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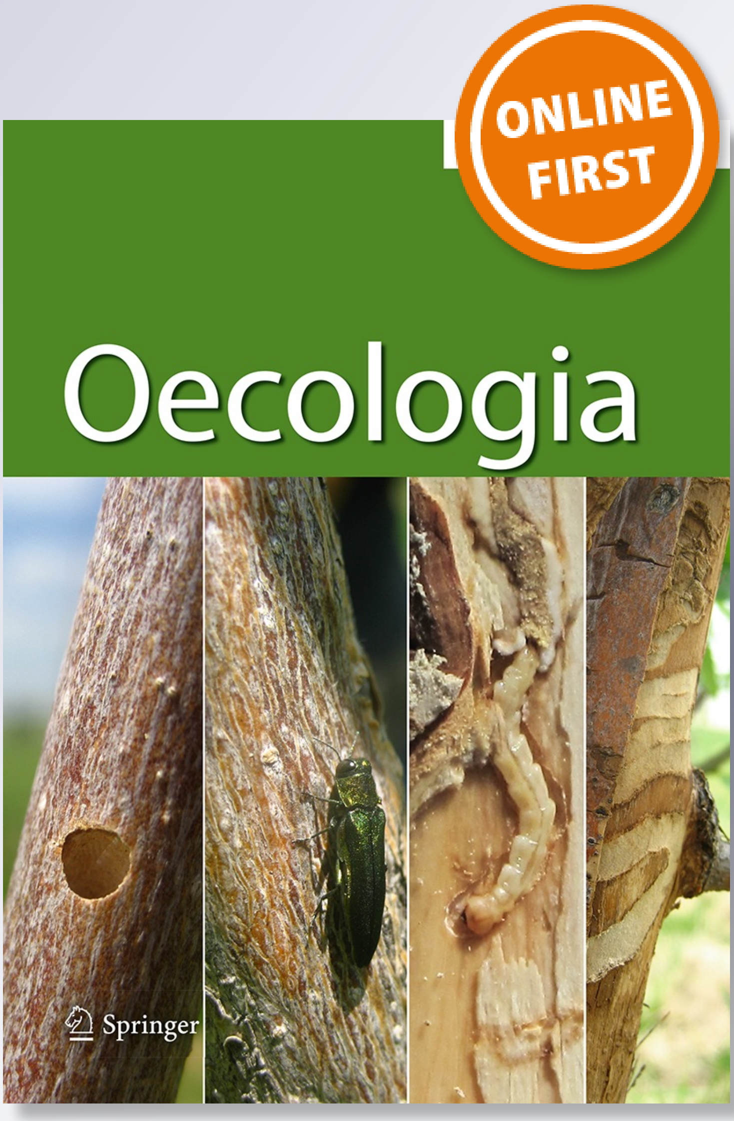
Oecologia

ISSN 0029-8549

Oecologia
DOI 10.1007/s00442-014-3183-4



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ECOSYSTEM ECOLOGY - ORIGINAL RESEARCH

Urine as an important source of sodium increases decomposition in an inland but not coastal tropical forest

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Received: 26 June 2014 / Accepted: 4 December 2014

Abstract Nutrient pulses can profoundly impact ecosystem processes and urine is a frequently deposited source of N and K, and Na. Na is unimportant to plants, but its addition can increase decomposition and change invertebrate community structure in Na-poor tropical forests. Here we used synthetic urine to separate the effects of Na from urine's other nutrients and contrasted their roles in promoting decomposition and detritivore recruitment in both a Na-poor inland Ecuadorian and Na-rich coastal Panamanian tropical forest. After 2 days, invertebrate communities did not vary among +Na, H_2O, Urine+Na, and Urine−Na treatments. But after 2 weeks, Ecuador wood, but not cellulose, decomposition was twofold higher on Urine+Na and +Na plots compared to H_2O and Urine−Na plots accompanied by >20-fold increases in termite abundance on these plots. Panama, in contrast, showed no effect of Na on decomposition. In both forests, plots fertilized with urine had nearly twofold decrease in detritivores after 2 weeks that was likely a shock effect from ammonification. Moreover, the non-Na nutrients in urine did not enhance decomposition at this time scale. On control plots, Panama had higher decomposition rates for both cellulose and wood than Ecuador, but the addition of Na in Ecuador alleviated these differences. These results support the hypothesis that in Na-poor tropical forests, urine can enhance wood decomposition and generate an important source of heterogeneity in the abundance and activity of brown food webs.

