An ecological assessment of Russian olive in western Canada: Predicted distribution across its invaded range and insect associations in southern BC

by

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# Abstract

Russian olive is a small tree or large multi-stemmed shrub that was introduced to Canada and the United States (US) from Eurasia in the early 1900s. It was provisioned in large numbers during the last century to prairie farmers as a shelterbelt plant, and remains a popular and widely-available ornamental. Now invasive within some riparian ecosystems in the western US, Russian olive has been declared noxious in the states of Colorado and New Mexico. With traits including high shade tolerance and a symbiotic association with nitrogen-fixing bacteria, Russian olive has the potential to dominate riparian vegetation, and thus radically transform riparian ecosystems. Despite its naturalization in many parts of Canada, especially in the south-west, little is known about its potential invasion range or impact within Canadian ecosystems. In this thesis, I conducted a 3 part ecological assessment of Russian olive in Canada. First, I critically evaluated the potential for Russian olive to become invasive and problematic within riparian ecosystems in Canada. Second, I predicted the potential distribution of Russian olive in North America through ecological niche modeling, building substantially upon previous work by using ecologically relevant predictors and North American occurrence records. I found that Russian olive has not yet filled its potential range within North America, including riparian zones along economically important salmon-bearing rivers and streams in southern British Columbia. Third, I conducted the first standardized assessment of insect assemblages on Russian olive in comparison to two co-occurring native shrubs species, Woods' rose and Saskatoon. I found that the insect family richness, diversity, community composition and community variance were no different from that of co-occurring native shrubs. These findings are consistent with a neutral response of insects to Russian olive compared to co-occurring native shrubs. The findings of this research will help guide management plans for Russian olive in Canada.

# Preface

The research in this thesis was designed, performed, analyzed, and written by me, Liana Collette, in collaboration with my supervisory committee, Drs. Jason Pither, Robert Lalonde, and Rosemarie De Clerck-Floate. Insect and Russian olive occurrence data were collected with the help of Emma Walker and Prairie Shelterbelt Program Russian olive planting data were obtained from Darren Bruhjell (Agriculture and Agri-Food Canada).

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# **Chapter 1: Introduction**

## **1.1 General introduction**

Russian olive (*Elaeagnus angustifolia* L., Elaeagnaceae) is a small tree or large multistemmed shrub that is native to southern Europe and to central and eastern Asia (Little 1961; Katz and Shafroth 2003). Introduced to Canada and the United States of America (US) in the early 1900s for use as an ornamental, a shade plant and a windbreak (Hansen 1901; Katz and Shaftroth 2003), Russian olive has since become naturalized within riparian ecosystems throughout the western US and parts of southern Canada. It can have detrimental ecological impacts (Katz and Shafroth 2003), especially in riparian ecosystems, and consequently has been declared noxious in the states of Colorado and New Mexico (Bean et al. 2008). It also is listed as potentially invasive and banned in Connecticut (Bean et al. 2008). By contrast, a federally-funded program sponsored the planting of Russian olive plants throughout the Canadian prairies from 1948 until as recently as 2002, as it was a valued shelterbelt tree/shrub that aided in the conservation of prairie soils. Russian olive continues to be sold as an ornamental throughout Canada.

My objective in this chapter is to call attention to Russian olive as an emerging exotic invasive plant within western Canada, and to highlight questions that urgently need answering if we are to minimize the risk of our riparian ecosystems suffering a similar fate to many in the western US that have been invaded by Russian olive. I begin by reviewing the biology of Russian olive, and describe what is known about its history within North America. Contributing to the latter are novel maps illustrating the numerical and geographical scope of the prairie shelterbelt planting program within Canada. Next, I describe what little is known about the current distribution and potential for naturalization of Russian olive in western Canada. I then review research concerning the ecological impacts that Russian olive can have, focusing especially on riparian ecosystems, and then shift towards management implications, and describe control efforts that are currently underway. I conclude by presenting a research agenda aimed at clarifying if and how Russian olive poses a threat to riparian ecosystems within western Canada.

### **1.2 Russian olive biology**

#### TAXONOMY

Phylogenetically, Russian olive remains enigmatic; its position within the angiosperms is not entirely resolved (Bartish 2002; Zhang et al. 2011), in part because the systematics of the family to which it belongs, the Elaeagnaceae, is itself uncertain. The most likely placement of the family has only 50% support in recent phylogenetic analyses (Savolainen et al. 2000; Soltis et al. 2000; Sytsma et al. 2002; Hilu et al. 2003; Stevens 2013) (Figure 1.1).





Both native and non-native confamilial species of Russian olive occur in Canada, and typically share the same habitat requirements as Russian olive (Table 1.1). The native species include *Elaeagnus commutata* Bernh. ex Rydb. (wolf-willow), *Shepherdia canadensis* (L.) Nutt. (soopolallie or buffaloberry) and *Shepherdia argentea* (Pursh) Nutt. (thorny

buffaloberry), and the two non-native comfamilials are *Hippophae rhamnoides* L. (sea buckthorn) and *Elaeagnus umbellata* Thunb. (autumn olive).

**Table 1.1** Ecozones, natural habitats and habitat requirements of Russian olive and its confamilials in Canada. Information adapted from Esser (1995), Li and Schroeder (1996), the Evergreen Native Plant Database (2013) and Muma (2013).

Species	Common name(s)	Ecozone(s)	Natural Habitats	Moisture Requirements	Light Requirements	Soil Requirements
Elaeagnus angustifolia	Russian olive	Atlantic Maritime	Forest Edge	Dry	Sun	Clay
		Mixedwood Plains	Prairie/Meadow/Field	Normal	Partial Shade	Sand
		Prairies	Wet Meadow/Prairie/Field	Moist		Calciphile
		Montane Cordillera	Riparian (edge)			
			Desert Lakeshores			
Elaeagnus commutata*	Wolf-willow	Boreal Shield	Forest Edge	Dry	Sun	Clay
	Silveryberry	Prairies	Prairie/Meadow/Field		Partial Shade	Sand
		Montane Cordillera	Riparian (edge)			
		Hudson Plains	Lakeshores			
Shepherdia canadensis*	Soopalallie	Taiga Plains	Woodland (35-60% cover)	Dry	Sun	Clay
	Silver buffalo-berry	Taiga Shield	Forest Edge	Normal	Partial Shade	Sand
		Boreal Shield	Riparian (edge)	Moist		Loam
		Atlantic Maritime	Swamp/Marsh (nutrient rich)			Calciphile
		Mixedwood Plains	Rocky Bluff			
		Boreal Plains Prairies Taiga Cordillera Boreal Cordillera	Lakeshores			
		Pacific Maritime				
		Montane Cordillera				
		Hudson Plains				
Shepherdia argentea*	Thorny buffalo-berry	Prairies	Woodland (35-60% cover)	Dry	Sun	Sand
urgenieu bunu	c.		Salt Water Shorelines	Normal Moist		Loam Clay
Hippophae rhamnoides	Sea buckthorn	Boreal Shield	Open Areas	Dry	Sun	Sand
		Prairies	Riverbanks	Normal		Loam
			Seashores	Moist		
Elaeagnus umbellata	Autumn olive	Atlantic Maritime	Forest Edge	Dry	Sun	Clay
		Boreal Shield Mixedwood Plains	Fields and Open Areas	Normal		Sand

\* Indicates species native to Canada

Like Russian olive, the latter two species were intentionally introduced to Canada in the early to mid-1900s (Li and Schroeder 1996; Catling et al. 1997; Oliver 2001). Superficially, *E. commutata* and Russian olive appear similar in the field owing to their silvery-grey leaves, but the latter species is distinguished by the reddish, sometimes shredding bark and sharp thorns that arm its branches. The other confamilial species show little resemblance to Russian olive.

#### PHENOLOGY

Although phenology will vary throughout its introduced, North American range (as it does within British Columbia (BC); Collette and Pither, unpublished data), bud break generally occurs in early spring, with flowering among mature trees commencing in mid- to late spring. The flowers are yellow and fragrant, and are pollinated by insects (Katz and Shafroth 2003; Pendleton et al. 2011). In late summer, the pollinated flowers mature into clusters of oval-shaped, 1-1.5 cm long fruits, each containing a single seed (Young and Young 1992; Lesica and Miles 2001). Fruit dispersal happens during the fall and winter, primarily through consumption and movement by birds (Borell 1962; Olson and Knopf 1986; Kindschy 1998), mammals (Kindschy 1998) and potentially through fluvial transport (Brock 1998; Pearce and Smith 2001).

#### NATURAL ENEMIES

In its native range, Russian olive is attacked by several fungi species, multiple insect species from the orders Coleoptera, Hemiptera, and Lepidoptera, and mite species from the families Tetranychidae and Eriophyoidae (Trombidiformes) (Zheng et al. 2006; CABI 2009). A moth, *Teia prisca* (Staudinger) (Lepidoptera: Lymantriidae), is believed to be a specialist on Russian olive (Zheng et al. 2006). Surveys for a biocontrol agent in Russian olive's native range indicate herbivores attack the trunk, shoots (young and old), leaves, flowers and fruits (CABI 2009). One particular fungus found in Russian olive's native range, *Phomopsis elaeagni* Sandu (Diaporthaceae), causes cankers in the branches and stems of Russian olive and is responsible for large-scale dieback of Russian olive stands in the US and Canada (Arnold and Straby 1973; James 1983).

#### IMPORTANT ECOLOGICAL TRAITS

Based upon research conducted in the US, Russian olive appears to be shade tolerant compared to co-occurring native species, such as cottonwood (Populus spp., Salicaceae) and willow (Salix spp., Salicaceae), and this may facilitate its dominance in the understory of habitats primarily composed of these pioneer species (Reynolds and Cooper 2010). Moreover, whereas cottonwood and willow seed germination requires flooding and highlight conditions, Russian olive will germinate in shadier, drier conditions (Shafroth et al. 1995; Reynolds and Cooper 2010), even under full canopies (Katz and Shafroth 2003). Furthermore, owing to a symbiosis with nitrogen-fixing actinomycetes of the genus Frankia (Miller and Baker 1985; Huss-Danell 1997), Russian olive can establish on bare, mineral substrates that are unfavourable for species lacking such symbioses (Shafroth et al. 1995). Russian olive has also been found to form associations with vesicular-arbuscular mycorrhizae (Riffle 1977), and this too may provide a competitive edge. Lastly, Shafroth et al. (1995) found that Russian olive seeds are much larger than seeds of the native cottonwoods (Populus spp.) (roughly 4 times heavier and 3.3 times longer than Populus *deltoides* seeds; Young and Young 1992), and this could provide an advantage during establishment in both disturbed and undisturbed areas (Shafroth et al. 1995; Lesica and Miles 1999; Katz et al. 2001).

#### **1.3 Russian olive distribution: past and present**

#### HISTORICAL PLANTINGS AND CANADA'S PRAIRIE SHELTERBELT PROGRAM

Russian olive's dense growth form, relatively large seeds, ability to tolerate colder climates (Gusta et al. 1983; Friedman et al. 2005), and a wide range of soil and moisture conditions (Lesica and Miles 2001; Reynolds and Cooper 2010) made it an ideal shelterbelt plant across the prairie provinces and states (Olson and Knopf 1986). From 1901 to spring 2013, the Government of Canada's (Prairie Farm Rehabilitation Administration, or PFRA) Prairie Shelterbelt Program (discontinued as of 2013) provided shelterbelt tree and shrub seedlings, including Russian olive, to eligible agricultural lands in Manitoba, Saskatchewan, Alberta and the Peace River region of British Columbia. The Prairie Shelterbelt Program in conjunction with another PFRA program, the Community Pasture Program, aimed to minimize the effects of drought by protecting and managing native prairie land and water resources (Marchildon 2009). The program administrators kept a database of planting records detailing the plant species, location, year, and amount distributed since its inception. I obtained program planting records for Russian olive from the current administrators, Agriculture and Agri-Food Canada (AAFC). I assumed that all plants distributed through this program were planted and therefore refer to these records as planting data. The planting locations were stored in the Dominion Land Survey format. Using open source Dominion Land Survey grids (source: GeoGratis, <u>http://geogratis.gc.ca/api/en/nrcan-rncan/ess-</u> <u>sst/f907a02c-f592-5261-ab4e-4bdae67a73ad.html</u>) and ArcGIS 10.1 (ESRI 2012), I mapped the plantings to section. Here, I define a planting as a section of land (1 square mile or ~2.60 km<sup>2</sup>) in which multiple Russian olive seedlings have been planted. These data contained 3,395 of 3,777 plantings, or 90% of plantings, with known locations.

From 1948 to 2002, a total of 1,086,654 Russian olive seedlings were planted. Of the records with locations provided, the majority of Russian olive seedlings occurred in Saskatchewan (335,945 plants), followed by Manitoba (98,368 plants), Alberta (17,975 plants), then British Columbia (975 plants) (Figure 1.2). According to Moore (1964), Canadian shelterbelt plantings of Russian olive were not nearly as extensive as those in the US.



**Figure 1.2** Number of Russian olive seedlings planted through the Prairie Shelterbelt Program. Projection: NAD 1983 CSRS UTM Zone 13N.

Historically, there were two peaks of Russian olive planting activity across the Canadian prairies; 1968-1974 and 1988-2000 (Figure 1.3, Figure 1.4a). The years 1969 and 2002 included particularly high numbers of plantings (Figure 1.4b). On average, 288 Russian olive seedlings were planted per planting. I could not find any evidence of plantings beyond the year 2002.



**Figure 1.3** The years in which Russian olive was planted through the Prairie Shelterbelt Program. Projection as in Figure 1.2.



**Figure 1.4** (a) Frequency of Russian olive plantings across the Canadian prairies from 1948-2002, (b) Number of Russian olive seedlings planted per year.

#### NATURALIZED DISTRIBUTION AND OCCURRENCE RECORDS

In its native range, Russian olive is found primarily along coasts and riparian areas, and is able to tolerate cold climates (Lamers et al. 2006; Singh et al. 2008). Similar patterns are emerging in its introduced, North American range. For example, Russian olive has a characteristically patchy distribution throughout riparian habitats in western US, and has begun to invade riparian areas in western Canada (Jarnevich and Reynolds 2011; Nagler et al. 2011). In the US, Russian olive thrives in riparian areas where cottonwoods typically dominate (Knopf and Olson 1984; Lesica and Miles 1999). However, in southern Alberta, it can also be found near small creeks and wetland areas where woody vegetation is absent (A. McClay, McClay Ecoscience and R. Bourchier, AAFC), personal communication, 2014). In BC, Russian olive has been observed to naturally occur in dry habitats in close proximity to water bodies, moist to dry roadsides, and the steppe zone (a large portion of the Bunchgrass Biogeoclimatic Ecosystem Classification (BEC) zone) (Douglas et al. 1999). Preliminary surveys conducted by myself indicate that it commonly co-occurs with willows (*Salix* spp.), cottonwoods (*Populus* spp.), sagebrush (*Artemisia* spp., Asteraceae), Saskatoon (*Amelanchier alnifolia* Nutt., Rosaceae) and roses (*Rosa* spp., Rosaceae).

Despite its obvious prevalence along waterways and drainages in south-western Canada, official occurrence records are lacking. For instance, as of fall 2013, only a single record of Russian olive had been entered into the Government of British Columbia's Invasive Alien Plant Program (IAPP) online application within the 8 years since the IAPP was initiated (L. Kristiansen, BC Ministry of Forests, Lands, and Natural Resource Operations, personal communication, 2013). I suspect this is primarily due to a lack of awareness of its status as an exotic and potentially invasive species.

