diversity

Article

The Disappearance of Small Mammal Carcasses in Human-Dominated Habitats: A Field Experiment in Northeastern Japan

Kyosuke Shizukuda [1,2] and Masayuki U. Saito [3,*]

1 Graduate School of Agricultural Sciences, Yamagata University, Tsuruoka 9978555, Yamagata, Japan
2 Chodai Co., Ltd., Sapporo 0600031, Hokkaido, Japan
3 Faculty of Agriculture, Yamagata University, Tsuruoka 9978555, Yamagata, Japan
* Correspondence: saito.ume@gmail.com

Abstract: Even in human-dominated regions such as urban and agricultural areas, there are organisms involved in the decomposition of animal carcasses. Therefore, it is possible that these complementary decomposition functions occur in different habitats. Here, we clarified the disappearance patterns of small mammal carcasses in forest and human-dominated (urban and agricultural) habitats in northeastern Japan, based on field experiments. All small mammal carcasses in both summer and autumn were removed by different scavengers within 6 days; therefore, there was little difference in the disappearance rate of carcasses between habitats. The scavenger groups that contributed to carcass removal of remains in the summer survey differed between sites, suggesting that the disappearance process varies with landscape and canopy openness conditions. Although many carcasses were removed by vertebrates during the autumn survey, the vertebrate species involved differed among the survey sites. This study suggests that ecological functions related to the decomposition of small mammal carcasses in anthropogenically modified habitats may be maintained by the complementary activities of vertebrates and invertebrates.

Keywords: agriculture; decomposition; ecosystem function; invertebrate; landscape ecology; urban; vertebrate; scavenger

Citation: Shizukuda, K.; Saito, M.U. The Disappearance of Small Mammal Carcasses in Human-Dominated Habitats: A Field Experiment in Northeastern Japan. *Diversity* **2023**, *15*, 339. https://doi.org/10.3390/d15030339

Academic Editors: Haitao Wu, Junhong Bai and Giovanni Bacaro

Received: 23 December 2022
Revised: 22 February 2023
Accepted: 22 February 2023
Published: 27 February 2023

1. Introduction

Urban and agricultural areas are dominated by humans, and therefore show the results of intensive anthropogenic activities [1]. Such areas have been reported to have a variety of effects on biological communities. Urbanization often reduces biodiversity and species richness, and alters biological communities through human impacts such as habitat loss and fragmentation [2–6]. Urbanization also leads to the homogenization of biological community structures at large scales [6,7]. Agricultural expansion and intensification can lead to changes in biodiversity and biological communities [8,9]. The effects of agricultural activity include a decrease in the diversity of insects such as pollinators [10], butterflies [11], and dung beetles [12]. Previous studies have also reported that the expansion of agricultural land causes a reduction in the range and abundance of some birds and large mammals [13,14]. The various effects of habitat alterations on biological communities in urban and agricultural areas can alter ecosystem functioning [15–17].

The consumption of vertebrate carcasses by wildlife accelerates the rate of decomposition and material cycling of animal remains [18–20]. Animal carcasses are scavenged by both vertebrates, such as mammals and birds, and invertebrates, including flies and carrion beetles [21–29]. The utilization and decomposition of animal carcasses by wildlife are important ecosystem functions [30–35]; however, few studies have identified the different species that contribute to the decomposition of vertebrate carcasses in urban and agricultural landscapes [36]. Because both vertebrates and invertebrates may scavenge carcasses in the field, these communities need to be assessed together to elucidate the process of carcass disappearance [28,37–40]. Given that vertebrate and invertebrate community structure varies among habitat types, it is important to understand the processes of utilization and decomposition and the interactions among organisms in human-dominated areas by identifying the community and composition of carcass consumers in each habitat [40].

The species responsible for an ecosystem's function may vary depending on the environment. For example, on remote islands where mammalian scavengers are absent, silphid beetles act as a substitute in the decomposition function of vertebrate carcasses [28]. Furthermore, Sugiura et al. [37] found that the rate of carcass burial by burying beetles was higher in large forests, whereas the rate decreased in small, fragmented forests where removal by medium-sized carnivores was greater. These results suggest that the function of carcass disappearance depends on different taxonomic groups, depending on the habitat type [41,42]. Although forest and human-dominated (urban and agricultural) habitats have different communities of scavenging beetles and vertebrates [43–47], some species are more abundant in human-dominated habitats than in natural environments. It is possible that the function of carcass disappearance is maintained by the presence of different taxonomic groups of animals including humans, even in highly anthropogenically modified landscapes. In such landscapes, it is important to determine which animals contribute to the disappearance of carcasses in a community that includes both vertebrates and invertebrates.

Here, we investigated the spatial and temporal disappearance patterns of small mammal carcasses in forest and human-dominated (urban and agricultural) habitats in northeastern Japan. We hypothesized that the removal rate would be similar in each habitat, but the spatial and temporal patterns of disappearance would differ. This is because, although urban and agricultural areas have different communities than natural environments, animals that contribute to the disappearance of small mammal carcasses are still likely to be found in such areas. To test this hypothesis, we implemented an experimental field approach using mouse carcasses. This approach is more empirical than trap-based consumer estimates because it reflects the actual field interactions of carcass scavengers based on interspecific relationships. Rodents and other small mammals inhabit diverse landscapes [48–50] and are likely to provide a large number of carcasses, making them suitable baits for this experiment. The aim of our study was to investigate how habitat modification affects the disappearance processes of small mammal carcasses by both vertebrates and invertebrates. The results will contribute to our understanding of the effects of human-induced landscape modification on biological interactions and the complementary and redundancy of ecosystem functions.

2. Materials and Methods

2.1. Study Area

This study was conducted in Tsuruoka City, northeastern Japan (38°43′ N, 139°49′ E; Figure 1). This area belongs to the cool temperate zone, with an annual mean temperature of 12.5 °C and annual precipitation of 2097.5 mm [51]. Parts of the mountainous areas receive heavy snowfall of more than 3 m in winter. Most of the mountainous area in the study region was covered by forests, mainly natural forests dominated by Fagaceae trees such as Japanese beech (*Fagus crenata*) and Japanese oak (*Quercus crispula*), and some cedar (*Cryptomeria japonica*) plantations. The plains consisted of agricultural land (approximately 15%), mainly paddy fields, and residential areas concentrated in certain regions (approximately 2%) (Figure 1).

In this study, we prepared two study sites as forest landscapes (Figure 2a), one site as an agricultural landscape (Figure 2b), and two sites as urban landscapes (Figure 2c). Since the degree of forest canopy affects the species composition and abundance of carrion beetles [47], the sites for forest and urban landscape sites were set up as closed and open canopy, respectively. The study sites for the forest and agricultural landscapes were established in the Kaminagawa Experimental Forest (forest-closed and forest-open sites) and Takasaka Farm (agricultural-open site) of Yamagata University, respectively. The study sites for the urban landscapes were established at the Biodiversity Conservation Study Site (urban-closed site) and the Tsuruoka Campus (urban-open site) of Yamagata University, respectively. We conducted experiments at each of these five sites.

