

# Effects of interannual snowfall variation on mammal consumption by mesocarnivores in a snowy area of northern Japan

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## Abstract:

Understanding the mechanisms by which climate change affects food webs is essential for predicting shifts in community structure and ecosystem functioning. Although the impacts of increasing temperatures and changing precipitation patterns on mesocarnivore diets are well documented, the influence of snowfall variation on their trophic interactions remains poorly understood, particularly based on multi-year dietary datasets. This study evaluated how interannual snowfall variation influences mammalian consumption by red foxes and Japanese martens during winter in northern Japan, one of the world's snowiest regions. Fecal samples were collected over five winters between 2019 and 2024 in and around forested areas of Tsuruoka City, northeastern Japan. Mammalian prey remains identified in fecal samples were classified into three categories: small mammals, lagomorphs, and medium- to large-sized mammals. We evaluated the effects of snowfall variation on mammal consumption using generalized linear models. The results demonstrated that low snowfall significantly increased the consumption of small mammals by mesocarnivores, whereas the consumption of lagomorphs and other mammals was unaffected by snowfall patterns. These findings suggest that mesocarnivores adjust their diet flexibly in response to snowfall changes. A long-term decline in snowfall may increase the predation success of mesocarnivores on small mammals, potentially affecting their population dynamics. Further research is required to elucidate how shifting snow conditions, driven by ongoing climate change, influence mammalian species interactions and their broader impacts on communities and ecosystems.

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## Short title

Effects of snowfall variation on mesocarnivore diets

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## Abstract

Understanding the mechanisms by which climate change affects food webs is essential for predicting shifts in community structure and ecosystem functioning. Although the impacts of increasing temperatures and changing precipitation patterns on mesocarnivore diets are well documented, the influence of snowfall variation on their trophic interactions remains poorly understood, particularly based on multi-year dietary datasets. This study evaluated how interannual snowfall variation influences mammalian consumption by red foxes and Japanese martens during winter in northern Japan, one of the world's snowiest regions. Fecal samples were collected over five winters between 2019 and 2024 in and around forested areas of Tsuruoka City, northeastern Japan. Mammalian prey remains identified in fecal samples were classified into three categories: small mammals, lagomorphs, and medium- to large-sized mammals. We evaluated the effects of snowfall variation on mammal consumption using generalized linear models. The results demonstrated that low snowfall significantly increased the consumption of small mammals by mesocarnivores, whereas the consumption of lagomorphs and other mammals was unaffected by snowfall patterns. These findings suggest that mesocarnivores adjust their diet flexibly in response to snowfall changes. A long-term decline in snowfall may increase the predation success of mesocarnivores on small mammals, potentially affecting their population dynamics. Further research is required to elucidate how shifting snow conditions, driven by ongoing climate change, influence mammalian species interactions and their broader impacts on communities and ecosystems.

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26 *melampus*

## 27 Introduction

28 Understanding the mechanisms by which climate change affects food webs is critical for  
29 predicting shifts in population dynamics, community structure, and biodiversity trends.  
30 Previous studies have shown a relationship between food webs, temperature, and rainfall  
31 patterns (e.g., Rosenblatt and Schmitz 2016); however, the impact of snowfall pattern shifts on  
32 food webs has been overlooked. Under global climate change, total seasonal snowfall is  
33 projected to decline in many regions, while extreme snowfall events may become more frequent  
34 and intense (Williams et al. 2015). Given that snow creates seasonally unique environmental  
35 conditions and drives ecosystem processes across vast regions of the Northern Hemisphere  
36 (Niittynen et al. 2018; Callaghan et al. 2011), elucidating how snowfall patterns affect food  
37 webs is essential for predicting the ecological consequences of global climate change. However,  
38 these responses remain poorly characterized (Penczykowski et al. 2017).

