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Assessing the vulnerability of rare plants using climate change velocity, habitat connectivity, and dispersal ability: a case study in Alberta, Canada

Quinn E. Barber¹ · Scott E. Nielsen¹ · Andreas Hamann¹

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Abstract Climate change generally requires species to migrate northward or to higher elevation to maintain constant climate conditions, but migration requirement and migration capacity of individual species can vary greatly. Individual populations of species occupy different positions in the landscape that determine their required range shift to maintain similar climate, and likewise the migration capacity depends on habitat connectivity. Here, we demonstrate an approach to quantifying species vulnerabilities to climate change for 419 rare vascular plants in Alberta, Canada, based on a multivariate velocity of climate change metric, local habitat fragmentation, and migration capacity. Climate change velocities indicated that future migration requirements ranged from 1 to 5 km/ year in topographically complex landscapes, such as the Alberta Foothills and Rocky Mountains. In contrast, migration requirements to maintain constant climate in relatively flat Boreal Plains, Parkland, and Grassland ranged from 4 to 8 km/year. Habitat fragmentation was also highest in these flat regions, particularly the Parkland Natural Region. Of the 419 rare vascular plants assessed, 36 were globally threatened (G1-G3 ranking). Three globally threatened species were ranked as extremely vulnerable and five species as highly vulnerable to the

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interactions among climate change velocity, habitat fragmentation, and migration capacity. Incorporating dispersal characteristics and habitat fragmentation with local patterns in climate change velocity improves the assessment of climate change threats to species and may be applied to guide monitoring efforts or conservation actions.

Keywords Climate change velocity · Climate refugia · Species conservation · Seed dispersal · Migration corridors · Managed relocation · Assisted migration

Introduction

Rapid climate change is anticipated to exceed species' tolerances to changes in their climatic habitat, which will likely lead to a decline in global biodiversity (Howe and Smallwood 1982; Hughes 2000; Thomas et al. 2004). Range shift through migration as well as genetic adaptation to new environments (e.g., in situ adaptation) may allow species populations to persist, but species and individual populations differ in their migration capabilities and their ability to acclimatize to climate change (Chen et al. 2011; Devictor et al. 2012; Savolainen et al. 2007). It is generally accepted that vulnerability is defined by the interactions between climate change exposure, species sensitivity, and species adaptive capacity (Williams et al. 2008). Climate change exposure refers to the magnitude of climate change experienced for a species or population, sensitivity refers to a species' inherent tolerance to climate change, and adaptive capacity refers to a species' ability to migrate or genetically adapt to new environments.

There are a variety of methodological approaches for assessing species' vulnerability to climate change, including correlative, mechanistic, and trait-based vulnerability



Quinn E. Barber qbarber@ualberta.ca

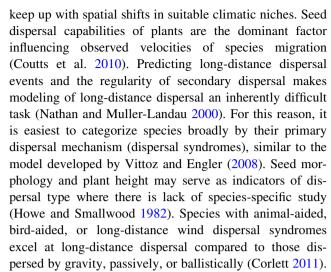
Department of Renewable Resources, University of Alberta, 751 General Services Building, Edmonton, AB T6G 2H1, Canada

assessments (Pacifici et al. 2015). Correlative approaches typically rely on realized niche models (Clark 1998; Pearson and Dawson 2003), while mechanistic models use species' functional traits and climate tolerances to define a species' fundamental climatic niche (Kearney and Porter 2009). Trait-based vulnerability assessments that infer function (e.g., migration capacity) from traits (e.g., dispersal mechanism) have been adopted by conservation and government organizations for their simplicity (Beardmore and Winder 2011). Estimates of climate change exposure have benefited from the concept of climatic landscape analyses that measure migration requirements instead of simply relying on the absolute value of climate change. These so-called climate change velocities measure instantaneous speed and direction of migration required to maintain constant climate conditions for any position within a landscape (Loarie et al. 2009).

