

Community-wide stable isotope analysis reveals two distinct trophic groups in a service-providing carabid community

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Abstract

Disentangling trophic interactions among species is important for elucidating mechanisms underlying ecosystem functioning and services. Carabid beetles are an important guild of predators that may regulate pest populations in arable landscapes, but their generalist feeding behavior hinders predictions about their actual contribution to pest control. In order to assess carabids' potential for pest control, we simultaneously analyzed the carbon and nitrogen stable isotope ratios of a community of 45 co-occurring species in wheat and oilseed rape fields. With the expectation to identify distinct trophic groups based on the mean and the variance of carabid isotopic signatures, we observed a high degree of overlap in trophic positions between species. However, we also observed that species could be successfully categorized into two groups according to whether or not their carbon signatures varied independently from variations in the crop baseline. We interpret these results as differential primary resource uptake or by differential mobility aptitude in foraging. Accordingly, we propose that the isotopic signal can inform us on the presence/absence of links between generalist predators and cultivated plants through the trophic networks they belong to, and consequently on their potential role as pest natural enemies. We therefore suggest the complementarity of stable isotope analysis for obtaining a time-integrated assessment of carabid trophic behavior that may be combined with more direct molecular diet analysis allowing the simultaneous quantification of specific trophic links within agricultural landscapes.

Keywords: $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, trophic interactions, ecosystem services, agroecosystems, biodiversity, pest control, ground beetles

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Introduction

The positive effect of biodiversity on ecological functions and processes is well documented (Johnson *et al.*, 1996; Loreau 2000; Cardinale *et al.*, 2003; Hooper *et al.*, 2005; Straub *et al.*, 2008). The general opinion is that more diversified

ecosystems sustain higher levels and higher number of ecological functions and services delivered to humans. However, for ecosystem services such as biological control, the effect of biodiversity is frequently ambiguous and highly dependent on the trophic level at which the biodiversity is considered (Montoya *et al.*, 2003). Indeed, while several studies showed a positive relationship between natural enemies biodiversity and pest biological control (Losey & Denno, 1998; Snyder *et al.*, 2006; Letourneau *et al.*, 2009), others have also indicated that species-rich predator assemblages could be more sensitive to competitive interactions or intraguild predation, diverting them from pest predation (Rosenheim, 1998; Finke & Denno,

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2005; Davey *et al.*, 2013). For instance, pest predation could be altered by diet shifting resulting from competitive interactions between generalist predators (Tixier *et al.*, 2013). Hence, our capacity to anticipate the effect of a change in predator diversity on biocontrol is directly dependent on our capacity to disentangle predator trophic interactions at the scale of the interacting community (Thompson *et al.*, 2012; Bohan *et al.*, 2013). However, empirically characterizing complex trophic interactions within a pest–predator food web is challenging, even in presumably simplified ecosystems such as intensively managed farmland areas (Pocock *et al.*, 2012; Mollot *et al.*, 2014). A typical community of service-providing predators frequently comprises dozens of small-sized arthropods with very wide diet spectrum (Agustí *et al.*, 2003; Eitzinger & Traugott, 2011; Staudacher *et al.*, 2016). Moreover, in response to frequent perturbations caused by management practices, predator–prey interactions could be very dynamic in space and time (Bommarco *et al.*, 2007; Bell *et al.*, 2010), requiring a significant capacity to track and integrate these spatio-temporal variations. This is particularly relevant with regard to carabid beetles – a major guild of generalist predators in agricultural landscapes (Kromp, 1999; Kulkarni *et al.*, 2015) that could feed upon a wide variety of resources (Larochelle, 1990) including numerous pests (Bohan *et al.*, 2011; Boreau de Roince *et al.*, 2012) but also beneficial organisms (King *et al.*, 2010; Davey *et al.*, 2013) or carrion (i.e., scavenging, Young, 1984, 2005). Additionally, carabids have been shown to dynamically change their feeding behavior in response to variations in prey abundance (Bohan *et al.*, 2000; Bell *et al.*, 2010). Hence, carabid contribution to biological control is yet hardly predictable, rendering the implementation of concrete management actions difficult. In this paper, we tackle the long-standing problem about the contribution individual species make to biological control within the carabid community. Previous studies have showed that carabid species could be lumped into broad trophic categories according to their feeding preferences (Larochelle, 1990) or according to functional traits, such as the mandible morphology or body size (Forsythe, 1983; Rouabah *et al.*, 2014; Rusch *et al.*, 2015). However, morphological trait-based categories do not provide a quantitative estimate of diet, also the link between functional attributes and feeding behavior is not always consistent, especially in such flexible feeders as carabids. Recently, molecular techniques were very successful in allowing the direct quantification of trophic links from predators' gut contents (Symondson, 2002; Clare, 2014). However, the main limitation with the molecular diet analysis is that it only provides a snapshot of a species diet – usually the most recent feeding event, thus making the incorporation of spatio-temporal variations in feeding choice of multiple species resource-demanding. Finally, both functional and molecular approaches fail to distinguish active predation from scavenging (Foltan *et al.*, 2005; von Berg *et al.*, 2012). The analysis of naturally occurring carbon and nitrogen stable isotope ratios (expressed as δ , the ratio of heavy to light isotope, and reported in parts per thousand as per mil) could help overcome some of the above-mentioned methodological challenges.

