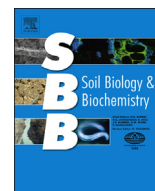




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Short-term sodium inputs attract microbi-detritivores and their predators

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ABSTRACT

Understanding individual nutritional requirements can generate good predictions for how communities should be structured over gradients of nutrient availability. Sodium (Na) bioaccumulates from plants to predators: it is relatively unimportant for plants, which concentrate very little Na in their tissues, but critical for consumers, which concentrate Na well above plant levels. Thus, plant consumers are likely Na-limited but their predators, which consume salty prey, are likely not. From this framework, we can make predictions about how an entire community should respond to Na subsidies in Na-poor environments. We tested these predictions in an interior Amazonian brown (detrital) food web. Specifically, we quantified the responses of microbi-detritivores and their predators to experimental pulses of Na by adding 250 ml 0.5% NaCl solution that mimicked patchy urine deposition, or river water as controls, to 55 paired 0.25 m² plots every other day. We regularly harvested plots over a 19 day period. Consistent with the hypothesis of Na-limitation among plant consumers, the response (effect size) to Na addition by microbi-detritivores like termites was >6 times that of predators. Moreover, consistent with the bioaccumulation of Na, fewer predatory invertebrates increased on +NaCl plots, thus trophic position alone was a good predictor of response. Our results support the Na bioaccumulation hypothesis and suggest that patchy, short-term Na inputs (like urine) facilitate heterogeneity in these leaf litter communities. Further, this study demonstrates that combining principles from nutritional and community ecology can generate predictions about how communities should be structured over gradients of nutrient availability with good accuracy.

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01 1. Introduction

Nutritional ecology combines principles of physiology and nutrient availability to predict how a given organism will respond to changes in essential nutrients (Aumann and Emlen, 1965; Raubenheimer et al., 2009). Low nutrient availability relative to the requirement of the organism forces organisms to spend more time acquiring these nutrients or suffer performance deficits (Arms et al., 1974; Sterner and Elser, 2002; Simpson et al., 2006; Geerling and Loewy, 2008). In this way, the stoichiometric imbalances

between consumers and their food can affect the composition and ecological functions provided by food webs (White, 1993; Wardle, 2002). Nutritional ecology often focuses on individuals, but a species rarely exists in solitude, and thus it is more realistic, although infrequent, to examine nutrient limitation at the community level of organization (Simpson et al., 2010). Identifying and quantifying the imbalances between consumers and their diet are necessary to understand how nutrient limitation of an individual ramifies to the community and ecosystem levels (e.g., Hawlena et al., 2012).

Within a community, herbivores and predators often face different nutritional challenges. This is evident even in the relative ability to acquire and maintain a balance of micronutrients; heterotrophs, more so than autotrophs, represent nutritionally balanced diets for their consumers (Galef, 1996). This pattern is particularly apparent for the micronutrient sodium (Na). Plants require and concentrate very little Na in general, but heterotrophs need to concentrate Na well above plant levels to maintain neural function, osmotic balance, reproduction and development (Ganguli

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et al., 1969; Bursey and Watson, 1983; Blumwald et al., 2000; Geerling and Loewy, 2008). Schowalter et al. (1981) measured plant, herbivore, and predator Na concentrations at 0.02, 0.31, 0.66% Na respectively, which demonstrates the large stoichiometric disparity between plants and herbivores. Herbivores and detritivores, as plant consumers, are thus potentially the most vulnerable to Na-limitation. Predators, in contrast, likely do not suffer from Na-deficits as their diet (other heterotrophs) is already rich in Na (Schowalter et al., 1981; Simpson et al., 2006; Kaspari et al., 2008). In fact, predators are generally insensitive to Na in choice tests (Bradshaw et al., 1996), but herbivores can taste and respond to Na even at concentrations as low as 0.005 M (Bell and Kitchell, 1966). Thus, Na bioaccumulates from plants to predators, but we know of no studies that compare Na-limitation among plant consumers and their predators in a given community.

In general, Na is abundantly available near coastlines due to its deposition in rainfall, but away from oceanic sources there is a Na shortfall (Stallard and Edmond, 1981; Kaspari et al., 2009, National Atmospheric Deposition Program, 2011). However, local historic, geological, biotic, or anthropogenic factors may create important sources of Na in otherwise Na-poor environments. These include salt or clay licks (Tracy and McNaughton, 1995; Dormaar and Walker, 1996; Powell et al., 2009), urine (McNaughton et al., 1997), and road salts (Canadian Environmental Protection Act, 2001; Kaspari et al., 2010). Larger animals such as sheep are able to travel to reliable salt licks (Poole and Bachmann, 2008), but smaller organisms like consumers of the brown food web (BFW) likely rely on patchy and ephemeral Na subsidies such as urine, feces and corpses. BFWs are donor-controlled and comprised of microbes, microbi-detritivores that consume plant detritus and associated microbes, and their predators that interact and ultimately decompose ca. 90% of the productivity (uneaten plant biomass) in green food webs (Fittkau and Klinge, 1973; Coleman et al., 1996; Wardle, 2002; Decaëns, 2010). Consequently, understanding Na-limitation and its effects on BFWs can facilitate our understanding of broad geographic community and decomposition patterns.