Russian olive naturalization is becoming increasingly evident in western Canada, though in most cases, the source is unknown. In regions that received shelterbelt plantings and that harbour favourable conditions for growth, program plants may have served as sources for naturalization. Horticultural plantings may also serve as sources, as Russian olive is a popular ornamental and remains available for purchase. Russian olive naturalization has been observed in southeastern Alberta, in particular in the Medicine Hat area (A. McClay, personal communication, 2014), however, whether the spread originated from Prairie Shelterbelt Program plantings or horticultural plantings in residential areas is

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uncertain (D. Young, City of Medicine Hat, personal communication, 2013). Within the City of Medicine Hat boundary, a single planting of 25 seedlings was established in 1970. Within a 15 km radius outside of the City of Medicine Hat boundary, three program plantings, totalling 1,300 seedlings planted, were established between 1969 and 1970. A total of 1,325 seedlings planted in and within the vicinity of Medicine Hat indicates the program may have played a part in Russian olive's spread, but more research is needed to assess this. Along the Old Man River in southern Alberta, Russian olive has been seen encroaching into the coulees from city back-yard plantings (R. De Clerck-Floate, AAFC, personal communication, 2013). Yet in central and northern Alberta, where Russian olive is a popular ornamental, it has not shown any signs of escaping cultivation (A. McClay, personal communication, 2014). In BC, Russian olive establishment is extensive along a 10 km portion of Highway 97 from Summerland to Osoyoos (L. Collette, personal observation, 2013). Extensive naturalization has also been observed along a 40 km reach of river upstream of Kamloops, BC on the Thompson River, most likely originating from riverbank plantings 100 years ago (Pearce and Smith 2009).

Pearce and Smith (2001) examined Russian olive dispersal along the Milk River starting at 40 km from the Alberta/Montana border and then extending 160 km into the US. In 1950, Russian olive was introduced to the Aageson Ranch in Montana, about 10 km downstream of the international border, as a windbreak and for erosion control, however, there are no known plantings on the Alberta side of the border. The 2001 study by Pearce and Smith, in conjunction with another one of their studies (Pearce and Smith 2009), found that Russian olive density was considerably greater downstream of Aageson Ranch compared to the upstream reaches in southern Alberta. Approximately 48 Russian olive plants (seedlings, saplings and trees) were found in the Canadian portion of the study, suggesting seeds were transported upstream by wildlife (Pearce and Smith 2001).

### **1.4 Ecological impacts**

Russian olive's establishment within many US riparian habitats has spurred a substantial amount of research and funding in the country over the past decade (Nagler et al. 2011), focused primarily on elucidating its potential impacts. Findings include; (i) lower bird

species richness and diversity than surrounding native plant species (Knopf and Olson 1984; Brown 1990), (ii) providing potential nesting habitat for the endangered southwestern willow flycatcher (*Empidonax traillii extimus* A.R. Phillips, Tyrannidae) (USDA 2012), and (iii) contributing significant nitrogen input to streams (Mineau et al. 2011) and soils (DeCant 2008; Follstad Shah et al. 2010). Reviews by Katz and Shafroth (2003) and Nagler et al. (2011) describe many additional examples of ecological effects; here I highlight new findings from the US that are especially relevant to riparian habitats and rivers in western Canada, where Russian olive is gaining a foothold.

Several studies indicate Russian olive invasion is drastically altering aquatic ecosystem functioning (Kominoski et al. 2013; Mineau et al. 2011; Mineau et al. 2012). Streams invaded with Russian olive are not as limited by nitrogen compared to uninvaded streams (Mineau et al. 2011). Furthermore, the primary limited nutrient of some invaded streams has been observed to shift from nitrogen to phosphorus, perhaps due to Russian olive's ability to fix nitrogen (Mineau et al. 2011). When coupled with anthropogenic sources of nitrogen from agriculture and urban-suburban areas where Russian olive planting is common, additions of nitrogen from Russian olive may contribute to stream nitrogen saturation, leading to eutrophication and oxygen deficiencies within the system (Mineau et al. 2011). Along Deep Creek in southeast Idaho, Mineau et al. (2012) found that allochthonous organic matter inputs from Russian olive leaf litter and the recalcitrant nature of Russian olive leaves caused a decrease in ecosystem efficiency. In that study, inputs of allochthonous organic matter increased 25-fold after Russian olive invasion and was most likely stored as benthic organic matter in the stream (Mineau et al. 2012).

Russian olive also appears to be providing a subsidy to the invasive, exotic common carp, *Cyprinus carpio* L. For example, in Deep Creek, Idaho, Russian olive material makes up on average approximately 66% of the stomach content of the common carp (C. Baxter, U. Idaho, personal communication, 2014). Carp have been found to be responsible for a multitude of deleterious ecosystem and community level effects (e.g. Parkos et al. 2003; Bajer et al. 2009; Weber and Brown 2011), thus making its invasion in North American freshwater systems a major concern. Furthermore, common carp has been found to decrease the growth (Wolfe et al. 2009; Wahl et al. 2011) and abundance (Weber and Brown 2011) of native fish species. It is therefore possible that Russian olive may be facilitating carp's dominance in some rivers.

In the US, Russian olive, along with saltcedar (*Tamarix* spp., Tamaricaceae), has the potential to serve as nesting habitat for the endangered southwestern willow flycatcher (*Empidonax traillii extimus* A.R. Phillips, Tyrannidae) (USDA 2012). This has led to conflicts between groups advocating for endangered species preservation on one hand, and those promoting invasive species management on the other (Hultine et al. 2010). Anecdotally, birders in the Okanagan Valley of BC have reported a variety of overwintering, berry-feeding birds consuming the fruits of Russian olive, including Western Bluebirds, American Robins, Northern Flicker, Bohemian and Cedar Waxwings, Varied Thrush and European Starlings. In the same region, there are areas where Russian olive has completely replaced all native, woody, vertical vegetative structures, thereby acting as the sole vertical structure for tree-nesting avian species (B. Harrison, Ducks Unlimited, personal communication, 2013). Clearly, a formal assessment of native bird use of Russian olive within western Canada is warranted.

Information regarding insect use of Russian olive in western Canada is also lacking, but several interesting observations have been made. I observed extensive feeding and habitation on Russian olive fruits by yellowjacket wasps (*Vespula* sp.) near Kamloops and Vernon, BC in October 2013 (Figure 1.5).



**Figure 1.5** (Upper) Yellowjacket wasps (*Vespula* sp.) on Russian olive. (Lower left) Yellowjacket wasp chewing on a Russian olive fruit. (Lower right) Holes in Russian olive fruits caused by yellowjacket wasp feeding.

Similar observations involving yellowjacket wasp use of Russian olive have been informally reported on the internet

(http://community.stretcher.com/forums/p/18888/197111.aspx,

http://www.countrylivinginacariboovalley.com/uncategorized/how-to-kill-wasps/). It would be interesting to determine whether Russian olive is subsidizing food resources for the yellowjacket wasp. Insect surveys conducted in the Okanagan Valley of BC found insects from the orders Thysanoptera, Hymenoptera, Hemiptera, Coleoptera, Diptera, Dermpatera, Psocoptera, Ephemeroptera, Trichoptera, and Orthoptera to be associated with Russian olive (Chapter 3).

#### **1.5 Potential for management and control**

Multiple control methods are in the process of being developed for Russian olive in the US. Mechanical control methods, such as mowing, cutting and bulldozing, have been used, but with varying success (Katz and Shafroth 2003). Additionally, these techniques can often have undesirable consequences; removal of Russian olive can cause severe soil disturbances, leading to increased erosion (Stannard et al. 2002), and the invasive species is often replaced by other exotic species (Gaddis and Sher 2012).

Biological control is an alternative control method currently being explored. However, because Russian olive is valued as an ornamental in North America, testing of candidate arthropod biocontrol agents in Europe by CABI (Centre for Agricultural Bioscience International) and BBCA (Biotechnology and Biological Control Agency) has focused on agents that only attack Russian olive flower buds, flowers, fruits, seeds, and seedlings. These types of agents would reduce the reproductive output of the tree and its spread while simultaneously preserving the horticultural value of existing trees (Bean et al. 2008). Promising host specific agents include Aceria angustifoliae Denizhan (Acari: Eriophyoidae), a mite which galls inflorescences, young fruits, leaves and shoots, and Ananarsia eleagnella Kuznetzov (Lepidoptera: Gelechiidae), a fruit and seed-feeding moth (CABI 2013; CABI 2014). Currently, the program is in the foreign exploration phase, which involves surveying for and host-range testing of potential agents within Russian olive's native range (Bean et al. 2008; CABI 2011; CABI 2014). The next planned phase for the US will focus on rearing and testing potential agents at the proposed USDA quarantine facilities in Temple, Texas and Sidney, Montana (Bean et al. 2008). Testing the mentioned candidate biocontrol agents for use in Canada has been postponed until information regarding Russian olive's invasiveness in Canada becomes available (R. De Clerck-Floate, personal communication, 2013).

Although Russian olive has yet to be classified as noxious or even "of concern" by any Canadian provinces, invasive species managers are taking notice. As in the US, suppression programs for Russian olive in western Canada face challenges due to potential conflicts between different stakeholders (see above). They are also subject to the same logistical challenges experienced in the US, including removal along stream banks leading to destabilization and erosion (Pollen-Bankhead et al. 2009). The following example illustrates these challenges. Russian olive suppression was initiated along a portion of the Milk River north of the Alberta/Montana border in 1999, and involved cutting trees and saplings (Pearce and Smith 2009; COSEWIC 2012). The stumps were then treated with the herbicide, triclopyr, in 2000 and 2001 (Pearce and Smith 2009; COSEWIC 2012). However, a follow up study conducted in 2005 found the herbicide treated stumps had begun to vigorously resprout and 236 new plants had established in the area (Pearce and Smith 2009).

To the best of my knowledge, there are currently no substantial or coordinated control programs for Russian olive in Canada, and efforts that I have witnessed (e.g. in the Okanagan Valley of BC) have been haphazard at best. Russian olive is still available for consumer purchase as an ornamental in Canada, further compromising management efforts. At greenhouses and nurseries, information about Russian olive is often incomplete or misleading. For example, during a recent visit to a Calgary, Alberta greenhouse, I found Russian olive for sale, the tag indicating it was "native to many areas", with no mention of it being non-native to Canada. Also, recommendations discouraging planting Russian olive in close proximity to bodies of water are not readily disseminated to consumers.

# 1.6 Anticipated impacts and future research needs

#### GEOGRAPHIC DISTRIBUTION

Acquiring accurate information about the current distribution of Russian olive in Canada is a priority. Previous studies have shown that if climate warming trends continue, Russian olive's southward invasion within the US could be limited (Friedman et al. 2005; Guilbault et al. 2012). However, no studies have focused on the projected climate change effects on northward expansion into or within Canada. Its ability to tolerate cold climates (Gusta et al. 1983; Friedman et al. 2005) suggests Russian olive's invasion front could easily shift northwards from affected states in the US.

Recently, Nagler et al. (2011) outlined several different factors that promote the present distribution and abundance of Russian olive in the US. These include; 1) a chilling requirement, potentially needed for bud break and seed germination (Friedman et al. 2005; Guilbault et al. 2012), 2) supplemental moisture in arid and semiarid regions, which is often provided in riparian areas, floodplains, reservoir margins and canals, 3) increased river flow

regulation leading to less flooding and less disturbance, conditions that are unfavourable for native plant seedling establishment (i.e. cottonwoods and willows), 4) silt loam and silty clay soil types (Madurapperuma et al. 2013), and 5) high soil salinity and alkalinity conditions in which Russian olive is more tolerant than native species (Nagler et al. 2011). Regions in Canada that support these conditions deserve both research and management attention.

The possibility of using "citizen science" as a means to record Russian olive locations is promising. Volunteers have been used to survey Russian olive in the US (Brown et al. 2001; Crall et al. 2011), and have also been used to survey other weedy shrubs and trees, including Lonicera species (Caprifoliaceae) (Brandon et al. 2003), Rosa multiflora Thunb. (Rosaceae) (Brandon et al. 2003), Celastrus orbiculatus Thunb. (Celastraceae) (Ibáñez et al. 2009), and Rhamnus cathartica L. (Rhamnaceae) (Brown et al. 2001; Brandon et al. 2003). This citizen science approach is promising for three reasons. First, due to Russian olive's popularity as an ornamental, the majority of Russian olive plantings occur in urban areas and are located on private land. Generally, property owners are reasonably knowledgeable of the plants located on their property. Second, Russian olive is easily identified (Crall et al. 2011) through its long, silvery-grey leaves and sharp thorns, which decreases the probability of misidentification. Third, tools and software used to record invasive plant locations, such as web-based application and mobile phone applications, are readily available to the public and easy to use. In addition to assisting Russian olive research, citizen science can help increase awareness about Russian olive's potential for invasion, and allows taxpayers to participate in and understand Russian olive research and management, to which they indirectly contribute financially.

The potential extent of Russian olive's naturalization in Canada is currently unknown and needs to be formally assessed. Planting records and outcomes from across the Canadian prairies can potentially be used as baseline data to determine potential naturalization. Water bodies and riparian areas in close proximity to Russian olive plantings may facilitate establishment of this plant and should be closely monitored as high risk for naturalization. Personal observations indicate Russian olive in western Canada typically spreads aggressively within ca. 1 km of a water body. This pattern is consistent with observations in the US (Lesica and Miles 1999; Pearce and Smith 2001; Narumalani et al. 2009; Madurapperuma et al. 2013). Using the Census of Canada Digital Boundary Files Rivers and Lakes shapefiles (Statistics Canada 2006), I identified 535 plantings (comprising 93,875 Russian olive plants) that occurred within 1 km of water bodies, and thus have the potential to naturalize (Figure 1.6).



**Figure 1.6** Russian olive plantings that have the potential to naturalize in areas within 1 km of a water body. Projection as in Figure 1.2.

This comprises 16% of the total plantings with known locations and 22% of the total amount of individual Russian olive seedlings that were planted (known locations). As these figures do not include the plantings with unknown locations (382 of 3,777 plantings, or 10% of plantings), there may in fact be more plantings that fall within this area of high naturalization risk. However, discussions with land owners have revealed that Russian olive plantings are often unsuccessful, requiring replanting in many prairie areas (G. Michener, U. Lethbridge, personal communication, 2013). Especially valuable would be surveys aimed at determining the fates of Russian olive plants from different planting periods (e.g. Figure 1.3), and within different climatic/soil regions. Data from such surveys could inform efforts to predict the current and future distribution of Russian olive (see below).

Ecological niche modeling (ENM) is a powerful tool currently being used to predict potential plant invasions (Peterson and Vieglais 2001; Peterson et al. 2003; Thuiller et al. 2005; Fiaboe et al. 2012; Sobek-Swant et al. 2012). A recent scientometric analysis, which analyzes trends, patterns and irregularities in publications of a particular field, showed that there has been a growing interest in using ecological niche models to predict invasive species distribution over the past decade (Barbosa et al. 2011). ENM could also be very useful for determining Russian olive's potential spread in Canada, as it has been with many other invasive species in Canada and the US (Anderson et al. 2006; Mau-Crimmins et al. 2006; Bradley 2009; Ensing et al. 2013). When coupled with the prairie planting data, the niche model predictions could be used to identify areas of concern for Russian olive naturalization and in turn, can be used to guide management plans.

