

# Rocks create nitrogen hotspots and N:P heterogeneity by funnelling rain

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**Abstract** We postulated that soil nutrient heterogeneity arises not only through physical and biological processes in the soil, but also through emergent rocks diverting precipitation containing nutrients to the surrounding soil. To test this idea—which we call the ‘funnelling effect’ of such rocks—we placed ion-exchange resin in small boxes beside rocks and in open soil on a pristine glacial forefield site in Switzerland, and measured the amounts of  $\text{NH}_4^+$ ,  $\text{NO}_3^-$ ,  $\text{NO}_2^-$  and  $\text{PO}_4^{3-}$  that were adsorbed. We also placed resin bags beneath PVC funnels of different sizes so that we could calibrate the natural funnelling effect of rocks.

We obtained strong linear relationships between nitrogen (N) adsorbed and rain-collecting area of both rocks and funnels. Although the mean rain-collecting area of rocks was only 0.02 m<sup>2</sup>, mean N adsorption was around 10 times higher within 1 cm of rocks than further away. In contrast, phosphorus (P) was not concentrated beside rocks, so that N:P stoichiometry varied spatially. *Rumex scutatus* and *Agrostis gigantea* plants that rooted beside rocks had significantly higher foliar N concentrations than those growing further away, in line with the resin data. However, the two species showed differing responses in foliar P and N:P. We propose that *R. scutatus* benefits from the increased N supply by increasing its uptake of soil P, while *A. gigantea* is unable to do so. This study clearly demonstrates that aboveground rain-funnelling structures can produce spatial heterogeneity in N supply, thereby creating a diversity of nutritional niches for plants.

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## Introduction

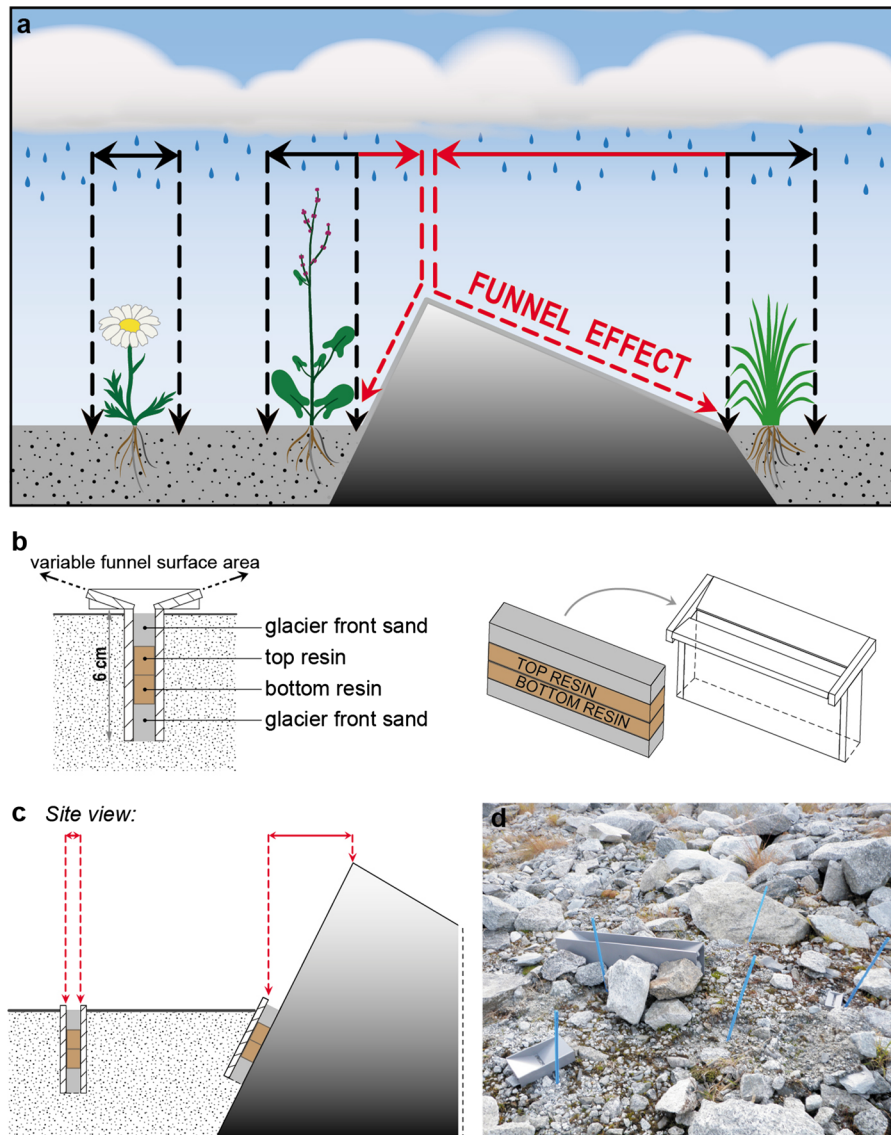
For various terrestrial ecosystems it is shown that nutrients are rarely distributed uniformly in the soil but exhibit patterns of spatial heterogeneity (Stenger et al. 1998; Schlesinger et al. 1996; Gallardo et al. 2005; Li et al. 2008; Mellert et al. 2008). In one study of an alpine ecosystem, nitrogen (N)-rich ‘hotspots’ contributed more than 50 % of the N availability even though they represented only 14 % of the area sampled (Darrouzet-Nardi and Bowman 2011). Similarly, soil P and other elements are often patchily distributed (Schlesinger et al. 1996; Fisher et al. 1998; Litaor et al. 2005; Liptzin et al. 2013). By increasing the diversity of microhabitats, soil nutrient heterogeneity can promote the co-existence of plant and microbial species, thereby increasing the overall species richness of communities (Pacala and Tilman 1994; Chesson 2000).

