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Land-sharing vs. land-sparing urban development modulate predator–prey interactions in Europe

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Abstract. Urban areas are expanding globally as a consequence of human population increases, with overall negative effects on biodiversity. To prevent the further loss of biodiversity, it is urgent to understand the mechanisms behind this loss to develop evidence-based sustainable solutions to preserve biodiversity in urban landscapes. The two extreme urban development types along a continuum, land-sparing (large, continuous green areas and high-density housing) and land-sharing (small, fragmented green areas and low-density housing) have been the recent focus of debates regarding the pattern of urban development. However, in this context, there is no information on the mechanisms behind the observed biodiversity changes. One of the main mechanisms proposed to explain urban biodiversity loss is the alteration of predator–prey interactions. Using ground-nesting birds as a model system and data from nine European cities, we experimentally tested the effects of these two extreme urban development types on artificial ground nest survival and whether nest survival correlates with the local abundance of ground-nesting birds and their nest predators. Nest survival (n = 554) was lower in land-sharing than in land-sparing urban areas. Nest survival decreased with increasing numbers of local predators (cats and corvids) and with nest visibility. Correspondingly, relative abundance of ground-nesting birds was greater in land-sparing than in land-sharing urban areas, though overall bird species richness was unaffected by the pattern of urban development. We provide the first evidence that predator–prey interactions differ between the two extreme urban development types. Changing interactions may explain the higher proportion of ground-nesting birds in land-sparing areas, and suggest a limitation of the land-sharing model. Nest predator control and the provision of more green-covered urban habitats may also improve conservation of sensitive birds in cities. Our findings provide information on how to further expand our cities without severe loss of urban-sensitive species and give support for land-sparing over land-sharing urban development.

Key words: birds; cats; corvids; land use; land-sharing development; land-sparing development; nest predation; nests; predator–prey interactions; urbanization.

Introduction

Globally, an increasing number of people are living in urban areas (United Nations 2014). At the same time, the expansion of urban areas has occurred twice as fast as current urban population growth, causing important landscape changes that could have harmful effects on global biodiversity (Seto et al. 2011, Beninde et al. 2015). Rapid and unplanned urban growth threatens the survival of many organisms (Francis and Chadwick 2013, Gagné et al. 2016), even though some species are favored by the proximity of human habitation (Blair

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1996, Møller and Díaz 2017*a, b*). In general, urbanization decreases biodiversity (Marzluff 2001, Marzluff et al. 2001*a*, Chace and Walsh 2006, McKinney 2008, Aronson et al. 2014, Ibáñez-Álamo et al. 2017) and promotes the biotic and phylogenetic homogenization of flora and fauna around the world (Blair 2001, Kühn and Klotz 2006, McKinney 2006, Morelli et al. 2016, Ibáñez-Álamo et al. 2017). Consequently, the process of urbanization and its environmental impacts are currently considered a major global challenge (United Nations, 2016). To prevent the further loss of biodiversity and to support sustainable populations of wild organisms in urban areas, there is an urgent need to reconcile urban expansion and biodiversity conservation (Miller and Hobbs 2002, Lerman and Warren 2011, Lepczyk and Warren 2012, Aronson et al. 2014).

Urbanization occurs in many different forms: development can vary from low-density private-house residential areas to compact, high-rise building areas with a high human density (Francis and Chadwick 2013). Earlier studies have shown reduced diversity in urban areas, but many show increases in diversity as one moves from more uniform wildland to highly diverse suburbs (e.g., Marzluff 2014). A long-standing debate about urbanization concerns the relative merits of scattered vs. compact development. In this context, a new approach has recently emerged in the form of the land-sharing vs. land-sparing framework (Lin and Fuller 2013, Soga et al. 2014, Stott et al. 2015), which explicitly considers the distribution and organization of green and built areas within cities. Land-sharing areas consist of low-density built areas (e.g., private-house settlements) interspersed with green spaces in the form of gardens and small-sized parks but lacking large, continuous forested areas or ancient parks (Lin and Fuller 2013). In contrast, land-sparing areas have high-density built areas (e.g., multi-story buildings) with set-aside, large-sized, continuous green areas (Lin and Fuller 2013). Although this dichotomy is somewhat arbitrary, as it emphasizes the endpoints of a continuum rather than its gradual nature (Kremen 2015, Finch et al. 2019), understanding how these two land-development approaches affect urban ecosystems and biodiversity is of key importance for city planning.

Despite its relevance for reconciling urban development with biodiversity conservation, our current knowledge on the topic is still very limited (Lin and Fuller 2013, Stott et al. 2015). The few studies on the topic support land-sparing as the best of the two development strategies for biodiversity conservation (Sushinsky et al. 2013, Caryl et al. 2016, Collas et al. 2017, Villaseñor et al. 2017). For example, Concepción et al. (2016) indicated that urban expansion into natural and seminatural areas decreases the species richness of plants and breeding birds, thus indirectly supporting densification (i.e., land-sparing) over dispersion (i.e., land-sharing) in urban development (see also Soga et al. 2014). Compact housing development minimizes the impacts of a given human population on forest vertebrates and arthropods, although there are some differences in its effects on animals inhabiting the forest interior and edges (Gagné and Fahrig 2010*a*, *b*). Some studies have also detected a positive relationship between species richness and household density (Araújo 2003, Evans and Gaston 2005, Tratalos et al. 2007, Ortega-Álvarez and MacGregor-Fors 2009), also providing support for land-sparing development. However, if the extra species are widespread species replacing more local ones, then positive relationship between species richness and household density does not necessarily provide an argument for land-sparing. Furthermore, it has been highlighted that a shift from a pattern-based to a mechanistic approach would be very useful in studying the effects of urbanization (e.g., Shochat 2004, Shochat et al. 2006, Gordon et al. 2009, Rodewald et al. 2011, McPhearson et al. 2016, Lepczyk et al. 2017, Marzluff 2017). This is particularly relevant to better understand the drivers of diversity and landscape practices (Tratalos et al. 2007) and is crucial for discerning whether urban habitats could represent ecological traps, e.g., for the ground-nesting birds (Stracey and Robinson 2012*a*, Bonnington et al. 2015).