#### ECOSYSTEM EFFECTS

The combined effects of differences in plant life history between Russian olive and co-occurring native species and altered hydrology have caused changes to successional pathways among riparian areas in the US (Friedman et al. 1997; Strange et al. 1999). As previously mentioned, in contrast to native cottonwoods, Russian olive germination and seedling establishment is not flood-dependent, and seedlings can establish under the canopy layer (Shafroth et al. 1995; Reynolds and Cooper 2010). Increased flood regulation through damming has led to fewer flooding events, decreased peak flow, and in turn, a decrease in the physical force of water to move sediment downstream. This decreased peak flow has reduced stream meandering, a process necessary to create point bars (where sediment accumulates on the inner bank of a meandering stream) and establish cottonwood germination sites (Friedman et al. 1997). With fewer point bars, cottonwood establishment and regeneration is limited, thereby shifting the successional processes to favour species that do not require flooding events to establish, such as Russian olive (Friedman et al. 1997; Strange et al. 1999). The beginning of this successional shift has been observed along eastern (Lesica and Miles 2001) and northern (Pearce and Smith 2001) Montana rivers. Although these findings concern rivers in the US, Canadian rivers are subject to similar flow regulation regimes and structures (Bradley and Smith 1986; Dynesius and Nilsso 1994; Rood et al. 2005) and might therefore experience similar fates. For instance, abrupt flow reductions and insufficient summer flows have been found to be partly responsible for riparian cottonwood declines

downstream of the St. Mary Dam in southern Alberta (Rood et al. 1995). Furthermore, historic declines in annual flow have been observed along the same portion of the Old Man River in southern Alberta (Rood et al. 2005) where Russian olive naturalization from backyard plantings has been observed (R. De Clerck-Floate, personal communication, 2013).

Russian olive's potential to subsidize streams in the US with nitrogen and allochthonous organic matter raises concern for Canadian aquatic ecosystems. The shift from a semiarid/riparian grassland to one dominated by woody plants, as appears to be happening with Russian olive in some areas of southern Alberta, is expected to affect nutrient dynamics and hydrologic function (Huxman et al. 2005; Ball et al. 2010). It follows that nutrient and/or organic matter inputs of any magnitude from these new woody inhabitants, especially from nitrogen fixing exotics such as Russian olive, will also have profound impacts on the system.

#### COMMUNITY AND SPECIES EFFECTS

Currently, peer-reviewed research concerning the potential impacts of Russian olive on Canada's native flora and fauna is lacking. A recently published report from the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) (COSEWIC 2012) raised concerns about the invasion of Russian olive and its potential displacement of native plants important to Weidemeyer's Admiral (*Limenitis weidemeyerii* W.H. Edwards, Lepidoptera: Nymphalidae), a brush-footed butterfly of special concern.

Russian olive invasion along river systems in southern Alberta, especially along the Milk River basin, may also impact the survival and reproduction of Mountain Sucker (*Catostomus platyrhynchus* Cope, Catostomidae) (Boguski and Watkinson 2013). The Mountain Sucker is primarily a benthic feeder, browsing on algae, diatoms, small invertebrates (Belica and Nibbelink 2006). If Canadian streams face the same fate as Deep Creek, Idaho, increases in benthic organic matter will have unknown effects on habitat quality for this fish. From an economic and ecological standpoint, any negative effects of Russian olive on fishery related waterways, such as the salmon bearing rivers in British Columbia, could be devastating. As such, Russian olive invasion impacts on Mountain Sucker and on the aquatic community in general require further study.

Russian olive's subsidization of other invasive species is also a concern. As mentioned previously, the common carp's invasion and dominance over native species may be facilitated by Russian olive. Carp's potential distribution (Zambrano et al. 2006) closely resembles the potential distribution of Russian olive predicted by Peterson et al. (2003), thus there is a high likelihood carp could be present in areas where Russian olive has naturalized. Areas in southern BC appear to bear this out; Russian olive is extensively naturalized near Kamloops, Penticton, and Osoyoos (L. Collette, personal observation, 2013), the same areas where common carp have been reported (FishBase, http://www.fishbase.org, accessed 25 March 2014).

# **1.7 Summary**

Recent research in the US on invasive riparian plants and their ecological impacts, such as salt cedar and Russian olive, provides a strong foundation for comparable research in Canada. Based on my literature review, I have identified five key research questions to guide research on Russian olive in Canada.

1. What is Russian olive's current and potential distribution? This includes deducing a northern limit to its range and potential distribution under climate change scenarios.

2. What capacity does Russian olive have to escape cultivation and naturalize in Canadian ecosystems?

3. What ecosystem level impacts will Russian olive invasion have? For example, will Russian olive alter nutrient cycling and shift succession patterns in Canadian rivers, as it has in the US?

4. What are the community level impacts of Russian olive? How might plant, bird, insect (e.g. pollinators), and fish communities be impacted?

5. What species-level impacts will Russian olive have, with initial focus on rare and endangered species?

#### **1.8 Research outline and objectives**

The majority of information about Russian olive's invasion in North America stems from research conducted in the US. To help inform management strategies in Canada, in particular BC and Alberta, I addressed the following objectives: 1) Predict the potential distribution of Russian olive in North America through ecological niche modeling, using ecologically relevant predictors and all available North American occurrence records.

2) Compare the resulting niche model predictions to previously published predictions, which were derived using limited occurrence records and a limited suite of predictors.

3) Survey and quantify the diversity of insects associated with Russian olive plants inhabiting riparian ecosystems within southern BC, and compare these diversity patterns to those associated with co-occurring native shrub species.

# **Chapter 2: Predicting the potential invasion range of Russian olive in North America**

### 2.1 Background

Most plant species that are intentionally introduced to novel regions fulfill their purpose (e.g. as ornamentals or shelterbelt plants) with limited impact on their surroundings. Some escape from cultivation and become serious pests (Reichard and White 2001). As these problematic, non-native plants proliferate and expand their ecological impact, predicting their potential distribution is an important step towards effective management (Gallien et al. 2010). Ecological niche models (ENMs), which correlate species occurrences with environmental variables to determine areas of suitable habitat, are often used to identify areas of potential invasion in efforts to direct management decisions (e.g. Chen et al. 2007; Jarnevich and Reynolds 2011; Trethowan et al. 2011; Motloung et al. 2014). Of the long list of non-native plants whose management could benefit from ENMs, woody plants introduced through horticulture warrant special attention (Mack 2005); Reichard (1997) found that 82% of 235 woody plant species originally introduced for landscape purposes had escaped cultivation. Russian olive (*Elaeagnus angustifolia* L., Elaeagnacae) is among these species. Intentionally introduced in the 1900s to the United States (US) and Canada as a shade plant, shelterbelt and windbreak, Russian olive is believed to have escaped cultivation within the US between the 1920s and 1950s (Christensen 1963). It has since become extensively naturalized across the western states, particularly within riparian ecosystems (Katz and Shafroth 2003), and is responsible for multiple deleterious effects (e.g. Katz and Shafroth 2003; Nagler et al. 2011; Mineau et al. 2011). Accordingly, it has been declared noxious and/or banned in multiple jurisdictions. Although naturalization of Russian olive is evident in parts of Canada, particularly within the southern interior of British Columbia (BC), efforts to estimate its current and potential range within Canada are lacking. In light of the impacts that Russian olive has had in the western US, and given that western Canada hosts many riparian ecosystems with similar characteristics to those impacted in the US Great Basin, such efforts are sorely needed.

Four previous studies used ENMs to predict the potential range of Russian olive within parts of North America (Peterson et al. 2003; Hoffman et al. 2008; Jarnevich and

Reynolds 2011; Liu et al. 2014), but the following limitations restrict their utility for US and especially Canadian stakeholders. First, despite extensive, naturalized populations of Russian olive within parts of Canada, Canadian occurrence records were not used in any of the four studies. Excluding occurrences from areas known to be part of the invaded range can lead to inaccurate predictions of potential range (Beaumont et al. 2009; Anderson and Raza 2010; Barbet-Massin et al. 2010; Sánchez-Fernández et al. 2011; Vale et al. 2013). For example, if naturalized populations within Canada are associated with environmental conditions that differ from those associated with US occurrences, then predictions based exclusively on the latter are likely to be misleading. Second, the predictions of Peterson et al. (2003) were derived using a limited number of occurrence records (41) exclusively from the native range. The exclusive use of native range occurrences to build predictions of the potential invasion range is risky for a variety of reasons (Beaumont et al. 2009; Jiménez-Valverde et al. 2011), particularly because species can occupy novel environmental conditions in the invaded region (see examples in Jiménez-Valverde et al. 2011). Moreover, Wisz et al. (2008) found that ENMs based on 100 occurrences performed consistently better than those with less. Third, Jarnevich and Reynolds (2011) and more recently Liu et al. (2014) each built ENMs using a suitably large number of Russian olive occurrence records (though all from the US), but the predictions from both studies were geographically restricted to the US, and the list of predictor variables used had some potentially key omissions (see below). Fourth, Jarnevich and Reynolds (2011) evaluated the importance of predictor variables based on "percent contribution", a heuristic method whose outcomes can vary depending on the path the model uses to achieve the optimal solution, and that is additionally sensitive to collinearity among predictors (see the Maxent tutorial: http://www.cs.princeton.edu/~schapire/maxent/). Lastly, the study by Hoffman et al. (2008) focused exclusively on a region of the North Platte River in Nebraska, and thus has limited relevance elsewhere.

My first objective here is to provide stakeholders with the best possible predictions of the potential invasion range of Russian olive within North America by using; (i) an updated and more extensive occurrence record dataset that includes all available North American records, (ii) methods that provide for reliable inferences regarding which variables exert the most influence over the potential invasion range, and (iii) predictor variables that are thought to be highly relevant to the ecology and physiology of the species (Nagler et al. 2011).

Nagler et al. (2011) discussed a variety of factors that are thought to contribute to Russian olive's current distribution in the US, and some of these can potentially be represented by geospatial data within ENMs. For example, standard climate variables, available through the worldlim.org website, could help account for the putative chilling requirement that Russian olive requires for bud break and seed germination (Friedman et al. 2005; Guilbault et al. 2012). Indeed, the ENMs of Jarnevitch and Reynolds (2011) included many relevant climate-related predictor variables. However, some characteristics of Russian olive are less readily accounted for by standard geospatial data. Increased river flow regulation, which results in less flooding and less disturbance within riparian zones, is thought to create conditions that favour the establishment of Russian olive over native riparian species, such as cottonwood (Friedman et al. 1997). Thus, in addition to a "length of water feature per grid cell" variable, I derive and include a variable "length of regulated water feature per grid cell". In the Methods and Materials section I explain why, in contrast with Jarnevitch and Reynolds (2011), distance to water features was not used. Soil conditions are also likely important to the establishment success of Russian olive. For example, Russian olive appears to favour silt loam and silty clay soil types (Madurapperuma et al. 2013), and importantly, it tolerates high soil salinity and alkalinity better than native species (Nagler et al. 2011). I therefore include soil texture, soil pH, and soil salinity as predictor variables. None of these variables have previously been included in ENMs of Russian olive.

As has been found with many other exotic, invasive plant species (Parendes and Jones 2000; Flory and Clay 2006; Birdsall et al. 2012), the presence of roads may also promote the establishment of Russian olive. Roads and roadsides create a distinctive habitat, where light availability (Parendes and Jones 2000), soil nutrients (Trombulak and Frissell 2000), and drainage patterns (Trombulak and Frissell 2000) can differ substantially from nearby natural habitat. Assuming that the interception and transportation of road run-off, overland flow, and subsurface flow by roadside ditches (Buchanan et al. 2013) increases soil moisture within those ditches, roadsides may provide the supplemental moisture that Russian olive requires in arid and semiarid regions (Nagler et al. 2011). Additionally, the use of deicing salts on roadways during winter seasons can increase roadside soil alkalinity (Skarie et al. 2004;

Gałuszka et al. 2011). As mentioned previously, such soil conditions may favour the proliferation of Russian olive. I therefore include "length of major road per grid cell" as a predictor variable in my models.

Despite its potential drawbacks, the practice of constraining occurrence records and the geographical scope of ENM predictions to a single, political jurisdiction (e.g. the US) is not uncommon (e.g. Liu et al. 2014; Mingyang et al. 2008). My second objective here is to use Russian olive as a case study for examining the potential practical implications of this practice. Specifically, I first assess if and how the exclusion of Canadian occurrence records alters the realized environmental niche of Russian olive, as quantified using conditions associated with occurrence record locations. I then compare predicted realized niches, the predicted geographical ranges, and the importance of predictor variables across two ENMs (built using Maxent; Phillips et al. 2006): one constructed using all North American occurrence records and the other using exclusively US records (cf. Jarnevich and Reynolds 2011; Liu et al. 2014).

#### 2.2 Methods and Materials

#### OCCURRENCE COLLECTION

Freely available, georeferenced Russian olive point occurrences were compiled from a number of sources (Table 2.1). NIISS occurrences were in the form of polygons and points and also included presence and absence data. Maxent is a point presence-only data model, therefore I excluded polygons and absence points.

Source	Date accessed or surveyed	Number of georeferenced points
Consortium of Pacific Northwest Herbaria (CPNWH, http://www.pnwherbaria.org/)	January 15, 2014	129
Gobal Invasive Species Information Network (GISIN, http://www.gisin.org)	January 15, 2014	3,234
National Institute of Invasive Species Science (NIISS, www.niiss.org/)	January 15, 2014	6,758
EDDMaps Ontario (www.eddmaps.org/ontario/)	April 2013	18
The Invasive Alien Plant Program (IAPP, www.for.gov.bc.ca/hra/plants.application.htm)	April 9, 2013	1
Russian olive research locations compiled from attendees of the 2014 Tamarisk Coalition's Research and Management Conference	February 2014	31
Google Street View remote survey	April 2014	1,162
On-ground survey in Kelowna	May-June 2013	39
Total		11,372

**Table 2.1** Sources of georeferenced Russian olive locations in Canada and the US.

As of April 2014, only 21 occurrence records were available within Canada, despite the occurrence of well-established, naturalized populations in western Canada, especially within the southern interior of BC. I therefore conducted surveys to add Canadian occurrence records. Between June and August 2013, I surveyed riparian and road-side habitats within the vicinity of Kelowna, BC, and throughout 2013, I conducted "remote" surveys along southern BC's major roads using Google Street View imagery within Google Earth (http://www.google.com/earth/index.html) (Figure 2.1). Accessible through Google Earth or Google Maps, Google Street View allows the user to view and navigate panoramic road-level imagery. Previously used to identify vulture (Olea and Mateo-Tomás 2013) and moth (Rousselet et al. 2013) habitat, Google Street View has the potential to be a promising tool for increasing occurrences of shrub/tree sized and easily recognizable plants (Visser et al. 2014). Russian olive is an ideal candidate for Google Street View mapping due to its stature and long silver-grey leaves. These features are not common among other plants in the region and allow Russian olive to be easily distinguished from other co-occurring species (Crall et al. 2011). This survey method is cost effective and several hundred kilometers of
road can be surveyed in just a few days. While I did not conduct a formal error assessment of identification, several occurrences were verified through on ground surveys. In general, misidentification was very low (less than 2%) but willows were the most often misidentified as Russian olive. Therefore, after studying the leaf and overall structure of willows on Google Street View, I re-checked all remotely identified occurrences (N=1,162) to ensure correct identification.



**Figure 2.1** Map of roads remotely surveyed for Russian olive using Google Street View. NAD 1983 UTM Zone 11 projection.

