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Dasvinder Kambo

Peter M. Kotanen

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**Latitudinal trends in herbivory and performance of an invasive species,
common burdock (*Arctium minus*)**

Dasvinder Kambo and Peter M. Kotanen¹

Department of Ecology & Evolutionary Biology

University of Toronto Mississauga

3359 Mississauga Road North

Mississauga, ON, L5L 1C6 CANADA

¹Author for correspondence

e-mail: peter.kotanen@utoronto.ca

tel: 905-828-5365; fax: 905-828-3792

Summary: Plants often lose natural enemies (herbivores and pathogens) while invading new geographic regions, as predicted by the Enemy Release Hypothesis. However, a similar reduction in attack might occur at a more local scale within an invader's range as plants in marginal areas escape enemies that fail to find them or cannot maintain local populations. In this study, we test the hypothesis that isolated populations near the northern edge of an invader's range escape the enemies present in more southern populations, using the non-native monocarpic biennial, common burdock (*Arctium minus*), as a model species. In southern Ontario, this plant is attacked by a wide range of insect herbivores, including generalist leaf chewers as well as leaf-mining flies (*Liriomyza arctii*, *Calycomyza flavinotum*) and an abundant lepidopteran seed predator (*Metzneria lappella*). Surveys over an 815 km transect from temperate southern to boreal northern Ontario indicate that damage by all of these enemies declines sharply with latitude, while plants in more northern areas are slightly larger and more fecund. Critically, seed parasitism drops from more than 85% in the south to less than 25% in the north. These results indicate that populations of *Arctium* near this species' northern limit escape many of their usual natural enemies, potentially counteracting less favourable environmental conditions. Such escape from enemies near invaders' range margins may accelerate further spread, including expected migration in response to climate change.

Key words: Herbivory; latitudinal gradient; leaf miners; *Metzneria lappella*; physical defense.

Introduction

Plants frequently lose natural enemies (herbivores and pathogens) when invading new geographic areas, as predicted by the Enemy Release Hypothesis (Keane and Crawley 2002; Torchin and Mitchell 2004; Mitchell et al. 2006). However, a new invader also acquires new enemies in its new range (e.g., Hill and Kotanen 2012), as local insects and pathogens shift to this novel host, and as enemies from its original range are accidentally or deliberately introduced (Levine et al. 2004; Hawkes 2007; Hatcher and Dunn 2011). As a result, exotic plants rarely are free of natural enemies; instead, whether they benefit from reduced damage depends on the balance between enemy loss and reacquisition. This balance may be influenced by factors including the geographic range which they invade (Kennedy and Southwood 1984; Strong et al. 1984; Hawkes 2007; Mitchell et al. 2010), their phylogenetic relationship to the native flora (Dawson et al. 2009; Hill and Kotanen 2011; Harvey et al. 2012), and the length of time since their introduction (Kennedy and Southwood 1984; Hawkes 2007; Brändle et al. 2008; Mitchell et al. 2010).

The extent to which an exotic plant escapes its natural enemies also may depend on the location of the population studied. There can be considerable spatial variation in attack within the range of a plant species; for instance, rates of attack often locally decline with a plant's distance from conspecifics (e.g., Condit et al. 1992; Packer and Clay 2000; Mackay and Kotanen 2008; Terborgh 2012), as predicted by the Janzen-Connell Hypothesis (Janzen 1970; Connell 1971). On a geographic scale, marginal populations might be expected to experience reduced damage if they occur in environments unsuitable for their enemies, or if enemies are unable to locate or persist in isolated host populations (e.g., Bach 1994; Garcia et al. 2001; Alexander et al. 2007; Stanton-Geddes et al. 2012; Vaupel and Matthies 2012). For example, western marginal

populations of *Carex blanda* (eastern woodland sedge) are less likely than more central populations to be attacked by fungal pathogens and pre-dispersal seed predators (Alexander et al. 2007). Similarly, leaf damage to *Asclepias syriaca* (common milkweed) is greater in central than marginal populations (Woods et al. 2012). Finally, geographic variation in herbivore attack may follow a latitudinal trend. For instance, insect herbivory often is claimed to decline with increasing distance from the equator (Coley and Aide 1991; Coley and Barone 1996; Schemske et al. 2009), suggesting populations of many plant species near northern range margins might escape some of the damage characteristic of more central areas. Most studies compare different species in temperate and tropical habitats, but some single-species studies also have found herbivory declines with latitude (e.g., Pennings et al. 2007, 2009; Kozlov 2007; Vaupel and Matthies 2012). Nonetheless, the latitudinal hypothesis remains controversial: a recent meta-analysis (Moles et al. 2011) found that only 37% of studies indicated higher average herbivory at lower latitudes. None of these spatial patterns are mutually exclusive; for example, a latitudinal trend in herbivore damage may also represent a trend with population marginality or isolation, a distinction that can be resolved only by a study that separately considers these components.

