Contrasting effects of urbanization on arboreal and ground-dwelling land snails: Role of

trophic interactions and habitat fragmentation

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Abstract

Urbanization generally reduces wildlife populations. Individual species responses, however, are often highly variable, and such variability can be explained by differences in species ecological traits. To examine this hypothesis, we focused on two co-occurring land snails, *Ezohelix gainesi* and *Euhadra brandtii sapporo*; the former is ground-dwelling and the latter is arboreal. We first estimated their population densities at nine sites distributed along an urbanization gradient: three were located in continuous natural forests, three at the edge of natural forests, and the rest in small isolated forests in urban areas. As a result, the ground-dwelling *E. gainesi* occurred at highest density in urban forests, followed by forest edges and continuous forests. By contrast, the arboreal *E. b. sapporo* occurred at highest density in continuous forests, but declined in forest edges and urban forests. We then conducted manipulative field experiments to quantify changes in predation pressure on these species. Ground-tethered *E. gainesi* and *E. b. sapporo* were repeatedly predated upon by forest-living mammals in continuous forests, but their survival rates increased in forest edges and urban forests. By contrast, canopy-tethered *E. b. sapporo* maintained high survival rates in all three forest types. The results indicate that a lack of mammalian predators enables ground-dwelling species to occur at high densities in urban forests, whereas the arboreal species was not affected by this predator relaxation effect. The combination of species-specific behavioural traits and changes in predator communities across an urbanization gradient has important effects on the biodiversity of urban ecosystems.

INTRODUCTION

Natural ecosystems are increasingly being affected by anthropogenic disturbances, and

urbanization is among the most impactful of these disturbances. Habitat loss and

fragmentation in urbanized areas promote local extinction (McKinney 2002; Marzluff 2005),

declining species richness (Miyashita et al. 1998; Martinson and Raupp 2013), increasing

populations of synanthropic and non-native species (Riley et al. 2005; Shochat et al. 2010),

and reduction of beta diversity or homogenization (Horsák et al. 2013; Hodges and McKinney

2018). Anthropogenic disturbances create drier and warmer environments (Gallo and Owen

1999; Kalnay and Cai 2003; Yang et al. 2017), and species sensitive to those changes (e.g.,

lichens and mosses) are known to develop markedly different communities in urban versus

non-urban areas (Lättman et al. 2014; Oishi 2018). Recent studies have demonstrated that

land-use changes have a large influence on functional diversity, which is closely related to

ecosystem services (Kissick et al. 2018).

Numerous studies have demonstrated that urbanization has tremendous effects on

biodiversity. Yet the actual mechanisms regulating these effects are poorly understood (Faeth

et al. 2005; Shochat et al. 2006, 2010; Fischer et al. 2012; El-Sabaawi 2018). In general,

species are highly variable in their response to anthropogenic disturbances (e.g., Patten and

Bolger 2003; Gagné and Fahrig 2011; Saito and Koike 2013; Ehlers et al. 2018). Many

species populations decline with increasing urbanization, but some species populations

actually increase (Hansen et al. 2005; McDonnell and Hahs 2008). We predicted that such

variability could be explained by differences in species' ecological traits. Species' responses to urbanization are often closely related to changes in predator–prey interactions (Gering and Blair 1999; Shochat et al. 2006; Ritchie and Johnson 2009; Rodewald et al. 2011; El-Sabaawi 2018). Loss of top-down control and release of prey populations are a common trophic consequence of land-use change (Crooks and Soulé 1999; Faeth et al. 2005; Fischer et al. 2012). However, this mechanism may not be applicable to certain functional groups; for example, two closely-related species may respond differently to land-use change because of differences in their anti-predator behaviours.

To examine this hypothesis, we investigated the effects of urbanization on two co-occurring land snails, *Ezohelix gainesi* and *Euhadra brandtii sapporo*; the former is ground dwelling and the latter is arboreal (Saeki et al. 2017a). We selected these species because they have differing behavioural traits that may trigger different ecological processes following anthropogenic disturbances. One of these processes, predator–prey interaction, is often difficult to quantify in the field, with the exception of a few bird studies that use artificial nests (Gering and Blair 1999). However, land snails' slow movement and low sensitivity to close human observation allow us to record predation rates in detail. The two snail species in our study are found predominantly in the same regional landscape of southern Hokkaido, Japan, which is severely affected by forest fragmentation and the introduction of non-native species. We took advantage of these regional characteristics to quantify changes in predator–prey interactions along a gradient of urbanization.

Although there has been increased interest in biodiversity–urbanization relationships in recent years, the available literature is biased towards vertebrate studies, especially birds (Ritchie and Johnson 2009; Gagné and Fahrig 2011). Yet invertebrates represent a majority of animal diversity (Groombridge and Jenkins 2002) and have distinctive ecological functions (Mason 1970; Kissick et al. 2018). Moreover, molluscs are important conservation targets because of their high diversity, large number of extinction records (Lydeard et al. 2004), and ability to be used as ecosystem indicators due to their limited dispersal ability (Hodges and McKinney 2018).

Our general objective was to identify the effects of urbanization on two ecologically-distinct land snails with a special focus on predator–prey interactions. Our specific objectives were to (i) compare the spatial distribution of arboreal and ground-dwelling land snails in continuous forests and forests that have been highly fragmented by urbanization, (ii) use manipulative field experiments to examine the effects of predation, or top-down control, on snail abundance, and (iii) analyse the relationship between species occurrence and predator communities along an urbanization gradient.

METHODS

Study area

Field studies were conducted in Tomakomai city, Hokkaido, Japan. Our study region covers latitudes of 42.64–42.71°N and longitudes of 141.55–141.70°E with an elevation range of 7–

128 m (Table 1, Fig 1). We used nine study sites in this region: three were located in large, continuous natural forests, three at forest edges, and three in small isolated forests in urbanized areas (hereafter 'continuous forests', 'edge forests', and 'urban forests', respectively). The forest area of continuous, edge, and urban forests ranged from over 50 km^2 (continuous forests) to less than 0.1 km^2 (urban forests) (Table 1). Data obtained from aerial photographs (provided by the Geospatial Information Authority of Japan) show that there was relatively little fragmentation of edge and urban forests until the 1950s. These forests were gradually fragmented and or converted to residential and industrial areas in the 1970s to 2000s. Of our nine sites, Itoi (ITO), Takuyuu (TKU), and Numanohata Centre (NUC) are managed by local governments, Uenae (UEN), Futou (FUT), and Numanohata South (NUS) are owned by private companies, and Horonai River (HOR), TOEF-North (TOE), and Takaoka (TAK) are located in the Tomakomai Experimental Forest, which is owned by Hokkaido University (TOEF).