Heterogeneous distribution of soil nutrients is driven by abiotic and biotic factors. Abiotic factors include effects of topography, rain, snow, fluvial processes, and wind (Burke 1989; Parsons et al. 1992; Fisk et al. 1998; Li et al. 2008; Liptzin et al. 2013). For instance topographical differences can cause variation in N mineralization rates (Burke 1989), and also in soil P pools, as shown in alpine tundra due to variation in snow depth (Litaor et al. 2005). The main abiotic factors causing the transport of nutrients are water and wind (Liptzin and Seastedt 2009). These factors can operate across a range of spatial scales from small (Parsons et al. 1992; Li et al. 2008) to very large; examples of the latter include downstream nutrient enrichment along a river corridor (River Continuum Concept; Vannote et al. 1980) and effects of wind on alpine ecosystems (Landscape Continuum Concept; Seastedt et al. 2004). Biotic factors causing heterogeneity in nutrient conditions include plants that modify their environment by taking up nutrients at a distance and returning them beneath the canopy, producing so-called ‘islands of fertility’ (Hook et al. 1991; Schlesinger et al. 1996). In some ecosystems such processes can produce remarkably regular spatial patterns in the vegetation and soil (Rietkerk and Van de Koppel 2008). Also, herbivores contribute to the redistribution of nutrients through grazing and excretion of dung and urine, sometimes producing patterns at several spatial scales (Augustine

and Frank 2001). In addition, biotic and abiotic factors may interact to produce more complex patterns of nutrient heterogeneity. For instance, trees can increase local atmospheric N deposition by intercepting particles from the air (Liptzin et al. 2013), (Fenn and Poth 2004), or concentrate rain through stemflow (Levia and Frost 2003; Johnson and Lehmann 2006).

The patterns of different nutrients can be spatially correlated (Schlesinger et al. 1996; Li et al. 2008), especially if their turnover rates in the ecosystem are largely controlled by the same biological process, such as mineralization. However, spatial distribution of nutrients such as N and P can also differ, for example because weathering of parent material and associated soil chemistry is a main source of P but not of N (Walker and Syers 1976; Liptzin et al. 2013). Also, N and P may differ in the extent to which they are transported by wind and water; in most regions on Earth, concentrations of N in rainwater are much higher than those of P (Penuelas et al. 2013), whereas P may adsorb more strongly to dust particles carried by the wind. These assumptions however need further investigation.

During fieldwork on a glacial forefield in Switzerland, we developed the hypothesis that emergent rocks can produce small-scale variation in soil nutrient concentrations by intercepting and redirecting precipitation. Specifically, we postulated that rocks act as funnels that concentrate rainwater, and the nutrients it contains, in their immediate vicinity (Fig. 1a). Although this idea appears to be obvious, it appears never to have been tested. Furthermore, since precipitation represents a more significant ecosystem input for N than for P (Olde Venterink et al. 2002; Penuelas et al. 2013), we expected that this funneling of rain would lead to different ratios of N:P availabilities for plants growing near rocks and further away. We tested these ideas on the forefield of the Damma glacier in Switzerland, where we placed ion-exchange resin in small boxes next to rocks with different funnelling areas, and in open soil. We measured the amounts of  $\text{NH}_4^+$ ,  $\text{NO}_3^-$ ,  $\text{NO}_2^-$  and  $\text{PO}_4^{3-}$  adsorbed to resin during 66 days, and predicted that these amounts would be higher next to the rocks, and would increase with the ‘rain-collecting area’ of the rocks (cf. Fig. 1c). We also compared the foliar N and P status of two plant species growing beside rocks with those growing further away. We predicted that the leaves of plants beside rocks would have higher N concentrations and higher N:P ratios than would plants further away.