Variation in herbivore pressure may correlate with trends in the performance of marginal populations. Theory predicts that a species' stable range limit may be set by a failure to adapt to extralimital conditions (Kirkpatrick and Barton 1997; Bridle and Vines 2007; Kawecki 2008; Sexton et al. 2009). It therefore might be predicted that increasing physical or biological constraints would be reflected by decreased performance (growth and reproduction) of a species as it approaches its range edge (Kawecki 2008; Sexton et al. 2009): ultimately, performance declines to such an extent that further populations are no longer sustainable. A review by Sexton et al. (2009) found that of 34 papers that studied size, growth and development of organisms

across range limits, 19 showed some decline in performance. Fecundity showed a similar pattern, with 15 of 31 studies indicating a decline. However, many exceptions exist; in some studies (e.g., Tsaliki and Diekmann 2009) performance has even been shown to increase approaching range margins. This unexpectedly good performance may indicate distribution is still expanding, or if limited, is set by habitat availability or metapopulation processes rather than physical factors *per se* (Holt et al. 2005); however, it also is possible that this maintenance of performance and/or further expansion into marginal habitats might reflect a decline in herbivore pressure counteracting any decline in physical conditions.

Most of these studies of geographic trends in herbivory and performance focus on native species, though evidence suggests that exotic species also may exhibit similar patterns (Colautti et al. 2009; Van der Putten et al. 2010; Alexander and Edwards 2010). Performance of marginal populations is likely to play an especially important role in the invasion process: as an exotic species spreads to fill its new range, or further extends it in response to climate change, escape from natural enemies might result in it occupying a greater area than expected on the basis of climate alone (Van der Putten et al. 2010; Gilman et al. 2010). For instance, the northern range limit of many invaders in North America likely reflects the harsher climate at higher latitudes; whether these northern populations might experience a compensating benefit of reduced damage by natural enemies is unknown.

To investigate how performance and herbivory change along a latitudinal gradient approaching the northern range edge of an invasive plant species, we studied the non-native plant, *Arctium minus* (common burdock) over an 815 km north-south transect. Specifically, we addressed the following questions; 1) does herbivore damage change with latitude; and 2) does plant performance change with latitude? Our results indicate damage by multiple guilds of

herbivores declines with latitude, with potential consequences for the distribution of this invasive plant; we are aware of no comparable study of an exotic species. For exotics as well as natives, latitudinal variation in herbivore attack and performance may have important ecological consequences.

Methods

Study Species

Common or lesser burdock (*Arctium minus*) (Asteraceae) is a Eurasian species now common throughout the USA and Canada except for northern areas (Gross et al. 1980). Burdock is a successful global invader, and is listed as invasive by many authorities in its introduced range (United States Department of Agriculture: <http://plants.usda.gov/java/noxiousDriver>). It is believed to have occurred in eastern North America since the 1600s (Gross and Werner 1983).

Burdock is monocarpic biennial, with a flowering, hollow stem originating from an overwintering rosette (Gross et al. 1980). Mature plants can reach heights of over 250 cm and individual rosette leaves can be over 90 cm long, but most mature plants grow to only 50-150 cm and rosette leaves grow to 35-50 cm. Flowering of the plant occurs in August, and seeds continually mature until middle to late September. Between 10 and 75 seeds are present in each capitulum, which is dispersed by attaching themselves to large mammals that pass by the plant, and possibly over snow in the winter (Hawthorn and Hayne 1978). Burdock is strongly disturbance-dependent, growing very well in perturbed environments such as roadside, footpaths, waste places, near fences and parking lots. Burdock is a competitive plant, as large rosette leaves can cover surrounding vegetation to block out light (Gross et al. 1980).

