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Contributions of ant mounds to soil carbon and nitrogen pools in a marsh wetland of Northeastern China

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ABSTRACT

Ant mounds often occur at high densities in marsh wetlands. However, little information is available regarding their impacts on soil nutrient pools in these ecosystems. We studied C_{org}, dissolved organic carbon (DOC), total nitrogen (TN), NO_3^- and NH_4^+ concentrations in above-ground ant mounds and in soils under mounds for three ant species (*Lasius flavus*, *Lasius niger* and *Formica candida*), and estimated their contribution to the total soil nutrient pools in a marsh wetland. Ant impacts were greatest in above-ground soils. All measured nutrient concentrations in above-ground mounds were significantly higher than the average values in reference soils (upper 25 cm). However, except for DOC, no significant differences for nutrient concentrations existed between soils under mounds and reference soils. The impacts of ant mounds on soil C and nutrient concentrations varied by ant species. *L. niger* above-ground mounds stored less C_{org}, TN and NO_3^- than *F. candida* and *L. flavus* mounds, or reference soils. At the ecosystem scale, soils in above-ground mounds and under ant mounds all contained less C_{org} per hectare than the reference soils. Total amounts in nutrient pools from mounds of the three ant species comprised from 5.3% to 7.6% of the total in natural marsh soils. More importantly, ant mounds increased the spatial heterogeneity of nutrient pools. Thus, ant mounds can be important to a fully integrated understanding of the structure and function of wetland nutrient cycles and balances.

1. Introduction

Ants can constitute a significant part of the animal biomass and also act as soil engineers in many ecosystems (Folgarait, 1998). Most ant species build their nests in mineral soil, but some species build mounds using organic material. The ability to build biogenic structures is a foundation of the soil engineering concept (Jones et al., 1997; Lavelle, 1997). In soil, the relative importance of regulation imposed by ecosystem engineers (*sensu* Jones et al., 1994) is likely to exceed regulation by foodweb complexity (Lavelle, 2002). Ants, as 'extended phenotype engineers', whose activities are concentrated at a few locations, have a large impact on the maintenance of ecosystem heterogeneity (Jouquet et al., 2006). The documented importance of ants to ecosystem functioning suggests that ants could affect soil structural heterogeneity (Folgarait, 1998; Boulton et al., 2003) and soil fertility (Holec and Frouz, 2006; Wagner and Jones, 2006; Ohashi et al., 2007; Jiménez et al., 2008). Besides soils, ants can also affect surface hydrological processes (Cammeraat and Risch, 2008), biological diversity and ecosystem functioning (see King, 1977; Moutinho et al., 2003; Wardle et al., 2011). At ecosystem scales, knowledge of ant mound densities and patterns will be crucial to understanding the impacts of ants, but this information is rarely available. Even less is known about the contribution of ant mounds to the total nutrient pools across ecosystems (Risch et al., 2005; Kilpeläinen et al., 2007).

Studies on the impacts of ant mounds to soil properties have been conducted in forests (Lenoir et al., 2001; Risch et al., 2005; Kilpeläinen et al., 2007), neotropical savannas (Jiménez and Decaëns, 2006), grasslands (Snyder et al., 2002; Wagner et al., 2004; Lane and BassiriRad, 2005) and agricultural lands (Amador and Görres, 2007). The ant species considered thus far include red wood ants (*Formica rufa* group, Lenoir et al., 2001; Domisch et al., 2008), leaf-cutting ants (*Atta sexdens*, Verchot et al., 2003; *Atta colombica*, Hudson et al., 2009), harvester ants (*Pogonomyrmex rugosus*, Whitford and DiMarco, 1995; *Pogonomyrmex occidentalis*, Snyder et al., 2002; *Pogonomyrmex barbatus*, Wagner et al., 2004) and red fire ants (*Solenopsis invicta*, Bender and Wood, 2003), because of their high densities and ecological importance. Ant mounds are also important biogenic structures in wetlands, where they can occur at high densities (Folgarait, 1998; Wu et al., 2010b). However, only a few studies have described ant mound characteristics in wetlands,

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or ant roles in the pedoturbation of wetland soils (Czerwinski et al., 1969; Pętal, 1980; Wu et al., 2013).

Wetland ecosystems comprise one of the most important carbon (C) and nitrogen (N) pools globally. Although wetlands occupy only 5–8% of the land's surface (Mitsch and Gosselink, 2007), they contain 20–25% of the terrestrial C and N pools (Batjes, 1996). Impacts of ant mounds on soil concentrations of C and N might potentially influence overall wetland C and N pools, but to what extent is unknown. Previous nutrient concentration studies have generally studied biogenic structures as a whole rather than analyzing the different components (Frouz et al., 2003; Jiménez and Decaëns, 2006; Hudson et al., 2009). For ant mounds, most research has focused on the above-ground portions of mounds, but Kilpeläinen et al. (2007) found soil nutrient concentrations under mounds were also influenced by ant mound-building.

