

## High niche overlap in the stable isotope space of ground beetles

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Classic theories on assembly rules and food-web structure are species-centered, so they largely ignore intraspecific variation. Intraspecific trophic variation, however, might be of key importance in understanding community organization. Here we study the variability of isotopic niche spaces of ground beetles and its consequences for the trophic structure of beetle assembly. Stable isotopes ratios ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) were measured in 1156 specimens of carabids belonging to 59 species inhabiting 20 island and two mainland sites of the Masuria Lakeland in northern Poland. Carabid species belonged to three different trophic guilds (named “phytophages”, “decomposer feeders” and “generalist predators”). However, this division is not sharp due to high intraspecific variability of isotopic signatures, which indicates the use of very different types of resources by conspecific individuals inhabiting different sites. As a consequence, most species studied did not differ significantly in the isotopic niche space. This high niche overlap corroborates the view that resource competition is not a major factor shaping the composition of ground beetles communities. Future studies should take into account the complex trophic structure of beetle assemblages and explore the intraspecific niche variability of ground beetles.

## Introduction

Classical theories on niche division (Sugihara 1981) and competitive exclusion (Gause 1934, Diamond 1975), and recent modeling of food web structure (e.g. Allesina *et al.* 2008), are all species-centered and focus on species interactions. Thus, they ignore intraspecific variability in trophic position for the purpose of mathematical modeling and conceptual ease (Chase & Leibold 2003, Violle *et al.* 2012). However, older works on character displacement (Brown & Wilson 1956) and competitive release (Connell 1961), and recent work on food web dynamics, all highlight the importance of spatial and temporal intraspecific variability (Grimm & Railsback 2005, Bolnick *et al.* 2011) in structuring trophic relationships (Nakazawa *et al.* 2010), species associations and competitive interactions (Lichstein *et al.* 2007). Therefore, research on trophic relationships within a community should acknowledge both intraspecific and interspecific variation in trophic position.

An appropriate approach to study simultaneously intra- and interspecific variability in trophic position and dietary niche width is stable isotope analysis (Oelbermann & Scheu 2002, Bearhop *et al.* 2004, Layman *et al.* 2007, 2011, Michener & Lajtha 2007). The carbon isotope ratio of body tissues ( $^{13}\text{C}/^{12}\text{C}$ , usually expressed as a standardized ratio  $\delta^{13}\text{C}$ ) is approximately stable across trophic levels, but depends on habitat and resource type — e.g. living *vs.* decaying organic material (Ponsard & Ardity 2000, Pollierer *et al.* 2009). The nitrogen isotope ratio ( $^{15}\text{N}/^{14}\text{N}$ , usually expressed as  $\delta^{15}\text{N}$ ) increases in insects by about  $2.5\text{‰} \pm 1.8\text{‰}$  (mean  $\pm$  1 SD) per trophic level (Ikeda *et al.* 2010) and thus indicates the relative position of an individual within its food chain. The comparison of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values within and among species allows therefore for an assessment of the degree of trophic overlap among species and among individuals of the same species (Halaj *et al.* 2005, Gratton & Forbes 2006, Wise *et al.* 2006 and references therein).

Stable isotope analysis is widely used in studies of all kinds of food webs (cf. Layman *et al.* 2007) including diverse invertebrate communities inhabiting the soil and litter (Scheu &

Falca 2000, Hyodo *et al.* 2010, Ikeda *et al.* 2010, Okuzaki *et al.* 2009, 2010, Wimp *et al.* 2013). These investigations have primary importance for understanding trophic structure and community organization of terrestrial arthropod communities. In particular, stable isotope research allows one to picture unidentified and complex trophic relationships within communities that cannot easily be explored using more traditional methods (Martinez del Rio *et al.* 2009).

One trophic interaction that could influence species assembly is resource competition. While overlap or separation of isotopic niches does not have to imply competitive interactions, resource competition could be reflected in isotopic niches. The study of isotopic niche spaces is therefore an indirect method of revealing whether a community is structured by food competition between species of the same trophic level. In such a case, species should be more segregated in isotopic niche space than expected by chance from a random occurrence model (Ponsard & Ardit 2000). Further, trophic segregation implies that intraspecific variability should be smaller than interspecific variability in order to reduce overlap in isotopic niche space (Bearhop *et al.* 2004, Araújo *et al.* 2011). In turn, if the level of intraspecific competition exceeds that of interspecific competition the opposite effect might occur: intraspecific variability in niche space should be large as compared with a random expectation and with the interspecific level. Thus, comparisons of intraspecific and interspecific variability might allow for the assessment of the relative importance of both levels of competition (Araújo *et al.* 2011). In this respect comparisons between the degree of variability of congeneric and non-congeneric species are of interest. Within the niche conservatism framework (Wiens & Graham 2005, Wiens *et al.* 2010) conspecifics and congeners should be more similar in phylogenetically conserved traits than non-conspecifics and non-congeners. While this prediction has been extensively tested for morphological traits (cf. Wiens *et al.* 2010) there are apparently no tests of trophic niche conservatism. Here we apply stable isotope analysis to explore this question. Particularly we hypothesize that if conspecifics and congeners are more similar in prey choice than specimens from dif-

ferent species and genera, they should have more similar isotope signatures with respect to trophic rank ( $\delta^{15}\text{N}$ ) and also with respect to the type of utilized carbon ( $\delta^{13}\text{C}$ ). Under the niche conservatism framework, this hypothesis further implies that prey choice is a conserved trait (Wiens *et al.* 2010).