Among many factors, predator–prey interactions, are one of the key mechanistic processes in community assembly (Lima 1998, Chase et al. 2002), that are known to be affected by urbanization (e.g., Møller and Ibáñez-Álamo 2012, Díaz et al. 2013, Uchida et al. 2016, Eötvös et al. 2018); consequently, they are candidates for explaining the differential effects of land-sharing and land-sparing development approaches on biodiversity. For example, Shochat et al. (2006) have suggested that predation could be one of the main factors modifying the urban assemblages. Reduced predation pressure in cities (i.e., safe-habitat or predator refuge hypothesis; Gering and Blair 1999, Tomialojć 1978, 1982) has been suggested to be a potential explanation for urbanization-induced changes (e.g., a high total number of individuals) in the biodiversity and community structure of birds (Tomialojć 1978, Gering and Blair 1999, Møller and Ibáñez-Álamo 2012, Møller and Díaz 2017*a*, *b*) and other taxa (Eötvös et al. 2018). Especially ground-nesting bird species have been shown to be sensitive for urbanization (Jokimäki and Huhta 2000, Clergeau et al. 2006, Croci et al. 2008, Evans et al. 2011, Jokimäki et al. 2016). However, the safe-habitat hypothesis has also been questioned (Jokimäki et al. 2005, Chamberlain et al. 2009) and, while cities are characterized by an overall decrease in the abundance of native predators, they also experience an increase in domestic (cats and dogs) and human-associated predators (rats and corvids; e.g., Gregory and Marchant 1996, Gering and Blair 1999, Jerzak 2001, Sims et al. 2008, Valcarcel and Fernández-Juricic 2009, Díaz et al. 2013, Jokimäki et al. 2017). Furthermore, the number of generalist predators increases with the level of urbanization, whereas the number of specialist predators decreases (Sorace and Gustin 2009), which might also suggest differences between land-sharing and land-sparing areas. Both nest predation relaxation and intensification can occur in the same urban system, suggesting that predator–prey dynamics can be diverse throughout urban areas (Rivera-López and MacGregor-Fors 2016). Moreover, some studies have noted that despite a low nest predation rate in urban areas, nest predator abundance can be high in urban areas (urban nest predator paradox; Shochat et al. 2006, Rodewald et al. 2011, Stracey and Robinson 2012*a*, *b*).

We suggest that urban development type, either land-sharing or land-sparing, can partly explain why some urban ecological studies have found predation relaxation, while others found predation intensification. In this study, we examined whether mechanisms driving biodiversity in urban areas, such as predator–prey interactions, differ between these two extreme urban development types (land-sharing vs. land-sparing). To do so, we carried out a large-scale experiment encompassing nine European cities. We used artificial ground nests while simultaneously evaluating the abundance of predators and their potential prey, ground-nesting birds (Jokimäki and Huhta 2000, Jokimäki et al. 2005, Smith et al. 2016). Nest predation of urban birds is still inadequately understood (Ibáñez-Álamo et al. 2015) despite several local studies on the topic (e.g., Tomialojć 1978, Gering and Blair 1999, Matthews et al. 1999, Jokimäki and Huhta 2000, Haskell et al. 2001, Blair 2004, Borgmann and Rodewald 2004, Kaisanlahti-Jokimäki et al. 2012). A recent meta-analysis on urban nest predation found very heterogeneous results attributed to different study methods, differences in local nest predator communities and differences in the urbanization level of the focal study areas (Vincze et al. 2017). The large-scale cross-city perspective of our approach is particularly important because many of the previous studies analyzed urban nest predation at a very small scale (i.e., park/woodlot level), making generalizations for management purposes difficult (Lepczyk et al. 2017).

Our specific study questions are as follows: (1) Does ground nest survival differ between the two extreme urban development types (land-sharing vs. land-sparing)? Given the previous findings on the effects of these urbanization approaches on biodiversity (see above), we predict lower nest predation in land-sparing areas. (2) What is the role of domestic (cats) and avian nest predators (corvids) on nest losses in the urban environment? Both cats and corvids are important nest predators known to increase with urbanization and human abundance (see above), although no information regarding the land-sharing/sparing context is available. Therefore, we would expect them to be directly associated with nest predation pressure. (3) What is the role of human disturbance (i.e., number of pedestrians) and nest visibility on nest survival in cities? Because predators might be deflected by human disturbance (Ibáñez-Álamo et al. 2012, Møller and Díaz 2017*a*, *b*), we expect a positive association with nest survival. In contrast, high nest visibility will increase detectability of nests by visually searching avian nest predators like corvids. Finally, (4) could nest predation predict the observed differences in the effects of land-sharing and land-sparing urbanization on the relative abundance of ground-nesting birds? If nest predation pressure is responsible for changes in urban avian populations, we would expect a direct association between ground nest survival and the abundance of ground-nesting species. Our large-scale experimental study will test, for the first time, whether predator–prey interactions might be responsible for the observed changes in abundance of urban-sensitive bird group, ground nesters, between the two extreme urbanizations types (land-sharing vs. land-sparing) and will provide useful insights into specific conservation practices that could help to reconcile urban development and urban-sensitive bird species conservation.

Methods

Study design

Because every ecological phenomena is at least partly scale dependent (Wiens 1989), multi-scale studies are needed to measure optimal land use allocation in urban landscapes (Hostetler 2001, Chong et al. 2019). Our data were collected at four spatial scales (European continent, landscape, study square, and study point scales). We assessed artificial ground nest survival, and the abundance of birds and potential nest predators as well as breeding bird species richness, in nine cities in six different European countries, encompassing a large latitudinal gradient that extends from Granada in southern Spain to Rovaniemi, near the Arctic Circle, in northern Finland (European continental scale; 3,700 km; Fig. 1). In each city (landscape scale; size of individual town; 84–8,018 km^2), we selected ten 500 × 500 m study squares (study square scale; 25 ha), half of them with land-sharing urban development (n = 5) and the other half (n = 5) with land-sparing urban development (Fig. 1; Appendix S1; Fig. S1). Minimum distance between squares within a specific city was an average of 574 ± 65 m (mean ± SE). The squares within each city were initially assigned to either the land-sharing development type (low-density housing and small-fragmented green areas) or land-sparing (high-density housing and >50% green area in a single patch) by the visual inspection of aerial photographs available on Google Earth. Every land-sharing square in a given city was paired with another land-sparing square in the same city containing a similar amount of overall green area (20–80%; forest remnants, parks, gardens). The total cover of green areas in the study squares was estimated by calculating number of cells (50 × 50 m; see Appendix S1; Fig. S1) with a high (>50%) green area cover by inspection of aerial photographs available on Google Earth.

