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Ilkka Hanski: The legacy of a multifaceted ecologist

Resource gradients and the distribution and flowering of butterwort, a carnivorous plant

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The transfer of materials such as nutrients from one ecosystem to another can establish gradients that affect the distribution and performance of species. We examined how a natural resource gradient influences the density and flowering of butterwort (*Pinguicula vulgaris*), a carnivorous plant. Mývatn, a lake in Iceland, produces large midge populations, generating a gradient in midge abundance on shore. The midge gradient was associated with butterwort flowering probability, which decreased by roughly 50% moving away from the shore. In a midge addition experiment, plants receiving midges had a four-fold increase in their subsequent likelihood of flowering, implicating carnivory in the flowering gradient. Nonetheless, the density of butterworts increased with distance from shore, in negative association with soil nutrient content and the abundance of grass species. This suggests that the positive effect of the midge gradient on butterwort flowering is overwhelmed by the negative effect of competition with grasses.

Introduction

Natural environmental gradients give insights into both the direct environmental impacts on species and the role of species interactions in determining species abundances (MacArthur 1972). In Finland, for example, dung-inhabiting beetles vary in abundance and species composition along environmental gradients consisting of dung age, season, and surrounding habitat type (fields, pine forests, and spruce forests) (Hanski & Kuusela 1977). The age of dung pats where they are found indicates resource preferences, the duration they are found indicates their degree of specialization, and co-occurrence patterns might suggest interactions (e.g., competition) with other species. For plants, there is a rich literature documenting the effects of environmental gradients on the composition and diversity of communities (Whittaker 1960, Weiher

Fig. 1. Midge mating swarm along the shore of Mývatn made up primarily of chironomids in the tribe Tanytarsini. The photo was taken along one of the butterwort transects in 2014. Photo by A. R. Ives.

et al. 2011, HilleRisLambers *et al*. 2012). These studies typically address how environmental gradients affect the occurrence and abundance of individual species, and also the species traits that are associated with environmental gradients (McGill *et al*. 2006, HilleRisLambers *et al*. 2012). A complication in understanding species responses to environmental gradients, however, is that the same environmental gradient may have multiple effects on species. For example, increased nutrient availability might increase seed production while decreasing seedling or adult survival. Thus, because the abundance of a species along an environmental gradient reflects the outcome of multiple life history events, any one life history trait may not track the environmental gradient in the way anticipated from species abundance.

Mývatn, a lake in northeast Iceland, generates an environmental gradient of above- and below-ground nutrients due to large-scale emergences of midges (Chironomidae) (Fig. 1). The movement of these aquatic insects to the adjacent land causes subsidies of nutrients to the terrestrial habitats surrounding the lake (Gratton *et al*. 2008, Hoekman *et al*. 2012). Averaged around the Mývatn shoreline, inputs of midges can exceed 40 g dry weight m^{-2} per year (Dreyer *et al*. 2012, 2015). Because the deposition decreases exponentially with increasing distance from the lake (Dreyer *et al*. 2015), midges generate a strong spatial gradient, with midge inputs disappearing beyond 500 m from shore (Dreyer *et al*. 2012, Dreyer *et al*. 2015).

The butterwort *Pinguicula vulgaris* is a carnivorous plant that takes advantage of Mývatn midge emergences by trapping insects with sticky secretions from their basal rosette of leaves (Heslop-Harrison & Knox 1971) (Fig. 2). Once the insects are digested, the plants allocate the nitrogen and phosphorus to growth and reproduction (Aldenius *et al*. 1983, Karlsson *et al*. 1991, 1994, 1996, Hanslin & Karlsson 1996, Worley & Harder 1996). The strong resource gradient from midge emergences and the benefits that butterworts derive from this above-ground nutrient source together suggest that there should be a strong, positive gradient in plant reproduction and/or survival, and hence a gradient in density decreasing from the shoreline along with midge inputs. Nonetheless, midges also increase soil nutrient content which favors other plant species, especially grasses (Hoekman *et al*. 2011, Webert 2016). Thus, the midge gradient around Mývatn could have positive effects on butterwort through carnivory but negative effects through competition or other consequences of increased soil nutrient content.