**Fig. 1** Schematic representation of the funnelling effect of rocks for rain and its chemical elements. Rain and chemical elements in it—which are not adsorbed to the rock surface—are concentrated near the rocks, causing local hotspots of resource availabilities for plants, and spatial heterogeneity of soil resources **a**. Panels **b–d** illustrate the methods to quantify this funnelling effect applied in this study. We placed PVC boxes, containing two resin bags on top of each, next to rocks of different sizes and away from rocks **b, c**. The top resin bag was

for measuring N and P adsorption derived from atmospheric deposition, the bottom resin was for control purposes, and for buffering against adsorption of N and P from soil release. We measured N and P adsorption to ion-exchange resin. Additionally, resin boxes with equal belowground design, but connected to PVC funnels of three different sizes (53, 176 and 660 cm<sup>2</sup>) were used for calibration purposes **b**. The photograph shows the experiment at the Damma glacial forefield, Switzerland in summer 2010 **d**

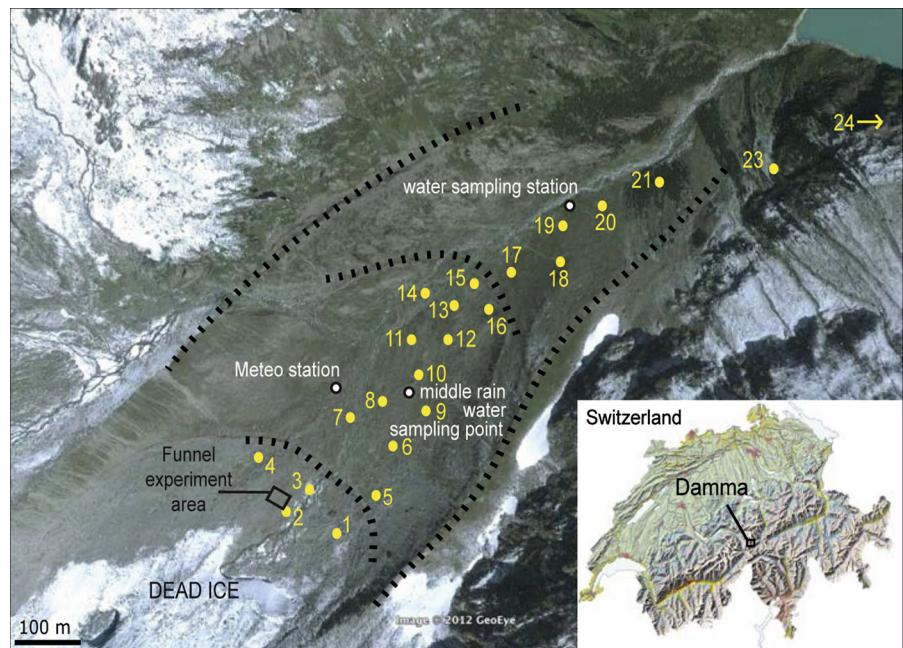
## Methods

### Study site

The research site was located at 2,050 m above sea level in the forefield of the Damma glacier in the

Central Alps of Switzerland (46°38'N 8°27'E). The front of the glacier has retreated since the end of the Little Ice Age (c. 1850), but the recession has not been continuous, it reversed two times during 1920–1928 and 1970–1992. The research site was close to site 2 of the 'Biglink' chronosequence, about 85 m from the ice

**Fig. 2** Location of the Damma glacier forefield in Switzerland. Points 1–24 refer to sampling sites of the Biglink chronosequence study (Bernasconi et al. (2011)). The study with resin boxes and funnels presented in this paper was carried out near site 2, close to the ice. Rainwater was collected in three rainwater sampling stations (meteo station, water sampling station ‘w.s.s.’ and middle rain water sampling point ‘middle’). The figure is adapted from Bernasconi et al. (2011) and Smittenberg et al. (2012)



