Annotations on what makes this grant particularly great are in Post-Its. These Post-Its should be viewable in Preview on Mac or Adobe Acrobat Reader on any operating system.

# <u>PROPOSAL:</u> How do positive and negative interactions with neighbours affect elevation gradients in fitness and species range limits?

Understanding the ecological factors that determine the size, shape, and location of species ranges is a foundational goal of ecology, and increasingly important to both conservation (e.g. predicting how species will respond to climate warming, or how fast exotic species will spread), and industry (e.g. forecasting future productivity of crops and forestry trees). Ecologically, species ranges can be limited by both abiotic and biotic factors. Testing their relative importance can be complex, however, because the outcome of interactions between species can vary along abiotic gradients. To date, the role of biotic interactions in limiting species ranges has been tested far less often than abiotic factors<sup>1</sup>, and generally testing one interaction and one set of abiotic conditions at a time. My PhD will provide one of the most detailed concrete studies of how biotic interactions interact with abiotic gradients to limit species ranges. Using ambitious field experiments along a 1275-m elevational gradient in Alberta, I am testing how beneficial and antagonistic biotic interactions combine to determine a native species' upper and lower elevational range.

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Hemiparasitic plants extract nutrients from hosts but also do their own photosynthesizing, thus offer an excellent model for addressing how contrasting species interactions shift across a species range. Root hemiparasites extract nutrients and water from the roots of other plants, relying on them for nutrition, but also compete with these same neighbours aboveground for sunlight<sup>2</sup>. Thus, **neighbouring plants are both essential resources and competitors for hemiparasitic plants**. Mountains also offer a useful model for studying biotic interactions along abiotic gradients, as we can traverse large climate gradients and, in some cases, an entire species range in a relatively short distance. I am using the annual hemiparasite *Rhinanthus minor*, which has both its high- and low-elevation range limits in Kananaskis, to test how of beneficial (nutrient provision) and antagonistic (competition) interactions with neighbours vary in intensity and fitness effects across a species range.



In Kananaskis, *Rhinanthus minor* occurs in open meadows from 1100 masl to treeline at 2300 masl. This elevational range coincides with an obvious gradient in the plant community. Meadow plants, including the grasses and legumes *R. minor* prefers as hosts, tend to be larger and denser at lower elevations, and rarer and smaller at higher elevations<sup>3</sup>. When transplanted above its upper range limit, *Rhinanthus minor* fitness is so reduced that populations are not self-sustaining<sup>4</sup>. Artificial warming increases fitness above the range, but not to levels within the range <sup>4</sup>, thus factors other than temperature likely also contribute to the range edge/limit. One potential factor is low quantity and/or poor quality of potential hosts in subalpine and alpine environments above *R. minor*'s range, where vegetation cover is sparser and grasses and legumes rarer.

In contrast, sites below *R. minor*'s range tend to have dense grass communities that form thick mats of dead vegetation and tall canopies of living vegetation. Thus, while host roots are presumably abundant, *R. minor* seedlings may often be outcompeted before they can establish.

To address the impact of host identity on *R. minor*'s entire range, I will reciprocally transplant *R. minor* seeds within and beyond *R minor*'s range, while simultaneously manipulating the interaction strength between *R. minor* and potential host plants.

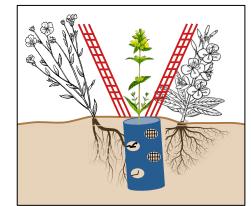
## Research objectives and hypotheses

Question 1) How do neighbouring plants affect *R. minor* fitness through their roles as both hosts and competitors across *R. minor*'s range? <u>Hypothesis:</u> *R. minor*'s fitness is highest where high quality and/or quantity host plants are available but declines where neighbouring plant density increases competition. Question 2) Does either interaction with neighbours contribute to *R. minor*'s low or high range edges? <u>Hypothesis</u>: Density of neighbouring plants' root and aboveground height decreases with elevation; thus *R. minor*'s high range edge is most strongly limited by lack of host-plant availability, while at the low range edge competition is the more important plant-plant interaction.

### Research methods

To test the relative importance of host availability and competition in limiting *R. minor*'s fitness across its elevational range, I am using two types of caging to experimentally reduce the strength of aboveground and belowground interactions between *R. minor* and neighbouring plants. To reduce the density of host root availability I will construct root exclusion tubes out of landscape fabric wrapped around 10 cm deep soil cores. Landscape fabric allows water and nutrient passage, but blocks root regrowth; the density of root regrowth is then manipulated by cutting holes in the fabric. To manipulate aboveground competition, I will create cages out of fine tree netting to push surrounding vegetation away from focal *R. minor* plants. This allows neighbouring plants to function as belowground hosts, while reducing light competition with focal *R. minor* plants. For each treatment type I will have four treatment levels: control (natural levels of host availability/competition), and low, high, and full host/competition reduction. Finally, a 9th treatment combining the high host reduction and high competition reduction treatments will test whether their effects on fitness are additive.