Keywords Urea · Nutrient subsidies · Brown food web · Latrine · Landscape heterogeneity · Biogeography · Biogeochemistry · Isoptera

Introduction

Foraging animals influence the quantity and quality of available resources for the microbes, detritivores, and their predators in belowground systems, and can thereby impact decomposition and nutrient mineralization (Fittkau and Klinge 1973; Wardle 2002; Bardgett and Wardle 2003). Herbivores, for example, can affect both the quantity and quality of litterfall inputs to detrital systems (Persson et al. 2000) and can alter resources across the landscape through vegetation trampling (Persson et al. 2000), soil turnover (Eldridge and James 2009), and activities like damming (Wright et al. 2002). Likewise, predators impact the behavior and densities of herbivores that can ultimately

Communicated by Stefan Scheu.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-014-3183-4) contains supplementary material, which is available to authorized users.

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alter decomposition processes (Fortin et al. 2005; Hawlena et al. 2012). But animals also provide some of the most important nutrient inputs to belowground systems via defecation, excretion, and corpses, which supply a direct and often concentrated source of bioavailable nutrients (Steinauer and Collins 1995; Drake et al. 2005; Weiss 2006). The deposition of these organic nutrient sources may alleviate nutrient limitation in otherwise nutrient-poor environments (e.g., McNaughton et al. 1997a).

Urine, in particular, is plentiful in N, K, Na, and to a lesser extent, micronutrients like Ca and Mg (Steinauer and Collins 1995). Its deposition rate can be roughly quantified via metabolic scaling. Urine deposition rates (U; ml 24 h^{-1}) scale to mass (M) as $U = aM^{0.75}$ (Peters 1983; Brown et al. 2004) and animal density (N km^{-2}) scales as $n = bM^{-0.75}$ (Peters 1983). Based on these scaling relationships, a corollary of the energy equivalence rule (Damuth 1981, 2007; Nee et al. 1991) predicts mammal urine deposition as a product of species richness and the two normalization constants: $U = Nab$ (Habeck and Meehan 2008), where $a = 60.85$ (Edwards 1975), and $b = 4.06$ (Ebenman et al. 1995). Thus, a lowland Ecuadorian forest with 199 non-volant, non-domesticated, terrestrial mammal species (InfoNatura 2007) should receive ca. 49 L urine km^{-2} day^{-1}. The nutrients in urine can enhance decomposition (Kaspari et al. 2008a, 2009; Waring 2012) and are relatively rare in many environments (White 1993; Wright et al. 2011; Kaspari et al. 2008b). Thus, urine is likely an important stimulus for detrital food webs and their function.

In particular, urine is a rich source of Na and likely creates Na hotspots in Na-poor environments away from oceanic Na sources (Stallard and Edmond 1981; National Atmospheric Deposition Program 2008). Inland tropical forests are ideal candidates for Na limitation because they are far from oceanic inputs, have high degrees of leaching, and high temperatures increase metabolic Na loss (Peters 1983; Kaspari et al. 2009; Dudley et al. 2012). Plants require and concentrate very little Na in their tissues, but plant consumers concentrate Na ten- to 100-fold above plants for neural function, osmotic balance, reproduction and development (Ganguli et al. 1969; Bursey and Watson 1983; Blumwald et al. 2000; Geerling and Loewy 2008). This stoichiometric disparity between plants and plant consumers drives detritivores, as plant consumers, to seek Na (Schulkin 1991; Geerling and Loewy 2008; Dudley et al. 2012). Previous research demonstrated rapid community and decomposition responses to Na subsidies in inland forests that mimicked patchy urine deposition (Clay et al. 2014, Kaspari et al. 2009); this suggests that these communities have likely evolved to capitalize on urine as a Na subsidy.

Most research has not separated urine into its nutritional components despite urine being a rich source of N, K, Na, Ca, and Mg, all of which can enhance decomposition processes (Steinauer and Collins 1995, 2001; Shand et al. 2000; Kaspari et al. 2008a, 2009; Waring 2012). Further, these nutrients may have additive or synergetic effects on belowground systems when one or more of these nutrients are limiting. Subsequently, the effects of urine deposition on decomposition processes may differ across sites depending on site-specific nutrient availability. For instance, in Na-poor inland tropical forests, urine deposition may enhance decomposition rates significantly more than in Na-rich coastal forests and these effects may be non-additive. Experimental factorial designs that use synthetic urine can discern the relative importance of these nutrients in driving decomposition processes by creating treatments that isolate and exclude specific nutrients.

We investigated the role of urine as a source of nutrients in two tropical forests using synthetic urine to separate the effects of Na from the other nutrients in urine. We tested the hypothesis that urine is an important source of Na for detrital communities and their function in inland but not coastal tropical forests with the predictions that:

1. Because inland detritivores are likely Na limited (Kaspari et al. 2009; Clay et al. 2014), Na addition should increase detritivore abundance in inland but not coastal forests.
2. Na addition should increase decomposition in inland but not coastal forests (e.g., Kaspari et al. 2009).
3. Because urine is also a source of many other bioavailable and often limiting nutrients, the addition of synthetic urine containing Na and all other nutrients may have additive or synergetic effects on detritivore abundance and decomposition.

