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Towards a geography of omnivory: Omnivores increase carnivory when sodium is limiting

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Abstract

1. Towards understanding the geography of omnivory, we tested three hypotheses that predict the proportion of animal tissue consumed: the sodium limitation hypothesis predicts that omnivores increase animal consumption in Na-poor environments because Na bioaccumulates from plants to predators; thus, heterotrophs are Na-rich sources. The nitrogen limitation and habitat productivity hypotheses use the same logic to predict more animal consumption in N-poor and productive environments respectively.

2. Omnivory is a common trophic strategy, but what determines the balance of plant and animal tissue omnivores consume is relatively unexplored. Most of what we know comes from single populations at local scales. Here we quantitatively test these three hypotheses at a large geographic scale and across 20 species of omnivorous ants.

3. We tested each hypothesis using N stable isotopes (δ^{15}N) to quantify the degree of carnivory in ant populations in 20 forests that span 12° latitude from Georgia to Maine, USA. We used the difference in δ^{15}N between 20 ant conspecifics in 10 genera between two paired forests (10 pairs of 20 forests) that consisted of a coastal and inland forests on the same latitude to determine if the proportion of animal tissue consumed could be predicted based on Na, N or net primary productivity.

4. Sodium gradients accounted for 18% of the variation in δ^{15}N, 45% if one outlier ant species was omitted. In contrast, the nitrogen limitation and habitat productivity hypotheses, which predict more animal consumption in N-poor and more productive environments respectively, failed to vary with δ^{15}N.

5. Our results reveal a geography of omnivory driven in part by access to Na.

KEYWORDS

ants, biogeography, nutritional ecology, stable isotopes, trophic ecology

1 | INTRODUCTION

Omnivory, once thought to be rare, is now recognized as common in most ecosystems (Digel, Curtsdotter, Riede, Klarner, & Brose, 2014). Omnivory is here defined as the consumption of both plant and animal tissue, the latter via scavenging, carnivory or predation. As omnivory increases in a community, so can food chain length, food web resilience and resistance, and linkages between food webs across the landscape (McCann & Hastings, 1997; Sprules & Bowerman, 1988; Vanni et al., 2005). While the ecological consequences of omnivory have long been studied, we still know relatively little about what drives its distribution. Omnivore diets are plastic (Sinia, Roitberg, Mcgregor, & Gillespie, 2004), and a variety of factors can increase an omnivore's prey consumption: reproductive demands and ontogenetic increases

in size and life stage (Dam, Peterson, & Bellantoni, 1994), limiting nutrients (Denno & Fagan, 2003), plant defences (Agrawal, Kobayashi, & Thaler, 1999) and competition (Brabrand, 1985). However, ecology still lacks a general theory for predicting spatial and temporal variation in the balance of plant and prey that omnivores consume. Towards developing a biogeography of omnivory, we investigated the explanatory power of three hypotheses centred on abiotic drivers of the relative proportion of plants to prey eaten by omnivores across the landscape.

1.1 | The sodium limitation hypothesis

Sodium is relatively unimportant for plants but critical for consumers. Plants concentrate very little Na in their tissues, but heterotrophs concentrate Na up to 100-fold more than plants in order to maintain neural function, osmoregulation, reproduction and development (Geerling & Loewy, 2008; Schulkin, 1991). The stoichiometric

disparity between plants and herbivores has resulted in a variety of adaptations to acquire Na such as puddling, visiting mineral licks and consuming low energy but salty plants (Botkin, Jordan, Dominski, Lowendorf, & Hutchinson, 1973; Dudley, Kaspari, & Yanoviak, 2012; Schulkin, 1991). Omnivores achieve Na tissue concentrations that are intermediate between herbivores and predators (Schowalter, Webb, & Crossley, 1981); this trophic bioaccumulation of Na renders heterotrophs as abundant sources of Na (Kaspari, Yanoviak, & Dudley, 2008). The sodium limitation hypothesis predicts that omnivores increase prey consumption when Na is scarce (e.g. Simpson, Sword, Lorch, & Couzin, 2006; Figure 1).

1.2 | The nitrogen limitation hypothesis

Nitrogen is essential to both plants and animals, but is less abundant in plant tissue: the C:N ratio of plants is $c.$ 38 compared to 6 in
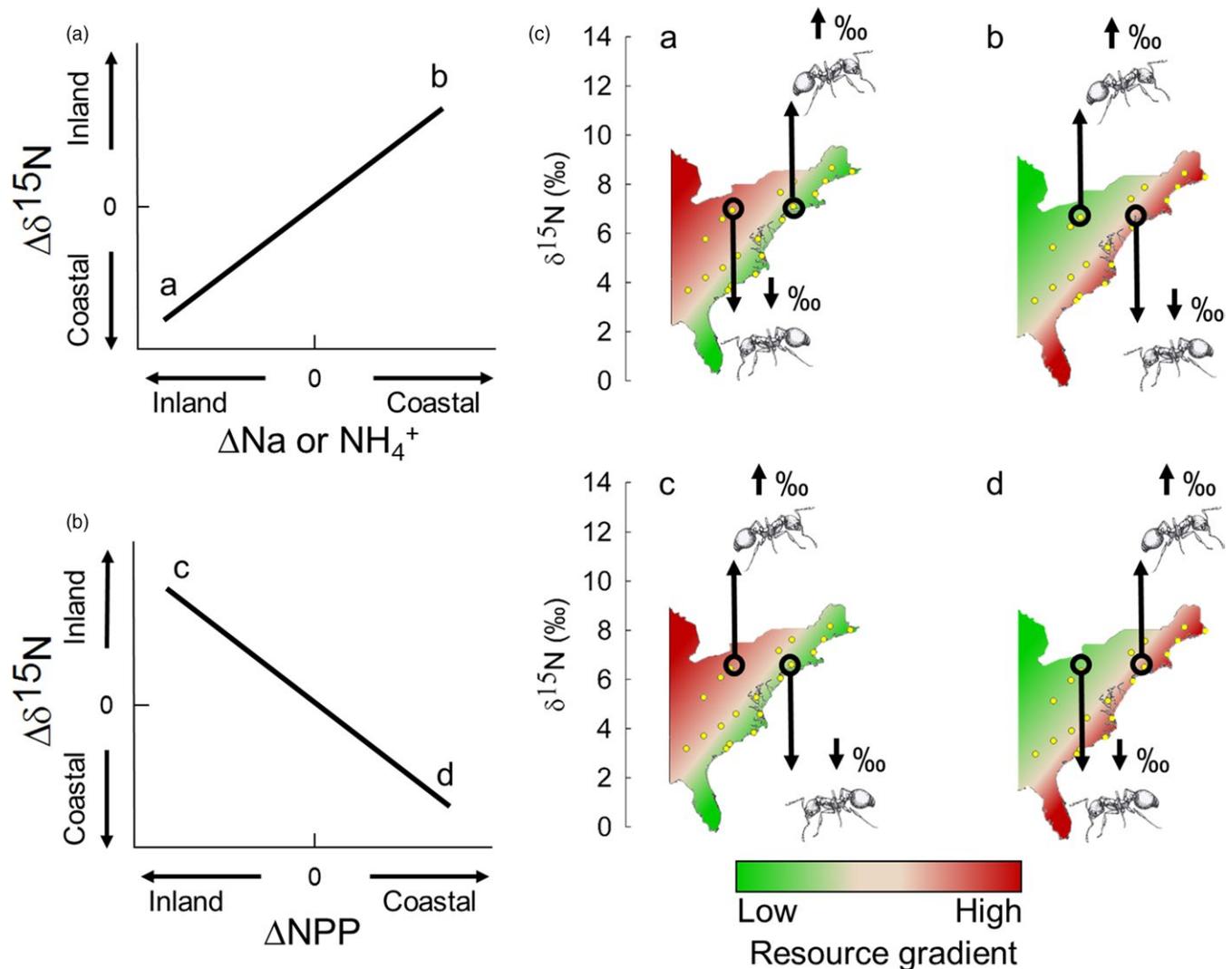

