# 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 bio-accumulation 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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## 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 subsides. 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 (Madigosky and Vatnick, 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 m$^2$ (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 m$^2$ treatment plot by collecting all leaf litter down to the topsoil and sifting it through a 1 cm$^2$ 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 cm$^2$ 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
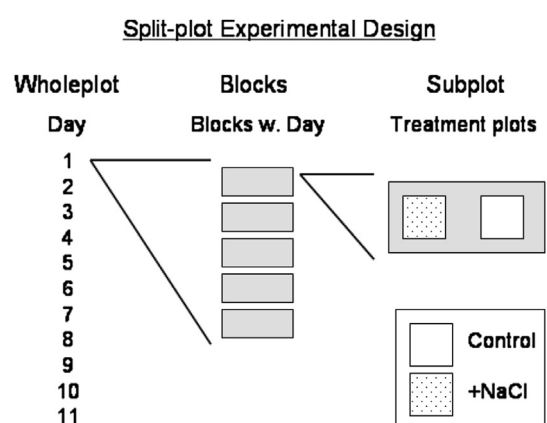


Fig. 1. Schematic diagram of the split-plot experimental design. The between-block effects at the wholeplot level are Day ($n = 11$), which is the day when 5 random blocks were destructively sampled, and Blocks w. Day ($n = 5$), which are the 5 random blocks sampled on each day. In a split-plot design, 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).
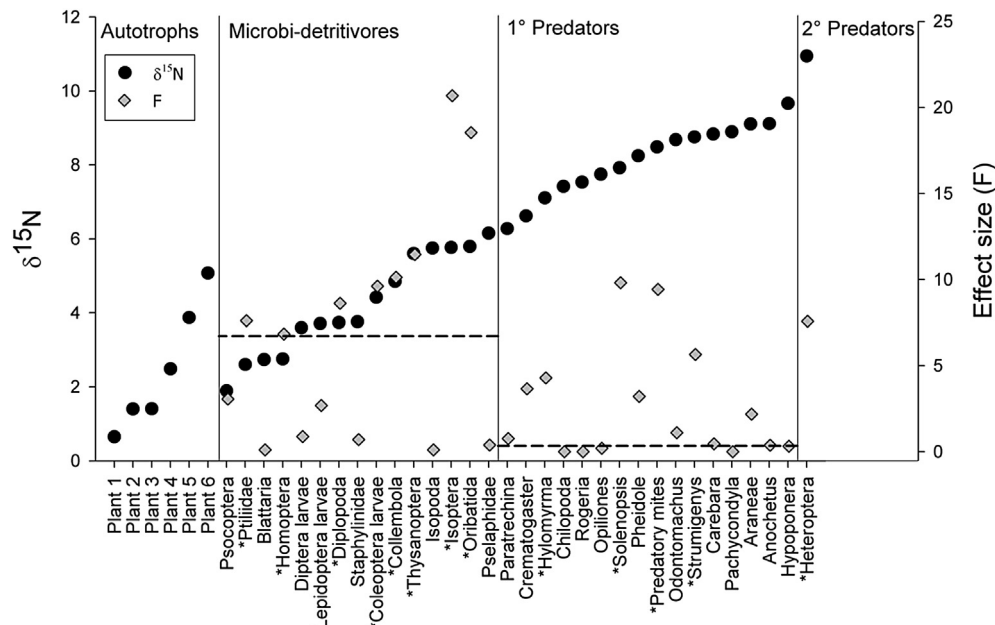
**Fig. 2.** Trophic position (black circles) and effect size (*F*) based on univariate Permanovas (gray diamonds) of the 32 invertebrates measured within the Amazonian brown food web. Vertical solid lines designate trophic position divides (autotrophs, microbi-detritivores, 1° predators, 2° predators, see Methods for how determined). Horizontal dashed lines are the mean *F* for each trophic position excluding the 2° predators that had only one invertebrate member. Stars in front of invertebrate labels represent significant ($p \leq 0.05$) increases in abundance on +NaCl plots determined from univariate Permanovas. Homoptera represents: Hemiptera: Sternorrhyncha and Auchenorrhyncha.