According to Soga et al. (2014), the conservation benefits of land-sharing and land-sparing development options depend on the level of urbanization. As urbanization can also affect the nest predation rate (e.g.,

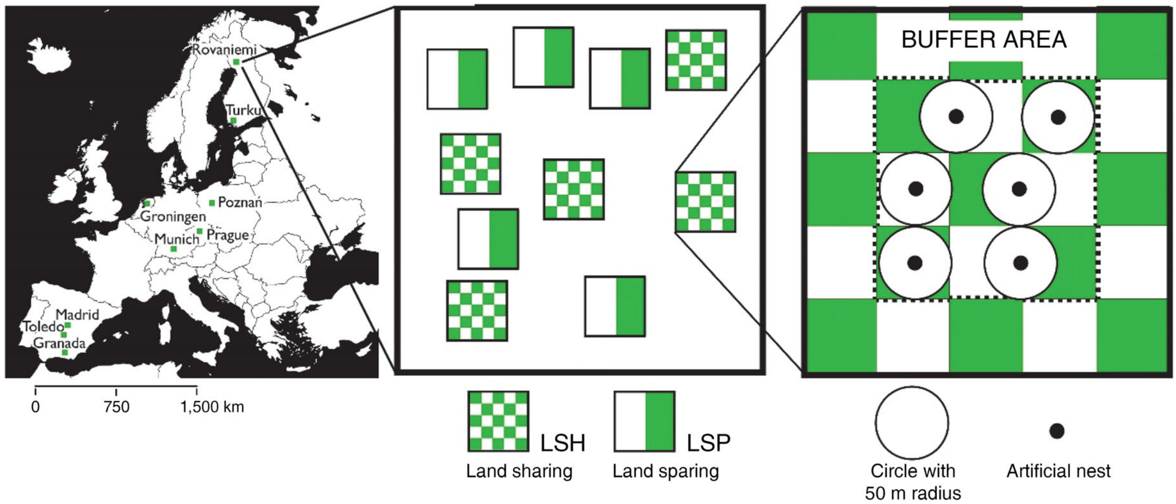

FIG. 1. Study design used to investigate nest predation in land-sharing and land-sparing areas across Europe. Each of the nine cities had five land-sharing and five land-sparing study squares. Each individual 500 × 500 m study square contained six artificial nests that were located at least 100 m from one another and the border of the study square. White represents built areas, while green corresponds to green areas. Circles with a 50 m radius in the third panel represent areas where nest predators, pedestrians, and birds were surveyed.

Eötvös et al. 2018), there is a need to control for the level of urbanization when comparing the benefits of land-sharing and land-sparing development. We controlled for this variable by calculating a commonly used urbanization score index (Liker et al. 2008) for each square that considers three major landscape features (built surfaces, green areas and roads). A general mixed model including land-sharing/sparing type as a fixed factor and city as a random factor showed that the land-sharing and land-sparing squares did not significantly differ in their urbanization index values ($F = 1.01$, df = 1,80; $P = 0.32$). This result was expected due to the paired selection of land-sharing and land-sparing squares according to their green cover and provides confidence that the potential results from our study are strictly related to the landscape organization of urban features rather than differences in the intensity of urbanization or amount of green area.

Artificial ground nest experiment

To evaluate the relative nest predation risk in a standardized way (McKinnon et al. 2010), a total of 554 artificial ground nests containing one Quail (*Coturnix coturnix*) egg each were established in the nine study cities within their 10 study squares (33–70 nests per town; Table 1; Fig. 1). By using artificial nests, we were able to use a similar nest design across all study areas and to obtain sufficient sample size without disturbing real nests. Within each 500 × 500 m study square, locations of artificial nests were randomly selected with at least 100 m apart and at least 100 m inside of study square border (Fig. 1). In a few cases when there were no small shrubs or trees at the selected random point, the nest was put under the nearest shrub or tree. A nest was a small-sized hand-made cup placed on the ground without any particular structures. Individual Quail eggs were directly placed on leaf litter in the nests, which were always located under a small shrub or tree. No physical nest markers (e.g., plastic strings) were used, but all locations were recorded using a GPS device with a very high accuracy. Because nest visibility can affect nest survival (Jokimäki and Huhta 2000, Martin and Joron 2003, Jokimäki et al. 2005), we estimated the visibility of each artificial nest. We used a slightly modified variation of the method of Rubio et al. (2018) to estimate the visibility of the nest. Just after placing the nest, we estimated the nest visibility by quantifying the visibility of the nest contents (i.e., the egg) from the four main compass directions at a distance of 2 m from the nest. Visibility was scored as 0 = egg nonvisible or 1 = egg visible, and these four measurements were then summed to obtain a score of 0 (egg not visible from any direction) to 4 (egg visible from all four directions).

The artificial nests were deployed during the main breeding period 2016 in each study city (i.e., late March–early April in the south, late April–early May in the mid-latitudes, and mid-May in the north), and the fate of the nests was checked after 30 d of exposure, hence including the typical duration of both the incubation and nestling stages of small European ground nesters (Cramp and Perrins 1977–1994). A nest was scored as preyed upon if the egg had disappeared or if we found egg remains at the nest location. The experiment was conducted over a single year, but earlier studies have indicated that the artificial nest predation rate do not vary a lot among study years (Jokimäki and Huhta 2000, Hoset and Husby 2018).