The field- and remote-surveys in southern BC were clearly biased towards roadside and riparian habitats, raising the risk of biased model predictions. However, for several reasons, I am confident that my surveys nonetheless provide for a reliable characterization of Russian olive distribution within the region. First, southern BC exhibits considerable relief, and most roads and waterbodies (lakes and rivers) are restricted to valley bottoms. The upland terrain is dominated by closed canopy forest that is unsuitable for Russian olive. Importantly, the remote digital surveys included highways that traversed upland areas between valleys, and I witnessed decreasing density of Russian olive with increasing elevation along these highways. Moreover, colleagues in my lab have conducted extensive field ecology research within most ecosystems of southern BC, and have never observed naturalized Russian olive plants beyond view of roadsides or homesteads.

Duplicate occurrence records were removed from the collated database, as were records representing known ornamental or shelterbelt plantings, and records whose coordinates did not overlap with predictor data.

Whereas Russian olive's naturalization in the western US states is well recognized, records pertaining to putative eastern North American occurrences raise some suspicions, especially those in south-eastern states (e.g. Georgia, Alabama). A close relative of Russian olive, Autumn olive (*Elaeagnus umbellata* Thunb., Elaeagnaceae), has similar thorny branches and leaf structure and is highly invasive in the eastern US (Catling et al. 1997). As several of the eastern occurrences have their origins within EDDMapS (Early Detection & Distribution Mapping System, www.eddmaps.org) and have not been verified, I suspect some of these occurrences are likely Autumn olive. Without being able to verify these eastern occurrences in person or through Google Earth, I chose to include only those eastern records where Russian olive has been observed as per the USDA map of present/reported occurrences. (http://plants.usda.gov/core/profile?symbol=ELAN, Accessed 15 April 2014).

After filtering, a total of 6,814 unique occurrence records remained for the entire invaded range (Canada and the US). Once these records were merged with the predictor variable raster data (see below), which had a spatial resolution of 30 arcseconds ( $\sim$ 1 km<sup>2</sup>), a total of 1,707 unique grid cells contained occurrence records (the total dataset), 1,482 in the US (the US dataset) and 225 in Canada (the Canada dataset) (Figure 2.2).



**Figure 2.2** Russian olive occurrence locations. Points represent data from Table 2.1 reduced to 1 occurrence per 1 km<sup>2</sup> grid cell. Projection: North America Albers Equal Area Conic.

## PREDICTOR VARIABLES

All predictor variables (Table A1) were represented using 30 arcsecond resolution raster grids. The inclusion of correlated variables can lead to model over-fitting (Elith et al. 2011). Pearson correlations were therefore calculated for all pairwise associations (Table A1), and for pairs that were strongly correlated (Pearson  $|\mathbf{r}| > 0.7$ ) (cf. Dormann et al. 2013), I retained the variable that I deemed to be most biologically relevant to Russian olive. This screening process yielded 12 predictor variables (Table 2.2). Despite its borderline strong correlation with annual temperature range (Table A1), mean temperature of coldest quarter was retained as Russian olive is thought to have a chilling requirement for bud break and seed germination (Friedman et al. 2005; Guilbault et al. 2012), and temperature annual range was not strongly correlated with any of the other predictors in the final predictor set. I chose to use topsoil predictors rather than subsoil predictors as topsoil predictors would most directly affect seed germination and establishment, which in turn would affect Russian olive's potential distribution.

I used the most recent, highest resolution hydrology datasets for Canada using the National Hydro Network (NHN) and for the US using the USGS National Hydrography Dataset (NHD). These datasets are harmonized between Canada and the US, represent skeletonized lines of rivers and lakes, and contain both perennial and ephemeral water bodies. Rather than including information solely about the larger, permanent waterways (cf. Jarnevich and Reynolds 2011), I included all waterway information, as Russian olive has been observed within riparian zones of ephemeral waterways. Moreover, rather than calculating a distance to waterway variable (cf. Jarnevich and Reynolds 2011), I calculated a "length of water feature per grid cell" variable, which can be interpreted as the amount of shoreline habitat within each grid cell. This was because at the resolution of my rasters (~1 km<sup>2</sup>), water features occur in nearly every grid cell, and therefore would have yielded distance to water values of 0 for the majority of cells. For consistency, I similarly calculated a "length of major road per grid cell" variable.

I used ArcGIS 10.1 (Environmental Systems Research Institute (ESRI) 2012) to clip each raster dataset to the conterminous US, Alaska, and Canada using the rectangle bounded by 83.117 and 24.517 latitude and -179.158 and -52.499 longitude.

Predictor variable	Source	Comments
Temperature annual range	bio7 from Worldclim.org (Hijmans et al. 2005)	
Mean temperature of wettest quarter	bio8 from Worldclim.org (Hijmans et al. 2005)	
Mean temperature of coldest quarter	bio11 from Worldclim.org (Hijmans et al. 2005)	
Precipitation seasonality	bio15 from Worldclim.org (Hijmans et al. 2005)	Standard deviation of the weekly precipitation estimates expressed as a percentage of the mean of those estimates (i.e. the annual mean)
Precipitation of warmest quarter	bio18 from Worldclim.org (Hijmans et al. 2005)	
Elevation	Global Land One-Kilometer Base Elevation (GLOBE) (http://www.ngdc.noaa.gov/mgg/topo/globe.html)	
Length of regulated water feature per grid cell	Derived from the National Hydro Network (NHN) ( <u>http://www.geobase.ca/geobase/en/data/nhn/index.html;j</u> sessionid=1CA5ECB447B642ED42C624912455AEAB) and the USGS National Hydrography Dataset (NHD) ( <u>http://nbd.usgs.gov/</u> )	Regulated water is defined as rivers and lakes downstream of dams. Derived from the NHD and NHN flowlines, which represent skeletonized lines of rivers and lakes
Length of all water feature per grid cell	Derived from the National Hydro Network (NHN) and the USGS National Hydrography Dataset (NHD)	Derived from the NHD and NHN flowlines, which represent skeletonized lines of rivers and lakes.
Length of major road per grid cell	Derived from U.S. and Canada Detailed Streets ( <u>http://www.arcgis.com/home/item.html?id=f38b87cc295</u> 541fb88513d1ed7cec9fd)	Major roads are defined as North America/Continental, Inter- and Intra-State, Inter- and Intra- Provincial, Inter and Intra- Metropolitan roads.
Topsoil pH	Harmonized World Soil Database ( <u>http://webarchive.iiasa.ac.at/Research/LUC/External-</u> World-soil-database/HTML/)	pH (measured in a soil-water solution) of 0- 30 cm soil below ground. Missing data in the Northwest Territories and Nunavut.
Topsoil USDA soil texture class	Harmonized World Soil Database	Categorical USDA texture class of 0-30 cm soil below ground. Missing data in the Northwest Territories and Nunavut.
Topsoil Salinity	Harmonized World Soil Database	Salinity (measured as the electrical conductivity of a saturated soil paste or a soil-water solution) of 0-30 cm soil below ground. Missing data in the Northwest Territories and Nunavut.

 Table 2.2 Predictor variables used to derive the total and US dataset models.

#### COMPARISON OF ENVIRONMENTAL NICHE PROPERTIES

Using ArcGIS 10.1 (ESRI 2012), I extracted predictor grid values associated with the US and Canada dataset occurrence points. Using R (version 3.1.0; R Development Core Team 2014), I compared the values of each predictor among the US and Canada dataset occurrences using boxplots and principal components analysis (PCA) based on the Hill and Smith method (Hill and Smith 1976; function *dudi.hillsmith* in the ade4 (Dray and Dufour 2007) R package). Standard PCA could not be conducted due to the categorical nature of topsoil USDA soil texture class. I assessed clustering using permutational multivariate analysis of variance (PERMANOVA; Anderson 2001; McArdle and Anderson 2001) and multivariate dispersion using PERMDISP within the vegan R package (Oksanen et al. 2013).

## ECOLOGICAL NICHE MODELING

The ENMs were generated using Maxent (version 3.3.3k; Phillips et al. 2006), a machine learning technique that builds a probability distribution of maximum entropy by correlating occurrence points with environmental variables (Phillips et al. 2006). Both models were run using default parameters with the exception of running 10 cross-validation replicates and increasing the maximum number of iterations from 500 to 3,000. Additionally, since the occurrence sample sizes differed between the US dataset and total dataset models, I followed a procedure similar to Ensing et al. (2013) to create the total dataset ENM. After generating 100 subsamples (N=1,482) from the total dataset, I then ran Maxent on each of these subsamples, each time using the same settings as those used to generate the US dataset model. To produce a single model to be compared with the US dataset model, I averaged the 100 subsamples of the total dataset using the 'raster' package in R.

I assessed the contribution of predictors to both models using jackknife tests of variable importance. Jackknife determines predictor importance in two ways. First, it sequentially isolates a variable and builds a model on this variable alone. It then evaluates the contribution of the variable by determining the model's training gain, test gain and AUC. Second, it sequentially omits a variable and builds a model based on all other variables. As in modeling in isolation, the effect of omitting a variable is assessed via the model's training gain, test gain and AUC. Because AUC has recently come under fire for its use in presence-only models (see below), I chose to assess variable importance using the jackknife training

and test gains. When used in isolation during modeling, the variable with the highest gain represents the variable that contributes the most useful information by itself to the model. When omitted during modeling, the variable that decreases the gain the most contains the most information not found in other variables.

I assessed how the US and total dataset model predictions depended on environmental variables by creating response curves for the five variables with the highest gain when modeled in isolation.

#### MODEL EVALUATION

I evaluated model performance using a threshold-dependent, omission rate of test occurrence records and a threshold-independent measure, area under the receiver operating characteristic curve (AUC). Omission rate of test occurrence is the proportion of test occurrences known to be present but predicted as absent and is calculated after a threshold has been applied (Phillips et al. 2006). In general, low omission rates imply high model quality and performance (Anderson and Gonzalez 2011; Boria et al. 2014). I applied the 10 percentile training presence threshold (see below) to both models. I used the average 10 percentile training presence omission rate of the 10 cross-validated total dataset replicates to evaluate the US dataset model, and the average 10 percentile training presence omission rate of the 10 cross-validated total dataset replicates for each subsample to evaluate the total dataset model.

The threshold-independent AUC is a rank-based approach that determines the probability of a random presence location being ranked higher than a random pseudo-absence location (Phillips et al. 2006; Baldwin 2009; Merow et al. 2013). Despite recent criticisms of its utility in model evaluation (e.g. Lobo et al. 2008; Merow et al. 2013), AUC is still the most popular Maxent model evaluator and equivalent alternatives are lacking for presence-only models (Merow et al. 2013). AUC values typically range from 0.5 to less than 1 for presence-pseudo-absence models, with a value of 0.5 representing a model that performs no better than random (i.e. it cannot discriminate between presences and pseudo-absences) (Phillips et al. 2006; Baldwin 2009). The higher the AUC value, the better the model is at discriminating between suitable and unsuitable habitat (Phillips et al. 2006). Like the omission rate, the average AUC value of the 10 cross-validated total dataset replicates was used to evaluate the US dataset model, while the average AUC value of the 100 subsample

models based on 10 cross-validated total dataset replicates for each subsample was used to evaluate the total dataset model.

#### COMPARISON OF NICHE SIMILARITY

I used the Niche Identity test within ENMTools (version 1.4.3; Warren et al. 2008; Warren et al. 2010) to measure the niche similarity/overlap between Maxent model predictions created using US occurrences and total occurrences. The Identity test works by first pooling occurrences from both sets of data, and then randomly draws occurrences from the pooled data to create two new datasets, such that the sample size of the original datasets are conserved in the new datasets (Warren et al. 2010). This pair of new datasets forms what is known as a pseudoreplicate. ENMTools calls Maxent to generate a predictive model for each dataset in the pseudoreplicate and then uses the model and predictability scores to calculate the niche overlap between the new datasets using two similarity indices that range from 0 (no niche overlap) to 1 (the niches are identical), Schoener's D and I (1-Hellinger distance) (Warren et al. 2010). The user can specify the number of times this process is repeated, resulting in a user-specified number of pseudoreplicates and thus a user-specified number of I and D values. A distribution of these values is created, forming a type of null distribution. The true overlap (I and D) between the models based on the original datasets is then compared to this null distribution. If the true overlap falls significantly lower on the null distribution, the two niches can be considered significantly different (Warren et al. 2010). I created 100 pseudoreplicates and then used ENMTools to generate the I and D null distributions. Following other studies that used ENMTools (e.g. Schulte et al. 2012; Ensing et al. 2013; Zhu et al. 2014), I chose to generate 100 pseudoreplicates, which yields a high degree of confidence when rejecting the null hypothesis (Warren et al. 2008). I then calculated the true overlap (I and D) between the models generated using the US and total datasets and compared the overlap values to their respective null distribution. Significance was determined by dividing the number of null replicates equal to or below their respective true I and D values by 100, yielding a p-value. If this p-value was less than or equal to 0.05, I considered the niches to be significantly different.

#### COMPARISON OF PREDICTED GEOGRAPHIC RANGE OVERLAP

I investigated the spatial differences in the predicted distribution of both ENMs by applying a threshold to deduce areas of suitable and unsuitable habitat. A variety of threshold options are available in Maxent and the choice of threshold can greatly affect the outcome of the map, but should ultimately depend on the map's intended use (Jiménez-Valverde and Lobo 2007; Freeman and Moisen 2008). I used the 10 percentile training presence threshold, the threshold previously used by Jarnevich and Reynolds (2011) for their Russian olive ENM. This threshold determines the probability value above which 90% of the training locations correctly classify presence based on Maxent's model testing procedure (Jarnevich and Reynolds 2011). Use of this type of threshold is recommended for management applications as it provides a conservative estimate of habitat suitability without overestimating prediction due to true absences misclassified as predicted presences (Freeman and Moisen 2008).

I created binary maps depicting suitable and unsuitable habitat based on the dataset's respective threshold value, where the average 10 percentile training presence threshold of the 100 subsample runs was used to produce the total dataset binary map. Using ArcGIS 10.1 (ESRI 2012), I compared the two maps and identified areas where the two models agreed the species would occur (agree present), where the two models agreed the species would not occur (agree absent) where the total dataset model predicted the species would occur but the US dataset did not (total) and conversely, where the US dataset model predicted the species would occur but the species would occur but the total dataset did not (US).

## **2.3 Results**

#### COMPARISON OF ENVIRONMENTAL NICHE PROPERTIES

With the exception of topsoil salinity, all environmental variable values associated with Canadian occurrences fell within the range of those associated with US occurrences (Figure 2.3). The ranges of temperature annual range, precipitation seasonality and elevation values associated with Canadian occurrences were, however, lower within the ranges of those associated with US occurrences (Figure 2.3). The topsoil values associated with Canadian occurrences were higher than those with US occurrences (Figure 2.3).

Hill and Smith based PCA analysis of the environmental variables associated with Russian olive occurrences shows that the majority of Canadian occurrences clustered together within the US occurrences in environmental space (Figure 2.4). PERMANOVA and PERMDISP revealed the Canadian realized niche to be significantly different from the US realized niche, in terms of both its variance and multivariate centroid.



**Figure 2.3** Boxplots of environmental predictor variables associated with Russian olive occurrences from Canada and the US. Note that because topsoil USDA soil texture class is categorical, only points have been plotted.



**Figure 2.4** Hill and Smith based principal components analysis of environmental variable predictors associated with Russian olive occurrences. Red spheres represent Canadian occurrences and blue spheres represent US occurrences. Inertia explained by the first three axes are 18.37%, 11.80%, and 9.30%, respectively.