Study sites

Study sites were chosen along an 815km latitudinal gradient (Fig. 1) from well within burdock's continuous range in Southern Ontario to near the edge of its range in Northern Ontario (Gross et al. 1980). To locate populations for study, we used a stratified searching scheme. First, a total of 12 focal locations were chosen based on accessibility and latitudinal coordinates (Table S-1). We then searched the region surrounding each focal location for separate burdock populations until we reached the desired sample size. The southernmost location was the Koffler Scientific Reserve (44°01'N, 79°31'W), west of the town of Newmarket, while the northernmost location was Moosonee (51°17'N, 80°36'W), near James Bay. The history of burdock at these sites is unknown, and it is possible that more northern sites might be younger, but this species has occurred in eastern North America since at least 1672 (Gross et al. 1980) and occurred to at least 47° by 1980 (Gross et al. 1980). We suspect this highly dispersive species colonized northern sites much earlier than these dates; trading posts have existed near Moosonee at 51° N (where it is now abundant) since the 1670s.

Burdock typically occurs in patches containing a few individuals (our largest examples had about 60 flowering plants) likely descended from a few parents; we refer to these groupings as populations but caution, we have no knowledge of gene flow; therefore, these "populations" represent convenient demographic units rather than genetic entities. A population was defined as a patch of burdock plants that consisted of at least 5 mature plants and 10 total plants (including rosettes and mature plants) at least 100m away from adjacent patches; however, the typical distance between populations was much greater than this minimum. On average, adjacent populations of burdock were 5.5km away from one another, and often separated by roads, streams, forest, and other barriers, while the average distance between consecutive populations

(travelling north) was 18 km; we feel it is reasonable to treat such populations as independent. We attempted to sample 8-10 populations surrounding each focal location, but only 7 populations were found near Peterborough and 6 in Moosonee (Table S-1). Total sample size therefore was 107 populations; however, logistic constraints meant that not all types of data could be collected from every population, so sample sizes vary among analyses. Approximately 45% of populations were found along roadsides or bike paths, 35% were found along walking paths in forests or walkways, while the other 20% were found in habitats including lawns, forest understories, parks and gardens; these habitats were sampled at multiple sites throughout the latitudinal gradient. Although population size (mature plants and rosettes) was estimated, population boundaries were often unclear; thus, these values should be treated as approximate.

With the exception of the Moosonee populations (sampled on 31 July 2011), sampling was split into two episodes; excluding Moosonee from our analyses did not qualitatively change our results. During the first sampling, over a 3 week span in August 2010, flowering was complete and no significant new growth of the plants was occurring. Our sampling proceeded from south to north; since frost free days began in our southernmost location 4 weeks before the northernmost location, the northward trajectory of our sampling helped to control for any additional growth during our sampling trip: northern populations (including Moosonee) had not experienced a longer growing season at the time of sampling. Morphological and herbivory data were collected from 5 randomly selected individuals in each population. Diameter of stem (mature plants) at ground height was measured using vernier calipers, the number of basal leaves was recorded by counting the number of petioles emerging from the ground around the main stem, height was measured to the nearest cm, and the number of mature capitulae (seed heads) was recorded. The number of mines on all leaves also was counted, as were small holes at the

base of affected leaves, showing successful emergence of serpentine miners. For each plant, the most basal live leaf was then selected for further analysis. These leaves were compressed using a plant press, brought back to the lab where leaf size were measured using a 2 cm transparent grid paper, and the fraction of tissue in each square damaged by herbivores was visually estimated and summed. The categories of damage recorded were serpentine mines, blotch mines, hole damage, and surface damage (chlorophyll stripped).

For all sites other than Moosonee, capitulae from each sampled individual were collected in a second trip in September, after maturation was complete. Since Moosonee was visited in July, before seed set had occurred, we instead collected overwintering capitulae from two populations; this may underestimate fecundity, but unless *Metzneria* affects dispersal this should not bias estimates of parasitism. Capitulae were then returned to the lab where 10 randomly selected capitulae per individual were opened and the number of seeds (total, viable and depredated) was recorded along with seed weight (determined as 1/10 the weight of 10 filled seeds). Conservatively, only seeds that were damaged and webbed together with silk by moth larvae were counted as depredated; isolated seeds with holes were assumed to have been damaged while opening capitulae.

