend on species preference of vegetation and tolerance to urbanization. That is, urban corridors managed for optimal human use can provide mainly tall trees without shrubs and understory vegetation for tree crown users, not for ground-forager species. Also, corridors located in urban areas can be benefit to species with low tolerance to urbanization to move around a hostile environment surrounding patches, rather than to species with high urbanization tolerance. More studies are needed to clarify the effectiveness of urban corridors focusing on their vegetation structure.

1.4 Urban landscape matrix

Matrix, surrounding patches and corridors, has long been viewed as hostile environment for wildlife (Arendt 2004). However, terrestrial habitat islands are not embedded in uniformly hostile matrix while oceanic islands are intervened by the sea where terrestrial species can't move (Franklin and Lindenmayer 2009; Prugh et al. 2008). Previous studies revealed matrix in terrestrial system provided species with secondary habitats (Umetsu and Pardini 2007; Perfecto and Vandermeer 2002) and movement pathways (Schooley and Wiens 2004; Haynes and Cronin 2006). The effectiveness of matrix depends on its component such as vegetation (Castelleón and Sieving 2005) or landuse type (Morimoto et al. 2006), and can also affect species movement through corridors by species colonization from the matrix or reduction of edge effects of the corridor (Baum et al. 2004). Baum et al. (2004) indicated the dispersal rate of planthopper *Prokelisia corcea* among connected patches with a corridor was significantly lower in a high-resistance matrix than in a matrix with relative similar components with habitats. That could imply a corridor in an urban setting with high resistance matrix could not perform effectively to facilitate species dispersal as we intended. Thus this study focused on the effects of surrounding matrix to evaluate the effectiveness of urban corridors for birds as well as those of their vegetation structure.

1.5 Ecological network and its implication to urban landscape planning

Ecological network is originally a phrase representing the aggregation of biological interactions in ecosystems where nodes (i.e., species, populations or individuals) are connected by interaction links. Recently, from a landscape ecological perspective, this phrase has also been used to indicate systems of habitat patches, wildlife movement corridors and stepping stones. The ecological network concept in landscape ecology originated from the theory of island biogeography (MacArthur and Wilson 1967) and metapopulation theory (Hanski 1998). They thought that appropriate ecological network can facilitate the movement of organisms among habitat patches by connecting isolated patches with movement corridors and stepping stones, thereby improving population viability and reducing the chance of population extinction (Beier and Noss, 1998; Brown and Kodric-Brown, 1977). In the thesis I use the phrase in the landscape ecological meaning.

Historically, the ecological network concept has been investigated in fragmented forest landscapes (Paetkau et al. 2009; Lees and Peres 2008; Castellon and Sieving 2006; Laurance et al. 2004; Sieving et al. 2000), agricultural landscapes (Haas 1995; Opdam 1995; Bennett 1990; Henderson et al. 1985), and riparian landscapes (Gillies and St. Clair, 2008; Skagen et al., 1998; Machtans et al., 1996), some of which indicated the effectiveness of ecological network on biodiversity conservation. Though the concept has also been applied in these days to urban landscapes where habitats are intensively isolated and there is little space to establish a lump of new greenspaces (Ignatieva et al., 2011; Hepcan et al. 2009; Jongman 2008; Parker et al. 2008), the effectiveness of ecological network in urban landscapes still remains equivocal (Gilbert-Norton et al. 2010) because the vegetation management of corridors and connected patches is for optimal human use, not for urban wildlife (Heyman, 2010; Hedblom and Söderström, 2008), and their surrounding urbanized matrix is too high resistant to facilitate species dispersal (Baum et al. 2004). Corridors and patches with inappropriate vegetation could be structural network but function as sinks (Weldon and Haddad 2005; Hess and Fischer 2001). In spite of uncertainty of the effectiveness of ecological network in urban areas, the concept is adopted into Green Master Plans set by local governments based on Urban Green Space Conservation Act in Japan in the paucity of alternative strategy to conserve and restore urban biodiversity. Green Master Plans have been made in 673 municipalities ("Urban Greening Database" Available at: <http://www.mlit.go.jp/crd/park/joho/database/toshiryokuchi/midori_kihon/> Accessed [31 May, 2016]), which covered 49 % of all. Sone et al. (2015) revealed ecological network was recommended in 19 plans among 20 best plans opened on the website (selected by Parks and Open Space Association of Japan), confirming it was paid greater attention. Establishment of ecological network is also a significant index to evaluate the actions for conserving biodiversity by local governments in "Urban Biodiversity Index (draft)" set by Ministry of Land, Infrastructure, Transport and Tourism. However, few plans propose concretely where is suitable to establish and maintain green infrastructures based on scientific knowledge (Sone et al. 2015). This is because few studies revealed the impacts of ecological network on species in urban areas (Sone et al. 2015; Ichinose 2010, but see Morimoto and Katoh 2005). Again, in urban landscape, patches and corridors do not often meet the habitat requirement for species due to small patch size, vegetation management for optimal human use and surrounding high resistant matrix, which may make the function of ecological network spoiled.

1.6 Purpose of this dissertation

This study demonstrates the availability of urban corridors for bird species focusing on their vegetation structures and the surrounding matrix. Testing their effectiveness on bird species distribution in connected or neighboring patches, I evaluate the utility of ecological network with corridors in urban areas. In this study, habitats are mainly characterized by woodlots because of their representatives of urban refuges. Bird species is targeted in this study, which has enough dispersal ability to use vegetation corridors, and is provided with ecological knowledge of the species, particularly for vegetation preference, and can often be major flagship species for conservation in urban planning. This study tests whether vegetation corridors can provide movement pathways or secondary habitats for species with low tolerance to urbanization or only for widely distributed species, indicating the effectiveness of conserving urban bird diversity.

This dissertation consists of the following parts. Chapter 2 demonstrates the relationship between vegetation structure of corridors and bird species observed in the corridors by comparing the species richness and abundance recorded in eight lines of corridors in and around Tokyo during wintering season. The effects of landuse (categorized into the three types: forest, agricultural field, and urban area) surrounding the corridors on the birds' distributions are tested on the purpose of exploring the potential species recruitment from the surroundings into the corridors. In Chapter 3, I showed the effectiveness of vegetation corridors on bird species in connected or neighboring woodlots. I compared the effects of three major corridors of varying their vegetation structure (trees with dense understory vegetation, trees with a sparse understory vegetation, and grassy areas with sparse trees) on the species richness and abundance of birds in 21 wooded patches in the center of Tokyo, during wintering and breeding seasons. In Chapter 4, from the view point of management of urban green spaces, I discuss management strategy of vegetation corridors in urban areas targeting conservation of avian species based on the research results shown in Chapter 2 and 3.

Chapter 2: Relationship between bird species and vegetation structures in urban corridors

2.1 Introduction

Vegetation corridors such as street trees and cycling tracks are important green infrastructures for residential people in urban areas, which provide ecosystem services such as enhancing recreational and aesthetic value of environments, reducing air pollution and noise damage, storing carbon and ameliorating heat-island effect (Mullaney et al. 2015; Seaman 2013). In addition, vegetation corridors are expected to take a role of movement pathways or secondary habitats for urban organisms by facilitating their movement or providing foods or refuges, which improve population viability to maintain biodiversity (Ignatieva et al. 2011; Savard et al. 2000). That has recently had publicity from the viewpoint of improving psychological well-being of residents with exposure to nature (Taylor et al. 2015).

However, management of vegetation in urban corridors is prioritized for optimal human use, which is not sure they are suitable habitats for urban wildlife (Mullaney et al. 2015). To assure scenic beauty and safety for residents, shrub and understory vegetation are often removed in urban corridors (Heyman 2010; Hedblom and Söderström 2008). This management practice can negatively affect species diversity, particularly for birds which are symbolic or popular wildlife for urban residents because some bird species exploit shrub and understory vegetation for foods, refuges and nesting sites (Heyman 2010; Katoh 1996). However, most of previous studies have suggested ways of vegetation management of urban corridors to reduce pavement damage by tree roots and improve tree growth rather than to provide habitats for urban organisms (Mullaney et al. 2015).

The present study aims to demonstrate urban corridors with different vegetation structures can affect bird species observed in corridors. My study area is located around Tokyo, Japan, and eight lines of vegetation corridors are surrounded by a mosaic of residential and commercial land uses including scattered green spaces and agricultural fields. I expected surrounding landuse also affected bird species observed in corridors. That means corridors surrounded by more green spaces may support more species and individuals of forest birds while those embedded in agricultural fields can attract bird species preferring croplands because species can drop in at those corridors from the surroundings. Therefore, I consider not only the effect of vegetation structure in corridors but also that of landuse in surrounding of corridors on bird species. Here I discuss management strategy to improve suitability of vegetation corridors as movement corridors and secondary habitats for bird species in urban areas considering surrounding landscapes to keep harmony with nature and humans.

2.2 Materials and Methods

2.2.1 Study area

The study area was located in the Kanto Plain, including Tokyo, Kanagawa, and Saitama prefectures (Fig 1). A mosaic of residential and commercial landuse dominates throughout the area including scattered green spaces and agricultural fields. Selected eight lines of corridors (for instance street trees, park way, pedestrian and walking path; ST_A~H) were characterized by different vegetation structures which would appeal to different bird species (Fig 2). ST_A, C, D and E are mainly composed of planted trees (height ~ 10 m). ST_B, F and G are linear stripes of scarce tall trees and relatively dense understory vegetation. ST_H is mainly a parkway planted with tall trees and dense understory vegetation. The minimum width of corridors is 9.3 m±3.8 m at ST_G and the maximum is 21.1 m±12.8 m at ST_H (Appendix A).

2.2.2 Bird sampling

I divided each corridor into transects with 500 m long, which are 157 transects in total. This is because Seven transects that included open water such as river and channel over 20 m wide, and roads with over two lines were excluded to avoid influences caused by water habitats or heavy traffics. Finally I used 150 transects in the following analysis.

I conducted bird surveys in wintering season (from February to March, 2012). Each transect was visited three times during the study period between 08:00 and 15:00 by following the method of Katoh (1996) that carried out bird surveys near my study area. During each observation period, I identified and recorded the abundance of each species observed within 10 m from each side of transects, walking at a speed of 2 km/h. The dawn period was excluded from my observation period, which was different from the typical bird sampling method, because detectability is likely to be low due to lower temperatures during wintering season.