front (Fig. 2). This location had been ice free for about 10 years, after being ice covered for 15 years, and ice free for the first time during 30 years. Organic material accumulated during the first ice free period was removed or buried under new moraine material during the 15 years of repeated ice cover (Bernasconi et al. 2011). Most of the site was covered by sand and gravel, but with many rocks ranging in size from a few centimetres to several metres in diameter protruding above the surface. The bedrock is Central Aar granite and the soil is a Eutric Hyperskeletal Leptosol. Since the soil had been free from ice for only about 10 years differences in soil characteristics among our measuring sites due to weathering or pedogenesis were probably rather small. The climate at the site is characterized by a short growing season for the vegetation (Late June–mid October), and about 2,400 mm precipitation per year. The vegetation was made up of scattered individual plants which accounted for only a few percent of the surface between the rocks. The species included both grasses (*Agrostis gigantea*, *A. rupestris*, *Poa alpina*) and forbs (*Rumex scutatus*, *Oxyria digyna*, *Leucanthemopsis alpina*, *Doronicum clusii*, *Sagina linnaei*, *Sedum alpestre* among other species). Additional information about soil physico-chemical and biological characteristics is presented in Bernasconi et al. (2011);

Göransson et al. (2011); Smittenberg et al. (2012) and Zumsteg et al. (2012).

#### Nutrient adsorption to resin

To assess the N and P deposited in the vicinity of rocks, we buried PVC-boxes (10-cm long, 1-cm wide, 6-cm deep) lengthwise next to rocks, so that the top of the box was flush with the soil surface (Fig. 1b, c). To prevent direct contact of the ion exchange resins with the soil, we first added a 1-cm layer of nutrient-poor sand to the bottom of each box. We stacked two resin bags (10 × 2 × 1 cm nylon bags with 13 g of mixed resin Amberlite IRN150, Sigma Aldrich, Switzerland) on the sand layer, and covered these with a further 1-cm of sand to protect the resin from sunlight (Fig. 1b). We selected ten rocks of different sizes and measured their intercepting areas. We then placed a resin box lengthwise next to each stone, and another c. 0.5 m away as a control (Fig. 1c). Apart from differences in size, the rocks were randomly selected, and also had a random North–South orientation.

The use of two resin bags on top of each other in the resin boxes served two purposes. First, we aimed to measure adsorption of nutrient derived from rain in the top resins. If the major source of N or P was indeed rain: adsorption to the bottom resins should be

marginal compared to adsorption to the top resins, since resin in the bottom bags would only capture nutrients that snuck past the top bags. Hence, the bottom resin bags were to check the effectiveness of the top resin bags adsorbing N and P from precipitation. Second, the bottom resins should also prevent contamination of the upper resin bag with nutrient released from the soil beneath the resin boxes (that could have passed through the 1-cm sand layer under the bottom resin). Such contamination could otherwise have resulted in overestimation of the N or P input from rain. As an additional check for N and P release rates from soil that could have led to N and P adsorption to the resin, we buried 6 resin bags—without boxes or sand around them—at a depth of 5–10 cm, at the same field site and period. None of the latter resin bags in the soil was located near rocks.

To calibrate the funnelling effect of rocks, we used PVC funnels with collecting areas of 660, 176 and 53 cm<sup>2</sup>, arranged so that any intercepted rainwater flowed into resin boxes like those described in the previous paragraph (Fig. 1b). We set out four replicate funnels of each size in the field, each paired with a control box a short distance away without a funnel (intercepting area 10 cm<sup>2</sup>).

The experiment ran from 28 July to 3 October 2010 (66 days). Before setting out the resin bags, they were pre-treated by shaking them in 2 M KCl for 2 h and rinsing them overnight in deionised water. At the end of the experiment, they were collected and kept frozen until extraction. They were then rinsed with deionised water to remove sand, and shaken for 2 h in 2 M KCL. The extract was analysed for NO<sub>3</sub><sup>-</sup>, NH<sub>4</sub><sup>+</sup> and PO<sub>4</sub><sup>3-</sup> using a continuous flow analyser (3 HR SEAL, Norderstedt Germany).

Atmospheric nutrient inputs were estimated from the quantities of N and P adsorbed by the upper resin bags. These values were extrapolated to a full year on the basis of the rain falling during the 66 days study period compared with that in a full year (i.e. 362 versus 2,300 mm; Kormann 2009). This extrapolation was done to enable comparison with the critical N load for alpine grasslands which is expressed per year.

### Rain sampling

The rain falling during the study period was measured continuously at a Meteo station in the middle of the forefield (Fig. 2). Rain was also collected at three

sampling stations in the forefield during the periods 28 July–19 August and 19 August–16 September (Fig. 2). Per station and period one sample was taken, including all rain of the entire 3–4 weeks periods. The quantity of rain during these two periods makes up 87 % of the rain that fell in the entire period of the experiment with the resin boxes and funnels (Table 1). Rain was collected 1 m above the ground, using a funnel with an insect net leading to an insulated bottle. A few drops of HgCl added to the collection bottles avoided transformation between different forms of the elements during the sampling periods. Rain samples were stored cool and in the dark without further preservation.