In this study, we investigated the impacts and contributions of ant mounds to soil carbon and nitrogen pools in a marsh wetland in the Sanjiang Plain, Northeast China. The Sanjiang Plain is one of the largest and most intact freshwater wetlands in China (Liu and Ma, 2002). Numerous ant mounds occur in wetlands of the Sanjiang Plain and often cover a large proportion of the soil surface. Wu et al. (2010a) reported that ant mounds altered soil C, N and P distributions in a wet meadow ecosystem of the Sanjiang Plain. However, impacts and contributions of ant mounds to soil nutrient pools have not been studied in the marsh wetlands, another wide-spread habitat type in Sanjiang Plain. The goals of our study were to: (1) determine whether the soil C and N concentration profiles of ant mounds differed from those of the surrounding wetland soil, and whether such differences varied among ant species and (2) assess the contributions of ant mounds to the total pools of C and N in marsh soils by estimating ant mound nutrient storage and ant mound distribution density. We hypothesized that ant mound soils have enhanced both above and below ground nutrient contents compared to reference soil, and variation in soil nutrient concentrations and contributions to nutrient pools of ant mounds were dependent on the type of ant species present.

2. Materials and methods

2.1. Study site

The Sanjiang Plain is a low floodplain, formed by the Heilong, Songhua and Wusuli rivers, located in Heilongjiang Province of Northeast China. The study was conducted in a *Calamagrostis angustifolia–Carex schmidtii* marsh at the Sanjiang Mire Wetland Experimental Station, Chinese Academy of Sciences (47°13″50′ N, 133°13″10′ E). In the Sanjiang Plain, wetland types vary with gradients in hydro-geomorphologic conditions. *C. angustifolia–C. schmidtii* marsh is seasonally inundated, and a dominant wetland type in the Sanjiang Plain. Besides *C. angustifolia* and *C. schmidtii*, other common plants included *Lythrum salicaria*, *Sanguisorba parviflora*, *Vicia cracca*, *Filipendula palmate*, *Trifolium lupinaster* and *Pedicularis sceptrum-corolinum*. This region experiences a temperate moist monsoon climate with a mean annual temperature of 1.9 °C and a mean annual precipitation of 600 mm. More than 60% of the annual precipitation falls between July and September. The study site is in a seasonally frozen zone and the frost-free period is 125 days. The average monthly temperature is −21 °C in January and 22 °C in July. The average altitude of the study area is 55 m.

Mounds of *Lasius niger*, *Lasius flavus* and *Formica candida* are common in *C. angustifolia–C. schmidtii* marsh of the Sanjiang Plain. The mounds are often constructed from soil excavated from deeper soil layers and plant materials such as leaf litter and twigs. Mounds can be easily identified in the marsh landscape by the pronounced above-ground portions, distinct edges, and the lack of plants growing on their surfaces. Mounds of the different ant species are all orange or yellowish domes, but other physical characteristics differ in many ways (Table 1). The density (number of mounds per hectare) of *L. flavus* and *L. niger* mounds were significantly higher than *F. candida* mounds. Mound heights, base diameters and base areas per mound for *L. niger* were significantly lower than those for *L. flavus* and *F. candida*, but no significant differences were observed between *L. flavus* and *F. candida* mounds (Wu et al., 2013).

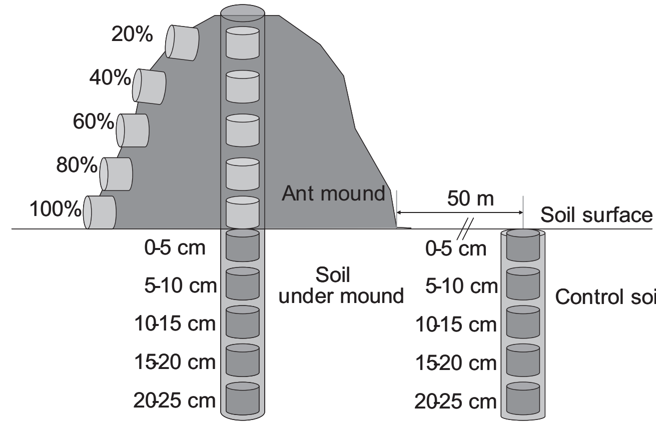

Fig. 1. Sampling methodology to collect soils for this study (adapted from Jiménez and Decaëns, 2006). Sampling locations from aboveground ant mounds were collected systematically along the distance (expressed as a percentage) from the top to the base of the mound. Soils under ant mounds and reference soils were sampled at 5 cm intervals to 25 cm depths.