Due to the scarcity of herbivory information on burdock, detailed observations of herbivores were carried out at the most southern location, Newmarket. Plants at this location were monitored every day and every other night for the first 3 weeks of growing season, beginning in May. After June, the populations were monitored twice a week until August. Samples of the five most commonly observed herbivores also were sent to the Canadian Centre for DNA Barcoding (Ratnasingham and Hebert (2007) at the Biodiversity Institute of Ontario (<http://www.ccdb.ca/>) for DNA barcoding analysis and further analysis.

Several variables were measured as possible indicators of food value to insects. Carbon: Nitrogen analysis was also performed using a CHN elemental combustion system (Costech model ECS 4010). Five leaves from each population were dried in a lab oven at 50°C for 48 hours and ground into a powder before analysis. Toughness was measured for fully expanded stem leaves using a Chatillon 516 series push-pull gauge to determine penetration force: three measurements were taken per leaf, three leaves were taken per plant and five plants were used in each population. Measurements were taken at a 90° angle, approximately 5 cm from the tip of the leaf, in the middle. Trichome density was also measured by removing two randomly selected leaves from each of two plants and counting the number of trichomes in three 0.5 cm diameter circles (0.2 cm² area) on the underside of each leaf using a dissecting microscope.

Statistical analysis

Analyses were performed using JMP 10 (SAS Institute Inc.). All variables were regressed against latitude. Each data point in a regression represents a mean or total for a single population: this simplified analysis while preserving the degrees of freedom associated with the factor of interest (latitude). An initial MANOVA model with stem diameter, mature plant height, number of capitulae, and number of basal leaves showed a significant trend with latitude ($F_{4,94} = 16.47$, $p < 0.001$); we then chose to analyze these variables separately to further explore relationships between our data and latitude. Since we chose to treat populations as independent, we did not include a "site" term in our models; in any case, preliminary Ordinary Least Squares analyses found that our major results were qualitatively unchanged if this term was included (analyses in Figs 2-5 retained their trends and statistical significance, other than $p=0.06$ for height, and variance components for site rarely differed from zero). Instead, a more flexible GLM (Generalized Linear Model) approach was used since many variables were obviously curvilinear

and/or non-normal. Count data were analyzed using a log link and a Poisson distribution, with correction for overdispersion. Proportional data were analyzed with a logit link. Since these data represented continuous fractions (e.g., proportion of leaf area damaged) rather than binomial counts, a binomial distribution was not appropriate for these data (Warton and Hui 2011); instead, we chose a normal error model. Other continuous measurements (including average seed and capitular production) were analyzed with a normal error model and an identity link (for measurements) or a log link (for ratios). For each type of model, R^2 is reported as the percentage of variance in the observed values explained by the fitted values.

Results

Herbivores observed

We observed a wide variety of herbivores on burdock plants (Table S-2); the identity of the most conspicuous species was confirmed by DNA barcoding analysis (Table S-3). Common leaf herbivores included the mining agromyzid flies *Calycomyza flavinotum* and *Liriomyza arctii*. The identity of *C. flavinotum* was confirmed with a barcoding BOLD match (Table S-3), but *L. arctii* was absent from the BOLD database, and our specimen had only an 88% match to the genus *Liriomyza* (Table S-3); still, *L. arctii* is the only serpentine miner commonly reported attacking *A. minus* in our area (Gross et al. 1980; <http://www.bugguide.net>), and visually matched our specimens. *L. arctii* lays eggs early May; the larva eats tissue in a linear, serpentine fashion until late May, when it emerges through a hole at the base of the leaf. *C. flavinotum* produces blotch mines later in the season (late June), until the larva emerges through a hole near the base of the leaf by late July.

Capitulae were host to a very abundant introduced Gelechid moth, *Metzneria lappella*, also noted as abundant by Hawthorn and Hayne (1978) and Gross et al. (1980). Larvae consume

multiple seeds and then glue damaged seeds together with silk to form a pupal case. The larvae over-winter inside the seed-case, and emerge as adults in late June or early July (Hawthorn and Hayne 1978; Gross et al. 1980). Other herbivores were observed rarely in capitulae, but included a Tephritid fly, thought to be either *Tephritis bardanae* or *Cerajocera tussilaginis*.

Finally, we also saw extensive evidence of chewing damage likely produced by a wide range of generalist herbivores, including both molluscs and insects; for instance, we commonly observed the Crambid moth, *Herpetogramma pertextalis* (Table S-2).