The climate of our study area is characterized by cool summers and cold winters. Maximum winter snow depth ranges from 20 to 50 cm. There was little pre-existing microclimatic data for our study sites; instead, we conducted our own monitoring of temperature at the forest floor (just below the litter layer, height = 0 m; TidbiT, Onset, Bourne, MA, USA) and in the canopy (height = ca. 6–8 m; HOBO U23 Pro v2, Onset), and measured canopy relative humidity at 4-h intervals from November 2017 to October 2018. Mean annual ground and canopy temperatures were 8.1–8.8 °C and 6.7–8.0 °C, respectively, and mean

annual canopy relative humidity was 78.9–85.2% (Supporting Information 1). Mean annual

temperature differed between canopy positions (canopy vs. ground) and also among the three

forest types (Supporting Information 2). These differences were small in magnitude, however

(<0.5 ºC). Relative humidity differed among the three forest types in summer ($F = 20.7$, $P =$

0.002), but did not differ in winter ($F = 1.54$, $P = 0.29$). Again, these differences were small in

magnitude (< 4%).

Our study area is situated within the cool-temperate deciduous forest zone. Dominant tree

species are *Quercus crispula*, *Acer pictum*, *A. amoenum*, and *Magnolia obovata*. The

topography is generally flat, with no steep slopes. The soil originates from volcanic ash,

which was deposited when Mt. Tarumae, located approximately 20 km away from the area,

erupted about 330 years ago.

Density of land snails

To estimate the population density of *E. gainesi* and *E. b. sapporo*, we counted the number of

individuals per unit land area in ground litter from 24 to 30 October 2017 at our nine study

sites. We conducted our investigation during this period because we found in previous

research that arboreal *E. b. sapporo* move to the ground in late fall and stay there until the

following spring (Saeki et al. 2017a). We established three 5.4 × 5.4 m plots at each study site

and recorded the number of living individuals and dead shells in the ground litter. Surveys

were conducted by two to four persons, and sampling effort was maintained at approximately

30 minutes/person/plot. *Ezohelix gainesi* and *E. b. sapporo* were the two most dominant land snails in our sample, and all the other snail species we found at our study sites were <5 mm in shell diameter. Relationships between forest type and *E. b. sapporo* and *E. gainesi* abundance were examined using a generalized linear model (GLM) constructed using the statistical software JMP 9.0 (SAS Institute, Cary, NC, USA).

Predation pressure

To quantify predation pressure at continuous, edge, and urban forests, we performed two manipulative field experiments. The first experiment was conducted from 24 August to 7 September 2017 (hereafter referred to as '2017-fall'), and the second was from 29 June to 12 July 2018 (hereafter referred to as '2018-summer'). In the first experiment, we collected 96 *E. b. sapporo* and 48 *E. gainesi* in a natural forest in the TOEF. We selected adult-sized individuals of shell diameter 20–27 mm for *E. b. sapporo* and 25–40 mm for *E. gainesi*. Sample collection was conducted over 2 days, and we brought the collected individuals alive to a laboratory at the TOEF. Then, an approximately 50-cm long string (Kevlar, diameter 0.25 mm) was tied around the shell of each snail, and a numbered label was also glued to the shell. A previous study (Saeki et al. 2017a) indicated that this treatment has little effect on snail survival and allows reasonably free movement within a radius equal to the length of the string. Attachment of strings and number labels was completed within 24 h after collection, and the snails were stored at room temperature for another 12–36 h until the first day of the

manipulative field experiment.

The first experiment in 2017-fall was performed at six study sites: three continuous forest sites, two edge forest sites, and one urban forest site (Table 1, Fig 1). We conducted this experiment at a relatively limited scale (i.e., six sites) to grasp the general trend of species occurrences in Tomakomai city along a gradient of forest fragmentation and urbanization. At each site, we selected one *Q. crispula* tree to serve as the location for the manipulative field experiment. For all selected trees, diameter at breast height was ca. 20–50 cm and tree height was ca. 15–20 m. Individual snails that had been collected and prepared as described above were brought to each site. For each selected tree, eight *E. b. sapporo* were tethered to the trunk at a height of 5–10 m, and eight were tethered on the ground. Eight *E. gainesi* were also tethered on the ground. We did not tether *E. gainesi* to tree trunks because mature individuals of this species are almost completely ground dwelling. Canopy-tethered *E. b. sapporo* were placed at least 0.5 m apart, and ground-tethered *E. b. sapporo* and *E. gainesi* were placed ca. 3–5 m apart.

Infrared camera trap (HGC SG-007, Shenzhen Siyuan Digital Technology, Dongguan City, China) were set up at each study tree to record predation events. One was placed in the crown of the study tree to monitor one of the eight individuals in the canopy treatment. The others were positioned to monitor individuals on the ground. The number of cameras on the ground was one to three per study tree depending on the availability of camera devices and batteries. After preparing this set-up, we visited the study trees every 1–3 days and noted whether each

of the total 144 land snails (i.e., 96 *E. b. sapporo* and 48 *E. gainesi*) was dead or alive. Because it took 2 days to place these snails in the field, we started the experiment 1 day earlier for two-thirds of the samples (i.e., four study sites), followed by the remaining one-third (i.e., two study sites) the next day. Canopy access was achieved by using single-rope techniques (Ishii 2000; Lowman et al. 2012).

In the first experiment, a clearly different survival trend was perceived across an urbanization gradient (see Results). Thus, we decided to perform the second experiment with a larger sample size by adding one edge and two urban forest sites. The total sample size was therefore 144 for *E. b. sapporo* and 72 for *E. gainesi*. The experimental procedure was similar to the one in the first experiment (Table 1). This second experiment (2018-summer) also enabled us to examine species responses in a different season from that of the 2017-fall experiment.

After the experiments, survival curves were constructed using the Kaplan–Meier method and compared by a log-rank test for each pair (Fox 2001) by using the statistical software JMP 9.0 (SAS Institute). Because of the small sample size (eight individuals) for each tree and the similarity of survival curves among the study trees within each treatment, data from the trees in the same treatment (i.e., land snail species × forest type) were pooled in the analysis. A few individuals escaped from the string during the experiment, and we treated them as "censored" in this model. When a land snail was found dead, the cause of death (predation or otherwise) was inferred from the available data.

Predator community

Four pitfall traps (9 cm in diameter, 12 cm in depth, without bait or preservatives) were placed approximately 20 m from the study tree during manipulative field experiments at each study site to identify the species composition of ground-dwelling beetles, which are putative predators of our two land snail species. The traps were opened for 12 days during both the 2017 and 2018 experiments. Invertebrates that fell into the traps were collected every 3 days, identified and counted in situ, and then released several metres away from the traps. Although a wide range of ground-living invertebrates was captured in the traps, we focused on carabine beetles (Carabidae: Carabinae) because this taxon contains specialists that consume land snails; their predation was also confirmed in the laboratory (S. Niwa, unpublished data).

In addition to the pitfall traps, we performed camera-trap surveys to identify putative mammal and bird predators. Animal sensor cameras were set up during the manipulative field experiments at each site as described above, as well as before and after the experiments. Camera-trap monitoring was conducted from 24 August to 26 October in 2017 and from 29 May to 27 September in 2018. These data were used to estimate mammalian and avian community differences among study sites. One camera, which was used in the canopy before and after the experiment, was excluded from the analysis because the frequency of animal detection was quite low (only 18 detections during the entire study period).

