

PRESENCE OF THE EXOTIC WEEVIL *RHINOCYLLUS CONICUS* FRÖELICH AT HIGH ELEVATIONS IN THE ROCKY MOUNTAINS OF COLORADO

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ABSTRACT.—We examined the presence of the exotic weevil *Rhinocyllus conicus* Fröelich on native thistles at high elevations in the Rocky Mountains of Colorado. We tested whether the distribution of *R. conicus* was related to elevation by performing 2 separate studies. First, transects along an elevation gradient were sampled in Rocky Mountain National Park and presence/absence of *R. conicus* was scored to infer relationships between environmental variables and weevil occurrence. Second, an experiment was conducted on Niwot Ridge to determine whether weevils were able to complete their reproductive cycle and overwinter at an elevation where they do not currently exist. Results of a logistic regression indicated that *R. conicus* presence was negatively correlated with elevation. In addition, weevils successfully reproduced at tree line, but climatic limitations suppressed their ongoing presence at this site. The ability of the weevils to utilize native thistles at tree line was unknown prior to this experiment, and our results suggest that within the context of climate warming, the range of *R. conicus* could expand to include more native alpine thistles in North America.

RESUMEN.—Estudiamos la presencia del gorgojo exótico *Rhinocyllus conicus* Fröelich en cardos nativos en Colorado, a altas elevaciones en las Montañas Rocosas. Nos propusimos investigar si la distribución de *R. conicus* tenía relación con el grado de elevación, a través de dos estudios diferentes. En primer lugar, tomamos muestras de transectos a lo largo de un gradiente de elevación en el Parque Nacional de las Montañas Rocosas, y registramos la presencia o ausencia de *R. conicus* para poder establecer la relación entre las variables ambientales y los gorgojos. En segundo lugar, realizamos un experimento en Niwot Ridge para determinar si los gorgojos podían completar su ciclo reproductivo y pasar el invierno a un nivel de elevación en el cual no están presentes actualmente. Los resultados de la regresión logística indicaron que la presencia de *R. conicus* estaba negativamente correlacionada con la elevación. Además, los gorgojos se reprodujeron de manera exitosa en la línea arbolada, sin embargo las limitaciones climáticas no permitieron su presencia en este lugar. Antes de este experimento, no se conocía la capacidad de los gorgojos de utilizar cardos nativos en la línea arbolada, y los resultados sugieren que, dentro del fenómeno de calentamiento climático, el área de *R. conicus* se podría expandir para incluir más cardos alpinos nativos en Norteamérica.

In the context of climate warming, exotic species in mountain ecosystems could shift their distributions further upslope. By examining the environmental parameters that limit such upward expansion, we can provide insight into the invasion potential of these exotic species. Understanding the spread of invasive species is critical to conservation research because invasive species disrupt human land-use activities, drive biodiversity loss, and are at the forefront of environmental damage worldwide (Sheley and Petroff 1999, Schaffner 2001, Russell et al. 2007, Vilà and Ibáñez 2011). Increased temperatures as a result of global climate change may induce species to expand their ranges into sensitive ecosystems such as the alpine zones (Lenoir et al. 2008). Here, we focus on a biological control agent that was introduced to North America and has become invasive.

Although classical biological control is often considered a cost-effective management technique for nonnative species (DeBach and Rosen 1991, Arnett and Louda 2002), the basis of this approach is complicated because it involves the unpredictable introduction of exotic species. One classic example is the weevil *Rhinocyllus conicus* Fröelich—a native European species introduced to North America as a biological control agent for the invasive musk thistle (*Carduus nutans*) but which subsequently targeted native thistle species in North America (Louda et al. 1997, 2005, Rose et al. 2005, Russell and Louda 2005, Rand and Louda 2006, Russell et al. 2007). Musk thistle is a noxious weed that reduces the quality of rangeland by suppressing the growth of desirable vegetation. It became a management priority because it overgrows in pastureland and reduces livestock

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carrying capacity (Sheley and Petroff 1999). In theory, biological control is a good alternative to other forms of management, such as pesticides and manual weeding, but it is hard to predict how an insect in a greenhouse experiment will behave when introduced into the field (Zwolfer and Harris 1984, Rand et al. 2004).