Herbivory

All types of herbivore damage showed a highly significant decrease with latitude; for instance, the fraction of leaf area damaged by the serpentine miner *Liriomyza arctii* ($\chi^2_1 = 48.71$, $p < 0.001$, $R^2 = 0.37$; Fig. 2a), the blotch miner *Calycomyza flavinotum* ($\chi^2_1 = 31.68$, $p < 0.001$, $R^2 = 0.26$; Fig. 2b), and hole-making invertebrates ($\chi^2_1 = 71.19$, $p < 0.001$, $R^2 = 0.49$; Fig. 2c). Other less well-defined types of herbivory showed similar patterns; for instance, surface damage (chlorophyll stripping) also declined ($\chi^2_1 = 90.85$, $p < 0.001$, $R^2 = 0.58$). As a result, the total leaf area damaged by herbivores strongly decreased with latitude ($\chi^2_1 = 100.27$, $p < 0.001$, $R^2 = 0.62$; Fig. 2d). At least in the case of leaf miners, this reduced damage reflected a reduction in the number of individual herbivores, as indicated by highly significant declines in the numbers of both serpentine ($\chi^2_1 = 100.91$, $p < 0.001$, $R^2 = 0.35$; Fig. 3a) and blotch miners ($\chi^2_1 = 139.35$, $p < 0.001$, $R^2 = 0.32$; Fig. 3b). Despite this, emergence success for serpentine miners increased with latitude ($\chi^2_1 = 8.36$, $p = 0.004$, $R^2 = 0.18$); emergence was not documented for the blotch miner. Seed damage caused by *Metzneria lappella* also showed a significant decrease with increasing latitude ($\chi^2_1 = 55.33$, $p < 0.001$, $R^2 = 0.63$; Fig. 4a). The number of viable seeds produced per plant was negatively correlated with seed predation ($R = -0.69$, $p < 0.001$) and significantly

increased with increasing latitude ($\chi^2_1 = 46.39$, $p < 0.001$, $R^2 = 0.56$; Fig. 4b), reflecting both decreased mortality and increased production. As a result, the absolute number of viable seeds increased by 894 for every degree of latitude of northward travel. As noted in the Methods, in Moosonee we were forced to sample last year's capitulae; nonetheless, the points from Moosonee matched the general trends, and these relationships remained highly significant even if Moosonee was excluded from the analysis (seed damage: $\chi^2_1 = 48.72$, $p < 0.001$; viable seeds: $\chi^2_1 = 38.44$, $p < 0.001$).

Nitrogen content of leaves showed a weak but significantly negative relationship with latitude ($\chi^2_1 = 4.49$, $p = 0.03$, $R^2 = 0.07$), though C:N ratio did not ($\chi^2_1 = 1.74$, $p = 0.19$, $R^2 = 0.03$). However other correlates of palatability showed higher significance; for example, force required to penetrate leaf tissue decreased with latitude ($\chi^2_1 = 105.69$, $p < 0.001$, $R^2 = 0.68$), as did number of trichomes ($\chi^2_1 = 130.97$, $p < 0.001$, $R^2 = 0.76$).

Plant performance

The total number of plants per population (rosettes plus mature plants) increased weakly with latitude ($\chi^2_1 = 3.96$, $p < 0.05$, $R^2 = 0.03$), primarily reflecting a significant, albeit small, increase in the number of reproductively mature plants per population ($\chi^2_1 = 14.39$, $p < 0.001$, $R^2 = 0.11$; Fig. 5a); in contrast, the number of rosettes per population did not vary with latitude ($\chi^2_1 = 0.24$, $p = 0.62$, $R^2 < 0.01$). As a result, the ratio of rosettes to mature plants decreased with latitude ($\chi^2_1 = 6.61$, $p = 0.010$, $R^2 = 0.06$). Since limits of populations often were difficult to define, and correlations were very low, these values should be treated cautiously; however, they conservatively suggest population size at least did not decline with latitude. Measures of growth also generally increased with latitude, including (weakly) mature plant height ($\chi^2_1 = 6.77$, $p = 0.009$, $R^2 = 0.06$; Fig. 5b), and (more strongly) mature plant stem diameter ($\chi^2_1 = 24.06$, $p <$

0.001, $R^2 = 0.20$; Fig. S-1a) and the number of basal leaves per mature plant ($\chi^2_1 = 51.95$, $p < 0.001$, $R^2 = 0.41$; Fig. 5c).