In both an inland and coastal tropical forest, we document the role of urine as a Na source for communities after one application simulating a migratory mammal, after 2 weeks simulating mammals with excretion site fidelity, and the effects of the other nutrients in urine on detrital communities and their function. Further, we discuss how animal behavioral ecology through urine deposition can impact landscape heterogeneity and ecosystem function.

Materials and methods

Fieldwork was conducted from 4 to 24 June in Barro Colorado Island (BCI), Panama (2009) and Yasuni National Park (YNP), Ecuador (2010), both lowland tropical rainforests. We a priori chose BCI and YNP as likely Na-rich and Na-poor forests based on distance from an ocean (National Atmospheric Deposition Program 2008; Kaspari et al. 2008b, 2009). BCI is a seasonal tropical forest located between two oceans (9°09′N, 79°51′W) receiving ca. 2,600 mm rain annually, the majority of which falls in the rainy season from mid-April to mid-December (Wieder and Wright 1995). The soils are described as Frijoles clay with Alfisols and Oxisols (Windsor et al. 1990). YNP is an aseasonal tropical rainforest located inland, west of the Andes (0°40′S, 76°24′W) that receives ca. 3,000 mm rain annually. The soils are not well described, but have been characterized as Typic Hapludult and Typic Paleudults characterized by clayey, kaolinitic, udic, isohyperthermic, and rich in Al with affinities to Inceptisols and Oxisols in at least one site (Korning et al. 1994).

In each forest, we demarcated 25 blocks of four treatments plots: Na addition (+Na), urine with Na (Urine+Na), urine without Na (Urine−Na), and a control (H_2O), which allowed us to separate effects of Na from those of the other nutrients in urine. Treatment plots within blocks were 0.25 m^2 (0.5 × 0.5 m) and separated by 3 m. Blocks were separated by ≥10 m. We made the synthetic urine the day of addition using the chemical formula from Steinauer and Collins (1995): 13.65 g urea L^{-1}, 0.75 g $MgCl_2{\cdot}6H_2O$ L^{-1}, 0.73 g $MgSO_4{\cdot}7H_2O$ L^{-1}, 0.09 g $CaCl_2$ L^{-1}, 7.02 g KCl L^{-1}, and 6.83 g $KHCO_3$ L^{-1}. In the Urine+Na treatment and the +Na treatment we increased the Na concentration to 5 g NaCl L^{-1}. This concentration mimics the upper range of predator urine Na content (Clarke and Berry 1992) and other Na fertilization research (Kaspari et al. 2008b, 2009; Clay et al. 2014). Prior to fertilization, we placed a polyester 0.75-cm-mesh litterbag containing pre-weighed and folded Whatman no. 1 nine-centimeter circular filter paper (Whatman) for cellulose and wooden dowels that were 11.4 × 0.95 × 0.32 cm (length × width × diameter) white birch (*Betula papyrifera*). We used standard substrates to minimize substrate-derived variation and increase comparability between sites and with other studies (Harmon et al. 1999). Every other day we added 250 ml of each respective treatment solution to treatment plots within each block.

Invertebrate communities

We randomly and destructively harvested five blocks on day 2, and 15 blocks after 2 weeks (days 15, 16, and 17). We harvested the 2-week plots over 3 days due to limited Berlese funnels. Invertebrate communities were unaffected by harvesting day after 2 weeks (Ecuador, $p = 0.267$; Panama, $p = 0.490$), and hereafter we refer to these 15 blocks as one group (2 weeks). We harvested after 2 days (one fertilizer application) to examine rapid effects that simulate a migratory mammal with patchy and ephemeral urine deposition. Plots harvested after 2 weeks simulated mammals with excretion site fidelity like many primates (Feeley 2005). We harvested the detrital invertebrates on each plot by collecting leaf litter down to the topsoil into a sifter with a 1-cm^2 metal mesh. We discarded the coarse leaf litter such as leaves and twigs above the metal mesh, and retained the "siftate" that contained the invertebrate communities within the fine leaf litter material that passed through the 1-cm^2 mesh (Bestelmeyer et al. 2000). We recorded the volume of the siftate and transferred a random 400-ml subset of each siftate to Berlese funnels through which invertebrates were extracted into 95 % ethanol over 24 h. We tested the null hypothesis of no difference in the community structure within blocks among treatments for 21 focal invertebrate taxa (Electronic supplementary material) on day 2 and after 2 weeks using a blocked permutational multivariate ANOVA (PERMANOVA) (Anderson 2001) in PC-ORD version 6 (McCune and Mefford 1999) with 9,999 permutations [see Anderson (2001) for a detailed description of PERMANOVA]. When we rejected the null hypothesis, we used a blocked indicator species analysis (PC-ORD) to determine which invertebrates differed among treatments.