TABLE 1. Study sites and nest survival rates (%) in the land-sharing (LSH) and land-sparing (LSP) urban areas over 30 d.

			Nest survival rate (%)		Number of nests		
City	Latitude	Longitude	LSH	LSP	LSH	LSP	Total
Granada	37°10′ N	3°36′ W	0.0	0.0	31	29	60
Groningen	53°13′ N	6°34′ E	0.0	8.6	35	35	70
Madrid	40°26′ N	3°41′ W	40.0	40.0	35	35	70
Munich	48°80′ N	11°31′ E	33.3	17.2	30	29	69
Poznan	52°25′ N	16°56′ E	0.0	20.0	35	35	70
Prague	50°50′ N	14°25′ E	21.7	20.0	23	10	33
Rovaniemi	66°29′ N	25°43′ E	29.0	61.3	31	31	62
Toledo	39°52′ N	4°20′ W	31.4	48.6	35	35	70
Turku	60°28′ N	22°17′ E	33.3	46.7	30	30	60
Average			21.0	29.2			
SD			14.7	18.5			
Total					285	269	554

Bird data collection

We collected data on bird species using standardized 5-minute point counts with a fixed 50 m radius (study point scale; 0.8 ha) detection distance (Bibby et al. 2000). Point counts provide good estimates of relative population density and are therefore a standardized method in ecology that is extensively used for monitoring bird populations across Europe (Voříšek et al. 2010). We surveyed birds during the main breeding season in 2016 (maximum 30 d after the placement of the artificial nests), when all migratory species had arrived at the specific study areas (i.e., in late April–early May in the south, mid-May–early June in midlatitudes, and later in June in the north). We surveyed birds within four hours after sunrise and under good weather conditions (without rain and heavy winds). We established survey stations at the same locations within each 500 × 500 m square at which the artificial ground nests had been placed. Therefore, the distance between the individual survey stations within a study square was at least 100 m, minimizing the risk of counting the same individual bird twice. We classified bird species as either ground nesters or other nesters based on Cramp and Perrins (1977–1994; see groupings in the Appendix S1; Table S1). We collected information from a total of 92 bird species, of which 23 were ground-nesting species. The percentage of ground-nesting species of the total number of species was 24.4% (n = 86 species) for land-sparing urban areas and 18.8% (n = 64 species) for land-sharing urban areas (Appendix S1; Table S1). Relative abundance of ground-nesting individuals (i.e., total number of ground-nesting individuals/total number of individuals of all species) was used later in analyses.

Nest predator surveys

We conducted nest predator and pedestrian surveys at the same study stations (Study point scale; 0.8 ha) where the artificial ground nest experiments and bird surveys were carried out. Because earlier studies have indicated that corvids are important nest predators in Europe (Andrén 1992, Groom 1993, Jokimäki and Huhta 2000, Haskell et al. 2001, Luginbuhl et al. 2001; but see Marzluff et al. [2007] for urban systems outside Europe), we quantified the number of Hooded or Carrion Crows (*Corvus corone corone/cornix)*, Jackdaws (*Corvus monedula*), Eurasian Magpies (*Pica pica*), and Eurasian Jays (*Garrulus glandarius*). It might be that different nest sites are vulnerable to different predators, e.g., in some areas, corvids might be the dominant nest predators of shrub nests, whereas mammals might predate mainly ground nests (e.g., Marzluff et al. 2007). However, the geographical location (e.g., tropical vs. temperate vs. boreal) and landscape context (e.g., urban vs. agricultural vs. wildlands) will also influence which nest predators (avian or mammal) are a driving force on different kinds of nests. We studied nest survival of ground nests in Europe, where many studies have indicated that corvids are the main nest predators of ground nests (e.g., Møller [1989], 90% of 301 depredated nests, plasticine egg study; Andrén [1992], 82% of 176 depredated nests, a board with a layer of grease study; and Jokimäki and Huhta [2000], 100% of 17 depredated nests, plasticine egg study). We also surveyed cats (*Felis catus*) because they can negatively affect avian abundance and breeding success (e.g., Woods et al. 2003, Sims et al. 2008, Stracey 2011, Woinarski et al. 2017). We surveyed pedestrians because they can affect nest predator abundance and modify predator searching efficiency and even nest survival (Jokimäki et al. 2005, Valcarcel and Fernández-Juricic 2009, Ibáñez-Álamo et al. 2012). We also surveyed red squirrels (*Sciurus vulgaris*) and Gulls (*Larus* sp.), but they were not used in analyses since they were observed only in a few study towns and survey points (red squirrels, three towns; 2.35% out of 554 survey stations; Gulls, four towns; 5.24% out of 554 survey stations). We did not detect any other potential nest predator species, such as red foxes (*Vulpes vulpes*), raccoon dogs (*Nyctereutes procyonoides*), badgers (*Meles meles*), raccoons (*Procyon lotor*), and *Mustela* species, in our sampling sites. We counted all corvids, cats, and pedestrians observed within the 50 m radius circle at each survey station during the 5-minute survey period while conducting the bird surveys. Predator sampling distances correspond relatively well with reported median home range size (0.9 ha) and maximum distance reached from home (79 m) of urban cats (Hanmer et al. 2017*a*) and Magpies that seldom collect food for their nestlings further than 75 m from their nest trees (Högstedt 1980).

Statistical methods

We checked for possible differences in the local-scale (nest-level) background variables between the land-sharing and land-sparing urban development types by using the estimated marginal means of each variable and statistical modeling with maximum likelihood estimates. Because of our multilevel hierarchical study design, we used city (n = 9 cities) as a random factor and square (n = 87 squares) was nested within city. We used a generalized linear mixed-effects model (GLMM) to analyze artificial nest survival. Nest survival was coded as 1 for surviving nests and 0 for predated eggs (i.e., binomial distribution), and the survival of nests at each survey point was modeled using a binary logistic regression analysis.