Samples were first analysed on total dissolved nitrogen (TDN). Thereto, subsamples were passed through 0.2 µm nylon membrane filters and acidified with 1 M HCl (to about pH 3.5). TDN was determined with a DIMATOC 2000 instrument (DIMATEC, Essen, Germany) equipped with a DIMA-N module for nitrogen measurement. Before analysis of all other variables, a second set of samples was filtered with cellulose acetate membrane disc filters of 0.45 µm pore size (Whatman, Schleicher & Schuell FP 30). Total dissolved phosphorus (TDP) was analyzed photometrically with the molybdenum blue method after digestion with peroxy-disulfate (K<sub>2</sub>S<sub>2</sub>O<sub>8</sub>) on a Procon autoanalyzer (Procon, Switzerland). The same procedure was applied for the determination of dissolved inorganic phosphate (DIP) only without digestion. Nitrate and ammonium were quantified with ion chromatography (Metrohm, Switzerland) using a Metrosep C4 100/4.0 column for cations. Anions were analyzed with suppression and a Metrosep ASupp 5 column.

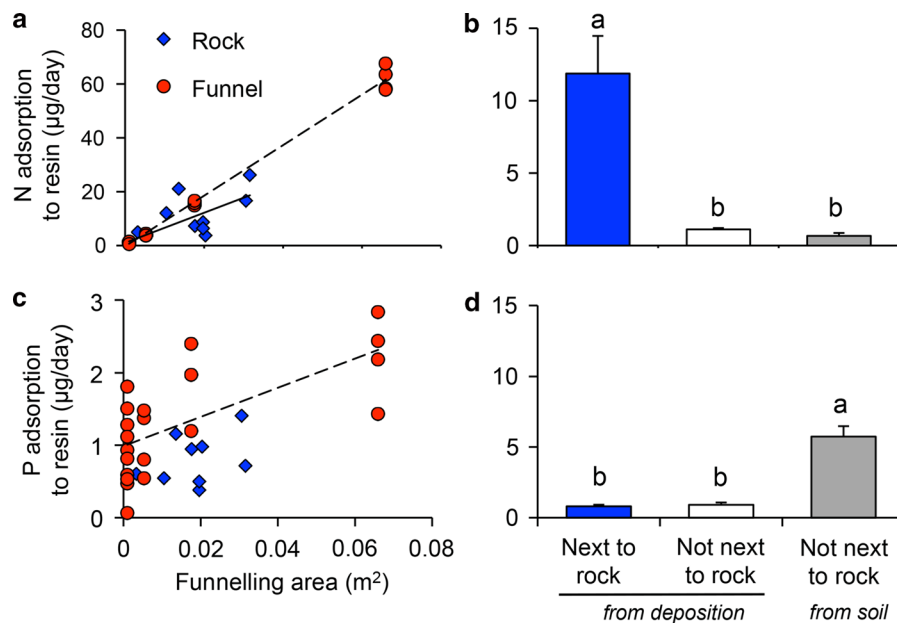
### Plant analyses

On 5 August 2011, we collected healthy, fully expanded leaves of two plant species common on the forefield, *Agrostis gigantea* and *Rumex scutatus*. We used a paired sampling approach, taking one sample from beside a funnelling stone (funnel area 144–1,972 cm<sup>2</sup> for *A. gigantea* plants and 164–675 cm<sup>2</sup> for *R. scutatus* plants), and the other 1–2 m away. We collected nine paired samples of *A. gigantea* but, for want of sufficient suitable material, only five of *R. scutatus*. The plants besides rocks were collected randomly with respect to North–South orientation of the slope of the rocks. The leaves were

**Table 1** Concentrations of N and P in rain collected at three sites in the Damma glacier forefield during the experimental period

Sampling station	Sampling period	Rain (mm)	NO <sub>3</sub> -N (µg/L)	NH <sub>4</sub> -N (µg/L)	DIN (µg/L)	TDN (µg/L)	DIP (µg/L)	TDP (µg/L)
Meteo	28-7-19-8	192	131	445	576	1,510	69	106
Middle	28-7-19-8	–	114	120	235	820	1.8	35
W.S.S.	28-7-19-8	–	118	120	237	1,390	1.6	48
Meteo	19-8-16-9	148	114	87	200	290	6.0	129
Middle	19-8-16-9	–	115	124	240	260	11	82
W.S.S.	19-8-16-9	–	–	–	–	–	–	–
Meteo	16-9-3-10	52	–	–	–	–	–	–