#### ECOLOGICAL NICHE MODELING

I found that the predicted extent of Russian olive was comparable among the US dataset and total dataset models, although the total dataset model predicted slightly higher habitat suitability values for BC, Alberta, Saskatchewan, Washington, Oregon, and Utah (Figure 2.5). Alternatively, the US dataset model predicted slightly higher habitat suitability values for southern Idaho and Nevada (Figure 2.5).

Based on the results of the jackknife tests of variable importance, the training gain and test gain of each model were similar with only slight deviations in lesser important variables (Figure 2.6, Figure 2.7). Mean temperature of coldest quarter increased the training gain and test gain the most when modeled in isolation among both models, indicating it contains the most useful, unique information (Figure 2.6, Figure 2.7). Topsoil pH was the second to most important variable common between both models, but the variables that followed it differed between models. Topsoil salinity ranked higher than elevation and length of regulated water per gird cell in the total dataset model, but this trend was reversed in the US dataset model (Figure 2.6, Figure 2.7). The relative ranking importance of the remainder of variables (all relatively unimportant compared to mean temperature of coldest quarter) varied slightly between the training gain and test gain of the models. Furthermore, for both datasets, mean temperature of coldest quarter decreased the training gain and test gain the most when it was omitted from modeling for both datasets, indicating it has the most information that isn't present in other predictor variables (Figure 2.6, Figure 2.7).

Marginal (variable in question is varied while all other environmental variables are kept at their average value; Figure A1) and single variable (variable in question is the only variable modeled; Figure A2) response curves of the five most important predictors differed between the US and total dataset models. In general, the marginal response curve for mean temperature of the coldest quarter for both models showed a gradual increase in probability of presence between  $-15^{\circ}$ C and  $-1^{\circ}$ C and then a abruptly dropped down to 0.27 probability of presence after 4.3°C. The highest probability of presence (0.66) occurred at -0.9°C for the total dataset, while the US dataset model's highest probability of presence (0.65) occurred slightly lower than that of the total dataset model, forming a plateau between -2.4°C and 4.3°C. Mean temperature of the coldest quarter was the only predictor variable that didn't show large differences between marginal and single variable response curves (Figure A1, Figure A2). Marginal and single variable response curves for topsoil pH and salinity differed, likely due to the fact that topsoil characteristics co-vary with climatic conditions. Therefore, the following observations for topsoil pH and salinity will be made using the single variable response curves, which facilitate interpretation in the presence of co-variation. In general, as topsoil pH increases, as did the probability of presence for both models (Figure A2). The highest probability of presence for both models (0.79) occurred at a pH of 8. Response curves for topsoil salinity between US and total dataset models were similar up to 1 dS/m, after which the total dataset model's curve was higher than that of the US dataset, but eventually falling below it at 2.3 dS/m (Figure A2). The highest probability of presence occurred at 2 dS/m (0.79 probability of presence) for the total dataset model and between 0.25 and 0.35 dS/m (0.79 probability of presence) for the US dataset model. Single variable response curves for elevation between US and total dataset models were similar, with the exception of the total dataset model showing higher probability of presence between 308 and 876 m in elevation (Figure A2). The highest probability of presence for both models (0.7) occurred between 1920 and 2085 meters in elevation. Both models responded similarly to

length of regulated water feature per grid cell, and in general, probability of presence remained the same across all values of length (Figure A1, Figure A2).



**Figure 2.5** Predictive maps of the potential distribution of Russian olive in Canada and the US generated using Maxent for the (a) US dataset and (b) total dataset. The higher the habitat suitability value of a given 1 km<sup>2</sup> cell, the higher the probability Russian olive would potentially occur there. White areas represents where predictor data is missing (e.g. Topsoil pH, salinity and texture class). Projection: North America Albers Equal Area Conic.



**Figure 2.6** Gain associated with training data of each predictor variable when modeled using only the variable (black bars) and when modeled without the variable but using all the others (grey bars) for the US and total dataset models. White bars represent the training gain associated with using all variables. Values represent the averages of 10 cross validated replicates for the US dataset and the averages of 100 subsample models based on 10 cross-validated total dataset replicates for each subsample of the total dataset.



**Figure 2.7** Gain associated with test data of each predictor variable when modeled using only the variable (black bars) and when modeled without the variable but using all the others (grey bars) for the US and total dataset models. White bars represent the test gain associated with using all variables. Values represent the averages of 10 cross validated replicates for the US dataset and the averages of 100 subsample models based on 10 cross-validated total dataset replicates for each subsample of the total dataset.

## MODEL EVALUATION

AUC values for both the US and total dataset models were very high (AUC>0.9) and both models produced low omission rates, indicating both models performed well and generated good to excellent predictions (Table 2.3).

**Table 2.3** The average results for the Maxent ENMs showing the test AUC, the AUC standard deviation, the 10 percentile training presence test omission rate, the 10 percentile training presence threshold, and the amount of area predicted suitable and unsuitable for both models.

Dataset	AUC	AUC standard deviation	10 percentile training presence test omission rate	10 percentile training presence threshold	Predicted suitable area (km <sup>2</sup> )	Predicted unsuitable area (km <sup>2</sup> )
US	0.9237	0.0056	0.1127	0.3458	1,171,346	22,353,462
Total	0.9241	0.0057	0.1132	0.3405	1,063,924	22,460,884

Note: AUC, AUC standard deviation, 10 percentile training presence test omission rate, and 10 percentile training presence threshold are the averages of 10 cross validated replicates for the US dataset and the averages of 100 subsample models based on 10 cross-validated total dataset replicates for each subsample of the total dataset.

## COMPARISON OF NICHE SIMILARITY

The true overlap value of predictions based random sampling of the US and total occurrences was not significantly different from the random samples (N=100) for *I* (true I=0.9956, P=0.68; Figure 2.8a) and *D* (true D=0.9417, P=0.47; Figure 2.8b). Models are considered significantly different from one another if the *I* and *D* values are significantly lower than their respective null distributions. In this case, the true *I* and *D* values were no different from their null distributions, thus, the predicted niches of the US and total dataset models were not significantly different.



**Figure 2.8** Results of the ENMTools Niche Identity test. Histograms represent the *I* (a) and *D* (b) (overlap) values of 100 pseudreplicates and the arrows indicate the true overlap (I= 0.9956, D= 0.9417) between the US and total dataset models. Note the different x-axes between plots (a) and (b).

## COMPARISON OF PREDICTED GEOGRAPHIC RANGE OVERLAP

The average 10 percentile training presence thresholds were similar among both models (Table 2.3). After applying these thresholds to produce binary maps of suitable and unsuitable habitat, I found that the US dataset (only US occurrences) model predicted 107,422 km<sup>2</sup> more suitable habitat (a 9.61% difference) than the total dataset (Canada and US occurrences) model (Table 2.3). Furthermore, comparison of these binary maps between both models shows that the habitat described suitable by the US dataset model but not by the total dataset model occurred primarily in the US, while habitat described as suitable by the total dataset but not by the US dataset occurred in Canada, particularly in BC, as well as throughout the US (Figure 2.9).



**Figure 2.9** Comparison of US and total dataset niche model predictions of Russian olive based on binary maps generated using the 10 percentile training presence threshold (a value of 0.3458 for the US dataset and 0.3405 for the total dataset). Above this threshold, areas are considered to be suitable and below it, areas are considered to be unsuitable. Green indicates where both models predict Russian olive to be absent, red indicates where both models predict Russian olive to be present, blue represents areas where the US dataset model

predicts Russian olive to be present but the total dataset model does not, and yellow represents areas where the total dataset model predicts Russian olive to be present but the US dataset model does not. White areas represents where predictor data is missing. Projection: North America Albers Equal Area Conic.

## **2.4 Discussion**

I have presented here predictions of Russian olive's potential invasion range in North America, based on the Maxent niche model algorithm using ecologically relevant abiotic predictors and the best available occurrence record data. Their extremely high AUC values suggest my models are robust. Furthermore, they predicted suitable habitat in disjunct regions that originally lacked associated occurrence records, but that have since been noted to host naturalized populations. I am therefore confident that my ENM predictions will help inform future management decisions. Below, I first discuss the variables that proved influential in the models, paying particular attention to their ecological relevance. I then consider how the inclusion of soil predictors may help explain the differences between my model predictions and those of previous studies. Lastly, I examine the predictions in more detail, highlighting geographic areas of concern within both Canada and the US.

## PREDICTOR IMPORTANCE

The predominant importance of mean temperature of coldest quarter is consistent with the hypothesis that Russian olive requires a chilling period for bud break and germination (Friedman et al. 2005; Guilbault et al. 2012). The highest probability of Russian olive presence occurred when the mean temperature of coldest quarter was -0.9°C for the total dataset and between -2.4°C to 4.3°C for the US dataset model (Figure A1). The sharp drop in probability of presence after 4.3°C is consistent with the hypothesis that Russian olive is constrained at its southern range edge by its chilling requirement (Friedman et al. 2005; Guilbault et al. 2012). In contrast, the gradual increase in probability of presence from -15°C to -1°C suggests that Russian olive's northern distribution may not be so limited. Russian olive is known to tolerate cold climates in both its native (Lamers et al. 2006; Singh et al. 2008) and invaded range (Klich 2000; Friedman et al. 2005; Fischer et al. 2012). However, a limit may exist. Gusta et al. (1983) conducted a controlled freezing experiment on branches obtained from 3 year old Russian olive plants in Saskatoon, SK and found that

branches were killed at a temperature of -55°C. The lowest minimum temperature of the coldest month for Canadian occurrences was -19°C (the occurrence in the southwestern corner of Saskatchewan), suggesting that given the correct combination of biotic and abiotic conditions, Russian olive's distribution is likely to expand northwards.

The inclusion of topsoil predictor variables seems to have influenced the predictions of both models. Topsoil pH ranked second most important to both models, and in general, as pH increased, probability of presence increased. The highest probability of presence for both models occurred at a pH of 8. This result is consistent with Russian olive, which has been found in soils with pH ranging from 5.7 (Zitzer and Dawson 1989) to 8 (Herman et al. 2010). The low probability of presence associated with lower pH values (Figure A2) may be the result of an inability to form root nodules. A study by Zitzer and Dawson (1989) found that nodulation of Russian olive plants found in soils with a pH of 5.41  $\pm$  0.24 was extremely sparse.

Topsoil salinity ranked 5<sup>th</sup> and 3<sup>rd</sup> most important in the US dataset and total dataset models, respectively. For both models, topsoil salinity values ranged from 0 to ~2.5 dS/m. When converted to ppm, this range (0 to ~1600 ppm) is somewhat consistent with Carman and Brotherson (1982), who found that Russian olive preferred sites with salt concentrations of 100–3 500 ppm. Interestingly, the salinity range observed in this study is much lower than that which cultivated Russian olive plants have been found to withstand (8-16 dS/m) (Whiting et al. 2011). This suggests that although Russian olive can tolerate very saline soils, its preference may coincide with low to slightly saline soils (Zhao and Harris 1992). In any case, its ability to tolerate saline and alkaline soils may enable Russian olive to escape direct competition with riparian species less tolerant of such conditions, and thereby achieve dominance where such conditions prevail.

Surprisingly, length of all water feature and major road per grid cell ranked relatively low according to jackknife tests of variable importance for both models. It is possible that this is due to the coarse ~1 km<sup>2</sup> resolution used in my models. Had I used finer resolution rasters, distance to these predictors would have been more appropriate and may have yielded different results.

#### COMPARISON WITH PREVIOUS ENMS

Given that none of the previously published ENMs for Russian olive incorporated soil data, variables considered relatively important for the models generated here, or used Canadian occurrences for modeling, differences between predictions found here and previous predictions are likely. In this section, I will highlight the main differences between previous Russian olive ENMs and the ENMs generated here.

The ENM produced by Peterson et al. (2003) predicted Russian olive's distribution to cover a large extent of North America. This is in stark contrast to what I found here, where both the US and total dataset models predicted Russian olive's distribution to occur primarily in western US and Canada.

Jarnevich and Reynolds (2011) produced two ENMs for Russian olive, one using a coarse-resolution water dataset and another using a fine-resolution water dataset. Unless specifically mentioned otherwise, the following comparison with the total dataset model generated here will be made with the coarse-resolution dataset, as it is more directly comparable to mine, and was shown to perform slightly better than the fine-resolution water model (Jarnevich and Reynolds 2011). The total dataset thresholded habitat suitability map generated here differs in notable ways from that produced by Jarnevich and Reynolds (2011), though there are some areas of agreement. The most notable differences occur in California, eastern Nebraska and Kansas, Texas, Oklahoma, northern Oregon, southern Arizona and New Mexico, north-eastern North Dakota, South Dakota, and central Montana, where Jarnevich and Reynolds (2011) predicted to be suitable but the total dataset model generated here did not. Areas where the models agree to some extent occur in southern Washington, southern Idaho along Interstate 84, south-eastern Montana, Colorado, southern Arizona, and north-western New Mexico. The models tended to agree on predictions in Utah. The total dataset model predicted considerably more suitable habitat in Washington, Oregon, Wyoming, central New Mexico, and Nevada, than did the Jarnevich and Reynolds (2011) model. Notably, the large portion of area in Washington which was predicted as suitable by the total dataset model but not by the US dataset model (Figure A3) was also not predicted suitable by models produced by Jarnevich and Reynolds (2011). Naturalization is known in this area (J. Pither, personal communication, 2014), so the fact that neither the US dataset nor the Jarnevich and Reynolds (2011) models consider this area suitable strengthens confidence

in my ENM predictions. Since Jarnevich and Reynolds (2011) did not predict Russian olive's potential distribution across the eastern states, comparisons of results for those states cannot be made. In general, it appears the Jarnevich and Reynolds' (2011) coarse-resolution water model generated using only US occurrences predicted far more habitat as suitable than the total dataset model generated here. This result is consistent with my results of the US dataset model predicting more suitable habitat than the total dataset model.

For the western states, the predictive presence probability of the models generated here is similar to that generated by Liu et al. (2014) (Figure 3 in Liu et al. 2014), with potential distribution occurring mainly within western US. The high probability of presence observed in Utah and the low probability of presence observed in California in the models generated here is consistent with what Liu et al. (2014) found. Nevertheless, there are also areas not deemed highly probable by Liu et al. (2014) but were by my models, such as in Washington, southern Idaho and New Mexico. In the eastern states, notable differences exist. Liu et al. (2014) predicted a higher probability of presence across the north-eastern states, whereas for my models, probability of presence was virtually zero across this area. Within the New England region, the models appear to agree on similar probability of presence.

As there have been no ENMs produced for Russian olive in Canada, comparisons can't be made with other studies for this area. However, the total dataset model did predict areas as suitable in Canada where there are no occurrences but where naturalization is known, such as Medicine Hat and along the Milk River in Alberta (see below), suggesting the predicted potential distribution within Canada is robust.