We investigated the effects of the midge-input gradient on butterwort individuals around Mývatn using both survey and experimental studies. We used surveys along transects around the lake to measure, as a function of the distance from shore, *P. vulgaris* densities, catch rate of

Fig. 2. Butterwort (*P. vulgaris*) with *Chironomus* sp. (large midge) and members of the tribe Tanytarsini (small midges). Photo by A. R. Ives.

midges, midge densities measured by passive infall traps, soil nitrogen content, vegetation cover by grasses, and the proportion of *P. vulgaris* that flowered. We further performed a midge-carcass addition experiment to determine whether increased catch rates caused within-season increases in flowering. We used these data to address how the gradient in midge inputs affected both butterwort flowering and density.

Material and methods

Study site and organisms

Mývatn is a large (37 km^2), eutrophic lake in northeast Iceland (65°40´N, 17°00´W). The lake is known for its large midge emergences (Jonasson 1979, Lindegaard & Jónasson 1979, Einarsson *et al*. 2004, Gratton & Vander Zanden 2009). After the midges emerge from the lake as adults, they fly to land to mate and often die there. The terrestrial habitats adjacent to the lake receive the highest input of midge carcasses, with deposition decreasing markedly with distance from the shoreline (Gratton *et al*. 2008, Dreyer *et al*. 2015).

Pinguicula vulgaris has a wide distribution across subarctic habitats (Mendez & Karlsson 2005). It is a perennial with an annual root system and overwinters by forming a “winter bud” belowground (Worley & Harder 1999). Vegetative reproduction can occur through subsidiary buds arising from the winter bud (Worley & Harder 1996). Floral primordia are evident in the bud stage over winter, and Worley and Harder (1999) found all plants had floral primordia, with 45% containing two or more. Flowers are borne singly on stalks that arise from the center of the rosette of leaves laying flat on the ground. Flowering and seed production occur from June to August, with plants producing typically a single flower stalk at our study site, although up to six flowering stalks are possible (Worley & Harder 1996, 1999). Flowering depends on the size of plant rosettes (Svensson *et al*. 1993, Worley & Harder 1999, Mendez & Karlsson 2004), and a long-term study in northern Sweden found that the proportion of *P. vulgaris* flowering varied among years between 10% and 50% (Svensson *et al*. 1993). Seed dispersal distance is apparently low, leading to locally isolated populations (Svensson *et al*. 1993).

Pinguicula vulgaris extract nitrogen and phosphorus from the insects they trap, leading to increased growth and reproduction (Aldenius *et al*. 1983, Karlsson *et al*. 1991, 1994, 1996, Hanslin & Karlsson 1996, Worley & Harder 1996). Experimental supplementation of insects to *P. vulgaris* increases plant photosynthetic rates (Mendez & Karlsson 1999), and growth and reproduction over a plant’s lifetime (Thoren & Karlsson 1998). Worley and Harder (1999) performed a detailed experiment on the allocation of supplemental resources to growth, vegetative reproduction (winter bud), and flowering. They found that, while insect supplementation increases same-year growth and vegetative reproduction, it did not increase same-year flowering and seed production. Instead, supplementation led to larger winter buds and larger plants in the following summer, which then had higher probability of flowering. Thus, insect supplementation affected reproduction in the following year but not in the same year. Consistent with the importance of between-year factors affecting reproduction, Svensson *et al*. (1993) found a positive effect of temperature in one year on the probability of *P. vulgaris* flowering in the following year. In contrast to these results showing delayed effects of carnivorous resource inputs on reproduction, Hanslin and Karlsson (1996) found that flowering *P. vulgaris* allocated roughly 1/3 of nitrogen from captured prey to reproduction and 1/3 to bud formation, with the remaining 1/3 lost. Furthermore, there was a large increase in root uptake of nitrogen for plants with supplemental prey. These results suggest the possibility of within-season effects of prey capture on flowering.

