

Integrating climate and trait models to predict the invasiveness of exotic plants in Canada's Riding Mountain National Park

R. Otfinowski¹, N. C. Kenkel¹, P. Dixon², and J. F. Wilmshurst²

¹*Department of Biological Sciences, University of Manitoba, 190 Dysart Road, Winnipeg, Manitoba, Canada R3T 2N2 (e-mail: umotfino@cc.umanitoba.ca); and* ²*Parks Canada, Western and Northern Canada Service Centre, 145 McDermot Avenue, Winnipeg, Manitoba, Canada R3B 0R9. Received 5 July 2007, accepted 9 January 2008.*

Otfinowski, R., Kenkel, N. C., Dixon, P. and Wilmshurst, J. F. 2007. **Integrating climate and trait models to predict the invasiveness of exotic plants in Canada's Riding Mountain National Park.** *Can. J. Plant Sci.* **87**: 1001–1012. Invasive exotic species threaten the biodiversity and function of native ecosystems. Existing models, attempting to predict successful invaders, often emphasize isolated stages of biological invasions and fail to formalize interactions between exotic species and recipient environments. By integrating the native climatic range and biological traits of exotic vascular plants reported inside and outside Riding Mountain National Park, Manitoba, Canada, we present a model where invasion risk is predicted using the likelihood of establishment and proliferation of exotic species. Exotic vascular plants constituted 11.5% (77/669) of the total vascular flora of Riding Mountain National Park and approximately 14.2% (202/1418) of the flora of Manitoba. Based on their climatic range in Europe, 155 among 174 exotic species absent from the Park, including those found in Manitoba and other natural areas in Canada, were predicted to establish within its boundaries. Among the biological traits of exotic plants, perenniality and vegetative reproduction correctly identified 61% of documented invaders of natural areas in Canada and helped to further define a subset of 40 exotic plants with the highest potential to proliferate within Riding Mountain National Park. Among these, 11 are still absent from inside its boundaries and 17 are not yet reported in Manitoba. Our results demonstrate that Riding Mountain National Park and natural areas in western Canada will continue to be impacted by exotic vascular plants. By integrating establishment and proliferation, key stages in the progress of biological invasions, our model offers a synthetic approach to the prediction and management of biological invasions inside natural areas; such integration is critical to the protection of Canada's endemic biodiversity.

Key words: Biological invasions, invasive alien plants, climate-matching model, life history, natural areas, risk assessment

Otfinowski, R., Kenkel, N. C., Dixon, P. et Wilmshurst, J. F. 2007. **Prévision de la nature envahissante des plantes exotiques dans le parc national Riding Mountain du Canada par des modèles intégrant le climat et les caractères biologiques.** *Can. J. Plant Sci.* **87**: 1001–1012. Les espèces exotiques envahissantes menacent la biodiversité et le fonctionnement des écosystèmes indigènes. En tentant de prévoir les risques d'une telle invasion, les modèles actuels insistent souvent sur des cas isolés d'envahissement biologique et négligent l'interaction des espèces exotiques avec le milieu d'accueil. Les auteurs ont intégré les changements du climat local et les caractères biologiques des plantes vasculaires exotiques répertoriées dans le parc national Riding Mountain, au Manitoba (Canada), et à l'extérieur de celui-ci, et créé un modèle permettant de prévoir les risques d'envahissement selon la probabilité qu'une espèce s'y implante et s'y multiplie. Les plantes vasculaires exotiques représentent 11,5 % (77 / 669) des plantes vasculaires recensées dans le parc national Riding Mountain et environ 14,2 % (202 / 1 418) de la flore du Manitoba. Compte tenu de leur aire climatique en Europe, 155 des 174 espèces exotiques absentes du parc, y compris celles existant au Manitoba et dans d'autres zones naturelles du Canada, pourraient s'y établir. Parmi les caractères biologiques, la rusticité et la multiplication végétative identifient correctement 61 % des plantes exotiques qu'on sait avoir envahi les zones naturelles du Canada et concourent à identifier un sous-ensemble de 40 autres plantes exotiques susceptibles de proliférer à l'intérieur du parc. Parmi elles, onze ne se sont pas encore implantées dans le parc et 17 n'existent pas au Manitoba. Ces résultats montrent que le parc national Riding Mountain et les zones naturelles de l'Ouest canadien continueront de subir l'assaut des plantes vasculaires exotiques. En intégrant l'établissement et la prolifération des espèces ainsi que les principaux stades de l'invasion biologique, le modèle adopte une approche systémique à la prévision et à la gestion des invasions biologiques dans les zones naturelles; pareille intégration est indispensable si l'on veut protéger la biodiversité endémique au Canada.

Mots clés: Invasions biologiques, plantes exotiques envahissantes, modèle climatique, histoire naturelle, zones naturelles, évaluation des risques

The cornerstone of biological invasions is the breakdown of natural biogeographical regions (Elton 1958). Non-native or exotic organisms, defined as those introduced intentionally

Abbreviations: GARP, genetic algorithm model

or unintentionally by human agents (Usher 1988), have always been associated with human travelers (di Castri 1989). In the past 100 yr, the geographic scope, frequency, and number of exotic species have grown enormously as a consequence of expanding travel and commerce (MacIsaac

et al. 2001). Globally, few habitats remain free of exotic species, and many pose serious threats to the biodiversity and function of native ecosystems (Mack et al. 2000; Ricciardi 2007). Exotic invaders, or those species whose introduction or spread threaten the environment, economy, or society (Environment Canada 2004), pose a particular threat to natural reserves, where protection of native biodiversity requires the prediction and control of a growing number of potential invaders (Palmer 2005).

Despite numerous attempts, predicting invaders has produced few generalizations (Henderson et al. 2006). Published models predicting invasiveness can be broadly divided into those based on climate and traits. Climate models emphasize correlations between the native and introduced environments of exotic species. In many cases, applications of this approach have successfully defined regions threatened by the expanding range of exotic invaders (Peterson 2003). Climate, however, does not solely dictate geographic distribution. Other biological constraints, such as dispersal vectors, habitat requirements, competition, mutualisms, and the genetic structure of invading populations often restrict the range of potential invaders (Thuiller et al. 2006). As a result, the presumption of climate models that species' geographic distributions correspond with their fundamental niches has often been criticized (Pearson and Dawson 2003).