First, we ran single-variable models (Table 2). We included urban development type (land-sharing vs. land-sparing) as a fixed factor and one of the several additional continuous (survey-level) covariates (number of pedestrians, number of cats, number of corvids, total number of breeding birds, relative abundance of ground nesters of the total number of breeding birds within 50 m from an artificial nest, and visibility score). Latitude (the mean point for each city) was also used as a continuous covariate in these models because it could be related to large-scale changes in nest survival (McKinnon et al. 2010). Second, we ran additive logistic regression models (Table 3) using a similar model design as that described for single-variable models but also adding multiple survey-level covariates simultaneously.

We used the total data set (n = 554 nests) for the logistic regression models. Before performing any multivariate logistic regression analyses, we explored the possible multicollinearity between continuous covariates with Pearson correlation coefficient tests. The Pearson correlation coefficients were between −0.42 and 0.50 for all paired comparisons. These correlations were clearly under 0.6, therefore minimizing concerns regarding collinearity problems in our data set (Tabachnick and Fidell 2001). We checked each logistic regression model for overdispersion, but the deviance/residual degrees of freedom ratio were always near 1, indicating no problems with overdispersion.

The models were fitted by the maximum likelihood method using the lme4 package in R (Bates et al. 2014). The selection of the best model was based on Akaike's information criterion (AIC) (Burnham and Anderson 2002), which was used to rank the candidate models and to select the models that best explained the variation in the data (Burnham and Anderson 2002). Models with $\Delta AIC \leq 2$ were considered to be equally supported (Burnham and Anderson 2002). The confidence intervals for the significant variables included in the best model were calculated by the maximum likelihood method with the lme4"package in R.

We estimated differences in species richness between LSP and LSH type of habitat with a GLMM. We calculated GLMM with link function Poisson because number of species was used as a dependent variable. We included urban development type (land-sharing vs. land-sparing) as a fixed factor. Because of our multilevel

TABLE 2. Generalized linear mixed models for the artificial nest predation experiment (binary variable: 0 = predated, 1 = not predated) over 30-d periods of exposure for all studied European cities combined.

	Parameter estimates		Model test (df = 1)			
Model	*I*	Variable	χ^2	*P*	AIC	(ΔAIC)
Cats	−1.47 (0.46)	−0.90 (0.41)	5.82	**0.019**	555.3	(0.0)
UDT	−1.88 (0.51)	0.62 (0.27)	5.01	**0.025**	556.1	(0.8)
Corvids	−1.34 (0.47)	−0.16 (0.08)	4.86	**0.028**	556.2	(0.9)
%Ground	−1.69 (0.47)	1.37 (0.82)	2.70	0.100	558.4	(3.1)
Visibility	−1.22 (0.53)	−0.18 (0.12)	2.27	0.132	558.8	(3.5)
Latitude	−4.26 (2.57)	0.05 (0.05)	1.13	0.288	560.0	(4.7)
Pedestrians	−1.54 (0.49)	−0.00 (0.01)	0.29	0.590	560.8	(5.5)
Tbirds	−1.58 (0.49)	−0.00 (0.01)	0.01	0.952	561.1	(5.8)

Notes: Predictor variables were urban development type (UDT, two categories: land-sparing and land-sharing as a reference category) and nest visibility score, number of cats, number of corvids, number of pedestrians, latitude, total number of individuals (Tbirds), and proportion of ground-nesting birds of the total number of birds (%Ground). In the models, city was used as a random variable and square was nested within city. Estimated parameter values for the intercept (*I*) and predictor variables are shown with SE in parentheses and are printed in boldface type if they differed from zero ($P < 0.05$). The adequacy of each model was tested by the goodness-of-fit test (χ^2) and AIC (Akaike's information criterion), and ΔAIC ($=AIC_{initial} - AIC_{min}$) values are presented. The model with the lowest AIC is considered to be the best model among all tested models.

Table 3. Twelve best (ΔAIC < 2.0 with respect to the best-fitting model) generalized linear mixed models for the nest survival experiment (binary variable).

Model	AIC	ΔAIC
UDT + Cats + Corvids + Visibility	549.6	0.0
UDT + Cats + Corvids + Visibility + %Ground	549.8	0.2
UDT + Cats + Corvids	550.2	0.6
UDT + Cats + Corvids + %Ground	550.8	1.2
UDT + Cats + Corvids + Visibility + Latitude	550.8	1.2
UDT + Cats + Corvids + Visibility + Pedestrians	550.9	1.3
UDT + Cats + Corvids + Visibility + %Ground + Pedestrians	551.2	1.6
UDT + Cats + Corvids + Visibility + %Ground + Latitude	551.3	1.7
UDT + Cats + Corvids + Latitude	551.4	1.8
UDT + Cats + Corvids + Pedestrians	551.6	2.0
UDT + Cats + Corvids + Visibility + Tbirds	551.6	2.0
UDT + Cats + Corvids + Visibility + %Ground + Tbirds	551.6	2.0

Notes: The included predictor variables were urban development type (UDT), nest visibility score (Visibility), number of cats (Cats), number of corvids (Corvids), number of pedestrians (Pedestrians), latitude, total number of individuals (Tbirds), and proportion of ground-nesting species among all bird species (%Ground). City was always used as a random variable in these models. The adequacy of each model was tested by AIC (Akaike's information criterion), and ΔAIC (=$AIC_{initial} - AIC_{min}$) values are also presented. The model with the lowest AIC is considered the best model of all the tested models.

hierarchical study design, we used city (n = 9 cities) as a random factor and square (n = 87 squares) was nested within city. All statistical tests were performed with R version 3.4.1 (R Development Core Team 2017).

Results

Species richness did not differ between the land-sparing (5.5 ± 3.4 [mean ± SD], n = 269) and land-sharing (5.7 ± 2.6, n = 285) urban development types (GLMM, χ^2 = 0.131, df = 1, P = 0.717). Urban development type was included in both the single-variable models (Table 2) and the 12 best (ΔAIC ≤ 2) additive models explaining nest survival after a 30-d period of exposure (Table 3). Nest survival was lower in land-sharing than in land-sparing urban areas (Table 1). According to the single-variable models, nest survival decreased with the number of corvids and cats and was greater in the land-sparing vs. land-sharing development type (P < 0.05; Table 2).