Survey

We took advantage of the natural gradient in midge deposition at Mývatn as a function of distance from the lake to assess the possible effects of midge inputs on *P. vulgaris* density and flowering. We established four transects around Mývatn that ran perpendicular to the shoreline. Transects were placed in areas with high *P. vulgaris* densities that had similar dominant vegetation and landscape. Each transect began at the lake edge and ran continuously away from shore. *Pinguicula vulgaris* were recorded at 50-m intervals between 82 m (the first observed butterworts) and 692 m from the shoreline. Starting at the lake, we identified sampling locations by walking 50 m inland and finding the nearest area containing at least two plants. We haphazardly placed a 2 × 2-m quadrat in that area and counted all *P. vulgaris* individuals within the quadrat, recording the number that had flowered. Additionally, we measured a random subset of ten individual plants in the quadrat (or all individual plants, in cases where there were fewer than 10) for width and midge catch rate. Width was measured as the maximum diameter of the rosette, and the observed midge catch rate was recorded as the number of midge carcasses present in the rosette. Midges were the primary arthropod found in rosettes, and all other arthropods were disregarded. All observations were taken on 2 July 2013.

In 2013, 20 infall traps were positioned at six transects around Mývatn and were collected roughly every 14 days over the course of the summer as part of a long-term survey (Dreyer *et al*. 2015). Two of the infall transects were close to two butterwort transects, and the remaining four were dispersed around the lake through similar habitat; one long-term infall transect in a different habitat type (lava field) was excluded from analysis. The infall traps were cups with a 95-cm^2 opening mounted about 1 m above ground and filled with propylene glycol to catch and preserve flying arthropods. Midges composed > 99% of arthropods captured, so we report only the numbers of midges caught in infall traps.

In 2009 at five of the six infall transects, 2-cm diam. × 10-cm deep soil cores were taken adjacent to the infall traps. At two of the transect sites, two separate transects were run, leading to seven sets of soil sample transects; each of the seven soil transects was analyzed as a separate transect. Soil cores were dried at 60 °C and stored in a refrigerator prior to transport to UW-Madison for total N determination on an elemental analyzer (Flash EA 1112 CN analyzer, Thermo Finnigan, Milan, Italy).

In 2009 at the six infall transects, plant cover was estimated in 25 × 25-cm quadrats adjacent to the infall traps. At three of the transect sites, two separate transects were run, leading to nine vegetation cover transects. Quadrats were systematically placed at five locations within a 5-m radius of each infall trap, and a photograph was taken of each quadrat from 3-m height. In the lab, photos had a grid with 25 intersections superimposed upon them, and the dicot species at each intersection was recorded. Cover was estimated as the number of hits of each species divided by 25 for each quadrat. For ease of data collection, all graminoid species were reported together as grasses.

Experimental midge addition

We performed a midge-addition experiment to investigate the short-term (within-season) effect of carnivory on plant reproduction. Using the quadrats from the butterwort transects, *P. vulgaris* individuals within the quadrat that had not yet flowered were numbered during the survey. The individuals were randomly assigned a treatment, with half receiving the experimental midge addition (midge treatment) and half receiving no supplemental midges (control). If a plot contained an odd number of plants without flowers, the assignment was randomly chosen for the last plant. The midge addition treatment consisted of applying 2.5 cm^3 of dried midge carcasses (1.91 ± 0.04 g) evenly over the rosette of the plant. Our goal was to saturate the plants in order to maximize nutrient intake. From the infall trapping data, the maximum catch rate was about 140 midges cm^{-2} yr^{-1} or 0.14 g dry weight cm^{-2} yr^{-1}. Thus, the experimental supplementation likely exceeded the annual catch of about 0.5 g yr^{-1} for a *P. vulgaris* plant. This prey capture rate is much higher than capture rates of 0.0006 g $plant^{-1}$ yr^{-1} estimated for a site in Sweden (Karlsson *et al*. 1994).

The experimental plants were revisited on 27 July 2013, 25 days after the experimental manipulations and after the peak flowering period had ended. They were scored for flowering, and widths of all experimental plants were recorded. Some numbered stakes were lost before the final sample, and these individuals were excluded from the analyses.