FIGURE 1 Predictions of the sodium limitation, nitrogen limitation (a) and energy limitation (b) hypotheses with regard to $\Delta\delta^{15}$N of conspecific ants between paired forests. Letters on prediction curve correspond to schematic representations of the predictions for ant δ^{15}N at coastal and inland sites (c). In c, gradient represents a generic low (green) to high (red) values of Na, NH_4^+ or net primary productivity (NPP), arrows from forest site pairs indicate the relative trophic position (δ^{15}N) of conspecific ants at each site (yellow dots) with respect to resource availability. Ant drawing by Natalie Clay

herbivores and 4 in predators driven by increased N content (Denno and Fagan, 2003; Matsumura et al., 2004). This trophic bioaccumulation of N suggests N-limitation is structured as: plants > herbivores > predators (White, 1993). Omnivores have N tissue concentrations that are intermediate between herbivores and predators (Matsumura et al., 2004). Plant N concentrations are typically low and also vary depending on the environment and soil N content (Deans, Behmer, Fiene, & Sword, 2016; Joern, Provin, & Behmer, 2012). The nitrogen limitation hypothesis predicts that omnivores increase prey consumption in N-poor environments (Figure 1).

1.3 | The habitat productivity hypothesis

Increases in the available energy of ecosystems (net primary productivity: gC m^{-2} year^{-1}) are often accompanied by increases in species richness, the number of trophic levels and food chain length (Kaspari, O'Donnell, & Kercher, 2000; Oksanen, 1990). The opportunity for omnivory (to feed on both plant and heterotrophs) thus increases with net primary productivity (NPP). The habitat productivity hypothesis predicts that increases in NPP (and thus carbohydrates) should provide the energy to support increased prey consumption by omnivores (Figure 1).

Ants are a model system for examining the geography of omnivory: they are ubiquitous, ecologically important, and although they occupy a diversity of trophic positions, they are mainly omnivores (Davidson, 2005; Hölldobler & Wilson, 1990; Kaspari et al., 2000; Wilder, Holway, Suarez, LeBrun, & Eubanks, 2011). Ants are easily manipulated in laboratory studies, and consistently implicated as indicators of Na-limitation, N-limitation and productivity (Davidson, 2005; Kaspari et al., 2000; Kaspari, Yanoviak, et al., 2008). Moreover, the trophic behaviour of ant populations varies across communities (Resasco, Porter, Sanders, & Levey, 2014; Wilder et al., 2011).

Here we use N stable isotope analysis to quantitatively compare the degree of carnivory in conspecific ants from paired forests. We test these three hypotheses towards exploring the underlying mechanisms driving the geography of omnivory. We used a field study that examined patterns of omnivory in 20 forests over 12° latitude (Figure 1) to identify a possible mechanism that could drive increased prey consumption by omnivores.

2 | MATERIALS AND METHODS

From 21 May to 22 July 2012, we sampled ants at 20 paired lowland forests from Georgia to Maine (n = 10 pairs; Figure 1). A pair consisted of one coastal and one inland forest on the same latitude, but 10–50 km and 200–400 km from the coast respectively (see Appendix S1; Table S1 for forests and coordinates). Restricting locations to the east coast of the USA maximized the likelihood of collecting conspecifics, and limited other potentially confounding abiotic variables such as historic factors. The sampling sites represented a broad geographic range (c. 12° latitude) that spanned multiple abiotic gradients, but the paired design allowed us to separate latitudinally

correlated effects from differences in Na, NH$_4^+$ and NPP between paired sites.

At each site, we laid twelve 100-m transects of one hundred 2.0-ml microcentrifuge vials between 10:00 and 17:00 hr. Just prior to deployment, each vial was half filled with cotton and soaked in solution until the cotton was saturated. The excess solution poured out, vial snapped shut, and the outside rinsed. Solutions consisted of: NaCl at 0.1%, 0.5% and 1.0% wt/vol; sugar at 1.0%, 5.0% and 10.0% wt/vol; and H$_2$O as controls. Sugar is phagostimulant for ants, and sugar usage was used as an indication of activity levels, while NaCl usage indicated the extent of Na-limitation (e.g. Kaspari, Yanoviak, et al., 2008). Each transect consisted of 15 vials of each NaCl and sugar concentration and 10 vials of H$_2$O. Upon deployment, one random vial was placed every metre with the cap open. After 1 hr, vials and ants were collected by snapping shut the vial with ants inside. This standardized ant collection while sampling a broad spectrum of ants in a short time. We identified the ants collected in vials to the species level and stored them in 35% by weight NaCl solution on ice.