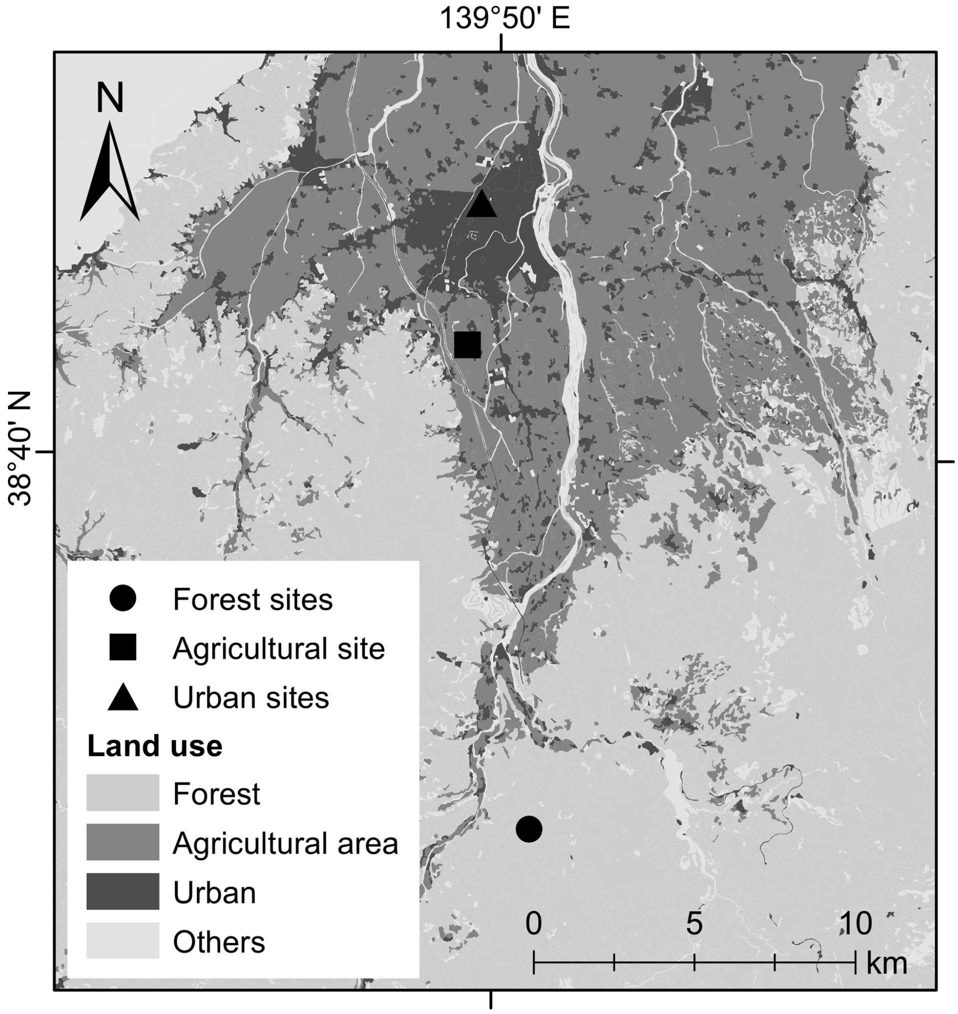

Figure 1. Locations of the study area and the sites that were surveyed.

The surrounding environment of the forest-closed site was a typical cool-temperate deciduous forest consisting mainly of Japanese beech, with some cedar plantations. The forest-open site was located near a forest road located approximately 200 m away from the forest-closed site, and the agricultural-open site was located along the causeway between the croplands. This cropland consisted mainly of rice paddies and dry fields, and there were no trees surrounding the area. The urban-closed site was an isolated forest of approximately 0.64 ha with a mixture of cedar, Japanese walnut (*Juglans ailantifolia*), and bamboo (*Phyllostachys edulis*), located approximately 400 m from the urban-open site. For each site, canopy openness was calculated based on a hemispherical photograph taken at a height of 1.2 m with a digital camera (Coolpix P5100, Nikon, Tokyo, Japan) equipped with a fisheye lens (FC-E8, Nikon, Tokyo, Japan) in August and September 2020. Photographs were taken five times at each site on a cloudy day. CanopOn2 [52] was used to obtain the degree of canopy openness from the hemispheric photograph, and the average value was used as the representative for each site. The degree of canopy openness was 5.9% for forest-closed sites, 30.1% for forest-open sites, 93.2% for agricultural-open sites, 7.3% for urban-closed sites, and 62.9% for urban-open sites.

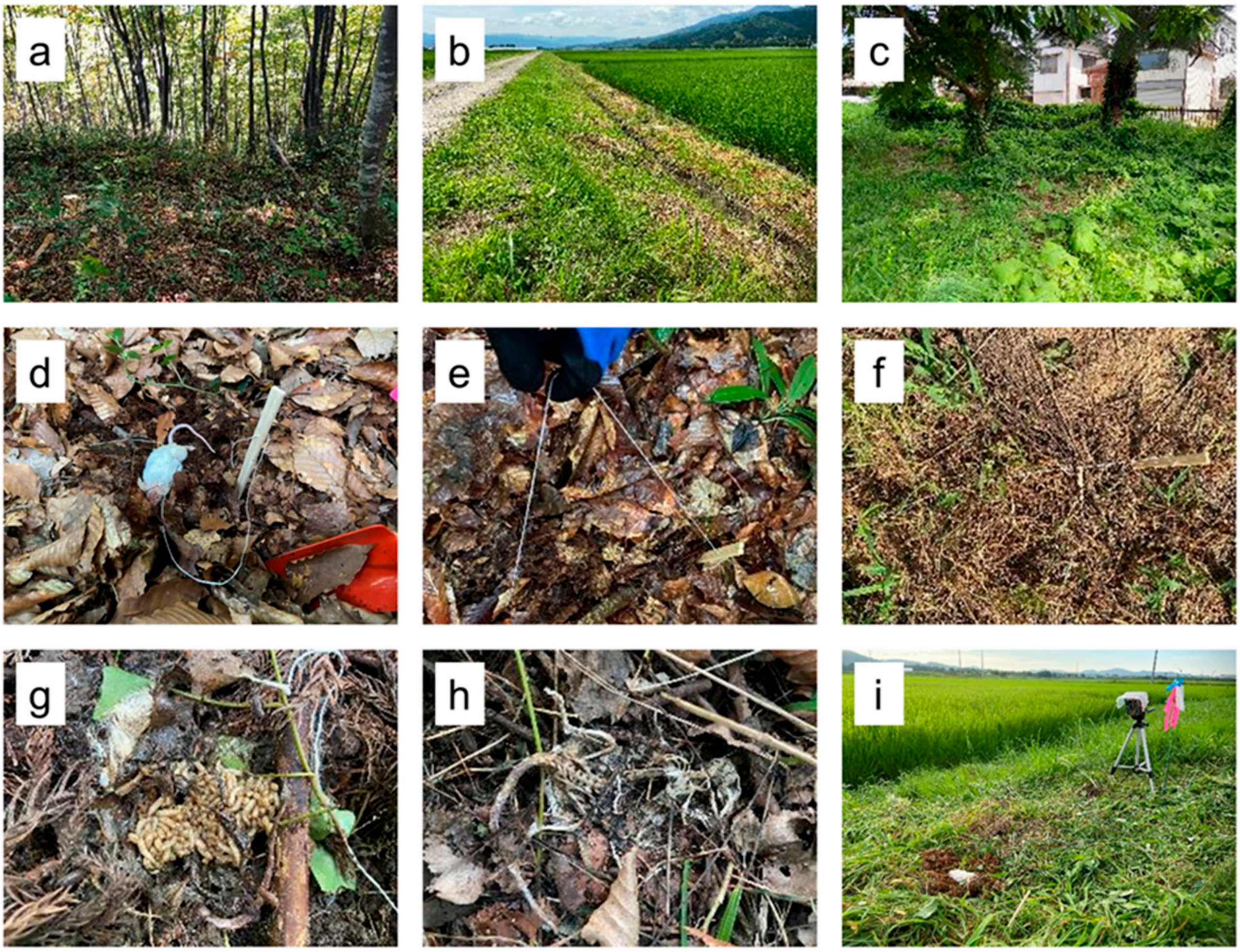

Figure 2. Photographs related to field survey. (**a**) An example of forest-closed sites, (**b**) an example of agricultural are-open sites, (**c**) an example of urban-closed sites, (**d**) a small carcass placed for field experiments, (**e**) removal of a carcass by vertebrates, (**f**) burial of a carcass by Nicrophorus beetles, (**g**) colonization of a carcass by flies, (**h**) colonization of a carcass by ants, (**i**) a camera trap in agricultural are-open sites.