## COMPARISON OF US AND TOTAL DATASET MODELS

Although there was no significant difference in niche overlap between the US and total dataset models, PCA on environmental data showed Canadian occurrences form a distinct subset within US occurrences, suggesting a unique environmental contribution from the Canadian data. Additionally, the inclusion of Canadian occurrences appears to have narrowed Russian olive's potential distribution in Canada and the US while simultaneously predicting areas in the US to be suitable that the US occurrences model did not. As such, it appears the exclusion of Canadian occurrences, prominent among known ENMs for Russian olive, has led to over-predictions of Russian olive's potential distribution. Two notable patterns emerge from comparing US and total dataset model thresholded maps. First, the total dataset model appears to predict more upland areas as suitable habitat than the US dataset model as one moves northward through western US and Canada, whereas the US dataset predicted more upland area as suitable than the total dataset as one moves southwards. Russian olive has been found to inhabit upland areas in Oklahoma, Oregon (Olson and Knopf 1986), and North Dakota (Madurapperuma et al. 2013). Second, the largest portion of continuous area predicted suitable by the total dataset model but not by the US dataset model occurs in central Washington (Figure A2). There were no occurrences from this area used in model building, yet naturalization in this area is known (J. Pither, personal communication, 2014). A possible explanation for these patterns can be gleaned from boxplots of variables associated with Canadian and US occurrences (Figure 2.4). Canadian occurrences were associated with higher topsoil salinity values and lower precipitation seasonality values than US occurrences, suggesting a change in soil and precipitation conditions with Canadian occurrences has resulted in small, but noticeable, differences between the US and total dataset models.

### AREAS OF CONCERN IN CANADA

There are several areas throughout Canada where there are currently no occurrences for Russian olive, but where the total dataset ENM binary map of suitable and unsuitable habitat generated here predicts to be suitable. BC appears to harbor the most suitable habitat in all of Canada (Figure 2.10). Incidentally, areas in BC predicted suitable but where there is currently no Russian olive occur primarily along major rivers (Figure 2.10). For example, suitable habitat is predicted along the Fraser River from the town of Lytton to as far north as Williams Lake, as well as along the Chilcotin River. The Fraser River hosts an economically important salmon fishery and any future Russian olive establishment along it could alter aquatic ecosystem functioning, as Russian olive has done along rivers in the US (Mineau et al. 2011; Mineau et al. 2012; Kominoski et al. 2013).

Suitable habitat is also predicted in areas where the invasive, exotic common carp (*Cyprinus carpio* L.) is found (Figure A4). Russian olive has been found to provide a subsidy to the common carp (C. Baxter, U. Idaho, personal communication, 2014) and carp are responsible for many deleterious ecosystem and community level effects (e.g. Parkos et al. 2003; Bajer et al. 2009; Weber and Brown 2011). Additionally, common carp has been found

to decrease the growth (Wolfe et al. 2009; Wahl et al. 2011) and abundance (Weber and Brown 2011) of native fish species. Therefore, the occurrence of common carp along waterways predicted to provide suitable habitat for Russian olive is concerning. Although the common carp has not yet made its way into the Fraser River, it is likely it will eventually. Thus, in addition to potentially negatively altering aquatic ecosystems, Russian olive has the potential to subsidize common carp in economically important salmon bearing rivers.

Areas adjacent to the Kettle River are also predicted to provide suitable habitat, yet there are no occurrences for these areas (Figure 2.10). Being a tributary of the Columbia River, establishment of Russian olive in this area could potentially act as source populations for areas downstream, areas which are also shown to provide suitable habitat. Overall in southern BC, it appears Russian olive has not yet filled all available suitable niches (Figure 2.10). Surveys for Russian olive across suitable areas lacking occurrences are needed to assess if Russian olive has already established in these areas.



**Figure 2.10** Suitable habitat depicted by the thresholded total dataset model in southern BC and northern Washington. Note the large amount of area predicted to be suitable but where occurrence records currently do not exist. Projection: NAD 1983 UTM Zone 10.

Southeastern Alberta and southwestern Saskatchewan are also predicted to provide suitable habitat, although not nearly as extensively as BC. The model predicted suitable habitat in the same area along the Milk River in Alberta where Russian olive naturalization has been noted but for which I did not have occurrence records (Pearce and Smith 2001; Pearce and Smith 2009). Additionally, habitat was predicted as suitable in and around Medicine Hat, AB, where naturalization is known and for which I was recently given occurrence data (D. Young, City of Medicine Hat, personal communication, 2013; A. McClay, McClay Ecoscience, personal communication, 2014).

It should be noted that, for the most part, areas across the Canadian prairies where Russian olive has been intentionally planted through the Prairie Shelterbelt Program have not been deemed suitable by the thresholded total dataset model. This suggests that shelterbelt plantings are unlikely to serve as sources for spread in most prairie regions. However, some areas exhibit approximately a 0.3 probability of providing suitable habitat for Russian olive, therefore establishment of naturalized populations is not inconceivable (Figure A5). To determine if these plantings are of concern, surveys of existing plantings and naturalization assessments must first be conducted. Once completed, any potential impacts these plantings may have on prairie habitats can be further explored.

## AREAS OF CONCERN IN THE US

The states of North Dakota, Wyoming, central New Mexico, and West Virginia show substantial amount of suitable habitat predicted by the thresholded total dataset model map, yet very little to no occurrences for these states were used in the model. It is possible that given the extensive shelterbelt plantings in the western states (Olson and Knopf 1986; Katz and Shafroth 2003), established Russian olive populations may already exist in these areas but their locations have not yet been made available. For example, Russian olive has been observed along the Rio Grande from Albuquerque, NM to El Paso, TX (Campbell and Dick-Peddie 1964; Olson and Knopf 1986), as well as throughout North Dakota (Olson and Knopf 1986), yet I did not have occurrences for these areas. Regardless, I recommend that these states should be carefully monitored for Russian olive establishment and/or spread.

Interestingly, suitable habitat was predicted in West Virginia, yet no occurrences from this state were used for modeling. Moreover, for the eastern states in general, Russian olive naturalization is less well noted. I was not able to find any mention of Russian olive establishment in West Virginia through literature searches, however, I still recommend this state be monitored for Russian olive naturalization and spread.

## CONCLUSION

I have provided what appear to be reliable and robust predictions about Russian olive's potential distribution in North America using novel predictor variables and occurrences. The models were able to predict suitable habitat in areas where documented occurrences were unavailable but for which naturalization is known. Additionally, the models predicted suitable habitat next to economically important salmon fisheries in southern BC. These areas currently lack Russian olive, highlighting the need for monitoring. Despite the fact that political boundaries hold little relevance to the distributions of organisms, they are nonetheless commonly used to constrain ENM predictions (e.g. Mingyang et al. 2008; Jarnevich and Reynolds 2011; Liu et al. 2014). My results show that excluding occurrences from a species' entire invaded range, based for example on political boundaries, can lead to over-predictions. Over-predictions can mislead management practices and efforts, and take away resources from areas that are actually predicted to provide suitable habitat. As such I strongly encourage that niche models be built upon all reliable occurrences from the species' entire invaded range.

# Chapter 3: Insect assemblages associated with the exotic riparian shrub Russian olive, and co-occurring native shrubs

## 3.1 Background

Invasive plant species can alter the dynamics (Ehrenfeld 2003; Chau et al. 2013), structure (Hawkes et al. 2006; Hladyz et al. 2011), and function (Ehrenfeld 2010; Weidenhamer and Callaway 2010; Spirito et al. 2014) of native ecosystems. Through cascading effects, invasive plants can affect other trophic levels (e.g. Levine et al. 2003), though comparatively little is known about these interactions (Simao et al. 2010). Differential reponses of arthropods to invasive plants have the potential to drastically alter ecosystems, as arthropods are key connectors between primary producers and higher trophic levels, and also provide important ecosystem services such as pollination (Potts et al. 2010) and decomposition (Lattin 1993).

When introduced into a native ecosystem, exotic invasive plant species have the potential to elicit a variety of responses from arthropods. Arthropod abundance and diversity has been shown to respond positively (Harris et al. 2004; Pearson 2009; Emery and Doran 2013), negatively (Simao et al. 2010; Holmquist et al. 2011; Ballard et al. 2013), and neutrally (Frenzel and Brandl 2003; Agrawal et al. 2005; Procheş et al. 2008) to the presence of an exotic invasive plant species. The direction and magnitude of the response could depend on a variety of factors, including phylogenetic relatedness and phenology. For example, the degree to which the exotic species shares traits in common with native plants in the region (e.g. defense compounds, volatiles, allelochemicals), which itself could depend on phylogenetic relatedness (Ricciardi and Ward 2006; Wiens et al. 2010), may influence the degree to which arthropods associate with the new invader (Agosta 2006; Bezemer et al. 2014). In general, invaders and their closely related native species are expected to share similar arthropod assemblages, as arthropods adapted to native plants may also find the invader attractive due to similar traits (Hill and Kotanen 2009; Ness et al. 2011).

Phenology, in particular the timing and frequency of flowering of native and exotic plants, may also alter insect responses (Bezemer et al. 2014). Several studies have found that insect pollinator communities do not differ between co-flowering native and exotic species (Bartomeus et al. 2008; Woods et al. 2012), however, exotic plants, on average, have more

pollinator visitations than co-occurring native plants (Morales and Traveset 2009; Montero-Castaño and Vilà 2012). Pyšek et al. (2011), however, found that the diversity of pollinator species associated with exotic plants increased with their time in the invaded area.

Regardless of the underlying causal mechanisms, any significant changes to arthropod assemblage structure, associated with the introduction of exotic plant species, can propagate through the food-web and ecosystem (e.g. Pearson 2009). Thus, investigating such changes within the invaded ranges of exotic species is crucial to devising biodiversity conservation plans (Spafford et al. 2013). A key first step is to determine how arthropods respond to the exotic plants. For example, do they consider the plants as suitable habitat, and/or as suitable food (Bezemer et al. 2014)? Or do they avoid the plants altogether? In the absence of exhaustive experimental trials, inferences about insects' response to exotic species could come from surveys of insects associated with exotic species. Three simplified, yet plausible, scenarios illustrate how arthropods might respond to the presence of an exotic species within their habitat. At one extreme, arthropods may perceive the exotic as unsuitable and may even avoid it, resulting in a depauperate arthropod assemblage on the exotic. From an ecosystem-scale perspective, the exotic plant is part of the invaded ecosystem and is competing with native vegetation that arthropods presumably consider more suitable. Avoidance of the exotic by the arthropod fauna would result in a decrease in diversity of the invaded ecosystem's arthropod community (e.g. Ernst and Cappuccino 2005; Simao et al. 2010; Holmquist et al. 2011). The other extreme involves an arthropod assemblage associating with the exotic that is unique compared to the arthropod assemblages of cooccurring native plant species. This scenario would result in an increase in diversity of the invaded ecosystem's arthropod community (e.g. Harris et al. 2004, Emery and Doran 2013), unless the added arthropods are detrimental to co-occurring native vegetation. As an intermediate scenario, arthropods may perceive the exotic plant no differently than cooccurring native plant species. Thus, arthropod diversity would remain unchanged in the invaded ecosystem (e.g. Dávalos and Blossey 2004; Hansen et al. 2009). Similar ideas were recently presented by van Hengstum et al. (2014), who conducted a meta-analysis on 56 peer-reviewed studies that compared arthropod abundance and richness in invaded and uninvaded habitat, and found that the presence of an invader significantly reduced arthropod abundance and richness.

Russian olive is an exotic shrub/tree that has become invasive in many riparian ecosystems throughout the great basin and western North America. Despite its prevalence and the potentially dramatic impacts it can have on riparian and aquatic ecosystems (Katz and Shafroth 2003; Mineau et al. 2011; Mineau et al. 2012), little is known about how Russian olive is perceived by arthropods, relative to native riparian vegetation. To my knowledge, only two previous studies have surveyed arthropods associated with Russian olive. Kennedy and Wilson (1969) examined the prevalence and diversity of insect pests on shelterbelt plants in North Dakota. Using observational surveys, they collected over 30 species of insects and mites from 23 species of shrubs and trees, yet, no insects were found on Russian olive (Kennedy and Wilson 1969). However, these results should be interpreted cautiously because the researchers were focused on quantifying the prevalence of insect pests, rather than insects more generally. Nevertheless, the absence of insect pests on Russian olive is consistent with the enemy release hypothesis (Keane and Crawley 2002), which would suggest that Russian olive's success as an invader in North America is due in part to a lack of arthropod enemies. Pendleton et al. (2011) sampled insects on Russian olive, saltcedar and willow (Salix exigua) plants, and found that willow had the greatest number of insect orders and families. However, sampling on Russian olive was severely limited (15 collection units, defined as 10 passes of the sweep-net over the plant, versus 80 collection units on willow and 79 on saltceder), precluding meaningful conclusions. Additionally, insects were collected using a sweep net on a portion of the plant, which can be ineffective when sampling trees and shrubby plants (Churchill and Arthur 1999).

In this study I had two objectives; (i) to survey and identify insects associated with Russian olive within invaded riparian areas of south-central British Columbia (BC), and (ii) to compare the diversity of insect assemblages associated with Russian olive to that of assemblages associated with native, co-occurring species of similar growth form: Woods' rose (*Rosa woodsii* Lindl., Rosaceae) and Saskatoon (*Amelanchier alnifolia* Nutt., Rosaceae).

It is commonplace for comparisons of insect fauna to be made between exotic species and native con-familials (e.g. Agrawal et al. 2005; Bezemer et al. 2014). Unfortunately this approach was not possible here because, although it shares similar habitat preferences as its native confamilials (see Chapter 1; Table 1.1), Russian olive is rarely found co-occurring with them in southern BC. Moreover, focusing on the rare sites where Russian olive cooccurs with its native confamilials would not be representative of the majority of its invaded range in southern BC.

Woods' rose and Saskatoon are shrubs that are widespread and locally abundant throughout the Bunchgrass Biogeoclimatic Ecosystem Classification (BEC) zones of southern BC, and therefore commonly co-occur with Russian olive where it has established. Native to the central and western US and Canada, Woods' rose is a long-lived shrub that can grow from 0.5-3 meters tall, and thrives in a variety of habitat types (Pavek and Skinner 2013). Like Russian olive (Katz and Shafroth 2003; Douglas et al. 1999), it is capable of surviving as an understory plant in moist and dry habitats and is commonly found in riparian areas, along lakeshores and roadways (Pavek and Skinner 2013). Species within the genus *Rosa* freely hybridize (Lewis and Basye 1961; Atienza et al. 2005; Joly and Bruneau 2006) and Woods' rose may form hybrids with other native roses across its range (Hitchcock et al. 1969).

Saskatoon is a shrub that can reach a height of 7 meters and is native across the US and Canada (Nesom 2006). Saskatoon is able to survive as an understory plant and is fairly drought tolerant, but prefers moist soils. It is most commonly found in thickets, woodland margins, low to montane hillsides and riparian areas (Lim 2012).

As discussed above, there is little consensus in the literature on how arthropod assemblages respond to the presence of an exotic plant species. Here I consider two factors that might influence an insect's reponse to Russian olive compared to its native, co-occurring shrubs, phylogeny and phenology.

Woods' rose and Saskatoon are phylogenetically more closely related to each other than either of them is to Russian olive (Figure 3.1). In general, closely related plant species are expected to share similar traits (Webb et al. 2002; Wiens et al. 2010) and thus, similar insect assemblages (Hill and Kotanen 2009; Ness et al. 2011). If these phylogenetically conserved traits are what influence insect reponses and if plant traits are the driving force governing insect assemblage diversity, then I predict insect assemblages to be least similar between Russian olive and Woods' rose or Saskatoon, and most similar between Woods' rose and Saskatoon. Woods' rose's flowering and fruiting time is more similar to Russian olive's than it is to Saskatoon's (Figure 3.2). One might expect that plants with similar phenologies will share similar arthropod communities, such as pollinators (Montero-Castaño and Vilà 2012). Thus, assuming that plant species with similar phenologies are more likely to share more similar insect assemblages, and if phenology is the driving force governing insect assemblage diversity, I predict that Russian olive will share a more similar insect assemblage with Woods' rose than with Saskatoon.