Species composition data obtained by the pitfall and camera traps were collated into a

matrix of site × species information, respectively. Then, we ran a non-metric

multidimensional scaling (NMDS) analysis to visualize predator–community changes with

urbanization. We used Bray–Curtis dissimilarity as a distance measure. The analysis was run

by using the package vegan (Oksanen et al. 2019) in R 3.5.2 (R Core Team 2018). All

experiments and sample collection procedures were performed in accordance with the

Institutional Policy on Animal Experimentation of the University of Tsukuba.

RESULTS

Density of land snails

The population density of arboreal *E. b. sapporo* and ground-dwelling *E. gainesi* differed

among our study sites (Fig 2). The density of *E. b. sapporo* was highest at site HOR followed

by TOE, both of which are located in continuous forests, and decreased markedly with forest

loss and fragmentation; it was low or zero in edge sites, and zero at all three urban sites. This

pattern was reversed with *E. gainesi*. Its density was lowest in continuous forests but

increased in edge forests, and was highest at site NUS, which is located in an urban forest.

Our GLM analysis shows that *E. b. sapporo* and *E. gainesi* abundance differed significantly

among forest types (χ^2 = 117.78, df = 2, *p* < 0.0001 for *E. b. sapporo* and χ^2 = 280.55, df = 2,

p < 0.0001 for *E. gainesi*). We obtained similar patterns based on our count of dead shells

(Supporting Information 3).

Predation pressure

For both species, the survival rate of ground-tethered individuals differed significantly among forest types in the 2018-summer experiment; it was highest in urban forests and decreased in edge and continuous forests (Fig 3, Table 2a). A similar pattern was found in the 2017-fall experiment, although the differences were not statistically significant due to a relatively small sample size. By contrast, the survival rate of canopy-tethered *E. b. sapporo* did not differ significantly among forest types in either experiment. Survival rates were consistently high in all forest types in both years. When comparing between canopy and ground-tethered treatments, the survival rate of canopy-tethered *E. b. sapporo* was significantly higher than that of ground-tethered individuals in continuous forests in both years (Fig 3, Table 2b). Yet these differences became less conspicuous in edge and urban forests. In edge forests, canopy-tethered individuals survived more than ground-tethered individuals in the 2018-summer experiment but not in the 2017-fall experiment, and no statistical difference was detected in urban forests in both years. In terms of comparisons between species, the survival rates of ground-tethered *E. gainesi* did not significantly differ from those of *E. b. sapporo* across all three forest types in both years (Table 2).

Mortality events among ground-tethered *E. b. sapporo* and *E. gainesi* were mainly due to predation by ground-dwelling mammals (Fig 4). We attributed a predation event to ground-dwelling mammals in instances when the shell was broken or the string was cut and the sample disappeared. This inference is consistent with our camera-trap data, in which we

observed multiple instances of mammalian predation leading to this outcome. At least four ground-tethered land snails were predated upon by *Nyctereutes procyonoides*, and two were predated upon by *Vulpes vulpes*, across the two experiments (Supporting Information 4). The average incidence rate of broken shells in the 2017-fall experiment was 23% for ground-tethered *E. b. sapporo* and 46% for *E. gainesi* in continuous forests, followed by 0% and 31% in edge forests and 0% and 13% in urban forests (Fig 4), respectively. We obtained similar results in the 2018-summer experiment: the incidence of broken shells was highest in continuous forests for both species. Some ground-tethered *E. b. sapporo*, however, were found dead without any discernible shell damage. We observed a few cases of carabine beetles (both larvae and adults) eating the soft body of snails (Supporting Information 4). Thus, we assumed that some portion of the mortality events without discernible shell damage were due to predation by beetles. The survival rate of canopy-tethered *E. b. sapporo* was consistently high across all forest types, and our camera traps did not record any canopy predation events in the 2017-fall or 2018-summer experiments, although birds were occasionally observed in the canopy.

Predator communities

The species composition of carabine beetles, which are known to prey on land snails, changed along an urbanization gradient. *Carabus arboreus* and *Cychrus morawitzi* were the dominant carabine beetles in all forest types in the 2017-fall experiment (Fig 5a). In the 2018-summer

experiment, *Carabus albrechti* was dominant in continuous and edge forests whereas *Carabus granulatus* and exotic *Carabus insulicola* were dominant in urban forests. *Cychrus morawitzi* and *Carabus blaptoides*, both snail specialists, were found in all three forest types.

Camera-trap records show that the species composition of ground-dwelling mammals also differed along the urbanization gradient (Fig 5b). In total, we recorded four omnivores (*Nyctereutes procyonoides*, *Vulpes vulpes*, *Procyon lotor*, *Sciurus vulgaris*), one carnivore (*Felis catus*), and one herbivore (*Cervus nippon*). *Nyctereutes procyonoides* and *C. nippon* were frequently detected in continuous forests, but *V. vulpes* appeared in edge forests, and exotic *F. catus* and *P. lotor* were observed in urban forests. We also recorded three bird species on the ground, but their detection was limited to the urban forest sites.

Ordination analysis (NMDS) of carabine beetle communities revealed marked differences in species composition among forest types and seasons (Fig 6a). Urban sites were assigned lower scores on NMDS Axis 2, whereas edge and continuous sites were assigned higher scores. Seasonal gradients were also detected: community composition data from the 2017-fall experiment were assigned low Axis 1 scores and high Axis 2 scores. The autumn-breeding carabine species (*C. morawitzi*, *Carabus opaculus*, *C. arboreus*) were assigned low and high Axis 1 and Axis 2 scores, respectively, whereas the spring-breeders (*C. albrechti*, *C. insulicola*, *C. granulatus*, *Carabus conciliator*, *C. blaptoides*) generally had high and low scores.

Changes in mammalian and avian species composition were also clearly detectable along

an urban to continuous forest gradient (Fig 6b). The community composition in continuous

forests was assigned a low score along NMDS Axis 1, and the community composition of the

2017-fall data was assigned a higher score along Axis 2. The 2017 data for the urban site

TKU were not plotted on these coordinates because we did not record any mammal or bird

species during that year at the site. There were distinct differences between the mammal and

bird communities observed in continuous forests versus those in urban forests, and those in

edge forests were of intermediate composition (Figs 6a, b). Inter-site differences in species

composition were larger for mammals and birds than for carabine beetles.

DISCUSSION

Urbanization commonly alters trophic interactions (Faeth et al. 2005, Fischer et al. 2012), but

the direction and magnitude of this alteration has rarely been estimated empirically. In this

study, we investigated changes in the abundance, predation rate, and putative predator

community of two land snails along a gradient of forest fragmentation. This approach enabled

us to characterize their contrasting responses to urbanization.

