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Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra

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Ecologists have long been intrigued by the ways co-occurring species divide limiting resources. Such resource partitioning, or niche differentiation, may promote species diversity by reducing competition^{1,2}. Although resource partitioning is an important determinant of species diversity and composition in animal communities³, its importance in structuring plant communities has been difficult to resolve⁴. This is due mainly to difficulties in studying how plants compete for belowground resources⁵. Here we provide evidence from a ¹⁵N-tracer field experiment showing that plant species in a nitrogen-limited, arctic tundra community were differentiated in timing, depth and chemical form of nitrogen uptake, and that species dominance was strongly correlated with uptake of the most available soil nitrogen forms. That is, the

most productive species used the most abundant nitrogen forms, and less productive species used less abundant forms. To our knowledge, this is the first documentation that the composition of a plant community is related to partitioning of differentially available forms of a single limiting resource.

Species-rich plant communities seemingly contradict the competitive exclusion principle, a fundamental tenet of ecology that predicts that species occupying the same niche cannot coexist, or that the number of species cannot exceed the number of limiting resources^{6,7}. Plants have nothing comparable to the 'food niche' of animals. At the global level the 300,000 terrestrial plant species may have only 20 different limiting resources (light, water, CO₂ and the same set of mineral nutrients), and field experiments indicate that at most three or four resources are limiting in any plant community². Consequently, some assert that resource partitioning is unimportant in maintaining species diversity in plant communities^{8,9}.

We studied tussock tundra in arctic Alaska where plant growth is primarily limited by soil nitrogen availability¹⁰. Despite this shared limitation, species with graminoid, deciduous shrub, evergreen shrub, cryptogam and forb growth forms typically co-occur in tussock tundra at scales of less than 0.1 m² (ref. 11). This 'paradox of diversity' could be resolved if variations in resource acquisition in space and time among plant species lead to resource partitioning¹², thereby allowing coexistence on a single limiting resource. There is abundant evidence that tundra plant species differ in rooting depth¹³, phenology¹⁴, and uptake preferences for different chemical forms of nitrogen (ammonium, nitrate and a variety of free amino acids)^{13,15}. Similar interspecific differences have been observed for many other plant communities^{12,16,17}. However, evidence that such differences contribute to resource partitioning within communities is limited¹⁸.

We used ¹⁵N-tracers in tussock tundra at Toolik Lake, Alaska (68° 38' N, 149° 34' W, elevation 760 m), to address two questions: how are species spatially, temporally and chemically differentiated in their use of soil nitrogen and are such niche differences consistent with community structure? We hypothesized that if niche differentiation reduces competition for soil nitrogen, its signature should be evident in patterns of species dominance (productivity). That is, dominant species should use the most available forms of soil nitrogen and subordinate species less available forms.

Soluble nitrogen fractions in tundra soils vary seasonally and are strongly dominated by organic forms, including free amino acids, with lower concentrations of ammonium and nitrate¹⁹. To trace how tundra species differ in uptake of different soil nitrogen sources, we injected three chemical forms (ammonium, nitrate and glycine) of ¹⁵N-labelled nitrogen at two soil depths (3 and 8 cm) twice (24 June and 7 August) in a growing season. Separate 1.5 m × 1.5 m plots were used for each of the 12 treatment combinations of chemical form, depth and time (3 × 2 × 2 factorial design). For each of the five most abundant vascular plant species (Table 1), we measured ¹⁵N tracers in aboveground tissues seven days after treatment for replicate plants (*n* = 3 to 6) in each plot. Uptake of the form of available nitrogen corresponding to the ¹⁵N label in each treatment

Table 1 Plant species analysed for uptake of ¹⁵N in tussock tundra at Toolik Lake, Alaska

Species*	Growth form	Peak aboveground biomass (% of community total)†	Aboveground net primary production (% of community total)‡
<i>Carex bigelowii</i>	Graminoid	1 ± 1	3 ± 1
<i>Eriophorum vaginatum</i>	Graminoid	19 ± 6	40 ± 14
<i>Vaccinium vitis-idaea</i>	Evergreen shrub	18 ± 3	10 ± 2
<i>Ledum palustre</i>	Evergreen shrub	32 ± 4	16 ± 2
<i>Betula nana</i>	Deciduous shrub	19 ± 5	16 ± 4

* The five species described here accounted for 89% of total community aboveground biomass and 84% of net primary production. Of the 15 vascular plant species we found in this community, these were the only species that occurred in all 12 treatments. There were an average of seven vascular species per quadrat within the 20 cm × 20 cm control quadrats used to measure biomass and productivity. On average, four out of the five species in Table 1 occurred in the same quadrats. Species' root systems were closely intertwined within the organic soil layer.