In Europe, *R. conicus* is the natural enemy of *C. nutans* and reduces thistle viability during stages of the insect's life cycle via seed predation. Weevils lay eggs on thistle flower heads between May and June. Eggs incubate for approximately 6–8 days, and then larvae emerge and consume developing seeds for 14–30 days. After the larval feeding period, the weevils pupate, and adult weevils appear 8–14 days later. The adults inhabit the plant, feed for about 2 more weeks, and then enter the soil where they overwinter and re-emerge the following spring (Surlles et al. 1974, Hodgson and Rees 1976, Surlles and Kok 1978, Louda et al. 2005). Because *R. conicus* effectively reduces seeds and therefore reproduction in musk thistles, it was tested for release as a biological control agent in North America. Prerelease studies specified that the North American *Cirsium*, *Silybium*, and *Onopordum* thistles would also be acceptable hosts, although not preferred (Zwolfer and Harris 1984, Louda et al. 1997, Rose et al. 2005). Zwolfer and Harris's (1984) study concluded that the larval mortality of *R. conicus* was high in *Cirsium* species and adults that developed in *Cirsium* species were smaller than those originating from *C. nutans*. These findings led to the conclusion that *R. conicus* would have little impact on *Cirsium* species (Simberloff 2012). The costs of introducing *R. conicus* appeared to be minimal; thus it was widely disseminated to North America in 1969 (Louda et al. 1997, 2005, Pemberton 2000). Consequences of this introduction proved much more extensive than originally thought; *R. conicus* exploits at least 22 native *Cirsium* species in North America (Simberloff 2012).

Rhinocyllus conicus presently uses about one-third of North American *Cirsium* species as hosts (Pemberton 2000, Arnett and Louda 2002, Louda et al. 2005). Research has explored the nontarget effect of this biological control agent in depth (Rand and Louda 2004, 2006, Rand et al. 2004, Rose et al. 2005, Russell and Louda 2005, Russell et al. 2007). A recent study revealed that *R. conicus* exerts more feeding pressure and destroys more seeds of

Cirsium canescens flower heads than native seed predators alone (Rand and Louda 2012). Additionally, because large musk thistle populations have persisted, weevil populations are subsidized, thereby increasing the chances that smaller, nontarget thistle populations will be driven to extirpation (Simberloff 2012). Evidence for the ability of *R. conicus* to limit population growth of native thistles continues to mount, but the weevil's ability to infest native mountain thistle species has not been assessed. Research into shifting species distributions in response to climate change is a growing field of scientific inquiry. Not surprisingly, the impact of climate change on wild species has been noted on every continent (Parmesan 2006). Mountaintop ecosystems are susceptible to the effects of climate change (Grabherr et al. 2000), and studies in these systems predict and report elevation shifts in distributions of both individual species and entire communities (Pimm 2007, Lenoir et al. 2008, Pauchard et al. 2009). As the climate warms, conditions that favor reproduction of *R. conicus*, as well as reproduction of its preferred host species, may move upslope. It is more likely that the weevil will alter its geographic range in response to increased temperatures rather than adapting locally to changing conditions (Parmesan 2006). This relocation could endanger what might otherwise be a thistle refugium at higher elevations in the Rocky Mountains and other regions throughout the continent.

Although a number of native thistles are impacted by *R. conicus* in the Colorado Front Range, survivorship of weevils at high elevations has not been tested. To date, there is only one study that has explored the presence of *R. conicus* in Rocky Mountain National Park (Louda et al. 1997). This work showed that thistles at lower elevation had much higher rates of damage by *R. conicus* than thistles at high elevation. On average, 44% of *Cirsium centaureae* and *Cirsium undulatum* flowerheads were damaged by *R. conicus* at an elevation of 2960 m, compared to <1% damage of *Cirsium tweedyi* flower heads at 4150 m. We re-examined the latter elevation and could not confirm *R. conicus* presence there. To better address the montane distribution of *R. conicus*, we conducted a more thorough survey in Rocky Mountain National Park (RMNP) and developed an experiment to determine the upper limits of the weevil's range.