Reproductive performance also improved with latitude. The number of capitulae per plant ranged from 28 to 618, and increased northward ($\chi^2_1 = 26.75$, $p < 0.001$, $R^2 = 0.22$; Fig. 5d). When total seed production per plant (including both viable and parasitised seeds) was estimated by multiplying the number of seeds per capitulum by the number of capitulae on that plant, the estimated number of seeds per plant increased with latitude ($\chi^2_1 = 25.00$, $p < 0.001$, $R^2 = 0.36$; Fig. S-1b). Seed weight was unrelated to latitude ($\chi^2_1 = 1.28$, $p = 0.26$, $R^2 = 0.03$).

Most measures of individual performance were positively correlated (Table S-4). Means and standard errors for all growth characteristics are provided in Table S-5.

Discussion

Trends in herbivore damage

Our results clearly show decreasing herbivory with increasing latitude. Burdock was damaged by a wide range of herbivores, with $85\% \pm 1.8\%$ of seeds parasitised (even higher than the 28%-71% reported by Hawthorn and Hayne 1978) and $25\% \pm 2.4\%$ of leaf area consumed in more southern sites (means $\pm$ standard deviations), versus starkly reduced rates of damage by all major guilds of herbivores at northern sites. As a result, plants from the northernmost areas experienced 99% less total leaf damage and 70% less capitular damage, relative to estimates at southern sites. Although many range margin studies have shown decreasing herbivory with increasing distance from the equator (Pennings et al. 2007, 2009; Zhang et al. 2011; Stanton-Geddes et al. 2012), nowhere have results been as striking.

In principle, herbivory might decline towards northern range margins either because insect populations are scarcer or because plants are less nutritious or better defended; however, the

limited evidence available does not support the hypothesis that plant food quality was lower in more northern sites. For instance, leaf nitrogen did decrease with increasing latitude, suggesting more northern plants might be less nutritious (Schoonhoven et al. 2005), but this trend was very weak, and did not seem to explain observed patterns of damage: when we regressed different categories of damage vs. N content, no significant relationships emerged ($p > 0.05$). With this exception, all measures of herbivory resistance declined with increasing latitude. For instance, leaf toughness and the number of trichomes often are correlated with resistance (Schoonhoven et al. 2005), but we found both of these measures to be reduced, not increased, in northern populations. In principle, we could have overlooked some important chemical defence: while not notably toxic, burdock chemistry is not well described. Still, the increase in emergence success by *Liriomyza arctii* in northern populations does not support the hypothesis that these plants are more toxic than southern plants.

If plant quality is not responsible for reduced levels of damage at northern sites, some other factor must be limiting herbivore abundance. For instance, many insects are highly sensitive to temperature (Hill et al. 2011), with lower temperature resulting in fewer herbivores. Cooler temperatures and shorter summers at higher latitudes in our study may inhibit the development of herbivore populations, especially if they have not had the time or ability to adapt to conditions near the edge of burdock's range (Bridle and Vines 2007; Kawecki 2008; Sexton et al. 2009). A second possibility is that herbivores are unable to reliably locate small and widely-separated marginal populations, as proposed to explain reduced rates of seed parasitism in marginal populations *Carduus deflorans* (Vaupel and Matthies 2012). This is unlikely to be true for *Metzneria*, which overwinters in capitulae and therefore is almost certainly co-dispersed with burdock seed, but it might explain reduced levels of attack by foliar herbivores at marginal sites.

As a result, peripheral populations may be partially protected by their isolation (Sexton et al. 2009), though this effect may be somewhat counteracted by burdock's association with disturbed corridors such as roads, which can guide dispersal of specialized insects to their host plants (Peralta et al. 2011). Smaller marginal populations also may be less able to stably support herbivore populations even if located, as also suggested by Vaupel and Matthies (2012); however, this explanation is unlikely for *Arctium*, given the weakly positive correlation between its population size and latitude. One final possibility is that herbivores may not yet have caught up to the expanding distribution of this invasive plant; the northernmost population reported in eastern Ontario by Gross et al. (1980) was only at about 47°N, though we suspect the real distribution at the time was much larger. Again, this seems unlikely for at least *Metzneria*, which likely co-disperses with *Arctium*, and has been in eastern Canada since at least 1898 (Gross et al. 1980). The other major herbivores that we observed (*Liriomyza*, *Calycomyza* and *Herpetogramma*) are less well-documented, and do not disperse with the host.