The density of the ground-dwelling *E. gainesi* was highest in urban forests, followed by

edge forests, and was lowest in continuous forests. By contrast, the density of the arboreal *E.

b. sapporo* was highest in continuous forests and decreased markedly in edge forests, and the

species was completely absent in urban forests (Fig 2). The high density of *E. gainesi* in urban

forests was likely due to a lack of predators. Our manipulative field experiments demonstrate

that *E. gainesi* mortality is extremely low in urban forests, whereas many individuals were predated upon in continuous forests (Figs 3, 4). Ground-living mammals, such as *N. procyonoides* and *V. vulpes*, were the principal predators (Supporting Information 4). Predation events were repeatedly recorded by camera-trap monitoring, and many dead individuals were observed with damaged shells. We interpret these density and predation patterns as a typical case of prey-population release by reduction of top-down control in urbanized areas (Faeth et al. 2005, Fischer et al. 2012). Similar patterns also were observed for the arboreal *E. b. sapporo* when individuals were tethered to the ground, indicating that a reduction of predation pressure in urban areas probably applies to a wide range of large ground-dwelling snails.

This predator relaxation effect, however, was not seen in non-ground-tethered *E. b. sapporo*, which markedly decreased in population density along an urbanization gradient. Instead, the species' survival rate in the canopy remained high in all three forest types (Figs 3, 4), most likely because arboreality allows it to avoid predators in both urban and continuous forests. This suggests that canopy-dwelling land snails may be more sensitive to dispersal limitations caused by forest fragmentation. Fragmentation causes a loss of canopy habitat, and likely interferes with the horizontal movement of arboreal species. In fact, a previous investigation revealed extremely low *E. b. sapporo* density in clear-cut and conifer-plantation forests (Saeki 2015). Unfortunately, we were unable to determine whether the presence of *E. b. sapporo* at the urbanized sites (TKU, NUC, and NUS) pre-dated the current state of severe

forest fragmentation. One possibility is that the species was originally present at the sites, but was extirpated due to habitat fragmentation or environmental perturbation caused by urbanization. We observed the presence of exotic *P. lotor* in these urban sites using camera trap surveys (Figs 5, 6). Unlike native predators, this species is able to climb trees and prey on arboreal land snails (Saeki et al. 2017b). Although we did not record any predation events during this experiment (Fig 4), episodic predation by exotic species may have driven local extinction in the past. In our study area, urban sites were warmer and more humid than non-urban sites (Supporting Information 1 and 2). However, this difference in microclimate is not likely to have substantially affected snail survival rates because the differences were slight and likely within the range of inter-annual variation in this region. Similarly, bottom-up processes (i.e., differences in food availability) are unlikely to have accounted for the effect of urbanization, as we did not observe large differences in ground litter, epiphytic lichen, or canopy moss availability (Saeki et al. 2017a).

The species composition of carabine beetles, which prey on land snails, changed from urban to natural forests (Figs 5, 6). This shift appears to have had relatively little effect on land snail survival rates in both the 2017-fall and 2018-summer experimental periods. In *E. gainesi*, almost all of the mortality was associated with shell-breaking predation by ground-living mammals (Fig 4). This species is known to display a unique anti-predator behaviour, whereby it attacks predatory beetles by swinging its shell (Morii et al. 2016). In addition, juveniles of the species climb woody and tall herbaceous plants (Morii, personal

communication), which is also an effective strategy for avoiding ground beetles. These behavioural traits likely account for the lack of mortality from ground-beetle predation. However, we did occasionally observe dead ground-tethered *E. b. sapporo* with undamaged shells (Fig 4), which is an indicator of ground-beetle predation, and found one individual that had been predated upon by *C. blaptoides* (Supporting Information 4). These results indicate that there is some predation pressure from beetles on the ground, which may be sufficient to affect snails that do not possess anti-predator traits.

Relative to carabine beetles and birds, predation by mammals had the greatest effect on land snail survival rates (Fig 4). Although ground beetles are closely linked to land snails both in terms of ecological interactions and evolutionary history (e.g., Konuma et al. 2011, Morii et al. 2016), predation by terrestrial mammals may be more important than predation by ground beetles in anthropogenically-disturbed landscapes. Comparative studies of top-down controls from multiple predators are extremely limited. Our results provide more evidence that prey responses to predators are highly variable in complex food webs, thereby highlighting the importance of identifying key predators and their effects. Regarding the trophic dynamics of urban ecosystems, a phenomenon called the predation paradox has been discussed (Fischer et al. 2012). That is, vertebrate predator populations increase with urbanization at the same time that predation rates decline. We suspect that this paradox may not apply to either of the snails we studied here, as we did not find any evidence of an increase in predator populations in edge and urban forests (Fig 5).

SUMMARY AND MANAGEMENT IMPLICATIONS

We hypothesized that differences in ecological traits influence species' responses to urbanization. This hypothesis was supported by the results of our study on land snails. Arboreal species, such as *E. b. sapporo*, are able to avoid predation simply by virtue of their arboreal behaviour. Thus, predation is not a major factor in the urban and non-urban survival rates of this species. Instead, habitat destruction and dispersal limitation caused by forest fragmentation may be more important for population sustainability than trophic interactions. By contrast, ground-dwelling *E. gainesi* experienced a marked decline in predation pressure from continuous to urban forests. The species has strong anti-predator defences against beetles but not against terrestrial mammals, which had a substantial role in regulating its abundance. These contrasting responses imply that the combination of species' behavioural traits and changes in predator communities across an urbanization gradient can strongly affect biodiversity in urban ecosystems.

Biodiversity conservation planning is often discussed in terms of the presence and absence of species of concern. Yet changes in species interactions should be included more often in management planning. For example, connecting isolated urban forests to more natural, continuous forests not only helps avoid local extirpation of fragmentation-sensitive species, but also helps to restore more natural food-web networks. Complex trophic systems tend to prevent runaway population growth of a few prey species, thereby helping to maintain total

biodiversity and ecosystem services. Nevertheless, it remains difficult to generalize the effects of urbanization on wildlife populations (Gagné and Fahrig 2011). We encourage further study on a wider range of taxonomic groups as well as in different geographic regions.

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AUTHOR CONTRIBUTIONS

IS, SN, and NO designed research, collected and analysed data, and wrote the manuscript.

WA and TH collected data and revised the manuscript. All authors contributed critically the

drafts and gave final approval for publication.

Table 1. Location of study sites, including a list of field studies that were conducted at each site.

Site No.	Forest type	Site name (Abbreviation)	Lat. (°N)	Long. (°E)	Elevation (m)	Area (km^2)	Length of forest edge (km)	Density investigation	Manipulative field experiment (Fall-2017)	Manipulative field experiment (Summer-2018)
1	continuous	Horonai River (HOR)	42.69	141.57	71	>50	32	✓	✓	✓
2	continuous	TOEF North (TOE)	42.71	141.57	128	>50	32	✓	✓	✓
3	continuous	Uenae (UEN)	42.70	141.63	39	>50	32	✓	✓	✓
4	edge	Itoi (ITO)	42.64	141.55	29	0.37	3.6	✓	✓	✓
5	edge	Takaoka (TKA)	42.66	141.60	48	0.26	4.0	✓		✓
6	edge	Futou (FUT)	42.65	141.70	5	2.93	12.0	✓	✓	✓
7	urban	Takuyuu (TKU)	42.67	141.67	6	0.01	0.51	✓	✓	✓
8	urban	Numanohata Centre (NUC)	42.67	141.68	7	0.03	0.96	✓		✓
9	urban	Numanohata South (NUS)	42.66	141.68	7	0.01	0.39	✓		✓

1   Table 2. Log-rank tests for comparisons among survivorship curves. Note that comparisons

2   could not be computed for treatments where mortality events were not observed during the

3   census period.