This study addresses 2 research questions: (1) whether present distribution of *Rhinocyllus conicus* in Rocky Mountain National Park is related to elevation (observational approach) and (2) whether weevils can reproduce and overwinter at an elevation where they do not presently exist (experimental approach). If experimentally introduced weevils can complete a reproductive cycle at a high elevation, then survival may not limit their presence and dispersal restrictions may be operating instead. In that case, management should focus on preventing opportunity for upslope dispersal of weevils. If weevils do not survive the experimental introduction, then a climatic limitation is supported, which may have dramatic implications in light of climate warming.

METHODS

To determine whether *R. conicus* presence/absence is related to elevation, we hiked multiple transects (trails) in RMNP, Colorado, from 15 June to 25 July 2010, when adult weevils and egg sacs were visible. Ten transects were chosen to maximize the area of RMNP covered and to represent the most diverse sample possible, such that the eastern side and the western side of the park were surveyed almost equally (5 transects per side). Transects were placed along designated hiking trails in RMNP and each was oriented from low elevation to high elevation. When a native thistle patch was spotted within 15 m on either side of the trail, at least 10 seed heads from the patch were dissected to check for *R. conicus* presence. If the patch only contained one thistle, then no more than 10 seed heads were removed. If more than one thistle was found in the patch, we randomly selected thistles to dissect by tossing a coin or stick and approaching the thistle nearest to where the coin/stick landed. We then checked all seed heads on the randomly selected plants to make sure we did not miss any weevils. Presence was counted if an adult weevil was found or if there were signature orange egg sacs on the external bracts of developing flower heads (Zwoller and Harris 1984, Russell and Louda 2005). A patch area with a 20×20 -m perimeter was established around the thistle patch, with highest thistle density at the center of the patch. If only a single thistle was located, that individual was designated as the center of the

20×20 -m patch. Thus, each thistle sampling area was 400 m^2 , and the number of bolting thistle plants within the patch was recorded to allow for density comparisons (patch size). GPS locations of all thistle patches found along trails were recorded. Elevation was noted at each thistle site, along with the dominant habitat type and the number of thistle plants. We cross-referenced our elevation recordings with a National Geographic topographic map (© 1988) to ensure the accuracy was within 50 m. Habitat types were tundra, rocky, aspen, spruce/fir, lodgepole, ponderosa, meadow, and riparian.

To test the prediction that *R. conicus* cannot survive on native high-elevation thistles, we introduced weevils to caged *Cirsium* species near tree line at Niwot Ridge, Colorado. Observations made in 2004, 2008, 2009 (T.R. Seastedt unpublished data), and 2010 indicated that this site did not have weevils. Cages were placed around 20 individual thistle plants located in the same patch at 3290 m elevation in the East Bowl of Niwot Ridge. Thistle species included in the experiment were *Cirsium eatonii* and *Cirsium centaureae*, which are highly similar morphologically and could actually be hybrids at this site because they are extremely difficult to distinguish (Tim Hogan personal communication, David Buckner personal communication). Thus, species type was not confounding in this case because both *C. eatonii* and *C. centaureae* are equally acceptable hosts. We placed cages only around bolting thistles because *R. conicus* requires flower heads for reproduction. The experiment included a total of 30 plants: 20 caged thistles (10 with weevils, 10 without weevils) and 10 marked control thistles that were not caged. Cages were constructed of insect-impenetrable remay cloth and chicken wire and were staked securely around each plant. Remay cloth was white and did not increase the temperature around the plant. The cloth was buried 3 inches deep and secured tightly around the cages to ensure that no weevils could escape. Cage size was 2 feet wide by 4 feet tall and adequately spacious so that no part of the cage touched the plant and plants remained unscathed. To monitor the cage effect, 2 mating weevil pairs were randomly placed in 10 of the cages, and the other 10 cages received no weevils. Mating pairs of *R. conicus* were collected on 15 July 2010 at a lower-elevation site (about 2950 m)

called “Elk Meadow” near the University of Colorado’s Mountain Research Station. That same day, weevils were transported in breathable containers to the experimental site on Niwot Ridge known as “tree line.” The 10 cages that received mating weevil pairs were checked each week to ensure none escaped. When thistles began to produce pollen, we hand-pollinated the caged thistles by using a brush. We cross-pollinated plants between cages to ensure seed maturation and hence a food source for the weevils. Three weeks post-introduction, we noted orange egg sacs on the bracts of flower heads in the enclosures containing weevils. We waited 2.5 months for the weevils to complete their reproductive process (oviposition to adult emergence) before dissecting the seed heads to evaluate weevil success rates and seed viability.

