Chapter 10
Characteristics and Temporal Trends of a Ground Beetle (Coleoptera: Carabidae) Community in Ooyamazawa Riparian Forest

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Abstract Over the course of a 10-year monitoring survey of ground-dwelling beetles in the Ooyamazawa riparian forest (2008–2017), 2381 individuals from 19 beetle families (including 1969 individuals of 36 carabid species) were collected. The carabid community was characterized by high species richness and a high proportion of endemic species, when compared with other monitored forest sites in Japan. Most of the carabid species exhibited drastic declines in abundance, and the annual catch of the carabids over the 10-year period decreased by 80%. These declines of the beetles were likely to be caused by changes in the forest floor environment due to overabundance of deer as well as climate warming.

Keywords Global warming · Long-term ecological research · Monitoring Sites 1000 Project · Pitfall trap · Sika deer overabundance

10.1 Introduction

The ground beetles (i.e., carabids; Coleoptera: Carabidae) comprise a species-rich family that contains over 40,000 described species. Carabids are globally distributed and are found in a wide range of terrestrial ecosystems (e.g., forest, grassland, wetland, seashore, desert, tundra, alpine zone, cave, arable land, and urban green area). Individuals live for one or several years and usually reproduce on an annual basis (Lövei and Sunderland 1996). Carabids that inhabit temperate forests are often flightless, live on the ground, and mainly prey on ground and soil invertebrates (Shibuya et al. 2014, 2018; Okuzaki et al. 2009; Vanbergen et al. 2010), while also serving as prey for a variety of vertebrates (Lövei and Sunderland 1996). The low dispersal ability of forest-dwelling carabids results in high rates of local endemism,

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as well as significant differences in the structure of geographically isolated communities, and may also increase the susceptibility of such species and communities to environmental changes.

The species composition of carabid communities largely varies by habitat, owing to differences in species' life histories (e.g., seasonality), dispersal abilities (e.g., flight ability), feeding habits (e.g., carnivore, granivore, or omnivore), habitat and microenvironment preferences (e.g., vegetation structure, shadiness, temperature, moisture, soil particle size, and hibernation site; Lövei and Sunderland 1996; Thiele 1977). The species composition is also likely affected by landscape structure, owing to the beetles' low dispersal ability, and is, therefore, likely sensitive to both natural and anthropogenic disturbances, including fire, grazing, grassland and forest management, agricultural practice, pollution, and habitat fragmentation (Rainio and Niemelä 2003; Koivula 2011). In addition, sufficiently large and quantitative carabid samples can be easily and cost-effectively collected by pitfall-trapping. For these features, carabid communities are often used as bioindicators (Rainio and Niemelä 2003; Koivula 2011) and have recently been adopted as a monitoring target for broad-scale, long-term ecological monitoring programs, including the Environmental Change Network (ECN) in the UK (Morecroft et al. 2009), the National Ecological Observatory Network (NEON) in the USA (Hoekman et al. 2017), and the Monitoring Sites 1000 Project in Japan (Niwa et al. 2016). Indeed, the data collected by the ECN from 1994 to 2011 allowed researchers to document substantial declines in carabid biodiversity throughout the UK and significant phenological shifts in many carabid species in Scotland (Brooks et al. 2012; Pozsgai and Littlewood 2014).

The Ooyamazawa riparian forest (Chichibu Mountains, Japan) was designated as a core site of the Forest and Grassland Survey in the Monitoring Sites 1000 Project, which is a nationwide, long-term ecological monitoring project that was launched by the Ministry of Environment (Japan) in 2003, and tree, bird, and ground-dwelling beetle surveys have been conducted at this site on an annual basis since 2008. For the Monitoring Sites 1000 Project, ground-dwelling beetle surveys have been performed in 22 forests across Japan (Niwa et al. 2016), and because most of these forests have not been subjected to direct human disturbance (e.g., logging) for over 100 years, the resulting data can be used to study natural gradients of beetle diversity within the Japanese Archipelago, as well as the effects of broad-scale environmental changes (e.g., climate change). The survey protocols and most of the data obtained in this project are publicly available *via* the internet (http://www.biodic.go.jp/moni1000/index.html, Ishihara et al. 2011; Suzuki et al. 2012; Niwa et al. 2016).

The Ooyamazawa riparian forest is a well-preserved old-growth forest and that possesses a diverse forest floor environment provided by the stream. Such a stable and continuous forest ecosystem with a diverse forest floor environment can be expected to harbor a rich and diverse carabid beetle community. Recently, however, sika deer populations have increased and the resulting heavy browsing pressure has completely changed the vegetation of the forest floor (Chap. 8). Indeed, the alteration of forest vegetation by deer overabundance has been reported all over Japan (Takatsuki 2009), as well as in subarctic and temperate zones all over the world, and the cascading effects of such population growth on other animals and ecosystem

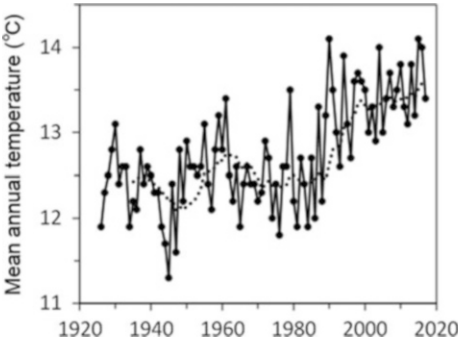

Fig. 10.1 Annual variation in mean air temperature at Chichibu weather station. Data were obtained from the Japan Meteorological Agency (http://www.data.jma.go.jp/obd/stats/etrn/index.php). Dotted line indicates the 10-year moving average

processes have become serious issues (Côté et al. 2004; Rooney and Waller 2003; Stewart 2001; Foster et al. 2014). In recent decades, the Ooyamazawa forest has also been affected by temperature increases associated with global warming. The mean air temperature in Chichibu City, for example, which is located 28 km east of Ooyamazawa, has increased at ~1.5 °C per 100 years, and the last decade was the hottest decade of the last 90 years in Chichibu (Fig. 10.1).

In this chapter, I will describe the diversity and characteristics of the carabid beetle community in the Ooyamazawa riparian forest and describe how the community has changed during the initial 10 years (2008–2017) of the long-term monitoring project.