39 In particular, understanding the effects of snowfall patterns on foraging strategies of  
40 mesocarnivores, defined as small- and medium-sized (< 15 kg) carnivorans, is important,  
41 given their role in ecological communities and ecosystem processes (Roemer et al. 2009). For  
42 instance, predation pressure can influence the behavior and population dynamics of prey  
43 species (Murano et al. 2022; Moll et al. 2020; Prugh et al. 2009). Mesocarnivores also  
44 facilitate energy and nutrient cycling in ecosystems by consuming dead animals (Rietz et al.  
45 2024; Shizukuda and Saito 2023; Wilson and Wolkovich 2011; DeVault et al. 2003). These  
46 trophic interactions modulate plant communities and landscape structure through cascading  
47 effects (Maron et al. 2006; Croll et al. 2005; Hambäck et al. 2004; Norrdahl et al. 2002) and  
48 facilitate key ecological services such as pest regulation and disease control (Patterson et al.

2022; Lim et al. 2020; Williams et al. 2018; Ćirović et al. 2016; DeVault et al. 2003).

Therefore, understanding how shifting snowfall patterns alter their foraging strategies is important for assessing the impacts on prey mammal population dynamics and ecosystem consequences.

Previous studies have suggested that snow cover affects the availability of prey for mesocarnivores through several mechanisms. First, snow cover can create subnivean spaces which act as a shelter for small mammals, enabling them to avoid predators (Murano et al. 2022). Second, snow cover can provide an escape advantage for prey mammals with low foot loading (small mass relative to foot area), such as hares, while simultaneously increasing the movement costs for larger-bodied mesocarnivores (Penczykowski et al. 2017). Third, snow cover can increase scavenging opportunities for mesocarnivores by precipitating higher mortality among large ungulates through elevated movement costs and reduced access to food resources (Okarma et al. 1995; Ochiai et al. 1993). Thus, interannual variation in snowfall may affect food habits of mesocarnivores by altering the availability of prey resources. However, empirical studies investigating the relationship between interannual snowfall variation and mammalian prey consumption by mesocarnivores are limited.

The red fox (*Vulpes vulpes*) and Japanese marten (*Martes melampus*) are common mesocarnivores active during winter in the heavy snowfall regions of northern Japan (Suzuki and Saito 2024; Watabe and Saito 2022). Both species are omnivorous and their diets vary seasonally, with mammalian prey becoming particularly important during winter and spring (Enomoto et al. 2023; Hisano et al. 2022). Among mammalian prey, they frequently consume small mammals such as rodents and insectivores (Tsunoda et al. 2026; Hisano et al. 2022). Red foxes are known to catch subnivean small mammals by plunging into the snowpack (Yuk et al. 2024). Although the winter hunting behavior of the Japanese marten remains poorly understood, a closely related species, the American marten (*Martes americana*), is known to

76 forage for subnivean small mammals by accessing subnivean spaces through snow excavation  
77 or areas of reduced snow cover around fallen logs and other structures (Jung et al. 2021). In  
78 addition to small mammals, both mesocarnivores also prey on hares and consume the  
79 carcasses beneath snow (Tsunoda et al. 2026; Enari and Enari 2021). These mesocarnivores  
80 exhibit flexible foraging strategies and adjust their diet in response to environmental  
81 conditions. Therefore, multi-year studies of their winter diets provide an important insight  
82 into how interannual snowfall variation influences mammalian prey consumption by  
83 mesocarnivores.

84 In this study, we aimed to reveal the effect of interannual snowfall variations on  
85 mammal consumption by red foxes and Japanese martens. We investigated dietary patterns of  
86 them over multiple years with varying snowfall in northern Japan. We hypothesized that  
87 during years of low snowfall, mesocarnivores would: (1) consume more small mammals due  
88 to reduced subnivean shelter provided by snow cover; (2) consume more lagomorphs due to  
89 the decrease in their escape advantage; and (3) consume fewer medium- and large-sized  
90 mammals due to reduced carrion supply.