Climate change velocity has been used to evaluate vulnerability of different ecosystems and geographic regions for projected climate change (Burrows et al. 2014; Loarie et al. 2009; Ordonez and Williams 2013) as well as recent (twentieth century) observed climate trends (Dobrowski et al. 2013; Pinsky et al. 2013). Climate change velocity forecasts can be highly variable but tends to be lower in mountainous biomes and regions possessing high climatic diversity (Burrows et al. 2014; Dobrowski et al. 2013; Loarie et al. 2009). More recent improvements in this basic concept allow for more applications to local conservation and management (Hamann et al. 2014). Not only can the climate velocity concept be used to compare climate change vulnerability among regions, but also across different species based on their present distribution (IPCC 2014).

Climate migrants are anticipated to move predominantly to higher latitudes and altitudes in response to warming temperatures, although observed migration patterns do not always conform to these expectations (Parmesan et al. 1999). Counterintuitive migration patterns are often due to multiple climate variables (Crimmins et al. 2011; Feeley et al. 2011; Tingley et al. 2012), and predictive methods involving the use of multiple climatic factors have proven more realistic than earlier approaches based on temperature change alone (Burrows et al. 2014). While mobile species have begun to respond to climate change by shifting their geographic range, many plant taxa have lagged behind expected rates of range shift (Chen et al. 2011; Zhu et al. 2012). This migration lag is driven by numerous factors that pose barriers to movement (Crooks et al. 2011), including habitat fragmentation and land use change. Quantifying these barriers to migration will be important to evaluate species' vulnerabilities to climate change.

Finally, species vary greatly in their adaptive tolerance and migration capacity, which in turn affect their ability to



Here, we provide a framework for estimating plant population vulnerability to climate change based on their local climate change velocities, habitat fragmentation, and their migration capacity inferred from their dispersal syndrome. This approach represents a combined approach that includes measures of exposure and adaptive capacity through a trait-based vulnerability assessment, and is most useful for rapid assessment of multiple species where a lack of species-specific data prevents correlative or functional assessment approaches (Pacifici et al. 2015). Our aim is to assess rare species' vulnerability to climate change in order to focus monitoring of their observed demographic response and, if necessary, recommend more direct management interventions, potentially including managed relocation (i.e., assisted migration). In the case of Alberta, 419 vascular plants are locally ranked as critically imperiled (S1), imperiled (S2), or vulnerable (S3) (Young et al. 2011). Rapid assessments and methods are needed to guide conservation actions and monitoring for species based on their location with respect to climate change velocity, habitat fragmentation, and dispersal capabilities. Here, we illustrate a spatially explicit approach to rank species vulnerabilities based on the interaction of these factors.

Methods

Climate data

Climate datasets were generated using the ClimateWNA software package (Hamann et al. 2013; Wang et al. 2012), available for anonymous download at http://tinyurl.com/ClimateWNA. The software provides lapse rate-adjusted climate surfaces at any resolution and in any projections, based on parameter-elevation regressions on independent slopes model (PRISM) climate grids (Daly et al. 2008). ClimateWNA further overlays anomaly surfaces for



historical data and future projections from atmosphere—ocean global circulation models (AOGCMs). We used seven AOGCMs projections for the A2 emission scenario from the CMIP3 dataset referenced in the IPCC's Fourth Assessment Report (IPCC 2007): CCMA CGCM3.1, CSIRO MK3.0, IPSL CM4, MIROC3.2 HIRES, MPI ECHAM5, NCAR CCSM3.0, and UKMO HADGEM. These seven models were chosen based on resolution, validation statistics, and representation of predictions for the study area according to Stralberg et al. (2014). The results were averaged into an aggregate estimate for concise reporting.

All climate datasets were generated in Lambert Conformal Conic projection at a 1-km resolution. Climate variables selected for the multivariate velocity analysis included: mean annual temperature, mean temperature of the warmest month, mean temperature of the coldest month, mean annual precipitation, mean growing season (May to September) precipitation, annual compound moisture index, summer (June, July, August) compound moisture index, degree days above 5 °C, and number of frost-free days. A baseline period of 1961–1990 (hereafter "normal period") was used as the climate normal, and 2041–2070 (hereafter "2050s") was used as our climate projection.