10.2 Study Site and Methods

In the Forest and Grassland Survey in the Monitoring Sites 1000 Project, ground-dwelling beetle surveys have been conducted at 22 forest sites, including Ooyamazawa, every year since 2004, 2005, 2006, or 2008 (Niwa et al. 2016). Each of the 22 forest sites is primarily composed of natural old-growth forests, and the sites span both the major climatic zones (subalpine, cool-temperate, warm-temperate, and subtropical) and forest types (coniferous, deciduous broadleaved, evergreen broadleaved, and conifer and broadleaf mixed) of Japan. At each site, one monitoring plot (100 m × 100 m) and five subplots (5 m × 5 m) within it have been established, and four pitfall traps (9-cm diameter, 12-cm depth, with no baits or preservatives) were installed in each subplot (Fig. 10.2). The traps were opened for 3 d each in four seasons per year (spring: May–June, summer: June–July, early-autumn: September–October, and late-autumn: October–November), and the animals captured in the traps during each sampling period were collected, identified to class, order, or family level, enumerated, dried, weighed, and preserved as dry specimens. Captured beetles were further identified to family, genus, or species level and individually weighed. The species were identified following the taxonomic system of Löbl and Löbl (2017).

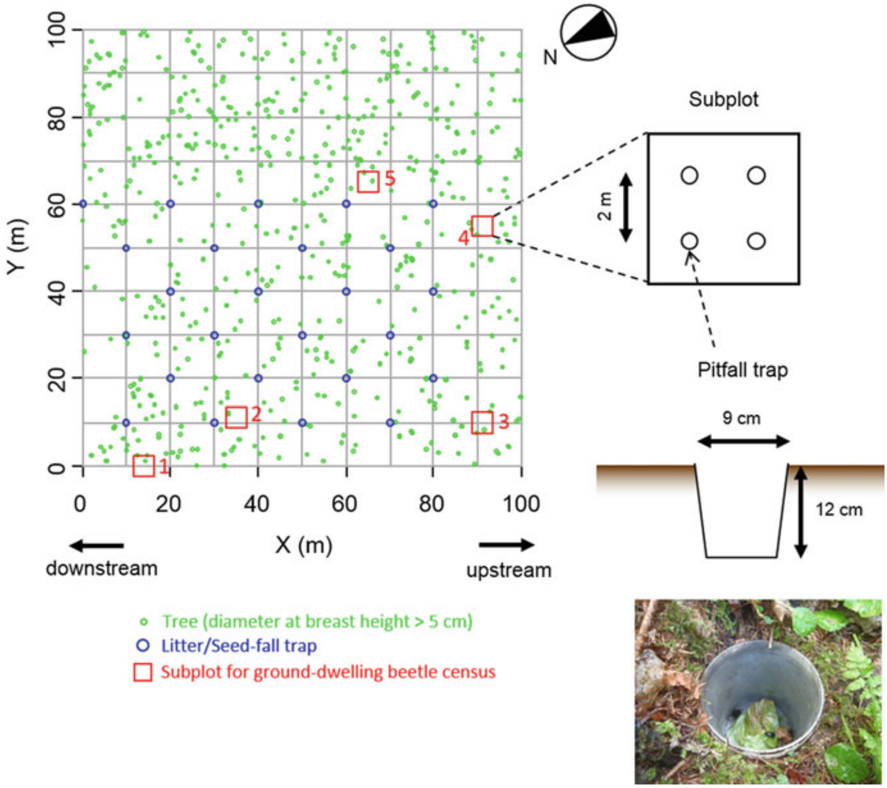

Fig. 10.2 Study plot established for the long-term monitoring of trees, litter and seed fall, and ground-dwelling beetles in the Ooyamazawa riparian forest

In Ooyamazawa, beetle sampling has been conducted in May, June, September, and October of every year since 2008. However, data from 2013 and 2015 have been excluded from the following analyses because the access road was temporarily impassable, owing to typhoon damage, and sampling could not be conducted in September of either year.

The general description of the monitoring plot in Ooyamazawa, including climate, geology, topography, soil and vegetation, is provided in Chap. 1. Subplots 1 and 2 were located on the bottom of a valley, along with a small first-order stream that usually flows belowground, and the colluvial deposits (gravels of various sizes) in these subplots were covered by soil, with a layer of litter. Meanwhile, Subplots 3 and 4 were located at the lower end of the slopes, and because the rich forest floor vegetation (e.g., ferns in Subplots 1–4 and dwarf bamboo in Subplot 4) had declined before the initiation of monitoring (Chap. 8), scarce vegetation was present in the subplots throughout the monitoring period (2008–2017). In contrast, Subplot 5 located in the middle of a slope had a relatively deep soil layer, and was, at least initially, covered with dense forest floor vegetation of dwarf bamboo (*Sasa* *borealis*). The bamboo vegetation, however, rapidly declined and almost disappeared during the monitoring period (Chap. 8).

10.3 Carabid Community Diversity and Distinctness

From 2008 to 2017, 2381 beetles from 19 families were collected (Table 10.1). Carabid beetles (36 species) accounted for 82.7% of them, and three predominant genera (*Carabus*, *Pterostichus*, and *Synuchus*) accounted for 92.5% of the carabids (Table 10.2, Fig. 10.3). The carabid community of Ooyamazawa was characterized by high species diversity, in comparison to the 21 other monitoring sites. The mean annual species number (17.8 ± 1.0, mean ± standard error) and diversity index (Shannon-Wiener's H': 2.19 ± 0.07) were the highest among these forests, whereas the mean annual catch (132.3 ± 32.5) was relatively high (sixth highest) and the evenness (Pielou's J': 0.768 ± 0.032) was about average.

The high species diversity of the carabids in Ooyamazawa can be partly attributed to the stable forest environment and to the presence of a stream, owing to higher soil moisture, greater habitat heterogeneity (including sand or gravel bars), a distinctive plant community, aquatic food resources, and occasional disturbance by flooding.

Table 10.1 Total catch of beetle families in the Ooyamazawa riparian forest, during 2008–2017

Family	Individuals
Carabidae	1969
Hydrophilidae	4
Ptiliidae	1
Leiodidae	66
Scydmaenidae	3
Silphidae	32
Staphylinidae	138
Geotrupidae	66
Lucanidae	8
Scarabaeidae	9
Nitidulidae	1
Cryptophagidae	5
Endomychidae	1
Corylophidae	1
Tetratomidae	1
Tenebrionidae	3
Pyrochroidae	1
Chrysomelidae	1
Curculionidae	7
Unknown (adult)	1
Unknown (larva)	63
Total	2381

Table 10.2 Annual catch and traits of each carabid species captured in the Ooyamazawa riparian forest, during 2008–2017