## 91 **Materials and methods**

### 92 *Study area*

93 This study was conducted in and around forested areas of Tsuruoka City, Yamagata  
94 Prefecture, northeastern Japan (Fig. 1). The study area ranged from approximately 90-770 m  
95 a.s.l. and covered approximately 640 km<sup>2</sup>. This area has a cool-temperate climate, with a  
96 mean winter (December–March) temperature of 3.7 °C and a mean total winter precipitation  
97 of 868.9 mm in the 2020–2024 period (Japan Meteorological Agency 2025). The study area  
98 mostly comprises broad-leaved forests (primarily Japanese beeches; *Fagus crenata*),  
99 coniferous forests (primarily Japanese cedars; *Cryptomeria japonica*), agricultural land, and

101 residential areas (Fig. 1). The mammalian community in the study area includes several  
102 mesocarnivores in addition to the focal species (red fox and Japanese marten), such as  
103 raccoon dog (*Nyctereutes procyonoides*), masked palm civet (*Paguma larvata*), Japanese  
104 badger (*Meles anakuma*), and Japanese weasel (*Mustela itatsi*) (Suzuki and Saito 2024).  
105 Potential prey species include small mammals such as mouse-like rodents (e.g., large  
106 Japanese field mouse; *Apodemus speciosus*), shrews (e.g., Dsinezumi shrew; *Crocidura*  
107 *dsinezumi*), and moles (e.g., Japanese shrew-mole; *Urotrichus talpoides*), as well as Japanese  
108 squirrel (*Sciurus lis*) and Japanese hare (*Lepus brachyurus*) (Komine and Ishikawa 2026;  
109 Suzuki and Saito 2024). Other medium- to large-sized mammals present in the study area  
110 include species such as Japanese macaque (*Macaca fuscata*), wild boar (*Sus scrofa*), Asian  
111 black bear (*Ursus thibetanus*), Japanese serow (*Capricornis crispus*) (Suzuki and Saito 2024).

#### 112 *Fecal sampling and diet analysis*

113 Fresh fecal samples of red foxes and Japanese martens were collected during the snowfall  
114 season (primarily December–March) from February 2019 to February 2024. Sampling was  
115 not conducted during the snowfall season of 2021–2022 (December 2021–March 2022)  
116 (Table 1). We searched for feces by walking on snow and by driving along roads in the study  
117 area, and collected only those found on the snow surface. Feces in contact with the ground  
118 were excluded from the analysis because they may have been deposited during the non-  
119 snowfall season. Red fox and Japanese marten feces were distinguished by their diameter and  
120 shape, and nearby tracks on the snow (Enomoto et al. 2023; Nakane et al. 2022; Hisano et al.  
121 2017; Tsuji et al. 2011). All fecal samples were stored at approximately -20 °C until analysis.

122 Fecal samples were washed with water using a 0.5–1-mm sieve. Undigested  
123 mammals were sorted and classified into three categories (small mammals, lagomorphs, and  
124 other medium- to large-sized mammals; hereafter, other mammals) based on morphological

126 characteristics of guard hairs and their medullary structure examined under a microscope,  
127 following published hair identification guides and morphological criteria (Murai et al. 2011;  
128 Yoneda 1982). Small mammals (mouse-like rodents, shrews, and moles) were primarily  
129 identified based on hair size and structure (typically <1 cm in length). Lagomorphs (Japanese  
130 hare) were identified by their relatively long (2–3 cm), white guard hairs and characteristic  
131 medullary patterns. Other mammals were defined as all remaining mammalian prey items not  
132 classified as small mammals or lagomorphs. In all categories, bones, teeth, or claws were also  
133 used for identification. To evaluate general mammal consumption, the frequency of  
134 occurrence (FO; i.e., the proportion of samples containing a given food category in the total  
135 sample) was calculated for each food category.