In summer 2019, I conducted a pilot experiment using natural *R. minor* seedlings at three within-range sites (Mt. Allen: 1400, 1885, and 2225 masl) along an elevational transect. In fall 2019, I set up the full experiment at 5 transplant sites, from below *R. minor*'s low range edge (Calgary: 1100 masl) to above its high range edge (Mt. Allen: 2375 masl), transplanting seeds into prepared soil core treatments. Due to COVID-19 travel restrictions in 2020, the above-ground treatments could not be deployed in time, so (with local help) we monitored the emergence, survival, phenology and reproduction of focal *R. minor* plants in the below-ground treatments only. In fall 2020 I was able to travel to Alberta, and finished fitness monitoring and quantified the



host community belowground root density and aboveground height, to test our assumption that host availability and competition for light decrease with increasing elevation. I also re-set the experiment at all 5 sites (25 plots with all 9 treatments per site) to be monitored in summer 2021.

<u>Predictions:</u> I first predict a gradient in host plant density: both root and aboveground height will decrease with elevation. Next, I predict that a lack of host-plant availability may limit *R. minor*'s growth at higher elevations, while at lower elevations competition may be the more limiting factor. **Therefore, I predict that reducing belowground host availability will most reduce** *R. minor* fitness at high elevations, whereas reducing competitors will most improve *R. minor* fitness at low elevations. I predict that reducing both hosts and competitors will have additive effects. The magnitudes of these effects should vary with elevation, i.e. competition is already weak at higher elevations. Thus, I predict no or little change in fitness at low elevation, and a decrease in fitness at mid and high elevations.

# **Significance**

Many modern conservation issues can be understood as changes to species geographic distributions, including range expansions of invasive species, range contraction of threatened-species, and range shifts of native species drive by climate change. While a great deal of effort has been spent predicting species future distributions, particularly under novel climate scenarios, realized shifts are highly idiosyncratic<sup>6</sup> and poorly predicted by models<sup>7,8</sup>. One of the most important factors that limits predictive ability is the role of biotic interactions, which can dramatically affect species range edges but about which we have little systematic data. My research will provide a concrete example of how abiotic and biotic factors interact to set species range limits within Alberta's fragile alpine habitat, which has high biodiversity yet is also a climate change hotspot.

#### References

- 1. Hargreaves, A. L., Samis, K. E. & Eckert, C. G. Are species' range limits simply niche limits writ large? A review of transplant experiments beyond the range. *Am. Nat.* **183**, 157–173 (2014).
- 2. Westbury, D. B. Rhinanthus minor L. J. Ecol. 92, 906–927 (2004).
- 3. Bocchinfuso, S., Ensing, D. J. & Eckert, C. G. Variation in beneficial host availability and performance of hemi-parasite *Rhinanthus minor* across and above its elevational range. *Undergr. honours thesis, Queens Univ.* (2017).
- 4. Hargreaves, A. L. & Eckert, C. G. Local adaptation primes cold-edge populations for range expansion but not warming-induced range shifts. *Ecol. Lett.* **22**, 78–88 (2019).
- 5. Freeman, B. G., Lee-Yaw, J. A., Sunday, J. M. & Hargreaves, A. L. Expanding, shifting and shrinking: The impact of global warming on species' elevational distributions. *Glob. Ecol. Biogeogr.* 27, 1268–1276 (2018).
- 6. Bayly, M. J. & Angert, A. L. Niche models do not predict experimental demography but both suggest dispersal limitation across the northern range limit of the scarlet monkeyflower (Erythranthe cardinalis). *J. Biogeogr.* **46**, 1316–1328 (2019).
- 7. Greiser, C., Hylander, K., Meineri, E., Luoto, M. & Ehrlén, J. Climate limitation at the cold edge: contrasting perspectives from species distribution modelling and a transplant experiment. *Ecography* (*Cop.*). 637–647 (2020) doi:10.1111/ecog.04490.

## **Budget** justification

The ASN Student Research Awards will help cover my travel costs associated with my fieldwork. Travel between the sites (>100km long transect) requires extensive driving and occasionally camping at locations that are 3+hours away. I will have access to a lab-owned vehicle, which I will use to drive from Montreal to Alberta (>4000km). I have also applied to the Quebec Center for Biodiversity Science (QBCS) Excellence Award to cover the other half of my travel expenses.

Non-travel costs of my fieldwork will be covered Dr. Hargreaves NSERC Discovery Grant. This includes housing at the University of Calgary's Biogeoscience Institute and material & equipment costs (eg caging material, field notebooks, flags, camping equip, coin envelopes

## **Budget breakdown**

Item	Cost per	# of units	Total Cost	Amount requested from ASN	QCBS Excellence Award (applied for)	Hargreaves NSERC Discovery Grant
Travel to & from Alberta: Gas	\$300 one- way	2 trips	\$600	0	\$600	0
Travel to & from Alberta: camping	\$40/night	6 nights	\$240	0	\$240	0
Gas/travel within Alberta, driving between sites	\$500/month	5 months	\$2500	\$,2,000	\$500	0
Camping at remote field sites	\$30/night	5 nights	\$150		\$150	0
Housing (field station fees)	\$775/month	5 months	\$3875	0	0	\$3875
Caging materials for experimental setup (Netting, skewers, glue, wood stakes, ground staples, & twist ties)	\$15/plot (based on 2019 costs)	125 plots	\$1875	0	0	\$1875
Other generic field supplies (Field notebooks, flags, camping equip, coin envelopes etc.)	\$350/season	1	\$350	0	0	\$350
Total:			\$9,590	\$2,000	\$1,490	\$6,100