Species	Annual catch[a] (indiv./20 traps·12 days)	Distribution[b]	Body length[c] (mm)	Hind wing[d]	Adult active season[e]	Note
Nebria sadona	1.63 (0.60)	HON, SHI, KYU, Sad	11.0–14.5	B	A	*N. chichibuensis*?
Notiophilus impressifrons	0.13 (0.13)	HOK, HON, SHI, KYU, Sak; **AS**, **EU**, **NA**	5.7–7.0	M	S	
Carabus albrechti	29.25 (8.20)	HOK, HON, Sad	19.0–24.0	B	S	ssp. *esakianus*
Carabus procerulus	5.25 (0.92)	HON, KYU	25.0–35.0	B	A	ssp. *procerulus*
Carabus arboreus	5.25 (1.38)	HOK, HON, Sak	18.0–25.0	B	A	ssp. *ogurai*
Carabus harmandi	9.13 (2.66)	HON	18.0–23.0	B	S	ssp. *okutamaensis*
Brachinus stenoderus	0.25 (0.17)	HOK, HON, SHI, KYU; **AS**	5.5–11.5	M	S	
Trichotichnus lewisi	0.13 (0.13)	HOK, HON, SHI, KYU	12.5–14.5	M	A	
Trichotichnus yoshiroi	1.50 (0.35)	HON (Kanto Mts.)	9.4–10.1	B	S	
Trichotichnus sp.	0.13 (0.13)	–	9.0	–	–	
Negreum bentonis	4.63 (2.43)	HON	9.0–12.0	B	S	
Platynus subovatus	0.13 (0.13)	HON	11.0–13.5	B	S	
Xestagonum xestum	0.25 (0.17)	HON, SHI, KYU; **AS**	8.0–11.0	B	S	
Myas cuprescens	2.88 (1.17)	HON, SHI, KYU, Sad	14.0–22.5	B	A	ssp. *cuprescens*
Pterostichus subovatus	5.63 (2.44)	HOK, HON, KYU; **AS**	11.0–14.5	M	S	
Pterostichus karasawai	0.13 (0.13)	HON	13.5–16.0	B	S	
Pterostichus koheii	0.13 (0.13)	HON (Kanto Mts.)	15.0–16.0	B	–	
Pterostichus mucronatus	0.63 (0.28)	HON	16.5–22.0	B	S	
Pterostichus yoritomus	0.50 (0.29)	HON, KYU	12.0–14.5	B	S	
Pterostichus katashinensis	3.13 (0.77)	HON	15.5–19.0	B	S	ssp. *naganoensis*
Pterostichus mitoyamanus	1.88 (0.77)	HON (Kanto Mts.)	15.5–18.0	B	S	
Pterostichus okutamae	1.25 (0.34)	HON (Kanto Mts.)	15.5–17.5	B	S	
Pterostichus rhanis	2.50 (0.95)	HON	13.5–16.0	B	S	ssp. *kantous*
Pterostichus tokejii	9.88 (2.36)	HON (Kanto Mts.)	17.0–19.5	B	S	

Pterostichus brittoni	0.25 (0.17)	HON	8.2–8.8	B	S	
Stomis prognathus	0.25 (0.17)	HON, SHI	9.0–12.0	B	S	
Pristosia aeneola	0.13 (0.13)	HON, SHI	11.5–16.0	B	A	
Parabroscus crassipalpis	–	HOK, HON, SHI, KYU, Izu	11.0–13.0	M	A	
Synuchus agonus	3.75 (1.19)	HON, SHI, KYU, Kur; **AS**	9.0–10.0	B	A	
Synuchus arcuaticollis	0.38 (0.28)	HOK, HON, SHI, KYU, Kur, Yak; **AS**	8.0–10.5	B/M	A	
Synuchus atricolor	0.13 (0.13)	HON; **AS**	11.0–15.0	B	A	
Synuchus crocatus	–	HOK, HON, SHI, KYU, Kur; **AS**	9.0–12.0	B/M	A	
Synuchus cycloderus	0.25 (0.27)	HOK, HON, SHI, KYU; **AS**	10.5–14.0	M	A	
Synuchus melantho	40.50 (17.05)	HOK, HON, SHI, KYU, Kur; **AS**	9.5–13.0	B/M	A	
Synuchus nitidus	–	HOK, HON, SHI, KYU, Kur, Tai; **AS**	12.5–17.0	M	A	
Synuchus tanzawanus	0.38 (0.20)	HON	7.4–9.0	B	A	
Synuchus sp.[f]	0.13 (0.13)	–	–	–	–	
Carabidae Gen. sp.[f]	0.13 (0.13)	–	–	–	–	

[a] Total of four seasons and five subplots. Average and standard error (in parentheses) from 2008 to 2017 (excluding 2013 and 2015). –, captured only in 2013 and/or 2015

[b] Main islands and continents (Ueno et al. 1985; Löbl and Löbl 2017; Imura and Mizusawa 2013; Habu 1978; Morita 1997): *HOK* Hokkaido, *HON* Honshu, *SHI* Shikoku, *KYU* Kyushu, *Sak* Sakhalin, *Kur* Kuril Isls., *Sad* Sado, *Izu* Izu Isls., *Tsu* Tsushima, *Yak* Yaku, *Tai* Taiwan, **AS** Asian continent, **EU** European continent, **NA** North American continent

[c] Ueno et al. (1985), Imura and Mizusawa (2013), Habu (1978), and Morita (1997)

[d] *B* degenerated (brachypterous), *M* developed (macropterous), *B/M* dimorphic

[e] *S* Spring–Summer, *A* Autumn

[f] Unidentifiable, due to damage

Nebria sadona, *Notiophilus impressifrons*, *Carabus albrechti*, *Carabus procerulus*, *Carabus arboreus*, *Carabus harmandi*, *Brachinus stenoderus*, *Trichotichnus lewisi*

Trichotichnus yoshiroi, *Trichotichnus* sp., *Negreum bentonis*, *Platynus subovatus*, *Xestagonum xestum*, *Myas cuprescens*, *Pterostichus subovatus*, *Pterostichus karasawai*

Pterostichus koheii, *Pterostichus mucronatus*, *Pterostichus yoritomus*, *Pterostichus katashinensis*, *Pterostichus mitoyamanus*, *Pterostichus okutamae*, *Pterostichus rhanis*, *Pterostichus tokejii*

Pterostichus brittoni, *Stomis prognathus*, *Pristosia aeneola*, *Parabroscus crassipalpis*, *Synuchus agonus*, *Synuchus arcuaticollis*, *Synuchus atricolor*, *Synuchus crocatus*

Synuchus cycloderus, *Synuchus melantho*, *Synuchus nitidus*, *Synuchus tanzawanus*

Fig. 10.3 Carabid species found in the Ooyamazawa riparian forest. Scale bars indicate 5 mm

For example, some of the species captured at Ooyamazawa (*Nebria sadona* and *Brachinus stenoderus*) have been reported to favor riverine gravel bars (Ueno et al. 1985; Terui et al. 2017). Multivariate analysis revealed that adjacent subplots possessed similar species compositions, which indicated the contribution of small-scale habitat heterogeneity to plot-level diversity (Fig. 10.4). In particular, the Autumn-breeding and more widely distributed species (i.e., *Carabus procerulus*,