Stable isotopes provide quantitative and time-integrative estimate about the trophic space occupied by an organism based on the dependency of isotopic signatures observed in consumers on their dietary resources (DeNiro & Epstein (1978, 1981)). For instance, measuring the stable isotope ratios of carbon ($\delta^{13}\text{C}$) allows pinpointing the actual food source among a pool of potential ones, provided that their ratios

differ (Gannes *et al.*, 1998). In contrast, for elements such as nitrogen ($\delta^{15}\text{N}$), a predictable enrichment of the heavier isotope from diet to consumer is observed (Martínez del Rio *et al.*, 2009), leading to identify the trophic level of an organism relative to a reference baseline (Eggers & Jones, 2000). Considering these advantages, we applied $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope analysis in order to estimate the degree of involvement in biological control of the most common carabid species in two dominant crop types. We measured the mean and the variance of the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ trophic space occupied by each species and compared it with the baseline crop plant. The crop plant is an important agronomical factor structuring arthropod assemblages through the frequency and the intensity of the different management practices (Marrec *et al.*, 2015; Puech *et al.*, 2015) but is also an important resource at the very basis of farmland food webs (Tixier *et al.*, 2013; Mollot *et al.*, 2014). Our objectives were twofold: (i) identify variations in the trophic position across species and between crop types for the same carabid species; (ii) assess whether variations in the crop plant baseline influence variations in carabid isotopic signatures. Our expectations were that (i) we would be able to identify distinct trophic positions – through strict herbivores to strict carnivores – within the carabid community; (ii) that variations in isotope ratios of the crop baseline will cascade at upper trophic levels, thus allowing the distinction between crop-derived and non-crop-derived trophic groups.

Material and methods

Collection and sample preparation

Carabid beetles were intensively sampled between 03 and 23 May 2012, period corresponding to the peak of carabid activity in our study area this year (Supplementary fig. S1). Sampling took place in two arable fields (winter wheat and oilseed rape, size 1–5 ha each), situated approximately 10 km apart within the long-term ecological research area 'Armorique' (<http://osur.univ-rennes1.fr/za-armorique/>, 48°36'N, 1°32'W), Brittany, France. For maximizing the number of species collected, each field was checked with a high number (>50) of dry pitfall traps. All traps were opened and closed in four sampling sessions of 24 h each. Carabid beetles were collected alive. Living individuals were freeze-killed at -20°C as soon as possible (and in all cases less than 5 h after collection), sorted out at the laboratory and identified to the species level (Roger *et al.*, 2012). For assessing the crop baseline, fresh plant tissues (stems, leaves, pods and ears) were sampled from randomly selected plants for each crop type: oilseed rape (*Brassica napus*, Brassicaceae) and wheat (*Triticum aestivum*, Poaceae). Plant tissues per crop were mixed together, frozen at -20°C within 5 h after collection and stored at -20°C prior analyses ($N=5$ for wheat and $N=8$ for oilseed rape). Both carabid and plant samples were freeze-dried for 24 h. To avoid bias induced by the presence of prospective prey within carabid gut contents, all species sizing >4.5 mm (90% of species) were dissected and gut contents were removed. Because of their small size, dissection was impractical for species smaller than 4.5 mm. These specimens were analyzed in their entirety. All freeze-dried samples were manually ground into fine powder. Tin capsules containing between 1 and 2 mg of tissue of each individual were processed with isotope-ratio mass spectrometer (Delta Plus, Thermo Quest, Waltham, MA, USA), coupled to an elementary analyzer (Flash EA, Thermo Quest, Waltham, MA, USA) at the Roscoff Biological Station,

Brittany, France. The stable isotopic composition of carbon and nitrogen ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) was expressed as a relative ratio, in parts per thousand, to an international standard:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1]1000,$$

where R_{sample} is the absolute isotopic ratio (heavy/light) of the sample and R_{standard} is the correspondent ratio in the standard (Peterson & Fry, 1987; Ehleringer & Rundel, 1988). The international standards used were Vienna Pee Dee Belemnite for $\delta^{13}\text{C}$ and atmospheric nitrogen for $\delta^{15}\text{N}$. Measurement uncertainty was $\pm 0.2\text{‰}$ for $\delta^{15}\text{N}$ and $\pm 0.1\text{‰}$ for $\delta^{13}\text{C}$.