For statistical analysis of bait usage, we used "hits" (number of vials that had at least one ant in it) rather than abundance (number of ants in a given vial) as the dependent variable, because strength of ant recruitment to resources is species-specific and the huge size variation among ants impacts the number of ants that can fit in a vial (e.g. *Camponotus* vs. *Monomorium*). We tested for differences in ant species composition between the 10 paired sites (pairs = coastal and inland forests on same latitude; 20 total forests) to account for any systematic differences in species based on geographic distance from the coast. We used a blocked PERMANOVA (Anderson, 2001) in PC-ORD (McCune & Mefford, 1999) and 9,999 permutations to test the null hypothesis of no difference in ant species composition between paired coastal and inland forests. Paired forests (n = 10) were used as the blocking factor with Bray–Curtis dissimilarities as the distance measure.

From each site we collected leaf litter, which was dried in the field and stored with drierite. We chemically analysed leaf litter samples (n = 4 per forest) for Na$^+$, NH$_4^+$ and NO$_3^-$, and additionally measured Total N, Total C, ADF (acid detergent fibre), ADL (acid detergent lignin), P, Ca, K, Mg, S, Fe, Zn, Cu and Mn to test for biogeochemical differences between paired forests (see methods from The Soil Analytical Laboratory at OSU, Stillwater, OK, USA). We tested the null hypothesis of no difference in leaf litter chemistry between paired forests using a blocked (by pairs: n = 10 pairs) PERMANOVA and 9,999 permutations of the data based on Euclidean distances.

We used stable isotope analysis to quantify trophic position of conspecific ants. N isotope values are reported using delta notation (δ^{15}N) where $\delta = ((R_{sample}/R_{standard}) - 1) \times 1,000$; 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). Nitrogen stable isotopes were analysed using a Finnigan Delta Plus mass spectrometer (Thermo-Finnigan) in the Stable Isotope Laboratory of the University of Georgia Odum School of Ecology. δ^{15}N values and precision were determined using a bovine protein (peptone) laboratory standard referenced against the international standard of atmospheric

nitrogen. Nitrogen stable isotope precision was ±0.08‰ ($n = 8$). To control for spatial variation in baseline $\delta^{15}N$, we used average $\delta^{15}N$ values from each forest's leaf litter ($n = 2$) as a baseline for isotope values for forests (Ponsard & Arditi, 2000; Post, 2002; Tillberg, McCarthy, Dolezal, & Suarez, 2006). We used average $\delta^{15}N$ for ant species in each forest so a given species is only represented once per forest.

Precipitation can impact omnivore $\delta^{15}N$ values in two ways: (1) during low precipitation, omnivores may increase their relative consumption of plants to alleviate water stress (Sinia et al., 2004) and (2) water-stressed animals often conserve water by concentrating urine, which alters N fractionation and enriches animals in $\delta^{15}N$ (Ambrose & DeNiro, 1986). We tested these two predictions and found that water-limited ants had higher $\delta^{15}N$ in dryer forest pairs (linear regression: $R^2 = 0.187$, $p = .006$; see Appendix S1; Figure S1). Thus, we rejected the former and accepted the latter: precipitation changes N fractionation. We accounted for potential water stress-derived variation in $\delta^{15}N$ by using the residuals from this regression to test the three hypotheses below.

2.1 | Testing the sodium limitation hypothesis

The terrestrial availability of Na is broadly determined through oceanic aerosol deposition (i.e. salty rain), which results in little or no oceanic Na input in land-locked environments (Botkin et al., 1973; National Atmospheric Deposition Program, 2012a). However, this pattern is not without exceptions, so we used $\%Na^+$ in leaf litter samples to determine Na availability for each forest. We used Wilcoxon signed ranks test to test the assumption that increased ant use of Na baits is a result of Na-limitation and not increased activity (determined by sugar use between paired forests). If per cent ant use of Na is greater in the Na-poor paired forests, but sugar use does not vary between pairs, then we can reject the null hypothesis of no difference in Na-limitation between paired forests.

If Na-limitation drives increased carnivory, then the difference (inland-coastal) in the average $\delta^{15}N$ values ($\Delta\delta^{15}N$) between conspecific ants in paired coastal and inland forests should be related to the difference (coastal-inland) in Na availability (ΔNa) between paired forests (Figure 1). $\Delta\delta^{15}N$ is a measure of trophic shift or change in the relative consumption of plants:prey between conspecifics. We used linear regression to test the null hypothesis of no difference in conspecific $\delta^{15}N$ values ($\Delta\delta^{15}N$) between paired forests ($n = 10$ pairs) with different Na availability (ΔNa). If as the ΔNa increases (regardless of which paired forest was saltier), $\Delta\delta^{15}N$ of conspecific ants increases (ants in the Na-poor forest have higher $\delta^{15}N$ values relative to conspecifics in the Na-rich pair), then this supports Na-limitation driving increased carnivory by omnivores (Figure 1).

2.2 | Testing the nitrogen limitation hypothesis

NH_4^+ and NO_3^- deposition is largely determined by rain patterns around industrial and agricultural areas, and NH_4^+ and NO_3^- are both bioavailable forms of N (National Atmospheric Deposition Program, 2012b; Paerl et al., 2001). We used NH_4^+ and NO_3^- (p.p.m.) in leaf litter samples

to determine NH_4^+ and NO_3^- availability. We first tested whether NH_4^+, NO_3^- and Na^+ availability were correlated using partial correlation analysis. NH_4^+ and NO_3^- were uncorrelated with Na^+ ($p = .120$ and .090 respectively), but correlated with each other (Pearson correlation = 0.865, $p \leq .001$). We therefore used only NH_4^+ as it had the highest explanatory power and least correlation with Na^+.

We used linear regression to test the null hypothesis of no difference in conspecific $\delta^{15}N$ values ($\Delta\delta^{15}N$: inland-coastal) between paired forests ($n = 10$ pairs) differing in NH_4^+ availability (ΔNH_4^+: coastal-inland). If as the ΔNH_4^+ increases (regardless of which paired forest was more N-rich), $\Delta\delta^{15}N$ increases (ants in N-poor forests have higher $\delta^{15}N$ values relative to conspecifics in the N-rich pair), then this supports N-limitation driving increased carnivory by omnivores (Figure 1).

