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Salted roads and sodium limitation in a northern forest ant community

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Abstract. 1. Road salt is a common, anthropogenic source of NaCl in many temperate ecosystems. Sodium is also an essential and potentially limiting element for inland animal populations. This suggests that Na limitation in inland ecosystems, and hence attraction to Na sources, should increase with distance from salted roads.

2. In a North Temperate forest, we tested the prediction that Na recruitment would increase, as soil [Na] decreased, with distance from a salted two-lane highway. We presented ants with three concentrations of NaCl and sucrose solution along four pairs of transects ca 1, 10, 100, and 1000 m from the road.

3. Consistent with the Na-limitation hypothesis, the ratio of NaCl to sucrose use increased with distance from the road from 1:13 vials at 1 m to 1:5 vials at 1 km. Genera characterised by high Na use did not accumulate farther from the road. For the common and widespread *Tapinoma sessile* (Say), a 10-fold increase in distance from the road resulted in ants doubling their use of NaCl relative to sucrose.

4. Road salt is a well-known pollutant, especially of freshwater ecosystems. However, by suppressing plants and potentially promoting consumers, road salt may have more complex effects on terrestrial ecosystems, especially those far inland from oceanic aerosols.

Key words. Biogeochemistry, foraging, pollution, landscape, nutrition, soil.

Introduction

Of the ca 25 elements required for life (Frausto da Silva & Williams, 2001) Na is unique. Sodium is relatively unimportant to terrestrial plants (Marschner, 1995) while plant consumers must concentrate Na 100–1000 fold over the 1.0 mg kg^{-1} found in their food. Na inputs from rainfall decrease 1000-fold with distance inland (NADP, 2006). Thus inland ecosystems are prime candidates for Na limitation of consumers (Chadwick *et al*., 1999). A variety of inland herbivore populations from butterflies to moose have been shown to crave Na (Blair-West *et al*., 1968; Arms *et al*., 1974; Belovsky & Jordan, 1981). Ants of inland ecosystems recruit more strongly to Na than ants from more coastal communities (Kaspari *et al*., 2008), suggesting a geography of Na limitation.

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Such geography may also arise through anthropogenic Na gradients (Mattson & Godfrey, 1994; Marschner, 1995; NRC, 2005) albeit at smaller scales. In seasonal ecosystems, road salt containing NaCl is frequently used to melt ice. Road salt can suppress roadside seed germination (Spencer & Port, 1988) as well as plant growth and survivorship (Thompson & Rutter, 1986). It can pollute inland freshwater streams via the accumulation of Cl anions (Jackson & Jobbgy, 2005; Kaushal *et al*., 2005) with lethal effects on plants and invertebrates (Hart *et al*., 1991). The ecological effects of roads regularly reach 100 m or more into surrounding forest (Schonewald-Cox & Buechner, 1992; Forman & Deblinger, 2000).

If roads represent local maps of NaCl availability, and inland populations of terrestrial consumers are Na limited, then we should see patterns of resource use that map onto roads. Specifically, we should see increased recruitment to supplementary NaCl by terrestrial consumers as one moves further from roadsides. Here we test this prediction using the ant communities of a North Temperate forest, 100 km inland, and criss-crossed with roads that are salted in the winter. Ants are ubiquitous and important consumers in such forests (Hölldobler & Wilson, 1990), and factors that shape their activity and abundance should ramify widely through the ecosystem. We find that ants increasingly use NaCl baits relative to sucrose farther from a highway and that these community-level changes arise, at least in part, from changes in behaviour within populations.

Materials and methods

This study took place at Harvard Forest (42°31′39″N, 72°11′13″W, elevation 120 m), characterised by a mix of hardwood and evergreens (Foster & Aber, 2004). From May to July 2008, ant activity was evaluated on a series of transects paralleling Massachusetts Rt. 32, a two-lane highway on which both NaCl and CaCl are applied during the winter (Massachusetts Department of Roads, 2010). During conditions of sub-0 °C precipitation, Massachusetts roads are treated with 68 kg of NaCl and 152 l of 32% liquid CaCl (by weight) per each 1.0 km of lane.

Two transects were arrayed, approximately 0.25 km apart, at 1, 10, 100, and 1000 m from the road. Transects at 1 m ran through an open stretch of grass and bare ground; transects at 10 and 100 m ran through a matrix of field and forest; transects at 1 km were embedded in a 30 m canopy forest. We characterised soil [Na] with an ICP spectrometer pooling 5 cm cores from the ends of each transect. We characterised forest canopy (% cover) and litter cover using a spherical densiometer and Daubenmire quadrat respectively, taking samples at four points equidistant along each transect (Southwood, 1978).