Multivariate climate change velocity and velocity trajectories

Multivariate climate change velocity surfaces were calculated using the protocol described in Hamann et al. (2014). Whereas univariate velocities are typically calculated as the temporal gradient of climate change divided by the spatial gradient of climate, Hamann et al. (2014) measured climate change velocity using the distance to nearest analogous climate. This allows the use of several climate variables summarized in a principal component analysis (PCA) with bins of unique climates used to define climate matches. Climate change velocities are then calculated as the minimum required geographic distance to a matching cell divided by the number of years between the baseline climate period and the future projection. Velocity calculations were completed using climate datasets for all of North America west of 100°0′W to avoid arbitrary edge effects associated with the boundary of Alberta; however, results are presented only to the extent of Alberta. Velocity data are available for anonymous download at http:// tinyurl.com/VelocityWNA.

Rare species data

We used rare vascular plants in Alberta, Canada, as a case study to demonstrate our methods of ranking climate change vulnerability. Of the different major terrestrial taxa, plants are considered the most vulnerable to migration stresses associated with climate change due to their poor dispersal capability (IPCC 2014). The Alberta Conservation Information Management System (ACIMS) is a biodiversity information database managed by Alberta Tourism, Parks & Recreation (2013) that contributes to North America's NatureServe system. ACIMS tracks species occurrence locations across Alberta using NatureServe protocols (Young et al. 2011). Rare plant species in this database are any species with a NatureServe subnational conservation rank of vulnerable (S3), imperiled (S2), or critically imperiled (S1).

Dispersal capability of each species was categorized using the NatureServe Climate Change Vulnerability Index dispersal criteria (Young et al. 2011). Young et al. classify species into seven categories according to how dispersal ability putatively affects climate change vulnerability, ranging from "greatly increases vulnerability," such as gravity-dispersed seed, to "greatly decreases vulnerability," such as avian-assisted seed dispersal. Dispersal mechanisms for the plant species covered in this study were obtained from the United States Department of Agriculture PLANTS database (USDA and NRCS 2014), the Encyclopedia of Life database (Encyclopedia of Life 2014), and botanical references. Following Young et al. (2011), classification is based on the primary dispersal mechanism of the plant and excludes dispersal mechanisms that rely on rare events that may result in extreme longdistance dispersal. In adopting Young et al.'s (2011) approach to our species portfolio, we consolidated the two most extreme classes (classes 1 and 2, and classes 6 and 7) for a total of five vulnerability classes based on dispersal.

Habitat fragmentation

We used the Human Footprint Map of Alberta (Alberta Biodiversity Monitoring Institute 2010) to derive habitat fragmentation for the year 2010. The "human footprint" refers to the temporary or permanent transformation of native ecosystems to human land uses (e.g., built-up area, roads, agricultural land, and surface mines). In addition, we considered water and snow/ice land cover as barriers to migration, obtained from the 2010 ABMI Land Cover Map (Castilla et al. 2014). Datasets were derived from SPOT 5, Landsat 5 and Landsat 7 satellite imagery with a minimum resolution of 30 m. We did not consider areas classified as "barren" and "exposed" as "not available" in our fragmentation index, since the dispersal of seeds is not normally inhibited by these features (Bacles et al. 2006). Habitat fragmentation (resistance to natural seed dispersal) was estimated as the proportion of habitat "not available" to plants within a 10-km moving window.



Vulnerability ranking

We defined an index of "migration stress" as the product of habitat fragmentation and climate change velocity at any given point in the landscape. Lacking empirical data to weigh the effects of habitat fragmentation versus climate change velocity, we assigned them equal weight by means of normalizing each index. Migration stress was reclassified into five equal ordinal groups, similar to seed dispersal capacity. Class 1 populations were anticipated to experience the highest migration stress, while class 5 populations were anticipated to experience the lowest.