**Figure 3.1** Phylogenetic comparison between Russian olive and several species it co-occurs with in southern BC. Comparisons are based on the large subunit of the ribulose-bisphosphate carboxylase gene (*rbcL*) nucleotide sequences of Russian olive, Woods' rose, Saskatoon, shining willow (*Salix lucida* Muhl., Salicaceae), narrowleaf willow (*Salix exigua* Nutt.), black cottonwood (*Populus trichocarpa* Torr. & A. Gray, Salicaceae), and ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson, Pinaceae).



**Figure 3.2** Flowering and fruiting periods of Russian olive, Woods' rose, and Saskatoon with sampling time overlaid.

## **3.2 Methods and Materials**

## STUDY REGION AND DESIGN

Six sites between Osoyoos, BC and Kamloops, BC were chosen for sampling (Figure 3.3). Five sites were located within the Bunchgrass BEC zone, while the Vernon site

belonged to the Interior Douglas-fir BEC zone. All sites were within the 'Very Dry Hot' BEC variant (Table 3.1).

Sites were separated by at least 1 km, and all host plants at each site were located no farther than 320 m from each other. At each site, I sampled insects on 2 or 3 of each Russian olive, Rose and Saskatoon, yielding a total of 15 Russian olive, 15 Rose and 15 Saskatoon plants across the entire study region. I sampled the same plants during three separate periods over the summer in 2013; late June, late July and late August. Each time, I sampled host plants between 9 am and 5 pm, and ensured that the date and time of sampling was haphazard among sites. I sampled exclusively on dry days, though cloud cover varied among sampling times.

Since Woods' rose can form hybrids with other native roses (Hitchcock et al. 1969), it is possible the Woods' roses I sampled are in fact hybrids. I therefore refer to the *Rosa* plants sampled as 'Rose' in my results.



Figure 3.3 Location of field sites. Projection: NAD 1983 UTM Zone 11.

**Table 3.1** Site descriptions and number of host plant types sampled per site. Longitude and latitude are decimal degree values(WGS 1984 datum).

		Site cen	Site centroid coordinates BEC				Number of host plants sampled			
Site number	Site	longitude	latitude	elevation (m)	Zone	Subzone	Variant	Russian olive	Rose	Saskatoon
1	Okanagan Lake Provincial Park	-119.728	49.6886	361	Bunchgrass (BG)	Okanagan	Very Dry Hot	2	2	2
2	Near north parking lot of Kal Tire Place, Vernon	-119.278	50.2784	394	Interior Douglas-fir (IDF)	Okanagan	Very Dry Hot	3	3	3
3	Next to LaFarge Cement Plant Bridge (Lafarge Rd), Kamloops	-120.062	50.6576	339	BG	Thompson	Very Dry Hot	3	3	3
4	Near Kickininee Provincial Park Pyramid Picnic Area	-119.637	49.554	350	BG	Okanagan	Very Dry Hot	2	2	2
5	Kickininee Provincial Park	-119.629	49.5429	348	BG	Okanagan	Very Dry Hot	2	2	2
6	Hayes Point Provincial Park, Osoyoos	-119.455	49.0142	280	BG	Okanagan	Very Dry Hot	3	3	3

## INSECT SAMPLING

I sampled insects using the beat method, which involves beating a branch and capturing any insects that fall onto a sheet held below. This method is commonly used for insect sampling on trees (Basset 1999; Riberiro et al. 2005; Campos et al. 2006) and was used for Russian olive biocontrol agent surveys in its native range (U. Schaffner, personal communication, 2013).

The beat sheet consisted of a 1 m<sup>2</sup> PVC frame overlaid with rip-stop Nylon. I cut a hole in the middle of the sheet and attached a 100 mL plastic vial lid, with the middle portion removed (leaving only the outer portion of the lid with threads), using a circular clamp. For insect sampling on each plant, the container portion of the vial was filled with 30 mL of 70% ethanol and secured to the lid in the beat sheet. This container was replaced after each individual plant was sampled. Five branches within arm's reach were haphazardly selected and beat five times each using a meter long PVC pipe. Any insects left on the beat sheet were gently moved into the vial using a paintbrush. I overturned the beat sheet, shook it vigorously and then visually inspected it for remnant insects prior to sampling another plant. The vials were placed in a freezer set at -18°C until they could be processed (debris removed and insects identified), which was usually no more than two days after sampling.

## INSECT IDENTIFICATION

I identified all adult insects to family using the keys in Borror et al. (1989). These keys were somewhat outdated with respect to family taxonomy, therefore for each family identified, I verified its current classification and name using relevant literature. Immature insects were not identified or included in the analyses due to difficulty in identification. Non-insect arthropods, such as spiders, mites, and collembolans were not identified. Following identification, the insects were stored in 70% ethanol in a freezer set at -18°C.

#### DATA ANALYSES

To obtain a synoptic picture of the host plant's insect community across the summer season, I pooled the abundance data for each plant across the different sampling periods. These pooled data were used for all analyses, as I had insufficient replication to evaluate site or date effects. All analyses were conducted using R (version 3.1.0; R Development Core

Team 2014), and community/diversity analyses were done using the vegan package (Oksanen et al. 2013).

To evaluate the thoroughness of sampling, I generated sample-based rarefied species accumulation curves using methods described by Gotelli and Colwell (2001).

I calculated the total insect abundance, family richness, and Shannon diversity among all plant types. I compared insect family richness among plant types using ANOVA and a Tukey-Kramer HSD post-hoc test. Due to unequal variances of Shannon diversity scores among plant types, comparisons were made using an unequal variances ANOVA and followed up with an unequal variances equivalent to a Tukey-Kramer HSD post-hoc test, the Games-Howell post-hoc test (R script obtained from

## http://www.psych.yorku.ca/cribbie/6130/games\_howell.R)

To compare insect community composition among host plant type, I applied permutational multivariate analysis of variance (PERMANOVA; Anderson 2001; McArdle and Anderson 2001), which is a non-parametric, permutational analysis of variance (ANOVA) that tests for interactions in multivariate data. PERMANOVA was conducted on a Bray-Curtis dissimilarity matrix of the untransformed insect data using 999 permutations, stratified according to site. PERMANOVA is sensitive to differences in multivariate dispersion (that is, variation in insect communities among plant types). Thus, a significant pvalue can indicate differences in insect community composition due to differences in the locations of each plant type's insect community in multivariate space, to differences in the dispersion of each plant type's insect community in multivariate space, or to both (Anderson 2001; Anderson 2006). After obtaining a significant PERMANOVA test, I applied PERMDISP to disentangle location and dispersions effects. PERMDISP is the multivariate analog of a Levene's test (Levene 1960) and tests for differences in the multivariate dispersion among groups. Within multivariate space, it first calculates the centroid of the arthropod assemblage associated with the given plant type, and then calculates the distance of each plant-specific arthropod assemblage to the plant type centroid. PERMDISP then compares the average distance to the centroid among plant types using a permutational ANOVA (Anderson 2004). To further investigate if a significant PERMANOVA test was due to differences in the location or dispersions of plant types, I visualized the Bray-Curtis

dissimilarity matrix in multivariate spacing using non-metric multidimensional scaling (NMDS).

PERMANOVA was conducted using the *adonis* function in the vegan R package and PERMDISP along with its post-hoc test were conducted using the *betadisper* and *permutest* functions, respectively, in the vegan R package.

## 3.3 Results

I caught and identified a total of 1360 adult insects belonging to 71 different insect families in 11 insect orders. Overall, the largest number of individual insects was caught on Saskatoon, followed by Russian olive, and then Rose (Figure 3.4).



Figure 3.4 Abundance of insects sampled on Rose, Russian olive, and Saskatoon.

In general, abundances of insect families were similar among Russian olive, Rose, and Saskatoon (Figure 3.5). There were, however, some notable differences in abundance of a few specific families. Among Thysanopterans, Russian olive hosted the highest number of insects from the family Thripidae. Saskatoon hosted the highest number of Hemipterans, made up primarily of insects from the Tingidae family, and Rose hosted the second highest number of Hemipterans, composed primarily of insects from the family Aphididae. Insects from the family Formicidae were more abundant on Russian olive and Rose, while insects from the family Eulophidae were notably more abundant on Russian olive (Figure 3.5).


**Figure 3.5** Abundance of insect families captured on Rose, Russian olive, and Saskatoon grouped by insect order. Abundance was pooled across sampling periods. The x-axis has been log<sub>10</sub> transformed to facilitate comparisons between plant types.

Rose was uniquely associated with 19 insect families, Russian olive with 13, and Saskatoon with 9, although the majority of these associations were due to singletons (Table B1). Excluding singletons, Rose was uniquely associated with 3 families (Chrysolmelidae, Aleyrodidae, and Cynipidae), Russian olive with 3 (Chloropidae, Trixoscelididae, and Gryllidae), and Saskatoon with 1 (Rhopalidae) (Table B1). Russian olive was also associated with 5 Lathridiidae individuals and 11 Anthicidae individuals (all from the subfamily Notoxinae), however, 1 individual from each of these families was also found on Rose (Figure 3.5).

The rarefied sample-based species accumulation curves showed that Rose hosted the highest insect family richness as number of individuals sampled increased, followed by Russian olive, and then Saskatoon (Figure 3.6). The curves for all three plant types are increasing, indicating I had not completely sampled the entire insect community found on Russian olive, Rose or Saskatoon. While still increasing, the curves for Russian olive and Saskatoon are less steep than the curve for Rose, suggesting I had sampled a lower proportion of the total insect community on Rose than Russian olive or Saskatoon.



**Figure 3.6** Rarefied sample-based species accumulation curves, showing mean insect family richness. Shaded areas show  $\pm 1$  standard deviation.

Insect family richness was significantly different among plant type (ANOVA;  $F_{2,42}$ =6.51, P= 0.003), with Rose having significantly higher insect family richness than Saskatoon (Tukey-Kramer LSD;  $\alpha$ =0.05, P= 0.002) (Figure 3.7). Insect family richness on Russian olive was not significantly different from either Rose (Tukey-Kramer LSD;  $\alpha$ =0.05, *P*= 0.282) or Saskatoon (Tukey-Kramer LSD;  $\alpha$ =0.05, *P*= 0.112) (Figure 3.7).



**Figure 3.7** Insect family richness on Rose, Russian olive, and Saskatoon. Plant types sharing the same letter indicate no significant difference as per the Tukey-Kramer LSD post-hoc test ( $\alpha$ =0.05).

Shannon diversity was significantly different among plant type (Unequal variances ANOVA;  $F_{2, 23.149}$ =6.33, P=0.006) (Figure 3.8). Shannon diversity was not different between Russian olive and Rose (Games-Howell;  $t_{19.93}$ =2.26, P=0.086), and Russian olive and Saskatoon (Games-Howell;  $t_{23.87}$ =1.35, P=0.380) (Figure 3.8). However, Shannon diversity was significantly higher on Rose compared to Saskatoon (Games-Howell;  $t_{16.55}$ =3.07, P=0.018) (Figure 3.8).



**Figure 3.8** Shannon diversity of insect families on Rose, Russian olive, and Saskatoon. Plant types sharing the same letter indicate no significant difference as per the Games-Howell posthoc test ( $\alpha$ =0.05).

Insect community composition among plant type differed significantly (PERMANOVA;  $F_{2,42}=2.76$ , P=0.001), however results from the NMDS analysis show that the insect community between plant types are clustered around each other, suggesting that the significant PERMANOVA result may be due to differences in the dispersion, rather than the location, of each plant type's insect community in multivariate space (Figure 3.9). Dispersion (measured as the distance to centroid) was in fact significantly different among plant type (PERMDISP;  $F_{2,42}=7.07$ , P=0.007), providing further evidence that dispersions of insect communities among plant types, are significantly different (Figure 3.10). Dispersions were found to be significantly different between Rose and Russian olive (PERMUTEST; permuted P=0.012), and Rose and Saskatoon (PERMUTEST; permuted P=0.241) (Figure 3.10). Based on these results, neither the phylogenetic- nor the phenology-related predictions suggested in the Background section gain support.



**Figure 3.9** NMDS of Bray-Curtis dissimilarity distances (species scores based on Wisconsin square root transformed values). Each point represents the insect community composition pooled across sampling period of a single plant.



**Figure 3.10** Dispersion of insect communities among Rose, Russian olive, and Saskatoon. Plant types sharing the same letter indicate no significant difference as per the PERMUTEST post-hoc test ( $\alpha$ =0.05).

# **3.4 Discussion**

I found that the richness, diversity and composition of insect assemblages associated with Russian olive plants were no different than those of assemblages associated with two co-occurring species, Rose and Saskatoon. Furthermore, the total insect abundance observed on Russian olive was intermediate to that observed on Rose and Saskatoon. Lastly, although composition varied more among Russian olive samples than it did among Rose samples, it was similar to that observed among Saskatoon samples. Taken together, the results of this study provide little evidence to suggest that insects respond differently to Russian olive than to co-occurring native shrubs. As such, my results do not follow either of the extreme scenarios described in the Background section, but instead are consistent with the intermediate scenario. Furthermore, these findings are inconsistent with both the phylogeny and phenology hypotheses described above, suggesting other factors, such as time since introduction, are responsible. Arthropod assemblages may change as the time since introduction of the plant increases (Strong et al. 1984; Brändle et al. 2008; Harvey et al. 2013). When a plant is first introduced, arthropods, specialists in particular, may not recognize the plant as suitable, and furthermore, may lack the necessary adaptations (e.g. enzymes to break down defensive chemicals, necessary mouthparts) to colonize the new host plant. However, over time, arthropods may evolve the necessary adaptations required to colonize the new host plant (Brändle et al. 2008). Russian olive was introduced to BC (Pearce and Smith 2009) and to North America in general around 100 years ago (Katz and Shafroth 2003). Although this is a relatively short time, it may have been long enough for insects to perceive Russian olive as a suitable habitat and/or food source.

#### COMPARISON OF RESULTS WITH PREVIOUS STUDIES

Only a few other studies have examined insect fauna associated with Russian olive. The vast majority of insect families found in this study to be unique to Russian olive were not observed on Russian olive in the Pendleton et al. (2011) study (Table 3.2). The families that were common to both studies were also found to be associated with willow and/or saltcedar by Pendleton et al. (2011) (Table 3.2). This fact, in conjunction with a still increasing species accumulation curve for Russian olive in this study, suggests that with additional effort, more insect families will be found to be associated with Russian olive. Furthermore, the families that I found to be unique to Russian olive, and that were not represented by singletons, were also observed on saltcedar and willow by Pendleton et al. (2011) (Table 3.2). This suggests that these families are unlikely to be specialists on Russian olive. Previous studies have also suggested that grasshoppers (*Melanoplus* spp.) (Dix et al. 1986) and blister beetles (Meloidae family) (Milliken 1921) feed on Russian olive leaves, but I did not find these taxa on Russian olive in this study. This may be an artifact of using the beat method, as grasshoppers have been observed on Russian olive in the Okanagan Valley of BC (B. Lalonde, personal communication, 2014), but quickly jump away from the plant as a person approaches. Interestingly, I found 11 individuals from the subfamily Notoxinae (Anthicidae family) on Russian olive, and several species within this subfamily are attracted to cantharidin (Dettner 1997), a potent defensive chemical synthesized by blister beetles (Carrel et al. 1993).