Each transect was run 13 times (one 1 m transect run was interrupted by a lawnmower); seven began at 09.00 h and six began at 14.00 h. Ant communities were sampled with transects of labelled 2 ml Eppendorf vials. Each vial was half-stuffed with cotton saturated with sucrose (1%, 5%, and 10%, by mass), or NaCl (0.1, 0.5, and 1% by mass) solution plus a distilled water treatment (which consistently received 0 hits and is dropped from further analysis). Fifteen vials of each solute concentration were snapped shut and mixed in a plastic bag. For each transect run, a vial was randomly selected, opened, and dropped on the ground every 1 m. After 1 h, we collected the vials, snapping the cap shut to capture the ants within (occasional escapes were identified on site to genus). Ants were returned to the laboratory, identified to genus, and counted. A large fraction were vouchered and later identified to species.

We tested two hypotheses. The first posits that carbohydrates and Na are limiting nutrients to the ant community; it predicts that ants prefer high over low concentrations of both. For each transect, we measured the per cent of vials for each solute concentration used by at least one ant, and took the mean. We used a two-way ANOVA to analyse concentration and distant effects for both solutes (d.f. $= 24$). The second hypothesis posits that the intensity of NaCl, but not sucrose, limitation increases with distance from the road: it predicts increasing use of Na relative to sucrose as we move from the 1 m to the 1 km transects. We calculated the average ratio of hits on NaCl to sucrose vials at maximum concentration, and used ordinary least squares regression ($n = 8$ transects) to evaluate the predicted increase of NaCl:sucrose with $\log_{10}$ distance from the road by the entire ant community.

The analysis above tests for a predicted gradient of increased NaCl use relative to sucrose use by the ant community. Such a gradient could occur because (i) taxa with higher fixed preference for NaCl are found further from the roads (i.e. species turnover) and/or (ii) individual colonies of widely distributed ant taxa increasingly prefer NaCl as its supply decreases (i.e. plasticity). To evaluate these two possibilities, we first characterised the generic composition of ants at baits for the four distances. We then characterised each genus by the fraction of total baits used that contained NaCl. If gradients in NaCl use arose from turnover of taxa with fixed NaCl preferences, we would see taxa with the highest Na use accumulating far from the road. Second, we tested for plasticity in NaCl:sucrose in *Tapinoma sessile*, our only common and widespread population by examining the gradient of NaCl:sucrose use as described above. We do not analyse Na use by all populations because most are rare, found along one part of the gradient, or both (any of which would lead to type II error). However, we do redo the analysis, *sans T. sessile*, to evaluate the hypothesis that the community pattern is driven by this common species.

Results

About one-sixth (15%) of NaCl and sucrose vials were used by ants. From them, we collected a total of 11 genera and 22 species (Table 1). Most species were rare or patchy. In contrast, *T. sessile* was both common (one-third of all vials

Table 1. Species composition of ants recruiting to baits in this study.

% genus	Genus	Species	% species
12	*Aphaenogaster*	*rudis*-group	100
8	*Camponotus*	*neararcticus*	5
		novaeboracensis	59
		pennsylvanicus	36
<1	*Crematogaster*	*cerasi*	100
11	*Formica*	*incerta*	5
		neogagates	60
		subsericea	35
5	*Lasius*	*alienus*	24
		neoniger	76
29	*Myrmica*	*americana*	11
		detrinodis	1
		fracticornis	7
		latifrons	8
		pinetorum	6
		punctiventris	66
		sculptilis	1
<1	*Solenopsis*	*molesta*	100
<1	*Stenamma*	*diecki*	100
33	*Tapinoma*	*sessile*	100
2	*Temnothorax*	*longispinosus*	100
1	*Tetramorium*	*caespitum*	100

% genus represents contribution of each genus to total ant activity; % species represents the contribution of each species to generic representation.