Statistical methods

The numbers of *P. vulgaris* plants within quadrats were analyzed as a function of distance from the Mývatn shoreline. To account for possible bias in counts caused by placing quadrats in areas in which at least two *P. vulgaris* were found, we first subtracted 2 from the total counts. The numbers of additional plants were regressed against distance using a quasi-Poisson Generalized Linear Model (GLM) to account for greater-than-Poisson variances, including transect as a factor. The numbers of midges found on *P. vulgaris* leaves were regressed against distance and plant width with a logit-normal Poisson Generalized Linear Mixed Model (GLMM) with transect as a factor and quadrat as a random effect to account for any quadrat-to-quadrat variation. The mean numbers of midges collected in infall traps over the summer of 2013 were regressed against distance with a quasi-Poisson GLM with transect as a factor. Logit-transformed percent nitrogen content and percent grass cover were regressed against distance including transect as a factor. From the survey data on 2 July 2013, whether or not *P. vulgaris* were flowering was regressed against distance from the shoreline and plant width using a binomial GLM including transect as a factor. A similar analysis was performed on experimental plants from 27 July 2013, with an additional factor for experimental treatment (midge addition or control). Interactions between distance and transect (i.e., whether the effect of distance differed among transects) were not significant in all of the regressions. All analyses were conducted in the computer language R (R Core Team 2016).

Results

Surveys

We surveyed 540 *P. vulgaris* individuals on 2 July 2013. *P. vulgaris* density increased with distance from shore ($\chi^2_1 = 6.15$, $p = 0.01$) and differed among transects ($\chi^2_3 = 8.10$, $p = 0.04$) (Fig. 3a). Because plant width was strongly related to the probability of flowering, we performed analyses of flowering on the subset of plants that were measured for width (295 individuals). The number of midges captured by butterworts decreased with distance from shore ($\chi^2_1 = 30.6$, $p < 0.001$) and differed among transects ($\chi^2_3 = 37.9$, $p < 0.001$) (Fig. 3b). In the six infall transects around the shoreline, the total numbers of midges collected per infall trap over the summer of 2013 decreased with distance from shore ($\chi^2_1 = 29.7$, $p < 0.001$) and differed among transects ($\chi^2_5 = 22.9$, $p < 0.001$) (Fig. 3c).