#### 136 *Environmental data*

137 We used the snowfall data collected at Kushibiki observation station (38°40'18" N,  
138 139°50'56" E; 33 m a.s.l.), located approximately at the center of the study area; these data  
139 were obtained from the Japan Meteorological Agency (2025). Annual snowfall was defined as  
140 the total snowfall from November to April of the following year. The sampling date may not  
141 correspond to the time of fecal deposition, as fecal samples found on the snow surface may  
142 represent scats deposited earlier and later revealed by snowmelt. Therefore, we used annual  
143 snowfall values in the analyses, rather than values matched to the collection date of each scat.

#### 144 *Statistical analysis*

145 To evaluate the effects of interannual snowfall variations on the mammal consumption by red  
146 foxes and Japanese martens, we employed generalized linear models (GLM) for each prey  
147 category with a binomial distribution and a logit link function. The response variable was the  
148 number of fecal samples containing a given prey category out of the total number of samples

150 analyzed in each year. The explanatory variables were the annual snowfall (m) of the  
151 sampling year. We also calculated the pseudo- $R^2$  value, defined as (null deviance – residual  
152 deviance) / null deviance, to evaluate the goodness of model fit. Statistical analyses were  
153 performed using R ver. 4.5.0. (R core Team 2025).

## 154 Results

155 A total of 316 fecal samples were analyzed, including 176 from red foxes and 140 from  
156 Japanese martens (Table 1). Regarding general mammal consumption by red foxes, small  
157 mammals occurred in 53 samples (FO: 30.1%), lagomorphs occurred in 5 samples (2.8%),  
158 and other mammals occurred in 41 samples (23.3%). Similarly, in Japanese marten feces,  
159 small mammals occurred in 50 samples (35.7%), lagomorphs occurred in 9 samples (6.4%),  
160 and other mammals occurred in 24 samples (17.1%).

161 GLM analyses showed that snowfall variation partially influenced mammalian prey  
162 consumption by mesocarnivores. The consumption of small mammals was significantly  
163 higher in low-snowfall years for both red foxes ( $P = 0.049$ ) and Japanese martens ( $P = 0.016$ )  
164 (Fig. 2; Table S1). In contrast, no significant effects of annual snowfall variation were  
165 observed on consumption of lagomorphs or other mammals in both mesocarnivores (red  
166 foxes-lagomorphs:  $P = 0.988$ , Japanese martens-lagomorphs:  $P = 0.487$ , red foxes-other  
167 mammals:  $P = 0.249$ , Japanese martens-other mammals:  $P = 0.989$ ) (Fig. 2; Table S1).

168 For small mammal consumptions, the pseudo- $R^2$  values were 0.557 and 0.872 for the  
169 red fox and Japanese marten models, respectively. In contrast, pseudo- $R^2$  values were  
170 substantially lower for lagomorphs and other mammal consumption models (red fox-  
171 lagomorphs: 0.000049, Japanese marten-lagomorphs: 0.104, red fox-other mammals: 0.279,  
172 Japanese marten-other mammals: 0.000021) (Table S1).

## Discussion

Our results showed that interannual snowfall variations influence the mammal consumptions of red foxes and Japanese martens, based on multi-year dietary data within the same region. Notably, supporting only Hypothesis 1, both mesocarnivores consumed more small mammals during low-snow years. Deep snow cover provides shelter for small mammals to evade mesocarnivores (Willebrand et al. 2017). Thus, in low-snowfall years, the reduced depth of snow cover may have increased the accessibility of small mammals to mesocarnivores. Small mammals are fundamental prey for red foxes and martens (Tsunoda et al. 2026; Hisano et al. 2022; Hisano et al. 2019; Tsuji et al. 2019); consequently, climatic shifts that alter these trophic interactions could potentially impact both predator and prey population dynamics. Further studies are needed to evaluate how changes in predation rates associated with winter snowfall variability affect their annual populations.