† Peak (August) total aboveground vascular plant biomass = 348 ± 30 g dry weight per m².

‡ Total aboveground vascular plant net primary production = 163 ± 21 g dry weight per m² per yr.

Data are shown ± 1 standard error.

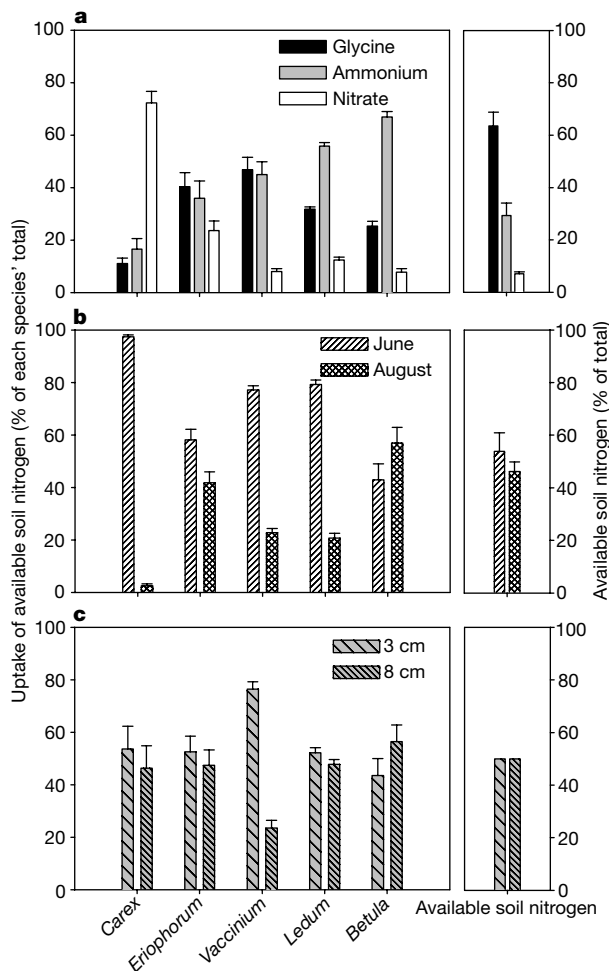


Figure 1 Aboveground uptake of available soil nitrogen by the five most common species in tussock tundra. Data is shown for chemical form, time and depth (left panels in **a**, **b** and **c**, respectively). The corresponding pools of available (1 M KCl-extractable) soil nitrogen are shown for comparison (right panels in **a**, **b** and **c**). Data are expressed as a percentage of each species' total uptake (left panels), or as a percentage of total available nitrogen (right panels). Data were summarized from Table 2 as the pooled means and standard errors for treatments having a common ¹⁵N label (chemical form, depth or time).

was calculated using an isotopic mixing model that included three variables: the amount of ¹⁵N label applied, the amount of the corresponding source of available nitrogen estimated to be within the diffusion zone of the ¹⁵N label, and the measured uptake of ¹⁵N label (Methods, equation (2)). To normalize, we expressed available nitrogen uptake per treatment as a percentage of each species' total uptake across all 12 treatments (Table 2).

The five most common species were well differentiated in chemical form, timing, and depth of available nitrogen uptake (left frames in Fig. 1a–c). Only *Carex bigelowii* Torr. (Bigelow sedge) used mainly nitrate. *Eriophorum vaginatum* L. (cottongrass) and *Vaccinium vitis-idaea* L. (low-bush cranberry) relied mainly on glycine and ammonium; however, *Vaccinium* obtained more of these forms earlier in the growing season and at a shallower depth than did *Eriophorum*. *Ledum palustre* L. (Labrador tea) and *Betula nana* L. (dwarf birch) used mainly ammonium but differed in timing of uptake. Thus each species occupied a different niche with respect to nitrogen use. We cannot be certain that some portion of tracer nitrogen was not microbially transformed to other compounds before plant uptake (for example, glycine-N may be transformed to ammonium-N or vice versa). Nonetheless, the data indicate that species used the original tracers in fundamentally different ways. Moreover, patterns of tracer use should also reflect how native forms of soluble nitrogen are transformed and ultimately partitioned among species.