4   a) Continuous forest vs. edge forest vs. urban forest

Year-season	Species	Position	χ^2	df	p
2017-fall	*Euhadra brandtii sapporo*	Canopy	0.5221	2	0.7702
	Euhadra brandtii sapporo	Ground	2.6446	2	0.2665
	Ezohelix gainesi	Ground	2.5071	2	0.2855
2018-summer	*Euhadra brandtii sapporo*	Canopy	2	2	0.3679
	Euhadra brandtii sapporo	Ground	9.8636	2	0.0072
	Ezohelix gainesi	Ground	11.619	2	0.003

5   b) *Euhadra brandtii sapporo*, canopy vs. ground

Year-season	Forest type	χ^2	df	p
2017-fall	Continuous	5.5329	1	0.0187
	Edge	1.956	1	0.1619
	Urban	0	0	NA
2018-summer	Continuous	6.0615	1	0.0138
	Edge	3.9176	1	0.0478
	Urban	0	0	NA

6   c) Ground, *Euhadra brandtii sapporo* vs. *Ezohelix gainesi*

| Year-season	Forest type	χ^2	df	p
2017-fall	Continuous	1.4505	1	0.2284
	Edge	0.2306	1	0.631
	Urban	1	1	0.3173
2018-summer	Continuous	0.1982	1	0.6562
	Edge	0.0472	1	0.8281
	Urban	0	0	NA

7   NA: not applicable

8

9   Fig. 1. Map of nine study sites in Tomakomai city, Hokkaido Island, Japan. See Table 1 for

10   abbreviation of site names. Sites 1–3, continuous forest; 4–6, edge forest; 7–9, urban forest.


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15   Fig. 2. *Euhadra brandtii sapporo* (a) and *Ezohelix gainesi* (b) abundance at nine study sites

16   located across un urbanization gradient in Tomakomai city, Hokkaido, Japan. Basis: three 5.4

17   × 5.4 m plots were surveyed by two to four persons (approximately 30 min/person/plot). Error

18   bars indicate standard deviation. Please refer to Table 1 and Fig. 1 for site numbers,

19   abbreviations, and locations.

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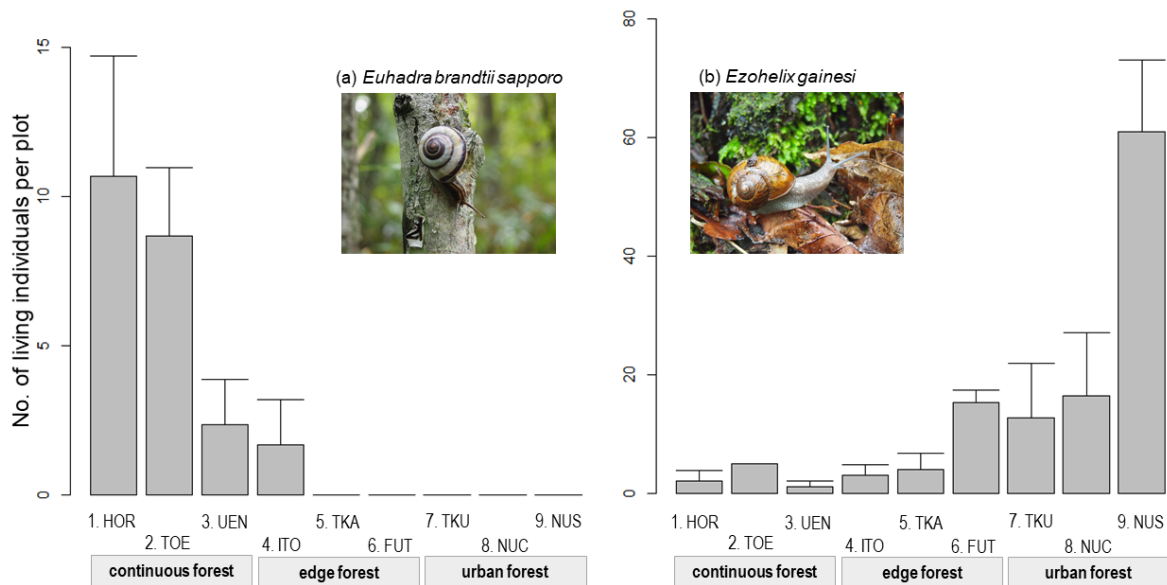
Fig. 3. Comparison of survival curves of *Euhadra brandtii sapporo* and *Ezohelix gainesi* for

25   canopy and ground treatments in the 2017-fall (left) and 2018-summer (right) experiments.

26   Error bars indicate 1 SE based on results of 8 samples × 3 sites (i.e., $n = 24$) for one forest

27   type. See Table 2 for results of pairwise comparisons by log-rank tests.

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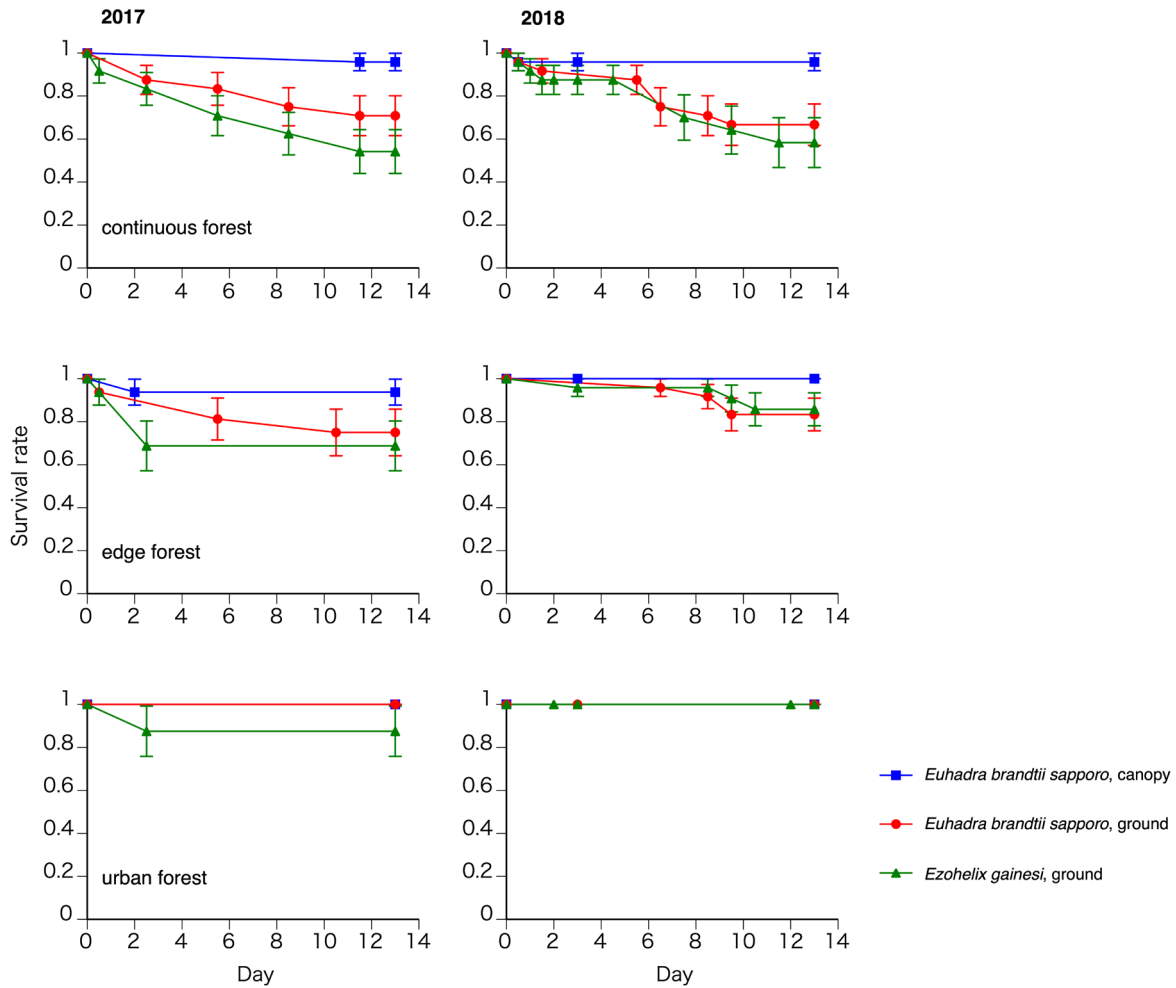
30   Fig. 4. Comparisons of mortality rate and its estimated causes for *Euhadra brandtii sapporo*