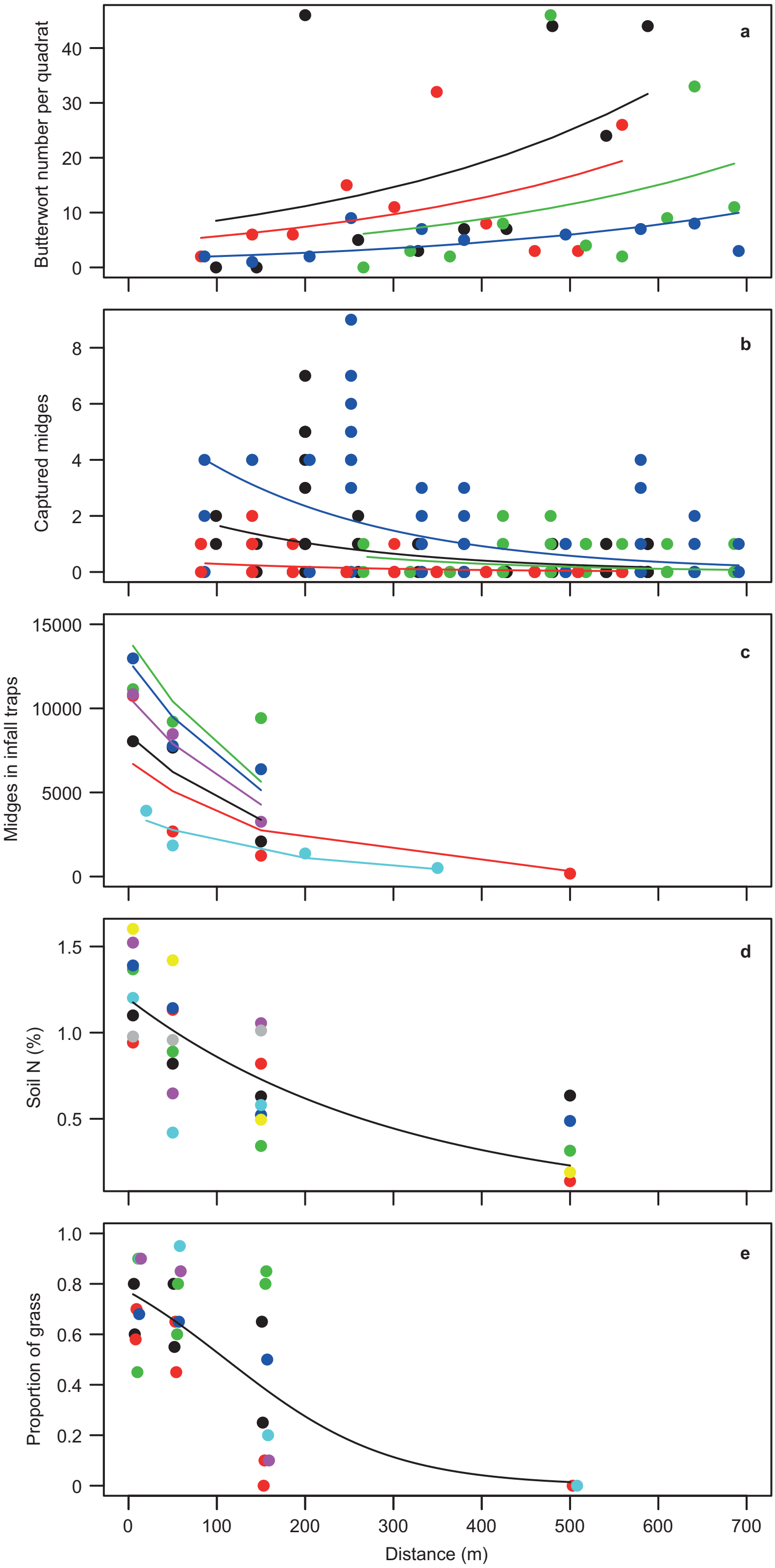

Fig. 3. (**a**) *P. vulgaris* density increased with the distance from the shore along four transects (colors); density was measured as the number of plants found in 2 × 2-m quadrats minus 2 (the minimum number of plants per quadrat); the effects of distance (χ^2_1 = 6.15, p = 0.013) and transect (χ^2_3 = 8.10, p = 0.044) were significant in a quasi-Poisson GLM regression (fitted lines). (**b**) The number of midge carcasses on *P. vulgaris* leaves decreased with the distance from the shore along four transects; the effects of distance (χ^2_1 = 30.6, p << 0.001) and transect (χ^2_3 = 37.9, p << 0.001) were significant in a logit-normal Poisson GLMM regression (fitted lines); the GLMM regression also showed high variance associated with quadrat (σ^2 = 0.25) and individual observations (σ^2 = 0.25), the latter indicating greater-than-Poisson variance among individuals. (**c**) Total number of midges captured in infall traps along six transects in summer 2013 decreased with the distance from the shore; the effects of distance (χ^2_1 = 29.7, p << 0.001) and transect (χ^2_5 = 22.9, p = 0.0003) were significant in a quasi-Poisson GLM regression. (**d**) Soil nitrogen content (%) decreased with distance from the shore along five transects in 2009. The effects of distance on logit-transformed percent N was significant (t_{27} = –6.21, p << 0.001), although there was no effect of transect. The line is a logit function fitted using nonlinear least squares. (**e**) Proportion grass decreased with distance from the shore along six transects in 2009; the effects of distance on logit-transformed proportion grass was significant (t_{27} = –4.07, p = 0.0004), although there was no effect of transect; the line is a logit function fitted using nonlinear least squares.

