

Original investigation

**Thermal forest zone explains regional variations in the diet composition of the Japanese marten (*Martes melampus*)**

Masumi Hisano<sup>1\*</sup>, Chris Newman<sup>2</sup>, Shota Deguchi<sup>3,4</sup>, and Yayoi Kaneko<sup>5</sup>

<sup>1</sup>*Faculty of Natural Resources Management, Lakehead University, 955 Oliver Road, Thunder Bay, ON P7B 5E1, Canada*

<sup>2</sup>*Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, The Recanati-Kaplan Centre, Tubney House, Abingdon Road, Tubney, Oxon OX13 5QL, UK*

<sup>3</sup>*Graduate School of Science and Technology, Niigata University, Ikarashi 2-8050, Nishi-Ku, Niigata 950-2181, Japan*

<sup>4</sup>*Fukui City Museum of Natural History, Asuwakamicho 147, Fukui city Fukui, 918-8006, Japan.*

<sup>5</sup>*Carnivore Ecology and Conservation Research Group, Tokyo University of Agriculture and Technology, Saiwaicho 3-5-8, Fuchu City, Tokyo 183-8509, Japan*

\* Corresponding author. *Email address:* [mhisano@lakeheadu.ca](mailto:mhisano@lakeheadu.ca) (M. Hisano).

## ABSTRACT

Examining biogeographical variations in species' diet is important for linking key ecological traits between consumers and their environment. While the trophic ecology of the Holarctic martens has been globally synthesised, systematic information on the feeding ecology of martens (*Martes* spp.) in Asia is still deficient compared to species in Europe and North America. Here we conduct a meta-analysis based on literature describing regional and seasonal variation in diet composition of the Japanese marten (*Martes melampus*). Across nine study areas in the Japanese archipelago, annual marten diet mainly comprised fruits, invertebrates, and mammals. Cluster analysis divided these into three groups according to the similarity in composition. Dietary niche breadth and the relative frequency of occurrence of the mammalian prey was significantly higher in sub-alpine/cool-temperate than warm-temperate thermal forest zones, whereas the occurrence of fruits was significantly higher in warm-temperate than sub-alpine/cool-temperate zones. Seasonal analysis showed significant effects across all four seasons on the frequency of occurrence of mammals, invertebrates, and fruits. The Japanese marten is a flexible and opportunistic feeder with the potential to maintain its key macronutrient requirements by adapting its feeding strategy to changes in resource variability and environmental conditions. This trophic plasticity may advantage the Japanese marten in coping with human-induced rapid

35 environmental change, as global analysis has projected for martens across other regions.

36

37 **Keywords:** Adaptive foraging; Biogeography; Climate; Dietary switching; Optimal foraging

## Introduction

Dietary examination is essential to fully understand the ecology and life-history strategies of species (Carr and Macdonald, 1986; Machovsky-Capuska et al., 2016), where the seasonal and spatial distribution of trophic resources can influence optimal foraging strategies, socio-spatial organisation, and mating systems (Macdonald and Johnsodn, 2015). Among available prey types, food choices are determined by various factors, including prey abundance, availability, quality (i.e., macro- and micro-nutrient, Mayntz et al., 2005; Machovsky-Capuska et al., 2016; and toxin content, Skelhorn and Rowe, 2007), and the energy expended while detecting, capturing, and handling these prey, along with the risk of predator injury (Pyke et al., 1977; Sundell et al., 2003). Predators thus generally favour prey types ranked highest by the ratio of energy gained to costs incurred by prey acquisition (Charnov, 1976).

Many species have evolved flexible strategies to exploit varied food sources, especially among opportunistic generalist carnivores, such as martens (*Martes* spp.; Zhou et al., 2011a). Martens are flexible food exploitation and composition generalists, feeding on various food types in different combinations/ratios (Machovsky-Capuska et al., 2016), with diets that interact substantially with regional primary productivity, connected to environmental and climatic conditions (Zalewski, 2004; Zhou et al., 2011, 2013; but see Remonti et al., 2016). Collectively,

a global analysis by Zhou et al. (2011a) showed that trophic diversity and niche breadth of Holarctic *Martes* species (eight species; Macdonald et al., 2017) are influenced significantly by geo-climatic conditions. This analysis was, however, based largely on data from Europe (pine marten (*Martes martes*) and stone marten (*M. foina*)) and North America (American marten (*M. americana*)/Pacific marten (*M. caurina*)) because of the greater number of publications arising from these regions compared to Asian countries. Moreover, how marten food composition is affected by seasonality and geo-climatic factors has only been examined for European species (the pine marten (Zalewski, 2004; Remonti et al., 2016) and the stone marten (Papakosta et al., 2014)). In comparison, systematic dietary information for Asian *Martes* species is data deficient, despite importance for formulating a comprehensive understanding of adaptive feeding behaviour in Holarctic martens, which is fundamental for linking their key ecological traits as consumers with their environment (e.g., Zhou et al., 2011a).

In this study, we focus on the Japanese marten (*M. melampus*), which is better known than other Asian martens and has been the subject of a sufficient number of dietary studies to support statistical analysis (cf. in a global analysis, Zhou et al. (2011a) compiled 36 publications for European martens and 15 for North American martens, but just six for the Japanese marten and only two for the sable (*M. zibellina*); note that other Asian martens, sub-genus *Charronia* (*M.*

72 *flavigula*/*M. gwatkinsii*), were not included). The Japanese marten is endemic to the Japanese  
73 islands of Honshu, Shikoku and Kyushu, and was introduced into Hokkaido and the Sado Island  
74 (Murakami and Ohtaishi, 2000) where they are not naturally indigenous. The endemic Japanese  
75 marten population is stable (Proulx et al., 2004; Masuda, 2009) and listed as ‘Least Concern’ on  
76 the IUCN Red List of Threatened Species (Abramov et al., 2015). Nevertheless, conservation  
77 efforts are still required for some local populations, which are listed in Japan’s national/regional  
78 red lists (e.g., ‘Nearly Threatened’ in Gunma Prefecture (2012), Aichi Prefecture (2015),  
79 Tsushima Island (Ministry of the Environment, 2017)) due to their sensitivity to habitat  
80 loss/fragmentation from forestry and urban development (Tatara and Doi, 1994; Proulx et al.,  
81 2004; Abramov et al., 2015). Furthermore, due to their wide trophic niche breadth, management  
82 of the Japanese marten is important when they predate protected prey species. For instance, in  
83 Sado Island, the marten was introduced to help control problematic hare (*Lepus brachyurus*)  
84 populations, which cause damage to commercial forestry. This has, however, caused unforeseen  
85 problems with martens hunting the Island’s highly vulnerable population of Japanese crested ibis  
86 (*Nipponia nippon*) (Osada, 2012), which was once extirpated, but was re-introduced in 2008  
87 (listed as ‘Endangered’ on the IUCN Red List of Threatened Species; BirdLife International,  
88 2016). Clearly, understanding the diet and range of prey utilised by the Japanese marten is a

research priority (Hisano and Deguchi, 2018), necessary to inform both effective conservation and management policy (Proulx et al., 2004).

