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ORIGINAL ARTICLE

Seasonal niche differentiation of *Camponotus morosus* and *Dorymyrmex goetschi* (Hymenoptera: Formicidae) in sandy beach habitats: Insights from stable isotope analysis

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Abstract. Quantifying the degree of ecological specialization of animals is essential for understanding the evolution of resource use in changing environments. Stable isotope analysis (SIA) is a powerful tool for investigating the ecological niches of animals and providing insights into their diet. This study focused on the ecological role of two coastal species of ants, *Camponotus morosus* and *Dorymyrmex goetschi*, in Chile. Their seasonal isotopic niches were characterised using carbon (δ^{13}C) and nitrogen (δ^{15}N) analysis. This was done on El Tabito Beach, a coastal area with a pronounced seasonality. The results indicated unique niches for each species and variation between them across seasons. While *C. morosus* maintained a consistent niche breadth throughout the year, *D. goetschi* displayed a narrower niche in summer. Our analyses showed that terrestrial-derived carbon constituted the primary food resource for both species of ants, with a slight increase in the marine component in summer. Overall, the results highlight seasonal variations in isotopic signatures, niche breadth, and diet composition and underscore the importance of considering temporal dynamics in ant ecology and, in particular, in trophic interactions.

INTRODUCTION

The ecological niche of a species encompasses a complex network of interactions taking place in an ecosystem, including feeding habits, resource utilization, and its role within a food web (Chase & Leibold, 2003; Phillips et al., 2020). Understanding the ecological niche provides insights into the species' position and function within an ecosystem, as well as its relationships with other organisms (Bearhop et al., 2004; Poisot et al., 2013). Coexisting species may have overlapping niches along multiple axes, but must differ in at least one to avoid competitive exclusion (Hutchinson, 1957). In ecology, quantifying species' niches and their overlap is crucial for understanding specialization, generalization, and resource use in changing environments (Bolnick et al., 2003; Carscadden et al., 2020). According to the principle of competitive exclusion, similar resource use by sympatric species may lead to local extinction or niche differentiation (Hardin, 1960; Schoener, 1974).

Advances in stable isotope ecology and mathematical techniques have provided valuable tools for determining niches (Newsome et al., 2007; Jackson et al., 2011; Balzani et al., 2020). Stable isotope analysis (SIA) has become a useful tool in ecology (Tillberg et al., 2006; Menke et al., 2010; Roeder & Kaspari, 2017), that uses the natural isotopic variation in ecosystems to estimate habitat use, evaluate trophic relationships, and understand various diet-related factors (Post, 2002; Martínez del Río et al., 2009; Feldhaar et al., 2010; Peña-Villalobos et al., 2024). Carbon stable isotope signatures, represented by δ^{13}C values, offer insights into the source of the diet of consumers (Farquhar et al., 1989; Robinson, 2001). Nitrogen stable isotope signals, δ^{15}N values, are closely associated with the trophic levels of consumers and help in establishing niche dynamics (Peterson & Fry, 1987). Combining these isotopic ratios enables the identification of the food of a species and an accurate estimate of its ecological role within a community (Post, 2002; Newsome et al., 2007; Martínez del Río et al., 2009; Navarrete et al., 2023; Hobson, 2023)._

The desert and semi-desert coasts in central and northern Chile are adjacent to one of the most productive ocean currents in the world (Ahumada et al., 2000). These highly

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productive marine environments often support consumers in the adjacent, less productive, terrestrial ecosystems (Polis & Hurd, 1996). This interdependence, however, can be influenced by seasonal variations in productivity (Drever et al., 2000). By adapting their foraging behaviour they can survive on land in areas where productivity is very limited (Polis & Hurd 1996). Despite the extensive coastal zone, our understanding of the terrestrial species that inhabit these areas remains limited. While numerous isotopic ecology studies have focused on terrestrial vertebrates, such as lizards and birds (Fariña et al., 2008; Martínez del Río et al., 2009), very few have explored invertebrates, which are mainly focused on ants (Catenazzi & Donnely, 2007; Garcia et al., 2011; Quinby et al., 2020).