The present work aims at testing hypotheses concerning the trophic structure of ground beetle communities. We focus on a species rich community of ground beetles spread among lake islands in northern Poland (Zalewski & Ulrich 2006). Our results present a complex trophic structure of carabid communities and show the degree of niche variability and overlap in trophic niche space within and between species.

## Material and methods

### Study sites and sampling

We sampled 27 sites on 18 lake islands and two adjacent mainland sites at two lakes in NE Poland: Lake Mamry ( $21^{\circ}30' - 52^{\circ}E$ ,  $54^{\circ}00' - 10'N$ ) and Lake Wigry ( $54^{\circ}00' - 05'N$ ,  $22^{\circ}01' - 09'E$ ). The islands vary in size (0.15–38.82 ha) and distance to the nearest mainland (30–375 m). In both archipelagos, humid alder (*Alnion glutinosae*) and lime-oak forests (*Tilio-Carpinetum betuli*) dominate. Additionally, three of the islands in Lake Wigry host abandoned pastures (*Arrhenatherion* and *Cynosurion* alliances).

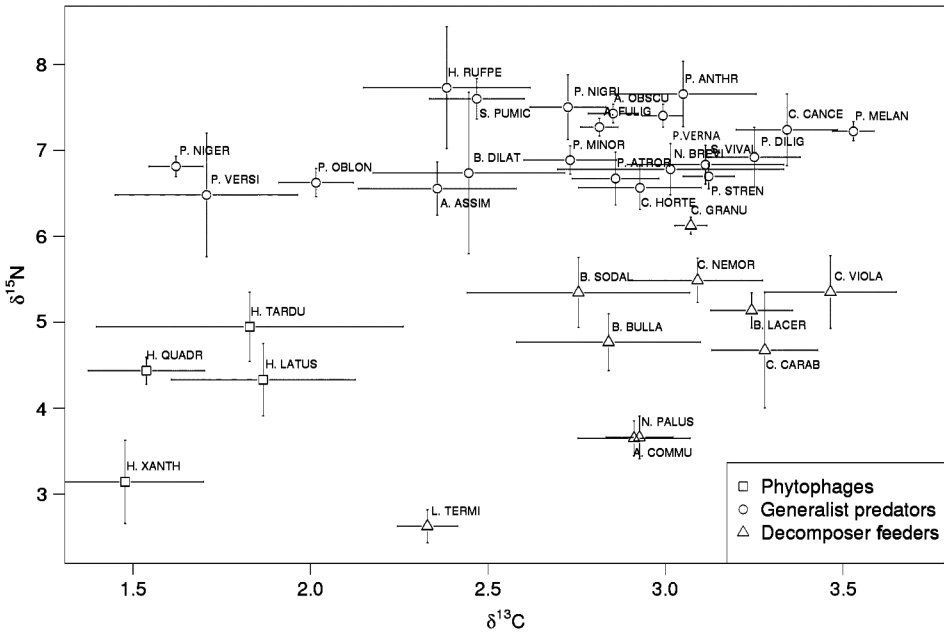
On each island and in each habitat, we installed a transect of 10 pitfall traps (0.5 l plastic mug, mouth diameter 120 mm, plastic roof, filled with pure monoethylene glycol) 10 m apart. The traps were emptied weekly and animals were preserved in 96% alcohol. This procedure does not affect the isotopic composition of carbon and nitrogen in beetles (Zalewski *et al.* 2012a). Emptied traps were refilled with new monoethylene glycol. Sampling was conducted over four weeks in June and August 2010.