Snowfall variation had no significant effect on lagomorph consumption by mesocarnivores, contrary to Hypothesis 2. These results suggest that snowfall variability may exert a limited influence on these predator–prey interactions, at least under the environmental conditions documented in this study; however, this finding should be interpreted with caution due to the consistently low frequency of lagomorph consumption. In the study area, total snowfall reached approximately 1 m, even in low-snow years; thus, lagomorphs may have been able to maintain their escape advantage in the year with the lowest snowfall. In the long term, climate change may lead to shifts in snow conditions and the eventual loss of snow cover (Kawase et al. 2021), which could alter trophic interactions, even in historically high-snowfall areas. Consequently, to fully evaluate the impact on trophic interactions, sustained long-term monitoring of mesocarnivore diet and population dynamics is essential.

In contrast with Hypothesis 3, snowfall variation had no significant effects on the consumption of other mammals by either mesocarnivore species. Previous studies have shown

200 that heavy snowfall increases the mortality of large ungulates (Okarma et al. 1995; Ochiai et  
201 al. 1993), which can increase the carrion supply for mesocarnivores. However, our results  
202 suggest that heavy snowfall did not necessarily lead to an increase in carrion availability for  
203 mesocarnivores. Heavy snowfall can trigger spatial niche shifts in large mammals (Enari et al.  
204 2024) and bury carrion under deep snow, potentially limiting their availability. Additionally,  
205 low temperatures and deep snow could increase the thermoregulatory and locomotion costs of  
206 mesocarnivores, restricting their activity budgets for scavenging (Enari and Enari 2021).

207 An important limitation of this study is its relatively short duration, which may not  
208 allow for a robust assessment of influence of snowfall variation on feeding strategies of  
209 mesocarnivores. In addition, temporal variations in the population dynamics of  
210 mesocarnivores and their prey were not considered in this study. As population densities can  
211 vary interannually and potentially influence trophic interactions (Gomo et al. 2021).  
212 Furthermore, although prey items were classified into broad taxonomic groups in this study,  
213 finer species-level resolution could provide more detailed insight into diet responses to  
214 snowfall variation. Snow conditions beyond annual snowfall, such as snow hardness, should  
215 be evaluated, as they could potentially influence the foraging strategies of mesocarnivores.  
216 Although our study provides initial insights into the influence of snowfall patterns on  
217 mammalian food webs, more long-term and detailed monitoring is needed to determine how  
218 climate-driven changes in snowfall affect mammalian trophic interactions.

219 This study showed the influence of interannual snowfall variation on the trophic  
220 interactions between mesocarnivores and small mammals, which are their main mammalian  
221 prey. These results suggest that a long-term decline in snowfall might increase the predation  
222 success of mesocarnivores on small mammals, potentially affecting their population  
223 dynamics. Furthermore, given the foundational roles of small mammals and mesocarnivores  
224 in ecosystems (Lacher et al. 2019; Roemer et al. 2009), understanding how these shifts trigger

226 cascading effects in ecosystems remains a crucial priority for future research. Our results also  
227 highlight the importance of long-term dietary monitoring to comprehensively understand  
228 feeding habits and characterize trophic interactions. Further studies are required to clarify  
229 how snowfall pattern shifts influence interactions among mammalian species, thereby shaping  
230 community structure and ecosystems under ongoing climate change.

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### 235 **Conflict of Interest**