I used the total abundance of each species observed at three visitations per transect in the following analysis. Shorebirds were excluded from the analysis because their distributions would strongly depend on water area.

2.2.3 Vegetation structure

I conducted vegetation structure surveys by sighting at six sections per bird sampling transect from August to October, 2013 to estimate vegetation coverage. Coverage was recorded for the following height layers: ground (0–0.5 m), shrub (0.6–2 m), sub-tree (2.1–8 m), and tree (>8 m) by seven ranks [0, 0.5, 1(1%-10%), 2(11%-25%), 3(26%-50%), 4(51%-75%), 5(76%-100%)]. The medians of each rank percentage (0%, 0.5%, 5.5%, 17.5%, 37.5%, 62.5% and 87.5%) per section were used to calculate the average scores at each transect. I used the average scores for the ground and shrub layers for the understory vegetation layer (UNDER), and those for the sub-tree and tree layer for the upper layer (UPPER). I recorded at each following part of a section; edges (EDGE) and center (CENTER) of a section. Edges cover 20 % of the width from both of the insides and the center part is a section excluding the edges. The scores of left and right edges were averaged for analysis. Finally, I had four kinds of variables about vegetation structure in corridors in total (i.e., two vegetation structures for two parts in a transect).

I checked correlations between four variables (EDGE_UPPER, EDGE_UNDER, CENTER_UPPER, CENTER_UNDER). EDGE_UPPER and CENTER_UPPER, which were also highly correlated (r = 0.83) were given a weighted average score based on percentage of width in a transect for EDGECEN_UP. Therefore, I used three variables about vegetation structure (EDGECEN_UP, EDGE_UNDER, CENTER_UNDER) in the following analysis.

2.2.4 Landuse coverage in surroundings of corridors

I considered the effect of landuse in the surrounding of corridors on the distribution of birds in corridors as well as the vegetation structure. Landuse in a surrounding is one of the important components of landscape affecting the distribution of birds in corridors (Dunford and Freemark, 2004; Wiegand, Revilla, and Moloney, 2005) by providing foods and improvement of permeability of surrounding landscape that leads to species recruitment into a corridor.

I used a landuse map with a spatial resolution of 100 m created by the National Land Numerical Information, Ministry of Land Infrastructure, Transport and Tourism, Japan. The classification used in the landuse map is 11 categories (paddy fields, other croplands, forests, wilderness, buildings, roads and rails, rivers and lakes, beaches, seawater, golf courses, and other artificial lands including airports, racecourses, and baseball grounds) from 1/25,000 topographic maps and ALOS satellite images. I summarized some of classifications into three types, namely FOREST (forests), AGRI (paddy fields and other croplands) and ARTIF (buildings, roads, rails and other artificial lands). Buffers from each transect within which landuse coverage was calculated were generated using 250 m and 1,000 m. Landuse coverage of each type was calculated for each buffer using ArcGIS version 10.0 (ESRI Inc.).

2.2.5 Classification of bird species

To examine the effect of vegetation corridors on the distribution of bird species with different tolerance to urbanization, for each habitat preference (forest or grassland including open habitat), I classified the observed bird species into two groups: urban avoiders and suburban adapters (Appendix B). This terminology is adopted from the study of Mckinney (2002), who suggested the classical terminology of the species depending on their tolerance to urbanization. My classification followed that of previous studies (Katoh, 2009; Okazaki and Katoh, 2005, 2004) in which metaanalyses were conducted to examine the association between the degree of urbanization and the occurrence of bird species around Tokyo and the bird species were classified into three groups, namely urban avoider, suburban adapter, and urban exploiter. *Columba livia*, adapter species preferring grassland or open habitat, was excluded because the distribution strongly depended on feeding by humans, causing wrong trends with the environmental factors about vegetation structure and surrounding of corridors I included. Forest species or grassland including open habitat are defined by the Japanese Avian Trait Database (Takagawa et al. 2011) and a guidebook about birds of Japan (Brazil 1991).

The urban avoider group of forest species mainly comprised ground-foraging species that prefer understory vegetation (e.g., *Horornis diphone* and *Emberiza Spodocephala*), foliage gleaners, and tree climbers that utilize tree tops (e.g., *Aegithalos caudatus* and *Dendrocopos kizuki*) that were observed in relatively large patches surrounded by less artificial land (Okazaki and Katoh 2005, 2004). That of grassland species is consisted of species preferring open cultivated fields or scattered bushes (e.g., *Phoeniourus auroeus* and *Lanius bucephalus*). The suburban group comprised urban bird species that are likely to utilize the landscape surrounding a habitat patch (Blair 1996).

2.2.6 Generalized linear mixed models and model selection

The number of species and total abundance of species belonging to each group (urban avoiders and suburban adapters) of each species preference in each transect were used as a response variable; thus I performed eight kinds of analyses in total (i.e., two groups and two preferences for two indices).

In all analyses, I used generalized linear mixed models (GLMMs) with a log-link function and corridors ID as a random effect. I assumed that response variables followed the zero-inflated Poisson distribution for the species richness of urban avoiders because of the large quantity of no-observation data but followed the zero-inflated negative binomial distribution for the total abundance to account for overdispersion. For suburban adapters, I employed the Poisson distribution for the species richness but a negative binomial distribution for the total abundances to account for overdispersion. Environmental variables included three types of vegetation structure in transects (EDGECEN_UP, EDGE_UNDER, CENTER_UNDER) and, three types of landuse coverage in surroundings (FOREST1000 and AGRI250 and 1000). FOREST250 was omitted due to high correlation with FOREST1000 (r = 0.83). FOREST1000 is a suitable range of influential environment because small and middle-sized bird species can utilize the environment up to 1.5 km^2 in urban areas (Hostetler 2000). ARTIF250 and ARTIF1000 were excluded because they had relative higher correlation with AGRI250 and AGRI1000, respectively (r = -0.70 and -0.79). I didn't include the width of a transect because of a correlation with CENTER_UNDER (r = 0.62).

To reveal parsimonious models for predictions, I computed Akaike's information criterion

(AIC) of all possible models, and ranked them by ΔAIC (difference of AIC between a candidate model and the best model). All statistical procedures were performed using the R package “glmmADMB” (Fournier et al. 2012).

2.3 Results

I recorded 8,857 individuals from 24 bird species during the study period, excluding water birds. The largest and smallest number of species richness recorded in a transect were 16 in ST_A and 2 in ST_C, ST_D, ST_F, and those in a corridor were 21 in ST_A and 13 in ST_G, respectively. The average of species richness and abundance of the observed species per transect were 6.8±2.7 SD and 47.5±37.2 SD, and those per corridor were 16.6±2.4 SD and 932.6±342.5 SD, respectively. The average number of species richness per corridor was much larger than that per transect, indicating beta diversity of transects increased the species richness in corridors.

2.3.1 Generalized linear mixed models and model selection

Influential explanatory variables depended on the habitat preference and tolerance to urbanization of each species group (Table 1 and 2). Vegetation structures within vegetation corridors delineated the species habitat preference. Regardless of tolerance to urbanization, more number and abundance of forest species were recorded in corridors planted with tall trees in the edges and centers, while no positive effect on grassland species were detected except for abundance of urban avoider species. Understory vegetation in the center of corridors appealed to all species group. In addition, forest species increased in the corridors surrounded by more forest area while grassland species decreased. The agricultural field coverage in the nearer surroundings increased both forest and grassland species particularly for urban avoiders, but that in the distant surroundings increased only forest species group.

2.4 Discussion

2.4.1 Factors affecting forest species in corridors

The number of species and abundance of forest birds increased in the corridors planted with both upper and lower vegetation (Table 1). This emphasized bird species observed in corridors will vary with the vegetation structures. For urban avoider species, woodland species such as *A. caudatu* and *D. kizuki* prefer tree crowns for perching (Kurosawa and

Askins, 2003; Natuhara and Imai, 1999), while ground-foraging species, such as *E. spodocephala* and *H. diphone* prefer to use shrub layer or understory vegetation (Katoh 1996). Also, suburban adapter species comprised of tree-top users (e.g., *Hypsipetes amaurotis* and *Parus major*) that mainly utilize tree crowns, and the species using shrubs and ground cover such as *Zosterops japonicas* and *Streptopelia orientalis*. Hense, the corridors with abundant tall trees and shrubs or understory vegetation appealed to both urban avoider and suburban adapter forest species. Shrubs and understory vegetation tend to be removed in urban green infrastructures to improve recreational and aesthetic values, leading to a decrease in forest bird species (Heyman 2010). My result indicated planting shrubs and understory vegetation in corridors can increase the number and abundance of forest bird species, particularly for ground-foragers. The surrounding forest cover increased the number and abundance of urban avoider forest species in corridors, but increased only the abundance of suburban adapter species, not the number of the species (Table 1). This is probably because more number of urban avoider forest species tend to be recorded in larger habitats (Okazaki and Katoh 2005, 2004; Natuhara and Imai 1999), while suburban adapter forest species are common in this study area independent of habitat area (Katoh 2009). Surrounding forest coverage comprised of wooded patches might function as a source that provided the urban avoider species to corridors. That indicated corridors could not stand as habitats but secondary habitats and pathways for urban avoiders. Also, agricultural field coverage in the surroundings also positively affected urban avoider forest species (Table 1). This is because agricultural field around Tokyo negatively correlated with urbanization (Ichikawa et al. 2006). It could be habitats providing shrubs and bushes to the ground-foragers, particularly for urban avoiders such as *Turdus pallidus* and *Turdus chrysolaus*, functioning as a source of those species into corridors.

2.4.2 Factors affecting grassland species in corridors

Grassland species increased in corridors with shrubs and understory vegetation (Table 2). They appealed to *Alauda arvenis* for urban avoider species and *Sturnus cineraceus* and *Turdus eunomus* for suburban adapter species that utilize grassland and open habitats. Planting tall trees showed positive influence on the abundance of urban avoider grassland species (Table 2). This is probably because corridors with tall trees and understory vegetation compose an edge environment, supporting the species such as *L. Bucephalus* and *P. auroeus* which inhabit in forest-edge and open habitat. The vegetation corridors would be preferred conduits for some urban avoider grassland species particularly for forest edge species, although grassy corridors are required to study to evaluate the utility of linear conduits for the species using grassy and open habitats.