### Stable isotope analysis

In total we determined isotopic ratios of 1156 ground beetles from 59 species. In line with Berg

*et al.* (2010) and Duyck *et al.* (2011), we determined whole body isotope signatures of the beetles. The beetles were dried in  $60^{\circ}\text{C}$  for about 70 hours and pulverized. Isotopic ratios of carbon and nitrogen were analyzed in three laboratories following the same methodology using a MAT-253 spectrometer at the Institute of Geological Sciences of the Polish Academy of Sciences in Warsaw, a Thermo-Finnigan Delta V Plus IRMS at the Joint Usage Center, Institute of Ecology and Evolution of the Russian Academy of Sciences in Moscow, and a Finnigan MAT Delta S at the Center for Ecological Research, Kyoto University. Analytical precision was cross-validated and the test measurements were almost identical in all three laboratories. Final results were based on calibration curves using the IAEA reference materials USGS 40, USGS 41, IAEA 6000 and IAEA CH-3 in Poland and Russia, and CERKU-01, CERKU-02 and CERKU-05 determined in Tayasu *et al.* (2011) in Japan. We used triple-point calibration and accepted a minimum signal intensity of 2 V on IRMS. Isotope ratios were expressed in delta ( $\delta$ ) units as a deviation from the international standards and recalculated into parts per thousand (‰), according to the formula:  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$  (‰) =  $(R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000$ , where  $R$  is the ratio of heavy/light isotope content for the considered element. The international standards were Pee Dee Belemnite for  $\delta^{13}\text{C}$  and atmospheric nitrogen for  $\delta^{15}\text{N}$ . The analytical error (standard deviation of the values measurements for the working standard) was less than  $\pm 0.15\text{‰}$  for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ .

To account for differences in isotopic baseline ratios among different sampling sites, we collected litter samples on each trap line in the vicinity of every second trap (in total 5 samples per line) in the middle of June and August 2010. Baseline samples were dried in  $60^{\circ}\text{C}$  for 48–70 hours and analyzed following the methodology applied to beetles. The carbon isotopic signature of the baseline was different in meadows and forested sites, but not among different islands (D. Dudek unpubl. data), therefore the mean value of  $\delta^{13}\text{C}_{\text{litter}}$  was calculated for each of the three habitats sampled (alder and lime forest and meadow) and was used as baseline correction of the isotopic ratio of beetles ( $\delta^{13}\text{C}_{\text{beetle}} = \delta^{13}\text{C}_{\text{raw}} - \delta^{13}\text{C}_{\text{average litter in habitat}}$ ). Due to high variability



**Fig. 1.** Mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  ratios of 35 ground beetle species represented by at least five individuals. Error bars denote standard errors. Stable isotope ratios are corrected by subtracting those of litter. The figure indicates the division of the community into three guilds; a “phytophagous” (low  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  ratios), a “decomposer feeders” (intermediate to high  $\delta^{13}\text{C}$  and low  $\delta^{15}\text{N}$  ratios), and a “generalist predators” guild (low to high  $\delta^{13}\text{C}$  and high  $\delta^{15}\text{N}$  ratios). The outlying springtail feeding *Leistus terminatus* (L. TERMI) belongs ecologically to the “decomposer feeders” guild. *Carabus granulatus* (C. GRANU) is situated at the boundary between the “decomposer feeders” and the “generalist predators” guild. *K*-means clustering classified this species into the “decomposer feeders” guild (cf. Table 2).

of  $\delta^{15}\text{N}_{\text{litter}}$  values (mean =  $-2.7$ , SD =  $1.3$ ,  $n = 135$ ), the mean  $\delta^{15}\text{N}$  were calculated for each trap line and were used as baseline correction ( $\delta^{15}\text{N}_{\text{beetle}} = \delta^{15}\text{N}_{\text{raw beetle}} - \delta^{15}\text{N}_{\text{average litter on trapline}}$ ).

## Statistical analysis

To avoid calculation biases due to small sample sizes, we compared isotopic niche spaces of the 35 most abundant species of which at least five individuals were analyzed (Table 1; total of 1108 individuals). We assessed interspecific differences in niche space from customary  $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$  biplots and intraspecific variability from *k*-means cluster analysis with *Z*-normalized ( $Z = (x - \mu)/\sigma$ , where  $x$  is the raw ratio,  $\mu$  is the mean, and  $\sigma$  is the standard deviation) ratios to avoid distortions due to differences in the mean and variance of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ . We used general linear modeling (GLM, orthogonal sums of squares) as implemented in Statistica 7.1 to infer

differences in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of carabids belonging to different species and originating from different islands. Subsequent post-hoc unequal sample size Tukey’s test was used for pair-wise comparisons of species differences in isotopic niche space. We used the numbers of significant differences between all pairs of species (separate analysis for each trophic guild) to estimate the degree of isotopic niche segregation and the degree of niche overlap.

## Results

Based on the plot of the species average isotopic positions, three major guilds of beetles were proposed (Fig. 1 and Table 1). The first guild, named “phytophagous”, contains four *Harpalus* species with low  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , which are mainly phytophagous (Lindroth 1985, 1986, Ribera *et al.* 1999), though high maximum  $\delta^{15}\text{N}$  values in some species (e.g. *Harpalus latus*; Table 1)

**Table 1.** A list of the 35 most abundant ground beetle species with numbers of colonized islands, numbers of studied individuals ( $n$ ), mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values along with their standard deviations (SD), minima (min), maxima (max) and ranges (range =  $\delta_{\text{max}} - \delta_{\text{min}}$ ). Stable isotope ratios are corrected by subtracting those of litter. Ratios for *Harpalus latus* should be treated with caution because some individuals were difficult to identify. Trophic guild classification (pr: "generalist predators" guild, de: "decomposer feeders" guild, pp: "phytophagous" guild) refer to the three guilds in Fig. 1.