Subsequently, the climate change vulnerability index was calculated for each species as the multiplicative interaction of migration stress (threat classes) and seed dispersal (capacity for response). Class 1 represents the most vulnerable species, characterized by high climate velocities, high habitat fragmentation, and weak dispersal capability, whereas class 25 represents the least vulnerable group. We used a multiplicative index since the two factors are unlikely to have additive effects without interactions (Renton et al. 2013). For example, high migration stress is likely to be disproportionately exacerbated by low dispersal capacity.

Results

Several regions of Alberta had disproportionately high habitat fragmentation (Figs. 1, 4). The Grassland and Parkland Natural Regions (south-central Alberta) had a mean fragmentation of 56 % and 78 %, respectively. Many parts of these regions exhibited near 100 % habitat loss due to agricultural land use, forming a significant barrier to migration for species incapable of long-distance dispersal. Mean fragmentation of other Natural Regions was much lower: 27 % in the Foothills; 22 % in the Boreal; 16 % in the Canadian Shield; and 9 % in the Rocky Mountains. Climate change velocities also varied markedly between Alberta's Natural Regions with the highest velocities in the Grassland Natural Region, a mean of 6.9 km/year (Fig. 4). The Parkland Natural Region also exhibited high climate velocities, with a mean of 5.3 km/year (Fig. 4). Overall climate change velocity for Alberta averaged 3.6 km/year.

Climate change velocity and habitat fragmentation were both spatially variable between and within Natural Regions (Fig. 4). The Rocky Mountain Natural Region had the highest variance, with climate velocity ranging from 0.05 to 20.8 km/year. Mountaintop species were forecasted to experience the highest climate velocities in the province, while montane climate shifts occurred at a significantly reduced rate (Fig. 2). Vulnerability of these mountaintop species is highly dependent on the population's elevation

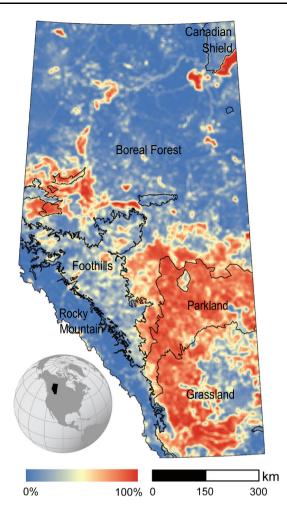


Fig. 1 Study area with divisions into major ecological regions and habitat fragmentation (%). The fragmentation index relevant for barriers to migration includes anthropogenic land conversion, water bodies, and permanent snow or ice cover

and dispersal mechanism. For example, rare high-elevation *Pinus* species such as *Pinus albicaulis* experience high climate velocity (Fig. 2), but are aided by avian seed dispersal (Keane et al. 1990), while high-elevation gravity-dispersed species are among the most threatened (Table 1).

Climate vectors generally conformed to expectation of latitudinal climate shifts, with an average bearing of 346° (NNW; Fig. 2). However, the Rocky Mountain and Foothills Natural Regions exhibited an upslope climate velocity toward the continental divide, generally at an overall lower climate velocity than the other Natural Regions. This divided climate vectors in Alberta into two distinct groups: those directed northward to boreal climates and those directed toward the Rocky Mountains. Velocity vectors in the Foothills Natural Region nearly always pointed southwest toward mountainous destinations. Migration stress was highest in unprotected regions of the Parkland Natural Region, although all six Natural Regions exhibited high migration stress across part of their extent (Fig. 5).



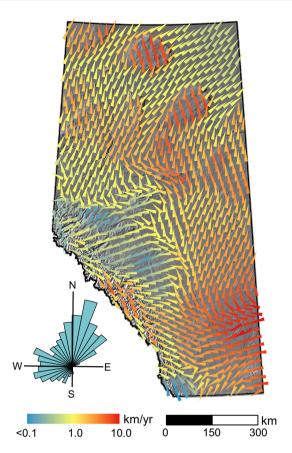


Fig. 2 Multivariate climate velocity vectors in Alberta summarized at 25-km resolution for a 2050s ensemble projection. Vectors are based on a continental-scale analysis to avoid Alberta boundary artifacts. The *rose* plot is the equivalent of a histogram, indicating the prevailing directions of climate shifts in Alberta

Protected areas had lower migration stress than unprotected regions, but this was not consistent across all Natural Regions (Fig. 5).