In Central Chile, two species of ants, *Camponotus morosus* and *Dorymyrmex goetschi*, usually dwell in coastal areas. These ants inhabit sandy or rocky regions, scavenging in the strand line for vegetation and marine animal remains at low tide. The proximity of their nests and overlapping foraging territories leads to constant interaction, potentially resulting in resource sharing or competition. Highly productive marine environments subsidize the resources available to these ants, likely reducing inter-species competition and facilitating coexistence (Vidal et al., 2019). The steady supply of marine resources and seasonal fluctuations in terrestrial food availability may influence the dynamics of resource use by *C. morosus* and *D. goetschi*. Resource partitioning may occur when two species coexist, especially during times of scarcity, such as summer.

While the biology of the two ant species has been studied to some extent, many important features remain unknown. *Camponotus* species are omnivorous, feeding on various plants, insects and sugary substances secreted by Homoptera and plants (Leviaux & Louis, 1975). However, the proportion of these materials consumed varies among species (Grez et al., 1986). In Central Chile, during summer, the diet of *C. morosus* consists mainly of insects. A high percentage (90.8%) of the total invertebrates being carried to the nest consists of insect remains or whole dead insects. Only 9.2% of the invertebrates are living insects (Grez et al., 1986). For *D. goetschi*, analysis of prey transported to the nest revealed that the percentage of insects in its diet ranges from 27% to 47% (Torres-Contreras & Vásquez, 2004). This study characterized the isotopic niches of the two species of ants coexisting on El Tabito Beach, where there is a pronounced difference in the seasons (Sabat & Martinez del Río, 2005). Furthermore, based on the ecology of the species, *D. goetschi* is less dependent on insects and nests closer to the beach (see below). It is predicted that both species will consume a different proportions of marine/terrestrial prey and/or occupy a different isotopic niche in both seasons of the year. Thus, the interaction between both species, which is likely to be characterized by an overlap in their isotopic niches, should decrease in summer.

MATERIAL AND METHODS

The study site was the El Tabito Beach, located in the province of San Antonio in the Valparaíso Region, Chile (33°27´00″S 71°40´00″W). According to the Köppen climate classification (Chen & Chen, 2013), the climate in this area is warm-temperate with winter rains and very cloudy. It is influenced by the cold ocean currents flowing along the coast and sea winds that moderate temperatures. As a result, this site experiences little variation in temperature and is generally characterized by moderate winter rainfall and summer drought. The temperature of the Humboldt Current determines the climate, with an average temperature of 20°C in summer and 15°C in winter. The average temperature difference between day and night in winter and summer is 5°C. The average relative humidity in summer is 65%.

While the biology of the two ant species has been studied to some extent, many important features remains unknown. *Camponotus morosus* and *Dorymyermex goetschi* are the most conspicuous and abundant species of ants at the study site. *Camponotus morosus* (Smith, 1858), belongs to the subfamily Formicinae and is conspicuous due to its large size (over 1 cm in length) and is abundant in the sclerophyllous shrubland of Central Chile (Torres-Contreras, 2001). *Dorymyrmex goetschi* (Menozzi, 1935), belongs to the subfamily Dolichoderinae (Snelling & Hunt, 1975) and weigh cca 1.7 mg (Torres-Contreras & Vásquez, 2004). The nests contain an average of approximately 300 workers (Torres-Contreras & Canals, 2010) and are constructed in open areas without trees or shrubs (Torres-Contreras & Vásquez, 2004).