2.3 | Testing the habitat productivity hypothesis

If NPP drives increased heterotroph consumption, then the difference in conspecific $\delta^{15}N$ values ($\Delta\delta^{15}N$: inland-coastal) should vary with ΔNPP (coastal-inland; Figure 1). We used ArcGIS v. 10.2 to extract NPP values (gC m^{-2} $year^{-1}$) for each forest site from the Moderate-Resolution Imaging Spectroradiometer (MODIS) MOD17 30-arcsec (1 km spatial resolution) data for September 2011 to August 2012.

We used linear regression to test the null hypothesis of no difference in conspecific $\Delta\delta^{15}N$ between paired forests ($n = 10$ pairs) differing in productivity (ΔNPP). If as the ΔNPP increases (regardless of which paired forest was more productive), $\Delta\delta^{15}N$ decreases (ants in the more productive forest have higher $\delta^{15}N$ values relative to conspecifics in the less productive paired forest), then this supports productivity driving increased prey consumption by omnivores (Figure 1).

Diet and $\delta^{15}N$ are plastic, but because we used multiple species to test each hypothesis and the amount of plasticity could be constrained by phylogeny , we tested for phylogentic signal. We took the chronogram from Moreau, Bell, Vila, Archibald, and Pierce (2006), pruned it to the 10 genera for which we had data, and then substituted species epithets and added the species for which we had data to the tree. When adding species, relationships within genera were based on published studies (*Aphaenogaster*: DeMarco & Cognato, 2015; *Crematogaster*: Johnson, 1988; *Formica*: Trager, MacGown, & Trager, 2007) and species were grafted onto the tree at branch midpoints (see Appendix S1; Figure S2 for our phylogeny). Each of the 20 species in the phylogeny was represented by a single value that represented the degree of their response; we used the average for species with more than one observation. We tested for phylogenetic signal in species responses using the phytools package in R (R Core Development Team 2009; Revell, 2012) and found that there was no significant phylogenetic signal based on either Pagel's λ ($p = .62$) or Blomberg's K ($p = .12$). Therefore, phylogenetic comparative methods that would account for phylogenetic nonindependence are not warranted and the use of conventional (nonphylogenetic) statistical methods is justified.

3 | RESULTS

Each of the 10 pairs of coastal and inland forests from 33° to 45° latitude were broadly similar in ant species composition, activity and biogeochemistry. Of the 18,198 ants collected in baited vials (72 species and 21 genera), species composition differed with latitude (PERMANOVA, Block [pairs]: $p = .0006$), but not between paired forests (Coastal vs. Inland: $p = .490$; see Appendix S1; Table S2). Two measures of ant activity indicated no difference in activity between paired forests: the use of control baits (H_2O, 3% of the total vial usage, median = 4 hits per forest) and sugar baits (76% of the total vial usage, median = 161 hits per forest) was consistent between paired sites (Wilcoxon signed ranks test, $df = 10$, $p = .090$, $p = .169$, for H_2O and sugar baits respectively). Overall average leaf litter biogeochemistry across 12 elements was also similar between paired forests (PERMANOVA: Between pairs: $p = .362$; Across pairs [block]: $p = .333$; see Appendix S1; Table S3).

These matched pairs of forests yielded 39 cases in which the same ant species was shared between a pair of coastal and inland forests, with an average of 3.9 species shared between each of the 10 forest pairs (20 species from 10 genera; Figure 2). The differences in $\delta^{15}N$ ($\Delta\delta^{15}N$ (Δ = difference between paired forests) between these conspecifics ranged from 0.004‰ to 3.09‰ with a median of 0.02‰. These pairs of species, in an otherwise similar biotic and abiotic environment provided our primary opportunity to contrast the three hypotheses.

3.1 | Sodium limitation

Leaf litter Na concentrations varied from 0.006% to 0.1% Na across the 20 sites; the median difference in Na between paired forests was 0.017% (IQR: 0.003% and 0.035%). Ants used Na baits twofold more overall in inland forests than in paired coastal forests (Wilcoxon signed ranks test, $df = 10$, $p = .041$). These differences arose from increased use of the intermediate of 0.5% Na baits in inland forests ($p = .021$; 0.1% or 1.0% Na bait use did not vary between paired forests: $p \geq .113$). Na bait usage at all concentrations varied independently of leaf litter Na concentration (Pearson correlation, $p \geq .636$).
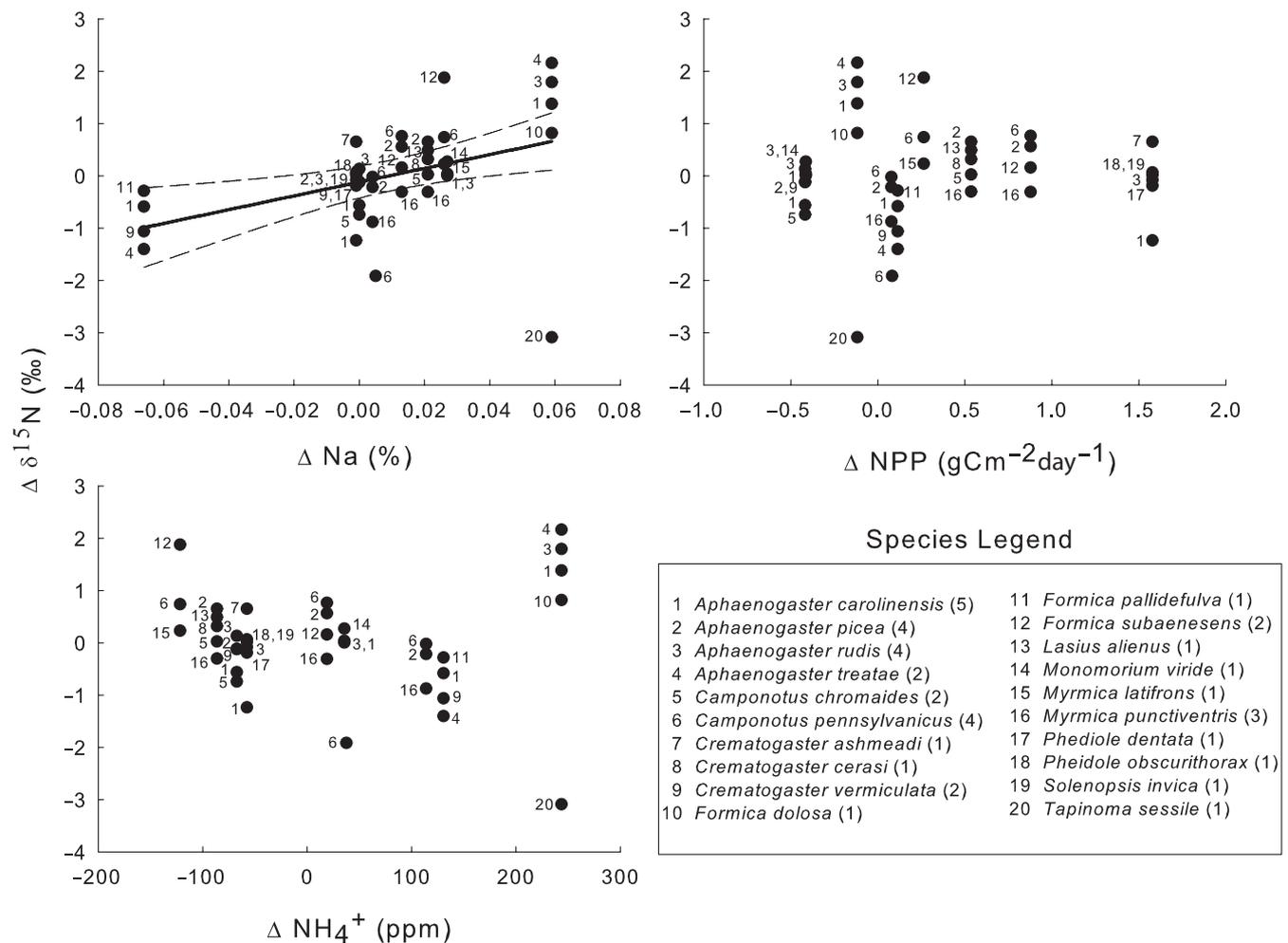