Statistical analyses

Statistical analyses were run with the R software version 3.1.0 (R Core Team, 2013). Variations in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ trophic position among carabid species and between crop types as well as their interaction were compared by fitting general linear models (GLM, Gaussian distribution family, link = identity) using the R function *glm*. The number of individuals per species and per field ranged between $N=1$ and $N=28$ (mode $N=2$ and $N=4$). Carabid species represented by less than two individuals in the whole dataset (seven species) were not taken into account in statistical analyses. Their individual $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values are provided in Supplementary table S1.

The effect of variations in the crop plant baseline on differences in the carabid $\delta^{13}\text{C}$ between crop types were also investigated using a GLM model (Gaussian distribution family, link = identity), including as variables the carabid species and the interaction carabid species \times crop field. Hence, the interaction carabid species \times crop field was an estimate of $\delta^{13}\text{C}$ variation between the two crop fields within the considered carabid species. The crop was also treated like a carabid species in this model. Thus, the interaction crop \times field was an estimate of the $\delta^{13}\text{C}$ variation between the two crop species as crop baselines consist in wheat in one field and in oilseed rape in the other. Then, for each pair of carabid species, *t*-tests were performed to assess whether the interaction carabid species \times field differed significantly. Similarly, *t*-tests were also performed to assess whether the $\delta^{13}\text{C}$ variation between the two fields for each carabid species differed significantly from the $\delta^{13}\text{C}$ variation between the two crop types (interaction crop \times field). Only the most abundant carabid species occurring in the both crop types were selected for these analyses (11 species, mode $N=10$).

Results

A total of 295 individuals belonging to 45 species and 26 different genera were analyzed (table 1). Of these 28 species were common in both cultures. Overall, the amplitude of $\delta^{13}\text{C}$ variation was higher in wheat (fig. 1a), whereas higher amplitude of $\delta^{15}\text{N}$ variation was observed in oilseed rape (fig. 1b). Average $\delta^{13}\text{C}$ values ranged from -14.3‰ (*Harpalus rubripes*) to -29.3‰ (*Amara familiaris*) in wheat (fig. 1a), and from -24.4‰ (*Pterostichus melanarius*) to -29.8‰ (*Leistus fulvibarbis*) in oilseed rape (fig. 1b). Average $\delta^{15}\text{N}$ values ranged from 4.4‰ (*Syntomus obscuroguttatus*) to 9.6‰ (*Pterostichus vernalis*) in wheat (fig. 1a), and from 2.2‰ (*Amara plebeja*) to 12‰ (*P. melanarius*) in oilseed rape (fig. 1b). Based on GLM analysis, the carabid species, the crop type and their interaction explained a significant part of the variation in

$\delta^{13}\text{C}$ and in $\delta^{15}\text{N}$ (table 2). The same results were observed when $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for only the most abundant species, present in the both crop types, were considered (Supplementary table S2). GLM analysis of the interaction carabid species \times field carried out on the species caught in both fields revealed two groups of species (fig. 2) depending on whether their $\delta^{13}\text{C}$ variation between fields differed significantly from the $\delta^{13}\text{C}$ variation between the two crops or not. For each species, isotopic signature was considered significantly different from plant isotopic signature for a probability threshold of 0.05. The first group included *Nebria salina* ($P=0.83$), *Anchomenus dorsalis* ($P=0.54$), *Poecilus cupreus* ($P=0.43$) and *Anisodactylus binotatus* ($P=0.50$). The second group included *Amara aenea* ($P=0.018$), *Brachinus sclopeta* ($P=0.042$), *Loricera pilicornis* ($P=0.021$) and *Ocydromus tetracolus* ($P=0.0018$). *Asaphidion flavipes* ($P=0.079$) was also included in the second group because its isotopic signature was almost significantly different from the isotopic signature of the crop plant as well as almost significantly different from the isotopic signatures of all the species belonging to the first group. All species belonging to group 1 did not differ significantly from each other in their interaction with the field (fig. 2), neither from the interaction crop \times field (fig. 2). In the group 2, species did not differ significantly from each other in their interaction with the field (with an interaction carabid species \times field not significantly different from 0), but the interaction carabid species \times field was significantly different from the interaction crop \times field (fig. 2, Supplementary table S3). Finally, the interaction with the field of species belonging to the group 1 was frequently significantly different from the interaction with the field of species belonging to the group 2, and when it was not, the difference was always close to the significance (Supplementary table S3). Two species exhibited intermediate behavior (*Agonum muelleri* and *Amara similata*), probably due to the relatively low sampling size (respectively, only four and one individuals in either of the two crop types). However, *A. muelleri* tended to belong to group 1 and *A. similata* to group 2 (Supplementary table S3).