2.2. Sampling and chemical analysis

Sampling was conducted between May and June 2010, when ants were active. However, mounds are created over many years, and thus much of the mound building activity had been conducted previously. To assess mound distribution across the marsh, five 10 m × 15 m plots were randomly selected, and counts of ant mounds and measurements of mound diameters and heights were made.

To assess individual mound soil characteristics, mounds were grouped by the ant species present. Four average-sized mounds of each ant species (*L. niger*, *L. flavus* and *F. candida*) were selected randomly over the whole marsh surface (7 ha). Mounds were at least 50 m apart to ensure independence. At the same time, four replicate natural soil sites were also selected randomly, at least 50 m from each other or from the ant mound sites to ensure independence. Thus, in total, 16 locations were selected for sampling. We did not pair reference soils with mounds samples because we wanted to generate a measure of nutrient concentration for the overall marsh to more accurately assess the contributions of ant mounds to the overall nutrient pools in the marsh.

Procedures for soil sampling for mound bulk density and chemical analyses are indicated in Fig. 1. We stratified our sampling into three areas: (1) soils from the aboveground portions of ant mounds, (2) soils under ant mounds, and (3) surrounding reference soils. For the aboveground portions of each ant mound, one sample was collected using a stainless steel corer with a diameter of 5 cm, and split into 0–20%, 20–40%, 40–60%, 60–80%, and 80–100% vertical sections from the top to the base of the mound. As per Jiménez and Decaëns (2006), a second sample was taken near the edge of the mound, also at 20%, 40%, 60%, 80% and 100% of the vertical distance from the top to the base. The two samples from the same vertical sections were then combined. Soil cores below the ant mound were taken by reinserting the corer through the center holes through the top of the mounds, to a depth of 25 cm. These cores were then

Table 1
Characteristics of ant mounds in a *Calamagrostis angustifolia–Carex schmidtii* marsh of the Sanjiang Plain, China. Data are average values (with standard errors) and values followed by the same lowercase letter are not significantly different ($p > 0.05$) (Wu et al., 2013).

Species	Density (mounds/ha)	Height (cm)	Base diameter (cm)	Total base area ($m^2\ ha^{-1}$)
Lasius niger	453 (49)[a]	16.2 (0.9)[b]	49.4 (2.9)[b]	96.7 (10.9)
Formica candida	267 (73)[b]	28.6 (1.0)[a]	65.9 (4.5)[a]	98.7 (17.3)
Lasius flavus	507 (104)[a]	29.3 (0.9)[a]	60.6 (3.2)[a]	160.5 (42.1)

subdivided into 5 cm intervals. Reference soil samples were obtained by coring through the top 25 cm of the soil column, and subdividing the core into 5 cm sections.

Soil samples were placed separately into labeled plastic bags, stored immediately on ice to stop further mineralization, and once back at the laboratory refrigerated at 4 °C until analysis. Subsamples, in which ants, stones and other impurities were carefully removed, were dried to constant weight at 40 °C, milled, and passed through a 2-mm sieve for elemental analysis. The chemical analyses were performed at the Key Laboratory of Wetland Ecology and Environment, Chinese Academy of Sciences. Total organic carbon (C_{org}) and nitrogen (TN) in soil were measured with a Carlo Erba FLASHEA 1112 CHN-S analyzer. Inorganic N concentrations in NO_3^- and NH_4^+ forms were measured using the colorimetric method (Lu, 1999). The DOC was extracted from field moist soils by the procedures as described by Ghani et al. (2003), and measured by a total organic C analyzer (TOC V_{CPH}, Shimadzu). Subsamples were dried at 105 °C to calculate bulk density. Total C and nutrient storage ($kg\ m^{-2}$) in ant mounds was calculated by multiplying the soil nutrient concentrations by the area-based ant mound masses (Wu et al., 2010a). Contributions of C and nutrient pools in ant mounds across the marsh ecosystem were calculated by multiplying the soil nutrient storage ($kg\ m^{-2}$ dry weight) by the ant mound densities and average basal areas for individual ant mounds.

2.3. Statistical analysis

Differences in soil C and nutrient concentrations and storages, C/N ratios and bulk densities among mounds of the different ant species, and between ant mounds and reference marsh soils were tested using a one-way ANOVA. A one-way ANOVA was also used to test differences in nutrient concentrations among the vertical soil layers for ant mounds and reference soils. C_{org}, TN and NH_4^+ concentration data, and nutrient storages ($kg\ m^{-2}$ dw) were all $\ln(x+1)$ transformed before analysis to improve normality and to reduce heterogeneity of variance. Least significant difference tests were used to compare treatment means. Results were considered statistically significant at $\alpha = 0.05$. The statistical analyses were conducted with the software SPSS 16.0 package. All figures were drawn using the OriginPro 8.0 software.