Including the latest publications as well as local anecdotal reports, here we (i) undertake a meta-analysis of the general diet composition of the Japanese marten; and (ii) investigate whether, and how, food type selection is associated with thermal forest zonation (which categorises unified climatic conditions arising through interaction between latitude, elevation, etc.; Kira, 1991) and seasonality (Zalewski, 2004; Díaz-Ruiz et al., 2013). We predict that, Japanese marten diet from within the same thermal forest zones will exhibit similar typologies, with diet composition adapting to temporal changes in seasonal food availability.

## **Material and methods**

### *Literature compilation*

We browsed both peer-reviewed papers and non-reviewed regional/local reports published by municipal governments on food types consumed by the Japanese marten (including a subspecies, the Tsushima marten (*M. melampus tsuensis*) in Tsushima Island, southern Japan) written in English and in Japanese up until April 2017, using *Google Scholar* (<https://scholar.google.com>), *ISI Web of Science* (<http://apps.webofknowledge.com>), and *Citation Information by National*

106 *Institute of Informatics* (<http://ci.nii.ac.jp>). We used various combinations of keywords: in  
107 English, “Japanese marten”, “*Martes melampus*”, “diet”, “food”, “frugivory”, “seed”; and in  
108 Japanese, “tenn” (martens), “Hondo-tenn” (the Japanese marten), “Nihon-tenn” (a synonym of  
109 the Japanese marten), “Tsushima-tenn” (the subspecies *M. melampus tsuensi*), “shushi-sanpu”  
110 (seed dispersal), and “shokusei” (diet). In addition, we also included regional government reports  
111 already known to us (Kanto Regional Office 2011, 2012, 2013, 2014) (Fig. 1).

112         We extracted two independent datasets from the mixed formats used in these reports,  
113 according with our objectives: (a) annual diet composition; and (b) seasonal diet composition.  
114 These required standardisation for quality prior to analysis, and we set the following criteria for  
115 inclusion; studies must have: (i) examined > 60 scats or stomachs for annual analysis, and > 15  
116 for each seasonal analysis (Zhou et al., 2011a; Díaz-Ruiz et al., 2013); (ii) reported all  
117 recognisable prey taxa (i.e., studies focused only on dominant foods or single taxa such as those  
118 exclusive for frugivory were not included); and (iii) covered at least one entire year for annual  
119 analysis and three seasonally consecutive months for seasonal analysis (spring: March – May;  
120 summer: June – August; autumn: September – November; winter: December – February; based  
121 on Nakamura et al., 2001); for example, Adachi et al. (2016a), which lacked dietary information  
122 for February, was excluded from the annual and winter seasonal dataset. Additionally, we



123 excluded Shiratsuki et al. (1973) because it presented data from across multiple regions. We also  
124 excluded dietary data from higher elevations (1,600 m – 2,600 m above sea level (a.s.l.))  
125 reported by Suzuki (1977), which did not meet our requirements for dataset standardisation;  
126 although we did include data from the lower elevations (1,200 – 1,600 m a.s.l.).

127

#### 128 *Data extraction*

129 From the text, tables and figures in studies that satisfied our criteria, we extracted values of the  
130 relative frequency of occurrence [RFO (%): the number of occurrences of each food category /  
131 the total number of food categories occurring  $\times 100$ ] and compatible metrics, such as the number  
132 of items belonging to each food category that occurred ( $n$ : trophic diversity), the frequency of  
133 occurrence [FO (%): the number of occurrences of each food item / the total numbers of faeces  
134 examined  $\times 100$ ], along with the sample size of number of faeces or stomachs examined. When  
135 necessary, *Plot Digitizer ver. 2.6.8.* (<http://plotdigitizer.sourceforge.net>) was used to digitise  
136 graphs to obtain values. To compile annual and seasonal dietary data, food types consumed were  
137 divided into six main categories: ‘mammals’, ‘birds’, ‘herptiles’ (reptiles and amphibians),  
138 ‘invertebrates’, ‘fruits’ (incl. hard fruits (pomes/drupes), citrus, berries and seeds), and ‘others’  
139 (minor foods not classified into other categories: fishes, fungi, human refuse, etc.). Note that, for

convenience, seeds of forbs/graminoids were categorised into ‘fruits’ (Hisano et al., 2017; Hisano and Deguchi, 2018). Some studies included martens’ own hairs and incidental plant materials (e.g., grasses, twigs) while some did not; hence for standardisation we excluded these items from our dataset.

Based on these six food categories, we initially calculated RFO, which provides an appropriate dietary comparison between different populations (e.g., Lozano et al., 2006; Zhou et al., 2011a) (among literature reviewed, only three studies presented biomass/volume information). We used RFO for annual food composition analysis.

Regarding seasonal studies, only two studies had compatible RFO values, and not all annual RFO data were suitable for being divided into seasonal data due to a deficiency of seasonal information (i.e., lacking the number of food categories occurring per season, or the number of faecal samples examined per season). As an alternative, we specifically calculated FO for the seasonal dataset, which has also been used widely for dietary meta-analysis studies of carnivores (e.g., Díaz-Ruiz et al., 2013; Doherty et al., 2015). We thus analysed seasonal FO data independently of annual RFO data.

156 *Environmental variables*

157 Previous meta-analyses of small carnivore diets have examined the relationship between dietary  
158 characteristics and numeric climatic variables using linear models (e.g., Lozano et al., 2006;  
159 Zhou et al., 2011a; Díaz-Ruiz et al., 2013); however, this approach was not applicable to our  
160 meta-analysis, due to small sample size. Within the latitude of the Japanese archipelago,  
161 temperature is the primary environmental factor determining the regional biome (e.g., thermal  
162 forest zone); where annual precipitation consistently exceeds 1000 mm across the archipelago,  
163 supported by moist soil types, and does not constrain woody primary productivity (see Kira,  
164 1991). Therefore we used thermal (climatographic) forest zones (Kira, 1948; Kira, 1991; see also  
165 Box, 1995) to encapsulate climatic conditions as a single categorical predictive variable and  
166 compared this to annual food composition, or dietary indices

167       The thermal forest zone of each study area was defined quantitatively based on Kira's  
168 warmth index ( $WI$ ),  $WI = \sum(t - 5)$ , where  $t$  represents mean monthly temperature  $\geq 5$  °C  
169 (temperature during growing season; i.e., when the mean monthly temperature was  $< 5$  °C, it was  
170 not used for the calculation). For this calculation, we used monthly temperature data recorded at  
171 the weather observatory nearest to each study area between 1981 and 2010 (Japan  
172 Meteorological Agency; <http://www.jma.go.jp>), corrected for moist adiabatic lapse rate of -