Discussion

Overall, the species identity explained a significant part of the variation in the carabid $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios. Despite these differences, we were not able to identify clear trophic groups within the carabid community based on the species $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. This is mainly due to the high intraspecific variation, especially for $\delta^{15}\text{N}$. This suggests that carabid beetles are indeed generalist, plastic foragers, particularly in agricultural areas (Lövei & Sunderland, 1996; Bennett & Hobson, 2009; Okuzaki *et al.*, 2010; Kamenova *et al.*, 2015), where such trophic generalism could be easily explained by important variations in resource availability (Bohan *et al.*, 2000; Bell *et al.*, 2010). However, similar levels of intraspecific variability in isotopic values have also been reported within carabid communities residing in more stable habitats (Zalewski *et al.*, 2014), suggesting that other mechanisms could be in play. For instance, numerous non-trophic sources of variation could also explain the high intraspecific variability in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of a consumer. Factors such as individual differences in metabolic rates, fasting time, or diet quality have all been shown to influence isotopic values without any direct link to differences in trophic choice (reviewed by Martínez del Río *et al.*, 2009). Carabid beetles typically could experience extended fasting periods (Bilde & Toft, 1998; Laparie *et al.*, 2012) and the

Table 1. Carabid species (and their taxonomic affiliation) analyzed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope ratios. Codes as presented in fig. 1.

Species code	Carabid species	Subfamily	Tribe
ACmerid	<i>Acupalpus meridianus</i>	Harpalinae	Stenolophini
AGmülle	<i>Agonum muëlleri</i>	Platyninae	Platynini
AGafru	<i>Agonum afrum</i>	Platyninae	Platynini
AGsexpu	<i>Agonum sexpunctatum</i> ¹	Platyninae	Platynini
ANdorsa	<i>Anchomenus dorsalis</i>	Platyninae	Platynini
AMaen	<i>Amara aenea</i>	Pterostichinae	Zabrini
AMcommu	<i>Amara communis</i> ¹	Pterostichinae	Zabrini
AMfamili	<i>Amara familiaris</i>	Pterostichinae	Zabrini
AMunic	<i>Amara lunicollis</i>	Pterostichinae	Zabrini
AMovata	<i>Amara ovata</i> ¹	Pterostichinae	Zabrini
AMplebej	<i>Amara plebeja</i>	Pterostichinae	Zabrini
AMsimil	<i>Amara similata</i>	Pterostichinae	Zabrini
ANbinot	<i>Anisodactylus binotatus</i>	Harpalinae	Anisodactylini
ASflav	<i>Asaphidion flavipes</i>	Trechinae	Bembidiini
BBulla	<i>Badister bullatus</i> ¹	Licininae	Licinini
BRsclope	<i>Brachinus sclopeta</i>	Brachininae	Brachinini
CAntri	<i>Carabus intricatus</i> ¹	Carabinae	Carabini
CAnemo	<i>Carabus nemoralis</i> ²	Carabinae	Carabini
CHnigri	<i>Chlaenius nigricornis</i> ²	Licininae	Chlaeniini
CIcindel	<i>Cicidella spp.</i> ¹	Cicindelinae	Cicindelini
CLfosso	<i>Clivina fossor</i>	Scaritinae	Clivinini
DEatric	<i>Demetrias atricapillus</i> ¹	Lebiinae	Lebiini
HAaaffin	<i>Harpalus affinis</i>	Harpalinae	Harpalini
HRubri	<i>Harpalus rubripes</i> ²	Harpalinae	Harpalini
LFulvi	<i>Leistus fulvibarbis</i> ¹	Nebriinae	Nebriini
LOpilic	<i>Loricera pilicornis</i>	Loricerinae	Loricerini
MEamp	<i>Metallina lampros</i>	Trechinae	Bembidiini
MEprope	<i>Metallina properans</i>	Trechinae	Bembidiini
NEbrevi	<i>Nebria brevicollis</i>	Nebriinae	Nebriini
NEsali	<i>Nebria salina</i>	Nebriinae	Nebriini
NObigut	<i>Notiophilus biguttatus</i> ¹	Nebriinae	Notiophilini
NOpalu	<i>Notiophilus palustris</i> ¹	Nebriinae	Notiophilini
NOquadri	<i>Notiophilus quadristriatus</i>	Nebriinae	Notiophilini
OCetra	<i>Ocydromus tetracolus</i>	Trechinae	Bembidiini
PAmacu	<i>Parophonus maculicornis</i> ¹	Harpalinae	Harpalini
PHbigut	<i>Philochthus biguttatus</i>	Trechinae	Bembidiini
PHobtu	<i>Phyla obtusa</i>	Trechinae	Bembidiini
POcupr	<i>Poecilus cupreus</i>	Pterostichinae	Pterostichini
PSrufi	<i>Pseudophonus rufipes</i>	Harpalinae	Harpalini
PTanthra	<i>Pterostichus anthracinus</i> ²	Pterostichinae	Pterostichini
PTmela	<i>Pterostichus melanarius</i>	Pterostichinae	Pterostichini
PTstren	<i>Pterostichus strenuus</i>	Pterostichinae	Pterostichini
PTvern	<i>Pterostichus vernalis</i>	Pterostichinae	Pterostichini
SYfovea	<i>Syntomus foveatus</i> ²	Lebiinae	Lebiini
SYobscu	<i>Syntomus obscuroguttatus</i> ²	Lebiinae	Lebiini
TRquadris	<i>Trechus quadristriatus</i>	Trechinae	Trechini