236 The authors declare no conflict of interest.

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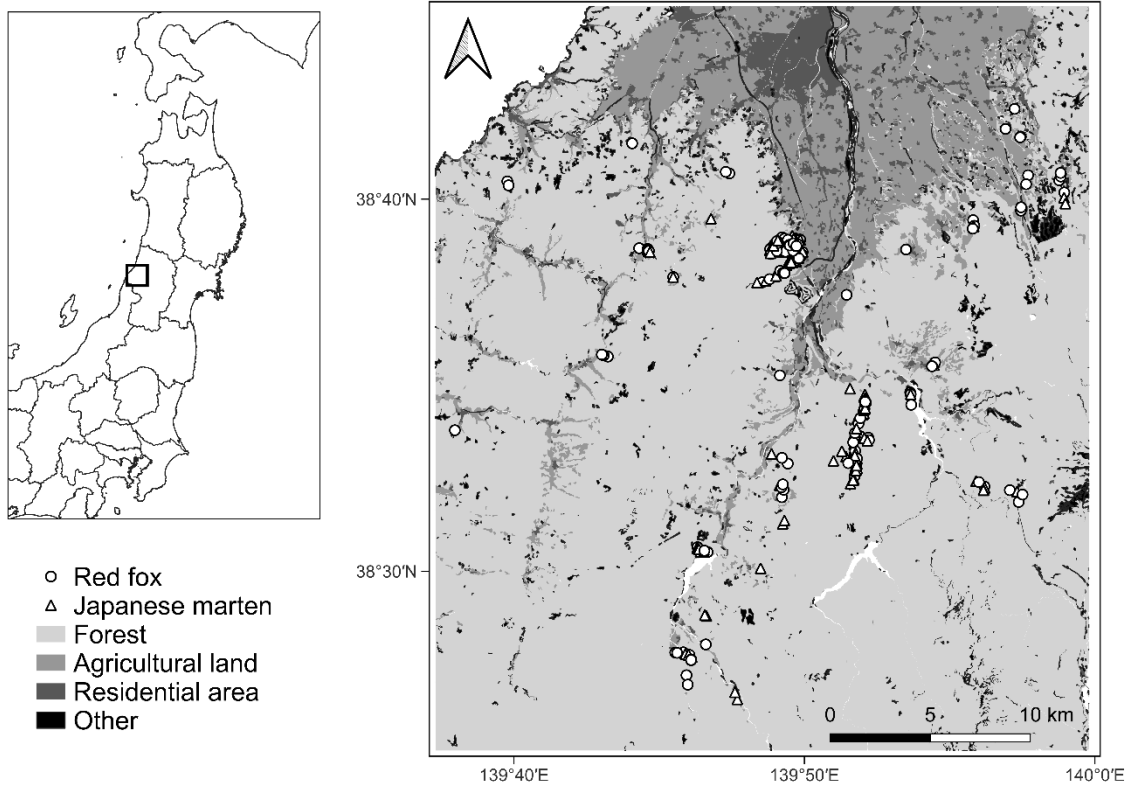
386 **Tables**

387 Table 1. Annual total snowfall, number of fecal samples collected, and frequency of occurrence (FO, %) of prey mammals in red fox and Japanese  
388 marten diets. The snowfall data was collected at Kushibiki observation station (38°40'18"N, E139°50'56"E), located near the center of the survey  
389 area and obtained from the Japan Meteorological Agency (2025). Annual snowfall represents the total snowfall from November of the given year to  
390 April of the following year.

Year	Total snowfall (m)	Red fox (n=176)				Japanese marten (n=140)			
		No. of fecal samples	Small mammals (FO, %)	Lagomorphs (FO, %)	Other mammals (FO, %)	No. of fecal samples	Small mammals (FO, %)	Lagomorphs (FO, %)	Other mammals (FO, %)
2018 (n=5)	3.93	3	0.0	33.3	0.0	2	50.0	50.0	0.0
2019 (n=61)	0.80	30	43.3	3.3	16.7	31	54.8	9.7	19.4
2020 (n=128)	4.01	52	21.2	1.9	23.1	76	28.9	5.3	22.4
2022 (n=107)	3.69	80	31.3	2.5	28.8	27	33.3	3.7	3.7
2023 (n=15)	2.42	11	36.4	0.0	9.1	4	25.0	0.0	0.0