Agricultural field in the near surroundings also affected the grassland species in the corridors, indicating the species recruitment into corridors from the surroundings (Table 2). Agricultural fields often comprise of open habitat with scattered tall trees and shrubs, which are suitable for the urban avoider species such as *A. arvenis* and *L. Bucephalus* as well as the suburban adapter species such as *Passer montanus* and *Sturnus cineraceus* (Brazil 1991). However, agricultural field coverage in the wider range of surroundings negatively affected the abundance of suburban adapter species. This is because less coverage of agricultural fields indicates urbanized area (Ichikawa et al. 2006) where suburban adapter species inhabit (Katoh 2009).

Suburban adapter species increased in the corridors surrounded by less forested area, but such an effect disappeared for urban avoider species. This is because the small number of open-habitat species such as *A. arvenis* was recorded in the present study. That is the surrounding forest could provide habitats to some urban avoider species such as *L. Bucephalus* and *P. auroeus* which inhabit in forest-edge, which made the negative effect of agricultural field unclear.

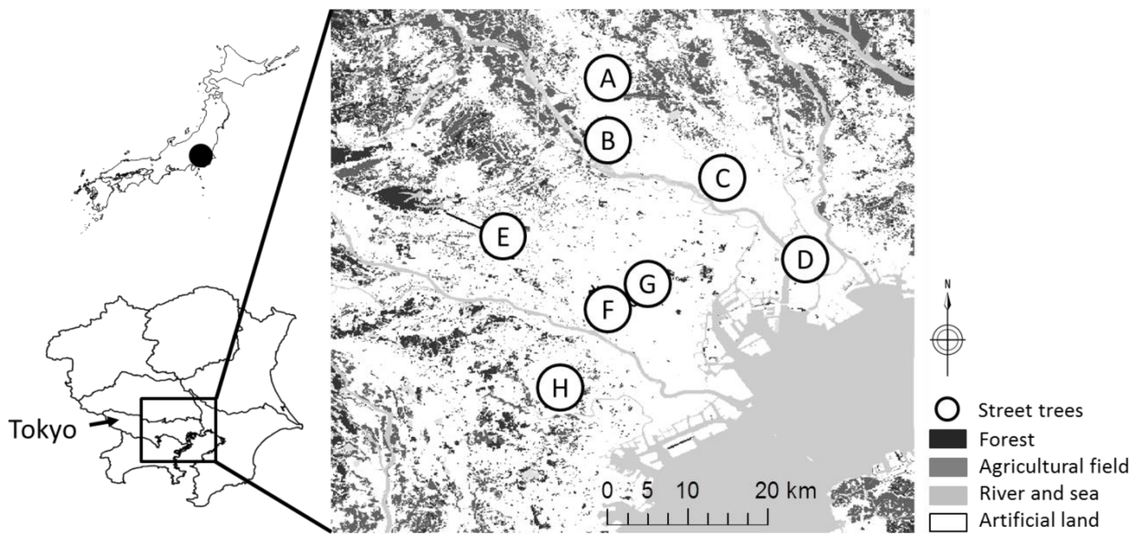


Fig. 1 Maps of the locations of corridors examined in this study.

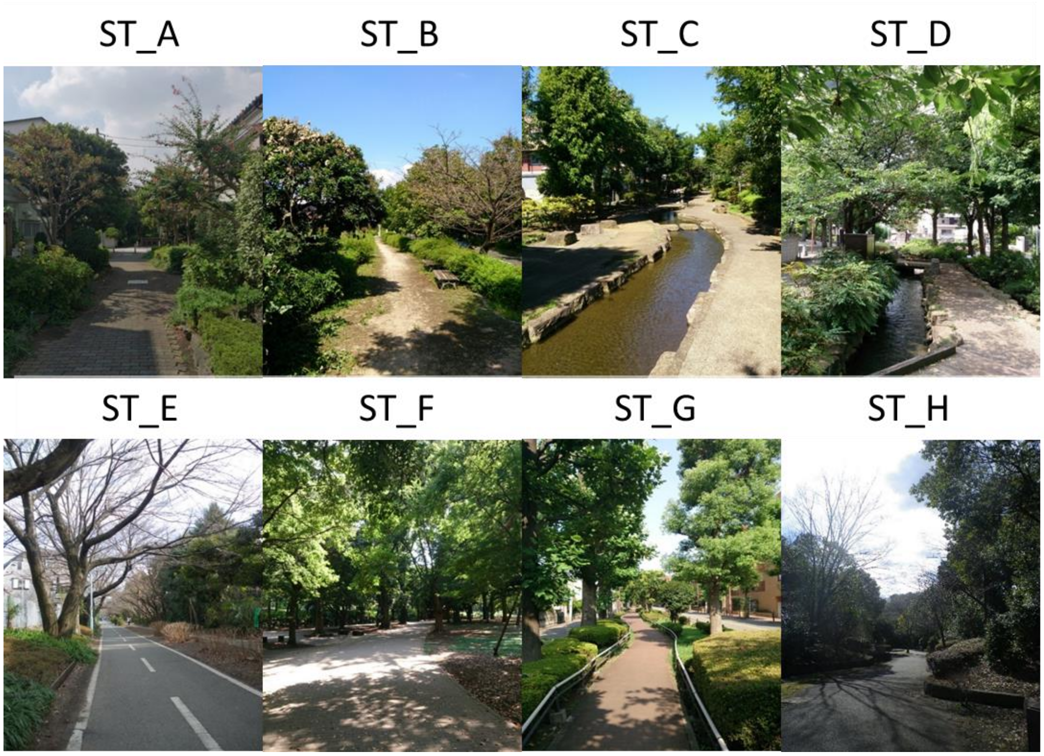


Fig. 2　Typical images of each corridor. ST_A, C, D and E are mainly composed of planted trees (height ~ 10 m). ST_B, F and G are linear stripes of scarce tall trees and relatively dense understory vegetation. ST_H is mainly a parkway planted with tall trees and dense understory vegetation.

Table 1 Results of the top five models and null model (without any predictors) for the species richness and total abundance of urban avoider and suburban adapter forest species. I show the estimate/standard error (z value) of each variable (z values over 2.0 corresponding to approximately $p < 0.05$ are in bold). Environmental variables included three types of vegetation structure in transects (EDGECEN_UP, EDGE_UNDER, CENTER_UNDER) and, three types of landuse coverage in surroundings (FOREST1000 and AGRI250 and 1000).

Forest species		Explanatory variables (Estimated/Standard Error)							
		EDGE UNDER	EDGECEN UP	CENTER UNDER	AGRI 250	AGRI 1000	FOREST 1000	AIC	ΔAIC
avoider	species richness		**2.3**	**2.0**	**2.8**	**2.6**	**3.8**	223.9	0.0
			2.2		**3.1**	**2.4**	**3.6**	225.5	1.6
		-0.3	**2.2**	**2.0**	**2.8**	**2.5**	**3.7**	225.8	1.9
				1.8	**2.3**	**3.3**	**4.3**	227.2	3.3
		0.1	1.9		**3.1**	**2.3**	**3.6**	227.5	3.6
				Null				269.9	46.1
	abundance		**3.0**	**2.1**	1.4	**2.4**	**4.1**	312.6	0.0
			2.8	**2.1**		**3.0**	**3.9**	312.6	0.0
		1.3	**2.5**	1.9	1.5	1.4	**4.0**	312.7	0.1
		2.3	**2.8**	1.9	**2.2**		**5.7**	312.7	0.1
		1.2	**2.2**	**2.0**		**2.1**	**3.9**	313.1	0.5
				Null				360.9	48.3
adapter	species richness		**2.3**	**2.0**			1.8	539.6	0.0
			2.3	**2.0**	1.1		1.7	540.5	0.9
			3.0	1.9				540.7	1.1
			2.6	1.9		1.3		541.1	1.5
			3.0	1.8	1.2			541.3	1.7
				Null				547.9	8.3
	abundance		**4.0**	**2.7**	1.7		**2.9**	1127.6	0.0
			3.9	**2.9**			**3.1**	1128.8	1.2
			4.0	**2.7**	1.7	-0.4	**2.6**	1129.4	1.9
		0.0	**3.8**	**2.6**	1.7		**2.9**	1129.6	2.0
			3.8	**2.7**		0.5	**2.4**	1130.5	2.9
				Null				1155.7	28.1

Table 2 Results of the top five models and null model (without any predictors) for the species richness and total abundance of urban avoider and suburban adapter grassland species. I show the estimate/standard error (z value) of each variable (z values over 2.0 corresponding to approximately $p < 0.05$ are in bold). Environmental variables included three types of vegetation structure in transects (EDGECEN_UP, EDGE_UNDER, CENTER_UNDER) and, three types of landuse coverage in surroundings (FOREST1000 and AGRI250 and 1000).