3. Results

3.1. Nutrient concentrations, bulk density

Overall concentrations of C_{org} ($F = 12.34$, df = 1, $p = 0.001$), DOC ($F = 7.20$, $p = 0.010$), TN ($F = 13.95$, $p = 0.001$), NO_3^- ($F = 4.87$, $p = 0.033$) and NH_4^+ ($F = 8.26$, $p = 0.007$) in above-ground ant mounds were significantly higher than in the surrounding reference soils (Fig. 2). However, C_{org}, TN, NO_3^- and NH_4^+ concentrations in soils under mounds and reference soils did not differ. DOC concentrations in reference soils were lower than in soils under *L. niger* mounds ($F = 9.87$, df = 3, $p < 0.001$), but not under *F. candida* or *L. flavus* mounds (Fig. 2B).

Among ant species, average C_{org} ($F = 8.07$, df = 2, $p = 0.002$) and DOC ($F = 11.86$, $p < 0.001$) concentrations were generally higher in *L. niger* above-ground mound than *F. candida* and *L. flavus* above-ground mounds, but these latter two species did not differ (Fig. 2A and B). TN, NO_3^- and NH_4^+ concentrations did not differ among above-ground mounds of the three ant species. DOC concentrations were higher ($F = 15.24$, df = 2, $p < 0.001$) and NO_3^- concentrations were lower ($F = 5.68$, $p = 0.009$) in soils under *L. niger* mounds than those under *F. candida* or *L. flavus* mounds (Fig. 2B and E). C_{org}, TN and NH_4^+ concentrations among soils under mounds of the different species were all similar (Fig. 2A, C and D).

C_{org} ($F = 20.08$, df = 4, $p = 0.003$), DOC ($F = 5.89$, $p = 0.039$), TN ($F = 22.40$, $p = 0.002$) and NH_4^+ ($F = 12.12$, $p = 0.009$) concentrations in reference soils were highest at the surface and decreased with depth, while soil layers under ant mounds were all similar (Fig. 2). In above-ground mound soils, NO_3^- concentrations varied among soil layers for all three ant species (*L. niger* $F = 13.21$, df = 4, $p = 0.007$; *F. candida* $F = 6.11$, $p = 0.005$; *L. flavus* $F = 30.85$, $p = 0.001$). An above-ground soil layer effect was also observed for C_{org} ($F = 146.08$, df = 4, $p < 0.001$) in *L. niger* mounds, NH_4^+ ($F = 5.50$, $p = 0.045$) in *F. candida* mounds, and TN ($F = 8.91$, $p = 0.017$) in *L. flavus* mounds. However, peak values did not necessarily occur in the upper-most layers. The interactions between ant species and soil layer were only significant for C_{org} ($F = 15.21$, df = 8, $p < 0.001$) in above-ground mounds.

Soil bulk densities in the above-ground mounds for all three ant species (0.42–0.49 $g\ dm^{-3}$) were much lower than reference soils ($F = 17.13$, df = 3, $p < 0.001$). Soil bulk densities under mounds and in reference soils were all similar (Fig. 3F).

3.2. Nutrient pools

C_{org} ($F = 32.26$, df = 2, $p = 0.009$), TN ($F = 9.78$, $p = 0.048$) and NO_3^- ($F = 7.64$, $p = 0.046$) storage in *L. niger* above-ground mounds was lower in comparison to *F. candida* and *L. flavus* mounds (Fig. 3) because *L. niger* mounds had lower soil bulk densities (Fig. 3F) and volumes (Table 1). Soil C_{org} storage under *L. niger* mounds was significantly lower than reference soils ($F = 56.10$, df = 1, $p = 0.005$), but not significantly different from the other two ant species (Fig. 3A). Soil NO_3^- storage under *L. niger* mounds was also lower than that under mounds of the other two ant species, or in reference soils ($F = 19.51$, df = 3, $p = 0.003$). DOC, TN, NO_3^- and NH_4^+ storage among soils under *F. candida* mounds, soils under *L. flavus* mounds, and reference soils were all similar (Fig. 3).

At the ecosystem scale, the total ant mound surface area in the marsh was low (ranging from 188.4 to 431.5 $m^2\ ha^{-1}$), and so nutrient pools in reference soils were many times larger than those associated with ant mounds (Table 2). Nutrient pools in above-ground and under-ground portions of all three ant species combined contributed 5.3–7.6% of the total (each species alone contributed <4%). Owing to the higher density and larger volume of *L. flavus* mounds (Table 1), the contribution of this species to the total soil nutrient pools was larger than for *F. candida* or *L. niger* (Table 2).