Underlined species were present in both crop types.

¹Indicates species present only in oilseed rape ($n = 11$).

²Indicates species present only in wheat ($n = 6$).

proportion of individuals displaying an empty gut within a population could be exceptionally high (Sunderland, 1975; Hengeveld, 1980), which in turn may significantly impact the isotopic fractionation. However, little is known about the specific factors affecting isotopic fractionation in insects in general, particularly in carabid beetles. Hence, identifying the most important sources of non-dietary variation and the magnitude of their effect is an important requirement for taking full advantage of the stable isotope analysis for this group of organisms. Another methodological constraint hampering the interpretation of stable isotope data in our case comes from the lack of information about the time lag in isotopic turnover associated with ontogenetic niche shifts (i.e., changes in the carabid isotopic signature between larval and adult

stages). Compared with the adult stages, carabid larvae usually exhibit distinct or more specialized trophic habits (Lövei & Sunderland, 1996), suggesting that a delayed response in isotopic turnover during the dietary shift after metamorphosis will result in an isotopic signature that does not match the actual adult's diet. Moreover, for some carabid species, two or more generations that are not distinguishable morphologically could co-occur at the same season (Thiele, 1977). This suggests that intraspecific variations in isotopic signature would have more to do with time since metamorphosis than with feeding habits. This point requires further consideration within the dynamic agricultural landscapes where spatio-temporal turnover of crops is high (Holland *et al.*, 2005; Fahrig *et al.*, 2010). For instance, an individual emerging in the late season on a