On 27 September 2010, thistle seed heads were collected at tree line from all weevil enclosures, whether the enclosure had received a weevil or not. Seed heads were stored in labeled airtight bags for dissection later that day. Seed heads were transported back to the University of Colorado and dissected to find and count larvae, pupae, and adult weevils. All larvae, pupae, and adult weevils found were placed in vials and frozen. Enclosures were left at tree line during the winter of 2010/2011 and were checked on 15 June 2011 to determine whether weevils had emerged from the soil.

To determine reproductive success of naturally occurring *R. conicus* for comparison to reproductive success of experimentally placed *R. conicus* at tree line, we sampled thistle plants at Elk Meadow on 10 July 2010 (2950 m). Plants were randomly sampled along five 6 × 50-m transects spaced along the entire meadow. All seed heads were removed from plants on each transect to gain a representative sample of the meadow (14 plants). Seed heads were dissected the same day, and the number of *R. conicus* larvae, pupae, and adults per seed head were recorded. The number of viable seeds per seed head was also noted. We did not cage any thistles at Elk Meadow because weevils attacked thistles equally at this site and there was no way to prevent weevils from locating thistles.

Statistical Analysis

Data analyses were performed using the statistical software package *R* Version 2.12.1 GUI

1.35 © 2004–2010 (R Development Core Team 2011). We used logistic regression to analyze the association between *R. conicus* presence/absence and 3 independent predictor variables (elevation, plant density, and habitat type). Logistic regression is the appropriate statistical test because the dependent variable is a binary (presence/absence) response. Logistic regression utilizes a logit, or a logistic transformation of the odds, as the dependent variable. The function represents the log odds of a “presence” response in the dependent variable and is described as follows:

$$\log(\text{odds}) = \text{logit}(P) = \log[P/(1 - P)].$$

The logistic regression equation was

$$\text{logit}(P) = a + bx.$$

The model was estimated using an iterative maximum likelihood process to optimize a goodness-of-fit criterion, rather than to minimize variance, so an R^2 statistic does not exist. We chose the model with the minimum AIC to maximize goodness of fit.

To determine whether the mean number of adults was different between experimental enclosures and control plants at the tree line site, a one-sample *t* test was used. We also conducted a 2-sample *t* test to compare mean number of weevils in the experimental cages at tree line to naturally occurring numbers at the lower-elevation Elk Meadow site. We conducted a 2-sample *t* test to compare average number of viable seeds between experimental and control samples at tree line and to compare average number of viable seeds between Elk Meadow and tree line.

RESULTS

On the 10 transects surveyed, weevil presence/absence and GPS coordinates were recorded at 55 thistle patches. Elevations ranged from 2513 m to 3601 m (median = 3012 m, \bar{x} = 3004 m). The number of thistles found per 400-m² sample area ranged from 1 plant to 70 plants (median = 6, \bar{x} = 12.4). Weevils were present in 19 patches and absent from 36 patches. Five different native thistles were found in all of the 8 different habitat types (see Methods). Of the 5 native thistles found, *Cirsium eatonii* was the most common (26

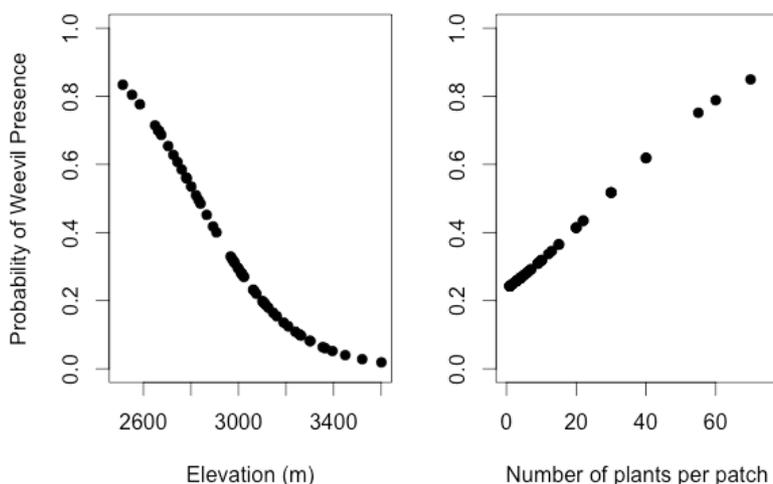


Fig. 1. Probability of weevil presence as a function of elevation (left) and thistle density per patch (right).