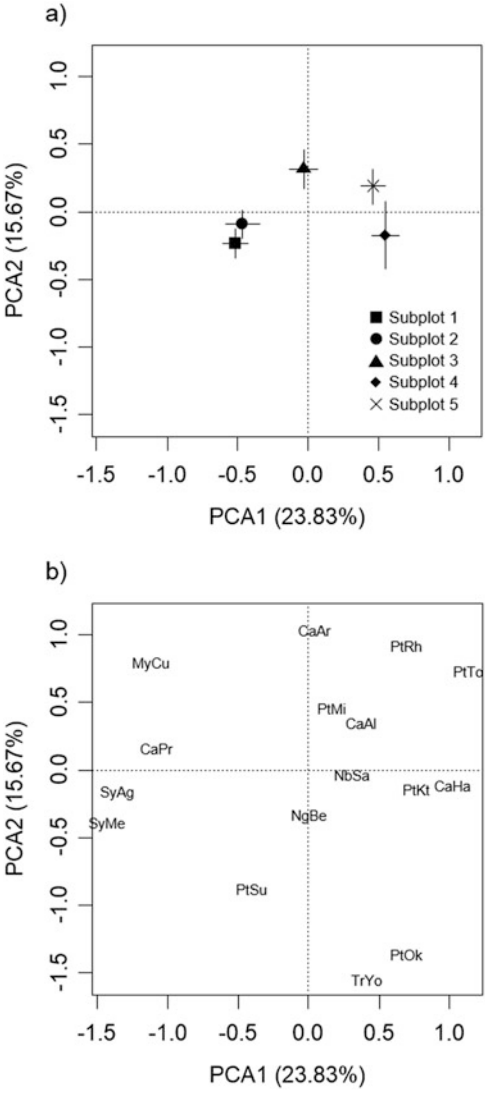

Fig. 10.4 Spatial variation in the species composition of carabids captured in the Ooyamazawa riparian forest. Data were ordinated using principal component analysis (PCA), with partialing out the effect of year, and rare species (<10 individuals) were excluded from analysis. (**a**) Mean and standard error of site scores among years in each subplot. (**b**) Species score for each carabid species. Species names are abbreviated by letters: NbSa, *Nebria sadona*; CaAl, *Carabus albrechti*; CaPr, *Carabus procerulus*; CaAr, *Carabus arboreus*; CaHa, *Carabus harmandi*; TrYo, *Trichotichnus yoshiroi*; NgBe, *Negreum bentonis*; MyCu, *Myas cuprescens*; PtSu, *Pterostichus subovatus*; PtKt, *Pterostichus katashinensis*; PtMi, *Pterostichus mitoyamanus*; PtOk, *Pterostichus okutamae*; PtRh, *Pterostichus rhanis*; PtTo, *Pterostichus tokejii*; SyAg, *Synuchus agonus*; SyMe, *Synuchus melantho*

Myas cuprescens, and *Synuchus* spp.) were dominant in the subplots close to the streambed (Subplots 1 and 2), where the ground was covered with colluvial deposits and where ferns used to dominate. In contrast, the Spring- and Summer-breeding Honshu-endemic species (*Carabus harmandi* and *Pterostichus* (*Nialoe*) spp.) characterized the beetle communities of subplots on the slope with dwarf bamboo (Subplots 4 and 5), which may reflect the beetles' preference for moist conditions, habitat stability, or both. Furthermore, the fact that Ooyamazawa is located in a vast and continuous forested area that ranges from lowland areas to alpine zones in central Honshu Island and that includes a variety of forest types may also contribute to the site's high beetle diversity. Indeed, the Ooyamazawa forest is located in the middle altitude zone of this huge species pool of forest carabids and harbors species that are often found in both subalpine to alpine zones (e.g., *N. sadona*, *Carabus arboreus*, *C. harmandi*, *Xestagonum xestum*, and *Pristosia aeneola*) and in lowland forests (e.g., *Carabus albrechti*, *C. procerulus*, *Pterostichus yoritomus*, *Synuchus arcuaticollis*, *S. cycloderus*, and *S. nitidus*).

Another distinctive feature of the carabid species composition in Ooyamazawa forest is the high proportion of Japan-endemic species (64.9%) which was third highest among the 22 monitored forest sites. In particular, the site harbored many locally endemic species and subspecies limited to the Kanto Mountains and the surrounding area. For example, the *C.* (*Ohomopterus*), *C.* (*Leptocarabus*), *C.* (*Pentacarabus*) *harmandi*, *P.* (*Nialoe*), *P. macrogenys*, and *Trichotichnus leptopus* groups mainly composed of forest-inhabiting and flightless species and that are finely differentiated on Honshu Island (Imura and Mizusawa 2013; Morita 1997; Sasakawa 2009; Sasakawa and Kubota 2009; Sota and Nagata 2008; Zhang and Sota 2007). Among the species and subspecies found in Ooyamazawa, *C.* (*L.*) *arboreus ogurai*, *C.* (*P.*) *harmandi okutamaensis*, *P.* (*N.*) *tokejii*, *P.* (*N.*) *mitoyamanus*, *P.* (*N.*) *okutamae*, *P.* (*N.*) *rhanis kantous*, *P. koheii* (*P. macrogenys* group), and *T. yoshiroi* (*T. leptopus* group) are endemic to the Kanto Mountains, and *C.* (*O.*) *albrechti esakianus*, *P. karasawai*, *P. mucronatus*, *P.* (*N.*) *katashinensis naganoensis*, *P. brittoni*, and *S. tanzawanus* are endemic to relatively narrow region (mainly the Kanto and Chubu districts) that includes the Kanto Mountains (Habu 1958, 1978; Imura and Mizusawa 2013; Morita 1997; Sasakawa 2005a, b, 2009; Ueno et al. 1985). Sasakawa (2005a) investigated the phylogenetic relationships within the *P.* (*N.*) *asymmetricus* species group, which includes *P. tokejii*, *mitoyamanus*, *okutamae*, *rhanis*, and *katashinensis*, and suggested that the Kanto Mountains are a hotspot for speciation in this group. Furthermore, recent studies of *Nebria* (*Sadonebria*) have revealed that the group has also finely differentiated within the Honshu, Shikoku, and Kyushu Islands (Sasakawa 2016). Because it is possible that the *N.* (*S.*) *sadona* recorded in our site is actually *N.* (*S.*) *chichibuensis*, which could be an endemic of the Kanto Mountains, further investigation is needed for this species.