0.65×10<sup>-2</sup> °C/m (Hasegawa, 1970). *WI* has been applied dependably to define thermal forest zonation in the East Asia, according to the following classification: ‘alpine (above tree-line; *WI* < 15)’; ‘sub-alpine (sub-arctic) forest (dominated by *Picea/Abies* spp. and/or *Betula* spp.; *WI* = 15-45)’; ‘cool-temperate forest (dominated by deciduous *Quercus* spp. and/or *Fagace* spp.; *WI* = 45-85)’; ‘warm-temperate forest (dominated by evergreen *Quercus* spp., *Castanopsis* spp., and/or *Lithocarpus* spp.; *WI* = 85-180)’; and ‘sub-tropical forest (containing Dipterocarpaceae such as *Vatica* spp. and *Hopea* spp.; *WI* = 180-240)’ (Kira, 1991). Study areas in our annual dataset all fell into two thermal forest zones, (i) sub-alpine/cool-temperate, and (ii) warm-temperate zones.

To ensure that these thermal forest zones represented variations in temperature regime across the studies accurately, we validated the geo-climatic characteristics of each study area’s thermal classification (Table 1) by obtaining mean annual temperature and precipitation (1981 and 2010) from the meteorological observatory nearest to each study area. Geographic information for each study area included latitude (0.1° resolution) and mean elevation (10 m resolution), which were extracted either directly from the publication, or from Google Maps (<https://maps.google.com>).

*Data standardisation*

The datasets we compiled included inconsistent sampling methodologies (faecal vs stomach contents analysis), sample sizes (number of analysed faeces/stomach ( $n$ )), and sampling durations (months). To inspect for potential bias caused by these factors (Putman, 1984), we performed a multivariate analysis of variance (MANOVA) for sampling methodology, and a multivariate analysis of covariance (MANCOVA) for sample size and duration, following the approach of previous studies (e.g., Lozano et al., 2006; Zhou et al., 2011a; Díaz-Ruiz et al., 2013). When testing annual RFO data, sample size and sampling duration were used as covariates, and the RFOs of food categories were used as response variables. For testing seasonal FO data, seasonal sampling duration (months per given season) was used as a covariate, and the FOs of food categories were used as response variables. Sample sizes of these seasonal data also varied among studies; however, it was not possible to test what influence this may have had on diet composition, because not all the studies included this information per month. For the winter data analysis, sampling methodology was included as a fixed factor because one winter study (Otsu, 1972) was based on stomach contents; all others studies used faecal analysis in winter and other seasons.

Across studies supplying annual data, variations in sample size (MANCOVA:  $F_{6,6} =$

0.60,  $P = 0.72$ ) and study duration ( $F_{6,6} = 2.02$ ,  $P = 0.21$ ) had no significant effect on annual food category RFO. For seasonal studies, study duration within season was also not influential on food category FO (MANCOVA: spring:  $F_{5,3} = 2.51$ ,  $P = 0.24$ ; summer:  $F_{5,3} = 0.52$ ,  $P = 0.75$ ; autumn:  $F_{5,3} = 0.65$ ,  $P = 0.69$ ; winter:  $F_{5,3} = 0.95$ ,  $P = 0.55$ ). Comparing the single stomach analysis study (Otsu, 1972) with the eight using faecal analysis revealed that sampling method had no effect on winter diet composition (MANOVA:  $F_{5,3} = 3.31$ ,  $P = 0.18$ ). Although we were unable to test whether sample size affected seasonal diet composition, we did not exclude any studies from the seasonal dataset, given that sample size and study duration were generally conflated in our dataset. Consequently, we could include all 20 studies we reviewed in subsequent annual/seasonal dietary analyses.

From these 20 studies, 14 satisfied our criteria for inclusion in the annual dataset (i.e., provided > 1 yr data), and these were compiled into nine geographical areas for the annual RFO analysis, by collating studies in similar geographical locations (see Table 1). These were then assigned to either thermal forest zone.

The seasonal FO dataset was divided into: spring = 10 studies, summer = 12 studies, autumn = nine studies, and winter = nine studies; and FO values were pooled within each season, regardless of geographical location. Note that seven studies from five study areas were subject to

223 both annual and seasonal analysis (Fig. 1).

224

#### 225 *Statistical analysis*

226 Thermal forest zonation was independent of latitude (Mann-Whitney  $U$  test:  $z = 0.98$ ,  $U = 6.00$ ,

227  $P = 0.49$ ) and mean annual precipitation ( $z = 0.00$ ,  $U = 10.00$ ,  $P = 0.89$ ); however, cool-

228 temperate/sub-alpine forest zone study sites were located at significantly higher elevations

229 (Mann-Whitney  $U$  test:  $z = 2.45$ ,  $U = 0.00$ ,  $P = 0.03$ ), with a mean annual mean temperature of

230  $7.9^{\circ}\text{C}$  (range,  $4.01 - 10.30$ ) compared to lower lying warm-temperate zone forest zones

231 averaging  $12.7^{\circ}\text{C}$  (range,  $11.56 - 14.52$ ). We were thus confident to be able to test the effect of

232 thermal zone type on marten diet.

233 To describe trophic diversity, we calculated Shannon-Wiener's diversity index ( $H'$ ),  $H'$

234  $= \sum_{i=1}^S P_i \ln P_i$  and Levins' niche breadth index ( $B$ ),  $B = 1 / \sum_{i=1}^S P_i^2$  based on annual RFO

235 values for each study area, where  $S$  represents the number of food categories and  $P_i$  represents

236 the ratio of the category  $i$  against total number of food categories present (Zhou et al., 2011a).

237 We then compared these trophic diversity indices between the two thermal forest zones using

238 Mann-Whitney  $U$  tests. To assess whether thermal forest zone type affected overall similarity in

239 diet composition, we performed a multivariate analysis of variance (PERMANOVA), using the

240 *adonis* function in the *R* package *vegan* (Oksanen et al., 2018) (see also Hisano et al., 2016;  
241 Tsunoda et al., 2017). If overall dissimilarity was detected, we then used Chi-squared tests to  
242 compare RFO of each food category between thermal forest zones (e.g., Lanszki et al., 2016).

243 To visualise similarities in diet composition among the study areas, i.e., ‘Diet Groups’,  
244 we applied a hierarchical cluster analysis to the annual RFO dataset and used the Ward method  
245 to derive Percent Similarity indices (shown in the output dendrogram, Fig. 3) (Mori and  
246 Bertolino, 2015). To identify the dietary characteristics of each Diet Group, we used  
247 PERMANOVA for overall-similarity examination and again applied Chi-squared tests, as  
248 appropriate, to compare RFOs of each food category between Groups.