Decomposition

We harvested litterbags from 20 blocks after 2 weeks. We included the additional five blocks to increase power in detecting treatment effects on decomposition, which is often highly variable. We did not examine decomposition after 2 days because this is insufficient time and sample size to detect effects. After harvesting litterbags, we gently rinsed substrates of debris, dried them at 60 °C until weight stabilized, and reweighed them. We used percent mass loss as our dependent variable and we tested the null hypothesis of no difference in substrate percent mass loss (both cellulose and wood) within blocks among treatments after 2 weeks. We used a blocked PERMANOVA in PC-ORD with 9,999 random permutations. We followed significant differences in decomposition among treatments with a posteriori ANOVAs.

Results

Invertebrate communities

After 2 days invertebrate communities were similar among all treatments in both Ecuador (treatment, $p = 0.819$; block, $p = 0.245$) and Panama (treatment, $p = 0.069$; block, $p = 0.0002$; Table S1). After 2 weeks, the detrital communities differed among treatments (Ecuador, treatment, $p = 0.0001$; block, $p = 0.0042$; Panama, treatment, $p = 0.0309$; block, $p = 0.0009$; Table S2). In both forests, detrital invertebrate abundance was similar between control and +Na plots, but decreased nearly twofold on plots that were fertilized with urine (Urine+Na and Urine−Na;

Figs. 1, 2). Seven taxa differed with treatment in Panama (Fig. 1), and six in Ecuador (Fig. 2).

Termites in Ecuador were a conspicuous exception to the above pattern. Inland Ecuadorian termites only recruited to plots that were fertilized with Na (Urine+Na and +Na plots; Fig. 2). Conversely, termites did not differ among treatments in coastal Panama.

Decomposition

The Panama and Ecuador forests differed in their decomposition rates; specifically, median decomposition rates on control plots were 1.5- and 1.4-fold higher for cellulose and wood respectively in the coastal Panama forest compared to the inland Ecuador forest (Mann–Whitney test, cellulose, $n = 20$, $U = 110$, $p = 0.015$; wood, $n = 20$, $U = 20$, $p < 0.001$; Fig. 3). Median cellulose mass loss after 2 weeks was 21.1 and 14.2 % for Panama and Ecuador respectively, and wood mass loss was 11.4 and 8.2 %. Adding Na alone eliminated the differences between the two forests (cellulose, $n = 20$, $U = 168$, $p = 0.387$; wood, $n = 20$, $U = 188$, $p = 0.745$; Fig. 3). This was not the case when Na was added with the other nutrients in urine, although differences were smaller (cellulose, $U = 127$, $p = 0.048$; wood, $U = 116$, $p = 0.023$).

Within Ecuador, wood decomposition was nearly twofold greater on Urine+Na and +Na plots than on Urine−Na or control plots after 2 weeks (treatment, $p = 0.007$; block, $p = 0.189$; Table S3; Fig. 3). Contrary to our prediction, cellulose decomposition was consistent among treatments (treatment, $p = 0.221$; block, $p = 0.027$; Fig. 3). This was not the case in Panama where 2 weeks of fertilization had no effect on decomposition for either wood (treatment, $p = 0.115$; block, $p = 0.356$) or cellulose (treatment, $p = 0.268$; block, $p = 0.214$; Table S4; Fig. 3).

Discussion

Here we demonstrated that urine is an important source of Na for inland tropical detrital systems. Both BCI, Panama and YNP, Ecuador are species-rich tropical forests (InfoNatura 2007), but BCI receives significant Na deposition from oceanic aerosols, and YNP does not (Stallard and Edmond 1981; National Atmospheric Deposition Program 2008; Kaspari et al. 2008b). Adding synthetic urine containing Na to the detrital system in Ecuador increased median wood decomposition nearly twofold above control and Urine−Na plots (Fig. 3). These decomposition effects were similar to those of just Na addition (Fig. 3), suggesting that the Na in urine drove these results. Termites increased >20-fold on plots containing Na in Ecuador (+Na and Urine+Na; Fig. 2). No other invertebrates responded to the Na treatments (Fig. 2). In contrast, the addition of Na as NaCl or in urine had no effects on decomposition or detrital community structure in coastal Panama as predicted (Figs. 1, 3). Contrary to our predictions, urine addition with or without Na decreased detrital invertebrate abundance twofold in both Ecuador and Panama despite the bioavailable N, K, and micronutrients in urine. Our results support the hypotheses that inland but not coastal tropical forests are Na limited, and that urine is an important source of Na in Na-poor forests.