The five most vulnerable rare species were spiked lobelia (Lobelia spicata), lance-leaved loosestrife (Lysimachia hydriba), low cinquefoil (Potentilla plattensis), goosefoot (Chenopodium atrovirens), and clammy hedgehyssop (Gratiola neglecta) (Table 2). None of these species, however, are imperiled on a global scale. Only 36 plant species in Alberta were listed with a NatureServe conservation status of globally vulnerable (G3), imperiled (G2), or critically imperiled (G1). Macoun's Cinquefoil (Potentilla macounii) and McCalla's Braya (Braya humilis ssp. maccallae) represented the only G1-ranked species assessed in Alberta. Macoun's Cinquefoil had the fourth highest vulnerability of the 36 globally rare species and is anticipated to spread seed passively, making it a priority target for considering conservation interventions. Table 1 summarizes rare Alberta plant species that occupy the highest category of climate change vulnerability, regardless of global conservation status (full records in Appendix S1).

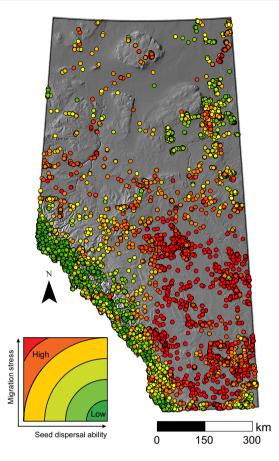


Fig. 3 Migration stress of rare plant populations across Alberta, Canada, between the normal period and 2050s. (*Inset*) Climate vulnerability is estimated by the product of dispersal capability and migration stress

Discussion

Our climate velocity estimates conform to the expectation that areas of high topographic and climatic heterogeneity reduce migration requirements for species under climate change (Loarie et al. 2009). Lower velocities in topographically diverse regions such as the Rocky Mountain and Foothills Natural Region present an opportunity for conservation planning of habitat connectivity by identifying source and sink populations (Burrows et al. 2014). Conversely, mean climate velocities exceeding 5.0 km/ year in the Grassland and Parkland Natural Regions may produce migration stresses too large for a plant response through natural range shifts, at least for dispersal-limited species with narrow climatic niches. Furthermore, Grassland and Parkland habitat is highly fragmented compared to the rest of Alberta, with both of these Natural Regions exceeding 50 % mean fragmentation (Figs. 1, 4). Fragmentation levels of 80 % or higher can completely inhibit species' migration capacity, even for strong dispersers under a moderate climate change scenario (Renton et al.



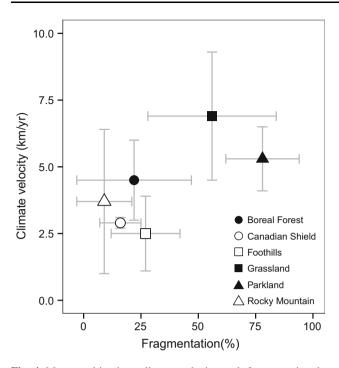


Fig. 4 Mean multivariate climate velocity and fragmentation by Alberta Natural Region, summarized by 1 km² cells. *Dots* represent the data mean, and *whiskers* represent the standard deviation

2013). Under climate change projections for this region, rare species will likely face increased climatic stress with expected declines in fitness and possibly local extirpation. Their protection may be best served through ex situ conservation, including considering managed relocation.