FIGURE 2 Results of the linear regression analyses testing the relationship between ΔNa, ΔNH_4^+ and ΔNPP, and $\Delta\delta^{15}N$ of conspecific ants between paired forests. All x-axes are coastal-inland, and all y-axes are inland-coastal (see Figure 1). Dashed lines are 95% confidence intervals and numbers next to points represent species. In the species legend, numbers in parentheses are the species-specific number of replicates (paired forests) included

Consistent with the hypothesis, ants occupied higher trophic positions in the Na-poor forests compared to the Na-rich pairs. Specifically, $\Delta\delta^{15}N$ increased with ΔNa (Δ = difference between paired forests; Figure 2). ΔNa accounted for 18% of the variation in $\Delta\delta^{15}N$ across 39 conspecifics (average of 3.9 conspecifics per paired forest; 20 ant species total) in 10 paired forests (linear regression: $13.17 \times \Delta Na - 0.12$, $R^2 = 0.181$, $p = .007$; Figure 2). At the extremes on the ΔNa axis ($\geq 0.06\%$), ants in the Na-poor forests were up to 2.2‰ enriched above conspecifics in the Na-rich paired forest (Figure 2). One outlier, *Tapinoma sessile* (the odorous house ant), decreased in $\delta^{15}N$ by 3.1‰ in the Na-poor forest (Figure 2), contrary to predictions. Omitting *T. sessile*, the Na gradient (ΔNa) accounted for 45% of the variation in $\Delta\delta^{15}N$ ($\Delta\delta^{15}N = 18.46 \times \Delta Na - 0.064$, $R^2 = 0.453$, $p < .001$).

3.2 | Nitrogen limitation

NH_4^+ concentrations varied from 74 to 372 p.p.m. across the 20 sites with a median of 143.1 p.p.m. (IQR: 107.1 and 203.7 p.p.m.). The median difference in NH_4^+ between paired forests (ΔNH_4^+) was 77.0 p.p.m. (IQR: 37.3 and 124.1 p.p.m.). There was no relationship between ΔNH_4^+ and $\Delta\delta^{15}N$ (linear regression: $3E^{-4} \times \Delta NH_4^+ + 0.007$, $R^2 = 0.001$, $p = .821$; Figure 2).

3.3 | Habitat productivity

Estimated NPP had a median value of 1.577 gC m^{-2} day^{-1} (IQR: −0.118 and 1.577 gC m^{-2} day^{-1}) varying independently of distance from the ocean (Wilcoxon signed ranks test, $df = 10$, $p = .285$). The median difference in NPP between paired forests (ΔNPP) was 0.34 gC m^{-2} day^{-1} (IQR: 0.11 and 0.62 gC m^{-2} day^{-1}). There was no relationship between ΔNPP and $\Delta\delta^{15}N$ (linear regression: $0.039 \times \Delta NPP - 0.013$, $R^2 = 0.001$, $p = .874$).

4 | DISCUSSION

Here we reveal geographic variation in omnivory among 20 common ant species in Eastern North American forests that spanned over 12° latitude. Among three hypotheses predicting the balance of plant and animal tissue in an omnivore's diet, only the Na-limitation hypothesis accounted for variation: at least 18% and as high as 45%, if we ignore one intriguing outlier species. Our results point to a geography of omnivory at least partially driven by the physiological need for terrestrial animals to find and ingest sufficient amounts of Na (Geerling & Loewy, 2008; Schulkin, 1991). These results support the mounting evidence that Na supplies constrain population and ecosystem processes (Ashraf, Öztürk, Athar, & Athar, 2009; Clay, Donoso, & Kaspari, 2015; Clay, Yanoviak, & Kaspari, 2014; Kaspari, Chang, & Weaver, 2010; Kaspari, Clay, Donoso, & Yanoviak, 2014; Kaspari, Yanoviak, Dudley, Yuan, & Clay, 2009; Kaspari, Yanoviak, et al., 2008; Ott et al., 2014; Simpson et al., 2006; Snell-Rood, Espeset, Boser, White, & Smykalski, 2014; Tyree, Clay, Polasky, & Entrekin, 2016). Thus, Na stoichiometry, via its effect on the health and activity of plant consumers, is an

ecological driver that parallels the well-documented effects of N and P (Fagan et al., 2002; Kaspari, Garcia, et al., 2008; Matsumura et al., 2004; McGroddy, Daufresne, & Hedin, 2004; White, 1993; Wilder & Eubanks, 2010).