TABLE 1. Logistic regression results of weevil presence/absence for 9 transects in Rocky Mountain National Park.

| Predictor variables | Coefficient | SE | Z value | P |
|---------------------|-------------|--------|---------|----------|
| Intercept | 13.6353 | 4.7657 | 2.861 | 0.0042** |
| Number of plants | 0.0581 | 0.0275 | 2.117 | 0.0343* |
| Elevation (m) | -0.0051 | 0.0017 | -3.054 | 0.0023** |

AIC: 58.908

Null deviance: 70.905 on 54 degrees of freedom

Residual deviance: 52.908 on 52 degrees of freedom

* $P < 0.01$

** $P < 0.001$

observations), and *Cirsium scariosum* was the least common (2 observations). *Cirsium centaureae* was observed 8 times. *Rhinocyllus conicus* was never observed on *Cirsium scariosum* or *Cirsium scopulorum*. *Cirsium* species that could not be identified were recorded as *Cirsium* spp.

The significant variables associated with weevil presence/absence were elevation and number of plants per patch (Fig. 1; Table 1). Habitat type was not significantly associated with weevil presence/absence. Number of plants was used instead of density because the density variable had an inflated coefficient due to its constrained range (0.0025–0.1750), and patch size was the same for every patch. Although there was a positive correlation between number of plants and *R. conicus* incidence, that correlation was not as strong as the negative one with elevation. The probability of weevil presence doubled when the number of thistles found in the patch increased from 20 to 60 individuals.

The final regression equation for our model was

$$\text{logit}(P) = 13.635 + 23.258X - 0.005X.$$

To interpret these results, the logit is transformed to get the odds ratio. For elevation, the odds ratio is calculated as $e^{-0.0051}$, such that for every meter of elevation gained, the probability of finding a weevil on a native thistle is multiplied by a factor of 0.995 ($P = 0.0023$). Weevil presence is negatively correlated with elevation, and weevils were never seen above an elevation of 3140 m (Fig. 2). Average thistle density in patches was similar at high and low elevations, so we deduced that there was no interaction between these 2 variables.

The weevil survivorship experiment indicated that weevils were able to successfully reproduce at tree line. At Elk Meadow, all seed heads were dissected from 14 different thistle (*C. centaureae* and *C. eatonii*) plants. The average number of seed heads per thistle

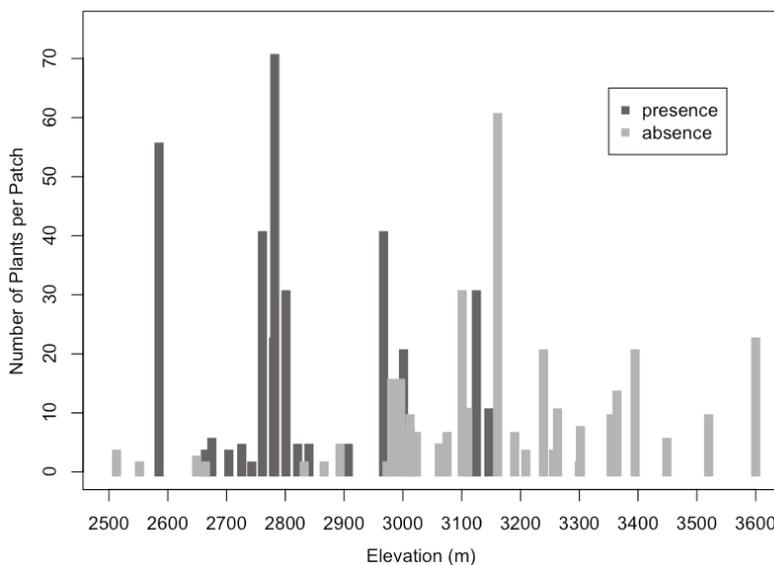


Fig. 2. Weevil presence/absence for the elevations sampled and the total number of thistles found in each sample patch.

was 6.71. The average number of *R. conicus* larvae, pupae, and adults found per seed head was 0.38, 1.38, and 0.53, respectively ($n = 14$). There was an average of 1.221 viable seeds per seed head, even though larvae of the weevils were actively feeding at the time of counting (Fig. 3).