In order to evaluate habitat preferences, samples were collected along a longitudinal transect near the edge of the coast. In an area of approximately 200 m long by 50 m wide, colonies of *C. morosus* and *D. goetschi* that were visible were identified and marked every 10 m along the transect. The sampling area was about 20 m from the coastline. Ants from different colonies were collected by sampling workers from nests that were far apart. Aggressive behavior between workers was used to identify overlapping boundaries of neighboring colonies, indicating they belonged to different nests (Ipinza-Regla et al., 1993). Each sample included one worker collected near the nest entrance to ensure independence. *C. morosus* nests were slightly more inland in the dunes, while *D. goetschi* nests were closer to the shoreline, though *C. morosus* foraged nearer to the coast. Plant material, including marine algae and terrestrial plants, was also collected for isotopic analysis (see Fig. 3). The first collection of individuals was carried out in September 2014 (austral spring), and the second in March 2015 (austral summer) in the same area. A total of 12 individuals of each species, *C. morosus* and *D. goetschi* (total N = 48), were collected in each season and analysed. Due to the potential for within-colony variation in isotopic values resulting from polymorphism in ants (see Roeder & Kaspari, 2017), and the recognized polymorphism exhibited by *C. morosus* workers, only intermediate-sized specimens were collected in the field. The samples were collected using entomological tweezers, deposited in Eppendorf tubes without preservatives and placed in ice buckets for transportation to the laboratory in Santiago. Ants were identified following Snelling & Hunt (1975). The samples were washed in mild detergent and a mixture of chloroform/methanol and rinsed with distilled water. They were then dried in an oven at 60°C for seven days.

Approximately 0.5–0.6 mg of dried tissue, corresponding to a single individual, was weighed into tin capsules, and carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope values were measured using a Costech 4,010 elemental analyser coupled to a Thermo Scientific Delta V Plus isotope ratio mass spectrometer at UNM-CSI. Isotope values are reported using standard delta (δ) notation in parts per thousand or per mil (‰) where $\delta X = (R_{sample} / R_{standard} - 1)$ and R_{sample} and $R_{standard}$ are the ratios of heavy to light isotopes in the sample and references [V-Pee Dee Belemnite (VPDB) for carbon, and atmospheric nitrogen (AIR) for nitrogen], respectively. The within-run precision (SD) for both $\delta^{13}C$ and $\delta^{15}N$ were estimated using three proteinaceous internal reference materials and are ≤0.2‰ for both isotope systems.

The individual isotopic compositions were used to estimate interspecific differences in the use of trophic resources. A two-way analysis of variance (ANOVA) and a post hoc Tukey test were carried out on individual $\delta^{13}C$ and $\delta^{15}N$ values in order to determine specific differences between species, between seasons and the effect of their interaction. The individual carbon and nitrogen isotopic signatures were plotted in bivariate space ($\delta^{13}C$ vs. $\delta^{15}N$), known as isotopic space or δ-space (Newsome et al., 2007). Isotopic niches were constructed using the indicators proposed by Jackson et al. (2011). These methods allow for evaluating species and population niche breadths and making comparisons based on statistical inference. In particular, the isotopic niche width and overlap of each species was estimated using standard ellipse areas corrected for small sample size (SEAc; Jackson et al., 2011). This metric has several advantages over convex hull polygons, especially when small or unequal samples are used or when there is variation in body size of the groups analysed. To assess the temporal variation in the isotopic niche, Bayesian standard ellipse areas (SEAb) were used with 10,000 Markov chain Monte Carlo simulations to analyse the two species. This analysis was done using the Stable Isotope Bayesian Ellipses package in R (SIBER; Jackson et al., 2011), which enabled the calculation of the proportion of posterior draws that are smaller between the 2 groups, which was used as the probability (P) that one group has a smaller isotopic niche width than the other (Jackson et al., 2011). Finally, a Bayesian isotope mixing model (Parnell et al., 2013) using the SIMMR (stable isotope mixing model with "R" package) (Govan et al., 2023) was used to assess the relative incorporation rates of terrestrial and marine organic matter into ant tissues. The SIMMR package estimates dietary contributions from food sources by measuring stable isotope ratios in animal tissues. In addition, the model incorporates uncertainty in source values and trophic discrimination factors, which account for the differences between diet and tissue isotope ratio. This method involved analysing the C isotopic signatures of local terrestrial plants and marine algae collected at the study site (see Fig. 3). Separate stable isotope mixing models were run for each species and season, using "terrestrial" and "marine" vegetation as the two source data sets and ants collected in each habitat as the "mixture" data sets. The SIMMR package in R was utilized to run Markov chain Monte Carlo (MCMC) functions, determining the proportion and 95% confidence intervals of terrestrial and marine-derived food consumed by ants based on C stable isotope ratios in ant tissues. Trophic discrimination factors of 1.1‰ ± 0.3 for $\delta^{13}C$ were used (Garcia et al., 2011; Quinby et al., 2020).

