

Research



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Community ecology

Changes in invertebrate food web structure between high- and low-productivity environments are driven by intermediate but not top-predator diet shifts

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Predator–prey interactions shape ecosystem stability and are influenced by changes in ecosystem productivity. However, because multiple biotic and abiotic drivers shape the trophic responses of predators to productivity, we often observe patterns, but not mechanisms, by which productivity drives food web structure. One way to capture mechanisms shaping trophic responses is to quantify trophic interactions among multiple trophic groups and by using complementary metrics of trophic ecology. In this study, we combine two diet-tracing methods: diet DNA and stable isotopes, for two trophic groups (top predators and intermediate predators) in both low- and high-productivity habitats to elucidate where in the food chain trophic structure shifts in response to changes in underlying ecosystem productivity. We demonstrate that while top predators show increases in isotopic trophic position ($\delta^{15}\text{N}$) with productivity, neither their isotopic niche size nor their DNA diet composition changes. Conversely, intermediate predators show clear turnover in DNA diet composition towards a more predatory prey base in high-productivity habitats. Taking this multi-trophic approach highlights how predator identity shapes responses in predator–prey interactions across environments with different underlying productivity, building predictive power for understanding the outcomes of ongoing anthropogenic change.

1. Background

Predator–prey dynamics play a central role in maintaining food web stability [1,2] and ecosystem functioning [3,4]. Anthropogenically driven perturbations can shift community composition [5,6] and the occurrence of predator–prey interactions [7,8]. Understanding how trophic attributes respond to shifting

environmental context will be important for predicting and mitigating ongoing and future loss of biodiversity [9–11].

One environmental context that is changing in the Anthropocene and which has known outcomes for food web trophic structure is basal ecosystem productivity [12,13]. Productivity drives changes in community composition and biomass and also shifts the trophic position, diet composition, and trophic breadth of top predators (e.g. 14–16). These shifts, likely driven by energy availability [17], are mediated by predator and prey traits or taxonomy [18,19], abiotic conditions that shape metabolism or hunting success [20–22], or the underlying stability of the prey community [23]. Because the context dependence of predator–prey interactions is driven by multiple biotic and abiotic factors [24], it is likely that changing ecosystem productivity shapes predator–prey interactions differentially based on predator identity [25]. As a consequence, any observed shifts in food web structure based on measures such as food chain length [14] likely result from the combined effects of top predator responses and responses occurring lower in the food chain (e.g. increased omnivory; [26]). Thus, to capture not only patterns but also mechanisms for productivity–food web relationships, it is crucial to examine food web changes using complementary measures of trophic ecology [27] and across multiple trophic groups [8,28].

Here, we combine trophic information across two predator groups (top predators and intermediate predators) using two complementary measurements of trophic ecology (diet DNA metabarcoding to capture diet community composition and diet community niche and stable isotope data $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ to capture trophic position and isotopic niche size) to explore how shifting basal ecosystem productivity alters food web structure. We examine both the isotopic and DNA-based trophic niches along with trophic position of a top predator (the active-hunting spider *Heteropoda venatoria* (Sparassidae)) and the DNA-based trophic niche of multiple other intermediate predator spiders in the order Araneae (web-building: *Neoscona theisi* (Araneidae), *Keijia mneon* (Theridiidae) and the sit-and-wait spider *Scytodes longipes* (Scytodidae))—which comprise some of the top predator's diet items [29,30]—across two different levels of ecosystem productivity (high and low). We ask (1) does ecosystem productivity alter top predator trophic niches and trophic position, and (2) does ecosystem productivity alter intermediate predator trophic niche? Previous work in this system demonstrates that top and intermediate predator trophic position increases with increased ecosystem productivity [14], though was unable to resolve mechanisms, which we predict are driven by changing trophic niches of top predators (question 1) or changes to trophic niches lower in the food chain (question 2). This study adds to our understanding of how ongoing anthropogenic change influences trophic structure [12].