among the 32 focal invertebrates (see Fig. 2 for focal ant genera). N isotope values are reported using delta notation ($\delta^{15}N$) where: $\delta = ((R_{sample}/R_{standard}) - 1) \times 1000$. $R$ = ratio of heavy to light isotope ($^{15}N/^{14}N$ for nitrogen stable isotopes) of the sample and standard. Delta N values are expressed in ‰ (per mil notation). All invertebrates were preserved in 95% ethanol prior to stable isotope analysis; as such, we only used N stable isotope values that are unaffected by ethanol (Fábián, 1998). A homogenate of multiple individuals was used in each sample to best represent each invertebrate's respective trophic position because many of the invertebrates are represented at the Class, Order, or Family level. Samples were dried at 60 °C and ca. 500 µg of each homogenate was encapsulated in tin capsules. We included plants (grass, shrubs, and tree leaves) haphazardly sampled from the experimental site to provide the basal $\delta^{15}N$ values within the system. Nitrogen stable isotopes were analyzed using a Costech Elemental Analyzer interfaced through a ConFlo III open split valve with a Thermo Finnigan Delta V isotope ratio mass spectrometer (Costech Analytical Technologies Inc., Valencia, CA, USA). $\delta^{15}N$ values and precision were determined using a laboratory standard referenced against the international standard for N of atmospheric nitrogen (international standards calibrated with USGS 40 and 41). Nitrogen stable isotope precision was ±0.128‰ ($N = 8$).

Trophic positions were calculated as: Trophic Position = $\lambda + (\delta^{15}N_{secondary\ consumer} - \delta^{15}N_{base})/\Delta N$. We used the average plant value (2.876 ± 1.875‰) as $\delta^{15}N_{base}$ (Scheu and Falca, 2000; Ometto et al., 2006; Hyodo et al., 2010), $\lambda$ was 1 (the trophic level of the organisms used to estimate the base, i.e., autotrophs), $\delta^{15}N_{secondary\ consumer}$ was directly measured, and we used the standard 3.4‰ enrichment per trophic level as our $\Delta N$ (Fry, 1988; Post, 2002). Organisms occupying Trophic Position 2 are hereafter referred to as microbi-detritivores, those in Trophic Position 3 as 1° predators and those in Trophic Position 4 as 2° predators. The placement of these organisms within each Trophic Position is consistent with other studies (Coleman et al., 1996; Scheu and Falca, 2000). The only exceptions were Staphylinids and Pselaphids (Coleoptera) which

are typically classified as predators. Since the purpose of using stable isotopes was to eliminate subjectivity in the assignment of organisms to Trophic Positions, we kept them as microbi-detritivores. Thus, a significant result in the analyses of Trophic Position and effect size would further indicate that the assumptions of our hypotheses are robust despite the few taxa that may have debatable Trophic Position placement.

### 2.4. Statistical analysis

We collected invertebrates on +NaCl and Control plots to test two predictions: 1) NaCl plots attract more invertebrates and 2) this effect diminishes with higher trophic position. In BFWs, leaf litter functions both as consumer habitat and food (Wardle, 2002). Litter depth is patchy and as with aquatic systems, deeper litter (i.e., a great volume of leaf litter) as habitat is positively correlated with invertebrate abundance and richness (Angermeier and Schlosser, 1989; Ettema and Wardle, 2002; Kaspari and Yanoviak, 2009; Shik and Kaspari, 2010). Average litter depth on plots varied from 0.28 to 13.37 cm, which is representative of the natural heterogeneity in tropical forest litter depth (Fauth et al., 1989; N.A. Clay, unpublished data). However, NaCl addition enhances decomposition and litter depth decreased on +NaCl plots (average litter depth of Control: 5.18 ± 3.15 vs. +NaCl: 4.18 ± 3.30 cm; Wilcoxon Signed Ranks Test, d.f. = 55, $p = 0.007$, see Kaspari et al., 2009 for further discussion). Consequently, litter depth on +NaCl plots accounted for 24.1% of the variation in invertebrate abundance ($\log_{10}$Abundance = 0.606*$\log_{10}$LitterDepth + 1.871, $R^2 = 0.241$, $p = 0.0001$), and 8.6% on Control plots ($\log_{10}$Abundance = 0.632*$\log_{10}$LitterDepth + 1.568, $R^2 = 0.086$, $p = 0.03$). To account for this variation, control for habitat size-abundance relationships, and reduce potential type II error from natural and non-random, treatment-derived variation in litter depth, we thus used abundance per habitat volume: the number of invertebrates m$^{-3}$ (plot area × litter depth) as is common in aquatic research (Downing and Leibold, 2002; Bagge et al., 2004).