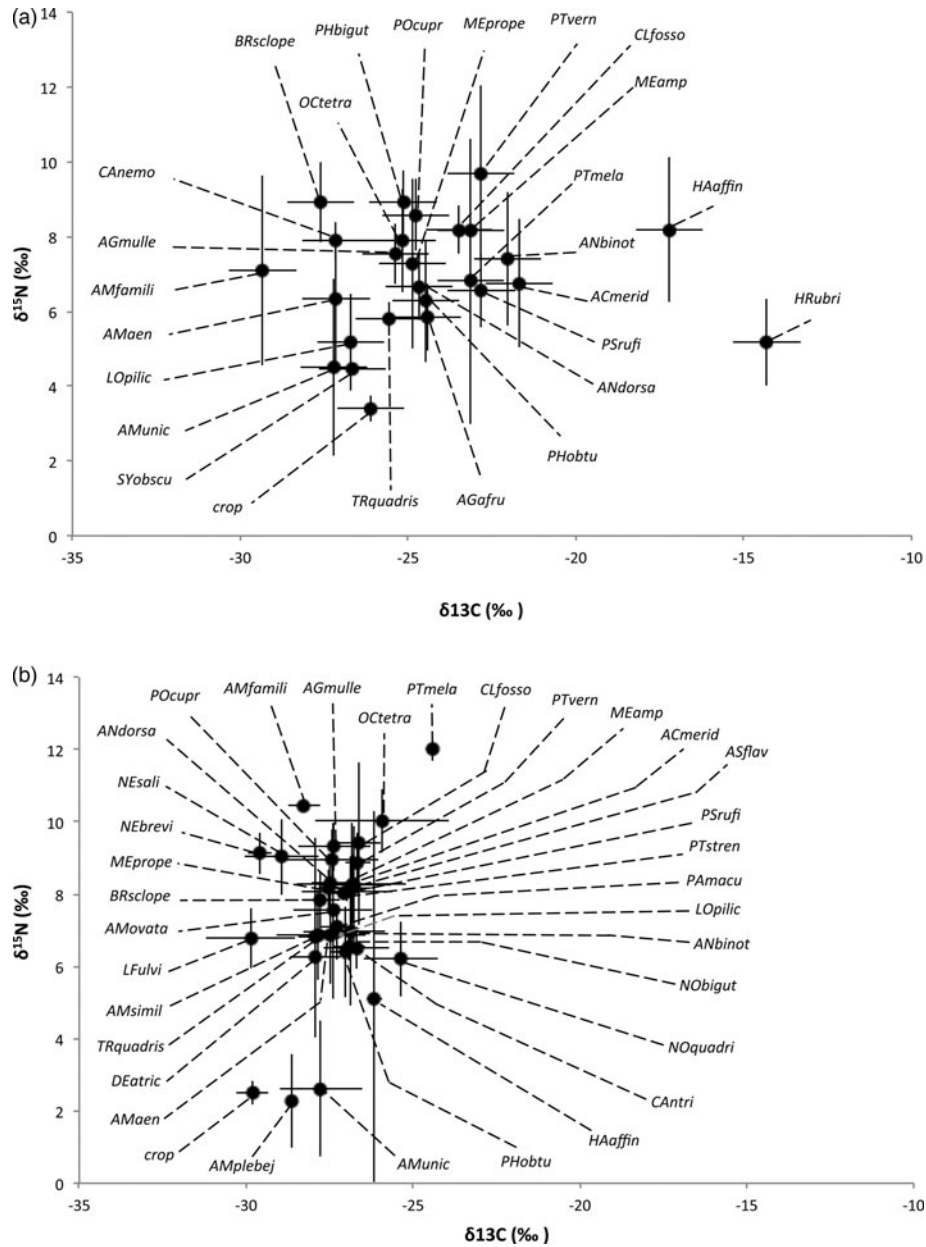


Fig. 1. Comparison of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope ratios of carabid beetles in (a) wheat; (b) oilseed rape. Means \pm SD are shown. Species codes are indicated in [table 1](#).

previous year may have experienced a very different basal resource, and still exhibit the isotopic signature of its previous diet at the moment of the field sampling. The same reasoning holds true for dispersal. One plausible scenario is that overwintering carabid beetles may migrate to other fields after emergence, while keeping the isotopic imprint of their native location (Girard *et al.*, 2011). Indeed, we cannot guarantee that no migrants from the nearby fields were present at the time of sampling, but we believe that such scenarios are highly unlikely in our case. First, it takes about 17 days for a mid-sized adult carabid to reach the isotopic level of its prey after overwintering (Makarov *et al.*, 2013). Second, beetles were collected in the middle of the reproductive season, when carabids usually

Table 2. Results of GLM analyses testing the effect of the carabid species, the crop type, and their interaction on $\delta^{13}\text{C}$ and in $\delta^{15}\text{N}$ variation.

Variable	df	Residual deviance	P
$\delta^{13}\text{C}$			
Species	39	855.96	<0.001
Crop	1	244.12	<0.001
Species \times crop	21	179.18	<0.001
$\delta^{15}\text{N}$			
Species	39	827.89	<0.001
Crop	1	36.08	<0.001
Species \times crop	21	108.40	<0.001