Soil nitrogen content that was measured in five of the six infall transects in 2009 decreased with distance from shore ($t_{27} = -6.21, p < 0.001$) and showed no difference among transects ($F_{7,20} = 0.51$, $p = 0.81$) (Fig. 3d). Similarly, in 2009 the proportion of vegetation cover that was grass decreased from an average of 75% to less than 10% from near-shore (5 m) to a distance of 500 m ($t_{27} = -4.07$, $p = 0.0004$) and showed no difference among transects ($F_{8,19} = 1.41$, $p = 0.25$) (Fig. 3e). Although measurements of soil nitrogen content and plant cover were taken four years before the observations on butterworts, the plant community and associated nutrient pools are relatively stable on a decadal time scale.

Of the 540 surveyed plants, 163 had flowered by the time of the survey on 2 July 2013. At each transect, the percentage that had flowered varied between 25% and 53%. For further analyses, we again included only the 295 plants whose width was recorded. The probability of flowering decreased significantly with increasing distance from the lake (Table 1 and Fig. 4a). The average width of plants that had flowered was 3.58 cm, whereas for non-flowering plants, it was 2.76 cm. There was a significant interaction effect on the probability of flowering between plant width and transect (Table 1).

Experimental midge addition

In the midge addition experiment, 321 plants were re-surveyed on 27 July 2013. In the 25 days between manipulation and re-survey, 5% of control plants flowered and 33% of midge-addition plants flowered; on average, within transects there was a roughly four-fold increase in flowering (Fig. 4b). There were strong statistical effects of treatment, plant width, and transect, but not distance from shore (Table 2).

Discussion

Our survey of the carnivorous plant *P. vulgaris* showed that whereas flowering was greater close to the shore of Mývatn, plant density was greater farther from shore. Near shore *P. vulgaris* benefited from the above-ground nutrient input of midge deposition and flowered at a significantly higher rate, as demonstrated by the midge catch rates (Fig. 3b), infall traps (Fig. 3c), flowering rates (Fig. 4a), and the midge addition experiment (Fig. 4b). In spite of this midge-induced increase in flowering, plant density was lowest near the shore and increased with distance from the lake (Fig. 3a), generating a negative association with below-ground nitrogen content and grass cover.

It is puzzling that density of *P. vulgaris* increased with distance from shore even though there was decreasing midge input, for three reasons. First, midge input close to shore increased flowering, and this should increase local recruitment of new plants. Although butterworts have

Table 1. Probability of flowering in *P. vulgaris* individuals as a function of log-transformed distance from the lake, transect and plant width, with 40 quadrats treated as a random effect in a logit-normal binomial GLMM. Higher-order interactions were not statistically significant at $p < 0.05$. Note that Distance and Width were not correlated ($\rho = -0.03$). The analysis included 295 plants from four transects, and data were collected on 2 July 2013; p values are from type II Wald's test.

Coefficient	χ^2	df	p
$\log_{10}$(Distance)	9.52	1	0.002
Transect	4.85	3	0.18
Width	23.8	1	<< 0.001
Distance × Width	4.47	1	0.034
Transect × Width	17.3	3	0.0006
σ^2 [quadrat]	0.34		

Table 2. Probability of flowering in *P. vulgaris* individuals as a function of log-transformed distance from the lake, transect, plant width and experimental midge carcass addition, with 30 quadrats treated as a random effect in a logit-normal binomial GLMM. Higher-order interactions were not statistically significant at $p < 0.05$. The analysis included 321 plants from four transects, and data were collected on 27 July 2013. p values are from type II Wald's test.

Coefficient	χ^2	df	p
$\log_{10}$(Distance)	2.14	1	0.14
Transect	12.1	3	0.007
Width	30.9	1	<< 0.001
Treatment	29.7	1	<< 0.001
σ^2 [quadrat]	0.00		