2.2. Field Experiments

We conducted the disappearance experiments of small mammal carcasses at each site from August to September (summer) and October to November (autumn) 2020. Based on previous studies [28,37,53], fresh mouse carcasses (*Mus musculus*, mean weight 42.3 ± 5.4 g) were placed on the ground at each study site (Figure 2d). To account for differences in the scavenger fauna depending on the time of day [46,54], we prepared two different installation times: within three hours after sunrise (morning) and within three hours before sunset (evening). We placed four to ten mice at each site and conducted three to six experiments at each study site. The mice were fresh carcasses sold as pet food for carnivores. The number of mice placed at each site in the summer and autumn was 40 and 29 for forest-closed, 40 and 30 for forest-open, 48 and 30 for agricultural-open, 40 and 35 for urban-closed, and 45 and 35 for the urban-open site, respectively. In previous studies on both vertebrates and invertebrates, as we did, the distance between mice was set to at least 2 m [28,37], whereas in this study each mouse was placed at least 10 m away from the others. To find the carcasses that had been removed or buried by scavengers, we attached approximately 60 cm of dental floss to the body of the mouse, tied it to a tree branch at the other end, and drove the branch into the ground [28] (Figure 2d). The placed mouse was checked for conditions after three days. If it was still present at that time, it was observed again after another three days. Similar to previous studies [28,37,55], we distinguished between removal by vertebrates, burial by *Nicrophorus* beetles, and consumption by other invertebrates. When dental floss and carcasses were buried underground, we determined that the carcasses were taken by *Nicrophorus* beetles (Figure 2e). Although some ant species cover carcasses with soil [56,57], in this study, we dug up buried carcasses and confirmed the absence of ants. When the dental floss was not buried underground and the carcass was not located in the surrounding area, we determined that the carcass was taken by a vertebrate (Figure 2f). If a particular species or group of invertebrates colonized the carcass, that species or group was considered responsible for the disappearance of the carcass. These were specifically classified as flies (Figure 2g) or ants (Figure 2h). Carcasses used by diverse species and groups were defined as other invertebrates.

2.3. Camera Trap

We used an infrared sensor camera (Trophy Cam HD119876, Bushnell, KS, USA; BTC-6HD-940 and BTC-6HD-APX, Browning, UT, USA; HykeCam SP2, Hyke, Hokkaido, Japan) to investigate the vertebrates that removed the carcasses. The camera trap was set to either three or five consecutive shots in response, with the interval between each shot set to one second. The survey was conducted at the same time as the carcass disappearance experiment, and the camera traps were positioned in the direction of specific carcasses. The survey period of the camera trap was three days after the placement of the carcass, and the total number of days was 60 (20 traps $\times$ 3 days) for the summer season and 45 (15 traps $\times$ 3 days) for the autumn season. Camera traps were placed at a height of approximately 60 cm, attached to standing trees at closed sites, and fixed on tripods at open sites (Figure 2i). The distance between the carcass and the camera trap was approximately 0.6 to 1.5 m. Based on the photographs taken, we identified the vertebrates that removed the carcasses, and vertebrates captured by the camera traps that did not exhibit carcass removal behavior were excluded from the data.

2.4. Statistical Analysis

To analyze the effect of habitat differences on the disappearance of small mammal carcasses, we used Firth's bias-reduced logistic regression for each disappearance type in each season [58]. In ordinary logistic regression, the solution may not converge, and the regression coefficients and standard errors may be overestimated if the response variable data are completely separated by explanatory variables [59]. Firth's bias-reduced logistic regression can be adjusted by adding a penalty term to the log-likelihood function to optimize the estimates [58,60,61]. We created five models for each season with the following response variables: removal by vertebrates (1) and other (0), burial by *Nicrophorus* beetles (1) and other (0), colonization by flies (1) and other (0), colonization by ants (1) and other (0), and remaining (i.e., unused) (1) and other (0). Survey sites were used as categorical variables for explanatory variables to show differences in habitat. The effect of the habitat was assessed by using the forest-closed site as a reference and estimating the relative impact of the other sites. As confounding factors, we used the time of carcass placement (1 in the morning and 0 in the evening) and the number of repeated carcass placements at each site as explanatory variables. The number of repeated carcass placements was used because some vertebrates are known to revisit sites where they once obtained food resources [46], and the cumulative number of surveys at each site in each season was defined as the number of repetitions. We calculated the value of the variance inflation factor (VIF) and confirmed that it was less than five, thus assuming that multicollinearity would not be a factor. All analyses were performed using R3.6.2 [62] and the packages logistf ver 1.24, car ver 3.0.10, and the functions logistf and vif.

3. Results

3.1. Field Experiment

In the summer, all mice disappeared by scavengers within three days of placement (Figure 3). Of the mice placed at the forest-closed site, 75% (30/40) were buried by *Nicrophorus* beetles, 17.5% (7/40) were removed by vertebrates, 5% (2/40) were colonized by flies, and 2.5% (1/40) were colonized by ants. At the forest-open site, 65% (26/40) were colonized by flies, 22.5% (9/40) were removed by vertebrates, and 12.5% (5/40) were buried by *Nicrophorus* beetles. At the agricultural-open site, 66.7% (32/48) were removed by vertebrates, and 20.1% (10/48) and 12.5% (6/48) were colonized by flies and ants, respectively. At the urban-closed site, 80% (32/40) were colonized by flies, and 10% (4/40) were used by other invertebrates. Colonization by ants and removal by vertebrates was 5% (2/40). At the urban-open site, 75% (34/45) were removed by vertebrates, 17% (8/45) were colonized by ants, and 6% (3/45) were colonized by flies.

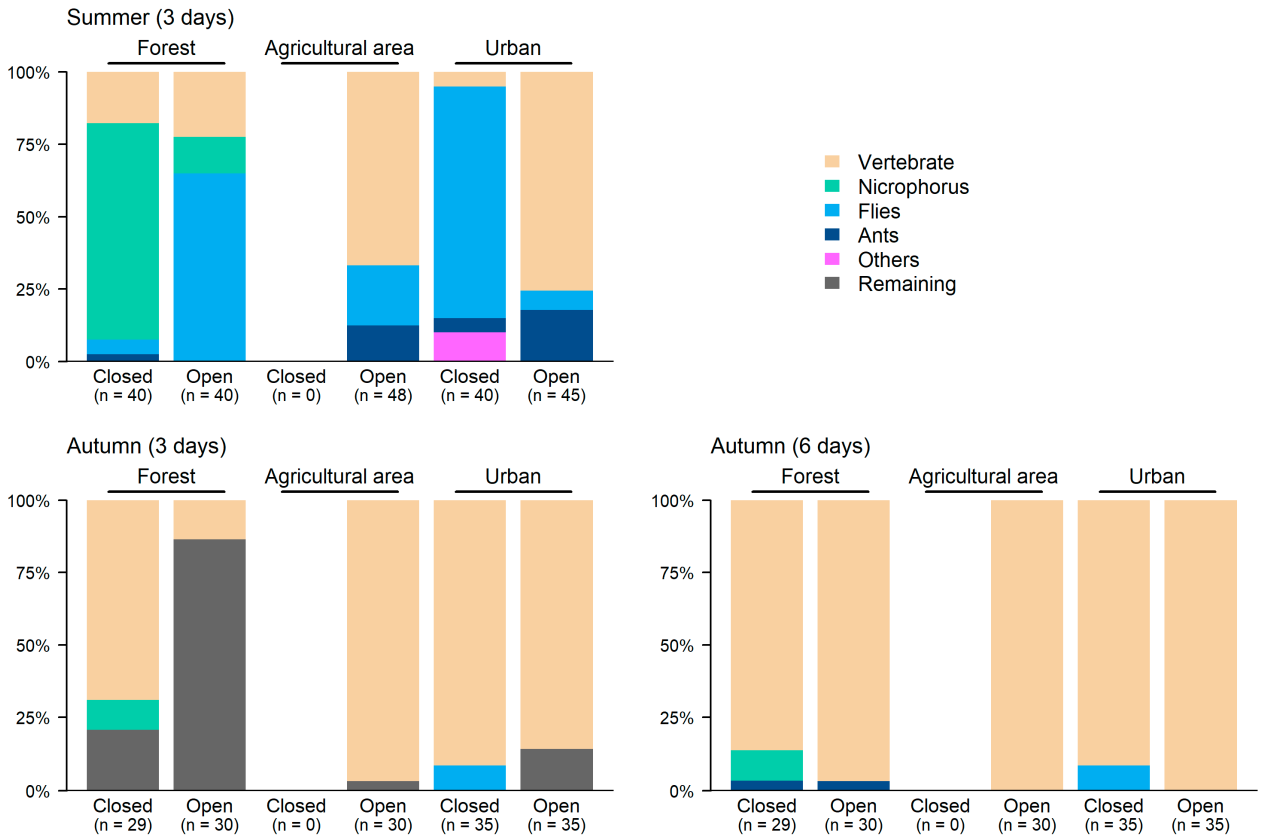

Figure 3. Percentage of scavenger groups of small mammal carcasses established at each survey site.