The low proportion of non-endemic continental species in the cool-temperate forests of Honshu Island, including Ooyamazawa, may be partly explained by the geohistorical background of the Japanese Archipelago. In particular, the history of land bridge formation between the Japanese Islands and the Asian continent can be an important factor affecting the distribution patterns of flightless animal species. Studies of paleoceanography and fossil records have revealed that southwestern Japan was often connected to the Asian continent by land bridges from the late Miocene to the Pleistocene (Tada 1994) and that land mammal species repeatedly immigrated to Japan using these bridges (Dobson and Kawamura 1998). During the late Pleistocene or last glacial period, Hokkaido was often connected to the Asian continent, and many land mammal species immigrated to Hokkaido during those periods, but most of those species did not immigrate to Honshu, which suggests that the connection between Hokkaido and Honshu, during this period, was temporal and unstable (Kawamura 2007). Dobson and Kawamura (1998) discussed that the terrestrial mammals that colonized Japan earlier than the middle Pleistocene have already speciated into Japan-endemic species, whereas some of the species that immigrated during later periods (middle to late Pleistocene) have not yet differentiated and remain non-endemic species. A phylogeographic study of *Carabus* (*Ohomopterus*), which is a representative group of the Japan-endemic carabids, showed that the ancestor of this group started to differentiate from its continental sister group (*C.* (*Isiocarabus*)) during the early Pleistocene, when stable connection between southwestern Japan and the Asian continent was broken, and then speciated rapidly in the Honshu, Shikoku, and Kyushu Islands (Sota and Nagata 2008). In a similar manner, Japan-endemic members of *C.* (*Leptocarabus*) differentiated from continental sister species and diverged into multiple endemic species when expanding eastward (Zhang and Sota 2007). In comparison to these endemic groups, non-endemic *Carabus* spp. exhibit smaller genetic differences with continental populations, which implies that they colonized Japan more recently using the southwestern or northern land bridges (Tominaga et al. 2000). For the continental carabid species that are adapted to warm-temperate climates and that have invaded Honshu *via* southwestern land bridges, the colonization of cool-temperate forests could be difficult. On the other hand, the dispersal from Hokkaido to Honshu by cold-adapted continental species that invaded Hokkaido using the northern land bridges during the last glacial period could be limited by the deep Tsugaru Strait, as has been reported for terrestrial mammals. Therefore, such geohistorical situations might have contributed to the current low proportion of non-endemic carabids in the cool-temperate forests of Honshu, including Ooyamazawa.

10.4 Trends in Carabid Abundance and Biomass

The annual abundance and biomass of carabid beetles decreased drastically over the last 10 years, by up to one-fifth and one-seventh, respectively (Fig. 10.5a, b), and these declines were the most prominent decreasing trends observed among the 22 forest monitoring sites. Furthermore, eight of the 12 dominant species ($\geq$20 individuals were caught over 10 years) exhibited significant decreasing trends (Fig. 10.6), and the overall richness decreases, as well. However, the diversity index was not reduced, owing to increases in evenness that mainly resulted from large reductions in predominant species (e.g., *Synuchus melantho*, *Carabus albrechti*; Fig. 10.5d–f).

Over the last two decades, the overabundance of sika deer has caused rapid reductions in the forest floor vegetation of Ooyamazawa (Chap. 8). For example, the coverage of forest floor vegetation was >80% in 1998 and was reduced to only 3% by 2004 (Sakio et al. 2013). The vegetation cover in the five subplots, which was measured during each beetle survey (2008–2017), has remained low (5–30% in June). Reductions in forest floor vegetation by mammalian herbivores reduce litter fall, destabilize the litter layer and surface soil, promote the loss of litter layer, and cause the erosion of soil from steep slopes. In addition, trampling by the mammals

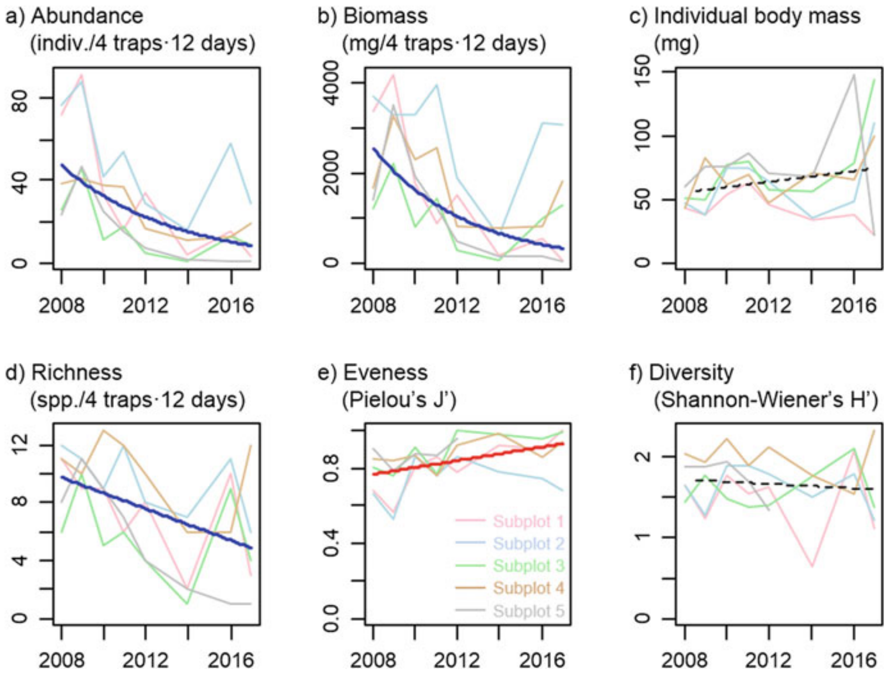

Fig. 10.5 Annual variation in the abundance, total biomass, individual mass, and species diversity of carabids in the Ooyamazawa riparian forest. Solid and dashed lines indicate significant and insignificant regressions by year, respectively (likelihood ratio test, $\alpha = 0.05$). Red and blue lines indicate increasing and decreasing trends, respectively. (**a**) Carabid abundance, Poisson regression; (**b**) Total carabid biomass, linear regression after log-transformation; (**c**) Individual body mass (biomass/abundance), linear regression; (**d**–**f**) Species diversity, linear regression. "Subplot" was used as a random factor

and the loss of forest floor cover, which protects soil from raindrop impact, are likely to promote the hardening of the soil surface and to reduce both the water permeability and water holding capacity of the forest soil. Loss of vegetation cover also reduced humidity, increases temperature, increases the variability of humidity and temperature at ground level, and reduces the availability of refuges for prey species to escape predators (e.g., mammals, birds). As a result, the changes brought by herbivore overabundance can generally reduce food resources and degrade the habitat of ground- and soil-dwelling animals, thereby reducing species density and diversity (e.g., Bressette et al. 2012; Lessard et al. 2012; Suominen 1999). In Ooyamazawa, the observed declines in carabid abundance, biomass, and richness could be caused directly by changes in the forest floor environment or indirectly by decreases in ground- and soil-dwelling invertebrates that serve as prey. The reduction of carabids occurred in all the subplots but was most conspicuous in Subplot 5, where the annual catch was reduced to almost zero (1 or 2 individuals per year) by 2014 (Fig. 10.5a). In this subplot, the dense cover of dwarf bamboo declined rapidly during the monitoring period. In addition, the beetles that initially inhabited Subplot