31   and *Ezohelix gainesi* obtained through the 2017-fall (left) and 2018-summer (right)

32   manipulative field experiments. See Table 1 for site name abbreviations.

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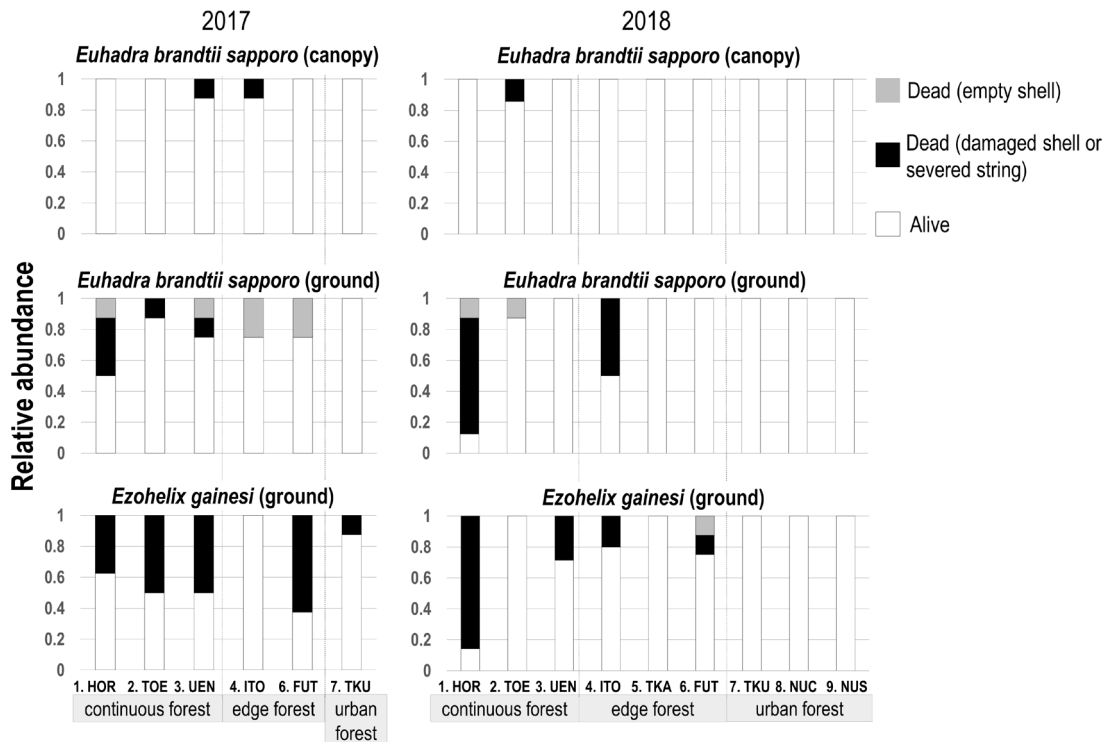
Fig. 5. Species composition of carabine beetles (a) and mammals and birds (b) in nine study sites along an urbanization gradient. See Table 1 for site name abbreviations. Carabine beetles were observed with pitfall traps, and mammals and birds were observed with camera traps. Specialist predators of land snails (carabine beetles) and species that preyed on land snails in our manipulative field experiments (mammals and birds) are indicated by red and yellow bars on the figure, and by an asterisk after the species name in the legend.
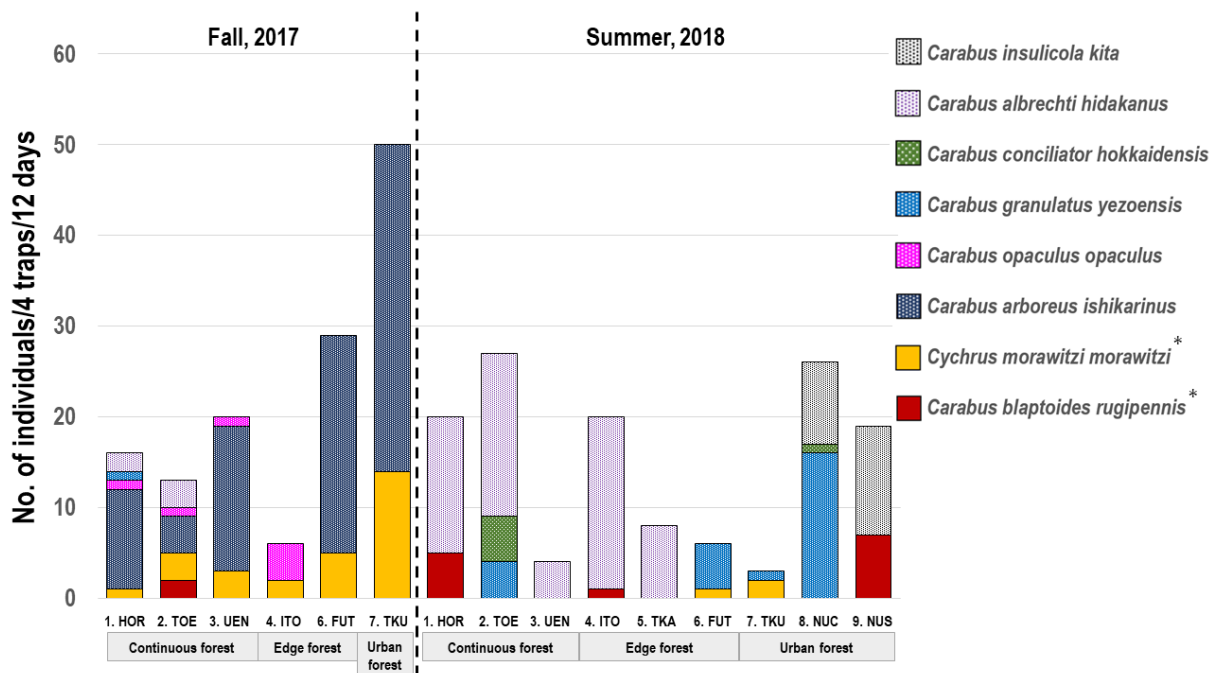
(a) Carabine beetles