At tree line, weevils successfully completed their life cycle (egg to adult) during a single growing season. We removed all of the seed heads from the thistles to obtain the total number of weevils per plant. During dissection all larvae, pupae, and adults were present, indicating that none had emerged prior to seed head collection. The average number of larvae, pupae, and adult weevils per seed head was 0.39, 0.92, and 1.66, respectively, in the enclosures that received mating weevil pairs ($n = 10$, Fig. 3). Tree line had significantly more mean adult weevils than Elk Meadow ($df = 12.743$, $P = 0.036$). At tree line, in the enclosures that did not receive weevils and on the control plants, there was no sign of weevil activity. Average number of viable seeds per seed head was 0.2 for cages without weevils and 0.535 for control plants. Compared to Elk Meadow, the average number of viable seeds per seed head was lower at tree line, although this difference was not significant ($df = 14.643$, $P = 0.1141$). Lastly, when the tree line site was revisited the following year on 15 June 2011,

plants were checked for adult weevils and none were found. At Elk Meadow, the weevil population had reemerged.

DISCUSSION

Our study examined the distribution of *R. conicus* along an elevational gradient in Rocky Mountain National Park and its ability to survive at tree line. By conducting a survey of transects from low to high elevation in RMNP, we were able to determine that the distribution of *R. conicus* was negatively associated with elevation and positively associated with the number of native thistles found within patches. *Rhinocylus conicus* was more likely to occur at low elevations than at high elevations and was more often found in dense thistle patches. Although weevils were associated with dense patches at low elevation, similarly dense patches at high elevation did not have weevils, indicating that density was not a limiting factor at high elevation (Fig. 2). Because *R. conicus* was not found at high elevations, the next step was to see whether survivorship at a high elevation was possible. To our knowledge, this was the first experimental test of the ability of *R. conicus* to reproduce at tree line. The controlled introduction was a success, with 100% survivorship in the enclosures with weevils and effective development from offspring to adults. We

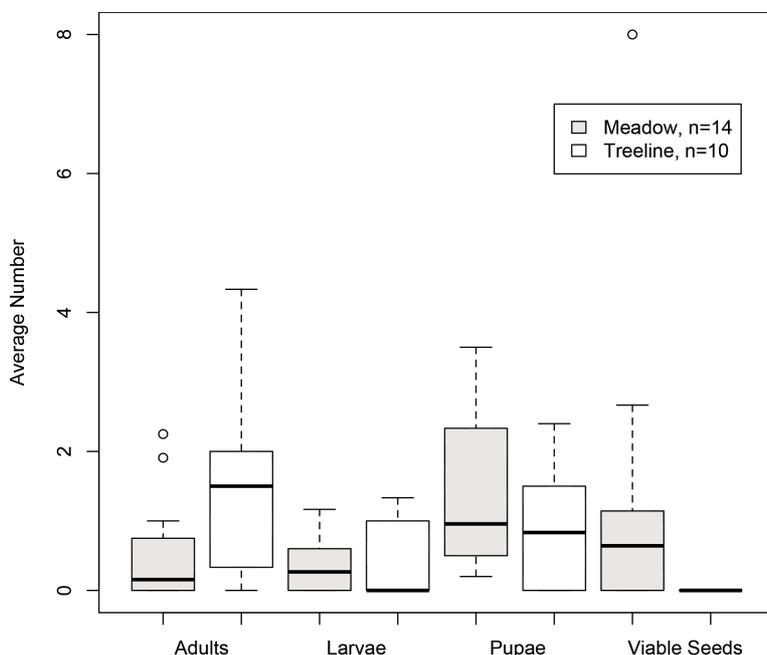


Fig. 3. Average number of weevils found at each life stage and total number of viable seeds.

conclude that weevils were able to reproduce at tree line, but they do not appear to overwinter successfully.