RESULTS

The carbon isotope signature ($\delta^{13}C$) was significantly different between species ($F_{1,44} = 22.18$, $p < 0.0001$), season ($F_{1,44} = 16.93$, $p < 0.001$) and was affected by the interaction between species and season ($F_{1,44} = 4.44$, $p = 0.031$). The posthoc analysis of $\delta^{13}C$ revealed that the tissues of *C. morosus* were richer in ^{13}C in summer than in spring (Tukey test, $p < 0.001$), which differs from the other three groups (Fig. 1). In the case of *D. goetschi*, the $\delta^{13}C$ values did not differ significantly between seasons (Tukey test, $p = 0.54$). When analysing the $\delta^{15}N$ values, significant differences were recorded between species ($F_{1,44} = 22.18$, $p = 0.0003$) and seasons ($F_{1,44} = 17.74$, $p = 0.0001$). However, there was no effect of the species x season interaction ($F_{1,44} = 0.58$, $p = 0.45$), indicating that both species respond similarly in the two seasons. Nevertheless, *C. morosus* had the lowest $\delta^{15}N$ value of the four groups during spring (Tukey, all $p < 0.01$). In the case of *D. goetschi*, the $\delta^{15}N$ values did not differ significantly between seasons (Tukey test, $p = 0.08$). In summary, *C. morosus* differed in both $\delta^{13}C$ and $\delta^{15}N$ in the two seasons, whereas *D. goetschi* had similar isotopic signatures in both seasons (Fig. 1).

The Bayesian analysis revealed that the isotopic niches of *C. morosus* and *D. goetschi* were different in the two seasons (Fig. 2). In the case of *Camponotus*, the size of the SEAb does not change between spring and summer (Table 1, $p = 0.77$), but in *D. goetschi*, it is smaller in summer than in spring (Table 1, Fig. 2; $P = 0.00$). When comparing both species in spring, the analysis reveals that the size of the SEA of *C. morosus* is twice that of *D. goetschi (*Table 1; $P = 0.028$) and the area of the standard ellipse of *C. morosus* is notably (six times) larger than that of *D. goetschi* in summer (Table 1; $P = 0.00$). When comparing the position of ellipses the greatest overlap is between *C. morosus* in summer and *C. morosus* in spring, although it is relatively small (12.3%, Table 2). As for *D. goetschi*, the overlap of ellipses in both seasons was very low, with a value of cca 1%. The overlap was almost negligible when comparing the two species within the same season (Table 2, Fig. 2).

The results of the mixing model in SIMMR are shown in Fig. 3. Overall, this analysis revealed that terrestrial-derived carbon made up most of the food of both species of ant, with 72 ± 4% for *Camponotus* and 83 ± 1% for *Dorymyrmex*. The lack of an overlap in the estimates of the consumption of marine and terrestrial resources by the two species indicates resource partitioning (Fig. 3). Both species, however, slightly increased their use of marine resources in summer. Specifically, the marine contribution to the diet of *Camponotus* was approximately 28% in summer and 18% in spring and in *Dorymyrmex* it ranged from 17% in summer to 14% in spring. However, the difference between seasons for *Dorymyrmex* is not significant, but that for *Camponotus* is (see Fig. 3).