249 For seasonal analyses, we performed one-way analysis of variance (ANOVA), using the  
250 FO of each food category as a response variable. If significant seasonal differences were  
251 detected, Tukey’s *post-hoc* tests were applied to determine in which season Japanese martens  
252 consumed food categories more/less frequently (Díaz-Ruiz et al., 2013).

253 Except for in the cluster analysis, values of RFO and FO were arcsine transformed to  
254 minimise potential departure from normal distributions (e.g., Zalewski, 2004; Díaz-Ruiz et al.,  
255 2013). All statistical analyses were performed using *R* 3.4.4. (R Development Core Team, 2018).

256



## Results

### *Overall diet*

Across all annual studies, the principal food categories consumed by the Japanese marten were: fruits (RFO  $\pm$  SE,  $46.41 \pm 3.14$  %), followed by invertebrates ( $27.29 \pm 3.00$  %; insects and arthropods) and mammals ( $19.04 \pm 2.4$  %; mostly Rodentia and Japanese hare with occasional occurrences of ungulate carcasses) (Table 1). Birds ( $4.76 \pm 0.54$  %; mostly songbirds) and herptiles ( $1.64 \pm 0.44$  %; lizards, snakes, and frogs) were eaten occasionally, while fish and human refuse ( $0.90 \pm 0.28$  %) were recorded infrequently. The average Shannon's diversity index was  $1.20 \pm 0.03$  with a Levins' index of  $2.81 \pm 0.11$  (Table 1).

### *Geographical variations in the marten food composition*

In cool-temperate/sub-alpine forest zones Japanese marten diet exhibited a significantly higher Levins' niche breadth index ( $2.96 \pm 0.17$ ) than in warm-temperate zone forest zones ( $2.66 \pm 0.11$ ) (Mann-Whitney  $U$  test:  $z = 2.20$ ,  $U = 1.00$ ,  $P = 0.03$ ); although Shannon's diversity index did not differ significantly between the two forest zones ( $1.25 \pm 0.04$  and  $1.15 \pm 0.04$ ;  $z = 1.96$ ,  $U = 2.00$ ,  $P = 0.06$ ).

The PERMANOVA indicated a marginally significant difference in the overall diet

composition between the forest zones ( $F = 3.59$ ,  $R^2 = 0.34$ ,  $P = 0.05$ ), attributable to differences in particular categorical food groups. That is, the RFO of mammals was significantly higher in the cool-temperate/sub-alpine than in the warm-temperate forest zone (Chi-squared test:  $\chi^2 = 745.68$ ,  $P < 0.001$ ; Fig. 2), whereas fruits were consumed significantly more often in the warm-temperate than in the cool-temperate/sub-alpine zone ( $\chi^2 = 659.34$ ,  $P < 0.001$ ). Consumption of other food categories did not differ significantly with forest zone type (Fig. 2).

In terms of percent dietary similarities among study areas, the cluster analysis separated diet composition into two primary groups, which generally accorded with forest zone type: Group A (Mt. Nyugasa, Okutama, and Kuju Highland), all of which represented the cool-temperate/sub-alpine forest zone and Group B (Akaya, Neko River, Mt. Momi, Tsushima Island, Hinode, and Mt. Yamato-Katsuragi) of which five out of six studies represented the warm-temperate forest zone) (Fig. 3). Overall diet composition differed significantly between the two Groups (PERMANOVA:  $F = 8.36$ ,  $R^2 = 0.54$ ,  $P = 0.01$ ). The RFO of animal prey (sum of mammals, birds, herptiles, and invertebrates) was significantly higher for Group A (mean RFO  $\pm$  SE,  $69.66 \pm 2.64$  %) than for Group B ( $47.74 \pm 2.11$  %); conversely, fruits were eaten significantly more frequently in Group B ( $51.73 \pm 2.05$  %) than in Group A ( $28.70 \pm 2.06$  %) (Chi-squared test:  $\chi^2 = 1214.90$ ,  $P < 0.001$ ). Group B sub-divided into Group B-1 (Neko River,

and Akaya) and Group B-2 (Mt. Momi, Tsushima Island, Hinode, and Mt. Yamato-Katsuragi) (Fig. 3). Although fruits were the primary food category, consumed with similarly high RFOs (Group B-1, mean RFO  $\pm$  SE,  $53.41 \pm 1.27$  %; B-2,  $50.90 \pm 4.14$  %) in both sub-groups, secondary food categories differed, leading to an overall diet compositional difference. Specifically, Group B-1 included a significantly greater frequency of invertebrates ( $31.55 \pm 2.72$  %) than B-2 ( $14.23 \pm 0.98$  %) (Chi-squared test:  $\chi^2 = 306.36$ ,  $P < 0.001$ ), whereas diet in Group B-2 compensated by including a significantly greater frequency of mammals ( $24.2 \pm 2.39$  %) than B-1 ( $11.23 \pm 1.42$  %) (Chi-squared test:  $\chi^2 = 6206.60$ ,  $P < 0.001$ ).

#### *Seasonal variations in Japanese marten diet composition*

A significant seasonal effect on Japanese marten diet was detected with regard to mammals (ANOVA:  $F = 8.61$ ,  $P < 0.001$ ), invertebrates ( $F = 11.41$ ,  $P < 0.001$ ), and fruits ( $F = 3.41$ ,  $P = 0.03$ ; Fig. 4). Martens consumed mammals most frequently in spring, with a significantly higher FO (mean FO  $\pm$  SE,  $54.59 \pm 5.82$  %) than in summer ( $29.79 \pm 5.39$  %; Tukey's *post-hoc* test:  $P = 0.01$ ), autumn ( $14.71 \pm 3.58$ ;  $P < 0.001$ ), and winter ( $26.11 \pm 6.05$ ;  $P = 0.02$ ; and FO tended to decrease from spring to autumn; Fig. 4a). The FO of invertebrates were significantly higher in summer ( $76.27 \pm 4.57$  %; Tukey's *post-hoc* test:  $P < 0.001$ ) and autumn ( $53.84 \pm 6.01$  %;  $P =$

0.02) than in winter ( $24.99 \pm 7.47 \%$ ); and FO tended to decrease from summer to winter/spring; Fig. 4b). The FO of fruits increased substantially from spring to autumn/winter, and FO in autumn ( $75.24 \pm 12.82 \%$ ) was significantly higher than in spring ( $30.73 \pm 7.63 \%$ ; Tukey's *post-hoc* test:  $P = 0.03$ ; Fig. 4c). There was no significant seasonal effect on the FOs of birds, herptiles, or other food categories.