Comparison of species' uptake patterns to the pattern of available nitrogen across chemical forms, seasons and depths (left versus right frames in Fig. 1a–c) suggests that dominance is related to a species' ability to exploit the most abundant resources. *Eriophorum*, the most productive species in this community, used nitrogen in a combination of chemical forms and seasons that closely matched the most available forms of nitrogen (glycine and ammonium). In contrast, *Carex*, the least productive of five dominants (Table 1), primarily used the least available nitrogen form (nitrate) and did not compete for nitrogen later in the growing season. More precisely, *Eriophorum* and *Carex* had patterns of uptake that were 71 and 31% similar, respectively, to the pattern of nitrogen availability across all treatments, as calculated from:

$$S_i = 100 - 0.5 \sum_{h=1}^T |u_h - a_h| \quad (1)$$

where, for species *i*, *S* is the percentage similarity between the pattern of uptake and the pattern of available nitrogen across *T* = 12 treatments, *u_h* is the percentage of species *i*'s total uptake of available nitrogen in treatment *h*, and *a_h* is the percentage of total available nitrogen in treatment *h* (Table 2)¹². Across all five species, productivity increased hyperbolically with the similarity between the pattern of uptake and pattern of available nitrogen (*r*² = 0.96, *P* = 0.004; Fig. 2). We tested the sensitivity of this result to uncertainties in our estimates of available glycine and the depth distribution of all three chemical nitrogen forms (see Methods). This analysis showed the relationship between productivity and *S* was very robust with respect to these uncertainties (Fig. 2).

Other studies^{13,16–18} have shown spatial, temporal or chemical differences in resource use among co-occurring plant species, but have not characterized mechanisms by which those differences

Table 2 Species' uptake and available amounts of native soil nitrogen for ¹⁵N-labelled treatments

Species	Percentage values												Total across treatments (μg m ⁻²)	I.s.d.*	
	Glycine				Ammonium				Nitrate						
	June		August		June		August		June		August				
	3 cm	8 cm	3 cm	8 cm	3 cm	8 cm	3 cm	8 cm	3 cm	8 cm	3 cm	8 cm			
Nitrogen uptake															
<i>Carex</i>	1	9	0	0	8	5	0	0	39	36	1	1	3	17	
<i>Eriophorum</i>	17	13	2	9	9	11	11	5	6	3	6	8	2	10	
<i>Vaccinium</i>	35	5	6	3	25	6	7	6	3	3	1	0	13	9	
<i>Ledum</i>	14	9	3	5	22	23	6	5	6	5	1	1	23	5	
<i>Betula</i>	9	6	6	5	10	11	16	30	3	1	2	1	4	12	
Available nitrogen	16	16	16	16	8	8	6	6	3	3	1	1	4,979	–	

* Least significant difference (I.s.d., *P* = 0.05) is given for comparing treatment means within rows.

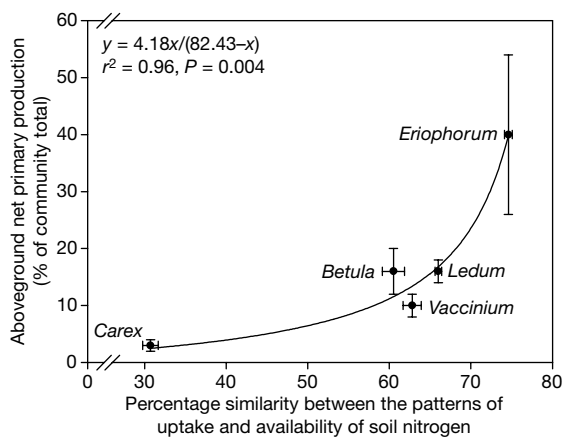


Figure 2 Aboveground net primary production (mean \pm standard error) of the five most common species in tussock tundra. Data is shown as a function of the percentage similarity (S) between the pattern of uptake and pattern of available soil nitrogen across three chemical forms, two seasons and two depths. S was calculated by applying equation (1) to the data in Table 2. Standard errors for S were calculated from a sensitivity analysis in which we assigned a maximum uncertainty of $\pm 50\%$ for estimated amounts of total available glycine and the depth distribution of available glycine, ammonium and nitrate (see Methods).