Six of the 20 ant species displayed the greatest trophic shifts ($\Delta\delta^{15}N$) coinciding with the greatest differences in Na (ΔNa) between paired forests. These ants in the Na-poor forests were nearly an entire trophic level (c. 3.4‰) above conspecifics in the Na-rich paired forest. Moreover, this pattern held regardless of distance from the ocean: ants were more carnivorous in the Na-poor forests even when inland forests were saltier than their paired coastal forest (Figure 2). The omnivorous ants of North America's eastern forests could be increasing trophic position in at least one of two ways: either by consuming more, or higher trophic level, prey. We have no data to distinguish between these possibilities, but both would increase access to Na. To acquire Na, plant consumers from arthropods to mammals will travel long distances to sources (Dudley et al., 2012), consume urine (Clay et al., 2015), and in a result similar to ours, Na-starved omnivorous crickets resorted to cannibalism to obtain this essential nutrient (Simpson et al., 2006). Here we show increased carnivory is systemic, widespread and driven by biogeochemistry.

In contrast, we found no support for increased trophic position when N was in short supply, or in more productive environments. Both measurements (N as NH_4^+ and productivity as NPP) are proxies for a more complicated reality. Despite widespread evidence of N-limitation's impact on plant consumers (Denno & Fagan, 2003; Matsumura et al., 2004; White, 1993), we found no correlation between omnivory and NH_4^+. But N exists in multiple forms, and N as a macromolecule in protein and amino acids may be a better predictor than N as an element (Wilder & Eubanks, 2010). As such the nitrogen limitation hypothesis may be most applicable at the microscale, where local or temporal N availability (as amino acids and proteins) may cause omnivores to increase prey consumption. Likewise, productivity, as gC m^{-2} day^{-1} was not correlated with shifts in trophic position of these omnivorous ants. Productivity here is averaged across the year, but at higher latitudes, the length of the productive season is significantly shorter than at lower latitudes. At least one recent study provides evidence for increased carnivory in more seasonal environments where shorter growing seasons increase the demand for high-quality and energy-rich food (Vulla et al., 2009). Field experiments, simultaneously manipulating productivity, N, and Na, will further clarify the roles of each. At least one such experiment, using synthetic urine with and without Na, highlighted the role of Na and not N in regulating termite activity (Clay et al., 2015).

Support for Na-limitation as a driver of omnivory was mixed in one key respect: Na bait usage at all concentrations varied independently of leaf litter Na concentration. Instead, inland ants consistently used 0.5% NaCl baits twofold more than ants in paired coastal forests. This concentration matches many animal dietary Na requirements (National Research Council (NRC), 2005). Studies of rats and humans reveal that Na appetite is rarely proportional to Na deficit, and Na ingestion typically far exceeds the specific need (Geerling & Loewy, 2008). Given inland forests generally have lower Na supplies than coastal forests (National Atmospheric Deposition Program, 2012a),

ants in inland forests may hedge towards higher Na intake, particularly because excesses in Na are easily balanced through losses in excretion. Alternatively, as Na is continuously lost through excretion, the ants' consumption of Na in its most accessible form, salty water, may represent a less risky and more expedient way to maintain a Na balance than consuming animal tissue, which is not without costs: foraging time, handling time, potential harm if prey is alive and potential competitive interactions over a valuable resource.

One species, *T. sessile*, was a conspicuous exception to the trend of increased carnivory in low-Na environments. The case of *T. sessile* points to other factors that may influence the degree of omnivory (e.g. Agrawal et al., 1999; Brabrand, 1985; Dam et al., 1994; Denno & Fagan, 2003). We suggest one possibility: competition with other ants. *Tapinoma sessile* is behaviourally subordinate (Fellers, 1987); if the majority of ants in Na-poor forests are increasingly carnivorous, *T. sessile* may be out-competed for animal tissue resources and instead use proportionately more sugar sources like hemipteran honeydew. In this case, these plant-derived resources may either be proportionately less used by other ants or just amply abundant. The most variation in $\Delta\delta^{15}N$ was located around 0 ΔNa (no difference between pairs; Figure 2) indicating that when omnivores are not Na-limited, other factors become more important in determining the proportion of plants to animal tissue consumed.

The biogeography of Na as a driver of the balance of plant and animal consumption in ecosystems should have consequences for the regulation and function of these ecosystems (Botkin et al., 1973; Clay et al., 2015; Kaspari et al., 2009, 2014). For example, omnivorous ants in the most Na-poor forests increased their trophic position nearly an entire trophic level above conspecifics in Na-rich paired forests. Increased carnivory could suppress prey density or activity and result in decreased herbivory (green food web) and detritivory (brown food web). This, in turn, should result in a greener (e.g. HSS: Hairston, Smith, & Slobodkin, 1960) and browner (e.g. Wu, Duffy, Reich, & Sun, 2011) worlds in Na-poor environments. Alternatively, nutrient cycling through the breakdown of carcasses may be faster in Na-poor environments due to increased scavenging in pursuit of salt. The majority of research has been on invertebrate omnivores, but these principles should also hold for vertebrates (e.g. Vulla et al., 2009).

Anthropogenic activity has altered the geography of Na by creating Na-rich veins (salting roads: Kaspari et al., 2010; Snell-Rood et al., 2014) and Na-hotspots (mining, agriculture: Ashraf et al., 2009) in otherwise Na-limited environments. Communities respond rapidly to changes in Na availability (Clay et al., 2014), which if sustained ultimately lead to changes in ecosystem function like increased carbon efflux from heterotroph respiration in decomposition processes (Kaspari et al., 2009, 2014). Understanding the geographic ecology of omnivore behaviour can provide a framework for predicting how ecosystem function is likely to change from human activity in the Anthropocene.

AUTHORS' CONTRIBUTIONS

All authors (N.C., R.L. and M.K.) provided intellectual contributions, and helped with writing and analyses. N.C. and R.L. conducted fieldwork. N.C. conducted laboratory work.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.26087 (Clay, Lehrter, & Kaspari, 2017).