## Discussion

From studies spanning the Japanese archipelago, we found that Japanese marten diet differed significantly between the two principal thermal forest zones they inhabit. Martens consumed mammals significantly more frequently in cool-temperate/sub-alpine forest zone study sites (i.e., lower mean annual temperature, higher elevation) than in warm-temperate forest regions, whereas they ate fruits more frequently in warm-temperate forest zone sites compared to cool-temperate/sub-alpine forest zone sites; a division mostly consistent with our cluster analysis, segregating Japanese marten diet into Group A (carnivorous/insectivorous biased) and Group B (frugivorous/omnivorous biased) (Table 1; Fig. 3). Indeed, this PERMANOVA similarity would have been perfect had one study area (Akaya) from cool-temperate zone not been assigned to Group B.

325 Japan's latitude (30 – 40° over the marten's range) leads to day length ranging from  
326 14.2-15.3 hrs of daylight in June to 9.4 – 10.2 hrs of daylight in December. Linked to this  
327 seasonality Japan experiences marked variation in weather conditions (Köppen-Geiger climate  
328 classification Cfa/Cfb and Dfa/Dfb), with an annual temperature range of 5.2 – 26.4 °C in  
329 Tokyo. This seasonal weather leads to shifts in food type availability, driving the Japanese  
330 martens' adaptable, opportunistic generalism and foraging plasticity (Pyke et al., 1977; Sundell  
331 et al., 2003). In terms of forest thermal zone influences, the abundance of fruiting plant species  
332 tends to be greater at lower, warmer elevations, where fruiting seasons are typically longer (see  
333 Rosenzweig, 1995; Ting et al., 2008), and Japanese martens can optimise their feeding ecology  
334 accordingly (*sensu* Charnov, 1976). In contrast, with less fruiting plant species, a shorter fruiting  
335 season, and a longer duration of wintry conditions, Japanese martens inhabiting cool-  
336 temperate/sub-alpine forest rely more on hunting vertebrate prey, especially mammals; where  
337 endothermic predators must consume a higher proportion of dietary protein under cold  
338 conditions to support thermogenesis and homeostasis (King and Murphy, 1985; see Zhou et al.,  
339 2013). Similarly, in an analysis where latitude was the main predictor of winter severity, and  
340 linked to the diet of pine martens, Zalewski (2004) also found that the RFO of small mammals  
341 was highest in cool-temperate forests (mid-high latitude), whereas fruit RFO predominated in

warm-temperate (lower latitude; including the Mediterranean) regions, linked to greater fruit availability (Zalewski, 2004; see also Pandolfi et al., 1996; Papakosta et al., 2014).

This dietary switching illustrates how distinct macronutrients can be important and potentially limiting within habitat zones exhibiting certain conditions. Indeed Remonti et al. (2016) applied a multi-dimensional nutrient geometric framework to the diet of pine martens across Europe and found that although marten food composition varied substantially between regional populations, annual macronutrient (protein, lipid, and carbohydrate) balance was similar (i.e., ‘macronutrient specialist’, *sensu* Machovsky-Capuska et al., 2016). From the details of studies contributing to our meta-analysis, we were able to characterise Japanese marten diet only in terms of RFO, whereas examination of foraging decisions aimed at selecting particular macronutrients, or energy based metrics, would ideally require biomass/volume analysis (Remonti et al., 2016). Nevertheless, the seasonal shifts in food composition we detected approximated patterns of macronutrient consumption reported for European pine martens (Remonti et al., 2016). We identified that despite peak fruit (low caloric density: high carbohydrate to protein and fat ratio; predominantly *Actinidia* spp., *Diospyros* spp., *Vitis* spp., etc.; see Hisano and Deguchi, 2018) and small mammal availability (high caloric density: high protein and fat ratio to carbohydrate) typically occurring in the autumn (see Pucek et al., 1993),

Japanese martens tended to consume (FO) fruit preferentially; the easier prey to acquire when protein was not a priority macronutrient. Outside of the fruiting season, even though small mammal numbers are usually lower in early spring (after cessation of breeding over winter), rodents were the primary prey, when protein supports breeding and embryonic development (Monteith et al., 2013); a finding congruent with Zhou et al. (2011b). Invertebrates were utilised most frequently in summer, in accord with their peak seasonal availability, established elsewhere (Tatara and Doi, 1994; Koike et al., 2012; Hisano et al., 2017), where we identified the principal consumption of Coleoptera (e.g., Carabidae, Harpalidae), Orthoptera (e.g., Rhaphidophoridae, Gryllidae, Acrididae), and Hymenoptera. In Europe, the meta-analysis by Zalewski (2004) identified similar patterns of summer insect consumption among pine martens. Throughout the year, however, Japanese martens consumed a mixture of food categories, suggesting they sought to achieve a suitably balanced diet through periodic nutrient complementarity (Remonti et al., 2016) despite differing diet compositions between thermal forest zones. These findings corroborate observations from regional studies, as well as the global consensus for other *Martes* species (Zalewski, 2004; Zhou et al., 2011a), and are consistent with Charnov's (1976) optimal foraging theory.

As with other predatory mustelids, martens must remain agile and able to climb

376 effectively, and so tend not to carry much body-fat (Macdonald and Newman, 2017). Combined  
377 with an elongated body-type, this causes them to lose heat quickly, and thus they have high  
378 dietary energy requirements (King and Powell, 2007; Newman et al., 2011; Kitchener et al.,  
379 2017). Dietary switching enables martens to (i) optimise choices for highest energy-ranked prey  
380 (i.e., the ratio of energy gained to costs incurred by prey acquisition) in accordance with changes  
381 in environmental/climatic conditions (Charnov et al., 1976) and the diversity of food types  
382 available in their environment (e.g., Thompson and Colgan, 1990; Zhou et al., 2011b); and (ii)  
383 modulate the quantity and balance of macronutrients eaten to achieve a suitable intake (Mayntz  
384 et al., 2005; Remonti et al., 2016; Machovsky-Capuska et al., 2016).

385         To conclude, as with other marten species (Zhou et al., 2011a), it appears that the  
386 dietary breadth and dietary switching capability of the Japanese marten will allow the species to  
387 be adaptive in the face of moderate extent of environmental change, making it a good model  
388 species with which to study mechanistic responses. Future integrated work on marten food  
389 composition and macronutrient ratios using a multidimensional geometric framework (Remonti  
390 et al., 2016) will improve our understanding on their feeding strategies and dietary generalism.