Emphasizing the importance of biological interactions, the traits of exotic species have alternatively been used to predict their invasiveness. Among characters most correlated with invasiveness, self-compatibility, fruit size, short- and long-range seed dispersal, wide germination and growth requirements, prolific and intermittent seed production, vegetative growth, a short vegetative period, competitiveness, and defense against herbivores are most often cited (Richardson and Pyšek 2006). Despite their appeal, trait models have proven poor predictors of invasion [but see Rejmánek and Richardson (1996), Herron et al. (2007)]. For example, even though exotic plants often possess traits that distinguish them from the native species they displace (Andersen 1995, Rejmánek 2000, Kolar and Lodge 2001), successful invaders represent a diversity of plant families and possess a wide range of life forms and breeding systems (Crawley 1987). As a result, other mechanisms, such as the biodiversity of the invaded community, attributes of the native organisms, physical disturbance and propagule pressure, have been invoked to account for the success of exotic invaders (Colautti et al. 2006; Thuiller et al. 2006).

Despite their individual shortcomings, climate and trait models highlight important elements in the life history of exotic organisms. By integrating both approaches, we conceptualized predicting potential invaders using a series of stages (*sensu* Williamson and Fitter 1996). We hypothesized that within natural areas, the threat of invasion corresponds to the potential of exotic species to establish and proliferate within recipient plant communities. Based on this approach, we sought to construct a predictive model to prioritize the monitoring and management of exotic plants in Riding Mountain National Park, Manitoba, Canada. Our effort was motivated by the limited knowledge of the Park's

exotic flora [but see Trottier (1986), Slogan (1997), Caners (1999)] and by the increasing threat posed by exotic plants to Canada's endemic biodiversity (Canadian Endangered Species Conservation Council 2006).

METHODS

Study Area

Riding Mountain National Park occupies an area of 2978 km² in Western Canada, 225 km northwest of Winnipeg (49°53'04"N-97°08'47"W). Most of the Park lies in the Mixedwood Section of the Boreal Forest Region (Rowe 1972) and consists of large areas of rolling upland (550–640 m), underlain by glacial tills, as well a section of the Manitoba Escarpment, characterized by exposed Cretaceous shale (Lang 1974). Small areas of fescue and mixed prairies, as well as western extensions of bur oak (*Quercus macrocarpa* Michx.) forests are also protected within the Park's boundaries (Cody 1988). The region is characterized by mean annual precipitation of 450–500 mm and a growing season of 168–173 d; mean temperatures range between –18°C in January and 18°C during July (Leeson et al. 2005).

The exotic flora of Riding Mountain National Park reflects its long human history. Before its establishment in 1933, logging, cattle grazing, and haying were important to the local economy and created opportunities for the introduction of exotic species (Trottier 1986). Continued agricultural expansion along the Park's boundaries, increasing visitation, and the construction of roads have escalated this trend. Today, the most intensively used area of the Park centers on the town of Wasagaming (seasonal pop. 4000), where campgrounds, accommodations, and services are offered to the 250 000 annual visitors (Parks Canada 1996). While preliminary surveys of the Park's exotic flora have focused on the fescue prairies (Trottier 1986; Slogan 1997; Caners 1999), its exotic species burden has not been reviewed prior to our study.

Model Design

We based our model on a summary of exotic plants found in Riding Mountain National Park and areas outside its borders. Lists of exotic species were compiled using published literature and separated into three categories: (1) exotic species found in Riding Mountain National Park (Cody 1988); (2) exotic species found in the province of Manitoba, but absent from the Park (Scoggan 1957; Leeson et al. 2005); (3) invasive species of natural areas reported in other regions of Canada (White et al. 1993; Haber 1996; Catling and Mitrov 2005). We confined our analysis to Eurasian vascular species, a predominant element in Canada's exotic flora (Haber 2002; McClay et al. 2007). Using information about each species' climatic range, biological traits, and habitat preferences, exotic plants were assigned to five classes of invasion risk based on their potential to establish and proliferate within the Park's natural habitats (Fig. 1).

The risk of establishment of exotic plants in Riding Mountain National Park was predicted using the climatic range of each species in Europe, estimated using long-term

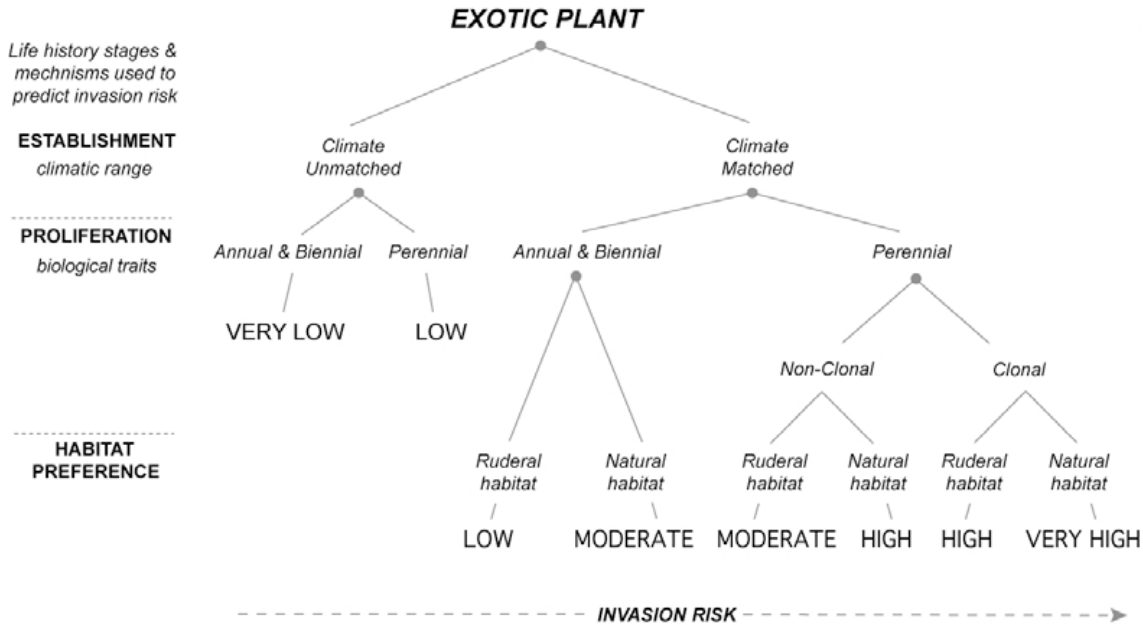


Fig. 1. Conceptualized model for predicting the establishment and proliferation of exotic plants in natural areas and their threat to native biodiversity. Model was used to assign invasion risks to exotic vascular plant species found in Riding Mountain National Park and in areas outside its borders, including the province of Manitoba and natural areas in other regions of Canada. Risks of invasion were assigned using each species' climatic range, biological traits, and habitat preferences. *Climatic range*: higher invasion risks were assigned to exotic species whose geographic distribution matched the climate of Riding Mountain National Park; *Biological traits*: higher invasion risks were assigned to perennial exotic plants capable of vegetative growth; *Habitat*: higher invasion risks were assigned to exotic species capable of proliferating in the Park's natural habitats, including prairies, wetlands, shorelines, and woodlands; lower invasion risks were assigned to plants confined to ruderal habitats, including gardens, lawns, roads, trails, and waste areas.

environmental data from 79 climate stations (Walter et al. 1975), distributed across 39 geographic regions of Europe (Tutin et al. 1964–1980). Depending on the physical area of each region we selected up to four evenly distributed stations to represent its climate (Fig. 2). Plants found in regions whose mean annual temperature and precipitation matched that of Riding Mountain National Park (Fig. 3) were considered more likely to establish within its boundaries and assigned to a higher class of invasion risk. We used principal component analysis (Legendre and Legendre 1998) to eliminate the multicollinearity inherent to large sets of climatic variables (Metzger et al. 2005; Thuiller et al. 2006). As a result, a more complex model, including the length of the growing and wet seasons and the number of frost-free and winter months produced similar results and is not presented here.