(b) Mammals and birds
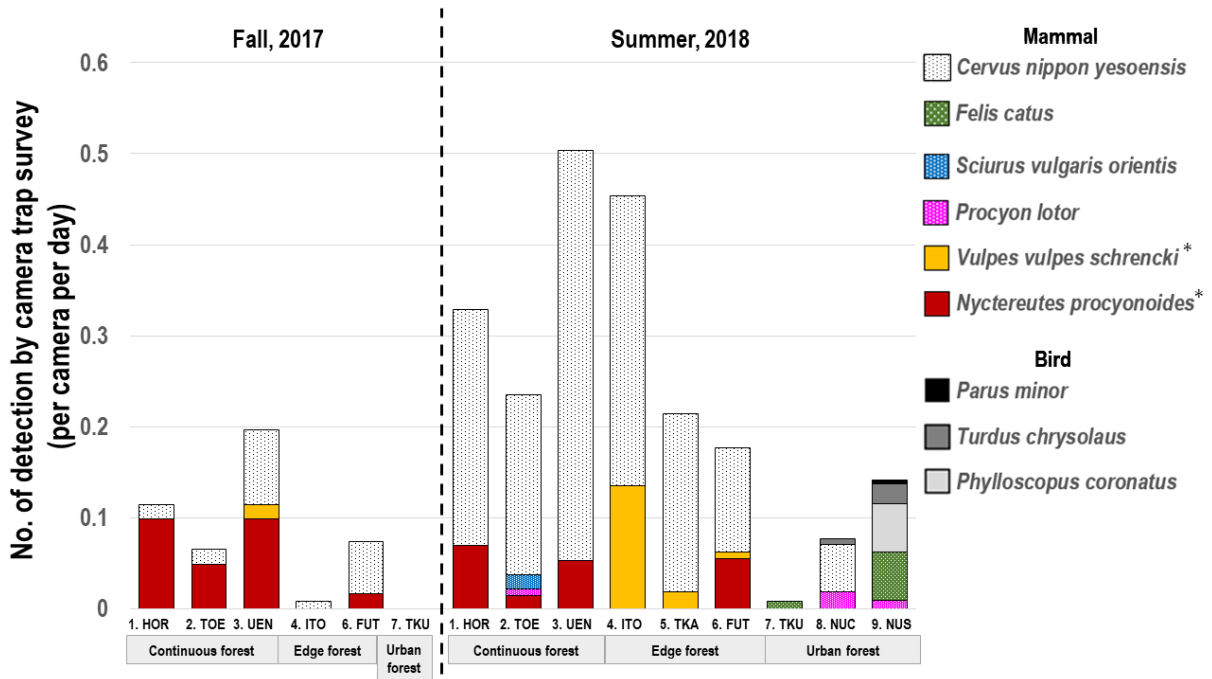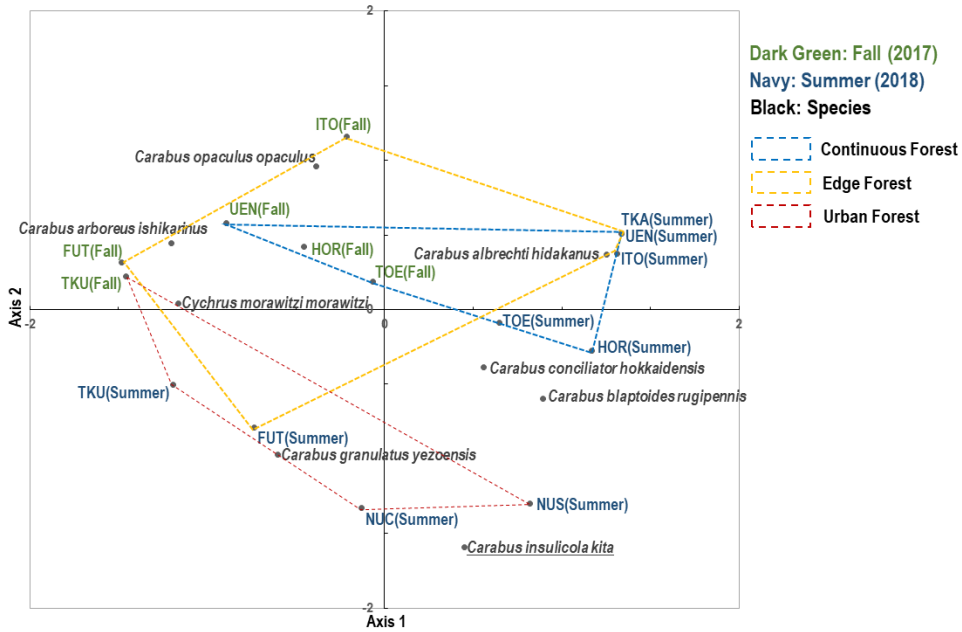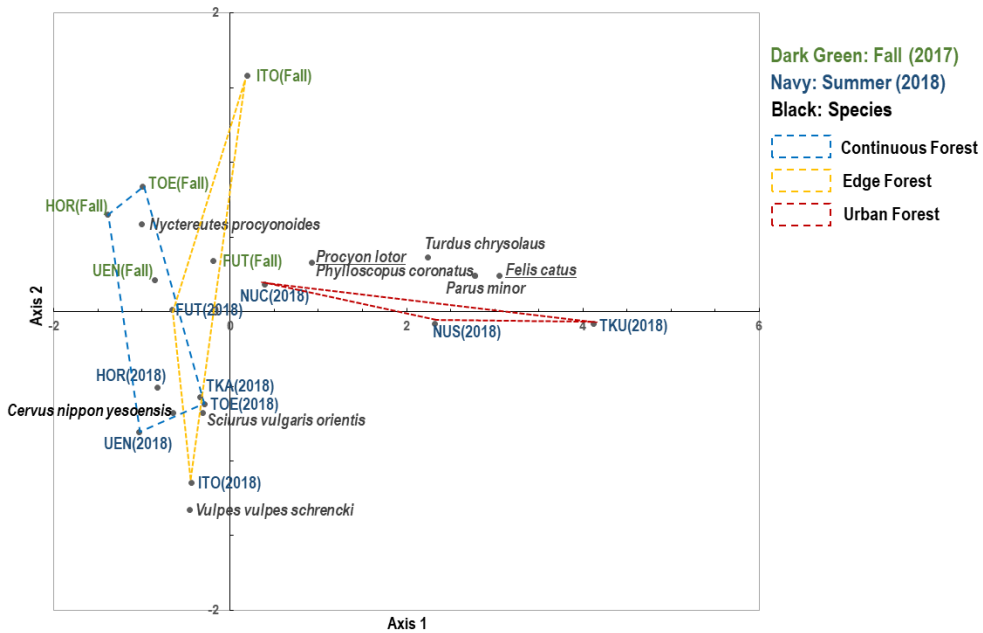
49   Fig. 6. Ordination analyses (non-metric multidimensional scaling) of carabine beetle (a) and