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REFERENCES

Agrawal, A. A., Kobayashi, C., & Thaler, J. S. (1999). Influence of prey availability and induced host-plant resistance on omnivory by western flower thrips. *Ecology*, *80*, 518–523.

Ambrose, S. H., & DeNiro, M. J. (1986). The isotopic ecology of East African mammals. *Oecologia*, *69*, 395–406.

Anderson, M. J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, *26*, 32–46.

Ashraf, M., Öztürk, M., Athar, H. R., & Athar, H. R. (2009). *Salinity and water stress: Improving crop efficiency*. New York, NY: Springer.

Botkin, D. B., Jordan, P. A., Dominski, A. S., Lowendorf, H. S., & Hutchinson, G. E. (1973). Sodium dynamics in a northern ecosystem. *Proceedings of the National Academy of Sciences of the United States of America*, *70*, 2745–2748.

Brabrand, A. (1985). Food of roach (*Rutilus rutilus*) and ide (*Leusiscus idus*): Significance of diet shift for interspecific competition in omnivorous fishes. *Oecologia*, *66*, 461–467.

Clay, N. A., Donoso, D. A., & Kaspari, M. (2015). Urine as an important source of sodium increases decomposition in an inland but not coastal tropical forest. *Oecologia*, *177*, 571–579.

Clay, N. A., Lehrter, R. J., & Kaspari, M. (2017). Data from: Toward a geography of omnivory: Omnivores increase carnivory when sodium is limiting. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.26087

Clay, N. A., Yanoviak, S. P., & Kaspari, M. (2014). Short-term sodium inputs attract microbi-detritivores and their predators. *Soil Biology and Biochemistry*, *75*, 248–253.

Dam, H. G., Peterson, W. T., & Bellantoni, D. C. (1994). Seasonal feeding and fecundity of the calanoid copepod *Acartia tonsa* in Long Island Sound: Is omnivory important to egg production? *Hydrobiologia*, *292/293*, 191–199.

Davidson, D. W. (2005). Ecological stoichiometry of ants in a New World rain forest. *Oecologia*, *142*, 221–231.

Deans, C. A., Behmer, S. T., Fiene, J., & Sword, G. A. (2016). Spatiotemporal, genotypic, and environmental effects on plant soluble protein and digestible carbohydrate content: Implications for insect herbivores with cotton as an exemplar. *Journal of Chemical Ecology*, *42*, 1151–1163.

DeMarco, B. B., & Cognato, A. I. (2015). Phylogenetic analysis of *Aphaenogaster* supports the resurrection of *Novomessor* (Hymenoptera: Formicidae). *Annals of the Entomological Society of America*, *108*, 201–210.

Denno, R. F., & Fagan, W. F. (2003). Might nitrogen limitation promote omnivory among carnivorous arthropods? *Ecology*, *84*, 2522–2531.

Digel, C., Curtsdotter, A., Riede, J., Klarner, B., & Brose, U. (2014). Unravelling the complex structure of forest soil food webs: Higher omnivory and more trophic levels. *Oikos*, *123*, 1157–1172.

Dudley, R., Kaspari, M., & Yanoviak, S. P. (2012). Lust for salt in the Western Amazon. *Biotropica*, *44*, 6–9.

Fagan, W. F., Siemann, E., Mitter, C., Denno, R. F., Huberty, A. F., Woods, H. A., & Elser, J. J. (2002). Nitrogen in insects: Implications for trophic complexity and species diversification. *American Naturalist*, *160*, 784–802.

Fellers, J. H. (1987). Interference and exploitation in a guild of woodland ants. *Ecology*, *68*, 1466–1478.

Geerling, J. C., & Loewy, A. D. (2008). Central regulation of sodium appetite. *Experimental Physiology*, *93*, 178–209.

Hairston, N. F., Smith, F., & Slobodkin, L. (1960). Community structure, population control, and competition. *American Naturalist*, *94*, 421–425.

Hölldobler, B., & Wilson, E. O. (1990). *The Ants*. Cambridge, MA: Belknap Press of Harvard University Press.

Joern, A., Provin, T., & Behmer, S. T. (2012). Not just the ususal suspects: Insect herbivore populations and communities are associated with multiple plant nutrients. *Ecology*, *93*, 1002–1015.

Johnson, C. (1988). Species identification in the eastern *Crematogaster* (Hymenoptera: Formicidae). *Journal of Entomological Science*, *23*, 314–332.

Kaspari, M., Chang, C., & Weaver, J. (2010). Salted roads and sodium limitation in a northern forest ant community. *Ecological Entomology*, *35*, 543–548.

Kaspari, M., Clay, N. A., Donoso, D. A., & Yanoviak, S. P. (2014). Sodium fertilization increases termites and enhances decomposition in an Amazonian forest. *Ecology*, *95*, 795–800.

Kaspari, M., Garcia, M. N., Harms, K. E., Santana, M., Wright, S. J., & Yavitt, J. B. (2008). Multiple nutrients limit litterfall and decomposition in a tropical forest. *Ecology Letters*, *11*, 35–43.

Kaspari, M., O'Donnell, S., & Kercher, J. R. (2000). Energy, density, and constraints to species richness: Ant assemblages along a productivity gradient. *American Naturalist*, *155*, 280–293.

Kaspari, M., Yanoviak, S. P., & Dudley, R. (2008). On the biogeography of salt limitation: A study of ant communities. *Proceedings of the National Academy of Sciences of the United States of America*, *105*, 17848–17851.

Kaspari, M., Yanoviak, S. P., Dudley, R., Yuan, M., & Clay, N. A. (2009). Sodium shortage as a constraint on the carbon cycle in an inland tropical rainforest. *Proceedings of the National Academy of Sciences of the United States of America*, *106*, 19405–19409.

Matsumura, M., Trafelet-Smith, G. M., Gratton, C., Finke, D. L., Fagan, W. F., & Denno, R. F. (2004). Does intraguild predation enhance predator performance? A stoichiometric perspective. *Ecology*, *85*, 2601–2615.

McCann, K., & Hastings, A. (1997). Re-evaluating the omnivory-stability relationship in food webs. *Proceedings of the Royal Society of London B: Biological Sciences*, *264*, 1249–1254.