4. Discussion

Our results confirmed that ant mounds contributed measurable amounts to soil nutrient pools in a marsh wetland. The contribution of C_{org} (5.3%) and N (TN 6.1%, NH_4^+ 6.9%, and NO_3^- 7.6%) was higher than that reported from European forests (C and TN 0.6–5.0%

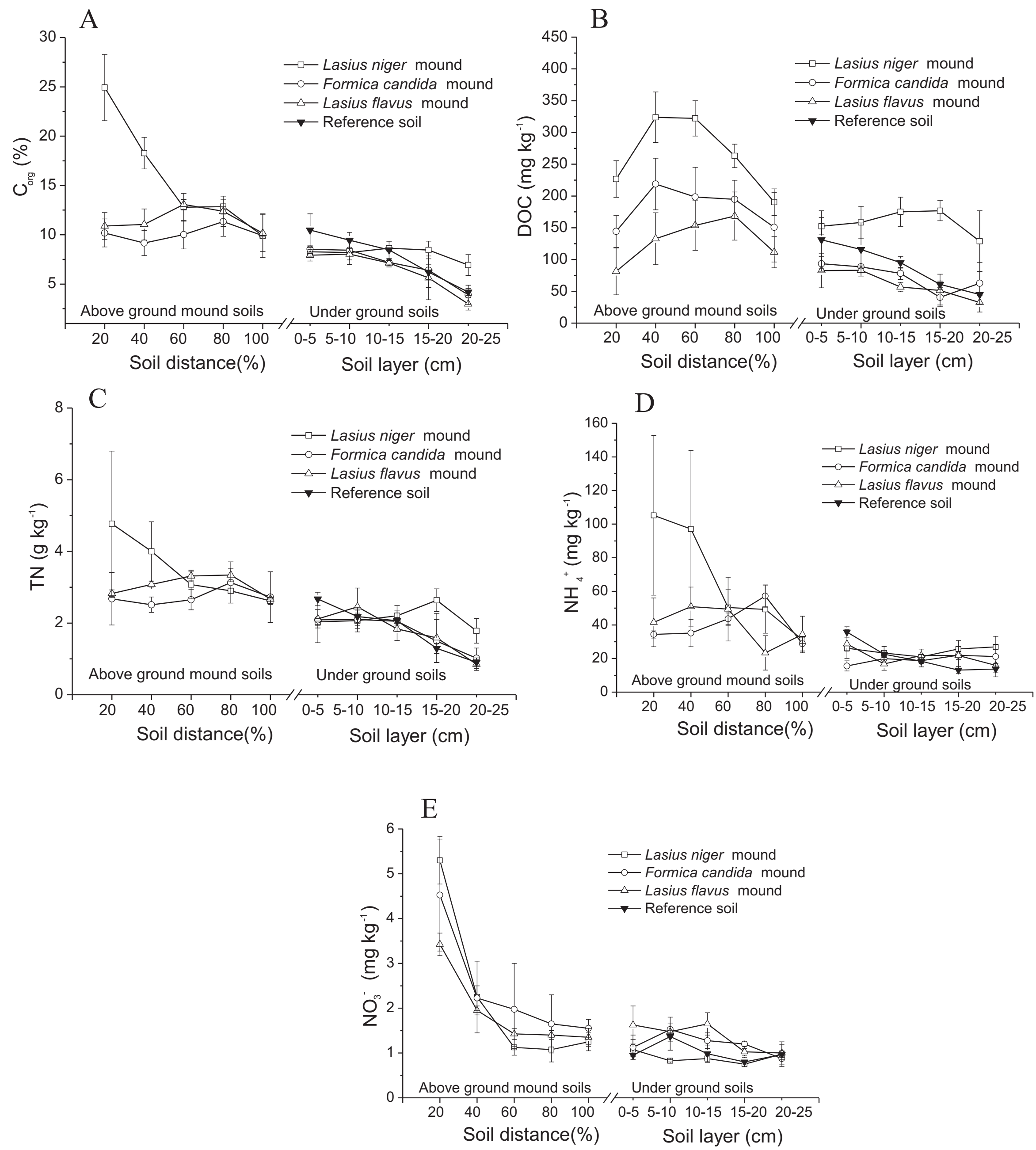

Fig. 2. C_{org} (A), DOC (B), TN (C), NH_4^+ (D) and NO_3^- (E) concentrations (dry matter basis) in ant mounds versus reference soils in a marsh of the Sanjiang Plain, China. C_{org}, organic carbon; DOC, dissolved organic carbon; TN, total nitrogen. Error bars indicate standard error.

by Risch et al., 2005; C and TN <1% by Kilpeläinen et al., 2007). Our field investigations suggest that ant mound frequency and area tend to increase with marsh ecosystem degradation (Wu, unpublished data). Thus ant mounds can be important to a fully integrated understanding of the structure and function of nutrient cycles and balances in wetland ecosystems, an important consideration given on-going global climate change (Osler and Sommerkorn, 2007).

