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Trophic structure of the spider community of a Mediterranean citrus grove: A stable isotope analysis

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Abstract

Spiders are dominant terrestrial predators that consume a large variety of prey and engage in intraguild predation. Although the feeding habits of certain species are well known, the trophic structure of spider assemblages still needs to be investigated. Stable isotope analysis enables characterisation of trophic relationships between organisms because it tracks the energy flow in food webs and indicates the average number of trophic transfers between a given species and the base of the web, thus being a useful tool to estimate the magnitude of intraguild predation in food webs. Using this technique, we studied the trophic groups of spiders and their links within the arthropod food web of a Mediterranean organic citrus grove. We assessed the trophic positions of the 25 most common spider species relative to other arthropod predators and potential prey in the four seasons of the year, both in the canopy and on the ground. The analyses showed great seasonal variation in the isotopic signatures of some arthropod species, as well as the existence of various trophic groups and a wide range of trophic levels among spiders, even in species belonging to the same family. Differences in $\delta^{15}N$ between spiders and the most abundant prey in the grove usually spanned two trophic levels or more. Our findings provide field evidence of widespread intraguild predation in the food web and caution against using spider families or guilds instead of individual species when studying spider trophic interactions.

Zusammenfassung

Spinnen sind dominante terrestrische Prädatoren, die eine große Vielfalt an Beute konsumieren und oft 'intraguild predation' zeigen. Obwohl die Nahrungsbiologie einiger Arten gut erforscht ist, bedarf die trophische Struktur von Spinnen-Gemeinschaften noch intensiver Untersuchung. Die Analyse natürlicher stabiler Isotope ist ein nützliches Verfahren um Nahrungsbeziehungen zwischen Organismen zu charakterisieren, denn sie kann Energieflüsse im Nahrungsnetz aufdecken, die Anzahl trophischer Transfers zwischen einer Art und der Basis des Nahrungsnetzes anzeigen und somit ein Maß zur Abschätzung des Ausmaßes der 'intraguild predation' liefern. Basierend auf dieser Technologie haben wir die trophischen Gruppen der Spinnen und ihre Verknüpfungen im Arthropoden-Nahrungsnetz auf einer biologisch bewirtschafteten mediterranen Zitrusplantage untersucht. Die trophischen Ebenen der 25 häufigsten Spinnenarten aus den Baumkronen und vom Boden wurden zu vier Jahreszeiten analysiert, jeweils im Vergleich mit anderen Prädatoren und potentiellen Beutetiergruppen. Die Analysen zeigten eine große

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saisonale Variation der Isotopensignatur einiger Arten sowie die Existenz verschiedener trophischer Gruppen mit einer großen Bandbreite an trophischen Ebenen, sogar zwischen Arten, die zur selben Familie gehören. Die Differenzen der $\delta^{15}N$ Werte zwischen Spinnen und den häufigsten Beutetiergruppen der Obstwiese reichten gewöhnlich über zwei oder mehr trophische Ebenen. Unsere Ergebnisse liefern, unter natürlichen Bedingungen, Belege für eine weite Verbreitung von Intraguildpredation im Nahrungsnetz. Wir mahnen somit zur Vorsicht, Spinnen-Familien oder Gilden als Ersatz für einzelne Arten zu nutzen, um trophische Interaktionen zu untersuchen.

Keywords: Agroecosystem; Ants; Food web; Intraguild predation; Trophic niche; $\delta^{15}N$; $\delta^{13}C$

Introduction

Over recent years, the complex network of species interactions in terrestrial arthropod communities has received increasing attention. Manipulative experiments have shown the impact of intraguild interactions on the strength of trophic cascades (Cardinale, Harvey, Gross, & Ives 2003; Finke & Denno 2005) and have pointed out the relevance of trait-mediated effects to the regulation of herbivore populations (Schmidt-Entling & Siegenthaler 2009; Werner & Peacor 2003). Ecologists have also begun to disentangle the trophic links that structure arthropod food webs, but data obtained with direct observations or captive feeding studies are limited in scope (Greenstone 1999; Tiunov 2007).