Grassland species		Explanatory variables (Estimated/Standard Error)							
		EDGE UNDER	EDGECEN UP	CENTER UNDER	AGRI250	AGRI 1000	FOREST 1000	AIC	ΔAIC
avoider	species richness	-1.5		**4.5**	**5.4**			198.7	0.0
				4.5	**5.1**			199.3	0.5
		-1.4		**4.0**	**5.5**		-1.0	199.6	0.9
				4.0	**5.2**		-1.1	199.9	1.2
		-1.5	0.3	**4.3**	**5.4**			200.6	1.9
				Null				228.1	29.4
	abundance	**-2.3**	**2.2**	**2.7**	**5.1**		**-2.0**	256.6	0.0
		-2.0	**2.2**	**2.7**	**3.5**	-0.3	-1.7	258.5	1.9
		-2.3	**2.0**	**3.2**	**4.6**			258.9	2.3
		-1.8		**2.1**	**4.6**		-1.7	259.3	2.7
		-1.7	**2.0**	**3.1**	**3.8**	-1.1		259.5	2.9
				Null				273.5	17.0
adapter	species richness			**2.6**	1.8		**-2.8**	461.7	0.0
				2.8			**-2.7**	462.7	1.1
				2.7		1.3	**-2.9**	463.0	1.4
			0.8	**2.6**	1.8		**-2.9**	463.1	1.4
				2.6	1.3	0.4	**-2.6**	463.5	1.8
				Null				476.0	14.4
	abundance		**-2.0**	**3.8**	**2.6**	**-3.3**	**-2.2**	1179.9	0.0
				4.2	**2.7**	**-3.5**	**-2.2**	1181.6	1.7
		0.0	-1.8	**3.8**	**2.6**	**-3.2**	**-2.2**	1181.9	2.0
			-2.0	**4.2**	**2.8**	**-5.1**		1182.3	2.4
		-0.7		**4.2**	**2.7**	**-3.3**	**-2.2**	1183.1	3.1
				Null				1224.0	44.1

Appendix A Information of vegetation structures, landuse coverage in surroundings and the width of corridors. The average values of transects for each corridor were shown. Except for WIDTH (m), the values ranged from 0 to 100 (%).

ID	EDGE_UNDER	EDGECEN_UP	CENTER_UNDER	AGRI250	FOREST250	ARTIF250	AGRI1000	FOREST1000	ARTIF1000	WIDTH
ST_A	8.8 ± 7.2 SD	33.9 ± 37.4 SD	6.4 ± 7.3 SD	11.2 ± 16.4 SD	1.7 ± 4 SD	86.5 ± 17.1 SD	6.2 ± 5.4 SD	2.8 ± 2.3 SD	89.2 ± 6.5 SD	14.2 ± 7.6
ST_B	6.4 ± 5.9 SD	19.4 ± 29.1 SD	9 ± 11.4 SD	0 ± 0 SD	0 ± 0 SD	98 ± 3.8 SD	0.9 ± 1.9 SD	0.1 ± 0.2 SD	96.1 ± 8.9 SD	18.1 ± 12.0
ST_C	4.2 ± 2.6 SD	13.3 ± 13.3 SD	8.4 ± 9.2 SD	0.5 ± 1 SD	0 ± 0 SD	98.7 ± 2.6 SD	1 ± 0.7 SD	0 ± 0 SD	97.8 ± 1.2 SD	14.3 ± 4.3
ST_D	4.3 ± 2.4 SD	23.3 ± 16.1 SD	8.6 ± 6.7 SD	0 ± 0 SD	0.1 ± 0.6 SD	99.4 ± 1.5 SD	0 ± 0 SD	0.2 ± 0.2 SD	91.7 ± 8.3 SD	14.5 ± 6.3
ST_E	14.4 ± 8.6 SD	39.5 ± 24.1 SD	4.6 ± 5 SD	5.8 ± 7.7 SD	5.8 ± 8.3 SD	87 ± 10.4 SD	4.3 ± 3 SD	4 ± 3.6 SD	89.3 ± 6.3 SD	10.0 ± 2.9
ST_F	12 ± 7.2 SD	21.8 ± 20.4 SD	4.6 ± 4.8 SD	0.1 ± 0.2 SD	1.2 ± 1.7 SD	98.7 ± 1.9 SD	0.1 ± 0.2 SD	0.9 ± 0.6 SD	99 ± 0.7 SD	9.7 ± 3.3
ST_G	10 ± 8.1 SD	22.1 ± 13.8 SD	6.2 ± 7.2 SD	0 ± 0 SD	0 ± 0.1 SD	100 ± 0.1 SD	0.1 ± 0.1 SD	0.9 ± 0.8 SD	99 ± 0.8 SD	9.3 ± 3.8
ST_H	14 ± 6.1 SD	50.5 ± 26.8 SD	6.1 ± 4.7 SD	2.3 ± 4.8 SD	15.6 ± 8.4 SD	81.6 ± 10.8 SD	12.1 ± 8.1 SD	9.1 ± 2.7 SD	78.5 ± 8.2 SD	21.1 ± 12.5

Appendix B List of bird species observed in corridors excluding water birds.

Scientific Name	Preference	Classification
Corvus macrorhynchos	forest	adapter
Cyanopica cyana	forest	adapter
Hypsipetes amaurotis	forest	adapter
Parus major	forest	adapter
Psittacula krameri manillensis	forest	adapter
Streptopelia orientalis	forest	adapter
Zosterops japonicus	forest	adapter
Aegithalos caudatus	forest	avoider
Horornis diphone	forest	avoider
Dendrocopos kizuki	forest	avoider
Emberiza spodocephala	forest	avoider
Turdus chrysolaus	forest	avoider
Turdus pallidus	forest	avoider
Caduelis sinica	grassland	adapter
Columba livia	grassland	adapter
Motacilla alba	grassland	adapter
Passer montanus	grassland	adapter
Sturnus cineraceus	grassland	adapter
Turdus naumanni	grassland	adapter
Alauda arvensis	grassland	avoider
Corvus corone	grassland	avoider
Emberiza cioides	grassland	avoider
Lanius bucephalus	grassland	avoider
Phoeniourus auroeus	grassland	avoider

Chapter 3: Effectiveness of urban corridors on bird species in connected and neighboring woodlots

3.1 Introduction

Vegetation corridors connect remnant woodland patches and mitigate isolation. The establishment of these corridors is expected to be effective for enhancing urban biodiversity (Ignatieva et al., 2011; Savard et al., 2000) by facilitating the movement of organisms among patches, thereby improving population viability and reducing the chance of population extinction (Beier and Noss, 1998; Brown and Kodric-Brown, 1977). However, the effectiveness of corridors in urban areas remains equivocal (Gilbert-Norton et al., 2010) because corridors, such as greenways, are often managed for optimal human use, which may not meet the habitat requirements of species present in urban areas. Street trees or cycling tracks are potential corridors within urban landscapes that can facilitate wildlife movement; however, the clearance of shrub or understory vegetation in urban corridors is a common management practice to enhance the recreational or aesthetic value of these areas (Hedblom and Söderström, 2008; Heyman, 2010). This management practice has been demonstrated to negatively affect bird species because shrub and understory vegetation frequently provide bird species with food items, refuges, and nesting sites (Heyman, 2010; Katoh, 1996).

Corridors with an inappropriate vegetation structure fail to fulfill their intended function as a corridor for wildlife movement and may threaten to function as a sink (Bennett et al., 1994; Hess and Fischer, 2001; Weldon and Haddad, 2005). However, most of the previous studies have tested the effectiveness of corridors for various organisms including birds, small mammals and butterflies by varying their proximity to habitat patches (Haas, 1995; Sutcliffe and Thomas, 1996; Tewksbury et al., 2002) and their widths (Andreassen et al., 1996; Haddad, 1999; King et al., 2009), rather than by varying the quality of the corridors (but see Haddad and Tewksbury, 2005).

The present study aimed to compare the effects of three corridors with different vegetation structures on the species richness and total abundance of bird species. My study areas were located in the center of Tokyo, Japan, and included wooded patches that were connected to or neighboring one of the three corridors, allowing me to overcome the paucity of the study fields of habitats connected to the corridors. I expected the corridors to result in a general increase in the distributions of bird species with a low tolerance to urbanization than those with a high tolerance to urbanization because species that generally avoid urban areas can move only through movement corridors, whereas urban-tolerant species can move through non-vegetated areas (McKinney, 2002). Therefore, I classified the observed bird species into two groups (urban avoiders and suburban adapters; named after McKinney,

2002) according to their tolerances to urbanization and analyzed the different manner in which the species richness and total abundance of each bird species group responded to the corridors, patch area, and vegetation in those patches. Here I also discuss how my results will contribute to the effective planning of ecological network with corridors for the conservation of diverse bird species in urban areas.

3.2 Methods

3.2.1 Study area

The study area was located in the center of Tokyo, Japan (Fig. 1). A suburban mosaic of residential and commercial land uses dominates central Tokyo, with certain areas utilized for agricultural purposes. In the study area, three extensive corridors that stretch from the east to the west are characterized by their vegetation structures. Each corridor may attract different forest-dwelling bird species to the various wooded patches present in the corridor (Appendix A). The middle corridor (trees with understory vegetation; CorridorTU) comprises a linear strip of 10–20 m width of mature broadleaf evergreen/deciduous woodland with dense understory vegetation growing along an old irrigation canal ("Tamagawa-jousui," built in the middle of the 17th century) (Appendix A) (Fig. 2a). The southern corridor (sparse trees: CorridorST) is a riparian corridor running along the Nogawa River, 5–20 m wide, and mainly covered with herbaceous vegetation and a few planted trees (Appendix A) (Fig. 2b). The northern corridor (trees without understory: CorridorT) comprises lines of planted trees (height, approximately 10 m) along both sides of a cycling track of 10–15-m width (Fig. 2c) with sparse understory vegetation (Appendix A). A total of 21 small wooded patches (<3.0 ha), including remnant woodlots, parks, shrines, temples, and university campuses, were selected surrounding these corridors.

Although many previous studies (Gillies and St Clair, 2008; Ibarra-macias et al., 2011; Vergnes et al., 2012) have focused on the patches that directly connect or are close to a corridor, in my study, I included patches away from the corridors (Fig. 1, Appendix C) for two reasons. First, some studies have revealed that small- and middle-sized bird species utilize the environments surrounding the patches ranging from 0.2–1.5 km^2 in urban areas (Hashimoto and Natuhara, 2002; Hostetler, 2000; Jokimäki, 1999). Second, in the context of managing greenspaces in urban areas, I am frequently forced to utilize the existing greenspaces for conservation because of heavy financial costs or insufficient space for creating new greenspaces, even if corridors are not typically established to connect habitat patches (Fuller and Gaston, 2009). Therefore, in the studied corridors, I considered patches located within the range influencing the bird species.

3.2.2 Bird surveys

Bird surveys were conducted during both winter (from December 27, 2009 to March 14, 2010) and breeding seasons (from April 15 to June 17, 2010) to evaluate seasonal variations in the effectiveness of corridors on the distribution of bird species. Each smaller wooded patch (0.26–1.24 ha; $N = 16$) contained one sampling point, and each larger wooded patch (1.25–3.00 ha; $N = 5$) contained two sampling points. All surveys were conducted by the same researcher (MM).