Species	Trophic guild	Island number	$n$	$\delta^{13}\text{C}$			$\delta^{15}\text{N}$					
				Mean	SD	Range	Mean	SD	Range			
<i>Agonum assimile</i>	pr	6	18	2.36	0.95	0.71	4.11	6.56	1.31	2.28	7.99	5.71
<i>Agonum fuliginosum</i>	pr	10	98	2.81	0.52	0.98	3.94	7.27	1.02	4.82	10.59	5.77
<i>Agonum obscurum</i>	pr	12	87	2.85	0.66	0.33	4.94	7.43	1.03	4.52	10.06	5.54
<i>Amara communis</i>	de	5	25	2.91	0.79	1.49	4.11	3.65	1.01	0.40	5.94	5.54
<i>Badister bullatus</i>	de	5	5	2.84	0.58	2.22	3.42	4.77	0.58	3.97	5.77	1.80
<i>Badister dilatatus</i>	pr	3	5	2.45	0.61	1.6	2.99	6.74	0.61	3.00	8.03	5.03
<i>Badister lacertosus</i>	de	5	14	3.24	0.43	2.36	3.85	5.14	0.43	3.72	6.31	2.59
<i>Badister sodalister</i>	de	5	6	2.76	0.77	1.62	3.44	5.35	0.77	3.54	6.55	3.01
<i>Carabus cancellatus</i>	pr	2	8	3.34	0.40	2.6	3.71	7.24	1.18	6.00	9.01	3.01
<i>Carabus granulatus</i>	de	12	145	3.07	0.55	1.54	4.22	6.12	0.55	2.50	9.66	7.16
<i>Carabus hortensis</i>	pr	4	11	2.93	0.78	1.82	3.38	6.56	0.84	5.53	8.37	2.84
<i>Carabus nemoralis</i>	de	11	18	3.09	0.78	1.36	4.18	5.49	1.10	4.43	8.07	3.64
<i>Carabus violaceus</i>	de	1	6	3.47	0.45	2.91	4.06	5.35	1.04	4.07	6.68	2.61
<i>Cychrus caraboides</i>	de	1	6	3.28	0.37	2.78	3.70	4.68	1.65	3.17	6.77	3.60
<i>Harpalus latus</i>	pp	4	19	1.87	1.13	-0.43	3.64	4.33	1.83	1.35	9.31	7.96
<i>Harpalus quadripunctatus</i>	pp	8	41	1.54	1.05	-0.39	3.09	4.44	1.01	2.22	6.35	4.13
<i>Harpalus rufipes</i>	pr	7	8	2.38	0.67	1.43	3.66	7.73	2.01	5.77	10.71	4.94
<i>Harpalus tardus</i>	pp	2	9	1.83	1.30	0.27	4.11	4.95	1.21	3.83	7.35	3.52
<i>Harpalus xanthopus</i>	pp	2	9	1.48	0.66	0.63	2.61	3.14	1.45	1.04	5.62	4.58
<i>Leisites terminatus</i>	de	5	16	2.33	0.34	1.85	3.02	2.63	0.76	1.28	4.10	2.82
<i>Nebria brevicollis</i>	pr	4	7	3.01	0.84	2.04	3.99	6.78	0.79	5.91	7.89	1.98
<i>Notophilus palustris</i>	de	7	13	2.93	0.34	2.37	3.65	3.66	0.89	2.29	5.15	2.86
<i>Pterostichus atrorufus</i>	pr	5	16	2.86	0.49	1.93	3.72	6.67	1.23	3.99	8.80	4.81
<i>Pterostichus anthracinus</i>	pr	2	5	3.05	0.46	2.63	3.66	7.66	0.85	6.77	8.92	2.15
<i>Pterostichus diligens</i>	pr	7	17	3.25	0.53	2.11	4.14	6.92	1.43	4.16	9.61	5.45
<i>Pterostichus melanarius</i>	pr	17	136	3.53	0.69	1.97	5.53	7.22	1.29	4.39	11.01	6.62
<i>Pterostichus minor</i>	pr	8	19	2.73	0.57	1.89	3.83	6.89	0.72	5.46	8.57	3.11
<i>Pterostichus niger</i>	pr	13	99	1.62	0.76	-0.23	3.51	6.81	1.18	2.44	10.96	8.52
<i>Pterostichus nigrita</i>	pr	8	19	2.73	0.47	1.97	3.59	7.50	1.64	5.03	11.00	5.97
<i>Pterostichus oblongopunctatus</i>	pr	16	69	2.02	0.87	-0.46	4.02	6.62	1.36	1.36	9.14	7.78
<i>Pterostichus strenuus</i>	pr	13	67	3.12	0.59	1.91	4.70	6.70	1.20	4.50	10.25	5.75
<i>Pterostichus vernalis</i>	pr	10	50	2.99	0.41	1.69	4.06	7.40	0.94	5.45	9.67	4.42
<i>Stomis pumicatus</i>	pr	2	7	1.71	0.68	1.23	2.99	6.48	1.90	3.65	9.88	6.03
<i>Synuchus vivalis</i>	pr	6	19	2.47	0.58	0.86	3.28	7.60	1.02	6.05	10.43	4.38
		5	11	3.11	0.73	1.83	4.54	6.83	0.75	5.35	7.65	2.30