2. Methods

(a) Study site

We conducted this study on Palmyra Atoll, Northern Line Islands, USA (5° 53'N, 162° 05'W). The atoll consists of approximately 20 islets that are dominated by either broadleaf vegetation and palms (*Pisonia grandis*, *Heliotropium arboreum*, *Pandanus tectorius*) or an introduced palm species (*Cocos nucifera*). Seabirds prefer to nest on islets that are dominated by broadleaf and *P. tectorius* palm forests and avoid nesting in forests dominated by *C. nucifera*

palms [31]. This habitat preference drives, in large part, differences in guano input, leading to 8.6 times higher soil nutrients and similarly increased productivity in broadleaf and *P. tectorius* palm habitat compared with *C. nucifera* palm habitat [32].

The atoll has a well-categorized species list [33] of which the animals are primarily invertebrate organisms (approx. 400 species), with top and intermediate predator species including several spider species (Arachnida: Araneae, [14,29]). These species respond in composition, diversity, diet and abundance to productivity in this system [15,32]. In this study, we examined trophic patterns for a spider top predator, *Heteropoda venatoria*, and for spider intermediate predators *Keijia mneon*, *Scytodes longipes* and *Neoscona theisi*, which are all common, habitat generalist, intermediate predator species on the atoll and are preyed by *H. venatoria* [29,30].

(b) Predator collection and sample processing

We collected all predator individuals for isotope and DNA diet samples across various islets that comprise two habitat contexts: (1) high productivity *P. grandis*, *H. arboreum* and *P. tectorius* forests (hereafter 'high-productivity') and (2) low productivity, *C. nucifera* palm forests (hereafter 'low-productivity'). For isotope samples, we followed procedures for bulk isotope sample processing in [14]. Specifically, we corrected consumer $\delta^{15}\text{N}$ values using a mixing model with two potential diet baselines—terrestrial plants and marine wrack. This mixing model corrects for elevated $\delta^{15}\text{N}$ that arises in terrestrial plants due to increased seabird guano subsidies. We also considered guano, rather than marine wrack, as a second-end source for (a) only consumers from high-productivity sites and (b) all consumers and found that isotopic trophic position stayed the same. Original explanations of sample processing for diet DNA data are in [29,30], although we adjusted bioinformatics filtering steps that were overly conservative from that original study to capture greater diet diversity, especially among predators. Specifically, while we originally removed all other predator species sequences from any sample that was run on the same sequencing run as those shared species, this step was likely overly conservative given that we followed best practices for both laboratory sample preparation and post-sequence filtering based on negative control samples [34]. Indeed, this filtering step likely biased diet estimates by under-representing the extent to which predators consume other predators. Please refer to the electronic supplementary material and these original papers for complete sample processing methodologies.

(c) Data analysis

To examine how stable isotope-based trophic niche of top predators shifts with environmental context, we calculated two common trophic niche metrics (standard ellipse area: [35], kernel utilization density: [36]). We calculated the 95% confidence interval for both metrics and used a generalized linear model to examine how habitat context shapes isotopic niche space. We also examined how trophic position ($\delta^{15}\text{N}$) shifted individually with environmental context using a set of linear mixed effects models. We used Gaussian error distributions for all linear models and random effects of islet and year to account for spatial and temporal non-independence. All models included abiotic context (categorical variable: high versus low productivity) as fixed effects ($n=88$ individuals from high-; 64 from low-productivity habitats).

To examine how diet DNA shifts with habitat context for both top and intermediate predators, we determined shifts in DNA diet niche (beta diversity) between the two environmental contexts using distance-based redundancy analyses [37]. This approach allowed us to separate the effects of niche 'turnover' (shifting to new prey items) and 'nestedness' (one prey community is a subset of the other) [38] in the event of shifts in diet