During the autumn survey, most of the mice disappeared within three days of carcass placement, but some remained (Figure 3). For each site, 20.6% (6/29), 86.6% (26/30), 3.3% (1/30), and 14.3% (5/35) remained at the forest-closed, forest-open, agricultural-open, and urban-open sites, respectively. All carcasses at the urban-closed site disappeared within three days. After another three days of observation, the remaining carcasses disappeared from all locations (Figure 3). Of the mice placed at forest-closed sites, 86.2% (25/29) were removed by vertebrates, 10.3% (3/29) were buried by *Nicrophorus* beetles, and 3.4% (1/29) were colonized by ants. At forest-open sites, 96.7% (29/30) were removed by vertebrates, and 3.3% (1/30) were colonized by ants. At the urban-closed site, 91.2% (32/35) were removed by vertebrates, and 8.6% (3/35) were colonized by flies. At the agricultural-open and urban-open sites, all mice were removed by vertebrates (30/30 and 35/35, respectively).

3.2. Firth's Bias-Reduced Logistic Regression

The results of logistic regressions for each disappearance pattern in summer showed that the rate of removal by vertebrates was significantly higher in the agricultural-open and urban-open sites and that the urban-closed site had significantly less vertebrate activity than the forest-closed sites (Table 1). The number of repeated carcass placements had a significant positive effect on the rate of removal by vertebrates (Table 1). The rate of burial by *Nicrophorus* beetles was significantly higher at the forest-closed site than at the other locations (Table 1). The colonization rate by flies was significantly higher in forest-open, agricultural-open, and urban-closed sites than in forest-closed regions (Table 1). The rate of ant colonization was significantly higher in agricultural-open and urban-open than in forest-closed sites, and the number of repeated carcass placements had a significant negative effect (Table 1).

Table 1. Parameter estimates of Firth's bias-reduced logistic regression for the pattern of the disappearance of the carcasses placed at each survey site in each season.

Variable	After Three Days in Summer					After Three Days in Autumn					After Six Days in Autumn				
	Coefficient	SE	95% CI		*p*-Value	Coefficient	SE	95% CI		*p*-Value	Coefficient	SE	95% CI		*p*-Value
			Lower	Upper				Lower	Upper				Lower	Upper	
Vertebrates or not															
Intercept	−2.71	0.61	−3.97	−1.58	<0.01	−1.70	2.32	−6.72	2.71	n.s.	−1.20	4.98	−19.40	7.95	n.s.
Survey site															
Forest-closed	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Forest-open	0.32	0.57	−0.79	1.45	n.s.	−2.58	0.66	−3.97	−1.38	<0.01	1.46	1.08	−0.49	3.92	n.s.
Agricultural area-open	1.65	0.54	0.64	2.74	<0.01	1.38	1.17	−0.83	3.98	n.s.	1.03	2.22	−5.12	6.52	n.s.
Urban-closed	−1.72	0.82	−3.52	−0.24	<0.05	0.46	1.08	−1.64	2.67	n.s.	−1.22	1.96	−7.17	2.59	n.s.
Urban-open	2.53	0.57	1.48	3.69	<0.01	−0.06	1.04	−2.12	2.03	n.s.	1.02	2.28	−5.12	6.61	n.s.
Installation time	−0.31	0.38	−1.05	0.43	n.s.	0.02	0.68	−1.33	1.41	n.s.	−2.47	1.59	−7.58	1.48	n.s.
Number of times installed	0.50	0.13	0.25	0.78	<0.01	0.41	0.36	−0.26	1.19	n.s.	0.81	0.77	−0.49	3.72	n.s.
Nicrophorus or not															
Intercept	1.99	0.92	0.12	4.11	<0.05	−5.20	5.46	−27.62	18.05	n.s.	−5.20	5.46	−27.62	18.05	n.s.
Survey site															
Forest-closed	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Forest-open	−2.92	0.59	−4.17	−1.84	<0.01	−2.23	1.56	−7.18	0.27	n.s.	−2.23	1.56	−7.18	0.27	n.s.
Agricultural area-open	−5.41	1.41	−10.28	−3.30	<0.01	−2.75	2.26	−9.83	4.87	n.s.	−2.75	2.26	−9.83	4.87	n.s.
Urban-closed	−5.30	1.43	−10.17	−3.21	<0.01	−2.99	2.72	−15.97	4.83	n.s.	−2.99	2.72	−15.97	4.83	n.s.
Urban-open	−5.38	1.43	−10.25	−3.29	<0.01	−2.99	2.72	−15.97	4.83	n.s.	−2.99	2.72	−15.97	4.83	n.s.
Installation time	−0.70	0.60	−2.01	0.53	n.s.	3.06	1.75	−2.23	8.81	n.s.	3.06	1.75	−2.23	8.81	n.s.
Number of times installed	−0.23	0.25	−0.81	0.31	n.s.	0.26	0.82	−3.39	3.61	n.s.	0.26	0.82	−3.39	3.61	n.s.
Flies or not															
Intercept	−3.10	0.79	−4.87	−1.70	<0.01	−0.57	4.83	−9.98	15.76	n.s.	−0.57	4.83	−9.98	15.76	n.s.
Survey site															
Forest-closed	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Forest-open	3.34	0.74	2.06	5.03	<0.01	0.00	2.01	−5.26	5.25	n.s.	0.00	2.01	−5.26	5.25	n.s.
Agricultural area-open	1.42	0.77	0.03	3.15	<0.05	1.54	2.49	−4.23	7.86	n.s.	1.54	2.49	−4.23	7.86	n.s.
Urban-closed	4.05	0.77	2.71	5.79	<0.01	3.74	2.26	−0.46	9.88	n.s.	3.74	2.26	−0.46	9.88	n.s.
Urban-open	0.22	0.87	−1.48	2.07	n.s.	1.56	2.54	−4.31	7.89	n.s.	1.56	2.54	−4.31	7.89	n.s.
Installation time	0.50	0.38	−0.25	1.26	n.s.	1.33	1.45	−2.23	6.41	n.s.	1.33	1.45	−2.23	6.41	n.s.
Number of times installed	0.04	0.13	−0.21	0.31	n.s.	−0.77	0.73	−3.39	0.50	n.s.	−0.77	0.73	−3.39	0.50	n.s.
Ants or not															
Intercept	−1.22	1.03	−3.66	0.67	n.s.	-	-	-	-	-	−5.60	5.38	−28.80	18.05	n.s.
Survey site															
Forest-closed	-	-	-	-	-	-	-	-	-	-					
Forest-open	−1.14	1.65	−6.14	1.84	n.s.	-	-	-	-	-	−0.01	1.19	−2.61	2.60	n.s.
Agricultural area-open	2.24	1.00	0.47	4.62	<0.05	-	-	-	-	-	−1.65	2.30	−9.00	6.15	n.s.
Urban-closed	0.73	1.08	−1.38	3.18	n.s.	-	-	-	-	-	−1.86	2.72	−15.18	6.08	n.s.
Urban-open	2.27	0.95	0.64	4.58	<0.01	-	-	-	-	-	−1.86	2.72	−15.18	6.08	n.s.
Installation time	−0.31	0.60	−1.56	0.90	n.s.	-	-	-	-	-	2.46	1.67	−2.84	8.20	n.s.
Number of times installed	−0.90	0.23	−1.43	−0.46	<0.01	-	-	-	-	-	0.24	0.80	−3.49	3.69	n.s.
Remain or not															
Intercept	-	-	-	-	-	0.53	2.60	−4.62	6.15	n.s.	-	-	-	-	-
Survey site															
Forest-closed	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Forest-open	-	-	-	-	-	3.03	0.68	1.79	4.46	<0.01	-	-	-	-	-
Agricultural area-open	-	-	-	-	-	−1.17	1.24	−3.89	1.22	n.s.	-	-	-	-	-
Urban-closed	-	-	-	-	-	−2.24	1.73	−7.36	0.70	n.s.	-	-	-	-	-
Urban-open	-	-	-	-	-	0.29	1.16	−2.12	2.60	n.s.	-	-	-	-	-
Installation time	-	-	-	-	-	−0.73	0.78	−2.39	0.83	n.s.	-	-	-	-	-
Number of times installed	-	-	-	-	-	−0.26	0.40	−1.13	0.52	n.s.	-	-	-	-	-

Logistic regression analysis showed that the rate of removal by vertebrates at the forest-open site was significantly lower than that at the forest-closed site after three days (Table 1). The number of unused carcasses at the forest-open site was significantly higher than that at the forest-closed site (Table 1). There were no significant results for burial by *Nicrophorus* beetles and colonization by flies (Table 1).