Predictions of our climate-matching model, based on regional means of annual temperature and precipitation, were validated using the genetic algorithm model (GARP), a predictive model integrated with global environmental data bases that include summaries of climate, topography, solar radiation, and substrate (Elith et al. 2006). We confined our comparisons to a subset of 100 exotic plants, randomly selected among 251 species in our data base, including those found in Riding Mountain National Park and areas outside its boundaries. For each species, we built 100 models predicting their potential range in North

America using all rule types and default environmental variables (0.001 convergence, 70% training data set; Stockwell and Peters 1999). We selected a subset of 20 best models for each species according to criteria proposed by Anderson et al. (2003) and used these to compile single mean projections of each species' predicted North American range using ArcView 9.2 (ESRI Inc., Redlands, CA). These, illustrating the potential climatic affinity of each species with Riding Mountain National Park, were used to predict their potential to establish within the Park's boundaries. Finally, we used chi-squared analysis (Zar 1999) to test the hypothesis that the predictions of our climate-matching model were not significantly different from those generated using GARP.

The risk of proliferation of exotic plants within natural areas of Riding Mountain National Park was predicted using their biological traits (Fig. 1). Based on published floras, we collected information about the perenniality, woody habit, vegetative reproduction, flowering period, and fruit type of each species in our data base (Scoggan 1957; Great Plains Flora Association 1986; Cody 1988; Gleason and Cronquist 1991). We eliminated redundancies among trait variables using principal component analysis (Legendre and Legendre 1998) and used the ordination scores of each species from the first three principal component axes in multiple logistic regression models to find independent sets of trait variables correlated with the invasiveness of exotic plants in Canada's natural areas. Using 251 species in our data base, including