At the ecosystem scale, we determined the contribution of ant mounds to total nutrient pools by estimating nutrient storage per m^{-2} for individual ant mounds and the total ant mound area. To our knowledge, only a few previous studies have similarly examined soil nutrient storage in mounds on an areal basis ($kg\,m^{-2}$) (Wagner et al., 2004; Kilpeläinen et al., 2007; Wu et al., 2010a). Thus, comparing our results to other studies is difficult. However, in general, our TC and TN storage values for three ant species are similar to above-ground mounds of red wood ants in boreal forests (Kilpeläinen et al., 2007), but larger than harvester ant mounds in grasslands (Wagner et al., 2004). TC storage levels were lower than *Formica sanguinea* mounds in a meadow wetland of the Sanjiang Plain, but TC concentrations were similar (Wu et al., 2010a). In the study marsh, the area occupied by ant mounds was extensive (Table 1), because of the high density of ant mounds and diversity of species. However, the individual mound areas were smaller than for red wood ant mounds in forests (Risch et al., 2005; Kilpeläinen et al., 2007). Contributions were also affected by ant species (Table 2), with the contribution of *L. flavus* mounds being larger than *F. candida* and *L. niger* mounds, owing to higher total basal area (Table 1).

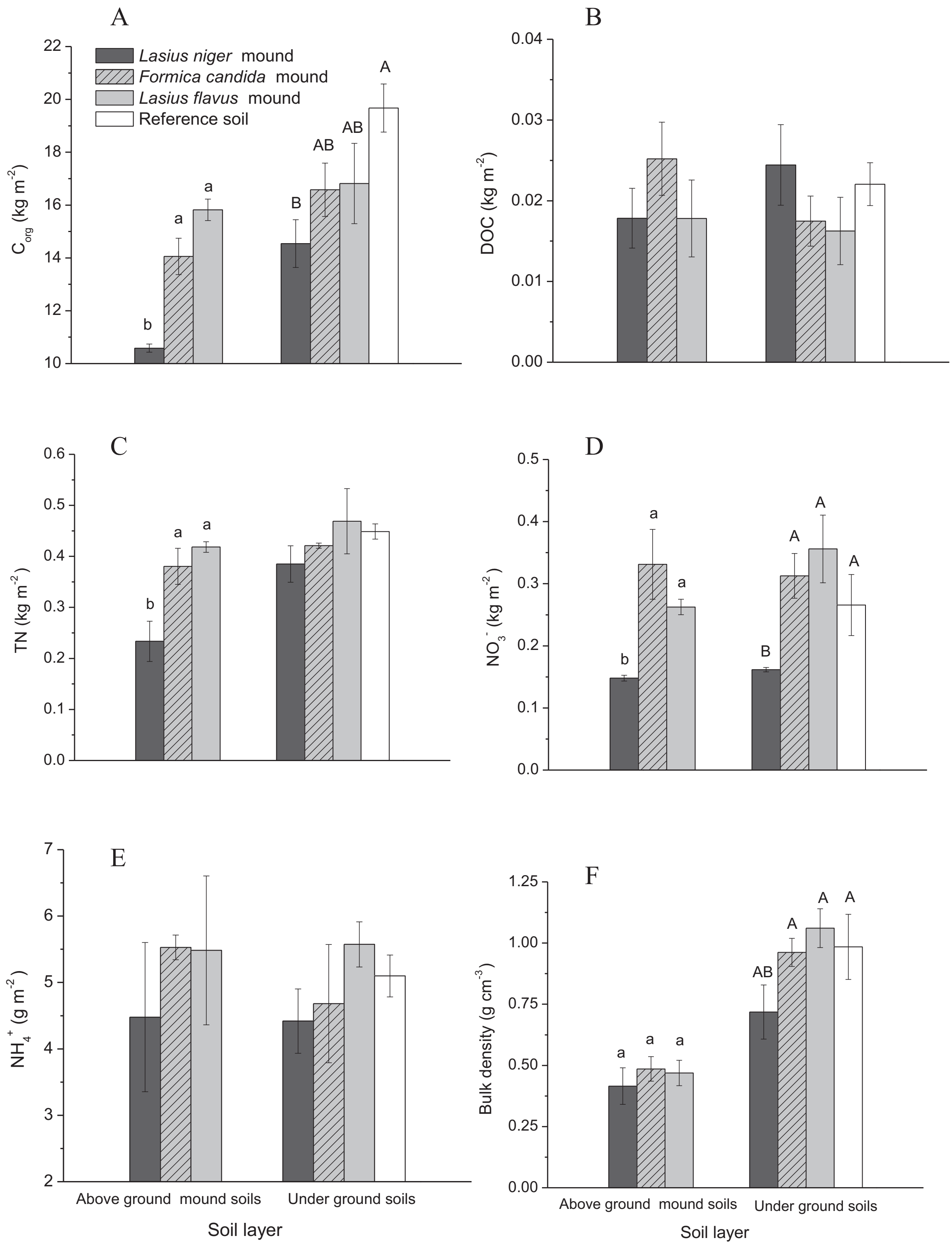

Fig. 3. Mean carbon and nutrient storages (dry matter basis) in aboveground ant mound soils and in soils under ant mounds down to 25 cm depths, and from surrounding reference soils to 25 cm depths in a marsh of the Sanjiang Plain, China. TC, total organic carbon; DOC, dissolved organic carbon; TN, total nitrogen. Error bars indicate standard error. Letters indicate significant differences ($p < 0.05$) for ant mounds versus reference soil (a and b for aboveground mound soils, A and B for under ground soils).

Soil nutrient storage on an areal basis is determined not only by soil nutrient concentrations, but also by soil bulk density and mound height. Even though above-ground mounds of *F. candida* and *L. flavus* had higher C and nutrient concentrations than surrounding marsh soils, and their average mound heights were greater than 25 cm, they stored lower or similar amounts of soil C and nutrient than surrounding soils, contrary to what Wagner et al. (2004) and Kilpeläinen et al. (2007) found. Ant activities reduced soil bulk density in above-ground mounds (Fig. 3), which was the key factor responsible for lower nutrient storage. However, for harvester ants, the bulk density of mounds and surrounding soils were similar (Wagner et al., 2004). In our study, nutrient storage in