### 2.5. Testing differences in community structure

To determine if communities on +NaCl plots differed from Control plots we used Primer 6 (version 6.1.11) computer program (Primer-E Ltd., Plymouth, United Kingdom) with the PERMANOVA add-on package (Anderson et al., 2008). Permanova is a mulit-variate permutational analysis of variance designed for community data (Anderson, 2001). We square-root transformed the abundance data from the 32 invertebrate taxa prior to analysis to control for rare taxa and used Bray–Curtis dissimilarities as the distance measure. The between-blocks effects were Day (wholeplot: $n = 11$) and Block ($n = 5$) and the within-blocks effects were Treatment (subplot: $n = 2$) and the Day $\times$ Treatment interaction (Kirk, 1982; Gotelli and Ellison, 2004, Fig. 1). We used 9999 permutations to test the null hypotheses of 1) no difference in BFW communities among Days and Blocks with Day at the wholeplot level, 2) no difference in BFW communities between treatments (pairs) at the subplot level, and 3) no interaction between Treatment and Day (Blocks w. Day) at the subplot level. A significant effect of Treatment was followed by a posteriori univariate Permanovas on the 32 focal invertebrates to determine which invertebrates within communities responded to Treatment effects and calculate their effect sizes.

### 2.6. Testing for diminished responses among predators

We then tested whether trophic position was a good predictor of response with the prediction from the Na bioaccumulation hypothesis that microbi-detritivores but not predators should recruit to +NaCl addition. First, we determined whether microbi-detritivores had a stronger response to +NaCl addition than predators using a t-test to test the null hypothesis of no difference in effect size between microbi-detritivores and 1° predators. We only compared the microbi-detritivores and 1° predators because only 1 invertebrate taxon occupied the 2° predators position (2° predator Hemiptera: Heteroptera, Fig. 2). We used the pseudo-$F$ value (see Anderson, 2001) as effect size from the a posteriori univariate Permanovas on the 31 invertebrate taxa. Effect size ($F$) was normally distributed (Kolmogorov–Smirnov, d.f. = 31, $p$ = 0.166). Second, we tested whether $F$ was a good predictor of group membership and how well it correctly classified invertebrate taxa to their respective trophic position using logistic regression (SPSS v. 10.0). We used $F$ of the 31 invertebrates in microbi-detritivore and 1° predator groups as our predictor variable and our binomial response was yes or no invertebrate is a microbi-detritivore.

We performed a second logistic regression where Collembola was broken into families (Onychiuridae, Hypogastruridae, Sminthuridae, Entomobryidae, Isotomidae) and Predatory mites were broken into Mesostigmatids and Prostigmatids to insure that differences in the taxonomic resolution among invertebrates did not introduce potential bias. These taxa were analyzed as groups in the stable isotope analysis to achieve sufficient mass. We chose these taxa because they were the most abundant in their respective Trophic Positions representing 42% and 27% of microbi-detritivore and predator abundances respectively. Because of their high abundances, these taxa would be the most likely to introduce potential bias when lower taxonomic ranks were grouped.

## 3. Results

We collected 16,367 invertebrates from the 55 paired +NaCl and Control plots. +NaCl plots had more invertebrates (Permanova, $p < 0.0001$). Median total invertebrate were 26 (IQR = 15–68) m$^{-3}$ on +NaCl plots versus 15 (IQR = 7–30) m$^{-3}$ on Control plots. The 32

focal invertebrates spanned 3 Trophic Positions: 15 microbi-detritivores, 16 1° predators, and 1 2° predator (Fig. 2).

### 3.1. Effects of NaCl on BFW composition

The addition of NaCl (Treatment) changed community composition (Within-blocks, Treatment: $p = 0.0127$; Table 1). At the wholeplot level, the community composition also differed among sample days (Between-blocks, Day: $p = 0.0001$), but the effects of NaCl addition on community composition were consistent regardless of the sampling Day (Treatment $\times$ Day: $p = 0.5208$; Table 1). In other words, as is characteristic of a dynamic tropical forest, there was daily variation in community composition for both +NaCl and Control plots, but the magnitude of the Treatment effect between plots remained constant over time (i.e., no interaction).