Trends in plant performance

Although exceptions are frequent (Sexton et al. 2009), it might be expected that a species' performance should decline approaching its range limits, as it experiences increasingly stressful conditions; for instance, Jump and Woodward (2003) showed that populations of *Cirsium acaule* and *C. heterophyllum* experienced significant declines in seed production on approaching northern latitudes. In contrast, we found little evidence of reduced performance with latitude in our analysis; instead, almost all measures of performance increased, including plant diameter, height, number of basal leaves, and capitulae. This is not due to northern populations being sampled at later dates: northern populations (especially Moosonee) had had an equal or lesser growing season than southern populations at the time of sampling. Though small in magnitude,

these trends clearly indicate performance of marginal populations was not reduced relative to more southern ones.

Latitudinal variation in climate might be expected to result in smaller, not larger, plants at more stressful northern sites (e.g., Clausen et al. 1948). Burdock extends south to at least Mexico (<http://www.usda.plants>); there is no reason to believe it cannot cope with warm climates. However, temperature is on average 10°C cooler in our northernmost population compared to our southernmost one, while the frost-free period in Newmarket is 75 days longer than in Moosonee (145 vs. 70 days; Environment Canada 2011: http://www.weatheroffice.gc.ca/canada_e.html). Most models of plant growth responses to climate predict a correlation between decreasing temperature and reduced plant growth. For instance, in *Carduus nutans* (nodding thistle), Zhang et al. (2011) showed that decreasing temperature and precipitation decreased plant height and emergence success, while Jonas et al. (2008) also showed that air temperature and snow cover had direct impacts on maximum plant height and growth rate in various alpine communities in Switzerland.

Alternatively, escape from herbivores may contribute to the ability of high-latitude populations to maintain growth and fecundity despite a much cooler environment. Reduced herbivory does not necessarily translate into improved performance (Maron and Vila 2001; Chun et al. 2010); however, reductions in foliar damage of the magnitude we observed potentially may contribute to improved growth and reproduction. Even if the reduction in foliar damage fails to result in an increase in growth, release from seed predation results in an obvious reproductive benefit for this monocarpic biennial in northern sites: northern plants experience much higher realized fecundity largely as the result of the greatly reduced proportion of seeds parasitised, which explains about half the total variation in viable seed crop ($R^2 = 0.48$). However, while our

results are consistent with enemy release in northern sites, more work is required to exclude other possibilities. For instance, greater absolute seed production could evolve in northern populations as a consequence of selection for greater dispersal near an invasion front (e.g., Darling et al. 2008), while larger size might be a side effect of such selection for increased seed production: Gross and Werner (1983) found a strong correlation between plant height and fecundity in *A. minus*.

Limits to the distribution of burdock

If performance of burdock does not decline approaching the northern margin of its distribution, what, if anything, prevents further range extension? One possibility is habitat availability. Burdock is a plant that thrives in highly disturbed environments in close proximity to human settlements (Gross et al. 1980). Of the 107 populations that we found, approximately 96 (90%) of them were found in highly disturbed human habitats such as bicycle and walking paths, roadsides, private lawns and parks. Few towns exist north of Moosonee in Ontario, and thus burdock currently may be limited by the distribution of suitable sites.

Poleward range extensions by exotic plants such as burdock are expected to occur in response to predicted changes in climate (Walther et al. 2009), both because marginal populations are likely to experience an ameliorating environment, and because a warmer climate is likely to encourage additional settlement and agriculture. Numerous examples now exist of both native and exotic plants and insects migrating poleward in response to climate warming (Hughes 2000; Parmesan 2006; Chen et al. 2011). Such migrations may be facilitated by enemy release if range-expanding populations outpace their natural enemies (Engelkes et al. 2008; Morriën et al. 2010). Marginal populations of burdock already have escaped many of their insect

herbivores; as this species expands its range in future in response to improving climate and/or associated expansion of northern settlement, enemy release may play an important role.