suggest that they also feed on animals. A second guild with similarly low  $\delta^{15}\text{N}$  but higher  $\delta^{13}\text{C}$  values comprised an assemblage of ten species including the partly phytophagous *Amara com-*

**Table 2.** *K*-means clustering analysis (three *a priori* clusters) of all 1108 individuals from 35 ground beetle species in comparison with the grouping of species derived from Fig. 1. The entries denote the number of individuals grouped into the clusters. Thus, 7 studied individuals of *Agonum assimile* were grouped into cluster one, 5 into cluster two and 6 into cluster three. Species that could be unequivocally (binomial  $p < 0.05$ ) grouped are indicated with boldface.

Species	Cluster		
	1	2	3
<b>Generalist predator guild</b>			
<i>Agonum assimile</i>	7	5	6
<b><i>Agonum fuliginosum</i></b>	<b>74</b>	21	3
<b><i>Agonum obscurum</i></b>	<b>62</b>	25	0
<i>Badister dilatatus</i>	4	0	1
<i>Carabus cancellatus</i>	3	5	0
<i>Carabus hortensis</i>	2	7	2
<i>Harpalus rufipes</i>	6	1	1
<i>Nebria brevicollis</i>	3	4	0
<i>Patrobis atrorufus</i>	6	7	3
<i>Pterostichus anthracinus</i>	5	0	0
<i>Pterostichus diligens</i>	6	10	1
<i>Pterostichus melanarius</i>	60	75	1
<i>Pterostichus minor</i>	9	8	2
<i>Pterostichus niger</i>	45	8	46
<b><i>Pterostichus nigrita</i></b>	<b>14</b>	4	1
<b><i>Pterostichus oblongopunctatus</i></b>	<b>36</b>	8	25
<b><i>Pterostichus strenuus</i></b>	25	<b>41</b>	1
<b><i>Pterostichus vernalis</i></b>	<b>32</b>	18	0
<i>Pterostichus versicolor</i>	4	1	2
<b><i>Stomis pumicatus</i></b>	<b>16</b>	3	0
<i>Synuchus vivalis</i>	4	6	1
<b>Decomposer feeder guild</b>			
<i>Amara communis</i>	0	11	14
<i>Badister bullatus</i>	0	3	2
<b><i>Badister lacertosus</i></b>	0	<b>12</b>	2
<i>Badister sodalis</i>	0	4	2
<b><i>Carabus granulatus</i></b>	36	<b>98</b>	11
<i>Carabus nemoralis</i>	3	10	5
<b><i>Carabus violaceus</i></b>	0	<b>6</b>	0
<i>Cychrus caraboides</i>	0	5	1
<b><i>Leistus terminatus</i></b>	0	0	<b>16</b>
<i>Notiophilus palustris</i>	0	6	7
<b>Phytophages</b>			
<b><i>Harpalus latus</i></b>	1	5	<b>13</b>
<b><i>Harpalus quadripunctatus</i></b>	0	9	<b>32</b>
<i>Harpalus tardus</i>	0	3	6
<b><i>Harpalus xanthopus</i></b>	0	1	<b>8</b>

*munis*, three omnivorous species of *Carabus* (*C. granulatus*, *C. nemoralis* and *C. violaceus*), as well as the mollusk predator *Cychrus caraboides*, a specialist collembolan feeder *Leistus terminatus*, and scavenging *Badister* spp. (LaRochelle 1972, Lindroth 1985, 1986, Sunderland & Sutton 1980, Gryuntal & Sergeyeva 1989, Turin *et al.* 2003). According to their increased  $\delta^{13}\text{C}$  values (Table 1), these species might be attributed to the decomposer food web (Ponsard & Ardity 2000, Pollierer *et al.* 2009, Hyodo *et al.* 2010, Potapov *et al.* 2014). The low average  $\delta^{15}\text{N}$  values suggest that members of this guild feed mostly on micro-phytophages and mycetophages like springtails, or on primary litter decomposers like mollusks, earthworms, diplopods, isopods or dead plant material (Scheu & Falca 2000, Pollierer *et al.* 2009). Hereafter, this rather heterogeneous guild is defined as “decomposer feeders” guild. The other 21 species (60%) had average  $\delta^{15}\text{N}$  ratios well above 6.0‰ and thus can be classified as being predominantly predators and were assigned to the “generalist predator” guild.