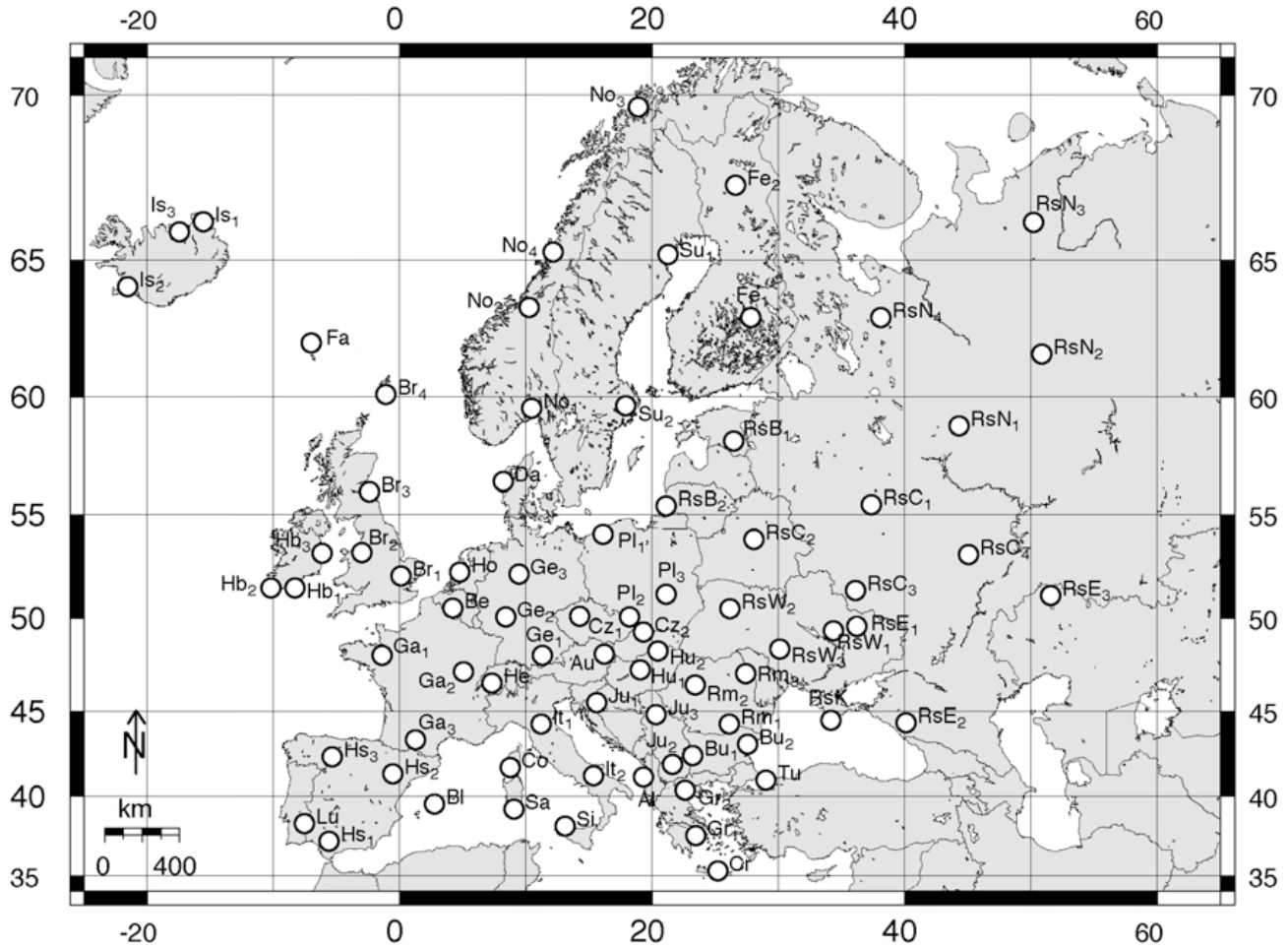


Fig. 2. The distribution of 79 climate stations across 39 geographic regions of Europe (Tutin et al. 1964–1980) used to predict the climatic range of European exotic vascular plants threatening Riding Mountain National Park, Manitoba, Canada. Climate summaries according to Walter et al. (1975). Abbreviations: Al (Durazzo, Albania), Au (Vienna, Austria), Az (Angra do Heroismo, Azores), Be (Brussels, Belgium), Bl (Palma de Mallorca, Balearic Islands), Br₁ (Cambridge, Britain), Br₂ (Liverpool, Britain), Br₃ (North Berwick, Scotland), Br₄ (Lerwick, Shetland Islands, Scotland), Bu₁ (Sofia, Bulgaria), Bu₂ (Warna, Bulgaria), Co (Ajaccio, Corsica), Cr (Khania, Crete), Cz₁ (Praha, Czech Republic), Cz₂ (Arvavaralja, Czech Republic), Da (Vestervig, Denmark), Fa (Thorshavn, Faroe Islands), Fe₁ (Kuopio, Finland), Fe₂ (Sodankyla, Finland), Ga₁ (Rennes, France), Ga₂ (Dijon, France), Ga₃ (Toulouse, France), Ge₁ (Munchen, Germany), Ge₂ (Frankfurt, Germany), Ge₃ (Hannover, Germany), Gr₁ (Athen, Greece), Gr₂ (Thessaloniki, Greece), Hb₁ (Cork, Ireland), Hb₂ (Valentia, Ireland), Hb₃ (Dublin, Ireland), He (Biel, Switzerland), Ho (Amsterdam, the Netherlands), Hs₁ (Sevilla, Spain), Hs₂ (Zaragoza, Spain), Hs₃ (Leon, Spain), Hu₁ (Budapest, Hungary), Hu₂ (Putnok, Hungary), Is₁ (Raufarhofn, Iceland), Is₂ (Reykjavik, Iceland), Is₃ (Teigahorn, Iceland), It₁ (Bologna, Italy), It₂ (Foggia, Italy), Ju₁ (Zagreb, Croatia), Ju₂ (Skopje, Macedonia), Ju₃ (Belgrade, Serbia and Montenegro), Lu (Evora, Portugal), No₁ (Oslo, Norway), No₂ (Trondheim, Norway), No₃ (Tromso, Norway), No₄ (Bronnysund, Norway), Pl₁ (Koszalin, Poland), Pl₂ (Raciborz, Poland), Pl₃ (Radom, Poland), Rm₁ (Bucharest, Romania), Rm₂ (Cluj, Romania), Rm₃ (Iasi, Romania), RsB₁ (Tartu, Estonia), RsB₂ (Memel, Lithuania), RsC₁ (Moscow, Russian Federation), RsC₂ (Minsk, Belarus), RsC₃ (Kursk, Russian Federation), RsC₄ (Pensa, Russian Federation), RsE₁ (Kharkov, Ukraine), RsE₂ (Maykop, Russian Federation), RsE₃ (Uralsk, Russian Federation), RsK (Yalta, Russian Federation), RsN₁ (Kologriv, Russian Federation), RsN₂ (Ust-Sysolsk, Russian Federation), RsN₃ (Ust-Sylma, Russian Federation), RsN₄ (Onega, Russian Federation), RsW₁ (Poltava, Ukraine), RsW₂ (Zdolbunov, Ukraine), RsW₃ (Uman, Ukraine), Sa (Sassari, Sardinia), Sb (Jan Mayen, Spitsbergen), Si (Agrigento, Sicily), Su₁ (Pitea, Sweden), Su₂ (Stockholm, Sweden), Tu (Istanbul, Turkey). Map generated using Generic Mapping Tools v. 4.1.1 (Wessell and Smith 2006).

106 documented invaders (White et al. 1993; Haber 1996; Catling and Mitrow 2005), we tested the null hypothesis that the invasion of natural areas by exotic plants is independent of their biological traits.

Finally, the potential threat posed by exotic plants to the endemic diversity and structure of natural areas inside

Riding Mountain National Park was further based on the habitat preferences of each species (Fig. 1). Exotic plants capable of proliferating within natural habitats, including prairies, wetlands, shorelines, and woodlands, were considered a higher management priority than those confined to ruderal habitats, including gardens, lawns, roads, trails, and