Locations of sampling stations are shown in Fig. 2



**Fig. 3** Rocks concentrate nitrogen (N), but not phosphorus (P), from atmospheric deposition. Adsorption of N and P to ion exchange resin placed next to rocks of different funnelling areas, in artificial funnels of different sizes or in the soil, incubated in the Damma glacier forefield for 66 days. **a** and **c** show N and P adsorption in relation to funnelling (deposition) area. Resin bags were placed in 10 × 1 cm PVC containers next to rocks or under the funnels with two resin bags on top of each other. Results are shown for the top resin bags and therefore show adsorption from deposition not from soil release. **b** and **d** show mean (±s.e.) adsorption rates to these top resins placed next to the rocks (mean area 0.02 ± 0.003 m<sup>2</sup>; n = 9) or in the PVC

containers without extra funnelling area (0.01 m<sup>2</sup>; n = 10); these bars show N and P derived from deposition. Additionally, **b** and **d** show N and P adsorption to resin bags that were incubated in the soil without PVC container; these bars show N and P release rates from the soil. All data from top and bottom resins are presented in supplementary material 1. Dashed lines in **a** and **c** are significant regressions for the funnels ( $P < 0.001$ ,  $R^2 = 0.97$  and  $P = 0.002$ ,  $R^2 = 0.40$  for **a** and **c**). The solid line in **a** is a significant regression for the rocks ( $P < 0.001$ ,  $R^2 = 0.64$ ), in **c** it was not significant ( $P = 0.991$ ). Different letters in **b** and **d** show significant ( $P < 0.001$ ) differences among bars (one-way ANOVA, Tukey)

dried, Kjeldahl digested and analysed for NH<sub>4</sub><sup>+</sup> and PO<sub>4</sub><sup>3-</sup> as described above. One pair of *A. gigantea* samples was excluded from the analyses because the control was a clear outlier with an exceptionally high N:P value (41:  $P < 0.01$ ).

## Results

We obtained linear relationships between collecting area and N adsorbed by the upper resin bag both for boxes placed beneath calibration funnels (Fig. 3a) and

for those beside rocks (Fig. 3b). Far less N was adsorbed by resin bags in the control boxes, and similarly low amounts of N were adsorbed by resin bags buried in the soil (Fig. 3b).

The results were very different for P, with no difference in the amounts adsorbed beside rocks, irrespective of their size, and the controls. For the calibration funnels, however, we did obtain a positive relationship between P adsorbed and collecting area, as for N (Fig. 3c). High amounts of P were adsorbed by resin bags buried in the soil (Fig. 3d).

We compared the adsorption of N and P to the resin under the PVC funnels during the 66 days with the sum of dissolved inorganic N (DIN) and dissolved inorganic P (DIP) in the rain that we collected during a large part of the measuring period; i.e., 87 % of the rain volume. For our largest funnels, the increase in N and P adsorption compared to the background adsorption were 60  $\mu\text{g N day}^{-1}$  and 1.3  $\mu\text{g P day}^{-1}$  (Fig. 3a,c). This increase came from 26 L of rain (392 mm on an area of 660  $\text{cm}^2$ ) (Table 1); hence, calculated DIN and DIP concentrations in rain were 153  $\mu\text{g N/L}$  and 3.3  $\mu\text{g P/L}$ . These concentrations were about 25–35 % lower than the normal range of concentrations measured in the rain at the nearby sampling stations (200–240  $\mu\text{g N/L}$  and 1.6–11  $\mu\text{g P/L}$ ; Table 1).

The two plant species studied, *A. gigantea* and *R. scutatus*, had higher N concentrations when growing beside rocks than in the open (Fig. 4a; Table 2). However, they differed in their P response (Fig. 4b; significant funnel  $\times$  species interaction in Table 2), with only *R. scutatus* having a higher leaf P concentrations beside rocks, albeit not significantly ( $P = 0.083$ ). As a consequence, the N:P response also varied (Fig. 4c; significant funnel  $\times$  species interaction in Table 2), with *A. gigantea* leaves having a higher N:P ratio beside rocks while there was no effect of position in *R. scutatus* (Fig. 4c).