402

Figures



403

**Fig1.** Study area and locations of sampling points of red fox and Japanese marten feces.

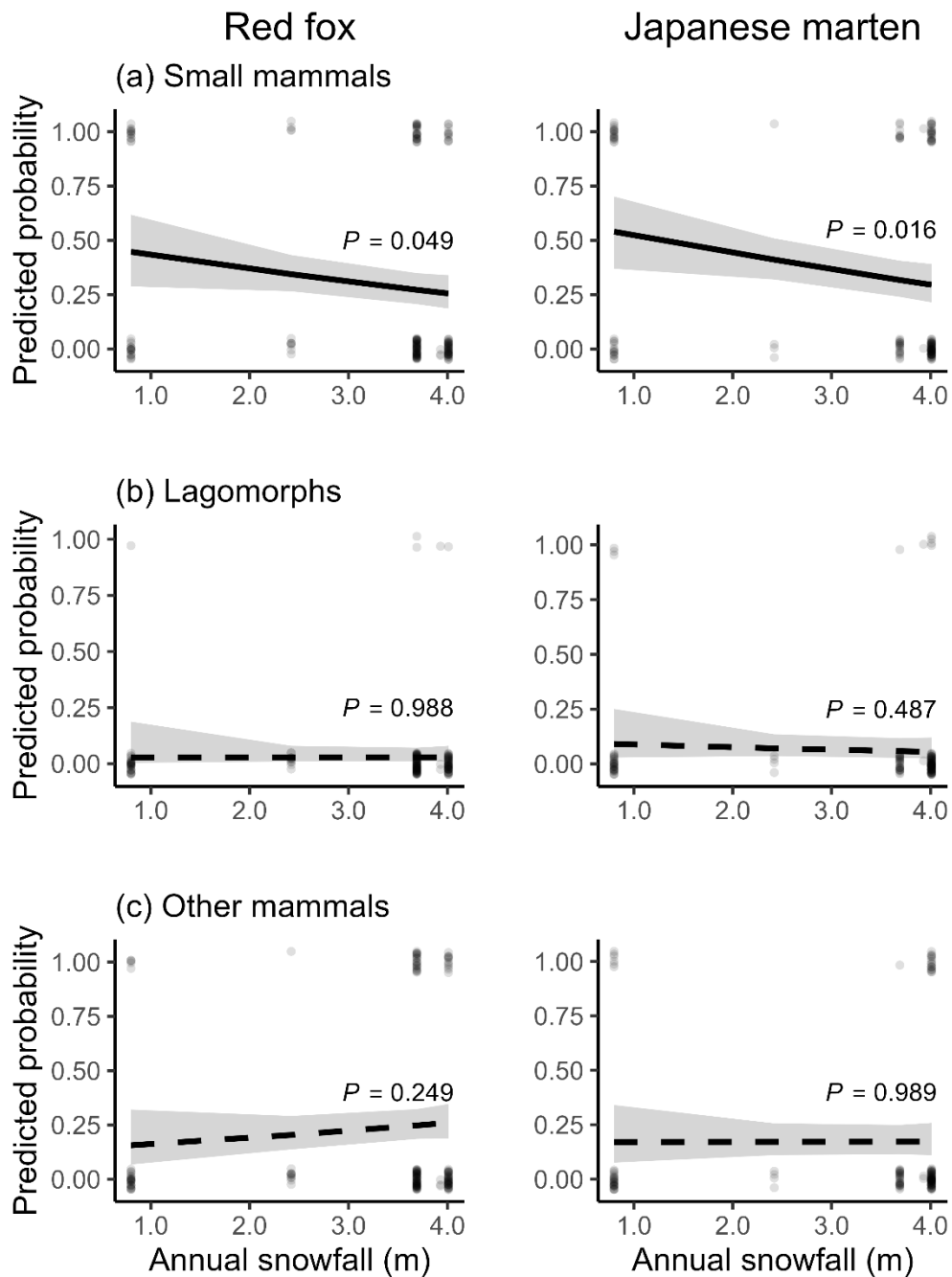
404

Land-use data were derived from the 1/25,000 vegetation data, a polygon-based digital

405

vegetation dataset, provided by the Ministry of the Environment (2012).

406



**Fig. 2** Relationships between occurrence of (a) small mammals, (b) lagomorphs, and (c) other mammals in red fox and Japanese marten feces, and total annual snowfall amount (m), estimated by logistic models. Dots represent observed values, lines represent estimates, and shading indicates the 95% confidence intervals of the model. Dots are vertically jittered slightly to reduce overplotting.

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