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395

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578

579 **Figure legends:**

580 Fig. 1. Geographical locations of dietary studies used in the meta-analysis across the Japanese  
581 archipelago.

582 MI: Mt. Iide (Yamagata Prefecture); MT: Mt. Tairappyo (Gumma/Niigata Prefecture); Ak:  
583 Akaya (Gumma Prefecture); Ch: Chichibu (Saitama Prefecture); Ok: Okutama (Tokyo); Hi:  
584 Hinode (Tokyo); CM: Chikuma Mountains (Nagano Prefecture); NS: Nishikoma Forest of  
585 Shinshu University (Nagano Prefecture); MN: Mt. Nyugasa (Nagano Prefecture); OH: Otome  
586 Highland (Yamanashi Prefecture); MY: Mt. Yamato-Katsuragi (Nara Prefecture); NR: Neko  
587 River (Wakayama Prefecture); KH: Kuju Highland (Oita Prefecture); MM: Mt. Momi (Fukuoka  
588 Prefecture); TI: Tsushima Islands (Nagasaki Prefecture).

589

590 Fig. 2. Comparing the relative frequency of occurrence (RFO; arcsine transformed; means  $\pm$   
591 SE) of each food category (annual diet data) of the Japanese marten between sub-alpine/cool-  
592 temperate forest and warm-temperate forest.  $*P < 0.05$  (Chi-squared test).

593

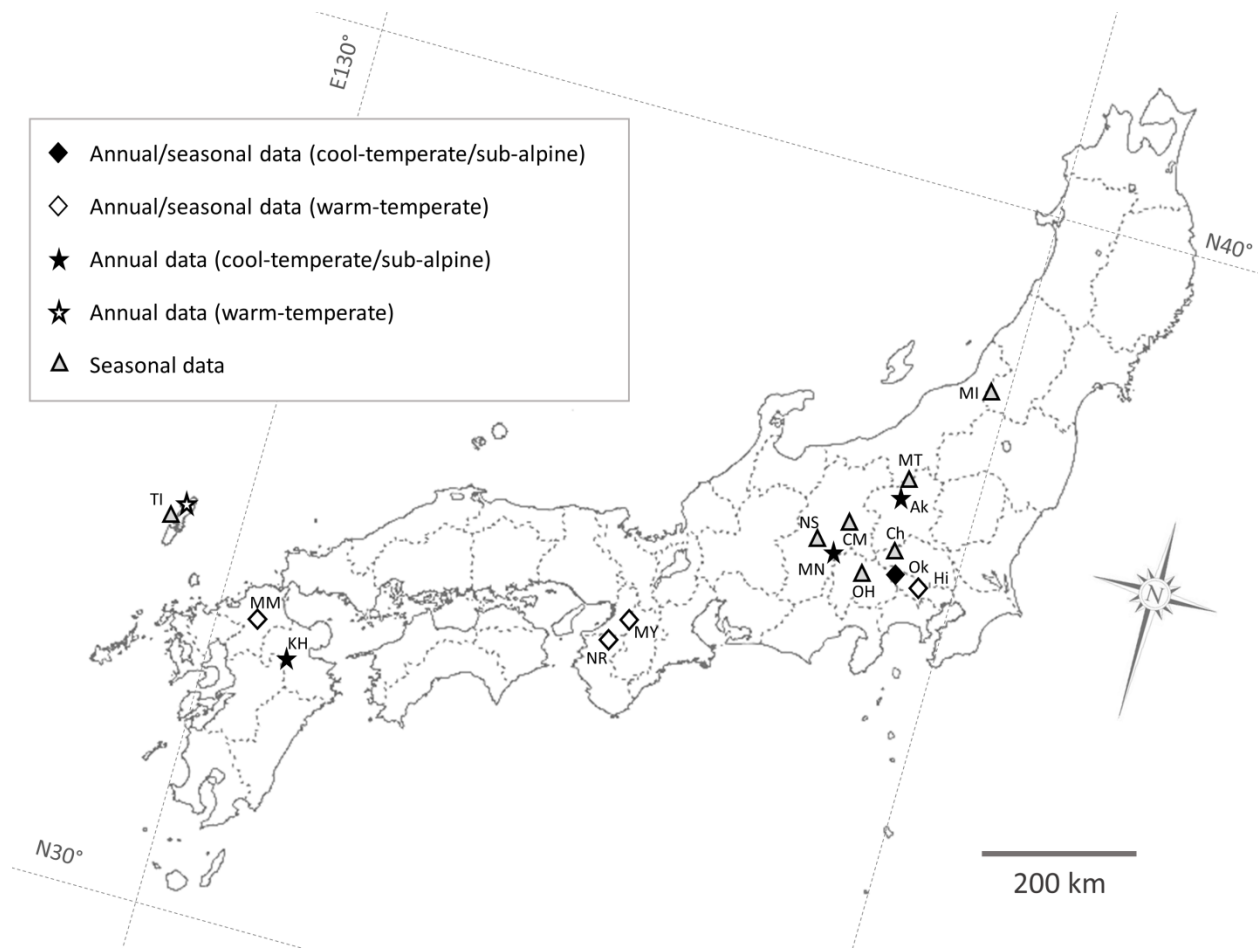
594 Fig. 3. Dendrogram derived from cluster analysis applying the Ward method, based on the  
595 percentage similarity of the relative frequency of occurrence (RFO) of annual marten diet.

596 \* Study areas from cool-temperate/sub-alpine forest zone. † Those from warm-temperate forest  
597 zone.

598

599 Fig. 4. Comparing the frequency of occurrence (FO; arcsine transformed; means  $\pm$  SE) of  
600 mammals (a), invertebrates (b), and fruits (c) in the diet of the Japanese marten. Capital letters  
601 (A, B, C) indicate that mean FOs are significantly different between categories ( $P < 0.05$ ;  
602 Tukey's *post-hoc* test).