Climate velocity metrics are an attractive alternative to established methods of estimating range shift, such as species distribution modeling, because they quantify migration requirements for individual populations in a landscape. While environmental niche models have been used extensively to assess potential climate change impacts in species (Peterson et al. 2002), these models typically do not account for migration requirements of populations (Beale et al. 2008). It should be noted, however, that the velocity approach does not account for different climatic tolerances of individual species or populations of species. Plants can acclimate to some degree to changed environments through plastic physiological or morphological responses. They could also adapt genetically over multiple generations to new climate environments (Chen et al. 2011). Unfortunately, species' capacity for plastic or genetic response is normally unknown and is understood to vary between populations (Savolainen et al. 2007). In our vulnerability ranking, we must treat adaptive capacity as uniform across all populations (i.e., not factoring into the vulnerability ranking), which is an important limitation.

Conservation priorities should, of course, not be determined by vulnerability rankings for individual populations

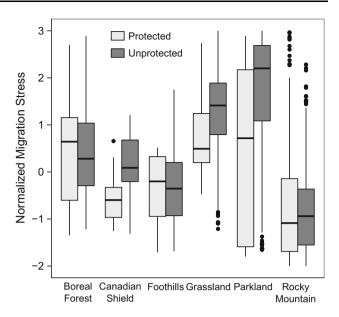


Fig. 5 Migration stress of rare plant species by Alberta Natural Region within and outside of protected areas. Note that the *box-plots* may not be fully representative of the entire ecoregion, but summarize known occurrences of rare species as shown in Fig. 3

of species alone. While vulnerability rankings, such as those proposed in this study, may be used to identify threatened populations, the global conservation status of a species is an important consideration as well. In the case study for Alberta, we identified spiked lobelia (Lobelia spicata) as the highest risk species of those studied. Nevertheless, Lobelia spicata is listed as "apparently secure" on a global (i.e., full range) scale (Encyclopedia of Life 2014; Natureserve 2014). For a globally oriented conservation strategy, the species in Table 1 would have a different focus in our Alberta case study: Macoun's Cinquefoil (Potentilla macounii) and McCalla's Braya (Braya humilis ssp. maccallae) are globally endangered and also have high vulnerability rankings. Weighing local threats and global conservation status of species will remain an important responsibility of conservation managers who operate within their jurisdictions.

Finally, our research indicates that ex situ conservation, including managed relocation, of some globally endangered species may be the only plausible conservation option for some populations if climate change continues as predicted for the study area. Identifying suitable future habitat for managed relocation will be a difficult task. First, it will be necessary to incorporate factors such as climate tolerance, specificity of edaphic requirements, and mycorrhizal and pollinator associations, among a host of other potentially important biotic and abiotic factors. This remains a challenge especially for rare species where it is difficult to even define their basic environmental tolerances (Schwartz et al. 2006). In setting conservation objectives,



Table 1 Plant species of highest vulnerability in Alberta, Canada, with a global conservation status of vulnerable (G3), imperiled (G2), or critically imperiled (G1)