Here we evaluate the responses of an interior Amazonian BFW to experimental patches of NaCl that simulate ephemeral Na subsidies. In Na-poor environments like interior Amazon rainforests (Stallard and Edmond, 1981; Kaspari et al., 2008; Dudley et al., 2012), microbi-detritivores, but not their predators, should seek Na (Geerling and Loewy, 2008). We test the prediction that microbi-detritivores will accumulate in response to NaCl, but predators, which should be less Na-limited (via the bioaccumulation of Na), should not. By comparing BFWs of paired Control and +NaCl plots over a period of 19 days, we tested for a difference in community composition between paired plots and we further tested whether trophic position (i.e., microbi-detritivore, 1° predator, 2° predator) via the bioaccumulation hypothesis was a good predictor of response. We document how short-term Na subsidies create predictable changes in community composition.

2. Materials and methods

2.1. Study site

We ran experimental plots from December 18, 2008 to January 6, 2009 at the Amazon Conservatory of Tropical Studies (ACTS) field station 67 km NE of Iquitos, in Loreto Province, Peru (3.25°S, 72.91°W). ACTS is a lowland tropical rainforest that receives ca. 3000 mm average rainfall per year and is characterized by variable soils in terms of geologic origins and fluvial inputs, but mainly consist of clay oxisols and ultisols (Madigovsky and Vatinick, 2000; Mäki et al., 2001).

2.2. Experimental design

We used a split-plot design (Lindquist, 1953) with Day sampled as the wholeplot factor, Blocks as the subplot factor, and within blocks were paired Treatment plots (Fig. 1). We used 55 paired 0.25 m² (0.5 × 0.5 m) plots that consisted of a +NaCl and a Control plot separated by 3 m and Blocks were separated by ≥5 m. Control plots received 250 ml stream water (see Kaspari et al., 2009 for stream description and water chemistry) and +NaCl plots received 250 ml 0.5% NaCl solution by weight in stream water from the same source. Although we added sodium in the form of NaCl, previous experiments separating the two elements demonstrate that sodium, and not chloride, is driving consumer response and decomposition (see Kaspari et al., 2009). Plots were fertilized on day 0 and every other day until the termination of the experiment on day 19.

We destructively harvested 5 random Blocks on Days 1, 2, 4, 7, 9, 14, 15, 16, 17, 18, and 19. This allowed us to examine both rapid effects that mimic a migrating mammal excretion event (1 day), and longer term subsidies that mimic latrines where mammals such as howler monkeys (as well as other primates) common throughout the Neotropics display excretion site-fidelity and deposit daily both urine and feces (Feely, 2005; Dos Santos Neves et al., 2010). Prior to each harvest, we measured litter depth 1 cm inside the four plot corners of both treatment plots using a wire gently inserted into the litter down to mineral soil. Invertebrates were collected from each 0.25 m² treatment plot by collecting all leaf litter down to the topsoil and sifting it through a 1 cm² metal mesh. We then discarded the coarse leaf litter and extracted invertebrates from the siftate (the fine leaf litter and inverts that fell through the 1 cm² mesh) over 24 h using Winklers (Bestelmeyer et al., 2000).

2.3. Trophic position

We used stable isotope analysis to assign 32 focal invertebrate taxa to a trophic level (see Fig. 2 for taxa list). These focal invertebrates accounted for 93% of individuals collected and are frequent subjects in other BFW studies (e.g., Coleman et al., 1996; Chen and Wise, 1999; Wardle, 2002; Decaëns, 2010). Ants (Hymenoptera: Formicidae) accounted for 21% of the total arthropod abundance and twelve of the common ant genera were included

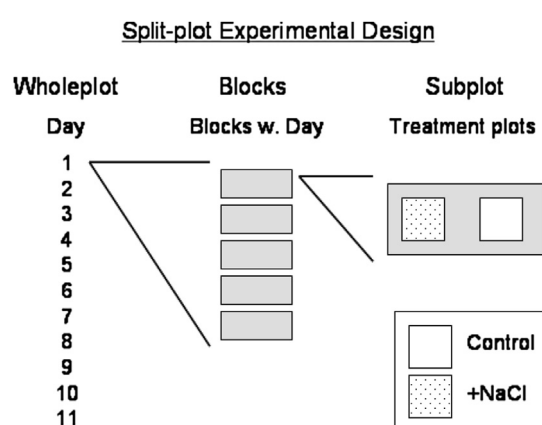


Fig. 1. Schematic diagram of the split-plot experimental design. The between-block effects at the wholeplot level are Day ($n = 11$), which is the day when 5 random blocks were destructively sampled, and Blocks w. Day ($n = 5$), which are the 5 random blocks sampled on each day. In a split-plot design, these effects are indistinguishable. The within-block effects at the subplot level are the paired Treatment plots ($n = 2$), Blocks ($n = 55$), which contain each paired Treatment plots, and the Treatment × Day (Blocks w. Day) interaction (see Table 1).

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