Plant consumers in inland tropical forests experience Na shortfalls in at least three ways: in their diet [Na-poor plants (Stamp and Harmon 1991)]; in environmental availability [Na-poor tropical forests (Stallard and Edmond 1981)]; and through temperature-enhanced metabolic Na loss (Peters 1983). This generally drives rapid Na-seeking behavior (Arms et al. 1974; Barrows 1974; Kaspari et al. 2008b). For example, Clay et al. (2014) found that detritivores strongly recruited to Na addition after just 1 day in an interior Peruvian forest near Iquitos. Accordingly, we expected to see similar responses from detritivores on +Na and Urine+Na treatments in inland Ecuador after 2 days, but communities were unaffected by treatment. Flooding regularly occurs at YNP and these frequently flooded soils have high concentrations of cations including Na^+ (Tuomisto et al. 2003), which may alleviate strong Na limitation at YNP. A comparison of soil cations between YNP, Ecuador and the Iquitos-Pebas region, Peru clearly demonstrates higher concentrations of cations in soils at the former (Vormisto et al. 2004) and may explain why we did not see evidence of Na limitation for the majority of detritivores in Ecuador.

Contrary to our predictions, urine addition did not enhance decomposition in either forest after 2 weeks (Urine+Na and Urine−Na treatments; Fig. 3; Tables S3, 4), and these plots had twofold decreases in detrital invertebrate abundance (Figs. 1, 2; Table S2). This was likely a "shock effect" to NH_3 production from urea hydrolysis (Marshall 1974). Initial reductions in soil fauna after urea application are commonly reported and followed by rapid recoveries at as early as 4 weeks (Marshall 1974; Lohm et al. 1977). Natural latrines are typically nutrient-rich sites where nutrient mineralization and decomposition occur rapidly and shock effects are likely insignificant because cell-free ureases can accumulate in areas of frequent urine deposition and accelerate mineralization (McNaughton et al. 1997b; Dos Santos et al. 2010). It is likely that we would have seen increased invertebrate abundance and enhanced decomposition on urine-fertilized plots had we sampled after a longer period. Alternatively, N input from urine may have little impact on decomposition because many lowland tropical forests are already N rich (Robertson