Rhinocyllus conicus was able to breed on thistles at tree line, even thistles that had an unsuccessful year, regardless of whether they were caged or not. Seed head dissection of both control and caged thistles from tree line revealed that seed heads were unfilled and desiccated. Mature seeds were found in previous years at this site (T.R. Seastedt unpublished data)—an indication that thistle reproduction is ongoing at tree line. Despite these conditions, *R. conicus* thrived in the enclosures, even without viable seeds to consume.

Our study introduced weevils to only one high-elevation site. Due to the time constraint, we could not perform the introduction at multiple locations throughout the Rockies. Although there is the possibility that the cages could have influenced the ability of *R. conicus* to survive at tree line, it seems unlikely, because during weekly checks of the cages, thistles with weevils and thistles without weevils were in similar flowering stages, as were the uncaged control thistles.

Our results demonstrated that *R. conicus* does not attack *Cirsium* species at their highest

elevations (at 40° N latitude and about 3200 m elevation) in Rocky Mountain National Park. We found that the weevils could complete their life cycle at about 3300 m, but these beetles apparently could not successfully overwinter in the tree line area. Soil temperatures at tree line can vary considerably depending on snow depth and duration at the specific site (Liptzin and Seastedt 2009). Hence, the successful movement of *R. conicus* will likely vary as a function of insulating snow cover, as well as ambient temperatures.

When placed in the context of a warming climate, this study has implications for the future of native North American thistles in the Front Range of Colorado. *Rhinocyllus conicus* is already a widespread invasive throughout the foothills of the Front Range. The thistles that have escaped infestation are those at higher elevations, outside the physiological limitations of *R. conicus*. The predator-prey interaction represented here has a strong spatial-climatic component generated by the elevational gradient. Currently, the weevil may be altering the distribution of *Cirsium* species by having a disproportionately large effect on lower-elevation thistles. With warming temperatures, or changes in snowpack amount and duration,

R. conicus may come to prefer higher-elevation host thistles as a response to the decline in fitness of lower-elevation thistles due to their inability to adapt to higher temperatures (Parmesan 2006). The current framework of global warming is likely to improve this weevil's success rate. Since the introduction of *R. conicus* in 1969, the weevil has spread to at least 22 native *Cirsium* species in North America, and infestation rates have increased (Babendreier 2007, Wiggins et al. 2010, Simberloff 2012). It is now clear that native, high-elevation thistles that were once protected by a colder climate may become acceptable hosts for *R. conicus* in warmer-winter scenarios.