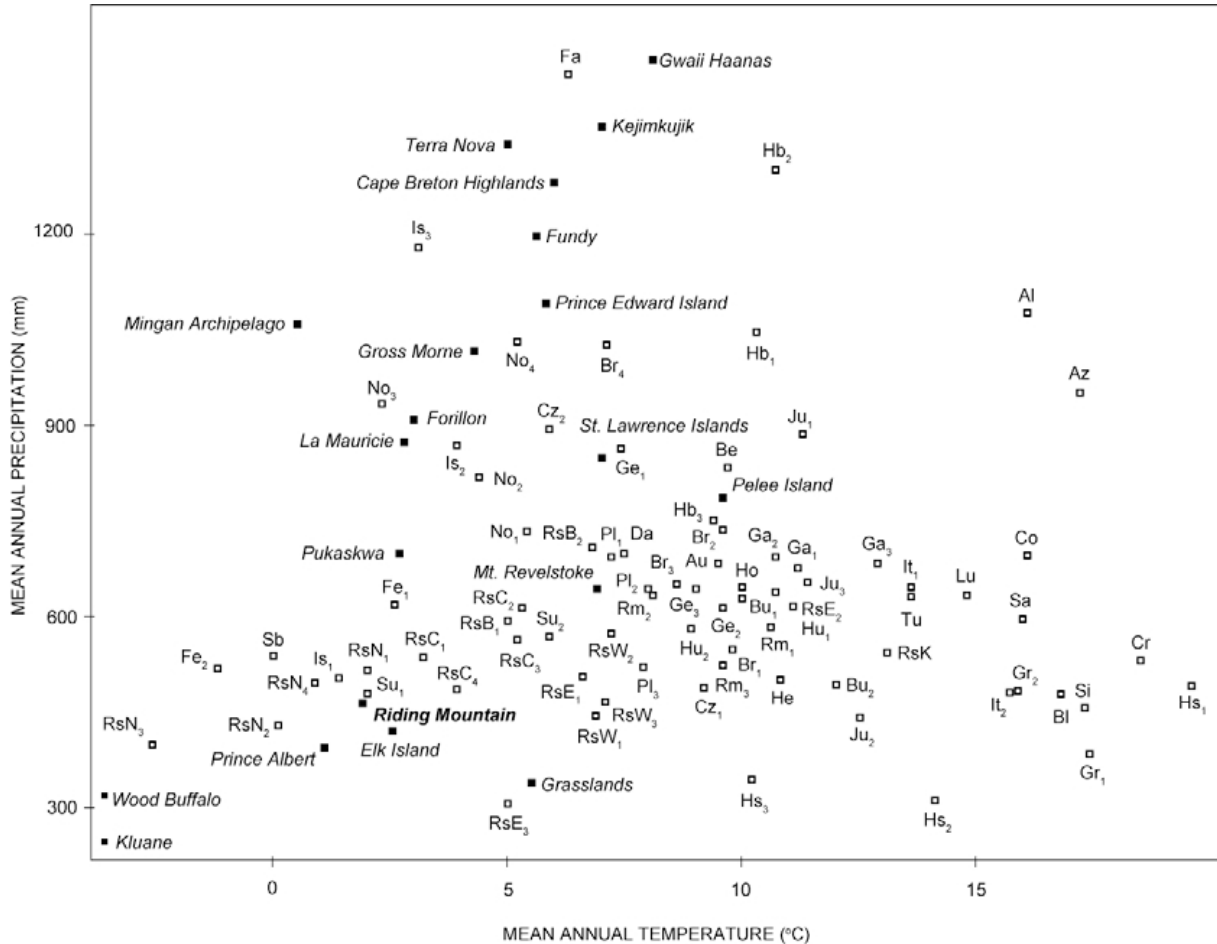


Fig. 3. Using climate data to predict the establishment of exotic vascular plants in Riding Mountain National Park, Manitoba, Canada. Plants found in regions of Europe whose mean annual temperature ($^{\circ}\text{C}$) and precipitation (mm) matched those of the Park were considered more likely to establish within its boundaries and assigned to a higher class of invasion risk. For climate station abbreviations refer to Fig. 2. Climate summaries according to Walter et al. (1975). The position of 21 national parks in Canada is provided for reference.

waste areas (Scoggan 1957; Great Plains Flora Association 1986; Cody 1988; Gleason and Cronquist 1991).

RESULTS

Climate

Exotic vascular plant species constituted 11.5% (77/669) of the total vascular flora of Riding Mountain National Park, and approximately 14.2% (202/1418) of the flora of Manitoba. The Park's climate closely corresponded with that of central and northern Russia and northern Scandinavia (Fig. 3). As a result, all exotic plants whose European range included Sweden, Iceland, and areas of central and northern Russia, were considered capable of establishing inside the Park. This condition was met by all exotic species in its flora (Table 1).

Outside the Park's boundary, only 12 of the 125 exotic plants found in Manitoba did not match the Park's climate (Table 1). Many of these, including green pigweed (*Amaranthus hybridus* L.), yellow star thistle (*Centaurea*

solstitialis L.), stink grass [*Eragrostis cilianensis* (All.) E. Mosher], and flower-of-an-hour (*Hibiscus trionum* L.), are confined to southern and central areas of Europe (Tutin et al. 1964–1980). Only two species in this group, including spotted and Russian knapweed (*Centaurea biebersteinii* DC. and *C. repens* L.), are invasive in natural areas in Canada (Haber 1996). As predicted, their range in North America is confined to more arid regions of western Canada and the northern intermountain areas of the United States (Frankton and Mulligan 1970; DiTomaso 2000).

Matching the climate of Riding Mountain National Park and geographic regions in Europe helped identify a high number of exotic plants, currently absent from Manitoba, with the potential to establish within its boundaries. Among 49 species invasive within natural areas in other regions of Canada, only seven did not match the Park's climate (Table 1). Of the remaining 42 species still absent from Manitoba, many, including garlic mustard [*Alliaria petiolata* (M. Bieb.) Cavara & Grande], continue to expand their range in North America (Welk et al. 2002).

Table 1. Summary of exotic vascular plant species found in Riding Mountain National Park (Cody 1988) and in areas outside the Park boundary, including the province of Manitoba (Soggan 1957) and natural areas in other regions of Canada (White et al. 1993; Haber 1996; Catling and Mitrow 2005). The increasing risks of establishment and proliferation of exotic plants inside the Park (Very Low – Very High) were predicted using their climatic ranges and biological traits, respectively. The potential threat of each species to the endemic diversity and structure of natural areas inside the Riding Mountain National Park was further based on its habitat preferences. Natural habitats include prairies, wetlands, shorelines, and woodlands; ruderal habitats include gardens, lawns, roads, trails, and waste areas. Nomenclature according to the Great Plains Flora Association (1986) and Gleason and Cronquist (1991). **Bolded** species are invasive in natural areas in Canada (White et al. 1993; Haber 1996; Catling and Mitrow 2005)