The additive logistic regression analysis showed that the best-fitting model (ΔAIC = 0.0) explaining nest survival included urban development type, nest visibility, and the number of cats and corvids (Table 3). Eleven additional models included the same variables as the best model. The proportion of ground nesters was included in the second-best model. As in the case of the single-variable models, the additive models show that nest survival decreased with the number of cats and corvids and was lower in land-sharing than in land-sparing urban areas (Table 3). Furthermore, nest survival was negatively related to nest visibility and positively associated with the proportion of ground-nesting birds (Table 3).

Although the number of corvids, number of cats, and nest visibility did not differ between the land-sparing and land-sharing urban development types (Table 4), the predicted probability of ground nest survival was greater in the land-sparing than in the land-sharing urban development type in association with a given number of corvids (Fig. 2a), number of cats (Fig. 2b) and nest visibility (Fig. 2c). The relative abundance of ground-nesting individuals was greater in the land-sparing than in the land-sharing urban development type (Table 4; Fig. 3).

We analyzed separately the possible role of green cover in a study square on nest survival and total abundance of birds, proportion of ground-nesting birds, corvids, and cats. Based on the logistic regression analysis, the amount of green area did not affect nest survival (χ^2 = 2.381; df = 1, P = 0.123). However, the amount of green area affected positively on the proportion of ground nesters (r_S = 0.327, P < 0.001, n = 554), but negatively on the total abundance of birds (r_S = −0.251, P < 0.001, n = 554), cats (r_S = −0.131, P < 0.002, n = 554) and corvids (r_S = −0.084, P = 0.048, n = 554).

We also checked whether the location of nests (within, edge, or outside of a large green area) within a land-sparing square influence nest survival. Nest survival did not differ between nest locations (within green area 32.3% [n = 99]; edge area 34.2% [n = 76]; and outside of the green area 24.5% [n = 94]; χ^2 = 2.11, df = 2, P = 0.348).

Discussion

Our large-scale experimental study offers the first evidence that ecological mechanisms (i.e., predator–prey interactions) can change between the two extreme urban development types and provides novel insight into the causes of within-city changes in abundance of urban-sensitive species. Our findings showed clear differences

TABLE 4. Estimated marginal means of the local (nest-scale) covariables used in our nest survival models for land-sharing (LSH) and land-sparing areas (LSP) in European cities.

	Estimated marginal means				Statistical model maximum likelihood estimates		
	LSH		LSP				
Variable	Mean	SE	Mean	SE	χ^2	df	*P*
Visibility	1.95	0.16	2.09	0.16	3.10	1	0.079
Pedestrians	13.48	5.48	12.86	5.49	0.14	1	0.713
Cats	0.18	0.07	0.16	0.07	0.50	1	0.480
Corvids	1.71	0.46	1.50	0.46	0.86	1	0.353
Tbirds	11.87	2.20	12.98	2.22	0.739	1	0.390
%Ground	5.0	3.1	10.0	3.1	20.55	1	**<0.001**

Notes: Variables are nest visibility score (0 = not visible to 4 = totally visible), number of pedestrians, number of cats, number of corvids, total number of birds, and percentage of ground-nesting species of the total number of bird species. The variable city was used as a random factor in the model. Statistically significant differences are shown in boldface type.

in nest predation pressure between land-sharing and land-sparing areas, thus suggesting that the urban-associated alteration of critical selection pressures, such as nest predation (Tomialojć 1982, Eötvös et al. 2018) is not homogeneous in city landscapes, potentially explaining the variability in the results found in previous local-scale studies (e.g., Vincze et al. 2017). Moreover, our results indicate that urban planning (i.e., the urban development type) plays a crucial role in affecting nest survival among urban birds, with land-sparing areas favoring a higher survival probability of ground nests.

Earlier studies have suggested that land-sparing development will benefit urban biodiversity over land-sharing development among different taxa, including plants (Collas et al. 2017), arthropods (Soga et al. 2014), mammals (Caryl et al. 2016, Villaseñor et al. 2017), and birds (Sushinsky et al. 2013). In agreement with this suggestion, we found that the relative abundance of ground nesters was higher in land-sparing areas. Eleven of the 23 ground-nesting species in the study were found exclusively in land-sparing and not in land-sharing areas, and all were native species (Appendix S1; Table S1). In addition, of the two ground-nesting species found in "land-shared" but not "land-spared" areas, one (*Alopochen aegyptiacus*) is nonnative in Europe (Appendix S1; Table S1). Sustaining abundance or richness in the "spared" areas may in part be reliant on movements of individuals between them (a metapopulation model), and both theory and empirical evidence suggests the matrix of habitat between the shared areas can be vital for this movement (Pearson 1993, McGarigal and McComb 1995, Jokimäki and Huhta 1996). Thus, shared land may at least partly help support the animals observed in spared land in cities.

Birds might avoid breeding in areas with high predation risk (Suhonen et al. 1994), or these areas might be sink habitats for their populations. Future studies should analyze whether land-sparing areas truly promote an increase in avian fitness over land-sharing urban areas or whether they act as ecological traps for ground-nesting bird species. Interestingly, even though urban land-sharing areas host avian communities containing a smaller proportion of ground-nesting species, the total abundance of birds did not differ between the land-sparing and land-sharing urban development types (Table 4). This suggests that other species, such as cavity nesters, with protected nest sites in urban areas (Stracey and Robinson 2012*b*), may experience lower nest predation rates in land-sharing areas in European cities, compensating for the negative effect on ground nesters. It has also been suggested that the most abundant threatened bird species in European towns are cavity nesters, probably because the main urban nest predators, corvids, are not able to predate cavity nests (Jokimäki et al. 2018). Additional studies focused on a functional approach (e.g., guilds affected differently by nest predation and urban predators) would be extremely useful for advancing our knowledge in this respect.