Enemy Release

These results also have implications for enemy release. Studies of enemy release have been severely criticized for not considering variation in attack among populations of invasive plants; for instance, estimates of herbivore diversity may be inflated by combining data from sites with different herbivore communities, while latitudinal trends may bias estimates of damage (Colautti et al. 2004, 2009). At least some of the enemies we observed on *Arctium* (primarily *Metzneria*) also attack this plant in Europe (Gross et al. 1980), but our results suggest that whether North American plants are considered to have escaped from these particular enemies may depend on the latitude of the population under study. As well, collective damage by the entire herbivore community (native plus non-native) is much lower in northern Ontario than in southern sites, suggesting that conclusions about reductions in net herbivory relative to European locations will vary with latitude. Finally, to the extent that improved performance of northern populations reflects reduced herbivore impacts, conclusions regarding the ecological importance of enemy loss also will depend upon the population studied.

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- 587

Figure Legends

Fig. 1. Map indicating focal sampling locations. The region surrounding each location was searched for populations of *Arctium minus* in a stratified sampling scheme. Each location has been labeled with the name of the nearest town: Newmarket (Nm), Peterborough (Pe), Barrie (Ba), Bracebridge (Bb), Huntsville (H), Parry Sound (Ps), Manitoulin Island (Mi), North Bay (Nb), Kirkland Lake (K), Timmins (T), Cochrane (C) and Moosonee (Mo).

Fig. 2. Fraction of leaf area affected by various types of herbivory. Data points are population means; N = 105 populations. 2a) Serpentine mine damage vs. latitude. $\chi^2_1 = 48.71$, $p < 0.001$, $y = 1 / [1 + e^{-(182.83 - 4.24x)}]$, $R^2 = 0.37$; 2b) Blotch mine damage vs. latitude. $\chi^2_1 = 31.68$, $p < 0.001$, $y = 1 / [1 + e^{-(77.39 - 1.84x)}]$, $R^2 = 0.26$; 2c) Total hole damage vs. latitude. $\chi^2_1 = 71.19$, $p < 0.001$, $y = 1 / [1 + e^{-(18.67 - 0.46x)}]$, $R^2 = 0.49$; 2d) Total leaf area damaged by herbivores vs. latitude. $\chi^2_1 = 100.27$, $p < 0.001$, $y = 1 / [1 + e^{-(23.14 - 0.55x)}]$, $R^2 = 0.62$

Fig. 3. Total number of leaf miners observed on 5 plants per population at different latitudes; N = 99 populations. 3a) Serpentine mines (*Liriomyza arctii*). $\chi^2_1 = 100.91$, $p < 0.001$, $y = e^{(89.41 - 1.89x)}$, $R^2 = 0.35$; 3b) Blotch mines (*Calycomyza flavinotum*). $\chi^2_1 = 139.35$, $p < 0.001$, $y = e^{(114.62 - 2.45x)}$, $R^2 = 0.32$

Fig. 4. Effects of pre-dispersal seed predation. Data points are population means; N = 56 populations. 4a) Fraction of seeds damaged by *Metzneria lappella* vs. latitude. $\chi^2_1 = 55.33$, $p < 0.001$, $y = 1 / [1 + e^{-(18.75 - 0.40x)}]$, $R^2 = 0.63$; 4b) Average number of viable seeds per plant vs. latitude. $\chi^2_1 = 46.39$, $p < 0.001$, $y = -39056.64 + 892.30x$, $R^2 = 0.56$

Fig. 5. Characteristics of *Arctium minus* populations vs. latitude. Data points are population means. 5a) Number of mature plants per population vs. latitude; N = 105 populations. $\chi^2_1 = 146.19$, $p < 0.001$, $y = e^{(-3.81 + 0.14x)}$, $R^2 = 0.11$; 5b) Average height of mature plants vs. latitude; N

611 = 105 populations. $\chi^2_1 = 6.77$, $p = 0.009$, $y = -51.71 + 3.98x$, $R^2 = 0.06$; 5c) Average number of
 612 basal leaves vs. latitude; $N = 99$ populations. $\chi^2_1 = 51.95$, $p < 0.001$, $y = -20.90 + 0.51x$, $R^2 =$
 613 0.41 ; 5d) Average number of capitulae per plant vs. latitude; $N = 105$ populations. $\chi^2_1 = 26.75$,
 614 $p < 0.001$, $y = -802.76 + 20.44x$, $R^2 = 0.22$

Fig. 1

Fig. 2

a)

b)

c)

d)

Fig. 3

a)

b)

Fig. 4

a)

b)

Fig. 5

a)

b)

c)

d)