The results of logistic regressions on the disappearance patterns of carcasses after six days showed that removal by vertebrates, burial by *Nicrophorus* beetles, and colonization by flies and ants had no significant effect on any of the variables (Table 1).

3.3. Camera Trap

In the summer, five mammal species and two bird species were recorded as follows: red foxes (*Vulpes vulpes*), raccoon dogs (*Nyctereutes procyonoides*), masked palm civets (*Paguma larvata*), cats (*Felis catus*), rodents (*Muridae* spp.), raptors (*Accipitriformes* spp.), and crows (*Corvus* spp.) (n = 27, Table 2). At the forest-closed and forest-open sites, masked palm civets and rodents were photographed once, whereas, at the agricultural-open site, raptors were the most frequently photographed (n = 4), but raccoon dogs and red foxes were also captured (Table 2). In the urban-closed site, a masked palm civet was photographed once, and in the urban-open site, crows were the most frequently detected (n = 10), followed by cats, raptors, and masked palm civets.

Table 2. Frequency of vertebrates that removed carcasses captured by camera traps. The number of camera days at each study site was 60 days in summer and 45 days in autumn.

Group	Species	Common Name	Study Site in Summer					Study Site in Autumn				
			Forest-Closed	Forest-Open	Agricultural Area-Open	Urban-Closed	Urban-Open	Forest-Closed	Forest-Open	Agricultural Area-Open	Urban-Closed	Urban-Open
Mammal	*Ursus thibetanus*	Asiatic black bear	0	0	0	0	0	1	0	0	0	0
	Vulpes vulpes	Red fox	0	0	1	0	0	0	0	12	0	0
	Nyctereutes procyonoides	Raccoon dog	0	0	1	0	0	3	0	0	0	0
	Paguma larvata	Maskec palm civet	1	1	0	1	1	3	0	0	2	0
	Felis catus	Cat	0	0	0	0	3	0	0	0	1	0
	Muridae spp.	Rodents	1	1	0	0	0	4	0	0	0	1
Bird	*Accipitriformes* spp.	Raptors	0	0	4	0	2	0	0	1	0	0
	Corvus spp.	Crows	0	0	0	0	10	0	0	0	9	10
Total			2	2	6	1	16	11	0	13	12	11

Results of the autumn camera traps included Asiatic black bears (*Ursus thibetanus*), red foxes, raccoon dogs, masked palm civets, cats, rodents, raptors, and crows (Table 2). Rodents (n = 4) were the most frequently photographed at the forest-closed sites, followed by raccoon dogs, red foxes, and Asiatic black bears. At the agricultural-open site, red foxes were the most commonly photographed species (n = 12), and one raptor was also captured. The most commonly photographed species at the urban-closed site were crows (n = 9), followed by masked palm civets and a cat. In the urban-open site, crows were frequently photographed (n = 10) and rodents were also captured.

4. Discussion

All small mammal carcasses placed in both the summer and autumn disappeared within 6 days by various scavengers (Figure 3); therefore, there was little difference in the rate of carcass disappearance between habitats. A previous study examining the use of carcasses by vertebrate scavengers along an urban-rural environmental gradient reported no significant differences in carcass removal rates and the maintenance of ecological functions in cities, although the species composition differed between landscapes [46]. Our results are consistent with this study. The groups of scavengers that contributed to the disappearance of carcasses in the summer survey differed among sites (Figure 3), suggesting that the disappearance process varies with landscape and the degree of canopy openness. Although many carcasses were removed by vertebrates during the autumn survey (Figure 3), the species varied among the sites. This suggests that different vertebrate species contribute to the disappearance of small mammal carcasses depending on the environment of the study site [40]. In urban and agricultural landscapes, different groups of vertebrates and invertebrates would perform functions related to carcass disappearance than in forest landscapes.

This study also showed that the disappearance pattern of small mammal carcasses varied greatly with the season (Figure 3 and Table 1). Inagaki et al. [29] reported seasonality in the use of carcasses by vertebrate scavengers. Previous studies have reported that carrion beetles, blowflies (Calliphoridae), and ants that utilize animal carcasses are more active in the summer and less active in the autumn and winter [40,47,63–67]. These findings are consistent with the results of the present study. Our results suggest that a single season is not sufficient to assess ecosystem functions and that multi-seasonal studies that take into account the activity and life history of vertebrates and invertebrates are needed. We found that in addition to habitat factors, seasonal effects were also significant in the disappearance pattern of small mammal carcasses.

4.1. Scavenging by Invertebrates

Burial by *Nicrophorus* beetles was found only in forest sites (Figure 3), and during the summer survey, burial by *Nicrophorus* beetles was significantly higher in the forest-closed sites (Table 1). Ueda [68] and Shizukuda and Saito [47] stated that a high degree of canopy openness is important for the abundance of carrion beetles, including *Nicrophorus* beetles. This is consistent with the results of our study, in which burial by *Nicrophorus* beetles was more common in closed environments. Burial by *Nicrophorus* beetles was not observed at urban or agricultural sites in our study area (Figure 3), although previous studies have reported that it is possible to maintain *Nicrophorus* beetle abundance even in urban landscapes if a large forest area is present [37,45]. The agricultural-open and urban-open sites examined in this study were sunlit environments, while the urban-closed site was a small, isolated forest, which may have prevented the presence of *Nicrophorus* beetles. The study by Shizukuda and Saito [47], which examined carrion beetle communities in the same study area, did not collect any *Nicrophorus* beetles.

The rate of colonization by flies during the summer was higher at the open site than at the closed site in the forest site (Table 1). *Nicrophorus* beetles are known to suppress flies by removing their larvae from the carcass [69,70]. In the forest-open site, there were fewer *Nicrophorus* beetles, which may have allowed flies to colonize the carcasses. In the forest-closed site, flies may have been less abundant as a result of competition with *Nicrophorus* beetles. In contrast to the forest sites, the urban sites had greater fly activity in the closed sites (Table 1). In the urban open sites, most of the carcasses were removed by vertebrates, particularly crows (Figure 3 and Table 2). In an urban landscape in the United Kingdom, Corvidae birds were reported to consume approximately 30–40% of the roadside carcasses [26,71]. In our study site, the rate of colonization by flies may have been low because vertebrates, primarily crows, removed the carcasses before flies could colonize them in the urban-open site.

The colonization of small mammal carcasses by ants in summer was more frequent in the agricultural and urban open sites (Figure 3 and Table 1). According to carrion traps for ants only, the frequency of use was highest in forests, followed by farmlands, and finally in cities [72], which differs from the results of our study. In nature, competition for food resources exists between different taxonomic groups, and the colonization of carcasses may be less frequent than expected from the results of trap surveys targeting ants only. Furthermore, a study examining the food decomposition function of ants found no significant difference in removal rates between urban and suburban areas [73]. This is consistent with the results of our study, in which the colonization of carcasses was higher in urban and agricultural areas, suggesting the importance of the decomposition function by ants in cities.

4.2. Scavenging by Vertebrates

Removal of small mammal carcasses by vertebrates during the summer was more common in agricultural and urban-open sites, and less common in urban-closed sites (Table 1). The number of removals by birds (crows and raptors) was higher in the urban and agricultural-open sites (Table 2). Gatesire et al. [74] reported that bird scavengers and raptors were more abundant in open environments such as wastelands, which is consistent with the results of this study. Visibility is a possible reason why birds remove more carcasses in open environments; since birds are able to search for resources efficiently due to their ability to fly [75], an open environment without visual barriers may be more efficient for resource acquisition. Some raptor species inhabiting Japan are known to rely on open habitats for foraging, such as grasslands and rice paddies [76–78]. These factors suggest that removal by birds is increased at open sites. In particular, crows are considered to be the most important scavengers in the United Kingdom [26,71], and our results suggest that they are also important in Japan. In autumn, removals by birds (crows) were higher at the urban site, as in the summer, but most removals at the agricultural-open site were by red foxes (Table 2). Some raptors make large autumn migrations and overwinter in the southwestern islands of Japan and Southeast Asia [79], and some vertebrate scavengers also show seasonality in their use of carcasses [29]. These results suggest that the vertebrate assemblages at the agricultural-open site differed by season.