Species name	Prov. rank	Global rank	Mean velocity (km/year)	Mean frag. (%)	Seed dispersal	Vulnerability rank
Onosmodium molle	S2	G3	4.9	69	Very weak	$1 \times 1 = 1$
Phacelia lyallii	S2	G3	1.4	6	Very weak	$1 \times 1 = 1$
Papaver pygmaeum	S2	G3	1.9	3	Very weak	$1 \times 1 = 1$
Potentilla macounii	S1	G1	5.2	33	Very weak	$3 \times 1 = 3$
Sisyrinchium septentrionale	S3	G3	5.0	32	Very weak	$3 \times 1 = 3$
Conimitella williamsii	S2	G3	2.4	13	Very weak	$3 \times 1 = 3$
Lupinus minimus	S1	G3	1.3	19	Very weak	$3 \times 1 = 3$
Pedicularis flammea	S2	G3	3.4	4	Very weak	$3 \times 1 = 3$
Chrysosplenium iowense	S3	G3	4.2	23	Very weak	$4 \times 1 = 4$
Braya humilis ssp. maccallae	S1	G1	3.7	8	Very weak	$4 \times 1 = 4$
Arnica louiseana	S1	G3	2.4	4	Weak	$2 \times 2 = 4$
Stellaria americana	S1	G3	1.8	1	Strong	$1 \times 4 = 4$
Braya humilis ssp. porsildii	S1	G3	6.8	15	Very weak	$5 \times 1 = 5$
Draba porsildii	S1	G3	4.2	5	Very weak	$5 \times 1 = 5$
Draba macounii	S2	G3	5.4	4	Very weak	$5 \times 1 = 5$
Draba ventosa	S2	G3	4.9	3	Very weak	$5 \times 1 = 5$
Botrychium lineare	S1	G2	1.3	4	Very strong	$1 \times 5 = 5$
Erigeron lackschewitzii	SU	G3	2.4	12	Weak	$3 \times 2 = 6$
Prenanthes sagittata	S2	G3	0.9	11	Neutral	$2 \times 3 = 6$
Carex cordillerana	S1	G3	4.1	14	Weak	$4 \times 2 = 8$
Packera contermina	S3	G3	3.6	6	Weak	$4 \times 2 = 8$
Poa gracillima	S2	G2	1.0	10	Strong	$2 \times 4 = 8$
Salix raupii	S1	G2	2.0	4	Strong	$2 \times 4 = 8$
Puccinellia distans ssp. hauptiana	S1	G3	2.8	92	Weak	$5 \times 2 = 10$
Erigeron radicatus	S2	G3	4.7	9	Weak	$5 \times 2 = 10$
Botrychium paradoxum	S1	G3	2.1	4	Very strong	$2 \times 5 = 10$
Stellaria arenicola	S1	G3	3.4	6	Strong	$3 \times 4 = 12$
Pellaea gastonyi	S1	G2	2.7	16	Very strong	$3 \times 5 = 15$
Pinus albicaulis	S2	G3	3.2	7	Very strong	$3 \times 5 = 15$
Botrychium ascendens	S2	G3	2.8	8	Very strong	$3 \times 5 = 15$
Botrychium pallidum	S1	G3	4.4	23	Very strong	$4 \times 5 = 20$
Botrychium campestre	S1	G3	3.5	28	Very strong	$4 \times 5 = 20$
Arenaria longipedunculata	S1	G3	5.7	14	Strong	$5 \times 4 = 20$
Botrychium crenulatum	S1	G3	4.2	16	Very strong	$4 \times 5 = 20$
Botrychium spathulatum	S2	G3	4.1	16	Very strong	$4 \times 5 = 20$
Botrychium pedunculosum	S1	G2	4.7	11	Very strong	$5 \times 5 = 25$

Table 2 Plant species of highest climate change vulnerability in Alberta, Canada. The full table is provided as Supplemental Information Table S1

Rank	Species name	Velocity (km/year)	Mean frag. (%)	Seed dispersal	Vulnerability rank
1	Lobelia spicata	7.9	86	Very weak	$1 \times 1 = 1$
2	Lysimachia hybrida	6.6	78	Very weak	$1 \times 1 = 1$
3	Potentilla plattensis	8.2	55	Very weak	$1 \times 1 = 1$
4	Chenopodium atrovirens	5.6	80	Very weak	$1 \times 1 = 1$
5	Gratiola neglecta	5.4	80	Very weak	$1 \times 1 = 1$
6	Cyperus squarrosus	7.2	59	Very weak	$1 \times 1 = 1$
7	Rorippa curvipes var. truncata	6.1	67	Very weak	$1 \times 1 = 1$
8	Viola pedatifida	6.3	64	Very weak	$1 \times 1 = 1$
9	Thelesperma subnudum var. marginatum	4.7	80	Very weak	$1 \times 1 = 1$
10	Hedyotis longifolia	5.0	71	Very weak	$1 \times 1 = 1$



migration prescriptions must overcome policy and administrative barriers, including international boundaries, private land ownership, conflicts with industrial resource extraction, and ethical considerations (Schwartz et al. 2012; Vitt et al. 2010). Success in this respect will require an open dialogue between stakeholders on how best to overcome the ethical and legal barriers to managed species movement.

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