Furthermore, the experimental part of our study found a parallel pattern in nest survival (i.e., higher in land-sparing urban areas) to that found for ground-nesting communities (see also Roos et al. 2018), which strongly suggests that nest predation can be the mechanistic cause of the observed changes in avian communities between these two urban development styles. Predation is the dominant cause of nesting failure in many bird species (Ricklefs 1969) and is acknowledged to be an important driver determining avian community structure and avian life history evolution (Martin 1988, 1995). Our findings match previous studies using nest predation to explain the higher density of urban birds (Tomialojć 1978, Møller and Díaz 2017*b*) and the decrease in the abundance of ground-nesting species with urbanization (Clergeau et al. 2006, Croci et al. 2008, Jokimäki et al. 2016), which seems to be associated with the higher vulnerability of ground nesters to avian nest predators, such as corvids (Gregory and Marchant 1996, Jokimäki and Huhta 2000, Marzluff et al. 2001*b*, Sorace 2002, Stracey and Robinson 2012*b*). In rural environments, indices of corvid abundance have typically been associated with higher overall avian nest failure rates (Andrén 1992). However, while some

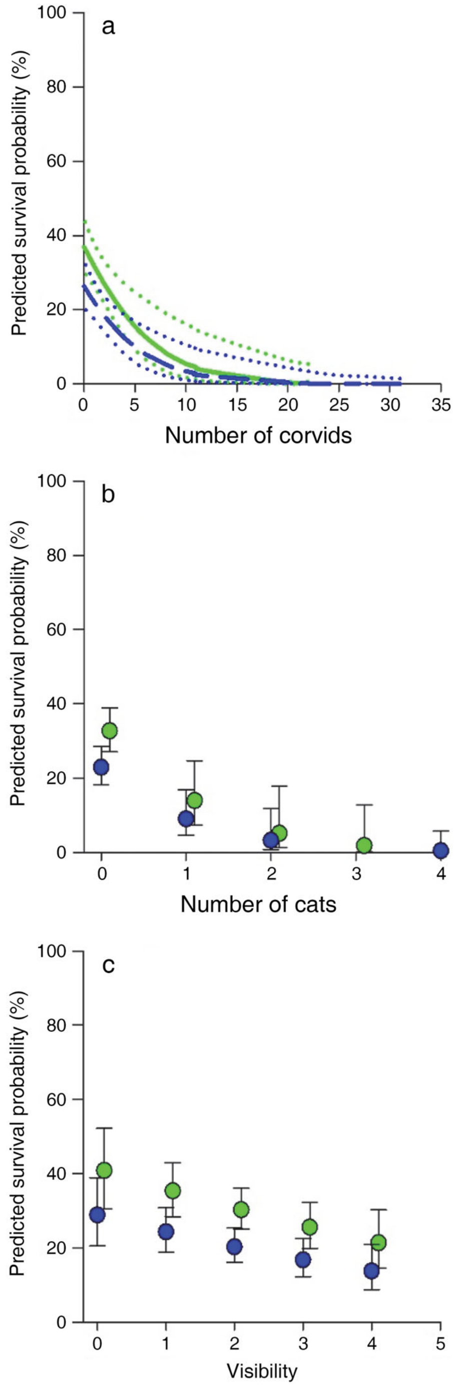

Fig. 2. (a) Predicted probability of nest survival estimated by the logistic regression model in land-sharing (dashed blue line) and land-sparing areas (continuous green line) in relation to the number of corvids. Dotted lines indicate 95% confidence intervals. (b) Predicted probability of nest survival estimated by the logistic regression model in land-sharing (blue dots; mean and 95% confidence intervals) and land-sparing areas (green dots) in relation to the number of cats. (c) Predicted probability of nest survival estimated by the logistic regression model in land-sharing (blue dots; mean and 95% confidence intervals) and land-sparing areas (green dots) in relation to the nest visibility index (0 = not visible to 4 = totally visible).

authors argue that corvids are major nest predators in cities (Groom 1993, Major et al. 1996, Matthews et al. 1999, Jokimäki and Huhta 2000), others indicate that this is not necessarily the case (Marzluff et al. 2001*b*, Borgmann and Rodewald 2004, Stracey 2011). Cats and squirrels are also highly abundant in many cities (Sorace 2002), and two recent reviews indicated that domestic cats are responsible for the majority of the predation pressure in urban environments (Kauhala et al. 2015, Eötvös et al. 2018). However, our results, despite supporting the importance of both corvids and cats in nest survival, do not show differences in corvid or cat abundance between the land-sharing and land-sparing urban areas and therefore do not indicate a direct link between these nest predators and the differential nest predation rate. According to Marzluff et al. (2007) correlation between nest predator abundance and nest predation is scale dependent. However, it is also possible that nest searching efficiency of predators may differ between land-sharing and land-sparing urban areas as even local vegetation composition may change it as indicated by Borgmann and Rodewald (2004).

Several authors have suggested that even if predator numbers tend to increase with urbanization (e.g., Sorace 2002), nest predation pressure will decrease as urbanization increases, suggesting the existence of a predator paradox (Shochat 2004, Rodewald et al. 2011, Fischer et al. 2012). This paradox might be due to differences in nest predator activities or nest-searching efficiencies by urban and nonurban predators. For instance, it has been experimentally shown that some nest predators, such as Eurasian Magpies and gray squirrels (*Sciurus carolinensis*), are frequent visitors to bird feeders and that this attraction effect increases the nest predation rate around feeding sites (Hanmer et al. 2017*b*). Land-sharing urban areas, which typically include private houses with gardens, present a higher abundance of bird feeders (Tryjanowski et al. 2015), which could therefore explain the higher rates of nest predation in these areas despite no differences in avian nest predators. Another important characteristic associated with land-sharing urban

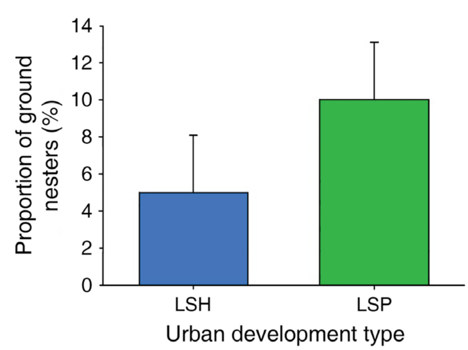

Fig. 3. Percentage (+ SE) of ground-nesting individuals from the total number of individuals in land-sharing (LSH; blue filling) and land-sparing (LSP; green filling) development types for all studied European cities combined.

areas, the fragmentation of green areas, might also be responsible for these results by affecting the nest predator searching efficiency. Several studies have indicated that the nest predator assemblages and predation rates increase with decreasing patch size and an increasing amount of edges (e.g., Møller 1988, Andrén 1992, Chalfoun et al. 2002).