McCune, B., & Mefford, M. J. (1999). *Multivariate analysis of ecological data, version 4.14*. Glenedon Beach, OR: MjMSoftware.

McGroddy, M. E., Daufresne, T., & Hedin, L. O. (2004). Scaling of C:N:P stoichiometry in forests worldwide: Implications for terrestrial Redfield-type ratios. *Ecology*, *85*, 2390–2401.

Moreau, C. S., Bell, C. D., Vila, R., Archibald, S. B., & Pierce, N. E. (2006). Phylogeny of the ants: Diversification in the age of angiosperms. *Science*, *312*, 101–104.

National Atmospheric Deposition Program. (2012a). *Sodium ion wet deposition*. Champaign, IL: National Atmospheric Deposition Program.

National Atmospheric Deposition Program. (2012b). *Ammonium ion wet deposition*. Champaign, IL: National Atmospheric Deposition Program.

National Research Council (NRC). (2005). *Mineral tolerance of animals*. Washington, DC: National Academies Press.

Oksanen, L. (1990). Predation, herbivory, and plant strategies along gradients of primary productivity. In J. Grace, & D. Tilman (Eds.), *Perspectives on plant consumption* (pp. 445–474). San Diego, CA: Academic Press.

Ott, D., Digel, C., Klarner, B., Maraun, M., Pollierer, M., Rall, B. C., … Brose, U. (2014). Litter elemental stoichiometry and biomass densities of forest soil invertebrates. *Oikos*, *123*, 1212–1223.

Paerl, H. W., Boynton, W. R., Dennis, R. L., Driscoll, C. T., Greening, H. S., Kremer, J. N., … Seitzinger, S. P. (2001). Atmospheric deposition of nitrogen in coastal waters: Biogeochemical and ecological implications. In R. A. Valigura, R. B. Alexander, M. S. Castro, T. P. Meyers, H. W. Paerl, P. E. Stacey, & R. E. Turner (Eds.), *Coastal and estuarine studies* (pp. 11–52). Washington, DC: American Geophysical Union.

Ponsard, S., & Arditi, R. (2000). What can stable isotopes (δ^{15}N and δ^{13}C) tell about the food web of soil macro-invertebrates? *Ecology*, *81*, 852–864.

Post, D. M. (2002). Using stable isotopes to estimate trophic position: Models, methods, and assumptions. *Ecology*, *83*, 703–718.

R Core Development Team. (2009). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Resasco, J., Porter, S. D., Sanders, N. J., & Levey, D. J. (2014). Assessing the effects of sodium on fire ant foraging in the field and colony growth in the laboratory. *Ecological Entomology*, *39*, 267–271.

Revell, L. J. (2012). phytools: An R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, *3*, 217–223.

Schowalter, T. D., Webb, J. W., & Crossley, D. A. Jr (1981). Community structure and nutrient content of canopy arthropods in clearcut and uncut forest ecosystems. *Ecology*, *62*, 1010–1019.

Schulkin, J. (1991). *Sodium hunger: The search for a salty taste*. New York, NY: Cambridge University Press.

Simpson, S. J., Sword, G. A., Lorch, P. D., & Couzin, I. D. (2006). Cannibal crickets on a forced march for protein and salt. *Proceedings of the National Academy of Sciences of the United States of America*, *103*, 4152–5156.

Sinia, A., Roitberg, B., Mcgregor, R. R., & Gillespie, D. R. (2004). Prey feeding increases water stress in the omnivorous predator *Dicyphus hesperus*. *Entomologia Experimentalis et Applicata*, *110*, 243–248.

Snell-Rood, E. C., Espeset, A., Boser, C. J., White, W. A., & Smykalski, R. (2014). Anthropogenic changes in sodium affect neural and muscle development in butterflies. *Proceedings of the National Academy of Sciences of the United States of America*, *111*, 10221–10226.

Sprules, W. G., & Bowerman, J. E. (1988). Omnivory and food chain length in zooplankton food webs. *Ecology*, *69*, 418–426.

Tillberg, C. V., McCarthy, D. P., Dolezal, A. G., & Suarez, A. V. (2006). Measuring the trophic ecology of ants using stable isotopes. *Insectes Sociaux*, *53*, 65–69.

Trager, J. C., MacGown, J. A., & Trager, M. D. (2007). Revision of the Nearctic endemic Formica pallidefulva group. In R. R. Snelling, B. L. Fisher, & P. S. Ward (Eds.), *Advances in ant systematics (Hymenoptera: Formicidae): Homage to E. O. Wilson – 50 years of contributions* (Vol. 80, pp. 610–636). Gainesville, FL: Memoirs of the American Entomological Institute.

Tyree, M., Clay, N. A., Polasky, S., & Entrekin, S. (2016). Salt in our streams: Even small sodium additions can have negative effects on detritivores. *Hydrobiologia*, *775*, 109–122.

Vanni, M. J., Arend, K. K., Bremigan, M. T., Bunnell, D. B., Garvey, J. E., González, M., … Stein, R. A. (2005). Linking landscapes and food webs:

Effects of omnivorous fish and watersheds on reservoir ecosystems. *BioScience*, *55*, 155–167.

Vulla, E., Hobson, K. A., Korsten, M., Leht, M., Martin, A.-J., Lind, A., … Saarma, U. (2009). Carnivory is positively correlated with latitude among omnivorous mammals: Evidence from brown bears, badgers and pine martens. *Annales Zoologici Fennici*, *46*, 395–415.

White, T. C. R. (1993). *The inadequate environment: Nitrogen and the abundance of animals*. New York, NY: Springer-Verlag.

Wilder, S. M., & Eubanks, M. D. (2010). Extrafloral nectar content alters foraging preferences of a predatory ant. *Biology Letters*, *6*, 177–179.

Wilder, S. M., Holway, D. A., Suarez, A. V., LeBrun, E. G., & Eubanks, M. D. (2011). Intercontinental differences in resource use reveal the importance of mutualisms in fire ant invasions. *Proceedings of the National Academy of Sciences of the United States of America*, *108*, 20639–20644.

Wu, X., Duffy, J. E., Reich, P. B., & Sun, S. (2011). A brown-world cascade in the dung decomposer food web of an alpine meadow: Effects of predator interactions and warming. *Ecological Monographs*, *81*, 313–328.

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