The difference in average  $\delta^{15}\text{N}$  ratios from the lowest ranking *Leistus terminatus* (litter-corrected  $\delta^{15}\text{N} = 2.6\text{‰}$ ) to the highest ranking *Harpalus rufipes* ( $\delta^{15}\text{N} = 7.7\text{‰}$ ) was more than two times the average increase in  $\delta^{15}\text{N}$  between trophic levels. In 31 species (89%) measured  $\delta^{15}\text{N}$  ratios spanned more than 2.5‰ suggesting that these species regularly feed on more than one trophic level. In three species (*H. latus*, *P. niger* and *P. oblongopunctatus*) this range was above 7.5‰ suggesting prey intake from over three trophic levels (Table 1).

To compare interspecific isotopic niche classification with intraspecific variability in isotopic space we used *k*-means cluster analysis with three predefined clusters (Table 2). This individual-based analysis redetected the “phytophagous” guild identified by the interspecific approach, enlarged by the partly phytophagous *A. communis* and the collembolan feeder *L. terminatus*. However, the intraspecific *k*-means clustering did not delineate clearly between the “generalist predators” and “decomposer feeders” guilds (Table 2). The majority of generalist predator species appeared to be highly variable and individuals of nearly all species overlapped with those of the “decomposer feeders” and even

the “phytophagous” guild. The intraspecific variability in the “decomposer feeders” guild was equally pronounced. These results point to a high intraspecific variability in C and N sources in both guilds that exceeds interspecific variability. General linear modeling indicated that at least part of these intraspecific variability in resource use stems from intraspecific differences in both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  ratios between islands as apparent from the highly significant species  $\times$  island interaction term, particularly among “generalist predators” (Table 3).

In the “generalist predator” guild, only *Pterostichus oblongopunctatus* and *Agonum obscurum* differed in their  $\delta^{15}\text{N}$  ratios from other species more often than would be expected solely from chance at the 5% error level (not shown). In line with Fig. 1, species of the “generalist predator” guild differed most in  $\delta^{13}\text{C}$ , indicating either difference in diet habits under different habitat conditions or food intake from different C-pathways, namely from grazers with low  $\delta^{13}\text{C}$  and decomposers or mycetophages with higher  $\delta^{13}\text{C}$  (Fig. 1). Particularly three species of the genus *Pterostichus* (*P. oblongopunctatus*, *P. niger*, *P. versicolor*) had significantly smaller and *P. melanarius* significantly larger  $\delta^{13}\text{C}$  ratios than the other species of this trophic guild (Fig. 1). Not counting the four mentioned

species, only 56 pair-wise comparisons within the “generalist predator” guild out of a total of 756 (= 7.4%) pointed to significant differences in isotopic niche space at the 5% error level. This is only slightly above the random expectation and does not point to marked niches differentiations. Instead the results suggest high intraspecific variability and isotopic niche overlap.

In the “decomposer feeders” guild the springtail feeding *L. terminatus* was set apart from the other species of this guild. *A. communis* (partly phytophagous) and *Notiophilus palustris* (feeding on springtails, Lindroth 1985, 1986) were separated with respect to  $\delta^{15}\text{N}$ . These three species had the lowest average  $\delta^{15}\text{N}$  ratios (Table 1). In the “decomposer feeders” guild (not counting the three mentioned species) 29 out of 170 (i.e. 17%) pairwise comparisons were statistically significant. Both results indicate that species of the “decomposer feeders” guild are better separated in the isotopic niche space than species of the “generalist predator” guild. Overall, 80% of species from the whole community (three guilds lumped together) did not differ significantly in the isotopic niche space (all possible pairwise comparisons of the isotopic scores in Table 1). A closer look to intra- and intergenus differentiation (Table 4) revealed that the *Agonum* and *Carabus* species were probably more similar

**Table 3.** General linear modelling of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  ratios as dependent on species membership and island as predictors.