I conducted five bird surveys at each point during each season between 08:00 and 15:00 by following the method of Katoh (1996), in which avian surveys were performed near the current study area. During each observation period, I identified and recorded the total abundance of each species observed within a 25-m radius from the survey point. Each point was surveyed until no new species were observed over a period of 10 min. By excluding the dawn period, my observation period differed from the typical bird sampling method. This approach was adopted because during winter, detectability is likely to be low because of lower temperatures, resulting in relatively few species being observed in urbanized areas.

For each season, I used the number of species and total abundance of each species recorded at five visitations per point (I only used the records in the first 10 min of an observation to calculate total abundance) in the analysis outlined below. To examine whether my sampling method could sufficiently detect bird species, I calculated the first-order jackknife richness estimator for incidence data (Smith and Belle, 1984) with the R package "vegan" (Oksanen et al., 2015). The jackknife estimator is non-parametric and is known to be a reliable estimator of species richness (Walther and Moore, 2005). For models of species richness throughout the surveys, I used the pooled data at five visitations per patch, whereas I separately used the data at five visitations per patch for the estimation of species richness and detectability for a patch.

3.2.3 Vegetation structure

To estimate the vegetation coverage, I conducted visual vegetation structure surveys at each bird sampling points in the wooded patches from November to December 2010. Coverage was recorded for the following layers: ground (0–0.5 m), shrub (0.6–2 m), sub-tree (2.1–8 m), and tree (>8 m) by seven ranks [0, 0.5, 1 (1%–10%), 2 (11%–25%), 3 (26%–50%), 4 (51%–75%), and 5 (75%–100%)]. The medians of each rank range (0%, 0.5%, 5.5%, 18%, 38%, 63%, and

88%) were used within the analyses described below. I recorded the coverage of the various vegetation structure categories at 25 sub-points that were randomly established within the bird observation radius of a point in a patch and used the average scores of the 25 sub-points as a point score. I used the average scores for the tree and sub-tree layers for the upper layer (TREE) and the shrub and ground layers for the understory layer (UNDER). Although tree type was recorded, I ignored this variable because of the small variation in tree type composition among patches.

3.2.4 Proximity to a corridor

Using ArcGIS version 10.0 (ESRI Inc.), I calculated the minimum distance from the edge of the nearest adjacent corridor to that of a patch using an ALOS/AVNIR2 satellite image with a spatial resolution of 10 m that was captured in September 2010. I used the distance to the corridor because avian fauna could be influenced not only in a connected patch but also in neighboring patches by their movement and dispersal among patches throughout the urban matrix comprising non-habitat areas (Ricketts, 2001).

3.2.5 Landscape matrix

I investigated the effects of the urban landscape surrounding a patch using the normalized difference vegetation index (NDVI). NDVI was used as an indicator to estimate vegetation coverage within the different patches and urban landuse coverage. The coverage of non-habitat areas surrounding habitat patches is an important component of a landscape affecting isolation and utility of corridors (Baum et al., 2004; Ricketts, 2001) through the improvement of matrix permeability (Bélisle and Desrochers, 2002; Bender and Fahrig, 2005; Castellón and Sieving, 2006; Morimoto et al., 2006) and food availability (Hodgson et al., 2007), thereby affecting the distribution of bird species in the patches (Dunford and Freemark, 2004; Wiegand et al., 2005).

A buffer area of 1,000 m extending from each patch was generated, within which the NDVI and urban landuse coverage, including buildings, roads, and rails, and other artificial lands, were calculated. The focal patch itself was excluded from NDVI and urban landuse coverage calculations. I used an ALOS/AVNIR2 satellite image with a spatial resolution of 10 m captured in February 2010 for winter and an image captured in September 2010 for the breeding season to calculate NDVI (the values were formatted in 8-bit numbers, ranging from 0 to 255). Urban landuse coverage was calculated using the existing landuse map from

2009. The map had a spatial resolution of 100 m and was obtained from the National Land Numerical Information, which classifies landuse into 11 categories (paddy fields, other croplands, forests, wilderness, buildings, roads and rails, rivers and lakes, beaches, seawater, golf courses, and other artificial lands including airports, racecourses, and baseball grounds) from 1/25,000 topographic maps and ALOS satellite images. The average NDVI from each season and urban landuse coverage were calculated separately for each buffer using ArcGIS version 10.0 (ESRI Inc.).

3.2.6 Classification of bird species

To examine the effect of corridors on the distribution of bird species with different tolerance to urbanization, within each season, I classified the observed bird species into two groups: urban avoiders and suburban adapters (Appendix B). This terminology is adopted from the study of McKinney (2002), who suggested the classical terminology of the species depending on their tolerance to urbanization. My classification followed that of previous studies (Katoh, 2009; Okazaki and Katoh, 2005, 2004) in which meta-analyses were conducted to examine the association between the degree of urbanization and the occurrence of bird species around Tokyo and the bird species were classified into three groups, namely urban avoider, suburban adapter, and urban exploiter.

I did not use urban exploiters (*Columba livia* and *Motacilla alba*) because they are open or semi-open land species and do not extensively utilize woody vegetation. The urban avoider group mainly comprised ground-foraging species that prefer understory vegetation (e.g., *Horornis diphone* and *Emberiza spodocephala*), foliage gleaners, and tree climbers that utilize tree tops (e.g., *Aegithalos caudatus* and *Dendrocopos kizuki*) that were observed in relatively large patches surrounded by less artificial land (Okazaki and Katoh, 2005, 2004). The suburban adapter group comprised forest edge and urban bird species that are likely to utilize the landscape surrounding a habitat patch (Blair, 1996).

3.2.7 Generalized linear models and model selection

The number of species and total abundance of species belonging to each group (urban avoiders or suburban adapters) during each season in each patch was used as a response variable; thus, I performed eight kinds of analyses in total (i.e., two groups and two seasons for two indices). I excluded *Eophona personata* and *Psittacidae* sp. from the analyses because they were observed as a flock at two points, and thus their inclusion would lead to a biased result. Shorebird species (*Anas poecilorhyncha*) that are defined by the Japanese

Avian Trait Database (Takagawa et al., 2011) were also excluded.

In all analyses, I used generalized linear models (GLMs) with a log-link function. I assumed that response variables followed the zero-inflated Poisson distribution for the species richness and total abundance of urban avoiders because of the large quantity of no-observation data. For suburban adapters, I employed the Poisson distribution for species richness but a negative binomial distribution for the total abundances to account for overdispersion. Explanatory variables included patch area (log-transformed; AREA), the coverage of each vegetation structure in patches (arcsine-transformed; TREE and UNDER), the nearest corridor among the three corridors from each patch (categorical; CorridorTU, CorridorST, CorridorT; the numbers of patches, seven, six, and eight, respectively), distance to the nearest corridor (DISTANCE), NDVI in a buffer zone during each season, and urban landuse coverage in each buffer (URBAN) (Appendix C). I displayed the results of GLMs that established CorridorT, the most poorly vegetated corridor, as the contrast of this categorical variable and confirmed that changing the contrast did not affect the relative importance of explanatory variables. Significant multicollinearity, which could potentially result in erroneous estimates of variable significance and overly complex models (Graham, 2003) was not observed among the explanatory variables ($r < 0.6$).

For the analyses of total abundance, I used the total abundance in each patch as the dependent variable and set the natural log of the number of observation points (i.e., one or two) in a patch as an offset term in the models to standardize bird species abundance by observation effort. For the analyses of species richness, I used the number of bird species across sampling point(s) in each patch as the dependent variable. The jackknife species estimator showed that species detectability in patches with two sampling points [86.6 % ± 7.1 standard deviation (SD) during winter, 88.8 % ± 7.7 SD during the breeding season] was slightly higher than that in patches with one sampling point (78.9% ± 7.3 SD during winter, 87.2% ± 8.2 SD during the breeding season). I then set the natural log of detectability in each patch (DETECT) as an offset term to analyze the effect of explanatory variables on actual species richness, including unobserved species.

To reveal parsimonious models for predictions, I computed Akaike's information criterion (AIC) of all possible models, and ranked them by □AIC (difference of AIC between a candidate model and the best model). I then checked the effect of spatial autocorrelation in residuals of the best models with Moran's I using R package "ape" (Paradis et al. 2004). The result showed that Moran's I for the best models were not significant ($P > 0.05$), indicating that my obtained results would be caused by selected explanatory variables themselves, rather than unconsidered variables with spatial autocorrelation. All statistical procedures were performed using the R package "glmmADMB" (Fournier et al., 2012).

3.3 Results

I recorded 1,536 individuals comprising 27 bird species during winter and 1,510 individuals comprising 18 species during the breeding season, excluding shorebirds (Appendix B). The first-order jackknife richness estimator demonstrated that real species richness, including unobserved species, was 29.9 [standard error (SE): 2.9] during winter and 19.9 (SE: 1.3) during the breeding season. Therefore, species detectability throughout the surveys was sufficiently high at 90.4% during both winter and the breeding season. The average species richness and total abundance of observed species per patch during winter were 9.8 ± 2.5 SD and 73.9 ± 29.2 SD, respectively, and those during the breeding season were 7.2 ± 1.4 SD and 69.5 ± 31.0 SD, respectively. The average estimates of species richness per patch were 12.2 ± 0.8 SE during winter and 8.6 ± 1.2 SE during the breeding season, resulting in species detectability per patch being sufficiently high at 80.1% during winter and 87.6% during the breeding season.

The total number of urban avoiders observed during winter was larger than that of suburban adapters (11 vs. eight, respectively) but marginally smaller during the breeding season (five vs. six, respectively). The total number of observed individuals of urban avoiders was considerably smaller than that of suburban adapters during both seasons, i.e., 85 vs. 1,156 during winter and 87 vs. 921 during the breeding season, respectively. Therefore, there was a considerably lower abundance of observed individuals per species of urban avoiders than that of suburban adapters: 7.2 ± 11.2 SD vs. 144.5 ± 152.3 SD during winter and 17.4 ± 18.3 SD vs. 153.5 ± 152.1 SD during the breeding season, respectively.