	Very low		Low		Moderate		High		Very high	
	Climate unmatched annuals/biennials	Climate unmatched perennials	Annuals/biennials in ruderal habitats	Annuals/biennials in natural habitats	Non-clonal perennials in ruderal habitats	Non-clonal perennials in natural habitats	Non-clonal perennials in ruderal habitats	Non-clonal perennials in natural habitats	Clonal perennials in ruderal habitats	Clonal perennials in natural habitats
RMNP			<i>Amaranthus retroflexus</i> <i>Avena fatua</i> <i>Brassica campestris</i> <i>Capsella bursa-pastoris</i> <i>Carum carvi</i> <i>Chenopodium album</i> <i>Descurainia sophia</i> <i>Crepis tectorum</i> <i>Erucastrum gallicum</i> <i>Galeopsis bifida</i> <i>Lappula echinata</i> <i>Malva rotundifolia</i> <i>Polygonum aviculare</i> <i>Polygonum convolvulus</i> <i>Senecio vulgaris</i> <i>Silene noctiflora</i> <i>Stellaria media</i> <i>Thlaspi arvense</i>	<i>Arcium minus</i> <i>Arcium tomentosum</i> <i>Ayris amaranthoides</i> <i>Brassica kaber</i> <i>Chenopodium glaucum</i> <i>Descurainia sophia</i> <i>Dracocephalum thymiflorum</i> <i>Erysimum cheiranthoides</i> <i>Hesperis matronalis</i> <i>Lolium perenne</i> <i>Tripleurospermum perforata</i> <i>Medicago lupulina</i> <i>Melilotus alba</i> <i>Melilotus officinalis</i> <i>Poa annua</i> <i>Polygonum lapathifolium</i> <i>Polygonum persicaria</i> <i>Setaria viridis</i> <i>Silene pratensis</i> <i>Sisymbrium altissimum</i>	<i>Artemisia absinthium</i> <i>Glechoma hederacea</i> <i>Humulus lupulus</i> <i>Lycchnis chalcidonica</i> <i>Medicago sativa</i> <i>Phleum pratense</i> <i>Plantago major</i> <i>Portulaca oleracea</i> <i>Puccinellia distans</i> <i>Silene latifolia</i> <i>Taraxacum officinale</i> <i>Tragopogon dubius</i> <i>Trifolium hybridum</i> <i>Trifolium pratense</i> <i>Vicia cracca</i>	<i>Lonicera tatarica</i>	<i>Achillea ptarmica</i> <i>Aegopodium podagraria</i> <i>Dianthus deltoides</i> <i>Elytrigia repens</i> <i>Festuca rubra</i> <i>Gypsophilia paniculata</i> <i>Leucanthemum vulgare</i> <i>Mantha spicata</i> <i>Ranunculus acris</i> <i>Saponaria officinalis</i> <i>Tanacetum vulgare</i> <i>Trifolium repens</i>			<i>Agropyron cristatum</i> <i>Agrostis solonifera</i> <i>Bromus inermis</i> <i>Caragana arborescens</i> <i>Cirsium arvense</i> <i>Euphorbia esula</i> <i>Festuca pratensis</i> <i>Juncus compressus</i> <i>Linaria vulgaris</i> <i>Poa compressa</i> <i>Poa pratensis</i> <i>Sonchus arvensis</i>
Manitoba	<i>Amaranthus hybridus</i> <i>Brassica juncea</i> <i>Centaurea solstitialis</i> <i>Delphinium ajacis</i> <i>Eragrostis cilianensis</i> <i>Hibiscus trionum</i> <i>Polygonum monspeliensis</i> <i>Silene cseretii</i>	<i>Centaurea biebersteinii</i> <i>Centaurea repens</i> <i>Knautia arvensis</i> <i>Rumex patientia</i>	<i>Alyssum abyssoides</i> <i>Asperugo procumbens</i> <i>Berteroa incana</i> <i>Borago officinalis</i> <i>Brassica hirta</i> <i>Centaurea cyanus</i> <i>Chaenorrhinum minus</i> <i>Daucus carota</i> <i>Elsholtzia ciliata</i> <i>Euphorbia peplus</i> <i>Fagopyrum tataricum</i> <i>Fumaria officinalis</i> <i>Lepidium rudrale</i> <i>Lithospermum arvense</i> <i>Malva verticillata</i> <i>Marricaria chamomilla</i> <i>Papaver rhoeas</i> <i>Pastinaca sativa</i> <i>Phalaris canariensis</i> <i>Raphanus raphanistrum</i> <i>Setaria verticillata</i> <i>Tragopogon portifolius</i> <i>Urtica urens</i> <i>Vaccaria pyramidata</i> <i>Veronica agrestis</i> <i>Veronica persica</i> <i>Vicia sativa</i> <i>Vicia villosa</i>	<i>Agrostemma githago</i> <i>Anethum graveolens</i> <i>Anthemis cotula</i> <i>Arcium lappa</i> <i>Atriplex hortensis</i> <i>Brassica nigra</i> <i>Bromus tectorum</i> <i>Bromus japonicus</i> <i>Camelina microcarpa</i> <i>Camelina sativa</i> <i>Carduus nutans</i> <i>Centaurea diffusa</i> <i>Cerastium glomeratum</i> <i>Conringia orientalis</i> <i>Cynoglossum officinale</i> <i>Digitaria ischaemum</i> <i>Echinocloa crassagalli</i> <i>Echium vulgare</i> <i>Erodium cicutarium</i> <i>Fagopyrum esculentum</i> <i>Geranium pusillum</i> <i>Hyoscyamus niger</i> <i>Koeleria scoparia</i> <i>Lactuca serriola</i> <i>Lamium plebeiale</i> <i>Lapsana communis</i> <i>Myosotis arvensis</i> <i>Neslia paniculata</i> <i>Oenanthe serotina</i> <i>Panicum miliaceum</i> <i>Rexada lutea</i> <i>Salsola iberica</i> <i>Senecio viscosus</i> <i>Setaria flauca</i> <i>Setaria italica</i> <i>Sisymbrium boeseldii</i> <i>Sonchus asper</i> <i>Sonchus oleraceus</i> <i>Tragopogon pratensis</i> <i>Verbascum thapsus</i>	<i>Ammoracia rusticiana</i> <i>Artemisia abrotanum</i> <i>Cichorium intybus</i> <i>Dianthus barbatus</i> <i>Dipsacis muralis</i> <i>Lolus corniculatus</i> <i>Nepeta cataria</i> <i>Plantago lanceolata</i> <i>Plantago media</i> <i>Potentilla argentea</i> <i>Rumex acetosa</i> <i>Sedum purpureum</i> <i>Stellaria graminea</i> <i>Taraxacum laevigatum</i>	<i>Alopecurus pratensis</i> <i>Bentla pendula</i> <i>Cirsium vulgare</i> <i>Dactylis glomerata</i> <i>Frangula alnus</i> <i>Rhamnus cathartica</i> <i>Rumex crispus</i>	<i>Artemisia pontica</i> <i>Artemisia vulgaris</i> <i>Campanula rapunculoides</i> <i>Candaria draba</i> <i>Convolvulus arvensis</i> <i>Euphorbia cyparissias</i> <i>Festuca ovina</i> <i>Geranium pratense</i> <i>Lathyrus tuberosus</i> <i>Linaria dalmanica</i> <i>Rumex acetosella</i> <i>Sabia nemorosa</i> <i>Ranunculus repens</i> <i>Rorippa austriaca</i>	<i>Batium umbellatus</i> <i>Hieracium aurantiacum</i> <i>Hypericum perforatum</i> <i>Iris pseudacorus</i> <i>Leonurus cardiaca</i> <i>Lythrum salicaria</i> <i>Myriophyllum spicatum</i> <i>Populus alba</i> <i>Rorippa sylvestris</i> <i>Rumex acetosella</i> <i>Sabia nemorosa</i>		

Table 1 Continued

Canada	<p><i>Buddleia davidii</i> <i>Cynanchum rossicum</i> <i>Morus alba</i> <i>Robinia pseudoacacia</i> <i>Robinia viscosa</i> <i>Rubus discolor</i> <i>Syringa vulgaris</i></p>	<p><i>Acinos arvensis</i> <i>Dipsacus sylvestris</i> <i>Milva neglecta</i> <i>Senecio jacobaea</i> <i>Tribulus terrestris</i></p>	<p><i>Althaea petiolata</i> <i>Angelica sylvestris</i> <i>Anthriscus sylvestris</i> <i>Barbarea vulgaris</i> <i>Chelidonium majus</i> <i>Cirsium palustre</i> <i>Impatiens glandulifera</i></p>	<p><i>Hippophae rhamnoides</i> <i>Pimpinella saxifraga</i> <i>Quercus robur</i></p>	<p><i>Acer platanoides</i> <i>Alnus glutinosa</i> <i>Elaeagnus angustifolia</i> <i>Ectonymus europaeus</i> <i>Pinus sylvestris</i> <i>Potentilla recta</i> <i>Rorippa amphibia</i> <i>Viburnum opulus</i></p>	<p><i>Polygonum cuspidatum</i> <i>Polygonum sachalinense</i></p>	<p><i>Carex acutiformis</i> <i>Cytisus scoparius</i> <i>Gadum molugo</i> <i>Geum urbanum</i> <i>Glyceria maxima</i> <i>Hedera helix</i> <i>Hydrocharis morsus-ranae</i> <i>Ligustrum vulgare</i> <i>Lysimachia nummularia</i> <i>Nymphoides peltata</i> <i>Origanum vulgare</i> <i>Phalaris arundinacea</i> <i>Phragmites australis</i> <i>Potamogeton crispus</i> <i>Tussilago farfara</i> <i>Ulex europaeus</i> <i>Vinca minor</i></p>
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Compared with GARP, matching regional climates using the means of annual temperature and precipitation identified a greater number of exotic species with the potential to establish in Riding Mountain National Park. According to this method, only two among the 100 randomly selected exotics were not expected to establish within the Park. In contrast, 35 species were less than 50% likely to establish inside the Park according to GARP (Table 2). Despite its conservative predictions, low risk categories frequently included exotic plants already found inside Riding Mountain National Park. For example, 17 of 55 species with a risk of establishment 0–60% are present in the Park, and several of these, including smooth brome (*Bromus inermis* Leys.), are invasive.