The analysis of stable nitrogen and carbon isotope ratios (expressed as $\delta^{15}N$ and $\delta^{13}C$, respectively) is a powerful tool for characterising trophic interactions between organisms (Boecklen, Yarnes, Cook, & James 2011; Vander Zanden & Rasmussen 2001) and it has been used to study trophic relationships in arthropod food webs both in natural (Collier, Bury, & Gibbs 2002; Kupfer, Langel, Scheu, Himstedt, & Maraun 2006) and in agricultural settings (McNabb, Halaj, & Wise 2001; Wise, Moldenhauer, & Halaj 2006). Stable isotopes undergo a fractionation process by which $\delta^{15}N$ and $\delta^{13}C$ are enriched in the heavy isotope with increasing trophic levels (trophic enrichment). The carbon isotope fractionation with each trophic transfer is very small and largely retrieves the isotopic signal of the food source, so it is used to track the energy flow in food webs. By contrast, the enrichment of $\delta^{15}N$ is considerable and is useful for estimating the trophic levels of individuals (Gannes, Obrien, & del Rio 1997; Post 2002). Therefore, the $\delta^{15}N$ of a species indicates the average number of trophic transfers between the species and the base of the food web, and the comparison of the $\delta^{15}N$ of predators with those of their potential prey gives an integrated measure of intraguild predation in the community (Cabana & Rasmussen 1994; Ponsard & Arditi 2000). This is an especially interesting application of stable isotopes because experimental studies show that intraguild predation interactions are extremely frequent in arthropods (Arim & Marquet 2004; Hunter 2009), yet the actual prevalence of intraguild predation within arthropod food webs is only beginning to be quantified in the field (Gagnon, Heimpel, & Brodeur 2011; Sheppard & Harwood 2005).

Spiders are dominant generalist predators that consume a great variety of prey, engage in intraguild predation, and reduce herbivore numbers in terrestrial habitats (Hooks, Pandey, & Johnson 2006; Riechert & Lawrence 1997). But despite the determinant role of spiders in food webs, detailed studies on the trophic ecology of spider communities are largely lacking. Indeed, identifying arthropods to species is extremely demanding, so almost all studies about trophic relationships in arthropods group species into families on the basis that taxonomical relatedness should translate into diet similarity (but see Sanders & Platner 2007). However, this approach is likely to prove inaccurate precisely because of our lack of knowledge about the biology and feeding habits of spiders in nature (Cardoso, Pekár, Jocqué, & Coddington 2011; Greenstone 1999).

We performed a stable isotope analysis to describe the trophic structure of the spider community of a Mediterranean organic citrus grove. Because in this system the spider assemblages of the canopies and the ground are totally different (Mestre, Piñol, Barrientos, Cama, & Espadaler 2012) we collected arthropods from both layers. The strong seasonality intrinsic to this climate should influence the arthropod community and the structure of the whole food web, so we (1) compared the trophic signatures of important spider species and other arthropods at different times of the year. Above all, we wanted to (2) assess the trophic positions of the 25 most common spider species relative to other predators and potential prey in the grove. Moreover, we aimed to (3) assess the extent of intraguild predation in the spider community at different seasons.

Materials and methods

Study site

The grove is located at La Selva del Camp (Catalonia, NE Spain; 41° 13′ 07″ N, 1° 8′35″ E), an area with a Mediterranean climate. There are ca. 300 Clementine trees (*Citrus clementina* var. *clemenules*) grafted on the hybrid rootstock Carrizo citrange (*Poncirus trifoliata* (L.) Raf. × *Citrus sinensis* (L.) Osb.); these are watered during dry periods. Grasses and other weeds form a permanent ground cover, which is mowed a few times every year.