3.3.1 GLM and model selection

Influential explanatory variables depended on the tolerance to urbanization and the seasonality of the species group (Tables 1, 2). The three corridors imposed different effects on urban avoiders during winter. The corridor with the most abundant trees and understory vegetation (CorridorTU) showed the highest bird species richness and total abundance in neighboring patches, followed by the corridor with abundant herbaceous plants and sparse trees (CorridorST) (Table 1, Fig. 3). In addition, vegetation coverage in the surrounding environments enhanced the species richness and total abundance of urban avoiders during winter.

During the breeding season, the corridors did not show a definite influence on either the species richness or total abundance of urban avoiders (Table 1). Understory vegetation in patches as well as patch area had a positive effect on the total abundance of urban avoiders, whereas no model was well constructed for species richness.

For the suburban adapter group, the corridor type had little effect on the species richness and total abundance in patches during both seasons (Table 2). The only influential variable on total abundance during the breeding season was tree coverage in patches, and no significant relationships between response and explanatory variables were revealed for total abundance during winter and species richness during both seasons.

3.4 Discussion

3.4.1 Factors affecting urban avoiders

The species richness and total abundance of the urban avoider group during winter were higher in the patches near CorridorTU, which comprised planted mature broadleaf woodland and dense understory vegetation (Table 1). This highlights the importance of vegetation structures on bird species in nearby small wooded patches, although additional surveys using a larger number of corridors are required to confirm the generality of the current results. Because the studied corridors varied in width, the effect of corridors might be a result of their widths rather than their vegetation structures. However, the widths of corridors did not correlate with the effectiveness of the corridors (CorridorST had the narrowest width but more understory vegetation), indicating that the vegetation structure of corridors was more important than their widths.

During winter, ground-foraging species, such as *H. diphone* and *E. spodocephala*, tend to utilize the shrub layer or understory, whereas *D. kizuki* and *A. caudatus* predominantly utilize the tree tops (Katoh, 1996). Hence, CorridorT and CorridorST were less suitable for ground-foraging and tree-top species, respectively. However, a small number of tree-top users (e.g., *D. kizuki* and *A. caudatus*) was observed in the patches neighboring CorridorST, indicating that sparse trees could contribute to the occurrence of these tree-top species, resulting in the marginal difference in the effects on species richness between CorridorTU and CorridorST.

Heyman (2010) demonstrated that understory vegetation in patches is likely to be poor in urbanized areas because of the improvement of recreational values in forest settings, which negatively affect the total abundance of forest bird species. My study indicated that the management of understory in corridors and in patches can also affect the species richness of urban avoiders during winter, particularly for ground-foraging species. In addition, patch area increased the species richness of forest bird species only in winter. The reason why patch area was not significant during the breeding season may be because the number of species observed during the breeding season was too small in urban areas to detect the species-area relationship.

Corridor type was a significant variable only during winter. This is probably because although individuals often move among patches during winter, they tend to remain within patches during the breeding season. This seasonal difference may reflect a temporal change in food availability and/or the behavior of particular species to avoid human disturbance during the breeding season. In other words, food availability during winter is lower than that during the breeding season (Haworth et al., 2006; Lovette and Holmes, 1995; Marra and Holberton, 1998); therefore, wintering bird species need to forage over a wider range (Haworth et al., 2006; Storch, 1995). Thus, higher permeability among patches is advantageous for these species during winter, and corridors can serve as an effective passage or a secondary habitat for them.

During the breeding season, breeding pairs feed their chicks and guard their nests, which restricts the size of their home range (Haworth et al., 2006; Wiktander et al., 2001), and the bird species become more vulnerable to human disturbances, which can result in low reproductive success (Miller et al., 1998; Murgui, 2009). Thus, the total abundance of breeding bird species can be increased by the presence of larger habitats containing abundant understory vegetation to provide more food and refuges (Carbó-Ramírez and Zuria, 2011; Fahrig, 2003; Uezu and Metzger, 2011; Wilson et al., 2009).

Importantly, the effectiveness of corridor vegetation appears higher in areas containing many scattered greenspaces (i.e., higher NDVI), particularly for abundance during winter (Figs. 3, 4). These patterns are evident because of the non-linear results of the log-link function in GLMs, although my analyses could not consider interaction terms between explanatory variables because of small sample sizes. My results are validated by Katoh & Yoshida (2011) who reported that vegetation coverage (agricultural and open lands) in a 1,000-m buffer extending from each wooded patch can have a positive effect on urban avoiders by providing secondary habitats and improving matrix permeability and the landscape-scale potential of species recruitment. Vegetation coverage in the landscape may play an important role in the persistence of urban avoiders in wooded patches during winter when individuals move more frequently among the patches. Urban landuse coverage did not influence the distributions of birds. This could be because there were fewer differences in urban coverage among patches located in the highly-fragmented urban landscape in the current study area than those in vegetation coverage in a landscape.

3.4.2 Factors affecting suburban adapters

The corridor type was not influential in top five models for the suburban adapter group (Table 2), suggesting that their distribution is independent of the vegetation types in corridors. This pattern might occur because of the higher capability of suburban adapters to exploit the matrix compared with that of the urban avoiders. Gilbert-Norton et al. (2010) indicated in their meta-analysis that corridors were less effective for species that can frequently utilize matrix environments. Suburban adapters, such as *Hypsipetes amaurosis, Parus minor*, and *Corvus macrorhynchos*, can exploit matrix surrounding a patch (Hashimoto and Natuhara, 2002; Katoh, 2009, 1996); thus, their dependence on the corridors was most likely low in the present study.

In addition, I determined that the coverage of tall trees was the only influential variable that increased the total abundance of these species during the breeding season. No model was well constructed for species richness during both seasons, probably because suburban adapters were common within the studied wooded patches. Tree coverage, which may indicate the availability of potential nesting sites, was significant because birds tend to remain within habitats associated with reproductive behavior (Haworth et al., 2006; Wiktander et al., 2001). Previous studies have indicated that although suburban adapters have greater tolerance to the urban environments, tree coverage remains essential for nesting (Hinsley et al., 1999; Yamaguchi and Saito, 2009). Therefore, I conclude that the wooded remnants in urban areas are necessary to support the presence of even those bird species that are adapted to suburban environments.

Appendix A. Comparison of vegetation coverage (%) with standard deviation in each corridor, the average of normalized difference vegetation index (NDVI), and urban landuse coverage (%) in a 300-m buffer extending from each corridor. I recorded the vegetation coverage at 100-m intervals and used the average scores of points in each corridor (total number of points was 100 in CorridorTU, 50 in CorridorST, and 87 in CorridorT). TREE indicates the average scores for the tree and sub-tree layers, whereas UNDER indicates average scores for the shrub and ground layers.

	TREE	UNDER	Wintering NDVI	Breeding NDVI	Urban Coverage
CorridorTU	34.5 ± 15.4	17.5 ± 6.3	86.6	86.0	0.88
CorridorST	2.4 ± 3.4	7.1 ± 7.4	90.1	89.9	0.89
CorridorT	13.5 ± 12.0	2.7 ± 2.8	86.2	82.6	0.90

Appendix B. List of bird species observed and their classifications. *Zosterops japonicus* and *Lanius bucephalus* were observed around urbanized areas only during winter and tended to be urban avoiders during the breeding season. Open land/semi-open land species and shorebirds were excluded from the analyses because of their habitat preferences. *Eophona personata* and *Psittacidae* sp. were also excluded because of irregular observations. The terminology I used was adopted from the study of McKinney (2002) that suggested the classical terminology of the species depending on their tolerance to urbanization.

Species	Wintering group	Breeding group
Parus major	Adapter	Adapter
Hypsipetes amaurotis	Adapter	Adapter
Corvus macrorhynchos	Adapter	Adapter
Streptopelia orientalis	Adapter	Adapter
Cyanopica cyana	Adapter	Adapter
Caduelis sinica	Adapter	Adapter
Zosterops japonicas	Adapter	Avoider
Lanius bucephalus	Adapter	Avoider
Dendrocopos kizuki	Avoider	Avoider
Cettia diphone	Avoider	Avoider
Aegithalos caudatus	Avoider	Avoider
Parus varius	Avoider	No records
Coccothraustes coccothraustes	Avoider	No records
Phoeniourus auroeus	Avoider	No records

Picus awokera	Avoider	No records
Emberiza spodocephala	Avoider	No records
Bambusicola thoracica	Avoider	No records
Accipiter gularis	Avoider	No records
Picoides major	Avoider	No records
Eophona personata	Irregularly observed	No records
Psittacidae sp.	Irregularly observed	Irregularly observed
Passer montanus	Open land/semi-	Open land/semi-
Sturnus cineraceus	Open land/semi-	Open land/semi-
Columba livia	Open land/semi-	Open land/semi-
Motacilla alba	Open land/semi-	Open land/semi-
Turdus naumanni	Open land/semi-	Open land/semi-
Corvus corone	Open land/semi-	Open land/semi-
Anas poecilorhyncha	Shorebird	Shorebird

Appendix C. Information of explanatory variables per patch in generalized linear models (GLMs). The values are shown as raw values before transformation [AREA, TREE, UNDER, normalized difference vegetation index (NDVI) wintering, NDVI breeding, DETECT, and sampling points]. The values of TREE, UNDER, URBAN, and DETECT ranged from 0 to 1.