Table 2
Mean carbon and nitrogen pools (dry weight, per hectare of natural marsh) and contributions (%) in above-ground ant mound soils and soils under ant mounds (0–25 cm) for three different ant species, and for reference soils (0–25 cm) in a marsh of the Sanjiang Plain, China.

	C_{org}		DOC		TN		NO_3^-		NH_4^+	
	Pool (kg ha^{-1})	Contribution (%)	Pool (kg ha^{-1})	Contribution (%)	Pool (kg ha^{-1})	Contribution (%)	Pool (g ha^{-1})	Contribution (%)	Pool (g ha^{-1})	Contribution (%)
Above ground mounds										
Lasius niger	1023 (149)	0.5 (0.07)	1.7 (0.17)	0.8 (0.07)	22.6 (3.8)	0.5 (0.08)	14.3 (2.5)	0.5 (0.02)	433 (108)	0.8 (0.21)
Formica candida	1387 (68)	0.7 (0.03)	2.5 (0.45)	1.1 (0.20)	37.6 (3.5)	0.8 (0.08)	32.7 (5.6)	1.3 (0.21)	545 (83)	1.0 (0.35)
Lasius flavus	2539 (65)	1.3 (0.03)	2.9 (0.76)	1.3 (0.34)	67.2 (6.4)	1.5 (0.04)	42.1 (2.0)	1.6 (0.08)	880 (180)	1.7 (0.34)
Soil under mounds										
Lasius niger	1406 (88)	0.7 (0.04)	2.8 (0.39)	1.2 (0.17)	37.2 (3.5)	0.8 (0.08)	15.6 (3.4)	0.6 (0.01)	427 (47)	0.8 (0.08)
Formica candida	1636 (100)	0.8 (0.05)	1.7 (0.31)	0.8 (0.13)	41.6 (3.1)	0.9 (0.01)	30.9 (3.6)	1.2 (0.14)	462 (87)	0.9 (0.17)
Lasius flavus	2698 (292)	1.4 (0.15)	2.6 (0.67)	1.2 (0.29)	75.3 (10.3)	1.6 (0.22)	61.9 (2.3)	2.4 (0.09)	895 (54)	1.7 (0.10)
Surrounding reference soils	189,750 (8785)	94.7 (4.4)	212 (26)	93.8 (11.3)	4327 (414)	93.9 (3.12)	2404 (161)	92.4 (6.17)	49,178 (3041)	93.1 (5.77)

mounds was affected by ant species. *L. niger* mounds had the lowest soil bulk densities (Fig. 3) and mound heights (Table 1), and in turn the lowest C_{org}, TN and NO_3^- storage. Lower nutrient storage in ant mounds than natural marsh soils suggests that the formation and development of ant mounds may induce declines in C and nutrient storage functions in marsh ecosystems. In addition, mound formation may alter water flow across soil surfaces and increase soil erodibility because mounds are highly erodible, contain large soil macropores and lack vegetative cover (Cerdà and Jurgensen, 2008; Cerdà and Doerr, 2010). These factors also would impact soil nutrient pool functions.