influence species diversity and composition. We have proposed that if niche differentiation promotes coexistence by ‘sufficiently’ reducing competition, its signature should be evident in the pattern of species dominance. Our results clearly support this hypothesis by showing that species dominance in tussock tundra is positively correlated with use of the most available soil nitrogen resources.

Our results are consistent with solution culture studies showing differential uptake of ammonium and free amino acids by excised roots¹³ or intact plants of these species in isolation¹⁵. However, because we measured nitrogen uptake in a competitive environment, our study and those conducted in solution culture are not directly comparable. In particular, uptake preferences of species isolated in solution culture should more closely reflect species’ fundamental niches²⁰. For example, when isolated in solution culture, *Ledum*, *Eriophorum*, *Betula* and *Carex* all preferred glycine over ammonium, albeit in different ratios (the glycine to ammonium uptake was 4.31, 1.45, 1.32 and 1.05, respectively)¹³. Our study shows that of these four species only *Eriophorum* took up more glycine than ammonium (ratio, 1.14) in the field, suggesting that our *in situ* measurements estimate realized niches²⁰. Taken together, these studies are consistent with the idea that dominance is the appropriation of potential (fundamental) niche space of subordinate species by other dominant species²¹. Thus, *Eriophorum* appears to have pre-empted the most favourable niches in this community.

Although our results clearly support the niche diversification hypothesis¹, our focus on the most abundant species in this community has emphasized factors (the competitive interactions involving *Eriophorum*) that are sufficiently common to have predictable effects on community structure. The importance of niche differentiation in facilitating the coexistence of the less abundant plant species in this community is an important, unresolved question. For example, the occurrences of rare species may depend primarily on infrequent or less predictable factors, such as random gaps in the spacing of dominant species, spatial heterogeneity in soil nitrogen resources, and small-scale disturbances⁹. However, across all 15 vascular plant species in this community, species productivity generally decreased in a rank-ordered geometric series ($r^2 = 0.96$, $P < 0.001$). This dominance pattern is commonly associated with plant communities of severe environments and is generally thought to be a result of niche pre-emption. In contrast, species-rich plant communities in temperate and tropical environments more commonly fit a lognormal distribution, a

dominance pattern that may reflect a larger number of controlling factors²². Our study provides a clearer view of belowground competitive interactions, and establishes a means to better examine fundamental questions about plant species diversity. □

Methods

Field site

This experiment was conducted in 1992 in moist tussock tundra near Toolik Lake, Alaska, at the Arctic Tundra Long Term Ecological Research (LTER) Site in the northern foothills of the Brooks Range. The soil is a histic pergelic cryaquept²³ and consists of a 10–50-cm peat layer over a silty mineral soil and permafrost. During the June–August growing season, mean air temperature is around 9.3°C, total precipitation is about 180 mm, and the depth of thaw moves from near the surface to just below the organic soil layer. The vegetation at the study site¹¹ is similar to tussock tundra across the Alaskan North Slope, northern Canada, and eastern Siberia²⁴.

Plant biomass and productivity

Species biomass (g m^{-2}) and net primary production ($\text{g m}^{-2} \text{ yr}^{-1}$) were measured on 26–28 June and 8–13 August to coincide with the times of ¹⁵N labelling. At each time, total aboveground biomass was destructively measured for 16 randomly located 20 cm \times 20 cm control quadrats near the ¹⁵N plots. Aboveground net primary production was determined from biomass of tissues produced during the current year, including leaves, apical stems and inflorescences, plus a separate measure of secondary stem production at this site²⁵.