In the autumn, some carcasses were still observed three days after the start of the experiment (Figure 3). Particularly in the forest-open site, the number of carcasses remaining was high, while the rate of removal by vertebrates was low (Table 1). The higher remaining rate in the forest-open site may be related to less removal by vertebrates than in the closed site, and the effect of reduced insect activity due to lower temperatures. At all sites, however, all carcass remains were cleared by scavengers after six days of the carcass placement (Figure 3). More than 80% of the carcasses that had disappeared were removed by vertebrates, and the disappearance rate did not differ significantly among the study sites (Figure 3 and Table 1). This may be the result of an increase in the removal by vertebrates due to a decrease in insect activity during the autumn [40]. This suggests that vertebrates serve as important scavengers in the autumn.

5. Conclusions

This study suggests that ecological functions associated with the disappearance of small mammal carcasses in anthropogenically modified habitats may be maintained by the complementary activity of vertebrates and invertebrates. This suggests that biological communities in urban and agricultural landscapes have redundancy in ecosystem functions in the study area. Species that can adapt to the human-dominated landscape may have a relatively higher contribution to the disappearance process than the same species living in natural landscapes. Small mammals such as mice and rats used in this field experiment are generally abundant in different landscapes including urban and agricultural areas [48–50]. This suggests that animals with carcass disappearance processes associated with the presence of these small mammals inhabit human-dominated landscapes. Urbanization has led to the homogenization of animal community structure [7], while even leading to more dissimilar communities between cities than between rural landscapes [6]. In such cases, there is room to consider whether ecosystem redundancy can be maintained in human-dominated landscapes through species turnover, including nonindigenous species [40]. As we were unable to identify species in the invertebrate community, further detailed analysis will reveal the effects of turnover on the decomposition of small carcasses.

The carcass decomposition function in this study was limited to the disappearance of small mammal carcasses. In the natural environment, the carcasses of small mammals as well as medium and large mammals and birds are all available. Depending on the size and taxonomic group of animal carcasses, the decomposition process may vary [80]. As shown in this study, the remains of small mammals are consumed only by certain taxonomic groups due to their size, whereas the carcasses of medium and large mammals are not monopolized by one species, but are used by a variety of vertebrate species [29,80]. The effects of taxonomic groups and carcass size on the decomposition process should be investigated not only in forest habitats but also in human-dominated habitats, leading to a further understanding of ecosystem functions.

Author Contributions: Conceptualization, K.S. and M.U.S.; Data curation, K.S.; Formal analysis, K.S.; Investigation, K.S.; Methodology, K.S. and M.U.S.; Writing—original draft, K.S. and M.U.S.; Writing—review & editing, M.U.S. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by YU-COE (M) grant from Yamagata University.

Institutional Review Board Statement: Not applicable.

Data Availability Statement: The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Acknowledgments: We thank the staff of the Field Science Center, Yamagata University and the associates of the Yamagata University for supporting our field survey.

Conflicts of Interest: The authors declare no conflict of interest associated with this manuscript.

References

1. Foley, J.A.; DeFries, R.; Asner, G.P.; Barford, C.; Bonan, G.; Carpenter, S.R.; Chapin, F.S.; Coe, M.T.; Daily, G.C.; Gibbs, H.K.; et al. Global Consequences of Land Use. *Science* **2005**, *309*, 570–574. [CrossRef] [PubMed]
2. McKinney, M.L. Urbanization, Biodiversity, and Conservation. *BioScience* **2002**, *52*, 883–890. [CrossRef]
3. McKinney, M.L. Effects of Urbanization on Species Richness: A Review of Plants and Animals. *Urban Ecosyst.* **2008**, *11*, 161–176. [CrossRef]
4. Faeth, S.H.; Warren, P.S.; Shochat, E.; Marussich, W.A. Trophic Dynamics in Urban Communities. *BioScience* **2005**, *55*, 399–407. [CrossRef]
5. Dolan, R.W.; Moore, M.E.; Stephens, J.D. Documenting Effects of Urbanization on Flora Using Herbarium Records. *J. Ecol.* **2011**, *99*, 1055–1062. [CrossRef]
6. Knop, E. Biotic Homogenization of Three Insect Groups Due to Urbanization. *Global Change Biology* **2016**, *22*, 228–236. [CrossRef]
7. McKinney, M.L. Urbanization as a Major Cause of Biotic Homogenization. *Biol. Conserv.* **2006**, *127*, 247–260. [CrossRef]
8. Matson, P.A.; Parton, W.J.; Power, A.G.; Swift, M.J. Agricultural Intensification and Ecosystem Properties. *Science* **1997**, *277*, 504–509. [CrossRef]
9. Emmerson, M.; Morales, M.B.; Oñate, J.J.; Batáry, P.; Berendse, F.; Liira, J.; Aavik, T.; Guerrero, I.; Bommarco, R.; Eggers, S.; et al. How Agricultural Intensification Affects Biodiversity and Ecosystem Services. *Adv. Ecol. Res.* **2016**, *55*, 43–97. [CrossRef]
10. Tscharntke, T.; Klein, A.M.; Kruess, A.; Steffan-Dewenter, I.; Thies, C. Landscape Perspectives on Agricultural Intensification and Biodiversity—Ecosystem Service Management. *Ecol. Lett.* **2005**, *8*, 857–874. [CrossRef]
11. Koh, L.P.; Wilcove, D.S. Is Oil Palm Agriculture Really Destroying Tropical Biodiversity? *Conserv. Lett.* **2008**, *1*, 60–64. [CrossRef]
12. Ueda, A.; Dwibadra, D.; Noerdjito, W.A.; Sugiarto; Kon, M.; Ochi, T.; Takahashi, M.; Fukuyama, K. Effect of Habitat Transformation from Grassland to *Acacia mangium* Plantation on Dung Beetle Assemblage in East Kalimantan, Indonesia. *J. Insect Conserv.* **2015**, *19*, 765–780. [CrossRef]
13. Medan, D.; Torretta, J.P.; Hodara, K.; de la Fuente, E.B.; Montaldo, N.H. Effects of Agriculture Expansion and Intensification on the Vertebrate and Invertebrate Diversity in the Pampas of Argentina. *Biodivers. Conserv.* **2011**, *20*, 3077–3100. [CrossRef]
14. Aikawa, E.; Saito, M.U. Effects of Intensive Agricultural Landscapes on Farmland Use by Medium and Large Mammals in Japan. *Écoscience* **2022**, *in press*. [CrossRef]
15. Tratalos, J.; Fuller, R.A.; Warren, P.H.; Davies, R.G.; Gaston, K.J. Urban Form, Biodiversity Potential and Ecosystem Services. *Landsc. Urban Plan.* **2007**, *83*, 308–317. [CrossRef]
16. Burton, M.L.; Samuelson, L.J.; Mackenzie, M.D. Riparian Woody Plant Traits across an Urban–Rural Land Use Gradient and Implications for Watershed Function with Urbanization. *Landsc. Urban Plan.* **2009**, *90*, 42–55. [CrossRef]
17. Knop, E.; Zoller, L.; Ryser, R.; Gerpe, C.; Hörler, M.; Fontaine, C. Artificial Light at Night as a New Threat to Pollination. *Nature* **2017**, *548*, 206–209. [CrossRef]
18. DeVault, T.L.; Rhodes, O.E., Jr.; Shivik, J.A. Scavenging by Vertebrates: Behavioral, Ecological, and Evolutionary Perspectives on an Important Energy Transfer Pathway in Terrestrial Ecosystems. *OIKOS* **2003**, *102*, 225–234. [CrossRef]
19. Barton, P.S.; Cunningham, S.A.; Macdonald, B.C.T.; McIntyre, S.; Lindenmayer, D.B.; Manning, A.D. Species Traits Predict Assemblage Dynamics at Ephemeral Resource Patches Created by Carrion. *PLoS ONE* **2013**, *8*, e53961. [CrossRef]
20. Barton, P.S.; Evans, M.J.; Foster, C.N.; Pechal, J.L.; Bump, J.K.; Quaggiotto, M.-M.; Benbow, M.E. Towards Quantifying Carrion Biomass in Ecosystems. *Trends Eol. Evol.* **2019**, *34*, 950–961. [CrossRef]
21. DeVault, T.L.; Brisbin, I.L., Jr.; Rhodes, O.E., Jr. Factors Influencing the Acquisition of Rodent Carrion by Vertebrate Scavengers and Decomposers. *Can. J. Zool.* **2004**, *82*, 502–509. [CrossRef]
22. Martín-Vega, D.; Baz, A. Sarcosaprophagous Diptera Assemblages in Natural Habitats in Central Spain: Spatial and Seasonal Changes in Composition. *Med. Vet. Entomol.* **2013**, *27*, 64–76. [CrossRef] [PubMed]
23. Pastula, E.C.; Merritt, R.W. Insect Arrival Pattern and Succession on Buried Carrion in Michigan. *J. Med. Entomol.* **2013**, *50*, 432–439. [CrossRef] [PubMed]