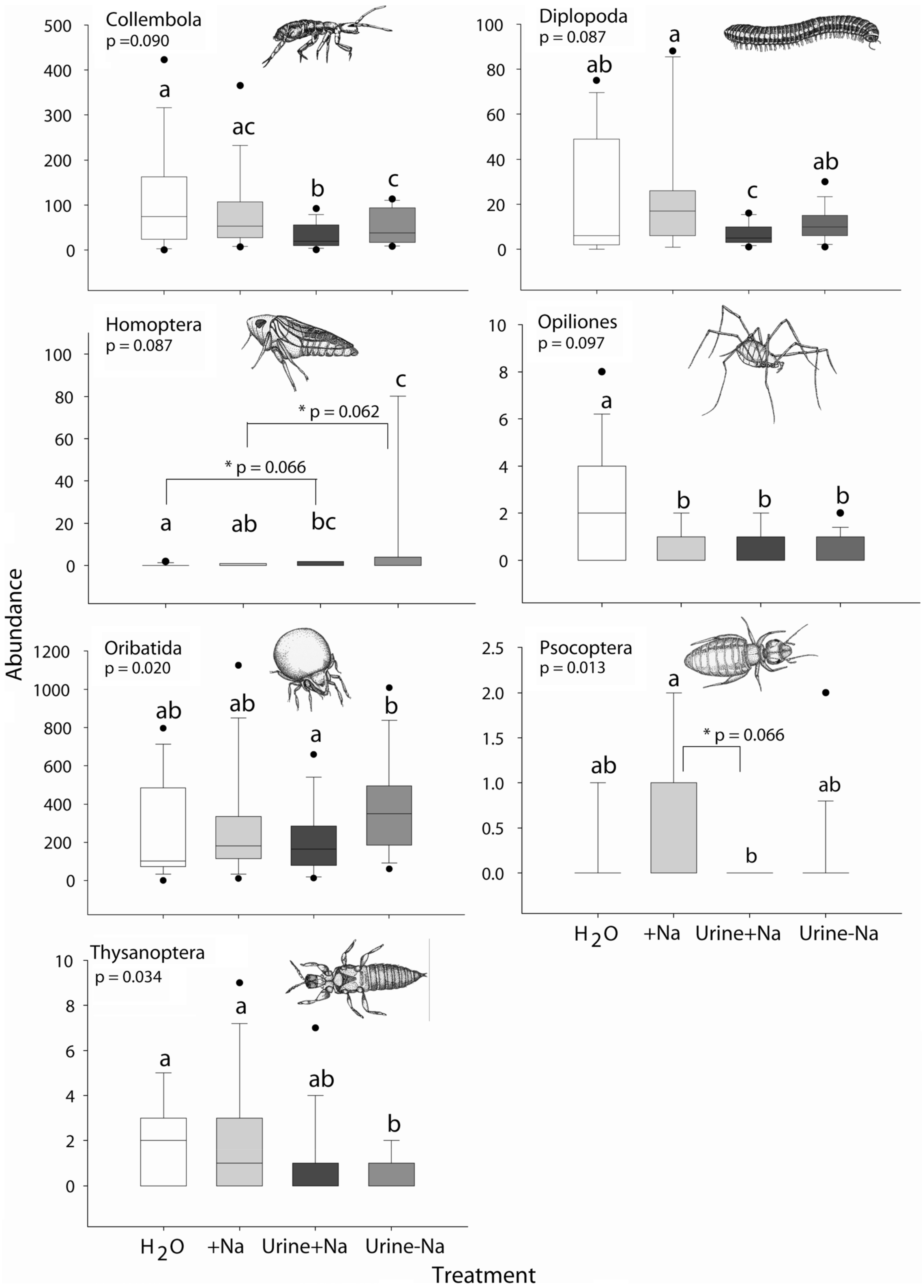

Fig. 1 The results of the blocked indicator species analysis showing the abundances of the seven Panamanian invertebrate taxa that differed among treatments after 2 weeks. Treatments: control (*H_2O; white*), NaCl additions (*+Na*; *light grey*), Urine+Na (*dark grey*) and Urine−Na (*medium grey*). Illustrations by Natalie Clay