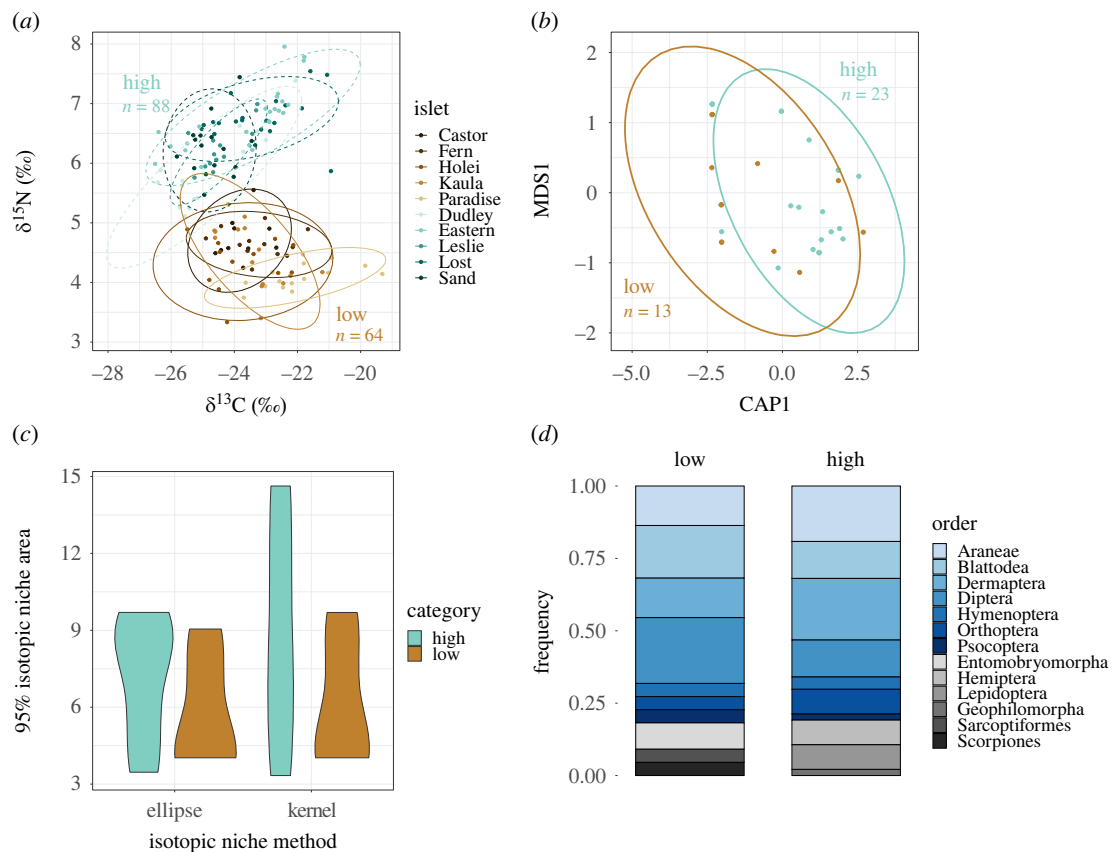


Figure 1. Top predators increased their trophic position (a), but neither shifted their isotopic niche size (a,c) or diet composition (individuals, (b); population relative frequency, (d)) across high- and low-productivity habitats. In (b), variation constrained by productivity is on the CAP1 axis; unconstrained variation is along the MDS1 axis.

composition. We ran one model for each predator category ($n = 23$ and 13 individuals for the top predator species in high- and low-productivity habitat, respectively; $n = 29$ and 7 intermediate predators from each habitat, respectively) and used the Jaccard dissimilarity index based on the presence-absence nature of our data. In the event of dissimilarity in diet composition with environmental context (p -value ≤ 0.05), we determined whether dissimilarity (beta diversity) was based on turnover or nestedness.

We ran all statistical analyses in R (v. 4.0.2; [39]) and cleaned data with the here (v. 1.0.1, [40]) and tidyverse packages (v. 1.3.0, [41]). We computed isotopic niches using the rKIN package (v. 0.1, [42]), ran mixed effects models in the glmmTMB package (v. 1.1.2, [43]), and ran model diagnostics using the DHARMA (v. 0.3.3, [44]) and effects (v. 4.2-0, [45]) packages [46]. We ran distance-based redundancy analyses using the vegan (v. 2.5-7, [47]) and betapart (v. 1.5.4, [48]) packages. Raw data and reproducible code are available on Dryad [49].