24. Mohr, R.M.; Tomberlin, J.K. Environmental Factors Affecting Early Carcass Attendance by Four Species of Blow Flies (Diptera: Calliphoridae) in Texas. *J. Med. Entomol.* **2014**, *51*, 702–708. [CrossRef] [PubMed]
25. Young, A.; Márquez-Grant, N.; Stillman, R.; Smith, M.J.; Korstjens, A.H. An Investigation of Red Fox (*Vulpes vulpes*) and Eurasian Badger (*Meles meles*) Scavenging, Scattering, and Removal of Deer Remains: Forensic Implications and Applications. *J. Forensic Sci.* **2015**, *60*, S39–S55. [CrossRef]
26. Inger, R.; Cox, D.T.C.; Per, E.; Norton, B.A.; Gaston, K.J. Ecological Role of Vertebrate Scavengers in Urban Ecosystems in the UK. *Ecol. Evol.* **2016**, *6*, 7015–7023. [CrossRef]
27. Barton, P.S.; Evans, M.J. Insect Biodiversity Meets Ecosystem Function: Differential Effects of Habitat and Insects on Carrion Decomposition. *Ecol. Entomol.* **2017**, *42*, 364–374. [CrossRef]
28. Sugiura, S.; Hayashi, M. Functional Compensation by Insular Scavengers: The Relative Contributions of Vertebrates and Invertebrates Vary among Islands. *Ecography* **2018**, *41*, 1173–1183. [CrossRef]
29. Inagaki, A.; Allen, M.L.; Maruyama, T.; Yamazaki, K.; Tochigi, K.; Naganuma, T.; Koike, S. Vertebrate Scavenger Guild Composition and Utilization of Carrion in an East Asian Temperate Forest. *Ecol. Evol.* **2020**, *10*, 1223–1232. [CrossRef]
30. Moleón, M.; Sánchez-Zapata, J.A.; Selva, N.; Donázar, J.A.; Owen-Smith, N. Inter-Specific Interactions Linking Predation and Scavenging in Terrestrial Vertebrate Assemblages. *Biol. Rev.* **2014**, *89*, 1042–1054. [CrossRef]
31. Moleón, M.; Selva, N.; Sánchez-Zapata, J.A. The Components and Spatiotemporal Dimension of Carrion Biomass Quantification. *Trends Ecol. Evol.* **2020**, *35*, 91–92. [CrossRef] [PubMed]
32. Mateo-Tomás, P.; Olea, P.P.; Moleón, M.; Vicente, J.; Botella, F.; Selva, N.; Viñuela, J.; Sánchez-Zapata, J.A. From Regional to Global Patterns in Vertebrate Scavenger Communities Subsidized by Big Game Hunting. *Divers. Distrib.* **2015**, *21*, 913–924. [CrossRef]
33. Sebastián-González, E.; Moleón, M.; Gibert, J.P.; Botella, F.; Mateo-Tomás, P.; Olea, P.P.; Guimarães, P.R., Jr.; Sánchez-Zapata, J.A. Nested Species-Rich Networks of Scavenging Vertebrates Support High Levels of Interspecific Competition. *Ecology* **2016**, *97*, 95–105. [CrossRef] [PubMed]
34. Sebastián-González, E.; Morales-Reyes, Z.; Botella, F.; Naves-Alegre, L.; Pérez-García, J.M.; Mateo-Tomás, P.; Olea, P.P.; Moleón, M.; Barbosa, J.M.; Hiraldo, F.; et al. Functional Traits Driving Species Role in the Structure of Terrestrial Vertebrate Scavenger Networks. *Ecology* **2021**, *102*, e03519. [CrossRef] [PubMed]
35. Probst, C.; Gethmann, J.; Amler, S.; Globig, A.; Knoll, B.; Conraths, F.J. The Potential Role of Scavengers in Spreading African Swine Fever among Wild Boar. *Sci. Rep.* **2019**, *9*, 11450. [CrossRef] [PubMed]
36. Baz, A.; Botías, C.; Martín-Vega, D.; Cifrián, B.; Díaz-Aranda, L.M. Preliminary Data on Carrion Insects in Urban (Indoor and Outdoor) and Periurban Environments in Central Spain. *Forensic Sci. Int.* **2015**, *248*, 41–47. [CrossRef]
37. Sugiura, S.; Tanaka, R.; Taki, H.; Kanzaki, N. Differential Responses of Scavenging Arthropods and Vertebrates to Forest Loss Maintain Ecosystem Function in a Heterogeneous Landscape. *Biol. Conserv.* **2013**, *159*, 206–213. [CrossRef]
38. Henrich, M.; Tietze, D.T.; Wink, M. Scavenging of Small Bird Carrion in Southwestern Germany by Beetles, Birds and Mammals. *J. Ornithol.* **2017**, *158*, 287–295. [CrossRef]
39. Muñoz-Lozano, C.; Martín-Vega, D.; Martínez-Carrasco, C.; Sánchez-Zapata, J.A.; Morales-Reyes, Z.; Gonzálvez, M.; Moleón, M. Avoidance of Carnivore Carcasses by Vertebrate Scavengers Enables Colonization by a Diverse Community of Carrion Insects. *PLoS ONE* **2019**, *14*, e0221890. [CrossRef]
40. Sawyer, S.J.; Eubanks, M.D.; Beasley, J.C.; Barton, B.T.; Puckett, R.T.; Tomeček, J.M.; Tomberlin, J.K. Vertebrate and Invertebrate Competition for Carrion in Human-Impacted Environments Depends on Abiotic Factors. *Ecosphere* **2022**, *13*, e4151. [CrossRef]
41. Dekeirsschieter, J.; Verheggen, F.J.; Haubruge, E.; Brostaux, Y. Carrion Beetles Visiting Pig Carcasses during Early Spring in Urban, Forest and Agricultural Biotopes of Western Europe. *J. Insect Sci.* **2011**, *11*, 73. [CrossRef]
42. Charabidze, D.; Vincent, B.; Pasquerault, T.; Hedouin, V. The Biology and Ecology of *Necrodes littoralis*, a Species of Forensic Interest in Europe. *Int. J. Legal Med.* **2016**, *130*, 273–280. [CrossRef] [PubMed]
43. Saito, M.; Koike, F. Distribution of Wild Mammal Assemblages along an Urban–Rural–Forest Landscape Gradient in Warm-Temperate East Asia. *PLoS ONE* **2013**, *8*, e65464. [CrossRef] [PubMed]
44. Saito, M.U.; Koike, F. Trait-Dependent Changes in Assemblages of Mid-Sized and Large Mammals along an Asian Urban Gradient. *Acta Oecol.* **2015**, *67*, 34–39. [CrossRef]
45. Fusco, N.A.; Zhao, A.; Munshi-South, J. Urban Forests Sustain Diverse Carrion Beetle Assemblages in the New York City Metropolitan Area. *PeerJ* **2017**, *5*, e3088. [CrossRef] [PubMed]
46. Welti, N.; Scherler, P.; Grüebler, M.U. Carcass Predictability but Not Domestic Pet Introduction Affects Functional Response of Scavenger Assemblage in Urbanized Habitats. *Funct. Ecol.* **2020**, *34*, 265–275. [CrossRef]
47. Shizukuda, K.; Saito, M.U. Effects of Human-Dominated Landscape on the Community Structure of Silphid and Dung Beetles Collected by Carrion Pitfall Traps. *Entomol. Sci.* **2021**, *24*, 157–168. [CrossRef]
48. Barko, V.A.; Feldhamer, G.A.; Nicholson, M.C.; Davie, D.K. Urban Habitat: A Determinant of White-Footed Mouse (*Peromyscus leucopus*) Abundance in Southern Illinois. *Southeast. Nat.* **2003**, *2*, 369–376. [CrossRef]
49. Silva, M.; Hartling, L.; Opps, S.B. Small Mammals in Agricultural Landscapes of Prince Edward Island (Canada): Effects of Habitat Characteristics at Three Different Spatial Scales. *Biol. Conserv.* **2005**, *126*, 556–568. [CrossRef]
50. Heroldová, M.; Bryja, J.; Zejda, J.; Tkadlec, E. Structure and Diversity of Small Mammal Communities in Agriculture Landscape. *Agric. Ecosyst. Environ.* **2007**, *120*, 206–210. [CrossRef]