Guild	Variable	$\delta^{13}\text{C}$				$\delta^{15}\text{N}$			
		SS	df	F	p	SS	df	F	p
Phytophages									
	Species	8.0	3	5.4	0.002	6.4	3	1.7	0.181
	Islands	52.1	10	10.5	< 0.001	44.8	10	3.5	0.001
	Species $\times$ Islands	2.3	2	2.3	0.106	5.5	2	2.1	0.126
	Error	30.7	62			78.9	62		
Generalist predators									
	Species	135.0	20	18.7	< 0.001	76.7	20	4.0	< 0.001
	Islands	30.5	19	4.7	< 0.001	137.8	19	8.0	< 0.001
	Species $\times$ Islands	82.4	120	2.0	< 0.001	268.9	120	2.5	< 0.001
	Error	211.8	617			560.1	617		
Decomposer feeders									
	Species	7.2	9	3.2	0.001	225.3	9	30.2	< 0.001
	Islands	9.8	16	2.5	0.002	45.5	16	3.4	< 0.001
	Species $\times$ Islands	18.0	26	2.8	< 0.001	23.1	26	1.1	0.380
	Error	50.0	201			166.7	201		

in their isotopic niches than species of other genera, while of the ten *Pterostichus* species, 49% of pairwise comparisons pointed to significant interspecific differences (Tukey's post-hoc comparisons). In turn, only 13% of the pairwise differences of the *Pterostichus* species and species from other genera were significant.

## Discussion

Classical theory on the coexistence of species (MacArthur & Levins 1967) focuses on species as the basic players in ecological games, and used average values of important niche axes to estimate species distances, limiting similarity and possible competitive interactions (May & MacArthur 1972). While both of the above-mentioned studies emphasize the importance of species distance in niche space and intraspecific variability, later work often ignored the variability aspect due to a lack of data, and instead centered on distances only (reviewed in Violle *et al.* 2012). This neglect of intraspecific variance in favor of species means is particularly obvious in the discussions around ecological assembly rules (Diamond 1975, Abrams 1983, Weiher & Keddy 1999) and community phylogenetics (Webb *et al.* 2002, Violle *et al.* 2011), which nearly treat species solely as statistical central tendencies. In turn, recent neutral (Hubbell 2001, Rosindell *et al.* 2012) and individualistic based modeling approaches (Grimm & Railsback 2005) and community and molecular ecology, highlight

the importance of intraspecific variability in the maintenance of species diversity and community structure (Lichstein *et al.* 2007, Yamauchi & Miki 2009, Clark 2010, Albert *et al.* 2011). Nevertheless the majority of studies still use average values for pattern analysis (Violle *et al.* 2012).

In the present analysis, our large sample of 1108 ground beetle specimens allowed us to simultaneously assess variability in the isotopic niche space among and within species. The major result is the high overlap in isotopic niche space between species of the same trophic guild (Tables 1 and 2, Fig. 1). In all three guilds, more than 80% of the species did not differ significantly in isotopic niche space. This high niche overlap explains the seeming contradiction between division into three trophic guilds (Fig. 1) and results of the cluster analysis (Table 2). While Fig. 1 suggests a rather clear classification of species into three major guilds, the cluster analysis (Table 2) points to an overlap among guilds. The reason is that the use of species averages in Fig. 1 masks high intraspecific variability. Further, the clustering suggests that members of the same species might occupy a different trophic position depending on the island on which they live (Table 3) and perhaps on habitat type. For instance, 60 individuals of *P. melanarius* were classified into the "generalist predator" guild and 75 into the "decomposer feeders" guild, which might be an indication of two subpopulations within this species that opportunistically use different types of resources. Similar trophic subpopulations appear to exist in the majority of other species, particularly in *A. fuliginosum*, *A. obscurum*, *P. niger*, *P. strenuus*, *P. vernalis*, and *C. granulatus* (Table 2).

Our results are in line with the antibody-based findings of Sergeeva (1994) who reported a comparably high diet overlap for 15 carabids. Recently, Semeniuk and Tiunov (2011) reported a similar broad overlap in the isotopic niche space in a moderate species rich community of saprophagous forest millipedes. Pollierer *et al.* (2009) applied isotopic biplots and found a strong segmentation of different soil functional guilds in connection with high niche overlap within trophic guilds. Our study adds additional data to this picture. Both mentioned studies and the present one indicate high niche overlap between species together with some guild seg-

**Table 4.** Comparisons of significant differences in isotopic niche space between all species pairs within the genera *Agonum*, *Carabus* and *Pterostichus* and the pairs including the species of these genera and other genera (non-congener differences). Given is the fraction of significant post-hoc Tukey's test (GLM in Table 3) in relation to the total number of single pairwise comparisons for each genus.

Genus	Species	Fraction of congener differences	Fraction of non-congener differences
<i>Agonum</i>	3	0.00	0.19
<i>Carabus</i>	3	0.00	0.11
<i>Pterostichus</i>	10	0.49	0.13



regation in niche space. This finding is in line with many studies on diversity and ecosystem functioning that have also reported a major influence of functional (i.e. guild) diversity (Hooper *et al.* 2005), and a less important role of species. As an exception to this picture, Schneider *et al.* (2004) found significant isotopic niche differentiation within species rich soil mite communities (Oribatida) that span three to four trophic levels. More detailed trophic studies on multi-species communities are necessary to gain a consistent picture of within and between guild differentiation and the important drivers of these patterns.