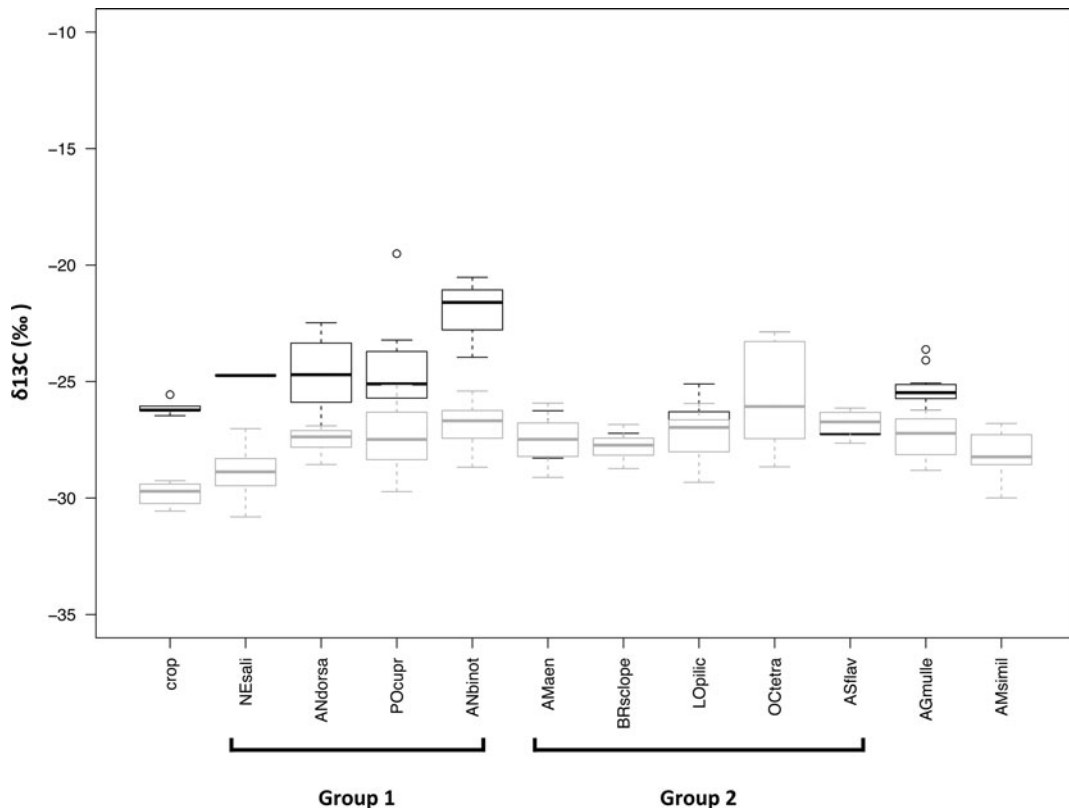


Fig. 2. Boxplot comparing the $\delta^{13}\text{C}$ values of the crop baseline and the 11 most common carabid species in wheat (black) and oilseed rape (gray). Carabid species has been arranged according to whether their $\delta^{13}\text{C}$ variation between the fields differed significantly (group 2) or not (group 1) from the $\delta^{13}\text{C}$ variation between the two crop types. The species *Agonum muëlleri* and *Amara similata* exhibited intermediate behavior. For *P* values see Supplementary table S3. Species codes are indicated in table 1.

tend to stay within the crop they select after emergence (Marrec *et al.*, 2015).

Yet, according to our dataset, some species occupied well-differentiated $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic niches. Interestingly, differences were more marked for carbon compared with nitrogen, possibly indicating that resource partitioning is mostly related to the identity of the basal resource rather than to a differentiation in the trophic position. This confirms results from at least three independent studies, suggesting that the primary resource uptake could be the prevalent axis of trophic differentiation between carabid species (as opposite to the $\delta^{15}\text{N}$ trophic position) (Ikeda *et al.*, 2010; Okuzaki *et al.*, 2010; Zalewski *et al.*, 2014). Here, *Harpalus* species were more carbon-enriched compared with all other species, even if enrichment was less pronounced in oilseed rape compared with wheat (fig. 1). In laboratory conditions, *Harpalus* species usually show marked granivorous preferences (Johnson & Cameron, 1969; Forsythe, 1982; Goldschmidt & Toft, 1997) as well as a capacity to consume a large variety of seed species (Honek *et al.*, 2003, 2007; Wallinger *et al.*, 2015). Thus, the carbon enrichment (compared with the crop baseline) as well as the relatively low $\delta^{15}\text{N}$ trophic position might suggest that in arable fields, *Harpalus* species not only consume plant material but also that this plant material probably originates from weed plants rather than the crop. Another genus of supposedly granivorous species, *Amara*, showed a rather intriguing pattern in $\delta^{15}\text{N}$ signature. Most species occupied intermediate-to-high $\delta^{15}\text{N}$ trophic positions

in both wheat and oilseed rape, while only two species in oilseed rape showed a trophic position compatible with phytophagous behavior (*A. plebeja* and *Amara lunicollis*). The explanation about this pattern is not evident, but it will be interesting to investigate at what extend observed differences in isotopic signatures among *Amara* species could be linked to various degrees of specialization in seed consumption within the genus (Saska, 2005; Honek *et al.*, 2007).