Contrary to our prediction, human disturbance does not seem to predict nest survival in European cities, which also contrasts with previous findings (Jokimäki et al. 2005). It is possible that the protective effect of human presence (Ibáñez-Álamo et al. 2012, Møller and Díaz 2017*a*, *b*) due to the higher disturbance to large-sized predators than to smaller-sized prey in both land-sharing and land-sparing areas is intrinsic to urban habitats and is not influenced by urban landscape organization. However, as we predicted, nest visibility seems also to determine nest survival. This confirms the potential key role that visual predators, such as avian nest predators (i.e., corvids), can play in nest failures among urban birds and at the same time provides useful information for the implementation of conservation actions to promote ground-nesting bird species in urban areas. While city planners and urban developers can implement such measures directly in land-sparing areas, private management of green areas in land-sharing urban areas suggest that working with citizens and private land owners will be crucial for the success of such practices where they are most needed (Belaire et al. 2014). The promotion of urban bird abundance and urban biodiversity in general is not only a matter of conservation concern but could also be useful for improving citizen well-being (Miller and Hobbs 2002, Lerman and Warren 2011, Lepczyk and Warren 2012).

The sparing-sharing debate is related to land allocation at a fairly large scale. However, our multiscale study identified effects at a variety of spatial scales. We observed some differences in nest survival rate between study towns and spared and shared types of study squares, and nest survival was dependent on nest visibility at the microhabitat level. Design of a private-house-gardens scale (study-point scale in our case) done by the homeowner may affect nest-site selection of ground-nesting bird species, whereas the design of a study-square or town scales done by the city planners may affect habitat use of large-sized species, like corvids (Hostetler 2001, Chong et al. 2019). Our results indicated that artificial nest survival was not related to the total amount of green area of the study square, however, nest survival decreased with the nest visibility, indicating the important role of small-scale vegetation cover for the ground-nesting bird species. We also detected that the amount of green area positively affected the proportion of ground nesters. However, the total abundance of birds, cats, and corvids were negatively related to the amount of green area cover. Highly urbanized areas associated with a lower green cover generally have a high total density of birds partly due to the great number of urban exploiters (Blair 2001, Jokimäki et al. 2018), such as sparrows and doves. However, less urbanized areas with a greater green cover offer more suitable nesting sites and niches for the ground-nesting bird species. We did not find any differences in nest survival of nests located within a large green area, edge area, or outside of the large green area located in the land-spared study squares. Apparently, the fragmentation level of green areas in cities is so high even in land-sparing study squares, that we did not detect any edge effect in nest survival rate.

As with all ecological studies, this study has some limitations. Our work relies on the use of artificial nests with quail eggs. However, it is not sure if artificial nests are sufficient to measure natural nest predation, e.g., due to lack of parental care and nestling activity in artificial nests and the relatively large size of quail or hen eggs that are normally used in artificial nest experiments (e.g., Haskell 1995). Some studies have observed a similar nest fate between natural and artificial nests (e.g., Yahner and DeLong 1992, Hoset and Husby 2019), whereas others have reported either lower (e.g., Roper 1992) or greater (e.g., King et al. 1999) nest losses of artificial than natural nests. However, we were interested in differences in *relative* nest predation pressure between two urban development types rather than in measuring nest losses accurately. In addition, our main nest predators, corvids and cats, had no problems consuming quail-sized eggs used in this study. Therefore, the use of artificial nests to get sufficient sample size with similar nest and sampling design would be acceptable in our case. Our nest predator surveys were conducted after sunrise, therefore, sampling of nocturnal nest predators was not the best possible. However, because the majority of nest predators in European cities are day-active corvids (e.g., Jokimäki and Huhta 2000, Czyzowski et al., 2009), we suppose that undersampling of nocturnal nest predators does not have a serious effect on our results. One shortcoming in our study design was that we did not identify predators responsible for nest losses, e.g., by using cameras or clay eggs. Our earlier results, based on clay eggs, from one of our study towns, Rovaniemi (Finland), indicated that corvids are the main nest predators in European cities (Jokimäki and Huhta 2000). However, it might be possible that the main nest predators differ between the land-spared and land-shared town areas (Jokimäki and Huhta 2000). Our assessment was done in European cities, and therefore our results are not directly applicable for tropical cities with different nest predator assemblages. The main purpose of this study was not to investigate general biodiversity patterns, but we think that our results about the relationship between disturbance-sensitive species and land-development types will also help managers to develop biodiversity-friendly cities.

In conclusion, urban planning can influence predator–prey interactions, with land-sharing areas promoting the lower survival of ground nests. This increase in nest predation, which is related to the differences in ground-nesting bird abundance, strongly suggests that predation pressure could explain the differences in abundance of disturbance-sensitive bird species between land-sharing and land-sparing urban areas. Future studies in other geographical areas and taxa are required before generalizing the importance of predation pressure in determining within-city biodiversity, but our findings offer a new approach for investigating the eco-evolutionary effects of urban planning and are in line with recent recommendations highlighting the importance of using more mechanistic studies in the urban context (Shochat 2004, Rodewald et al. 2011, Lepczyk et al. 2017, Marzluff 2017). Finally, our results highlight an important threat faced by wild organisms during the urbanization process and provide some new insights that can help implement specific conservation measures to balance urban development and biodiversity conservation.

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Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.2049/full

Data Availability

Data are available from ResearchGate: https://doi.org/10.13140/rg.2.2.33740.16002