DISCUSSION

The ants studied had $\delta^{15}N$ values close to 10‰ in the summer. *Camponotus morosus* had lower values in spring of around 7‰ (Fig. 1). Assuming an enrichment of 3.4–3.7‰ for each trophic level (Minagawa & Wada, 1984; Post, 2002; Hyodo, 2015) and $\delta^{15}N$ values for C3 plants in the study area of 3.44 ± 1.99 ‰, this could suggest that during summer ants are in trophic level 3, which indicates they are secondary consumers, whereas in spring *C. morosus* is in trophic level 2, which indicates they are primary consumers. Previous studies on the genus *Camponotus* also report it is in a low trophic level based on its $\delta^{15}N$ signatures (Blüthgen et al., 2003; Fiedler et al., 2007; Ottonetti et al., 2008) and does not change with season (Plat-

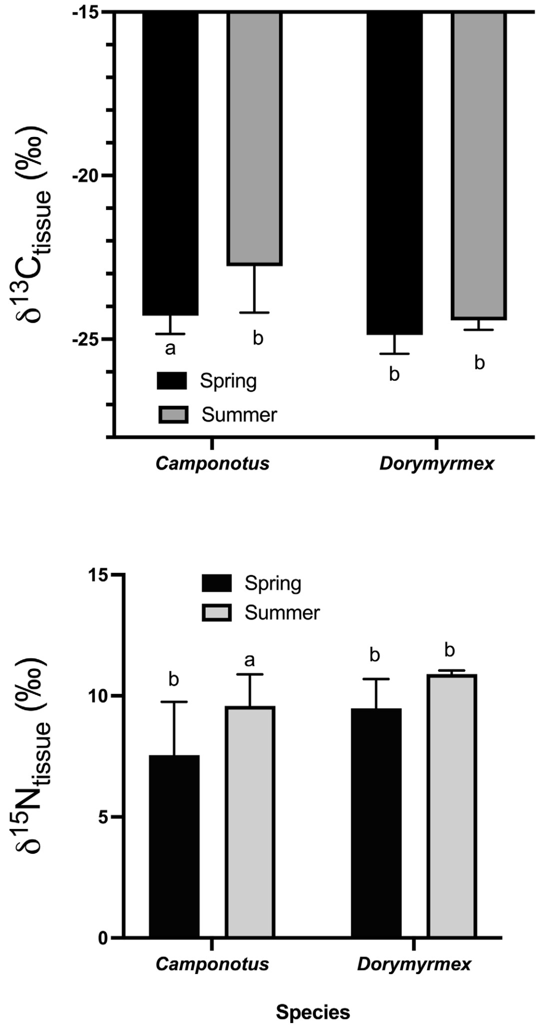

Fig. 1. Carbon isotopic ($\delta^{13}C$, Mean ± SD, Panel A) and nitrogen isotopic composition ($\delta^{15}N$, Mean ± SD, Panel B) of tissue from two ants, *Camponotus morosus* and *Dorymyrmex goetschi*, collected during spring and summer. Different letters represent significant differences between groups based on aTukey post hoc test.

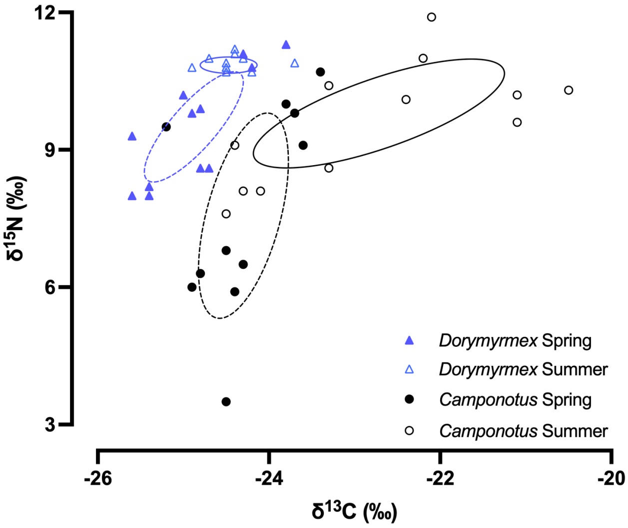

Fig. 2. Standard ellipses (SEA_C) estimated from stable carbon and nitrogen isotopes recorded in in body tissues of two ants (*Camponotus morosus* and *Dorymyrmex goetschi*) in two seasons (spring and summer) are illustrated. The solid ellipse lines are for species in summer and the segmented ones for spring. Each point represents an individual and ellipses consist of 95% of the standard ellipse area. The isotopic niche of *D. goetschi* is smaller in spring, and there are no significant differences in the isotopic niche between seasons for *C. morosus* (see Table 1 for statistics).