Patch ID	AREA (ha)	TREE	UNDER	DISTANCE (km)	CORRIDOR	NDVI wintering	NDVI breeding	URBAN	DETECT	Sampling points
A	2.4	1.0	0.8	0.7	CorridorT	88.6	86.7	1.0	0.9	2
B	1.7	0.8	0.4	1.6	CorridorT	85.9	81.0	0.8	0.9	2
C	0.5	0.6	0.1	<0.01	CorridorT	85.3	80.1	0.9	0.9	1
D	0.7	1.0	0.7	0.2	CorridorT	86.0	82.0	0.9	0.9	1
E	0.9	0.8	0.6	0.1	CorridorT	84.9	80.1	0.9	0.9	1
F	0.6	0.9	0.6	0.7	CorridorT	81.8	73.3	1.0	0.7	1
G	0.4	0.7	0.9	0.1	CorridorT	85.9	80.4	0.9	0.7	1
H	0.6	1.0	0.8	0.1	CorridorT	85.8	80.3	0.9	0.8	1
I	0.4	1.0	0.3	<0.01	CorridorTU	80.8	73.0	1.0	0.7	1
J	0.7	0.9	0.4	<0.01	CorridorTU	84.1	77.5	0.9	0.8	1
K	0.3	0.9	0.6	1.2	CorridorTU	83.1	75.3	1.0	0.7	1
L	0.4	1.0	0.5	0.8	CorridorTU	83.0	76.3	0.9	0.8	1
M	0.7	1.0	0.9	0.0	CorridorTU	86.0	83.6	0.9	0.8	1
N	1.2	1.0	0.6	0.2	CorridorTU	90.9	97.6	0.8	0.9	1
O	2.6	1.0	0.6	<0.01	CorridorTU	86.6	83.1	0.8	0.8	2
P	1.7	0.8	0.8	0.1	CorridorST	87.8	84.9	0.9	0.9	2
Q	1.1	1.0	0.8	0.1	CorridorST	86.2	80.8	1.0	0.7	1
R	0.6	1.0	1.0	0.1	CorridorST	86.9	75.4	1.0	0.8	1
S	1.3	1.0	0.9	0.1	CorridorST	85.8	81.4	0.9	0.8	2
T	0.7	0.8	0.2	0.1	CorridorST	87.7	85.4	1.0	0.8	1
U	1.2	1.0	0.5	0.5	CorridorST	85.4	81.0	1.0	0.7	1

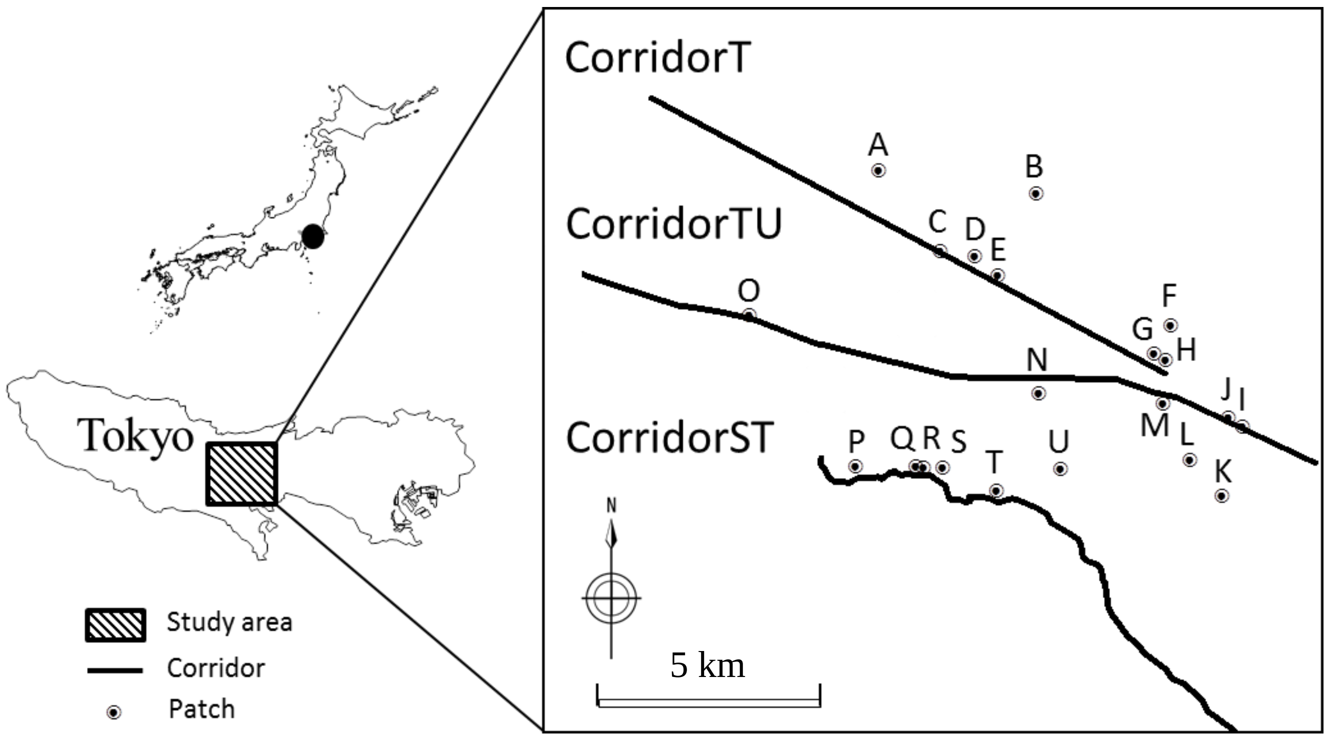


Fig. 1. Map of the locations of small wooded patches and corridors examined in this study

(a) CorridorTU (b) CorridorST (c) CorridorT

Fig. 2. Typical vegetation structures observed in the three corridors used in this study. CorridorTU is a linear strip of mature broadleaf evergreen/deciduous woods with dense understory vegetation. CorridorST is a riparian corridor along the Nogawa River that is mainly covered with herbaceous vegetation and a few planted trees. CorridorT comprises rows of planted trees (height, approximately 10 m) along both sides of a cycling track with scarce understory vegetation

Table 1

Results of the top five models and null model (without any predictors) for the species richness and total abundance of urban avoiders during each season. I show the estimate/standard error (z value) of each variable (z values over 2.0 corresponding to approximately $p < 0.05$ are in bold). Explanatory variables included patch area (log-transformed; AREA), the coverage of each vegetation structure in patches (arcsine-transformed; TREE and UNDER), the nearest corridor among three corridors from each patch (categorical; CorridorT was set as a contrast), distance to the nearest corridor (DISTANCE), normalized difference vegetation index (NDVI) in a buffer zone during each season, and urban landuse coverage in a buffer (URBAN).

Avoiders	Explanatory variables (Estimate/Standard Error)									
	AREA	TREE	UNDER	CorridorTU	CorridorST	DISTANCE	NDVI	URBAN	AIC	ΔAIC
species richness	**2.6**	−1.5	**2.1**	**2.6**	1.4				68.5	0.0
in winter	**2.3**		1.6	**2.2**	1.4				68.9	0.4
	1.7	−1.7	1.9	**2.5**	1.4		1.1		69.3	0.8
				1.9	1.8		**2.3**		69.4	0.9
	2.3			**2.1**	1.9				69.4	0.9
				Null					72.9	4.4
species richness							**2.1**		56.7	0.0
in breeding season		0.7					1.7		58.2	1.5
						0.5	**2.1**		58.5	1.7
				Null					58.5	1.7
				0.8	−0.8		1.8		58.5	1.8
abundance	1.8			**2.5**	1.3		**3.0**		89.6	0.0
in winter						−1.4	**3.0**	−1.6	90.8	1.1
	1.6					−1.6	**2.3**		90.8	1.2
			0.8	**2.0**	0.9		**4.1**		90.8	1.2
	1.9			**2.6**	1.0		**2.8**		90.9	1.3
				Null					102.0	12.4
abundance	**4.5**		**3.3**						87.4	0.0
in breeding season	**4.3**		**3.2**	1.3	1.9				87.5	0.1
	4.5		**2.8**			−0.9			88.7	1.2
	3.5	0.6	**3.1**	1.2	1.9				89.1	1.7
	3.8		**3.0**				0.5		89.2	1.7
				Null					116.1	28.7

Table 2

Results of the top five models and null model (without any predictors) for the species richness and total abundance of suburban adapters during each season. I show the estimate/standard error (z value) of each variable (z values over 2.0 corresponding to approximately $p < 0.05$ are in bold). Explanatory variables included patch area (log-transformed; AREA), the coverage of each vegetation structure in patches (arcsine-transformed; TREE and UNDER), the nearest corridor among three corridors from each patch (categorical; CorridorT was set as a contrast), distance to the nearest corridor (DISTANCE), normalized difference vegetation index (NDVI) in a buffer zone during each season, and urban landuse coverage in a buffer (URBAN).

Adapters	Explanatory variables (Estimate/Standard Error)									
	AREA	TREE	UNDER	CorridorTU	CorridorST	DISTANCE	NDVI	URBAN	AIC	ΔAIC
species richness					Null				80.0	0.0
in winter								0.8	81.4	1.4
						0.6			81.6	1.6
	−0.5								81.8	1.8
		0.4							81.8	1.8
species richness					Null				73.0	0.0
in breeding season						1.2			73.7	0.7
									75.0	2.0
	−0.1		−0.1						75.0	2.0
								−0.1	75.0	2.0
abundance					Null				172.9	0.0
in winter		1.4							173.0	0.1
								1.0	174.1	1.1
		1.4						0.9	174.2	1.2
							0.8		174.3	1.4
abundance		**2.2**							164.3	0.0
in breeding season		**2.0**		0.8	−1.2				164.8	0.5
		2.3				0.6			165.9	1.6
	−0.2	**2.2**							166.3	2.0
		2.1	−0.2						166.3	2.0
					Null				166.7	2.4