¹⁵N treatments

The twelve ¹⁵N treatment plots were randomly located along a transect parallel to the slope contour (slope angle, $\sim 5^\circ$). Plots were separated by at least 2 m. We injected the ¹⁵N (99 atom percentage ¹⁵N) in solution (11 mmol l⁻¹) as ammonium chloride, potassium nitrate or glycine. A syringe fitted with a four-sideport needle was used to deliver 2 ml to the desired depth (3 or 8 cm) at each of 431 injection sites per plot (test injections with dye showed a diffusion radius of about 1.5 cm around points of injection). The injection sites were spaced in a 7.5 cm \times 7.5 cm grid, with alternate rows offset to distribute the ¹⁵N more evenly. This spacing delivered 65 mg ¹⁵N per m².

Plant ¹⁵N analyses

Seven days after ¹⁵N injection, the aboveground biomass of up to six replicate plants of each of the five dominant species (Table 1) was randomly sampled from the central 1 m \times 1 m area of each 1.5 m \times 1.5 m treatment plot. We used a Finnigan MAT Delta S isotope mass spectrometer to determine atom percentage ¹⁵N on dried, milled plant samples. Background nitrogen content and natural abundance of ¹⁵N were determined from replicate samples ($n = 3$) of each species collected from the 20 cm \times 20 cm control quadrats.

Available nitrogen

Native concentrations (g N per g dry soil) of available ammonium, nitrate and glycine were determined for the upper 10 cm of organic soil in mid-June, mid-July and mid-August for a related study near the ¹⁵N plots (K.K., unpublished data). Concentrations for the 24 June and 7 August ¹⁵N treatment dates were linearly interpolated from the concentrations for the three times of soil sampling. Ammonium and nitrate concentrations were measured by autoanalyser methods on 1 M KCl extracts. Glycine concentrations were measured by high-performance liquid chromatography (HPLC) on water extracts, a method that does not include total exchangeable (KCl-extractable) glycine. Other work has shown that concentrations of water extractable glycine are 5 to 20 times lower than concentrations of KCl-extractable glycine (T. Nasholm, unpublished data; ref. 26). As an initial estimate, we multiplied our glycine data by 10 to express availabilities of all three forms of nitrogen on a 1 M KCl-extractable basis. Also as an initial estimate, we assumed total available nitrogen was equally distributed by depth within the 10-cm soil layer. To test the sensitivity of our results to uncertainties in these two estimates, we recalculated each species’ uptake of available nitrogen (equation (2)) and S (equation (1)) for all combinations of a 0, +50 or -50% change in available glycine and the depth distribution of available glycine, ammonium and nitrate (a 50% decrease in available nitrogen for the 3-cm treatment depth corresponded to a 50% increase for the 8-cm treatment depth and vice versa).

Nitrogen uptake calculations

Species aboveground uptake of the ¹⁵N labels ($\mu\text{g m}^{-2}$) was calculated from data on nitrogen content, atom percentage ¹⁵N in excess of natural abundance, and biomass per m². Uptake of the form of available nitrogen corresponding to the treatment ¹⁵N label was calculated using an isotopic mixing model:

$$U_{\text{unlabelled}} = U_{\text{labelled}}(m_{\text{unlabelled}}/m_{\text{labelled}}) \quad (2)$$

where m_{labelled} is the total mass (g m^{-2}) of ¹⁵N-labelled nitrogen injected per treatment, $m_{\text{unlabelled}}$ is the mass of the ‘target’ pool of available nitrogen estimated to be within the diffusion zone of injected ¹⁵N (for example, the mass of 1 M KCl-extractable ammonium within a 1.5-cm spherical radius of injections of ¹⁵N-ammonium at the 3-cm soil depth in late June), U_{labelled} is uptake (g m^{-2}) of ¹⁵N from the source m_{labelled} , and $U_{\text{unlabelled}}$ is uptake of available nitrogen from the source $m_{\text{unlabelled}}$.