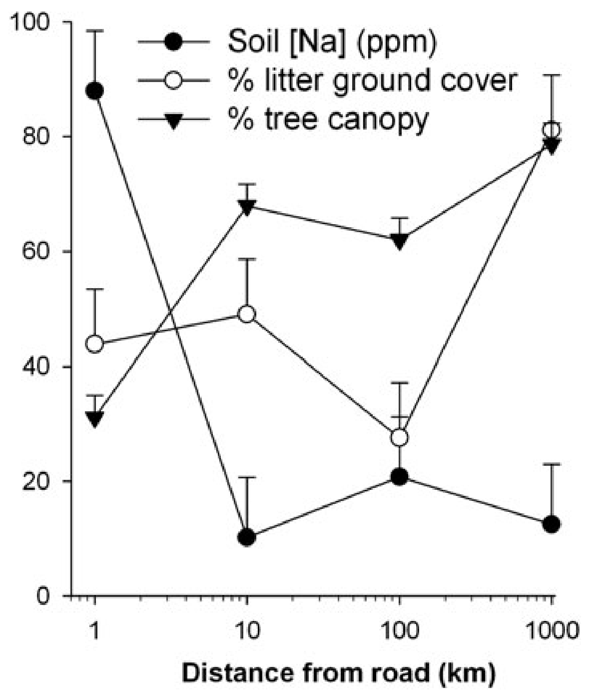

Fig. 1. Habitat variables (+SE) for pairs of sample transects at increasing distance from a road cutting through a Northeastern forest.

hit) and widespread (collected on 102 of the 103 transect runs, and 16–56% of all hits at a given distance). The second most common species, *Aphaenogaster rudis*-group, was collected on only about half (57) of the transect runs, made up only 12% of the ants, and constituted 3–28% of hits at a given distance.

Soil and vegetation changed as one moved roadside towards and into the forest (Fig. 1). Sodium concentrations in the soil were 10-fold higher next to the road ($F_{3,8} = 12.34$, $P = 0.0172$); a Tukey's test (threshold $P = 0.05$) showed that Na ppm at 10, 100, and 1000 m were indistinguishable. Tree canopy cover increased from 33% roadside to 79% 1 km from the road ($F_{3,8} = 25.51$, $P = 0.0045$); litter ground cover was patchy but failed to vary significantly with distance ($F_{3,8} = 5.45$, $P = 0.07$).

Use of both solutes increased with concentration (Fig. 2). Ants collected from vials, especially *Lasius*, *Formica*, and *Tapinoma*, frequently had distended gasters suggesting that they were not simply visiting, but imbibing solution. In a two-way ANOVA, ant use of NaCl increased from 2% to 5% with concentration ($F_{11,23} = 5.81$, $P = 0.017$). It also increased with $\log_{10}$ distance from the road ($F_{11,23} = 3.74$, $P = 0.0417$, interaction NS). Sucrose use also increased with concentration ($F_{11,23} = 111.54$, $P < 0.0001$). Unlike NaCl, sucrose use peaked at 100 m (28%, vs. 22% at 1 and 10 m, and 23% at 1 km). Preference for NaCl by the ant community, measured as the ratio of NaCl:sucrose, increased with distance from the road [Fig. 2, OLS regression NaCl: sucrose $= 0.094 + 0.034 \log_{10}$ (distance), $F_{1,8} = 6.9$, $P = 0.039$, $r^2 = 0.53$]. Next to the road, ant use averaged one NaCl vial for every 13 sucrose; 1 km from the road, that average was 1:5.

We next evaluated if the above pattern arose through taxa turnover. The six genera that accounted for 98% of collections (Fig. 3, Table 1) were non-randomly distributed with distance from the road ($\chi^2_{15} = 371$, $P < 0.0001$) and in the use of NaCl versus sucrose ($\chi^2_5 = 84.6$, $p < 0.0001$). However, both roadside (1 m) and deep forest (1 km) transects yielded the peak abundances of genera with a high Na use (*Tapinoma* and *Camponotus* respectively) and low Na use (*Formica* and *Aphaenogaster*). Thus the community-wide pattern of increasing NaCl use farther from the road did not arise primarily by the accrual of genera with higher recruitment to Na.