50   mammal and bird (b) communities at nine sites along an urbanization gradient. See Table 1

51   for site name abbreviations. Exotic species are underlined.
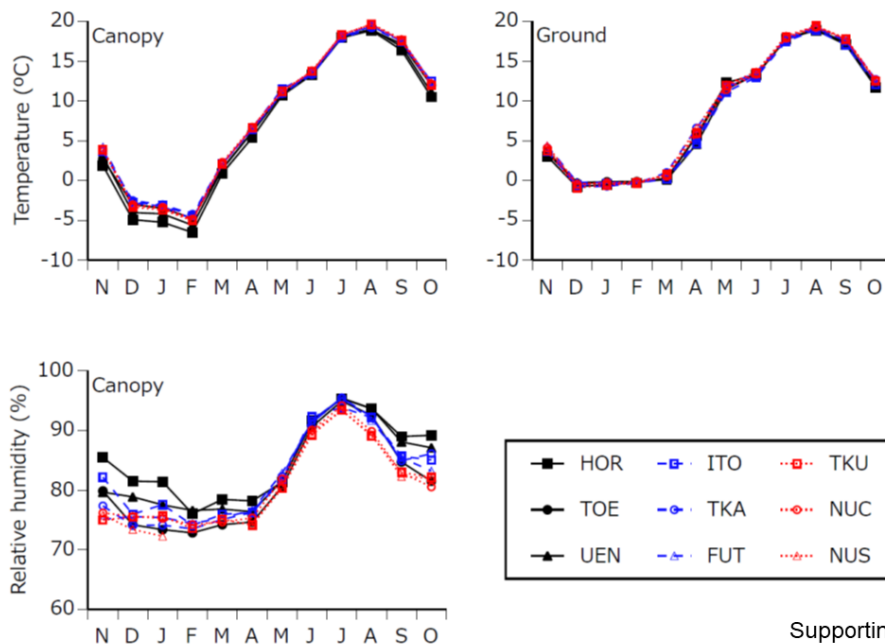
52   (a) Carabine beetles (Stress = 0.07)

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54   (b) Mammals and birds (Stress = 0.03)

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56 Supporting Information 1. Relative humidity and canopy and ground temperature at nine

57 study sites. See Table 1 for site name abbreviations.

Supporting Information 1

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60 Supporting Information 2. Differences in temperature among forest types and canopy

61 positions.

		df	F	p
Year	Forest type	2	10.6143	0.0022
	Position	1	63.8064	<0.0001
	Interaction	2	3.7134	0.0555
Dec–Feb	Forest type	2	2.6728	0.1096
	Position	1	345.9901	<0.0001
	Interaction	2	4.0798	0.0445
Jul–Sep	Forest type	2	24.1639	<0.0001
	Position	1	3.2878	0.0949
	Interaction	2	2.3776	0.135

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63   Supporting Information 3. Comparison of the abundance of dead *Euhadra brandtii sapporo*

64   (a) and *Ezohelix gainesi* (b) shells at nine study sites located along an urbanization gradient in

65   Tomakomai city, Hokkaido, Japan. Basis: three 5.4 × 5.4 m plots were surveyed by two to

66   four persons (approximately 30 min/person/plot). Error bars indicate standard deviation.

67   Please refer to Table 1 and Fig. 1 for site numbers, abbreviations, and locations. Our

68   generalized linear model analysis shows that the abundance of dead *E. b. sapporo* and *E.*

69   *gainesi* shells differed significantly among forest types (χ^2 = 130.11, df = 2, p < 0.0001 for *E.*

70   *b. sapporo* and χ^2 = 447.30, df = 2, p < 0.000 for *E. gainesi*).

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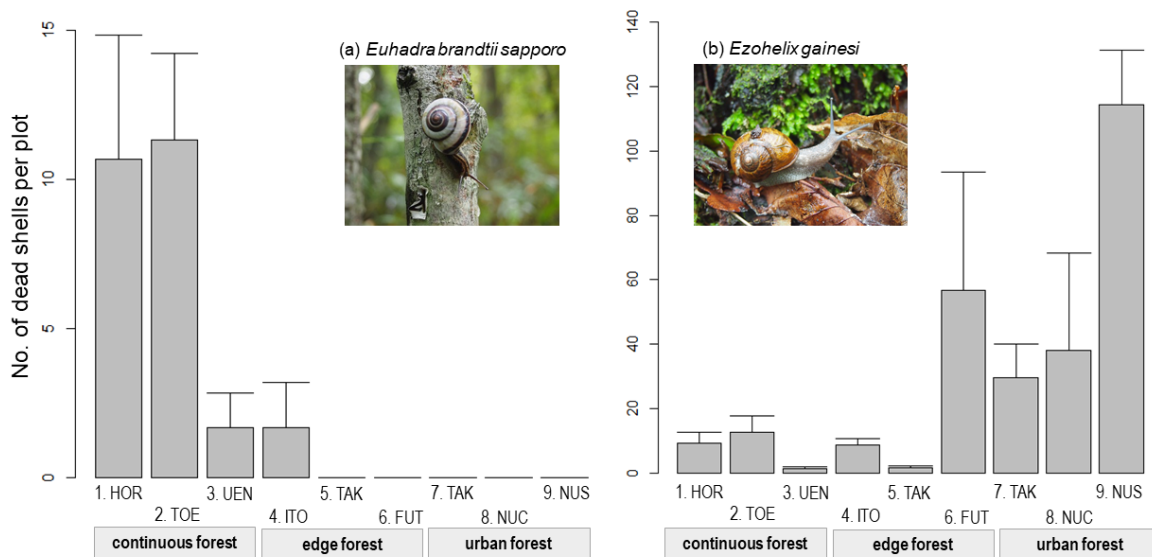
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74   Supporting Information 4. Photographs showing predation on *Euhadra brandtii sapporo* and

75   *Ezohelix gainesi* in manipulative field experiments.

76   (a) *Nyctereutes procyonoides*. 2 July 2018. Uenae (UEN) site.

77   https://www.youtube.com/watch?v=CYSVrp6G6mA&feature=youtu.be

78

79   (b) *Vulpes vulpes schrencki*. 5 July 2018. Itoi (ITO) site.

80   https://www.youtube.com/watch?v=kvZ8CUEN8n8&feature=youtu.be

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85   (c) *Carabus blaptoides rugipennis*. 30 June 2018. Horonai River (HOR) site

86   https://www.youtube.com/watch?v=usUXnxIiqiM&feature=youtu.be

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