ner et al., 2012). In the case of *C. morosus*, the higher $\delta^{15}N$ value recorded in summer could be explained by a change in its feeding behaviour, altered nitrogen levels due to the presence or absence of bacterial endosymbiotic activity (Davidson et al., 2003; Fiedler et al., 2007), or a change in its diet that includes remnants of other animals and even vertebrate faeces (Grez et al., 1986). This enrichment in ^{15}N could also come from the excreta of lizards, birds and other animals, which indicates that *C. morosus* may be utilizing these resources for feeding its larvae (Curtis, 1985).

The dry summer conditions in areas with a Mediterranean-like climate induce stomatal closure in plants to reduce evaporation, resulting in an enrichment of $\delta^{13}C$ during this period (Platner et al., 2012). This could contribute to the increase in $\delta^{13}C$ in both ants in summer. The small difference between seasons recorded for *D. goetschi* indicate that the changes in $\delta^{13}C$ between seasons in *C. morosus* are due to a dietary shift that includes a different carbon source, possibly incorporating carbon from marine algae (and arthropods feeding on that source) (Fry, 2006). The results of the mixing model indicate that *Camponotus* relied more on terrestrial than marine food sources, with a higher difference recorded in summer than in spring. On the other hand, *Dorymyrmex* ants also showed a preference for terrestrial over marine resources, with their reliance on marine-derived resources being consistently lower in both seasons. Thus, the findings of this study partially support the initial hypothesis of a significant seasonal variation in the reliance on marine resources for *Camponotus,* with peak percentages occurring during summer. While it

Table 1. Standard ellipse area (SEA), standard ellipse area corrected for small sample size (SEAc) and Bayesian standard ellipse area (SEAb) are presented in ‰². The probability (P) resulting from the proportion of posterior draws of SEAb for one group (G) was higher than those from the other group is shown for statistical comparison of isotopic niche widths. Differences in SEAb size were considered significant when ≥ 95% of posterior draws (10,000) for one species were smaller than the other. When P: Gx > Gy is higher than 0.95, it indicates that the ellipse area of group x is larger than that of group y. Conversely, when P < 0.05, it means that the SEAb of group x is smaller than that of group y. Bold values denote statistical differences between groups, when probability (P) is > 0.95 or < 0.05.

Group / Species	SEA	SEAc	SEAb	P: G > G1	P: G > G2	P: G > G3	P: G > G4
G1. *Camponotus* Summer	4.25	4.68	4.71	—	0.777	**1.00**	—
G2. *Camponotus* Spring	3.21	3.53	4.38	0.223	—	—	**0.972**
G3. *Dorymyrmex* Summer	0.14	0.16	0.76	**0.00**	—	—	**0.00**
G4. *Dorymyrmex* Spring	1.28	1.41	2.30	—	**0.028**	**1.00**	—