The enriched nutrient concentrations in above-ground mounds confirmed that ant mounds can impact soil nutrients in marsh ecosystems, which is in agreement with previous work in meadow wetlands (Pętal, 1980; Pętal and Kusinska, 1994; Wu et al., 2010a). Compared to the results for *Formica*-group mounds in forests (Risch et al., 2005; Kilpeläinen et al., 2007), C concentrations for *F. candida* mounds in our study were lower. In contrast, C concentrations for *L. flavus* and *L. niger* mounds in our study were higher than those reported by Holec and Frouz (2006). In our study, nitrogen concentrations in aboveground ant mounds were higher than natural reference marsh soils, but did not significantly differ among ant species. However, Holec and Frouz (2006) found TN concentrations were lower in *L. niger* and *L. flavus* mounds than the reference soils. Beattie and Culver (1983) showed no significant differences in nitrogen content between *F. canadensis* nests and surrounding soils. Studies on *Pogonomyrmex* showed mounds to be enriched in nitrogen (*P. rugosus*, Whitford and DiMarco, 1995; *P. occidentalis*, Snyder et al., 2002; *P. barbatus* Wagner et al., 2004).

Enrichment of soil nutrients in ant mounds indicates that rates of nutrient input exceed the rates of loss. Inputs of organic matter to ant mounds result from ant foraging and construction activities (Folgarait, 1998; Laakso and Setälä, 1998; Wagner et al., 2004; Kilpeläinen et al., 2007). *L. niger* has generalized food habits and adds plant litter, insect remains, floral nectar, and Homoptera honeydew to mound surfaces. *L. flavus* mainly feeds on honeydew from root-feeding aphids. *F. candida* is omnivorous, carrying plant litter and dead insects into their mounds. The inputs of many different types of organic matter into the mounds of *L. niger* may have caused the high C_{org} and nutrient content in the upper soil layers.

Nutrient concentrations are also influenced by changes in soil nutrient processes such as respiration, decomposition, mineralization and denitrification (Dauber and Wolters, 2000; Risch et al., 2005; Domisch et al., 2008). Decomposition rates in ant mounds of wetlands should be larger than natural soils because ant mound formation converts an anoxic environment to an aerobic environment. High C/N ratios usually suggest slow decomposition rates (Berg and McClaugherty, 2003). In our study, the soil C/N ratio was higher in *L. niger* above-ground mounds than in *F. candida* or *L. flavus* above-ground mounds ($F = 4.95$, df = 2, $p < 0.05$). Thus higher C/N ratios in *L. niger* mounds may indicate slower organic matter decomposition rates compared to the other two ant species, which may in turn lead to the higher C_{org} content. In terms of N, higher NH_4^+ and NO_3^- content suggests higher rates of N mineralization (Lenoir et al., 2001; Verchot et al., 2003). Studies elsewhere (Dauber and Wolters, 2000; Ginzburg et al., 2008) reported N-fixing microbes are more abundant in ant mounds than in the surrounding soils. Further, Stadler et al. (2006) found that enzyme activities increased in ant mounds. Numerous factors may affect relative C and N concentrations between ant mounds and natural soils, and among mounds of different ant species.

Our results indicate the ant activities mostly affect above-ground soils. But this does not mean there were no effects of ant activities on soils under mounds. As reported elsewhere (Levan and Stone, 1983; Holec and Frouz, 2006), we assume ants transport soils from deep horizons, and mix upper organic and deeper mineral soils, thus changing nutrient profiles. In our study, soil layers under ant mounds were fairly homogenous (Fig. 2), while reference soil layers were stratified with highest values at the surface, suggesting mixing of soils under mounds during the process of mound development.

5. Conclusions

Our results confirm that ant mounds alter soil C and N concentrations and spatial characteristics among soil layers in marshes. Our study also demonstrated that formation of ant mounds can change overall soil C and N storage. Ant mounds contributed measurable amounts (5.3–7.6%) to the total nutrient pools of marsh soils. The impacts and contributions of ant mounds varied by ant species. Thus, ant mounds increased the spatial heterogeneity of nutrients pools, and are important for a more complete understanding of C and N pool functions and balances in wetland ecosystems.

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