Chapter 4: General discussion

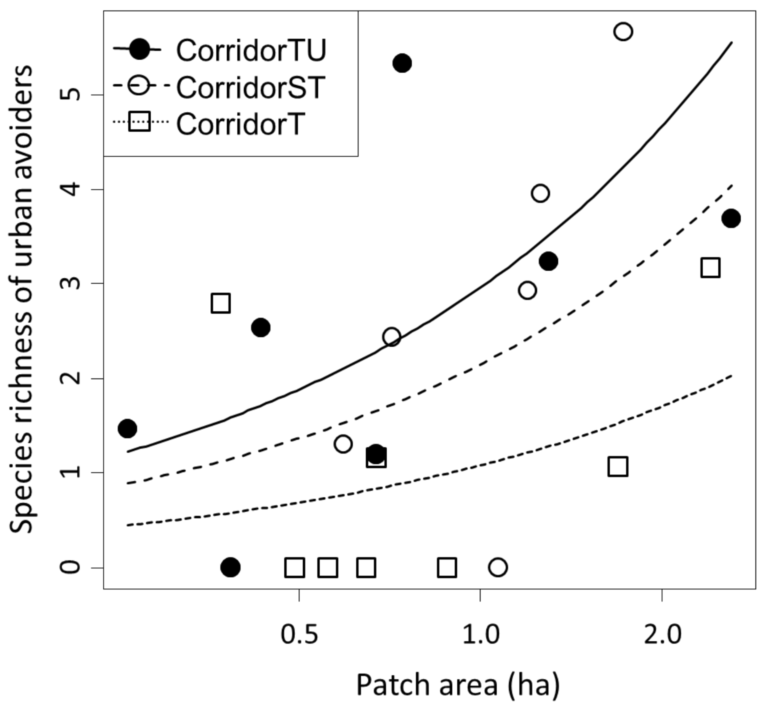
In this study, I investigated the effectiveness of urban wooded corridors on the distributions of bird species in connected or neighboring to a corridor. In Chapter 2, I compared the distributions of avian species observed in eight lines of wooded streets located in and around Tokyo and found they were explained by the vegetation structures in wooded corridors and the surrounding landuse. The corridors planted with both tall trees and understory vegetation appealed to forest bird species. The surrounding forest and agricultural field coverage positively influenced on the species richness of urban avoider species group. These results suggest the distribution of bird species varied with vegetation structures in corridors and the species might be moved from the surroundings. In Chapter 3, I showed the effectiveness of wooded corridors on avian species in connected or neighboring woodlots. I compared the effects of three major corridors of varying vegetation structures (trees with a dense understory, trees with a sparse understory, and grassy areas with sparse trees) on the species richness and abundance of birds in 21 wooded patches in the center of Tokyo, during wintering and breeding seasons. I found that the effectiveness of corridors depended on the tolerance of birds to urbanization. Urban avoider species, having low tolerance to urbanization, demonstrated lower species richness and abundance in patches close to the corridor with a sparsely vegetated understory as compared with patches close to the understory-richer corridors during winter, although such an effect disappeared during the breeding season. The corridors did not have a significant effect on suburban adapter species with a high tolerance to urbanization. These results suggest that corridors with scarce understory vegetation may limit the persistence of birds avoiding urban areas.

Based on the above results, I obtained the following two findings: (1) the bird species will increase in urban corridors planted with tall trees, and shrubs or understory vegetation; (2) these urban corridors can function as an ecological network to increase the species richness and abundance of urban avoider species in connected or neighboring woodlots. These findings can provide significant evidence showing the effectiveness of urban corridors as an ecological network, which has been equivocal due to the paucity of the empirical studies in urban areas. Urban corridors for bird species, particularly for urban avoiders need to provide both tall trees, and shrub and understory vegetation, which is consistent with habitat requirements of the species (Katoh 1996). It is notable that little attention to the quality of a corridor has been paid in a landscape planning aiming at establishment of ecological network (Sone et al. 2015). Haddad and Tewksbury (2005) indicated low-quality corridors can work as movement conduits for butterflies. That is corridors may not always need to provide the quality as a habitat because of their expected roles as a pathway and a secondary habitat. However, as the results shown in this study, even a movement corridor needs appropriate vegetation structures as well as a habitat patch. Also, the surrounding matrix affected urban avoider species in a corridor and a connected or neighboring patch, indicating the species recruitment from the surroundings and necessity of matrix management for effective urban corridors. Few landscape plans have included matrix management yet in Japan (Sone et al. 2015). My results indicate that corridors independent on management of the surroundings may limit the effectiveness of urban corridors for the birds avoiding urban areas.

From the view of management of greenspaces, the maintenance of shrub or understory vegetation is encouraged not only in patches but also in corridors. However, this may be in conflict with safety and aesthetic values of the environments for humans in urban landscapes (Heyman, 2010). Understory vegetation decreases the aesthetic value (Tyrväinen et al., 2003) and recreational value (Heyman et al., 2011) of urban woodlots and arouse the fear of clime (Jansson et al., 2013), whereas well-managed vegetation mitigates these negative impacts by increasing the utilization of public space and surveillance (Wolfe and Mennis, 2012). One possible strategic approach is to differentially select and manage corridors for forest-dwelling bird species, particularly for urban avoiders. On the basis of my results in Chapter 3 (Fig.1b), I suggest that the management practice of increasing vegetation in corridors will be better implemented in a landscape with numerous scattered greenspaces (as in Fig.2a) or that neighbor larger patches (Fig. 1a), whereas management for humans should be prioritized in a landscape with more artificial land use (as in Fig.2b).

The results obtained in this study of scattered greenspaces in the surroundings support the roles of private gardens, which are major components of greenspaces. These gardens are considered to be refuges for urban organisms (Goddard et al., 2010; Ikin et al., 2015) and provide ecosystem services, such as human health and well-being (Barbosa et al., 2007). As a conclusion, corridors with appropriate vegetation structure, which might be originally established for human use, can contribute to the persistence of urban bird species and possibly encourage the harmony of nature conservation with human well-being.

(a)



(b)

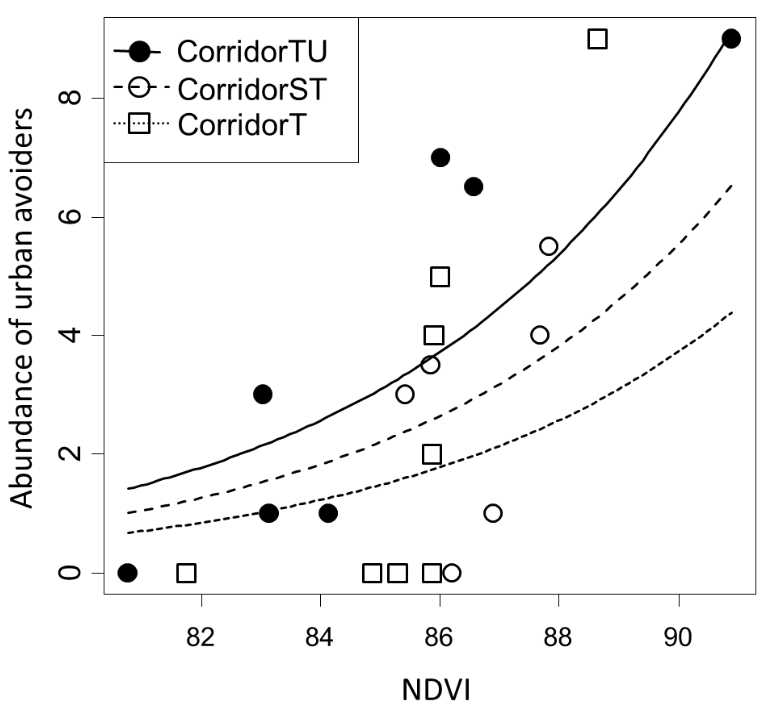


Fig. 1. Relationships between the urban avoider group in winter and the influential

explanatory variables showed in Chapter 3: (a) species richness and patch area; (b) total abundance and the values of the normalized difference vegetation index (vegetation coverage surrounding the patches; NDVI) in the area surrounding the patches. The vertical axis in (a) is species richness divided by detectability (i.e., estimated richness including unobserved species). The values were formatted in 8-bit numbers, ranging from 0 to 255. I show the response curves using the estimate of the three corridors in each best model of general linear models for species richness and total abundance.

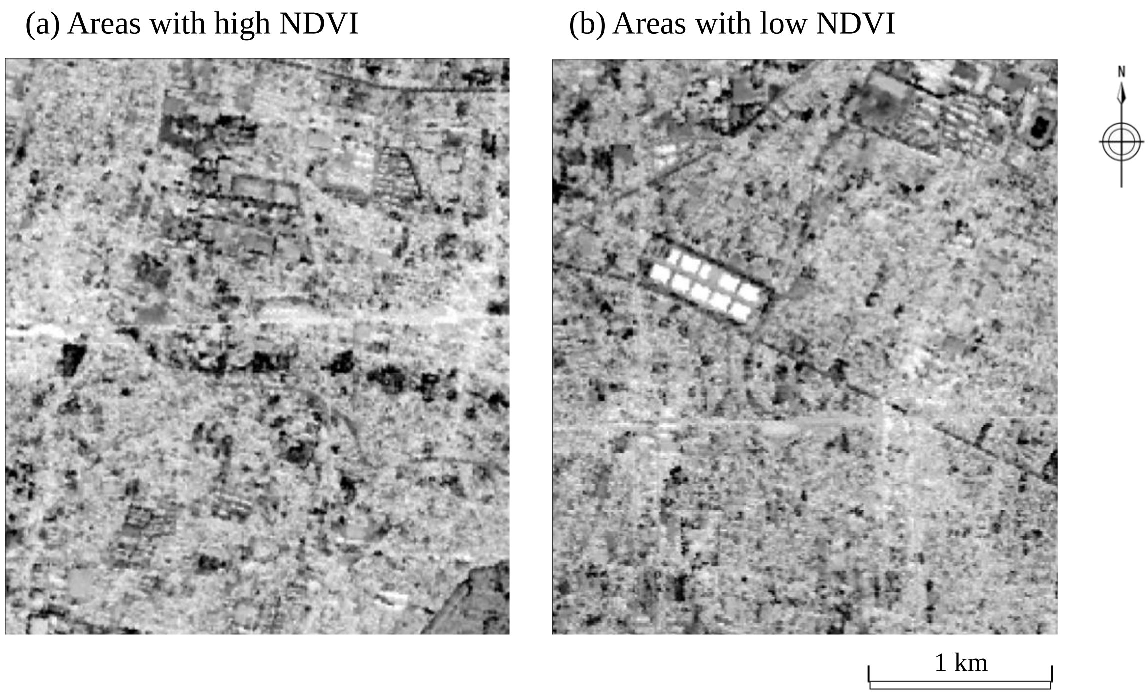


Fig. 2. Examples of the areas with a (a) high (86.9) or (b) low (80.8) normalized difference vegetation index (vegetation coverage in the areas surrounding the patches; NDVI) during winter. The values were formatted in 8-bit numbers, ranging from 0 to 255. Dark areas indicate greenspace, whereas white areas indicate more artificial land use.

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