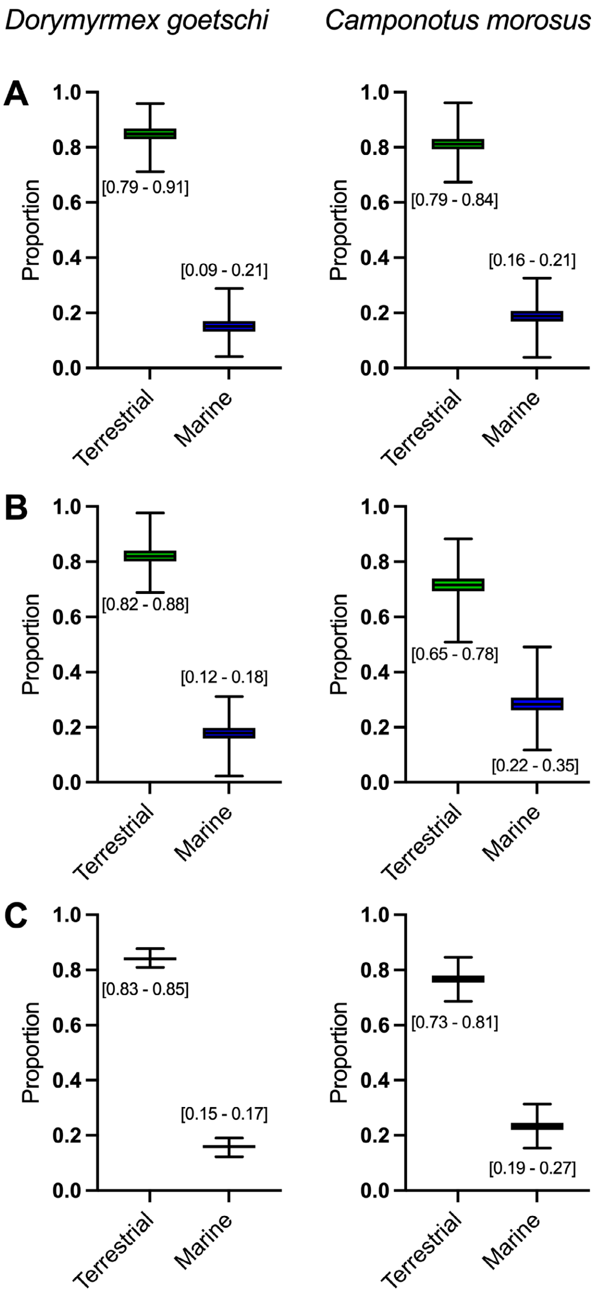

Fig. 3. Proportion (Mean ± SD) of terrestrial and marine food in in the diet of two species of ants at a coastal locality in central Chile obtained using SIMMR (Govan et al., 2023). Values in parentheses show 95% posterior interval estimates of terrestrial and marine-derived food consumed by ants. Stable isotope data for the endpoints for the mixing model (marine and terrestrial baselines) were obtained by analysing $\delta^{13}C$ for the most abundant species collected in the dunes and adjacent intertidal areas during spring (A) summer (B) and in both seasons (C). Terrestrial plants ($\delta^{13}C$ = –28.20 ± 1.51) includes the most abundant species *Baccharis linearis*, *Baccharis poeppigiana*, *Carpobrotus* spp., *Podanthus ovatifolius, Juncus* sp. and *Senecio* sp. Marine algae ($\delta^{13}C$ = –12.9 ± 1.79) includes the most abundant species *Ulva lactuca, Porphyra coumbina* and *Nothogenia fastigiata.*

is acknowledged that using a mixing model is useful, it is important to recognize that it relies on many assumptions, some of which may be inaccurate. For instance, variations exist in the discrimination between tissue and diet in ants (Quinby et al., 2020). Nonetheless, altering the values for the diet-tissue discrimination in our mixing model would have affected its quantitative, rather than qualitative, assessments. The proportion of marine items in the tissues of *Camponotus* and *Dorymyrmex* differed and increased in summer in *Camponotus*.

Table 2. Overlap (%) of the isotopic niche (SEAc) for each species, *Camponotus morosus* and *Dorymyrmex goetschi*, and for each season (summer and spring).

Comparison	Overlap (%)
C. morosus (Summer) / *C. morosus* (Spring)	12.32
D. goetschi (Summer) / *D. goetschi* (Spring)	1.08
C. morosus (Summer) / *D. goetschi* (Summer)	< 0.0001*
D. goetschi (Spring) / *C. morosus* (Spring)	< 0.0001**

Note: The exact percentage estimates were: * = 1.8×10^{-14} and ** = 6.9×10^{-14}.

The documentation of marine resource utilization by terrestrial animals along coastlines is not new. For instance, a substantial proportion of the diet of intertidal-foraging black fire ants (*Solenopsis richteri*) originates from marine sources and reach levels as high as 88% (Garcia et al., 2011). This study emphasizes the significant impact of ant foraging across ecosystems on marine resources, potentially leading to declines in intertidal invertebrate populations by up to 50%. Furthermore, the roles of *Camponotus* and *Dorymyrmex* in resource transfer and associated top-down effects are still largely unexplored and warrant further investigation.