Traits

Logistic regression of principal component scores, separating along the first ordination axis clonal, perennial species from annuals (Table 3), correctly identified 76.6% of non-invasive and 61% of the invasive plants of natural areas in Canada, yielding an overall correct classification rate of 70% ($\chi^2 = 58.361, P < 0.001$). Inside Riding Mountain National Park, a large number of clonal exotics consisted of escaped forages. For example, crested wheatgrass [*Agropyron cristatum* (L.) Gaertn.], smooth brome (*Bromus inermis*), and Canada and Kentucky bluegrass (*Poa compressa* L., *P. pratensis* L.) continue to be cultivated in areas surrounding the Park (Table 1). Also in this group were weeds of overgrazed rangelands such as Canada thistle [*Cirsium arvense* (L.) Scop.], leafy spurge (*Euphorbia esula* L.) and toadflax (*Linaria vulgaris* Hill.). Clonal perennials also included caragana (*Caragana arborescens* Lam.), which threatens the Park's woodlands.

The integration of climate and trait models helped identify the proliferation risk posed by exotic species currently absent from Riding Mountain National Park. For example, the Park's wetlands remain vulnerable to purple loosestrife (*Lythrum salicaria* L.), creeping yellow cress [*Rorippa sylvestris* (Crantz) Bess.], European milfoil (*Myriophyllum spicatum* L.) and flowering rush (*Butomus umbellatus* L.), clonal perennials that continue to expand their range in western Canada (Frankton and Mulligan 1970; Lindgren 2003; Olson 2004). According to our model, invaders of natural areas in other regions of Canada, including frog-bit (*Hydrocharis morsus-ranae* L.) and curly pondweed (*Potamogeton crispus* L.), are also capable of establishing and proliferating inside the Park (Table 1).

Distinguishing between natural and ruderal habitats also helped prioritize the monitoring and management of exotic plants found in Riding Mountain National Park. For example, escaped ornamentals confined to roads, gardens, or waste areas, including bouncing bet (*Saponaria officinalis* L.), sneezeweed (*Achillea ptarmica* L.), and goutweed (*Aegopodium podagraria* L.), were considered a lower threat to the Park's native diversity (Table 1). Also common in these habitats were weedy perennials, such as meadow buttercup (*Ranunculus acris* L.), ox-eye daisy (*Leucanthemum vulgare* Lam.), quackgrass [*Elytrigia repens* (L.) Nevski], tansy (*Tanacetum vulgare* L.), as well as Dalmatian toadflax [*Linaria dalmatica* (L.) Miller] and

Table 2. Contingency between the predictions of a climate-matching model, based on regional means of annual temperature and precipitation, and GARP, a genetic algorithm model integrated with global environmental data bases (Elith et al. 2006). Models were used to predict the establishment of 100 vascular exotic plants in Riding Mountain National Park, Manitoba, Canada. For each species, its potential to establish within the Park was predicted using its climatic range in Europe. Establishment risks represent the proportion of 20 among 100 GARP models, selected according to criteria proposed by Anderson et al. (2003), predicting the potential establishment of each species in Riding Mountain National Park. Predictions of both models were compared using chi-squared analysis of contingency tables (Zar 1999). Probabilities of Type I error (P) illustrate the likelihood that predictions of the climate-matching model differ from those generated using GARP

Number of Species	Maximum establishment risk according to GARP	Contingency between climate-matching model and GARP	
		χ^2	P
7	> 80 %	–	–
13	70 – 80 %	0.15	0.6700
25	60 – 70 %	0.51	0.4750
20	50 – 60 %	1.67	0.1960
11	40 – 50 %	3.79	0.0516
11	20 – 40 %	8.16	0.0043
13	< 10 %	13.66	0.0002

creeping buttercup (*Ranunculus repens* L.) reported outside the Park boundary. Threats posed by these species likely depend on the extent and persistence of disturbances inside the Park (Olson and Wallander 1999; Rose and Hermanutz 2004; Hendrickson et al. 2005).

The majority of exotic species inside and outside Riding Mountain National Park were considered a moderate threat to its biodiversity. Most of these were annuals, confined to disturbed areas (Table 1). In this category, sweet clover [*Melilotus alba* Medic., *M. officinalis* (L.) Pallas], burdock (*Arctium minus* Schk., *A. tomentosum* Miller), and scentless false mayweed [*Tripleurospermum perforata* (Merat) M. Lainz] pose an ephemeral threat to prairies, stream banks, and open woodlands (Frankton and Mulligan 1970). Among species absent within Park boundaries, this group includes red bartsia [*Odontites serotina* (Lam.) Dumort.], as well as diffuse knapweed (*Centaurea diffusa* Lam.), nodding thistle (*Carduus nutans* L.), and downy brome (*Bromus tectorum* L.), whose range in western Canada continues to expand (Frankton and Mulligan 1970; Douglas et al. 1990; Manitoba Agriculture Food and Rural Initiatives 2003). Moderately invasive species also included non-clonal perennials confined to ruderal habitats. Most species in this category, such as common dandelion (*Taraxacum officinale* Weber), timothy (*Phleum pratense* L.), and common purslane (*Portulaca oleracea* L.), are confined to trails, ditches, and campgrounds and pose little threat to the Park's natural areas (Cody 1988).

Low risks of proliferation were most often associated with weedy, agricultural species (Table 1). In the absence of soil disturbance, plants in this category, including field pennycress (*Thlaspi arvense* L.), shepherd's purse [*Capsella bursa-pastoris* (L.) Medic.], and lamb's quarters (*Chenopodium album* L.) do not threaten native biodiversity. As expected, a high diversity of annual exotic species was found outside the Park (Table 1).