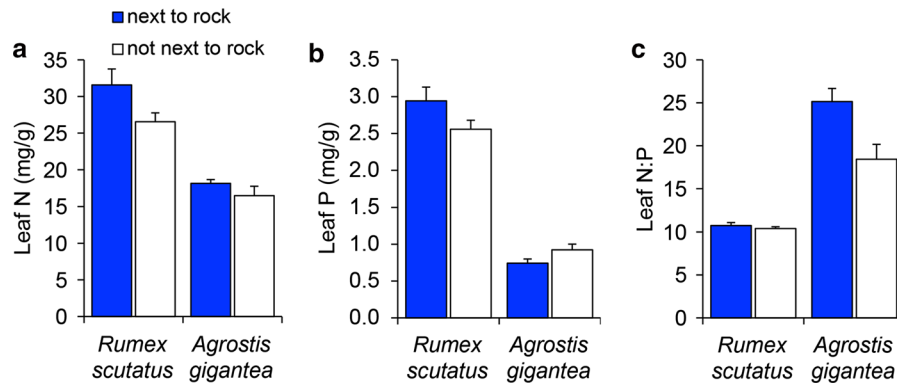
## Discussion

The hypothesis that rocks concentrate nutrients by funnelling rainwater is supported by the positive correlation between N adsorbed and collecting area (Fig. 3). Although the mean intercepting area of the rocks was only 0.02  $\text{m}^2$ , mean N adsorption was around 10 times higher within 1 cm of rocks than further away. This indicates that this funnelling mechanism creates

N-rich hotspots in the vicinity of rocks, which presumably leads to spatial heterogeneity in soil N availability. Although we did not measure other potentially relevant processes, such as N mineralization, N-fixation and denitrification, previous studies have shown that these were of negligible importance at our pristine glacial forefield site (Noll and Wellinger 2008; Brankatschk et al. 2010). Moreover, extrapolating our results to a full year on the basis of N concentrations in rainfall during the measuring period, we obtained a mean N input of 4.9  $\text{g m}^{-2} \text{y}^{-1}$  beside rocks compared to 0.5  $\text{g N m}^{-2} \text{y}^{-1}$  further away. According to location, therefore, these values are either close to the critical N load for alpine grasslands (0.5–1  $\text{g m}^{-2} \text{y}^{-1}$ ; Bobbink et al. 2010), or 5–10 times higher. This critical N load represents the threshold above which detrimental ecological effects may occur, mostly associated with loss of species diversity (Bobbink et al. 2010). Indeed, the fact that these local N inputs on the forefield span an ecologically critical range makes it likely that funnelling influences the distribution of plant species and soil microbes.

Phosphorus was also significantly concentrated by funnels (though the data were much more variable than for N), but not by rocks (Fig. 3c,  $P = 0.991$ ). We think it is likely that this difference was because inorganic-P was adsorbed onto the surface of rocks but not onto the plastic of the funnels. Indeed, compounds such as iron oxyhydroxides, which are likely present in the Central Aar granite of our study site (G. Furrer; pers. comm.), are known to bind inorganic-P (Arias et al. 2006; Kim et al. 2011), though further study would be needed to assess the relevance of such adsorption nutrient inputs. In any case, much less P was adsorbed in the boxes than by resin placed directly in soil (Fig. 3d), indicating that precipitation was relatively unimportant as a source of P for plants at our site, at least in comparison to inorganic P release in the soil from for instance Fe-bound P compounds (associated with Fe reduction) or through weathering of mineral P.

We predicted that the relatively N-rich hotspots near rocks—due to the stronger funnelling effect of rocks for N than for P—would be reflected in higher foliar N concentrations and N:P ratios in *A. gigantea* and *R. scutatus* plants growing besides rocks than further away. This prediction was confirmed for foliar N concentrations, with higher values in plants beside rocks (Fig. 4a; Table 1). However, the N:P ratios of



**Fig. 4** The N enrichment next to rocks is reflected in enhanced leaf N in plants, but species vary in their response with leaf P and N:P. Bars show mean ( $\pm$ s.e.) N and P concentrations and N:P ratio in green leaves of the forb *Rumex scutatus* and the grass

*Agrostis gigantea* at a 10-years young site in the Damma glacier forefield, Switzerland. Samples were collected in rock—non-rock pairs; 5 and 8 pairs for the two species, respectively. ANOVA results are shown in Table 2

**Table 2** F values and significance of 2-way ANOVA for the data in Fig. 4

	log (leaf N)	log (leaf P)	Leaf N:P
Rock	5.9*	0.3 <sup>N.S.</sup>	5.6*
Species	80.8***	244.3***	56.2***
Rock $\times$ Species	0.2 <sup>N.S.</sup>	5.1*	4.5*