3. Results

(a) Top predator trophic position and isotopic niche

Top predators did not have different isotopic niche sizes between high- and low-productivity habitats (p -value = 0.51) for either the standard ellipse area or kernel utilization density method (figure 1c). However, $\delta^{15}\text{N}$ values clearly increased in high-productivity habitat (p -value < 0.001 , $\beta = 1.93$, CI = 1.56–2.31; Nakagawa $R_m^2 = 0.75$, $R_c^2 = 0.85$) compared to top predators from low-productivity habitat (figure 1a).

(b) Diet composition

We detected an average of 2.1 (± 0.1) unique diet orders in each individual predator's diet DNA (1–5 orders in each individual).

Thirty-four per cent ($n = 587$ out of 1738) of the total ASVs found in predator samples received taxonomic assignments from GenBank and BOLD at the order level or lower. As a group, top predators most often consumed Araneae, Blattodea, Dermaptera and Diptera across habitats (figure 1d). As a group, intermediate predators in high-productivity habitat more often consumed more predatory diet orders than in low-productivity habitat, including Araneae, Diptera and Coleoptera (figure 2b). Beta-diversity of prey consumed by top predators was not significantly different between habitats (dbRDA: p -value = 0.45). Beta-diversity of prey consumed by intermediate predators (other Araneae) was significantly different between habitats (p -value = 0.01). Turnover in prey composition (p -value = 0.01) explained differences between habitats while nestedness did not (p -value = 0.45).

4. Discussion

In this study, we provide evidence of one mechanism by which food web structure shifts with ecosystem productivity, specifically, a shift in intermediate predator species diet composition. While top predator (the spider *H. venatoria*) trophic position clearly increased with productivity, this was not driven by changes in top predator diet composition. However, intermediate predators (the spiders *N. theisi*, *K. mneon* and *S. longipes*), which are consumed by *H. venatoria*, shifted their diet composition between productivity contexts, consuming more other predators in high-productivity environments. This study demonstrates the dynamic nature of predator–prey interactions [8] and how predator identity can inform these dynamics—some predators maintain consistent diets across

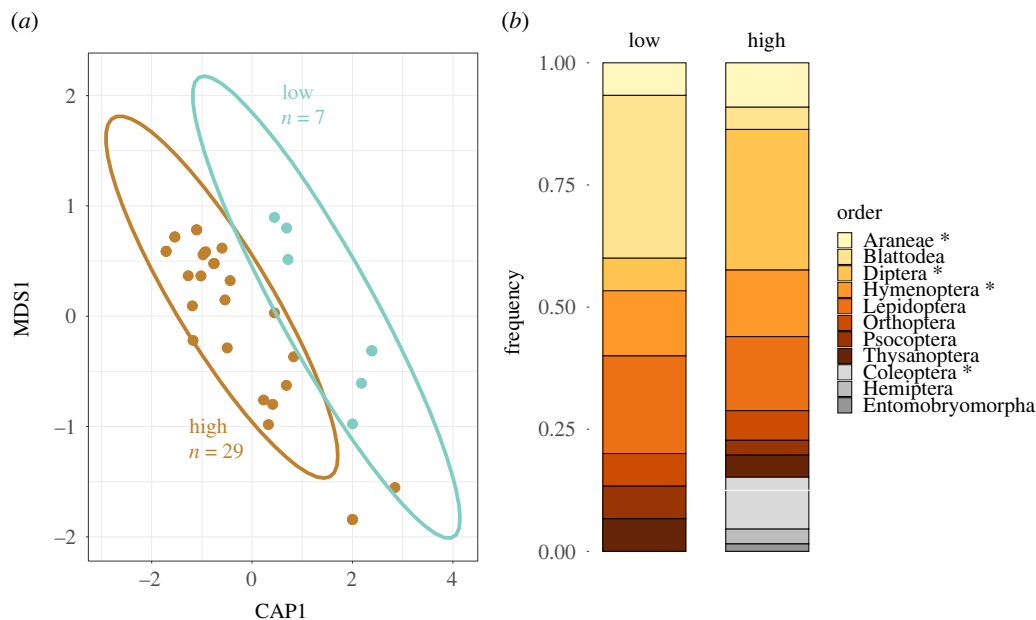


Figure 2. (a) Intermediate predators (other Araneae) substantially shifted diet composition with habitat productivity, indicated by shifts along the CAP1 axis (variation constrained by productivity; the MDS1 axis represents unconstrained variation). (b) Intermediate predators consumed predatory orders (indicated by *) at a higher frequency in high-productivity habitat (population relative frequency).

different environments, while others change. Furthermore, this study shows how realized shifts in top predator trophic position can be driven by trophic shifts in lower-level trophic groups rather than shifts in diets of top predators themselves.