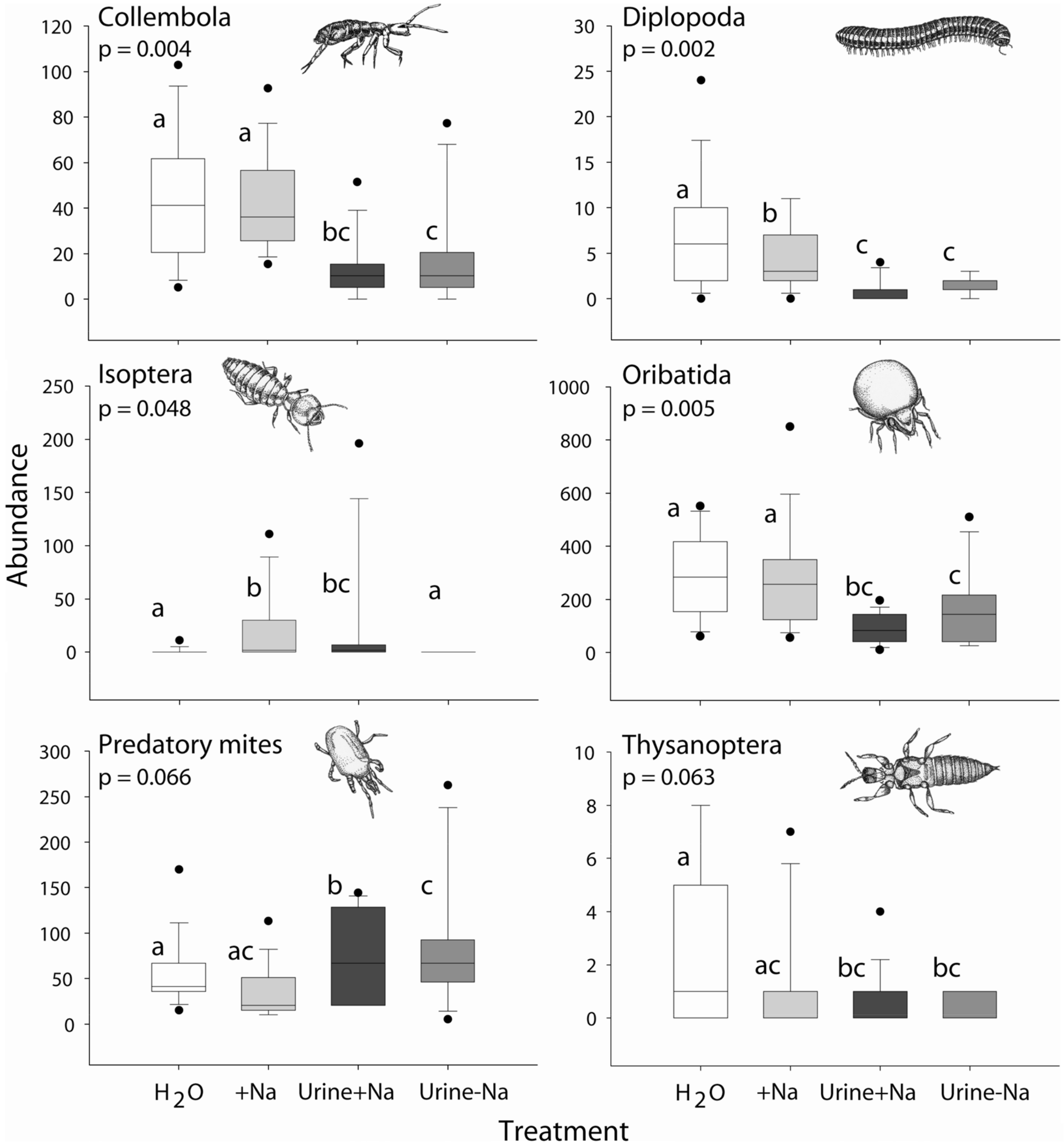

Fig. 2 The results of the blocked indicator species analysis showing the abundances of the six Ecuadorian invertebrate taxa that differed among treatments after 2 weeks. Treatments: control (*H*$_2$*O; white*), +Na (*light grey*), Urine+Na (*dark grey*) and Urine−Na (*medium grey*). Illustrations by Natalie Clay

and Vitousek 1981; Kaspari et al. 2008a; Sayer et al. 2012). The leaf litter landscape is heterogeneous and patchy N input from urine may be more or less stimulatory based on soil chemistry and types. Further investigation into mammalian excretion patterns and short- and long-term effects of urine deposition in tropical forests are needed.

As predicted, decomposition increased with the addition of Na in inland Ecuador (+Na and Urine+Na treatments; Fig. 3; Table S3), and was accompanied by >20-fold increases in termites (Fig. 2). Termites in Ecuador recruited to Na despite potential NH_3 toxicity on Urine+Na plots, whereas coastal Panamanian termites did not differ among treatments. Kaspari et al. (2009, 2014) also demonstrated strong recruitment of termites to Na addition in inland tropical forests while investigating Na limitation of decomposition, and hypothesized that termites drove the enhanced decomposition rates. The termites collected in this study were *Nasutitermes* and *Reticulitermes*, both of which are wood-feeding termites (Jones and Eggleton 2011), and wood within litterbags on Na-fertilized plots had conspicuous termite tunneling and was often covered in termites (N. A. Clay, personal observation). This suggests that