Treatment comparisons

The calculated nitrogen uptake data (Table 2) were used to compare how species differ in their patterns of uptake across treatments. We emphasize that the data cannot be used to compare how species partition total nitrogen uptake within treatments because the total amount of ¹⁵N uptake by each species strongly depends on the relationship between lateral rooting distance and the spacing of ¹⁵N injections. In this experiment, where ¹⁵N injections were spaced in a 7.5-cm grid, *Ledum* took up six times more ¹⁵N across all treatments than *Eriophorum* (¹⁵N data not shown). In a different experiment designed to determine species' lateral rooting distances, we injected a constant amount of ¹⁵N (114 mg as a mixture of 25 mmol l⁻¹ each of glycine, ammonium and nitrate) at different treatment radii (5, 10, 20, 40, 60 and 100 cm) around individual plants of *Eriophorum* and *Ledum*. That design allowed ¹⁵N uptake data to be spatially integrated across all treatment radii, simulating how ¹⁵N would be taken up from injections spaced infinitely close together over an area with a radius of 100 cm. Although those results showed that the primary lateral radius of uptake (about 60% of total uptake) of *Eriophorum* was about half that of *Ledum* (5 versus 10 cm), *Eriophorum* took up almost twice as much ¹⁵N as *Ledum* when the data were extrapolated on a community basis (uptake per unit ground area) (R.B.M., unpublished data). The results of both experiments show that widely spaced tracer injections disproportionately label species with larger rooting areas but lower uptake capacities per unit ground area (for example, *Ledum*). In contrast, species' patterns of uptake across treatments (within rows), as presented here, should be relatively robust with respect to the spacing of tracer injections.

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Competing interests statement

The authors declare that they have no competing financial interests.

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Polyandrous females avoid costs of inbreeding

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Why do females typically mate with more than one male? Female mating patterns have broad implications for sexual selection^{1,2}, speciation³ and conflicts of interest between the sexes⁴, and yet they are poorly understood. Matings inevitably have costs⁵, and for females, the benefits of taking more than one mate are rarely obvious. One possible explanation is that females gain benefits because they can avoid using sperm from genetically incompatible males, or invest less in the offspring of such males^{6,7}. It has been shown that mating with more than one male can increase offspring viability^{8–12}, but we present the first clear demonstration that this occurs because females with several mates avoid the negative effects of genetic incompatibility¹³. We show that in crickets, the eggs of females that mate only with siblings have decreased hatching success. However, if females mate with both a sibling and a non-sibling they avoid altogether the low egg viability associated with sibling matings. If similar effects occur in other species, inbreeding avoidance may be important in understanding the prevalence of multiple mating.

Previous studies of the highly polyandrous¹⁴ (mating with more than one male)¹⁰ field cricket *Gryllus bimaculatus* have shown that polyandry is associated with increased egg hatching success¹⁰. This benefit appears to stem from males having higher fertilization success when they mate with females with whom they are genetically more compatible. As yet, the source of this incompatibility is unknown. Within natural populations the negative effects of homozygosity for deleterious recessive alleles and at loci with heterozygote advantage¹⁵ mean that mating with a close relative is likely to be a major source of genetic incompatibility. We suggest that females may be able to avoid this threat to their reproductive success through some mechanism that enables them to preferentially fertilize their eggs with sperm from genetically compatible males. To test this hypothesis we conducted a study in which females were allocated matings with males of known relatedness. Our prediction is that females mating with two relatives will have low offspring viability, but that polyandrous females mating with both closely related and unrelated males will have offspring viability comparable with females only mating to unrelated males.

Blocks of four sibling females were assigned to one of four treatments, all of which involved one mating with each of two different males, either with two siblings (SS), two non-siblings (NN) or a sibling and a non-sibling in either order (SN and NS) (see Methods). After mating, the hatching success of eggs was recorded. Randomized block analysis of variance reveals a significant effect of mating treatment on proportional egg hatching success ($F_{3,75} = 6.01$, $P = 0.001$) (Fig. 1). Hatching success does not differ significantly between experimental blocks ($F_{25,75} = 1.48$, $P = 0.10$). Post hoc analysis (Tukey test) of egg hatching indicates that the significant effect of treatment is due to the lower hatching success of females mated to two siblings relative to females mated to at least one non-sibling (Fig. 1) (Tukey test: NN versus SN or NS, minimum $P = 0.68$; SS mating versus other treatments, maximum $P = 0.05$). This suggests that females mating with a sibling and a non-sibling have egg viability similar to that of completely outbreeding females, rather than halfway between completely outbreeding and completely inbreeding females. We can test this explicitly by comparing the hatching success of females within each block using a paired *t*-test of mean hatching success of NN