Ecosystem productivity drives changes in food web structure [14,16] and elucidating possible mechanisms is a crucial step for predicting how ongoing environmental change will influence species interactions [24]. Our study adds an important contribution to this literature: specifically, shifting ecosystem productivity does not lead to trophic shifts for all predator species, suggesting a combination of multiple mechanisms (e.g. traits, taxonomy, relative abundance and environmental context; [18,50]). The top predator, *H. venatoria*, has a general habitat association as well as an active hunting strategy; perhaps this combination of traits allows this predator to seek out preferred prey regardless of prey abundance in the environment (e.g. [16,19]). Conversely, intermediate predator species (*N. theisi*, *S. longipes* and *K. mneon*) all have more specific habitat preferences (e.g. tree canopies and forest understories) and at least two of these species employ passive hunting strategies (web-building: *N. theisi*, sit-and-wait *S. longipes*). This combination of traits may mean these predators are more reliant on prey abundance, and thus, have more limited ability to select for specific prey taxa [23,26].

Our results also highlight next steps in examining predator–prey interactions across ecosystem productivity. For example, explicit trait-based studies (e.g. habitat and diet generality, hunting strategy, body size) within and across environments and trophic groups would illuminate generalizable trends, thereby improving predictive capacity [18,51]. Our study highlights the importance of quantifying trophic interactions across multiple trophic levels using distinct but complementary approaches [52]: conflicting results across trophic groups and diet tracing methods can help illuminate where in food webs trophic restructuring occurs [8,27]. Examining even more trophic levels via both methods (e.g. adding isotopic data for intermediate predators), especially in food webs with detrital basal resources may illuminate additional

patterns [53]. While in this system, trait differences among predators manifested between top predators and intermediate predators, in other systems, these patterns may be more multi-trophic, with predators across trophic levels displaying diet shifts.

5. Conclusion

Biological communities continue to shift due to anthropogenic change across the globe [54]. As biological communities change, the interactions between those species also face new constraints and may disappear altogether [11]. Some interactions may be resistant to change, perhaps due to predictable organismal traits like hunting strategy or diet breadth, while some may shift or disappear. Taking a holistic approach by combining information on multiple trophic groups and using multiple diet tracing methods (e.g. EcoDiet; [55]) will help recognize generalities (e.g. trait-based approaches; [18]) in how interactions are influenced by environmental context and change. Not only will these insights build ecological theory, but they may help mitigate the effects of ongoing biodiversity loss [56].

Data accessibility. All data and code used for the analyses in this manuscript are available from the Dryad Digital Repository: <https://doi.org/10.25349/D9C334> [49].

The data are provided in the electronic supplementary material [57].

Authors' contributions. A.M.K.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, resources, software, supervision, visualization, writing—original draft, writing—review and editing; A.A.: conceptualization, formal analysis, methodology, writing—original draft, writing—review and editing; A.B.: conceptualization, data curation, formal analysis, investigation, methodology, software, visualization, writing—review and editing; K.B.: conceptualization, formal analysis, methodology, software, writing—review and editing; J.N.C.: investigation, writing—review and editing; S.C.: investigation, writing—original draft, writing—review and editing; B.P.D.: conceptualization, validation, writing—review and editing; E.S.F.: investigation, writing—review and editing; M.K.: investigation, writing—original draft, writing—review and editing; C.I.M.: investigation, writing—original draft, writing—review and

editing; D.O.: investigation, writing—original draft, writing—review and editing; K.A.P.: investigation, writing—original draft, writing—review and editing; D.L.P.: conceptualization, validation, writing—original draft; H.S.Y.: conceptualization, funding acquisition, project administration, resources, supervision, writing—review and editing.

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Conflict of interest declaration. We declare we have no competing interests.

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