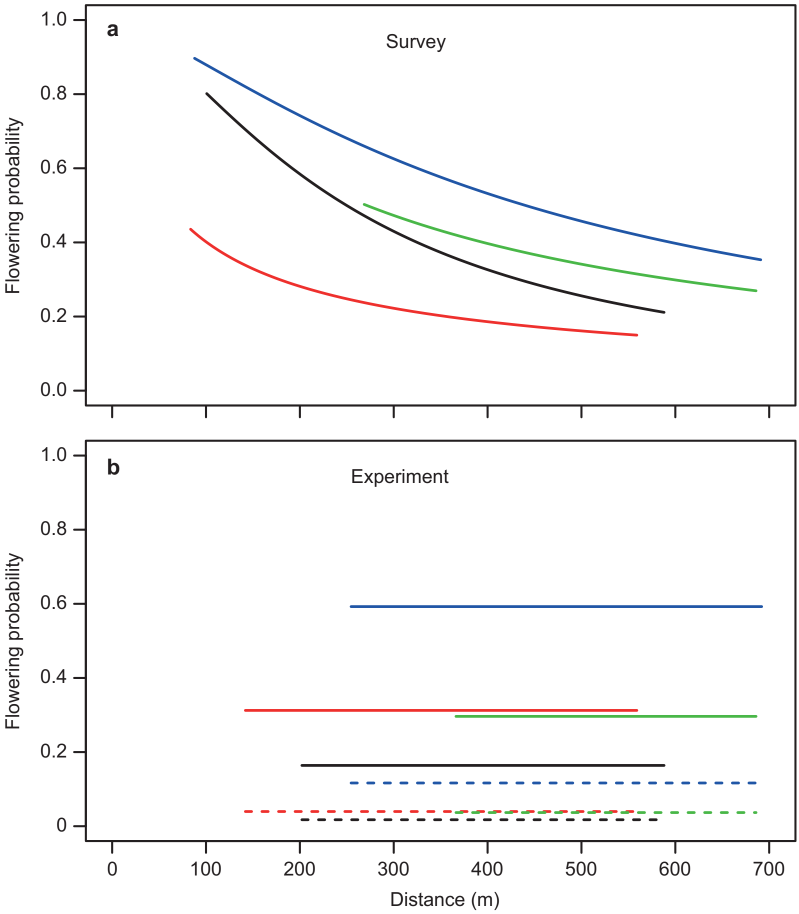

Fig. 4. (**a**) *P. vulgaris* individuals nearer to the lake had a greater probability of flowering. The effect of log-transformed distance ($\chi^2_1 = 13.0$, $p << 0.001$) was significant in a logit-normal Poisson GLMM regression (Table 1); the plotted lines for each transect are predicted probabilities of flowering from a logit-normal Poisson GLMM regression; for the lines, the estimated flowering probability was calculated for a plant with the average width for the transect. (**b**) *P. vulgaris* individuals that received experimental midge carcass additions (solid lines) had a greater probability of flowering than experimental controls (dashed lines); the effect of log-transformed distance was not significant in a logit-normal Poisson GLMM regression (Table 2); transect and plant width both had significant effects on flower; for the lines, the estimated flowering probability was calculated for a plant with the average width for the transect.

wind-dispersed seeds, and their seeds float to allow water-borne dispersal, populations show localized dynamics (Svensson *et al*. 1993) that suggest limited effects of immigration/emigration on density. The negative correlation between flowering probability and density — repeated across four transects around the lake in different geographical directions — does not have an obvious explanation involving seed dispersal, such as seeds being blown from the shoreline farther inland. Second, carnivory not only increases reproduction in *P. vulgaris*, it also increases underground resource storage and the subsequent size of plants in the following year (Karlsson *et al*. 1991, Worley & Harder 1996, 1999). This might increase the survival of plants, either over winter or in the longer term. Third, increased carnivory increases vegetative reproduction through the production of subsidiary winter buds that subsequently form new individuals (Worley & Harder 1996, 1999). This would be expected to lead directly to increasing densities in areas with greater midge inputs.