1    **Fig. 1**



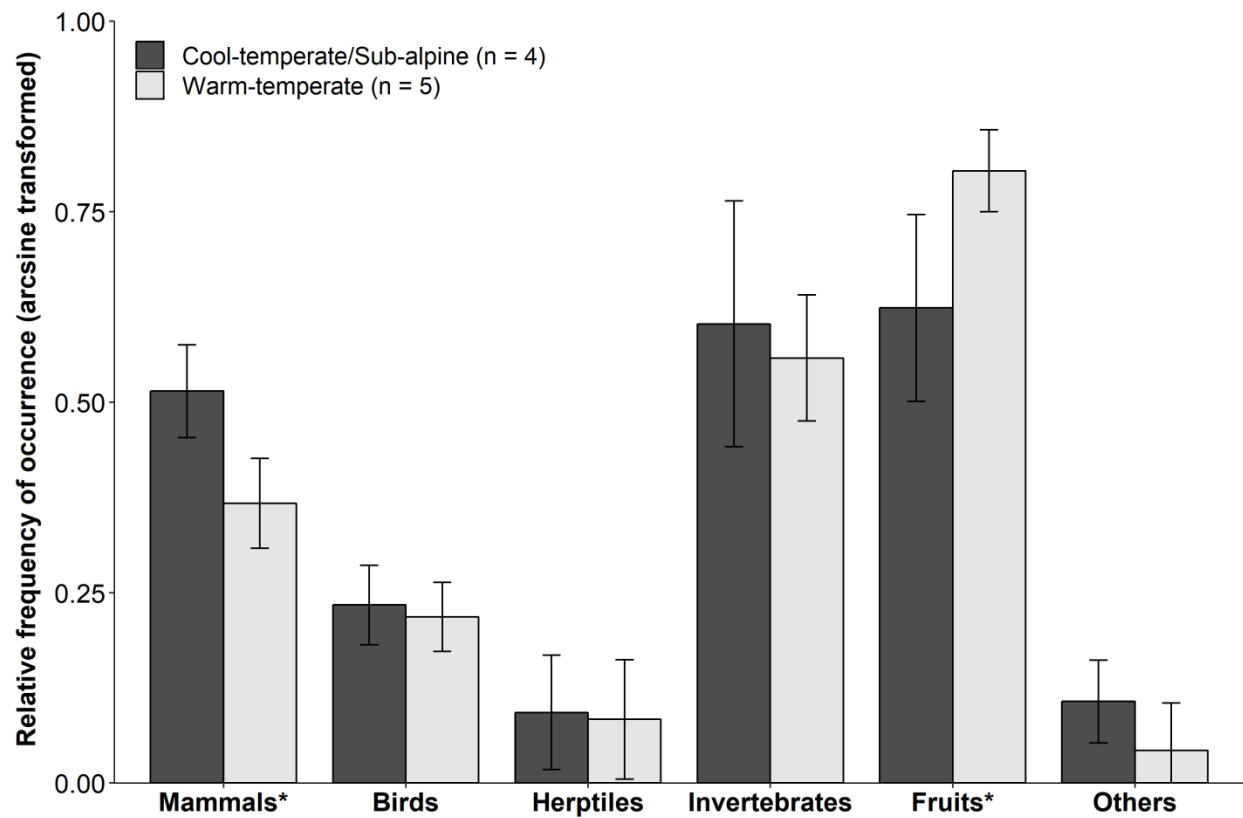
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4 **Fig. 2**

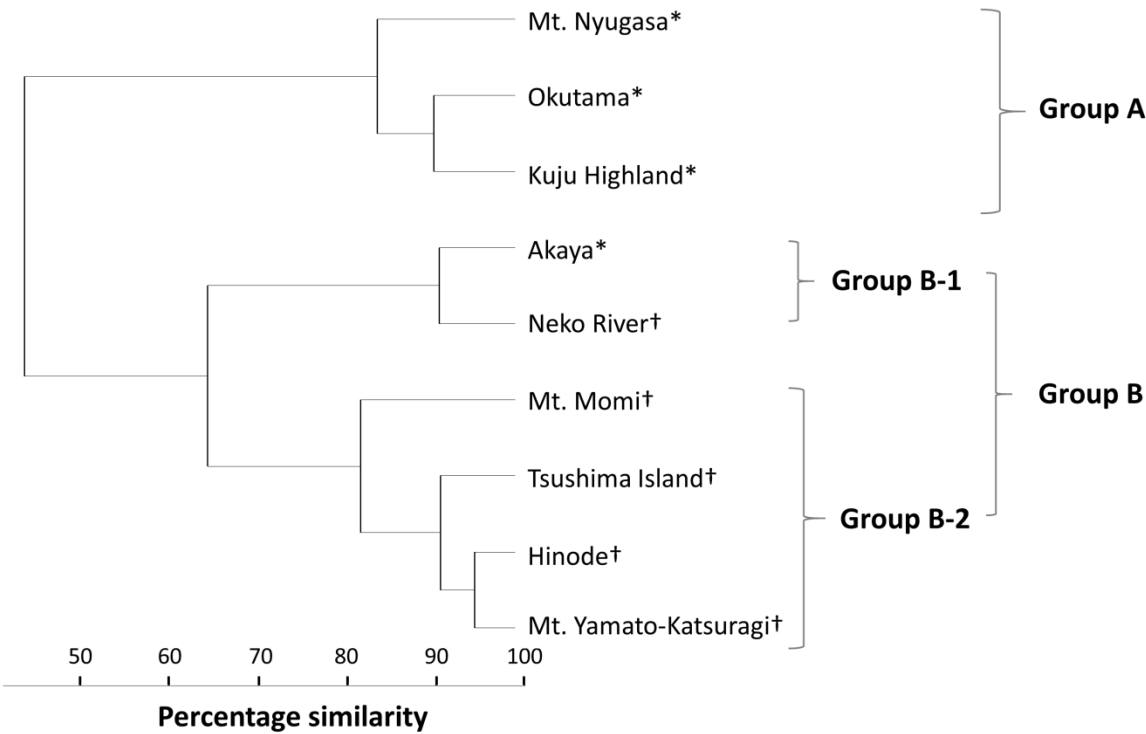
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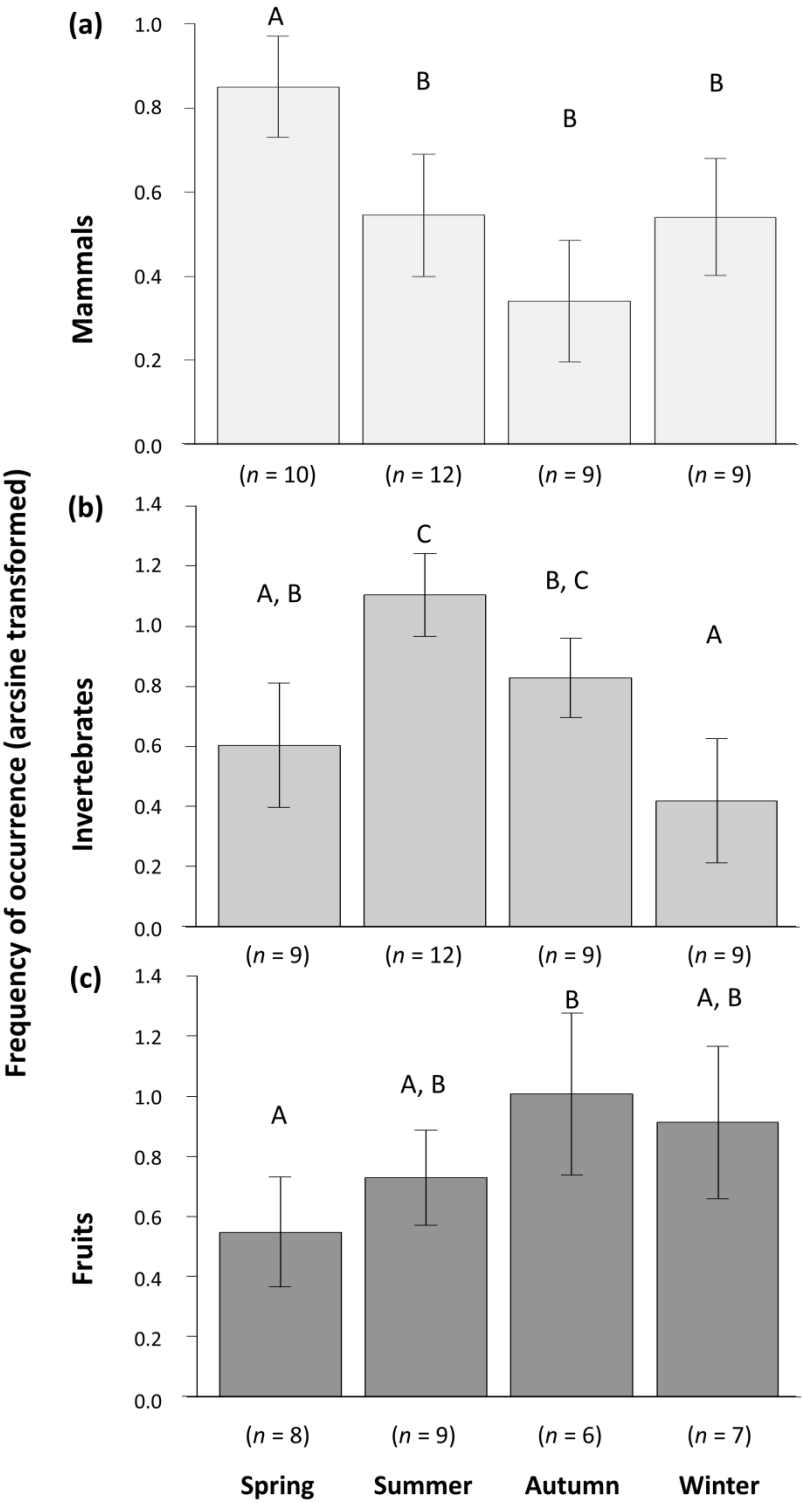
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8    **Fig. 3**