From applied perspective, our results show that solely based on the mean and the variance of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures, it seems challenging to consistently infer carabids' potential to contribute to biological control. Nevertheless, when comparing variations in carbon signatures between carabid species and the crop baseline, we identified two distinct groups. The first group varied in a similar pattern to the variations in $\delta^{13}\text{C}$ observed between the two crop plants. The carabid species forming this group – *N. salina*, *A. dorsalis*, *P. cupreus* and *A. binotatus* – are all supposedly mid- to large-sized carnivorous or omnivorous beetles, usually indicated as feeding upon a large variety of insects, comprising aphids and other pests (Sunderland, 1975). The second group of species had their $\delta^{13}\text{C}$ ratios varying independently from the variations in the crop. These species include *A. aenea*, *L. pilicornis*, *O. tetracolum*, and *A. flavipes*, which are all small- to mid-sized species, mainly phytophagous or carnivores, specialized in the consumption of small detritivores like *Collembola* (Sunderland, 1975; Hintzpetter & Bauer, 1986). The carabid *B.*

sclopeta, which also belongs to this group of species, is most likely an ectoparasitoid of *Amara* species (Saska & Honek, 2004, 2008). This apparent trophic partitioning mediated by the baseline resource allows distinguishing between crop-derived and non-crop-derived trophic groups of species, and thus confirms our expectations. Consequently, based on our results and on previous information about carabid trophic behavior, we were able to indirectly assess the likely contribution of these generalist predators to biological control. For example, large carnivorous or omnivorous carabids most seemingly rely on the crop plant for their carbon uptake suggesting the consumption of animal species directly associated with the crop (i.e., herbivorous pests). On the other hand, small granivorous or detritivore feeders probably rely on alternative carbon resources with no direct link to the crop. The latter might still be contributing to biocontrol of weeds (Girard *et al.*, 2011), as weed plants constitute another important and diversified source of carbon at the basis of agricultural food webs (Marshall *et al.*, 2003; Tixier *et al.*, 2013; Mollot *et al.*, 2014).

Overall, the stable isotope analysis we applied in this study shows to be practical, rapid, and relatively cheap method for directly assigning carabid species into loose trophic categories. However, in order to take more advantage of such stable isotope data, it would be beneficial to diversify the tools and the methods. For instance, more quantitative tools such as mixing models or functional metrics (Layman *et al.*, 2007; Parnell *et al.*, 2013; Chucherousset & Villéger, 2015), or methods for more direct assessment of diet (e.g., DNA metabarcoding, Pompanon *et al.*, 2012; Vacher *et al.*, 2016) could help characterizing with more precision the carabid contribution to biological control (Boreau de Roince *et al.*, 2012).

Yet, carabid beetles are also notorious scavengers, but DNA techniques cannot tease apart active predation from scavenging (Foltan *et al.*, 2005; Juen & Traugott, 2005; Heidemann *et al.*, 2011; von Berg *et al.*, 2012). Thus, the question about the importance of carrion in carabid diet remains open. Stable isotope analysis could possibly inform about scavenging, but it is not known yet how the consumption of carrion impacts the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures as well as the trophic groups we observe here. In order to elucidate if scavengers could be clearly delimited based on their isotopic signature, it would be interesting to experimentally feed carabid beetles with fresh or decayed prey (Wallinger *et al.*, 2013), and compare their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures.

In conclusion, stable isotope analysis appears as a straightforward, relatively cheap, and complementary tool that could be used to assess species trophic behavior and possibly provide a mean for the functional categorization of carabid beetles based on their diet. Although our study does not provide direct evidence about carabid contribution to biological control, we show that the isotopic signal can inform us about the juxtaposition in arable fields of two independent and functionally complementary carabid trophic groups, comprising each several functionally redundant species. Based on these results, we argue that maintaining high levels of species richness within farmland carabid assemblages appears as an important prerequisite for preserving the integrity of ecological functions that could be important to humans (Jonason *et al.*, 2013; Trichard *et al.*, 2013; Peralta *et al.*, 2014).

Supplementary material

The supplementary material for this article can be found at <https://doi.org/10.1017/S0007485317000542>.

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Author contribution

S.K. and M.P. designed the study, collected and analyzed the data. C.L. ran the stable isotope analysis. S.E.P. helped with data collection and statistical analyses. S.K. wrote the paper and M.P. provided comments.

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