51. Japan Meteorological Agency Normal Value 2020. Available online: http://www.data.jma.go.jp/obd/stats/etrn/view/nml_amd_ym.php?prec_no=35&block_no=0263&year=&month=&day=&view=a (accessed on 1 December 2020).
52. Takenaka, A. CanopOn 2. Available online: http://takenaka-akio.org/etc/canopon2/ (accessed on 20 February 2023).
53. Wolf, J.M.; Gibbs, J.P. Silphids in Urban Forests: Diversity and Function. *Urban Ecosyst.* **2004**, *7*, 371–384. [CrossRef]
54. Ito, M. Study of Community Assembly Patterns and Interspecific Interactions Involved in Insect Succession on Rat Carcasses. *Entomol. Sci.* **2020**, *23*, 105–116. [CrossRef]
55. Trumbo, S.T.; Bloch, P.L. Habitat Fragmentation and Burying Beetle Abundance and Success. *J. Insect Conserv.* **2000**, *4*, 245–252. [CrossRef]
56. Lindgren, N.K.; Bucheli, S.R.; Archambeault, A.D.; Bytheway, J.A. Exclusion of Forensically Important Flies Due to Burying Behavior by the Red Imported Fire Ant (*Solenopsis invicta*) in Southeast Texas. *Forensic Sci. Int.* **2011**, *204*, e1–e3. [CrossRef]
57. Eubanks, M.D.; Lin, C.; Tarone, A.M. The Role of Ants in Vertebrate Carrion Decomposition. *Food Webs* **2019**, *18*, e00109. [CrossRef]
58. Firth, D. Bias Reduction of Maximum Likelihood Estimates. *Biometrika* **1993**, *80*, 27–38. [CrossRef]
59. Albert, A.; Anderson, J.A. On the Existence of Maximum Likelihood Estimates in Logistic Regression Models. *Biometrika* **1984**, *71*, 1–10. [CrossRef]
60. Heinze, G.; Schemper, M. A Solution to the Problem of Monotone Likelihood in Cox Regression. *Biometrics* **2001**, *57*, 114–119. [CrossRef]
61. Heinze, G.; Schemper, M. A Solution to the Problem of Separation in Logistic Regression. *Stat. Med.* **2002**, *21*, 2409–2419. [CrossRef]
62. R Core Team. *R: A Language and Environment for Statistical Computing*; R Foundation for Statistical Computing: Vienna, Austria, 2019.
63. Růžička, J. Seasonal Activity and Habitat Associations of Silphidae and Leiodidae: Cholevinae (Coleoptera) in Central Bohemia. *Acta. Soc. Zool. Bohem.* **1994**, *58*, 67–78.
64. Lingafelter, S.W. Diversity, Habitat Preferences, and Seasonality of Kansas Carrion Beetles (Coleoptera: Silphidae). *J. Kansas Entomol. Soc.* **1995**, *68*, 214–223.
65. Nagano, M.; Suzuki, S. Phenology and Habitat Use among Nicrophorine Beetles of the Genus *Nicrophorus* and *Ptomascopus* (Coleoptera: Silphidae). *Edaphologia* **2003**, *73*, 1–9. [CrossRef]
66. Suwabe, M.; Ohnishi, H.; Kikuchi, T.; Kawara, K.; Tsuji, K. Difference in Seasonal Activity Pattern between Non-Native and Native Ants in Subtropical Forest of Okinawa Island, Japan. *Ecol. Res.* **2009**, *24*, 637–643. [CrossRef]
67. Zabala, J.; Díaz, B.; Saloña-Bordas, M.I. Seasonal Blowfly Distribution and Abundance in Fragmented Landscapes. Is It Useful in Forensic Inference about Where a Corpse Has Been Decaying? *PLoS ONE* **2014**, *9*, e99668. [CrossRef]
68. Ueda, A. Response of assemblages of carrion beetles (Carrion Silphid and Scarabaeoid dung beetles) in a forest consisting of small, different-aged stands. *J. Jpn. For. Soc.* **2016**, *98*, 207–213, (In Japanese with English summary). [CrossRef]
69. Satou, A.; Nisimura, T.; Numata, H. Reproductive Competition between the Burying Beetle *Nicrophorus quadripunctatus* without Phoretic Mites and the Blow Fly *Chrysomya pinguis*. *Entomol. Sci.* **2000**, *3*, 265–268.
70. Suzuki, S.; Nagano, M. Resource Guarding by *Ptomascopus morio*: Simple Parental Care in the Nicrophorinae (Coleoptera: Silphidae). *Eur. J. Entomol.* **2006**, *103*, 245–248. [CrossRef]
71. Schwartz, A.L.W.; Williams, H.F.; Chadwick, E.; Thomas, R.J.; Perkins, S.E. Roadkill Scavenging Behaviour in an Urban Environment. *J. Urban Ecol.* **2018**, *4*, juy006. [CrossRef]
72. De Carvalho Moretti, T.; Solis, D.R.; Godoy, W.A.C. Ants (Hymenoptera: Formicidae) Collected with Carrion-Baited Traps in Southeast Brazil. *Open Forensic Sci. J.* **2013**, *6*, 1–5. [CrossRef]
73. Hosaka, T.; Di, L.; Eguchi, K.; Numata, S. Ant Assemblages on Littered Food Waste and Food Removal Rates in Urban–Suburban Parks of Tokyo. *Basic. Appl. Ecol.* **2019**, *37*, 1–9. [CrossRef]
74. Gatesire, T.; Nsabimana, D.; Nyiramana, A.; Seburanga, J.L.; Mirville, M.O. Bird Diversity and Distribution in Relation to Urban Landscape Types in Northern Rwanda. *Sci. World J.* **2014**, *2014*, 157824. [CrossRef] [PubMed]
75. Ruxton, G.D.; Houston, D.C. Obligate Vertebrate Scavengers Must Be Large Soaring Fliers. *J. Theor. Biol.* **2004**, *228*, 431–436. [CrossRef] [PubMed]
76. Azuma, A.; Tokita, K.; Takeuchi, K.; Tsunekawa, A. Land condition of Gray-faced Buzzard, *Butastur indicus* habitats in watershed of Tega Marsh, Chiba Prefecture. *J. Rural Plan. Assoc.* **1999**, *18*, 253–258, (In Japanese with English summary). [CrossRef]
77. Momose, H.; Ueta, M.; Fujiwara, N.; Uchiyama, T.; Ishizaka, T.; Morisaki, K.; Matsue, M. Factors affecting the number of breeding grey-faced buzzard-eagles *Butastur indicus*. *J. Jpn. Inst. Landsc. Archit.* **2005**, *68*, 555–558, (In Japanese with English summary). [CrossRef]
78. Kadoya, T.; Washitani, I. The Satoyama Index: A Biodiversity Indicator for Agricultural Landscapes. *Agric. Ecosyst. Environ.* **2011**, *140*, 20–26. [CrossRef]

79. Shiu, H.-J.; Tokita, K.; Morishita, E.; Hiraoka, E.; Wu, Y.; Nakamura, H.; Higuchi, H. Route and Site Fidelity of Two Migratory Raptors: Grey-Faced Buzzards *Butastur indicus* and Honey-Buzzards *Pernis apivorus*. *Ornithol. Sci.* **2006**, *5*, 151–156. [CrossRef]
80. Enari, H.; Enari, H.S. Not Avian but Mammalian Scavengers Efficiently Consume Carcasses under Heavy Snowfall Conditions: A Case from Northern Japan. *Mamm. Biol.* **2021**, *101*, 419–428. [CrossRef]