### 3.2. Do invertebrates lower in trophic position respond more strongly to NaCl?

Microbi-detritivores had a stronger response to +NaCl than 1° predators ($t_{31} = 2.209$, $p = 0.039$). The mean effect sizes ($F$) for microbi-detritivores and 1° predators were 6.8 and 0.4 respectively (Fig. 2). Further, $F$ was a good predictor of trophic position (logistic regression, d.f. = 1, $\chi^2 = 5.153$, $p = 0.023$). The model correctly classified 67.7% of invertebrates to their respective trophic position, and predicts the odds of increasing on +NaCl plots is 1.2 times higher for microbi-detritivores than predators. The second logistic regression with Collembola and Predatory mites analyzed at finer taxonomic resolution (36 taxa total) yielded similar results: the model correctly classified 63.9% of invertebrates to their respective trophic position, with the same odds ratio of increasing on +NaCl plots ($\text{Exp}(\beta) = 1.2$; d.f. = 1, $\chi^2 = 5.281$, $p = 0.022$). These results are further supported by the results of the univariate Permanovas on response of the 32 invertebrates (Fig. 2). As predicted, the majority of invertebrates feeding low in the food web (Microbi-detritivores) increased on +NaCl plots ($p \leq 0.044$; Fig. 2), including each family of Collembola separately ($p \leq 0.027$). In contrast, most 1° predators did not increase on NaCl addition plots. The exceptions to this pattern were Predatory mites (Acari: Mesostigmata and Prostigmata; but when analyzed separately only Prostigmata increased on +NaCl plots), and the ant genera Strumigenys, Hylomyrma, and Solenopsis ($p \leq 0.033$, Fig. 2). The large responses of microbi-detritivores and the small responses of 1° predators support our predictions of how Na-limitation is structured within a food web: large bottom-up effects within the detrital community in response to direct consumer resource provisioning. Additionally, the one 2°

**Table 1**
Results of the split-plot permutational manova in Primer-E with PERMANOVA add-on based on Bray–Curtis dissimilarities for the abundances of 32 invertebrates within an Amazonian brown food web (see Fig. 1 for experimental design). Invertebrate abundance (number of individuals) was analyzed as per volume (m$^{-3}$ = plot area $\times$ litter depth).

| Source | d.f. | SS | MS | Pseudo-$F$ | $p$ |
|---|---|---|---|---|---|
| *Between-block effects (Wholeplot level)* | | | | | |
| Day | 10 | 23,518 | 2351.8 | 3.590 | 0.0001 |
| Blocks w. Day | 4 | 4670.2 | 1167.2 | 1.782 | 0.0009 |
| Residual | 40 | 26,203 | 655.08 | | |
| *Within-block effects (Subplot level)* | | | | | |
| Treatment | 1 | 5619.1 | 5619.1 | 5.884 | 0.0127 |
| Blocks | 54 | 108,780 | 2014.5 | 2.053 | 0.0001 |
| Treatment $\times$ Blocks w. Day | 4 | 3819.8 | 945.94 | 0.973 | 0.5208 |
| Residual | 50 | 49,064 | 981.28 | | |
| Total | 109 | 167,290 | | | |

predator, Heteroptera (Hemiptera), increased on +NaCl plots ($p = 0.021$, Fig. 2).

## 4. Discussion

Sodium has long been known to impact the behavior and performance of individual organisms (Arms et al., 1974; Belovsky and Jordan, 1981; Simpson et al., 2006; Kaspari et al., 2008), but its role in structuring communities had remained unexplored. Here we demonstrated that by using the principles of nutritional ecology at the individual level, we could predict with good accuracy how an entire community should respond to subsidies of a limiting nutrient. Because Na bioaccumulates from plants to predators, heterotrophs low in trophic position like microbi-detritivores rapidly recruited to pulses of NaCl that mimicked urine deposition in a Na-poor forest, whereas predators in general did not (Fig. 2). NaCl addition attracted >33% more invertebrates than Control plots largely driven by microbi-detritivores, which had >6 times the average effect size of 1° predators (Fig. 2), and this pattern remained consistent over time regardless of daily variation in this dynamic tropical forest (Table 1). Further, Trophic Position alone was a good predictor of invertebrate response (effect size: $F$). These results document the strong effects of NaCl additions on a large fraction of the BFW and demonstrate that we can largely predict community composition changes in response to nutrient addition using principles of nutritional ecology pertaining to individual invertebrates.

Although from the Na bioaccumulation hypothesis, predators are not predicted to increase on +NaCl plots from Na-limitation, predictions from classic food web ecology provide an obvious mechanism for predator increase: increases in prey. Our experimental design and time scale were not adequate to test this directly, but three of the four predators that responded were ants, which forage widely and rapidly, and strongly recruit to increased prey availability (Lach et al., 2010). Increased prey may also explain the increase in the only 2° predator, Heteroptera (Hemiptera, including Reduviids, Aradids, and Mirids; Fig. 2). Future studies should combine principles from nutritional and energy-based trophic ecology to fully understand the multiple mechanisms that shape community structure based on resource availability (Simpson et al., 2010).