9

10



1 **Table 1. Diet composition (the mean relative frequency of occurrence (RFO)  $\pm$  standard error (%)) of the Japanese marten**  
2 **from the reviewed annual dietary studies.**

	Sub-alpine/cool-temperate				Warm-temperate					Total
	Ak <sup>a</sup>	Ok	MN	KH	Hi	MY	NR	MM	TI	
Compiled publication ( <i>n</i> )	4	1	1	1	2	2	1	1	1	14
Analysed faecal sample ( <i>n</i> )	2,123*	158	217	1,387	425*	509*	92	7,091	1,236	13,238
<b><i>Food categories</i></b>										
Mammals	27.58 $\pm$ 4.11	17.53	29.14	23.19	9.32 $\pm$ 1.33	11.34 $\pm$ 1.49	20.83	9.82	14.47	19.04 $\pm$ 2.4
Birds	4.19 $\pm$ 0.64	5.50	3.39	9.12	3.02 $\pm$ 0.36	4.52 $\pm$ 0.50	8.33	2.77	5.74	4.76 $\pm$ 0.54
Herptiles	3.26 $\pm$ 0.53	0.00	0.51	1.39	1.44 $\pm$ 0.49	0.00 $\pm$ 0.00	0.00	0.71	4.47	1.64 $\pm$ 0.44
Invertebrates	12.84 $\pm$ 0.68	43.64	33.15	42.41	33.29 $\pm$ 0.82	36.38 $\pm$ 0.58	15.63	25.89	30.64	27.29 $\pm$ 3.00
Fruits	51.62 $\pm$ 5.30	30.93	31.51	23.66	50.24 $\pm$ 2.86	47.46 $\pm$ 1.42	55.21	60.57	45.32	46.41 $\pm$ 3.14
Others	0.51 $\pm$ 0.14	2.41	2.32	0.23	2.68 $\pm$ 0.13	0.00 $\pm$ 0.00	0.00	0.24	0.00	0.90 $\pm$ 0.28
<b><i>Trophic indices</i></b>										

$H^b$	1.2 ± 0.12	1.28	1.32	1.34	1.18 ± 0.14	1.1 ± 0.1	1.15	1.03	1.30	1.20 ± 0.03
$B^c$	2.71 ± 0.45	3.12	3.38	3.35	2.68 ± 0.41	2.67 ± 0.27	2.63	2.25	3.07	2.81 ± 0.11
<b><i>Geographical variables</i></b>										
Latitude <sup>d</sup>	36.7	35.5	35.9	33.1	35.7	34.5	34.4	33.5	34.5	34.87 ± 0.3
Elevation <sup>e</sup>	800	1,000	1,800	850	500	600	350	690	200	754.44 ± 117.12
Annual mean temperature <sup>f</sup>	8.55	8.85	4.01	10.30	11.56	13.25	12.07	11.93	14.52	10.56 ± 0.79
$WI^g$	68.06	66.76	40.16	79.32	89.36	104.13	92.95	92.61	114.36	83.08 ± 5.63
Annual mean precipitation <sup>h</sup>	1733.7	1623.5	1284.1	1949.5	1507.8	1358.4	1470.6	1860.4	2235.2	1669.24 ± 77.26

<sup>a</sup> Ak: Akaya (Gumma; Kanto Regional Office, 2011, 2012, 2013, 2014), Ok: Okutama (Tokyo; Koike et al., 2012), Hi: Hinode (Tokyo; Nakamura et al., 2001; Tsuji et al., 2014), MN: Mt. Nyugasa (Nagano; Yamamoto, 1994), MY: Mt. Yamato-Katsuragi (Nara; Kusui and Kusui, 1995, 1998), NR: Neko River (Wakayama; Shiratsuki, 1972), KH: Kuju Highland (Oita; Arai et al., 2003), MM: Mt. Momi (Fukuoka; Adachi et al., 2016b), TI: Tsushima Islands (Nagasaki; Tatara and Doi, 1994).

<sup>b</sup> Shannon's diversity index

<sup>c</sup> Levins' niche breadth index

<sup>d</sup> (°): based on Google Maps (<https://maps.google.com>) with 0.1° resolution.

<sup>e</sup> (m): the mean of the highest and the lowest elevation noted in the reference; if the elevation was not presented, approximate value was taken from Google Maps with 10 m resolution.

- 12 <sup>f</sup> (°C): based on the climate records from the nearest observatory between 1981 and 2010 (Japan Meteorological Agency;  
13 <http://www.jma.go.jp/>) corrected by lapse rate ( $-0.65 \times 10^{-2}$  °C/m).
- 14 <sup>g</sup> Kira's warmth index
- 15 <sup>h</sup> (mm): based on the climate records from the nearest observatory between 1981 and 2010 (Japan Meteorological Agency;  
16 <http://www.jma.go.jp/>).
- 17 \* Sample size of each study was summed.