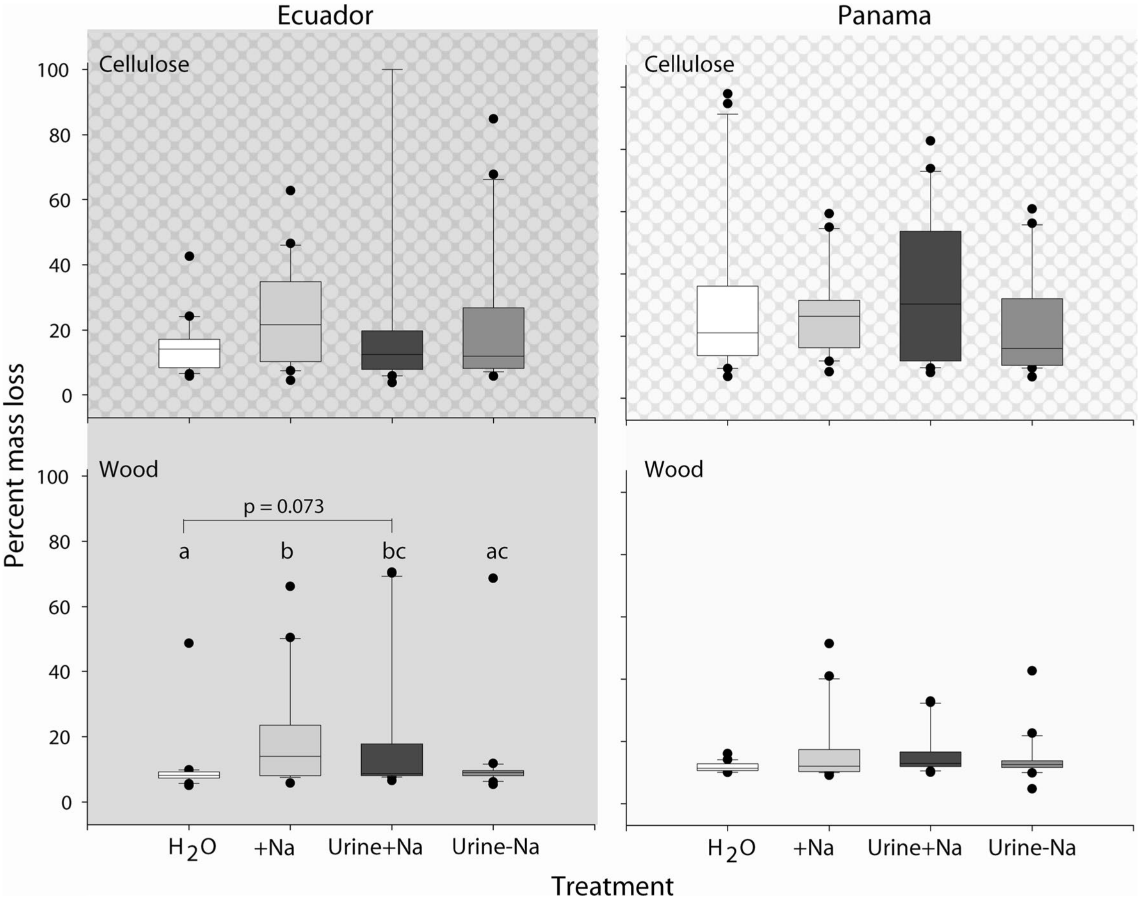

Fig. 3 Decomposition results for inland Ecuador (*left dark panels*) and coastal Panama (*right light panels*). Within each forest are the wood (*lower untextured panels*) and cellulose (*upper textured panels*) decomposition after 2 weeks of fertilization. Treatments: control (*H_2O; white*), +Na (*light grey*), Urine+Na (*dark grey*) and Urine−Na (*medium grey*)

our enhanced wood mass loss on plots fertilized with Na resulted from termite recruitment to, and consumption of, the salted wood (Figs. 2, 3). Wood-feeding termites may have a higher Na demand than other detritivores because lignin fermentation by their symbionts is a Na-intensive process (Yoshimura et al. 2002; Boiangiu et al. 2005). If wood-feeding termites are tracking Na sources and increasing wood consumption in the presence of Na, this could have important implications for C cycling and pest management across micro- and macro-geographies of Na availability.

When organisms are nutrient limited, they often suffer performance deficits (Arms et al. 1974; Sterner and Elser 2002). Decomposition of cellulose and wood was 50 and 40 % higher respectively in coastal Panama than inland Ecuador. However, the addition of Na (+Na treatment) alleviated these differences, but not for Urine+Na treatments—likely because of the ephemeral shock effect. Given sufficient time, urine deposition should have the same or even enhanced effects (from urine's other nutrients) on decomposition in inland tropical forests as +Na treatments. These results support the hypothesis that Na shortages slow the degradation of cellulose and lignin and promote C storage, ultimately constraining the C cycle in inland tropical forests (Kaspari et al. 2009, 2014). Increased replications of this design in more paired forests and across longer timeframes will provide a better understanding of urine's role as a Na source for inland detrital food web structure and function.

These decomposition results would likely be similar for natural dead organic material. One possibility is that contrary to the results we found with filter paper, the nutrients in local leaf litter may interact with those in urine and increase its palatability for microbes and detrital invertebrates. However, termites seemed to recruit to wood rather than cellulose, in which case, termite and urine interactions may impact coarse woody debris in inland tropical forests. A growing body of literature supports termite lust for salt (Kaspari et al. 2009, 2014; Clay et al. 2014), and termites are often important drivers of coarse woody debris decomposition, particularly in tropical forests (Lavelle et al. 1993). Thus, mammal selection of excretion sites could have a significant impact on the rates of coarse woody debris decomposition and nutrient cycling in tropical forests via termite recruitment and activity. If mammals excrete preferentially on or around fallen trees or branches, then where mammal densities are highest, coarse woody debris standing stock may be lower and wood average decay stage later than where mammals are less abundant.

Together, our results suggest that mammals act as nutrient conduits between above- and belowground processes through urine deposition and that urine is an important source of Na in inland tropical forests shaping forest floor heterogeneity and ecosystem function. Our results further supported the hypothesis that Na limitation constrains the C cycle of inland tropical forests likely due in part to Na limitation of wood-feeding termites. Thus, patchy and long-term urine deposition can increase detritivore abundance and activity creating hotspots of productivity on the tropical forest floor. Understanding mammal behavioral ecology can increase our understanding of how tropical forest ecosystems function and patterns of landscape heterogeneity.

Acknowledgments We thank D. Flatt, K. Tholt, J. Burks and D. Rinehart for help in the laboratory. Special thanks to N. Velasco and T. Zumbusch, who were invaluable in the field. We also thank Oris Acevedo and Belkys Jiménez and Smithsonian Tropical Research Institute staff on BCI, Panama, and ANAM for permit SEX/AP-3-09. Miguel Rodriquez and Alvaro Barragán provided logistical help in Quito and Yasuni. We thank the Ministerio de Ambiente del Ecuador for research permit 0020-2010-IC-FUN-DPO-MA. All experiments comply with the current laws of the countries in which the experiments were performed. Funding was provided from NSF DEB-0948762 (principal investigator M. Kaspari).

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