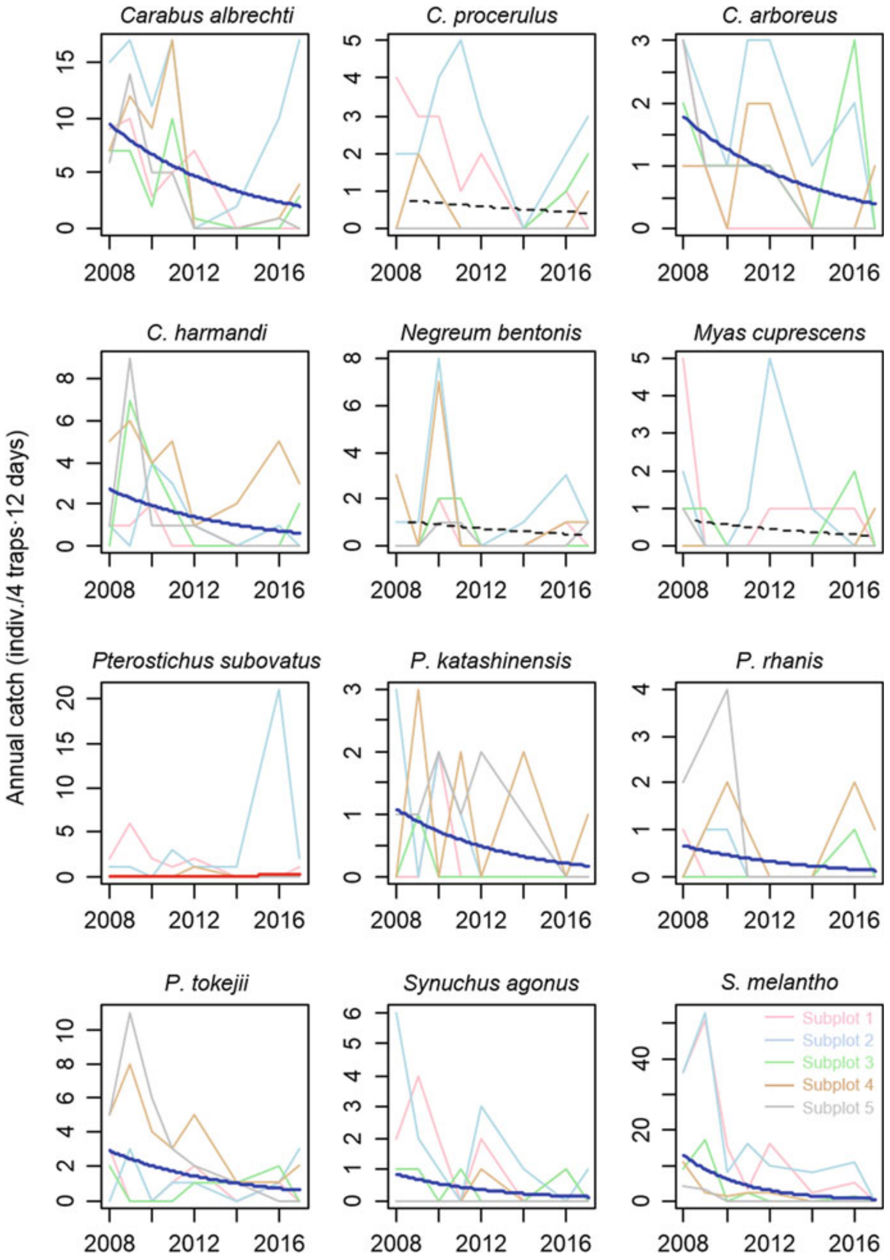

Fig. 10.6 Annual variation in the capture of dominant carabid species in the Ooyamazawa riparian forest. Dominant species were defined as those for which ≥20 individuals were captured over 10 years. Solid and dashed lines indicate significant and insignificant Poisson regressions by year, respectively (likelihood ratio test, $\alpha = 0.05$). Red and blue lines indicate increasing and decreasing trends, respectively. "Subplot" was used as a random factor

5, which were characterized by a high proportion of local endemics (Fig. 10.4), could have been most susceptible to deer overbrowsing because the subplot is located on a steep slope and because the litter layer and surface soil of the subplot are more likely to move without the support of forest floor vegetation.

However, the responses of ground- and soil-dwelling animals to increasing populations of large mammal herbivore are not always negative and vary, depending on taxon, ecological characteristics (e.g., body size, feeding habit, and habitat preference), environment (e.g., biome and productivity), and herbivory intensity (Bardgett and Wardle 2003; Stewart 2001; Foster et al. 2014; Allombert et al. 2005; Wardle et al. 2001; Flowerdew and Ellwood 2001). In the case of carabid beetles, the response of total abundance was highly variable because species that prefer open, warm, or dry conditions can be positively affected by the effects of large herbivores (Stewart 2001). For example, carabid beetles populations are reportedly increased by ungulate browsing in boreal forests, possibly owing to temperature increases and humidity decreases at the forest floor (Melis et al. 2006, 2007; Suominen and Danell 1999; Suominen et al. 2003). On the contrary, in Japanese temperate forests, many studies have reported that populations of certain small carabids increase in response to deer browsing, whereas populations of most large carabids (*Carabus* spp.) tend to decrease, and that, as a result, the dominancy of small species increased (Ueda et al. 2009; Okada and Suda 2012; Sato et al. 2018; Takakuwa et al. 2007; Yamada and Takatsuki 2015). In the Ooyamazawa forest, however, most species exhibited decreasing trends, regardless of body size, and only one small species (*Pterostichus subovatus*) exhibited a slight increasing trend (Figs. 10.6 and 10.7). Consequently, neither reductions in mean body mass nor directional changes in species composition were detected during the monitoring period (Figs. 10.5c and 10.8), possibly because few of the species at this site responded positively to deer browsing. Among the 12 dominant species, only one species (*P. subovatus*) had been reported by previous studies to respond positively to deer browsing, whereas negative responses had been reported for *C. procelurus*, *C. arboreus*, *P. tokejii*, and *P. rhanis* (Ueda et al. 2009; Okada and Suda 2012; Sato et al. 2018; Takakuwa et al. 2007). However, *C. procelurus*, which is the largest carabid species that was captured in Ooyamazawa, was not negatively affected, even though previous studies have reported that *C. procelurus* is highly sensitive to