In contrast, colonies of the species *T. sessile* increasingly used NaCl relative to sucrose farther from the road [OLS

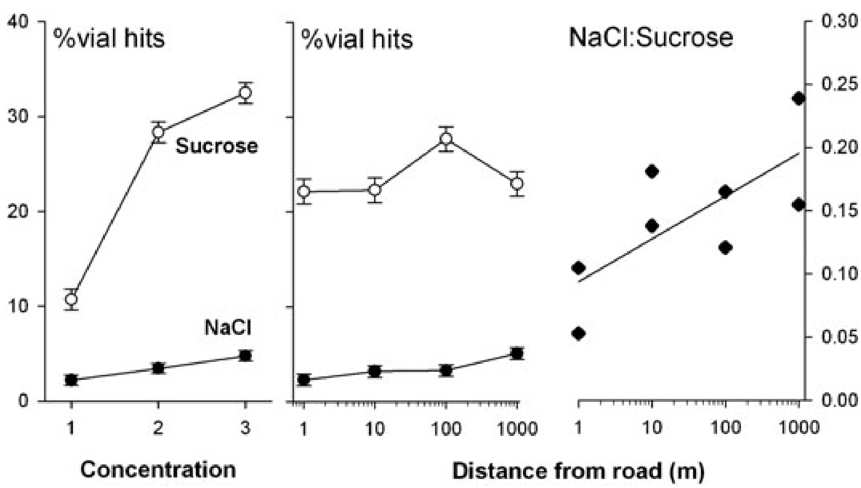

Fig. 2. Use of NaCl and sucrose by ant communities at four distances from a salted road (left and middle: least square means ± 1 S.E.). Left: % vial hits reflects activity at baits of increasing concentration (NaCl: 0.1%, 0.5%, 1.0%, sucrose: 1%, 5%, 10%). Middle: average activity for two compounds at increasing distance from road. Right: ratio of activity at 1% NaCl versus 10% sucrose baits at increasing distances from the road (line OLS regression).

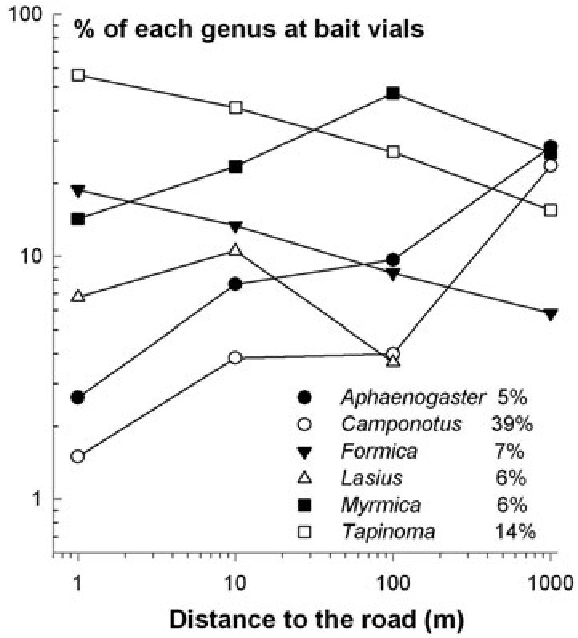

Fig. 3. Composition of ant assemblages coming to baits, by genus, at four distances from the road (note both axes $\log_{10}$-transformed). Inset: genera's per cent use of NaCl.

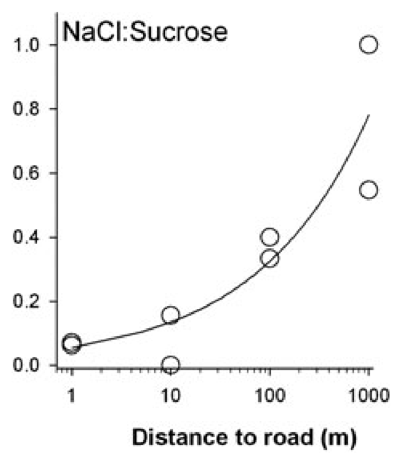

Fig. 4. Ratio of NaCl to sucrose use as a function of distance from the road for the most common species in the ant community using baits, *Tapinoma sessile*.

regression NaCl: sucrose $= -0.04 + 0.24 \log_{10}$(distance), $F_{1,8} = 17.6$, $P = 0.006$, $r^2 = 0.75$, Fig. 4]. This curve was better described by a quadratic regression of this semi log plot ($P = 0.0013$, $r^2 = 0.85$), suggesting a monotonic increase in Na preference with distance from the road. However, *Tapinoma* alone was not responsible for the community pattern. When *Tapinoma* records were extracted from the community dataset, the ratio of NaCl:sucrose use still increased with distance from the road [OLS regression NaCl: sucrose $= 0.017 + 0.05 \log_{10}$ (distance), $F_{1,8} = 19.9$, $P = 0.004$, $r^2 = 0.77$].