Guild-wide comparisons mask the fact that the vast majority of all pair-wise comparisons that pointed to interspecific differentiation came from a few genera, particularly from the species rich genus *Pterostichus*. These species were on average closer to species of other genera than to congeners (Table 4). Such a pattern suggests a pronounced intragenus trophic segregation of *Pterostichus* species. This result also sheds some light on frequently suggested competition and predation between different *Pterostichus* species (e.g. Brandl & Topp 1985, Niemelä 1988, Currie *et al.* 1996, Kotze 2008).

Most work on ground beetle community structure highlighted dispersal and temporal variability in species composition (Niemelä 1993). Interspecific competition, in turn, seems to be of minor importance in these dynamic communities (Niemelä 1993, Lövei & Sunderland 1996, Ulrich & Zalewski 2006). Our results strengthen the view that competition for food resources does not strongly structure ground beetle communities. More clear signs of trophic segregation appeared only in the genus *Pterostichus* and in the “decomposer feeders” guild. The formation of competitive community structures needs some temporal stability, which might be rare in these communities. The above argument is closely related to the temporal aspect in isotopic analysis. The ground beetles of our study form meta-populations with frequent local colonization and extinction events (Zalewski 2004, Zalewski *et al.* 2012b). Thus, short-term studies to determine isotopic ratios in local populations might miss temporal variability when estimating whole species trophic niches. To assess the realized variability in isotopic space — but also

mean values — time series rather than single observations should be used (Layman *et al.* 2011). Our eight-week sampling campaign was shorter than the annual reproductive and dispersal period and thus we probably underestimated the potential intraspecific variability and overlap between species in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  ratios. Our study did not include the spatial aspect of species occurrences among islands. In previous studies (Ulrich & Zalewski 2006, 2007) we found a significant tendency towards species segregation among islands. Subsequent studies have to show whether such spatial segregation forms another dimension of trophic niche space that segregates species, or whether the space dimension expands the potential niche space while the realized niches on single islands overlap even more.

Ground beetles are a trophically diverse group and Fig. 1 provides a rare insight into trophic structure of their communities. Carabidae contain predominately predators but also species considered as being either omnivorous or mainly phytophagous (Lövei & Sunderland 1996, Kotze *et al.* 2011) although detailed studies on the fraction of omnivory in carabid communities are hitherto lacking. Our results indicate a high level of omnivory. Of the nine species with a minimum  $\delta^{15}\text{N} < 2.5\text{‰}$  (indicating phytophagy), eight had a maximum ratio of 5.0 and thus feed on more than two trophic levels and probably on plant and animal tissues. Using the more general definition of omnivory applied in food web theory as being an animal feeding on more than one trophic level, 31 species can be classified as omnivorous (Table 1, range of  $\delta^{15}\text{N} > 2.5$ ); more than a third utilized up to three trophic levels. The high  $\delta^{15}\text{N}$  ratios of several *Pterostichus*, *Agonum*, *Stomis* and one *Harpalus* species (Table 1) might indicate intraguild predation or cannibalism of some individuals as observed by Currie *et al.* (1996) and Zetto-Brandmayr *et al.* (2004). It elevates trophic span of the community even higher. Thus our results show a higher intraspecific and interspecific trophic diversity of ground beetles than is often assumed (e.g. Vanbergen *et al.* 2010, Duyck *et al.* 2011). The study therefore ought to have implications for meta-analytical and comparative studies that persistently treat ground beetles as predators only (e.g. Bengtsson *et al.* 2005, Zvereva & Kozlov 2010).

Members of the “generalist predator” guild were mainly separated by their  $\delta^{13}\text{C}$  ratios but not by  $\delta^{15}\text{N}$  ratios (Fig. 1).  $\delta^{13}\text{C}$  ratios are either linked to habitat peculiarities with respective differences pointing to spatial segregation of species (Layman *et al.* 2007), or to differences in food web membership: with higher  $\delta^{13}\text{C}$  ratios indicating connection to the decomposer and lower  $\delta^{13}\text{C}$  ratios connection to herbivorous food web (Ponsard & Arditi 2000, Hyodo *et al.* 2010, Okuzaki *et al.* 2010). The “generalist predator” guild partly overlaps with the “decomposer feeders” guild, and several species are located in-between, e.g. *Carabus granulatus* (Table 2). Therefore the majority of species (66% of species had litter-corrected  $\delta^{13}\text{C}$  ratios over 2.5‰) could be connected to food chains stemming from detritus rather than to food chains that come from living plants. This information have some importance for our understanding of the role of ground beetles in the functioning of ecosystems, but also in practical terms — e.g. the suggested role of carabids in biocontrol (e.g. Thies *et al.* 2011).

To conclude, our stable isotope analysis revealed a complex trophic structure of the ground beetle assembly, with three partly overlapping guilds and a very high isotopic niche overlap between species. Subsequent research should establish generality of such organization and attempt to explain coexistence of trophically similar species.

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