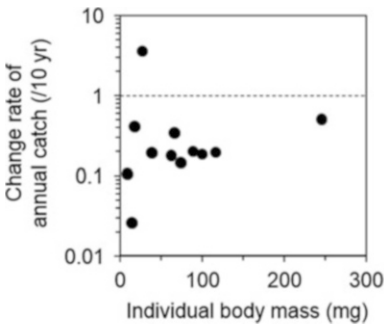

Fig. 10.7 Effect of mean body mass on changes in the annual catch of dominant carabid species. Vertical values were calculated using the coefficients of Poisson regression for each species (Fig. 10.6)

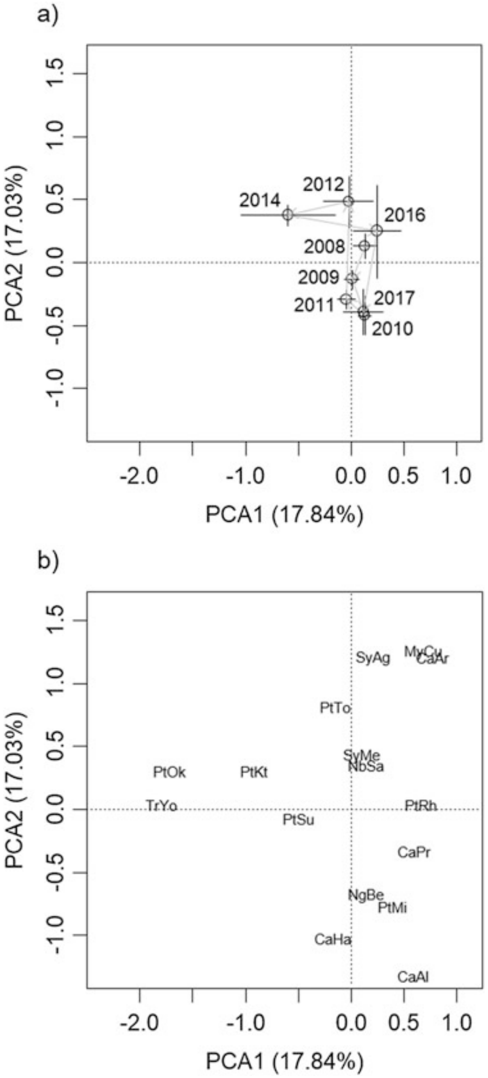

Fig. 10.8 Annual variation in the species composition of carabids captured in the Ooyamazawa riparian forest. Data were ordinated using principal component analysis (PCA), with partialing out the effect of subplot, and rare species (<10 individuals) were excluded from analysis. (**a**) Mean and standard error of site scores among subplots in each year. (**b**) Species score for each carabid species. Species names are abbreviated by letters: NbSa, *Nebria sadona*; CaAl, *Carabus albrechti*; CaPr, *Carabus procerulus*; CaAr, *Carabus arboreus*; CaHa, *Carabus harmandi*; TrYo, *Trichotichnus yoshiroi*; NgBe, *Negreum bentonis*; MyCu, *Myas cuprescens*; PtSu, *Pterostichus subovatus*; PtKt, *Pterostichus katashinensis*; PtMi, *Pterostichus mitoyamanus*; PtOk, *Pterostichus okutamae*; PtRh, *Pterostichus rhanis*; PtTo, *Pterostichus tokejii*; SyAg, *Synuchus agonus*; SyMe, *Synuchus melantho*

reductions in forest floor vegetation cover (Sato et al. 2018). It is possible that the *C. procelurus* population had already been reduced by vegetation reductions that occurred before the monitoring project was initiated and that the resulting low density was maintained thereafter or that the effect of increased temperature mitigated the negative impact of deer browsing (discussed below).

The last decade was the hottest one among the last 90 years in the Chichibu region. Although the mean annual air temperature of the region has exhibited constant fluctuation (±1°C, until the late 1980s), it subsequently increased by ~1°C during the next 10 years and has remained high since 2000, as documented by the weather station in Chichibu (Fig. 10.1). Such long-lasting warm conditions in these years may affect the carabid community. However, if warming was the main influencing factor of the observed community changes, the observed trends would be expected to differ between species with different temperature preferences. In general, species that are distributed at higher latitudes or altitudes (i.e., adapted to colder climates) are more negatively affected by warming than other coexisting species that are adapted to warmer climates. According to Ishikawa (1986) and Sasaki and Chishima (1991), who investigated the vertical distribution (150–2100 m alt.) of *Carabus* spp. in the Kanto Mountains, *C. arboreus ogurai* and *C. harmandi okutamaensis* are distributed at higher altitudes (850–2100 m), whereas *C. albrechti esakianus* and *C. procelurus procelurus* are distributed at lower altitudes (300–2000 m). In addition, only the two lower-altitude species were found in the lowland forests at the foot of the Kanto Mountains (90–230 m; Matsumoto 2005, 2009, 2012; Soga et al. 2013), and only *C. p. procelurus* was found in the forests of the Kanto Plain at lower altitude (20–90 m) and similar latitudes (Shibuya et al. 2008, 2011, 2014; Taniwaki et al. 2005a). In Ooyamazawa, *C. a. ogurai*, *C. h. okutamaensis*, and *C. a. esakianus* exhibited similar decreasing trends, whereas *C. p. procelurus* did not (Fig. 10.6), and another species that was found in lowland forest and was also dominant in Ooyamazawa was *Myas cuprescens* (Matsumoto 2005; Shibuya et al. 2008, 2011, 2014; Soga et al. 2013; Taniwaki et al. 2005b), which also failed to exhibit any significant change (Fig. 10.6). These two species (*C. p. procelurus* and *M. cuprescens*), which can survive in warm lowland forests, might be positively affected by temperature increases, thereby compensating for the negative effects of deer overabundance. However, distinct directional changes in species composition were not detected by the principal component analysis (Fig. 10.8). It is possible that the warming effects were overwhelmed by the overall negative impacts of deer overabundance or that the species composition might have already reached a new equilibrium after the major warming event that occurred from the late 1980s to the 1990s, before the initiation of beetle monitoring in Ooyamazawa. The species that are dominant in lowland forests and are also reported to respond positively to deer-mediated reductions in forest floor vegetation (e.g., *P. yoritomus* and *S. cycloderus*) are currently rare in Ooyamazawa but could increase with additional increases in temperature.