The increase in *P. vulgaris* density with distance from shore suggests that there are one or more negative effects of midge inputs on butterwort life history events. Butterworts are typically found in gravelly or disturbed areas around Mývatn, and they have an Ellenberg nitrogen score of 2 indicating they are found in nitrogen-poor soils (Ellenberg & Leuschner 2010). High midge densities close to the shore are associated with higher grass cover, reaching 80% ten meters from shore and decreasing to almost zero at 500 m (Fig. 3e). Grass cover has been shown experimentally to increase with midge addition, a response likely caused by greater soil nutrient input (Hoekman *et al*. 2011, Webert 2016). This is consistent with the much higher soil nitrogen content found near shore (Fig. 3d). *Pinguicula* *vulgaris* benefits from soil nutrient inputs (Karlsson *et al.* 1991, Hanslin & Karlsson 1996). Nonetheless, grasses also benefit and can be tall, likely shading butterworts. Furthermore, the thick grass thatch may decrease *P. vulgaris* seed establishment or growth of young butterworts produced vegetatively. Grasses are especially thick near shore, and the closest we found butterworts was 82 m from the lake.

Although competition with grasses is a likely explanation for the lower density of *P. vulgaris* near the lakeshore, there are additional or alternative explanations. For a different species, *P. moranensis*, Alcala *et al.* (2003) found that reproduction among populations did not increase linearly with prey capture rates, but instead had a hump-shaped relationship that was determined not just by prey capture but also by environmental conditions including light and moisture. This suggests that, for our study, there might be additional factors that vary with distance from shore that are important for determining butterwort density. One factor might be grazing pressure from sheep that occur at all of our study sites. Nonetheless, distance from the shore did not affect the experimental response of plants (Fig. 4b) in which flowering probability increased in response to midge addition independently of distance. Thus, even though there may be other environmental gradients that run parallel to the gradient in midge deposition (e.g., soil moisture, grazing pressure), the effect of experimental midges on *P. vulgaris* flowering was strong and positive regardless of an individual plant's location.

Our finding that experimental midge addition increased the flowering probability of *P. vulgaris* within the same growing season contrasts with previous studies that show an effect on flowering only in following years through the increased storage of resources in winter buds (Thoren & Karlsson 1998, Worley & Harder 1999). Nonetheless, the study of Worley and Harder (1999) on 80 experimental plants showed a trend (p = 0.08) towards increased flowering in the same year with experimental prey addition, and with 321 experimental plants, our experiment had more statistical power. Thoren and Karlsson (1998) conducted a supplementation study over six years with two populations each containing 240 experimental plants and found an increase in flowering of roughly 5% in the first year of supplementation and much larger increases in later years; data were not presented to determine whether the response in the first year was statistically significant. A second explanation for the rapid response we observed was the magnitude of the experimental additions, which were intended to saturate the butterworts. The supplementation rates for Worley and Harder (1999) and Thoren and Karlsson (1998) were 2–3 *Drosophila* fruit flies per week, or roughly 0.001 to 0.002 g plant^{-1} year^{-1}. In contrast, our supplementation was 1.9 g plant^{-1} as a one-time input. Although this was much higher than those of the other studies, it is not unrealistic for the high abundance of midges in the Mývatn system (Fig. 1). Our estimated passive rates of midge deposition reached a maximum of 0.14 g dry weight cm^{-2} yr^{-1} in one of our infall traps, translating to roughly 0.5 g dry weight plant^{-1} yr^{-1} in 2013, a year that had moderate but not high midge abundances. Our results are also consistent with Hanslin and Karlsson (1996) who found that flowering *P. vulgaris* allocated roughly 1/3 of nitrogen from captured prey to reproduction, and that prey capture increased nitrogen uptake from roots. Finally, while we measured only the within-year effect of midge addition to flowering, there are likely to be longer-term benefits to growth and reproduction, which we would expect to generate much higher butterwort densities near the Mývatn shore.

Our results show that an environmental gradient which has clear benefits to a species measured by one life history variable, in our case flowering, does not necessarily lead to a similar gradient in species abundance. This conclusion is not surprising, because population densities are set by multiple life history events and multiple environmental gradients that together determine the "success" of a species at the population level. For *P. vulgaris* at our study site, the midge environmental gradient is strong, and the positive response of butterwort flowering is also strong. We suspect, however, that this same environmental gradient establishes a strong negative response of *P. vulgaris* caused by competition especially with grasses that themselves benefit from the midge inputs into soil nutrients. This indirect negative impact of competition on *P. vulgaris* appears to outweigh the direct, positive benefits of midge capture, leading to higher butterwort densities farther from Mývatn.

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