In terms of niche width, *C. morosus* exhibited a larger SEA in both seasons compared to D. goetschi (Fig. 2, Table 1). This larger area may indicate a broader trophic niche (Layman et al., 2007) and suggest that *C. morosus* is a more generalist species (Freeman & Hannan, 1983). In contrast, *D. goetschi*, could have a narrower trophic niche and be more selective or a specialist. It is reported that when food becomes scarce, some species become less selective, resulting in a broader trophic niche (i.e., larger SEAs) (Evans et al., 2005; Lesser at al., 2020). This is in accord with optimal foraging theory, in which the expansion of the trophic niche results from reduced food availability, forcing consumers to include more poor-quality items in their diet (Calizza et al., 2017). For *C. morosus*, this could also be explained by the scarcity of nectar and sugary secretions from aphids during the dry season or by a change in metabolic needs due to increased demands for nitrogen for larval development at the beginning of summer, as described in other species (O'Grady et al., 2010). One possible explanation for this is that many ants are opportunistic feeders (Holway et al., 2002). As previously mentioned, the diverse roles of *Camponotus* workers might indicate different foraging behaviours and resource preferences (Roeder & Kaspari, 2017) that would broaden the isotopic niche within colonies. Despite this potential variability, the consistent differences in isotopic niche width and low overlap between stable isotope ellipses of both species indicate clear distinctions in resource utilization. In fact, when comparing the isotopic niches (SEA) of the two ants in the same season, there is practically no overlap (Table 2), indicating that there is no significant competition for food between the two species in the two seasons (Wang et al., 2019; Carscadden et al., 2020).

The changes in the isotopic niches of the two ants studied highlight the dynamic nature of resource utilization and the complex interactions between organisms in response to changing environmental conditions. The ability of ants to adjust their foraging to productivity levels highlights the importance of the interplay between marine and terrestrial ecosystems and in particular the complex relationships that shape these interconnected habitats along the Chilean coast. The results of this study support the hypothesis of resource partitioning by revealing significant differences in the $\delta^{13}C$ and $\delta^{15}N$ of the two species, indicating different ecological niches. The study also demonstrates that *C. morosus* is more of a generalist, incorporating a significant proportion of food of marine-origin in summer. In contrast, *D. goetschi* is more of a specialist with marked differences in isotopic niche width between seasons, but maintaining a preference for terrestrial prey throughout the year. This is based on the near-constant use of marine resources in both spring and summer (Fig. 3). These results indicate that they do not significantly compete for food, with differences in feeding behaviour contributing to their coexistence.

Furthermore, this study has some limitations that deserve attention. A key concern is that recently ingested food in the crop could bias isotopic signatures if it is processed along with the rest of an ant's body (Blüthgen et al., 2003; Tillberg et al., 2006). Since individual workers were analysed without removing their abdomens and the sample size was small, this could introduce biases. In this context, outliers, such as those recorded for *Camponotus* in spring (i.e., low value of $\delta^{15}N$), might reflect differences in feeding habits or amounts of nectar or prey in their abdomens at the time of collection. While this study revealed differences between individuals, it complicates statistical inference by introducing potential biases related to crop content, potentially widening confidence intervals and weakening conclusions. Although analysing entire workers provides unique insights, especially in large species of ants, including their abdomens might skew results towards recent feeding. Although the head and thorax may reflect nutrients acquired during the larval stage, focusing on these parts alone could offer a more accurate approximation of carbon and nitrogen sources assimilated by workers (Blüthgen et al., 2003).

Finally, although the isotopic niches of both species were characterized and compared in two seasons, there is still more to determine about their sources of food and behaviour. It is concluded that this research needs to be continued over a longer period, in order to analyse the effects of climate change and human intervention on this coastal ecosystem. As pointed out by Salas-López et al. (2022), comparative studies on trophic niche partitioning within ant communities can reveal differences in their nutritional ecology, which, in turn, could have larger-scale effects on colony sizes, their spread and interactions with other species.

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