DISCUSSION

Predictions

Climate matching provided a rapid method of predicting the potential establishment of exotic plant species absent from

Riding Mountain National Park. Among 174 exotic plants absent from the Park, but found in Manitoba or natural areas in other regions of Canada, only 19 were not expected to establish in the Park. Several among these, including garlic mustard (*Alliaria petiolata*), purple loosestrife (*Lythrum salicaria*), creeping yellow cress (*Rorippa sylvestris*), European milfoil (*Myriophyllum spicatum*) and flowering rush (*Butomus umbellatus*) continue to expand their range in North America (Frankton and Mulligan 1970; Lindgren 2003; Olson 2004; Welk et al. 2002).

While climate matching based on regional means of temperature and precipitation offered a simple means of identifying potential invaders, predictions based on this method likely exaggerate the number of exotic species threatening the Park's natural areas. Despite the sophistication of competing approaches (Elith et al. 2006), climate models frequently over-predict potential species' distributions by identifying habitats to which they are unable to disperse (Dormann 2007). Other factors, including the strength of dispersal vectors, the importance of mutualisms, the resilience of native communities, and the availability of suitable establishment areas often constrain the geographic range of species (Peterson and Vieglais 2001; Araújo and Guisan 2006; Colautti et al. 2006). While our model cannot predict these and other interactions, incorporating the biological traits of exotic species offered an effective method of anticipating potential biotic interactions relevant to the scale of native plant communities (Renne et al. 2006). Our findings, emphasizing the role of perenniality and vegetative reproduction in the invasion of natural areas, are consistent with reports from other regions (Andersen 1995; Pyšek 1997; Reichard and Hamilton 1997; Acosta et al. 2006; Cadotte et al. 2006).

Limitations

Predictions of our climate-matching model depend on the accuracy of native range distributions. Poor accuracy of distributional data can lead to an under-representation of species limits and result in higher invasion risks from species that appear outside a climatic area (Peterson and Vieglais 2001; Welk et al. 2002). The underestimation of

Table 3. Principal component analysis of five plant traits describing 251 exotic vascular plants found in Riding Mountain National Park, Manitoba, Canada, and areas outside its borders, including the province of Manitoba and natural areas in other regions of Canada. Summaries of traits were compiled from the following sources: Scoggan (1957), Great Plains Flora Association (1986), Cody (1988), Gleason and Cronquist (1991)

Variable	Eigenvector elements		
	Axis I	Axis II	Axis III
Life history (annual/biennial; perennial)	0.8446	-0.2747	0.1528
Vegetative reproduction	0.7160	-0.5259	0.2295
Woody habit	0.5617	0.6074	-0.1224
Length of flowering period (months)	-0.5030	-0.2030	0.7286
Fruit type ^z	-0.2468	-0.6698	-0.5747
Eigen value	0.3711	0.2421	0.1904
Variance (%)	37.1	61.3	80.4

^zFruit types were separated into four categories, each with an assigned dummy variable: indehiscent (11), fleshy (10), dehiscent (01), other (00); fruit categories summarized the following fruit types: indehiscent (achene, caryopsis, nut, nutlet, samara, schizocarp), fleshy (berry, drupe, druplet), dehiscent (capsule, follicle, pod, silicle, silique), other (catkin, cone, utricle).

the fundamental niches of exotic species may help explain the conservative predictions of GARP (Anderson et al. 2003). Although more extensive data, summarizing species distributions, may have reduced the disparity between our climate-matching model and GARP, the choice of environmental variables may also account for the observed differences (Stockwell and Peterson 2002).

Equally important in predicting species' establishment risks may be the origins of founder populations (Wilson et al. 2007). Widespread species often show local adaptations, and modeling these sub-populations together may overestimate their ecological breadth (Stockwell and Peterson 2002). For example, several exotic plants currently absent from Riding Mountain National Park, including European birch (*Betula pendula* Roth), orchardgrass (*Dactylis glomerata* L.) and scots pine (*Pinus sylvestris* L.), are characterized by regional adaptations (Sannikov et al. 1997; Li et al. 2002; Annese et al. 2006). It is possible that, despite their wide distribution in Europe, the introduced climatic ecotypes may not be well adapted to the environments of Riding Mountain National Park. In such cases, the plasticity, genetic diversity, and rapid adaptation of introduced populations may further determine their threat to natural areas (Roy et al. 2000; Sexton et al. 2002). Despite these and other potential limitations, climate models provide an important predictive tool, the results of which must be thoughtfully interpreted in the context of their application (Fielding and Bell 1997).

Our findings must also be considered in the context of natural areas. For example, the separation of native and human disturbed habitats in our model reflects a bias towards the conservation of "natural" habitats such as prairies, wetlands, and woodlands. While inside natural reserves, this focus places a justifiable emphasis on the preservation of native biodiversity, human as well as natural disturbances often fragment protected areas, providing staging points for the proliferation of exotic species into undisturbed habitats (Underwood et al. 2004; Rose and Hermanutz 2004; Mandryk and Wein 2006). Equally important in the management of exotic invasions may be considerations of their

suppression (D'Antonio and Meyerson 2002). For example, MacDougall et al. (2006) warned against the impacts of disturbance during the removal of exotic invaders.

A New Integrative Method

The likelihood of biological invasion is a function of the environment, an exotic organism's traits, and the nature of its impacts on native communities (Smith et al. 1999). Despite the large number of exotic species in most regional floras, the majority fail to become invaders and many simply contribute to local species richness (Rosenzweig 2001). The challenge of managing exotic organisms rests in our ability to predict and contain species posing the greatest threat to endemic biodiversity and the function of native ecosystems (Usher 1988; Underwood et al. 2004). Current models, emphasizing isolated stages of biological invasions, often fail to formalize interactions between exotic organisms and recipient environments that frequently determine the outcome of introductions (Dietz and Edwards 2006; Thuiller et al. 2006). Using combinations of climate and the biological traits of exotic plants, our model offers a synthetic approach to the prediction of invasions and the prioritization of their management inside natural areas.

We suggest that the contingent nature of biological invasions (*sensu* Puth and Post 2005), consisting of transitions between stages in the invasion process, likely accounts for the poor performance of most predictive models and the lack of general principles attributed to invasion biology (Colautti et al. 2006; Dietz and Edwards 2006). In order to resolve this impasse, we propose an approach integrating the characteristics of exotic plants, which enable them to establish and proliferate within native communities. We suggest that, within the context of natural areas, only plants capable of successfully completing these two life-history stages should be considered a threat to native biodiversity and warrant the highest management concern. Our model demonstrates that Riding Mountain National Park and other natural areas in western Canada will continue to be impacted by exotic plants. By integrating the native climatic range, biological traits, and habitat preferences of exotic species, our

model offers a synthetic approach to the prediction and management of biological invasions inside natural areas; such integration is critical to the protection of Canada's endemic biodiversity.

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