Discussion

Road salts are a significant source of NaCl inputs in North Temperate ecosystems (Mattson & Godfrey, 1994). The ant assemblage in one such forest increasingly used NaCl relative to sucrose, as one moved away from a road salted months before. One kilometre into the forest, one in five vial hits were on NaCl baits, a surprisingly high number given the metabolic demands for carbohydrates. The community level pattern did not appear to arise through the accumulation of Na-craving genera far from the road. Instead, colonies of the generalist *T. sessile*, an omnivorous ant of moist habitats (Smith, 1928), used little NaCl within 10 m of the road, and approximately doubled use relative to sucrose at 10-fold increments deeper into the forest. Our data suggest that far from the road salts of Massachusetts Highway 32, colonies of *T. sessile* of the Harvard Forest would recruit roughly equally to solutions of 10% sucrose and 1% NaCl. Furthermore, given the stronger Na limitation in herbivorous versus predacious taxa (Kaspari *et al*., 2008), *T. sessile* is probably among the most herbivorous ants at Harvard Forest.

This landscape pattern of resource use by a dominant terrestrial arthropod is recapitulated at larger scales when the Na source is oceanic: ant communities increasingly prefer NaCl to sucrose as one moves from coastal forests into Amazon forests 2500 km inland (Kaspari *et al*., 2008). Contrary to that geographic study, here there was little evidence of a decrease in ant activity (measured as the total number of sucrose hits) when Na supply decreased at the landscape scale.

Here, however, we studied a sequence of habitats – from a busy open roadside to mixed forest (Fig. 1). Furthermore, we sampled ants both in cool New England mornings and warm afternoons. The commensurate changes in temperature (Cerda *et al*., 1998; Hurlbert *et al*., 2008), humidity (Kaspari, 1993; Kaspari & Weiser, 2000), and habitat structure (Kaspari & Weiser, 1999; Farji-Brener *et al*., 2004) probably combined to affect ant activity and confound any Na effects. For example, the high sucrose use at 100 m appeared to represent an ecotone – with comparatively heavy forest canopy, but still ample bare ground – which allowed ants in a productive environment to move around freely, enhancing local capture rates. Press experiments – adding Na to the ecosystem and observing changes in population density and activity – represent the next step in testing Na limitation in these forests. Such additions double ant densities in a Peruvian forest (Kaspari *et al*., 2009), and based on a three-fold increase in queens, likely nest densities (N. Clay, unpublished). More generally, multifactorial experiments are needed to contrast the relative importance of nest site limitation (Herbers, 1986), cold temperatures (Heinze *et al*., 1998), food availability (Deslippe & Savolainen, 1994), and parasitism (Foitzik *et al*., 2004) on population and community structure of North Temperate ants.

At the same time, the biogeography of Na limitation can be profitably explored using salted roadways as templates. The application of 68 kg of NaCl per lane for every freezing precipitation event is standard across Massachusetts (Massachusetts Department of Roads, 2010); the precise quantities probably vary in different districts and countries. That said, a protocol similar to this one applied from coast to inland, and matched for habitat, should show increasingly positive effects of road salt on the abundance of ants and, presumably, other consumers (especially herbivores and decomposers, Kaspari *et al*., 2008), far from the road.

This use of Na by the terrestrial consumer community may account for a puzzle noted by Jackson and Jobbgy (2005). In the U.S.A., road salt inputs have long since exceeded by at least four-fold, wet deposition of NaCl from oceanic aerosols. Only Cl, however, has been accumulating in surrounding freshwater streams and lakes. Jackson and Jobbgy's explanation is that Na is accumulating in soils and, in turn, displacing useful cations like Ca, Mg, and K. Cafeteria experiments with butterflies (Arms *et al*., 1974) and ants (Kaspari *et al*., 2009) point to Na, not Cl, as the element driving NaCl recruitment. Perhaps some of the Na missing from freshwater ecosystems is bound up in the cells of terrestrial microbes and animals.

NaCl, at the ecosystem level, can play the role of toxin and limiting nutrient. Compared to the clear damage from road salt pollution (Schonewald-Cox & Buechner, 1992; Forman & Deblinger, 2000), especially to aquatic ecosystems (Kaushal *et al*., 2005), road salt effects may be more nuanced for terrestrial consumers. Adding NaCl to busy roadways may have consequences for the animals attracted to it (Smith-Patten & Patten, 2008) and for plants that may already be doubly impacted by physiological stress (Spencer & Port, 1988) and enhanced herbivore vigour (NRC, 2005).

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