In contrast to predators, microbi-detritivores strongly recruited to +NaCl plots (Fig. 2). Here we only examined invertebrate response and did not explore changes in the microbial community. Increased microbial necromass or biomass from Na application could be an indirect mechanism for increases in microbi-detritivores. However, microbi-detritivores responded from day 1 and remained consistent over time (Table 1). As such, sustained microbi-detritivore recruitment to microbial necromass seems unlikely as the necromass is finite. While increased microbial biomass may play a role in microbi-detritivore recruitment, numerous studies have used Na-soaked substances and demonstrated that Na itself is sufficient to attract herbivores (e.g., Arms et al., 1974; Barrows, 1974; Kaspari et al., 2008, 2010), and microbi-detritivores would still obtain Na by increasing consumption of salty organisms (e.g., Simpson et al., 2006).

Although microbi-detritivores increased nearly 1.5 fold on +NaCl over Controls plots, a handful of microbi-detritivores had similar abundances between treatments: Psocoptera, Blattaria, Diptera larvae, Lepidoptera larvae, Staphylinidae (Coleoptera), Isopoda, and Pselaphidae (Coleoptera). Together, these invertebrates represented only 5% of the total microbi-detritivore abundance. A suite of mechanisms could potentially cause this pattern such as increased predation pressure, ontogenetic constraints, competitive exclusion, physiological Na adaptations, or a cryptic predatory behavior, among others. However, without testing each specifically, it is impossible to discern the mechanism from our results. But, these exceptions provide opportunities to delve deeper into individual differences in Na physiology and species interactions to better understand when we should and should not predict Na-seeking behavior.

At the time scale of weeks, increases in invertebrates on +NaCl plots most likely arose from immigration rather than population increases. The rapid response of BFW invertebrates in this study suggests that they have evolved to quickly capitalize on ephemeral resources like NaCl pulses. Rapid recruitment of plant consumers to NaCl has also been documented in bees (Barrows, 1974), Lepidoptera (Arms et al., 1974), and ants (Kaspari et al., 2008) among other invertebrates and vertebrates. Na is lost during any metabolic water loss process such as sweating or excretion and these processes increase with temperature (Peters, 1983). Thus, in Na-poor environments, particularly in the hot tropics, short-term Na subsidies are likely vital to consumers maintaining a Na-balance (Dudley et al., 2012). Further experiments investigating the role of urine deposition in structuring BFWs and their ecological functions like decomposition over a gradient of Na availability will contribute to a multi-scale understanding of the patchiness of BFWs.

The increased microbi-detritivores like termites and Collembola on +NaCl plots likely drove the pattern of decreased litter depth with the addition of NaCl. Here we tested Na's effects on food web structure and invertebrate response and controlled for differences in habitat space between treatments, but Kaspari et al. (2009) demonstrated that the addition of Na increases both leaf litter and experimental filter paper decomposition and documented a similar response in termite recruitment to NaCl treated cellulose. The inverse relationship between habitat space and decomposition rates in BFWs—the "more food-less habitat effect" (Shik and Kaspari, 2010; Jacquemin et al., 2012)—suggests a dynamic mix of limiting factors for invertebrates as litter decomposes. Our results and those of Kaspari et al. (2009) demonstrate that even ephemeral patchy Na subsidies can have rapid and large effects on both BFW structure and function in Na-poor environments.

Our study is the first to apply concepts of Na-limitation to entire food webs and it demonstrates how nutritional ecology can provide a predictive framework for community ecology. Over 80% of earth's terrestrial surface is potentially Na-poor as oceanic inputs (i.e., "salty rain") exponentially decrease with distance inland (Stallard and Edmond, 1981; Kaspari et al., 2009, National Atmospheric Deposition Program, 2011). Na should be included as one of the major nutritional resources foci in future research in community ecology, biogeography and classic trophic theory. Lastly, future research should include effects of both short-and long-term Na subsidies on food webs at both macro-and micro-spatial grains to fully understand how Na availability impacts individuals to ecosystem level processes.

6                                    *N.A. Clay et al. / Soil Biology & Biochemistry xxx (2014) 1–6*

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