\*  $P < 0.05$ ; \*\*\*  $P < 0.001$ ; <sup>N.S.</sup>  $P > 0.5$

the two species responded differently to location (Fig. 4c); while *A. gigantea* leaves had a higher N:P ratio beside rocks (Fig. 4c), reflecting the pattern recorded in the resins, there was no effect of position in *R. scutatus* (Fig. 4c). The relatively high foliar P concentration of this species, particularly when growing besides rocks, suggests that it is effective in acquiring P from soil providing it has sufficient N. An important mechanism to acquire P in early successional rocky ‘soils’ is releasing phosphate from mineral-P fractions, such as apatite, which plants stimulate through root exudation of protons or organic acids (Hoffland et al. 1989, Hinsinger 1989). *Rumex scutatus* probably had a much higher exudation activity than *A. gigantea*, as we also observed in the rhizospheres of these plant species at older successional stages in the Damma forefield (J. Luster and H. Göransson unpublished). In addition, large differences in the response of plant species to variation in soil N availability was also demonstrated for root phosphatase activity under controlled conditions (Olde Ventenink 2011). Such interspecific differences in how plants respond to variation in N supply or in the ratio of

N and P supplies—as observed for the two plant species in the Damma glacier forefield—support the idea that species differ in their nutrient niches. Indeed, it has been suggested that such differences may contribute to species coexistence (Pacala and Tilman 1994; Chesson 2000; Amarasekare 2003).

It is usually supposed that primary production in the early stages of terrestrial ecosystem development is N-limited, since most soil parent materials contain reserves of P but not N. Gradually, N accumulates through N<sub>2</sub>-fixation and atmospheric deposition, and the ecosystem may eventually become P-limited as P is lost through leaching (Walker and Syers 1976; Wardle et al. 2004). Our results suggest that this traditional view may be too simple, however: because of the differing importance of atmospheric deposition as sources of N and P, the funnelling effect produces a stoichiometric gradient of N:P availabilities from the vicinity of rocks to open soil. Thus, the shift from N to P limitation for growth of plants or soil microbes does not necessarily depend only on a slow gradual accumulation of N and losses of P, but may develop patchily even in the early stages of a primary succession. The example of the two plant species sampled in this study illustrates that species will differ in their response to these patchily distribution of variation in N and P availabilities.

In order to evaluate our method of assessing nutrient deposition by means of adsorption to ion exchange resin, we compared our results with rainfall data, as was successfully done by Fenn and Poth (2004) in a previous study. Our comparison, however,



was complicated by large local spatial and temporal variation in rain quality in the Damma glacier forefield (Table 1), for which we do not have a good explanation. Particularly, the c. 1 mg DON in the rain of two sampling stations during the first measuring period was rather high and might have resulted from some dry deposition in the measuring funnel. This would indicate that the concentration of total N from rain in the vicinity of rocks through the funnelling of rain was probably even higher than our estimates based on nitrate and ammonium. When comparing our assessed N and P deposition rates by means of resin in the PVC funnels with the ‘normal range’ of DIN and DIP concentrations in rain (200–240 µg N/L and 1.6–11 µg P/L; Table 1), the calculations based on adsorption to resin were about 25–35 % lower. A difference in this order of magnitude may be due to local variation in rain, to measuring errors at these low nutrient concentrations, and to a fraction of ions in the rain that might not have adsorbed to the top resin in our resin boxes.

The influences of rocks in concentrating atmospheric N, which was clearly demonstrated in the young, nutrient-poor soil of a glacial forefield, provides an alternative explanation to micro-climatic factors for why plants often establish better beside rocks (Jumpponen et al. 1999; Marteinsdóttir et al. 2013). The funnelling mechanism is not restricted to early successional ecosystems, but is applicable to all ecosystems where bare rocks are present, such as many mountain areas. In cases where these rocks are very large (some inselbergs, for example, may be several hundred metres in diameter), they may have a profound effect upon local nutrient conditions. Moreover, any other structure that intercepts dry deposition and channels precipitation, such as the canopies of some trees and ferns, may have the same effect as rocks. And since funnelling causes spatial heterogeneity in the availability and stoichiometry of N and P, and plant species may vary in their response to this, it is a process that may contribute to species diversity in communities (Pacala and Tilman 1994; Chesson 2000). Funnelling structures should therefore be taken into account when assessing processes of soil nutrient heterogeneity, or the effects of nutrient deposition on plant communities and soil ecosystems. In addition, future studies should attempt to distinguish between effects of funnelling upon nutrients and water, since increased soil moisture could have important

ecological consequences in ecosystems where drought is an important factor (e.g. Fisk et al. 1998).

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