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LITERATURE CITED

- ARNETT, A.E., AND S.M. LOUDA. 2002. Re-test of *Rhinocyllus conicus* host specificity, and the prediction of ecological risk in biological control. *Biological Conservation* 106:251–257.
- BABENDREIER, D. 2007. Pros and cons of biological control. Pages 403–418 in W. Nentwig, editor, *Biological invasions*. Ecological Studies Series 193, Springer, Berlin, Germany.
- DEBACH, P., AND D. ROSEN. 1991. *Biological control by natural enemies*. 2nd edition. Cambridge University Press, Cambridge.
- HODGSON, J.M., AND N.E. REES. 1976. Dispersal of *Rhinocyllus conicus* for biocontrol of musk thistle. *Weed Science* 24:59–62.
- GRABHERR, G., M. GOTTFRIED, AND H. PAULI. 2000. GLOBRIA: a global observation research initiative in alpine environments. *Mountain Research and Development* 20:190–191.
- LENOIR, J., J.C. GÉGOUT, P.A. MARQUET, P. DE RUFFRAY, AND H. BRISSE. 2008. A significant upward shift in plant species optimum elevation during the 20th century. *Science* 320:1768.
- LIPTZIN, D., AND T.R. SEASTEDT. 2009. Patterns of snow, deposition, and soil nutrients at multiple spatial scales at a Rocky Mountain tree line ecotone. *Journal of Geophysical Research Biogeosciences* 114:2005–2012.
- LOUDA, S.M., D. KENDALL, J. CONNOR, AND D. SIMBERLOFF. 1997. Ecological effects of an insect introduced for the biological control of weeds. *Science* 227:1088–1090.
- LOUDA, S.M., T.A. RAND, A.E. ARNETT, A.S. MCCLAY, K. SHEA, AND A.K. MCEACHERN. 2005. Evaluation of ecological risk to populations of a threatened plant from an invasive biocontrol insect. *Ecological Applications* 15:234–249.
- PARMESAN, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics* 37:637–669.
- PAUCHARD, A., C. KUEFFER, H. DIETZ, C.C. DAEHLER, J. ALEXANDER, P.J. EDWARDS, J.R. ARÉVALO, L.A. CAVIERS, A. GUIGAN, S. HAIDER, ET AL. 2009. Ain't no mountain high enough: plant invasions reaching new elevations. *Frontiers in Ecology and the Environment* 7:479–486.
- PEMBERTON, R.W. 2000. Predictable risk to native plants in weed biological control. *Oecologia* 125:489–494.
- PIMM, S.L. 2007. Biodiversity: climate change or habitat loss—Which will kill more species? *Current Biology* 7:117–119.
- R DEVELOPMENT CORE TEAM. 2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria; [cited 5 March 2011]. Available from: <http://www.r-project.org>
- RAND, T.A., AND S.M. LOUDA. 2004. Exotic weed invasion increases the susceptibility of native plants to attack by a biocontrol herbivore. *Ecology* 85:1548–1554.
- _____. 2006. Invasive insect abundance varies across the biogeographic distribution of a native host plant. *Ecological Applications* 16:877–890.
- _____. 2012. Exotic weevil invasion increases floral herbivore community density, function, and impact on a native plant. *Oikos* 121:85–94.
- RAND, T.A., F.L. RUSSELL, AND S.M. LOUDA. 2004. Local- vs. landscape-scale indirect effects of an invasive weed on native plants. *Weed Technology* 18:1250–1254.
- ROSE, K.E., S.M. LOUDA, AND M. REES. 2005. Demographic and evolutionary impacts of native and invasive insect herbivores on *Cirsium canescens*. *Ecology* 86:453–465.
- RUSSELL, F.L., AND S.M. LOUDA. 2005. Indirect interaction between two native thistles mediated by an invasive exotic floral herbivore. *Oecologia* 146:373–384.
- RUSSELL, F.L., S.M. LOUDA, T.A. RAND, AND S.D. KACHMAN. 2007. Variation in herbivore-mediated indirect effects of an invasive plant on a native plant. *Ecology* 88:413–423.
- SCHAFFNER, U. 2001. Host range testing of insects for biological weed control: how can it be better interpreted? *BioScience* 51:951–959.
- SHELEY, R.L., AND J.K. PETROFF. 1999. *Biology and management of noxious rangeland weeds*. Oregon State University Press, Corvallis, OR.
- SIMBERLOFF, D. 2012. Risks of biological control for conservation purposes. *BioControl* 57:263–276.
- SURLES, W.W., AND L.T. KOK. 1978. *Carduus* thistle seed destruction by *Rhinocyllus conicus*. *Weed Science* 26:264–269.
- SURLES, W.W., L.T. KOK, AND R.L. PIENKOWSKI. 1974. *Rhinocyllus conicus* establishment for biocontrol of thistles in Virginia. *Weed Science* 22:1–3.

- VILÀ, M., AND I. IBÁÑEZ. 2011. Plant invasions in the landscape. *Landscape Ecology* 26:461–472.
- WIGGINS, G.J., J.F. GRANT, P.L. LAMBDIN, J.W. RANNEY, J.B. WILKERSON, A. REED, AND R.A. FOLLUM. 2010. Host utilization of field-caged native and introduced thistle species by *Rhinocyllus conicus*. *Environmental Entomology* 39:1858–1865.
- ZWOLFER, H., AND P. HARRIS. 1984. Biology and host specificity of *Rhinocyllus conicus* (Frol.) (Col., Curculionidae), a successful agent for biocontrol of the thistle, *Carduus nutans* L. *Zeitschrift der Angewandte Entomologie* 97:36–62.

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