Temperature changes can affect carabid body size. For example, certain *Carabus* spp. are reportedly larger in warmer regions or at lower altitudes (Sota et al. 2000a, b). This is likely owing to adaptation or plastic responses to climatic conditions or prey availability. Among the dominant carabid species in Ooyamazawa, *C. procelurus*, *P. tokejii*, and *S. melantho* exhibited increasing trends in individual body mass (Fig. 10.9), and the growth rate of *C. procelurus*, in particular, which is distributed in warm lowland forests, might have been enhanced by the temperature increase. Meanwhile, it is also possible that body size increases were caused by the relaxation of inter- or intraspecific competition. In contrast, the body size of *P. subovatus* was observed to decrease, which may reflect an intensification of intraspecific competition, owing to slight increases in the species' abundance (Figs. 10.6 and 10.9).

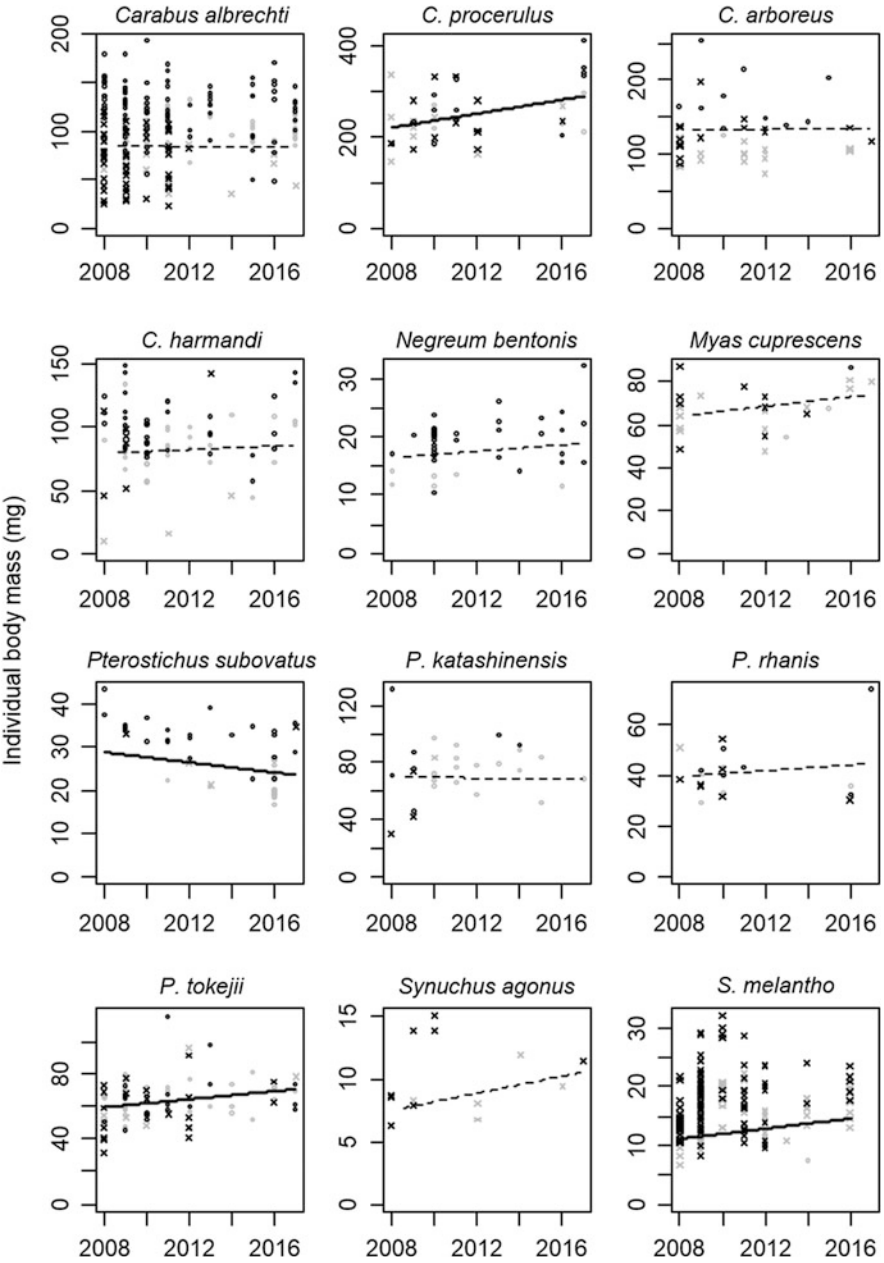

Fig. 10.9 Annual variation in the individual body mass of dominant carabid species in the Ooyamazawa riparian forest. Damaged individuals were excluded. Circle, Spring–Summer (May–June); cross, Autumn (September–October); grey, male; black, female. Solid and dashed lines indicate significant and insignificant regressions by year, respectively (likelihood ratio test, $\alpha = 0.05$). "Sampling season" and "sex" were used as random factors

10.5 Conclusion

The ground-dwelling beetle survey revealed that the Ooyamazawa riparian forest harbors a remarkably diverse and unique community of carabid beetles, including many locally endemic species. The characteristics of this community could be supported by the well-preserved stable forest environment, diverse microenvironments within riparian areas, huge species pool of forest-inhabiting carabids in central Honshu, and the geohistory of the Japanese Archipelago.

Sadly, the 10-year monitoring project also confirmed drastic or critical reductions in most species that prevailed throughout the plot. Two profound and long-lasting environmental pressures that have been introduced during the last two to three decades (i.e., deer-mediated reductions in forest floor vegetation and temperature increase) may have interactively caused the observed declines. If the present situation persists, most species, including many local endemics, will be extirpated from the site and be replaced by the species that are dominant at lower altitudes and that either tolerate or prefer deer-related disturbances.

The long-term and quantitative monitoring data allowed the identification of significant trends in the carabid beetle community that, generally, would have been difficult to understand using short-term or less frequent observation, mostly because the abundance of short-lived and rapidly reproducing animals, such as insects, often exhibits large annual fluctuations. It is necessary to continue this monitoring, in order to document the response of the beetle community to the persistence or alteration of the current deer density and climate conditions. Moreover, the observation of such pronounced species declines demonstrates the urgency of conserving the Ooyamazawa ecosystem. Indeed, Sato et al. (2018) described the effectiveness of providing early protection for forest floor communities against deer overbrowsing in the preservation of carabid species that are sensitive to declines in vegetation. A conservation project, the goal of which is to install deer exclosures in this area, has been just launched by the prefectural office, and the exclusion and population management of deer are expected to promote the recovery of the forest floor vegetation and, subsequently, of carabids and other vegetation-dependent animals. The monitoring data presented here also provides a basis for estimating the extent and direction of carabid community recovery.

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