This study			Pendleton et al. (2011) study	
Order	Family	Number captured	Present on Saltcedar or Willow?	Present on Russian olive?
Coleoptera	Mordellidae	1	Yes	No
Diptera	Chloropidae	4	Yes	Yes
	Muscidae	1	Yes	No
	Trixoscelididae	2	Yes	No
Ephemeroptera	Ephemeridae	1	No	No
	Heptageniidae	1	No	No
Hemiptera	Adelgidae	1	No	No
	Pseudococcidae	1	No	No
Hymenoptera	Eupelmidae	1	No	No
	Perilampidae	1	No	No
	Sphecidae	1	Yes	No
Orthoptera	Gryllidae	2	Yes	No
Psocoptera	Psocidae	1	No	No

**Table 3.2** Comparison of insect families unique to Russian olive in this study to insect families found on Russian olive in the Pendleton et al. (2011) study.

### TRAITS OF RUSSIAN OLIVE RELEVANT TO INSECTS

Although the coarse taxonomic resolution used in this study precludes assignment of insects to functional guilds (e.g. pollinators, herbivores), it is nonetheless informative to consider the traits of Russian olive that may be important to insects. Russian olive flowers emit a strong, fragrant smell (Katz and Shafroth 2003; Farkas and Zajácz 2007) which may

be attractive to pollinators, specifically bees. A study conducted in China found methyl cinnamate, a benzenoid (Willmer 2011), was the most abundant (>50% of all volatiles) volatile in the odor of Russian olive flowers (Xin-yao et al. 2009). Several bee taxa are attracted to methyl cinnamate volatiles; Euglossine bees (*Euglossa* spp., Hymenoptera: Apidae) are highly attracted to the methyl cinnamate volatiles produced by orchids (Williams and Whitten 1983) and methyl cinnamate emitting snapdragon flowers (*Antirrhinum*, Sonnet cultivar) are visited by bumblebees (*Bombus* spp., Apidae) (Odell et al. 1999). In Russian olive's native range, nectar flow is described as excellent and honeybees frequently visit Russian olive flowers throughout the day. However, the sugar content of the nectar itself is quite low and is most likely used for brood rearing (Farkas and Zajácz 2007). Although Russian olive has been promoted for the production of honey in the US (Hayes 1976), there were no honeybees or bees in general captured on Russian olive in this study or in the Pendleton et al. (2011) study, nor have I ever observed bees on Russian olive while flowering. Thus, bee visitation of Russian olive may potentially be region specific.

The structure of the flowers appears to be attractive to Thysanopterans, which may in turn act as both pollinators and herbivores. Thysanopterans prefer flowers with narrow openings (Mound 2005), like those presented by Russian olive. The largest collection of Thysanopterans among all plant types and sampling times was made on Russian olive during flowering in May (Table B2), and was overwhelmingly dominated by individuals from the family Thripidae. Thysanopteran larvae are known to develop in flowers (Sakai 2002) and are often described as pollen parasites. Depending on the size of the pollen grain, larvae and adults can consume more than 1500 grains per day (Kirk 1987; Mound 2005). Their impressively high reproduction rate allows them to produce large numbers of offspring (Sakai 2002), and as such, the likelihood that individual thrips come in contact with and successfully deposit pollen is high (Mound 2005). Given the enormous numbers of Thysanopterans observed on Russian olive during flowering, it is likely that these insects not only use the flowers as breeding sites, but also serve as key pollinators for the exotic species.

The high nitrogen and low carbon:nitrogen ratios of Russian olive leaves (Tibbets and Molles 2005; Moline and Poff 2008; Abelho and Molles 2009) may be attractive to herbivores (Abelho and Molles 2009). Nitrogen is essential for the growth, survival, reproduction, and protein synthesis of herbivorous invertebrates (Huberty and Denno 2006).

Because of this, terrestrial and aquatic herbivorous invertebrates are generally considered nitrogen limited (Mattson 1980; Polis 1999; Elser et al. 2000). Herbivores choose food based on nutritional quality and energy content (Polis 1999), where high quality food is considered as having high nitrogen content (Scriber and Slansky 1981; Bryant et al. 1983) and a low carbon:nitrogen ratio (Cross et al. 2005). Insect performance (e.g. growth and reproduction) and preference (Dixon 1970; Johnson et al. 1987; Minkenberg and Ottenheim 1990) has been found to increase with increases in plant host nitrogen. Owing to their high diversity (Jander and Howe 2008), it would not be surprising to find arthropod herbivores that benefit from the high leaf nitrogen content of Russian olive.

In contrast with their leaves, the fruits of Russian olive are poor in nitrogen and have a high carbon:nitrogen ratio. Nevertheless, the fruits – specifically the mesocarp – may be attractive to herbivores due to their high sugar content (Ayaz and Bertoft 2001; Doležal et al. 2001). Numerous adult Vesipdae, for example, were observed feeding on the mesocarp of Russian olive fruits near Kamloops, BC (Figure 1.5). This behaviour could be attributable to these insects' affinity for carbohydrates (Spadbery 1973).

#### CONCLUSION AND FUTURE WORK

My finding that the richness, diversity and composition of insect assemblages associated with Russian olive was no different than those of co-occurring native vegetation is similar to findings on other invasive plant species (Frenzel and Brandl 2003; Agrawal et al. 2005; Procheş et al. 2008) and suggests that the insect community of Russian olive's invaded range respond to its presence in a neutral manner. This study is the first to have conducted standardized sampling of insects associated with exotic Russian olive plants and co-occurring native vegetation. As such, there is still much more information that can be gleaned from future arthropod studies of Russian olive in its invaded range. For example, time since introduction is a possible explanation for why insect assemblages were no different than those of co-occurring vegetation. It would be interesting to compare arthropod communities on Russian olive along a gradient of time since introduction. Conducting arthropod gut content analyses on arthropods found on Russian olive would help distinguish between true Russian olive herbivores and arthropods using Russian olive as habitat. Furthermore, as this study and the Pendleton et al. (2011) study examined insect families on Russian olive, increasing the taxonomic resolution of identified arthropods to that of genus or species will enable the assignment of arthropod functional groups, which in turn will help identify Russian olive pollinator, herbivore, and predator communities.

# **Chapter 4: Conclusion**

# 4.1 General discussion

In this work, I sought to provide an assessment of Russian olive's potential distribution and its associated insect community in Canada to more fully understand Russian olive's integration into the ecosystems of its invaded range. My literature review, presented in the introductory chapter, revealed that although much is known about Russian olive in the US, very little research has been conducted in Canada. Therefore, I sought to fill this gap by providing the first assessment of Russian olive's potential distribution in Canada and, specifically within southern BC, its associations with the insect community of its invaded range.

I provide the following novel contributions to research concerning Russian olive. First, I present maps of government-sponsored Russian olive plantings across the Canadian prairies, and these provide the basis for future research on naturalization patterns. I also provide new occurrence records derived using "remote surveys", using Google Street View. To my knowledge, this is the only the second time this method has been used to survey an invasive plant (Visser et al. 2014).

I then provide comprehensive niche model predictions of Russian olive's potential distribution within North America. Specifically, the inclusion of roads, regulated water, and soil pH, salinity and texture as predictors and the use of Russian olive occurrences from across Canada and the US to predict Russian olive's potential distribution across these countries is novel and builds on ENMs previously constructed for Russian olive. With this new model, I found that Russian olive has the potential to inhabit a large portion of southern Canada, including areas where Russian olive was intentionally promoted and planted by government agencies. Additionally, this model shows Canadian locations in which Russian olive has the high probability of inhabiting, but has not yet been recorded there, suggesting it has not yet filled all of the available niches in Canada.

Third, I explored the implications of excluding Canadian occurrences from ENMs, a common practice among the ENMs produced for Russian olive to date. I found that adding Canadian occurrences added new environmental niches. Including them in the ENM led to a reduction in the total amount of suitable habitat relative to a model using just US occurrences

while also predicting habitat as suitable in the US that the US occurrences model did not. Therefore, excluding Canadian occurrences has potentially led to the over-prediction of previous Russian olive ENMs.

Finally, I addressed the question: how does the diversity of insect assemblages respond to the presence of Russian olive within riparian vegetation? In the first study of its kind, I used standardized surveys to compare the diversity of insect assemblages associated with Russian olive and co-occurring native shrubs. I found that the insect family richness, diversity, community composition and community variance were no different from that of co-occurring vegetation, suggesting that insects are not responding in any peculiar way to Russian olive's presence.

# 4.2 Applications

Being the first assessment of Russian olive's potential distribution and its associated insect community in Canada, this work provides invasive species groups and managers much needed information regarding Russian olive's potential distribution and faunal responses in Canada. Preventing invasions is often less costly and more feasible than eradicating or controlling already established populations of invasive species (Hobbs and Humphries 1995), however, preventing future invasions can be difficult (Peterson and Vieglais 2001; Jiménez-Valverde et al. 2011). Therefore, identifying areas of potential suitable habitat for invasion are needed to coordinate management efforts (Peterson 2003; Venette et al. 2010). The Russian olive ENM I generated here will allow invasive species managers to identify areas of potential suitable habitat currently devoid of Russian olive. These areas can then be put under surveillance and should they become infested by Russian olive, early detection rapid response initiatives can be used to suppress complete establishment (Simberloff et al. 2013). Additionally, nurseries in these areas could be discouraged or banned from selling Russian olive.

### **4.3** Assumptions and limitations

#### PRAIRIE PLANTING DATA

Due to the discontinuation of the Prairie Shelterbelt Program in the spring of 2013, I could not confirm whether the planting data I obtained reflected the number of Russian olive plants distributed, or the number of Russian olive plants actually planted. However, given that landowners had to pay for the plants, I assumed they were not wasted and were in fact planted.

#### ECOLOGICAL NICHE MODELING

Although ENMs are powerful and important tools for predicting species distributions, recent ENM literature has pointed out several caveats (e.g. Lobo et al. 2008; Jiménez-Valverde et al. 2011; Araújo and Peterson 2012; Merow et al. 2013). Use of AUC as a measure of presence-only model evaluation has been criticised as it can be a misleading measure of model performance (Lobo et al. 2008). Currently, however, there are no equivalent suitable alternatives (Lobo et al. 2008; Merow et al. 2013). I attempted to minimize any drawbacks associated with current model performance measures by using an additional model evaluator, the threshold dependent omission rate of test occurrence.

Sampling bias is also a concern among ENMs, particularly among presence-only models such as Maxent (Phillips et al. 2009; Merow et al. 2013). Background samples, known as pseudo-absences, are used to train and test presence-only models and are by default chosen uniformly at random across the study region as Maxent models assume that the likelihood of sampling a species is equal across the region of study (Elith et al. 2011). However, this is often not the case, as easily accessible areas such as near roads and populated places are often more heavily sampled (Merow et al. 2013). One way to account for sampling bias in Maxent ecological niche modeling is by supplying Maxent with a bias grid that identifies areas where sampling for the species has occurred and has not occurred. Maxent will then generate a model using background points from sampled areas, thereby reducing the effect of sampling bias (Phillips et al. 2009). Although I knew where Russian olive was surveyed for in British Columbia, I did not know the survey area of occurrences obtained on online invasive species databases. Therefore, I could not apply a bias grid that would cover Russian olive's entire invaded range. Assuming occurrences obtained from online invasive species databases were sampled from easily accessible areas such as roads, the effect of this bias may not be profound due to the fact that road ditches provide environments suitable for Russian olive growth and indeed, Russian olive is commonly found near roads.

I could not determine if occurrences obtained from various online invasive species databases were cultivated or naturalized. Given the amount of occurrences used for the models, it is likely that some of these occurrences are in fact cultivated but have not necessarily naturalized. Environmental conditions where cultivated invasive plants occur may allow them to survive but may not be suitable for naturalization or spread (Guilbault et al. 2012). As such, including them in the model may have influenced the results.

Furthermore, there may be factors other than the bioclimatic and abiotic predictors used in the ENMs here influencing Russian olive's potential distribution. Biological interactions, such as competition for resources, geographic barriers, and the presence of mutualists or parasites, could not be accounted for in the ENMs. As an example of one such biological interaction, Russian olive's ability to establish in shaded areas under canopies (Shafroth et al. 1995; Katz and Shafroth 2003; Reynolds and Cooper 2010) is a trait thought to contribute to its dominance in riparian areas (Reynolds and Cooper 2010). However, growth rates in shaded habitats are most likely lower than growth rates in unshaded habitats, suggesting Russian olive's spread could potentially be slowed in riparian areas with heavy canopy cover. I did not account for canopy cover in the ENMs I generated, and as such, this is an improvement that can be made for future ENMs (see below).

#### INSECT SURVEY

Several aspects of my insect survey conducted on Russian olive and its co-occurring plants, Woods' rose and Saskatoon, were limiting and could be improved. Firstly, Saskatoon was not sampled during its flowering period (Figure 3.2), which may have resulted in the absence of an important arthropod guild, as arthropod assemblages change with respect to the plants phenology (Lawton 1983; Yano and Ohsaki 1993; Intachat et al. 2001). Woods' rose and Saskatoon are more closely related to each other than either of them is to Russian olive (Figure 3.1) and previous studies have found that phylogenetically closely related species share similar insect/arthropod assemblages (Weiblen et al. 2006; Dinnage et al. 2012). The lack of sampling on Saskatoon during flowering may be a possible explanation for why

insect families found on Saskatoon and Woods' rose were different across all analyses, with the exception of insect community composition.

Secondly, the beat sampling method I used was limited in that it only helped to determine what insects were incidentally occurring on Russian olive. I could not determine if the insects were feeding on Russian olive, something which might be of interest to those developing biocontrol agents. Regardless, identifying what insects use Russian olive –as a perch and/or a food source – is still informative for determining how insects respond to Russian olive in its invaded range. Another limitation of the beat sampling method is that it is biased to collecting insects who respond to disturbance by dropping to the ground. Insects that respond to disturbance by flying or jumping away (e.g. grasshoppers) were likely not captured using the beat sampling method. However, given that sweep nets would not withstand Russian olive's thorny branches, and fumigation would also disturb insects prior to collection, there was a lack of suitable alternative sampling methods. Future studies could benefit from the use of observational sampling in addition to sampling using the beat method.

Thirdly, due to the coarse resolution of insect identification (family level), I was unable to group insects by functional group, which is commonly done for arthropod surveys on invasive plant species (Simao et al. 2010; Holmquist et al. 2011; Emery and Doran 2013; Spafford et al. 2013). However, family level identification was sufficient in detecting significant differences in insect assemblages among plant types, indicating that in general, it was an appropriate level of identification for the focus of the study. Regardless of its shortcomings, the survey I conducted provides a good starting point for future insect surveys on Russian olive.

# **4.4 Future directions**

Given the lack of information regarding Russian olive in Canadian ecosystems, there are several avenues of research stemming from this work that can be further explored. PFRA Prairie Shelterbelt Progam planting records for Russian olive provide an excellent opportunity to test hypotheses prominent in invasive plant biology literature, such as the enemy release hypothesis (ERH) and time since introduction. The ERH states that upon introduction to a novel range, exotic plant species are potent invaders due to a lack of suitable enemies (Keane and Crawley 2002). However, overtime, native enemies may expand, or even switch, their host ranges to include the invader (Bowers et al. 1992; Creed and Sheldon 1995; Mitchell et al. 2010). These planting data provide year of planting and as such, can be used to establish a gradient of invasion to test the ERH and determine how native enemies respond to Russian olive over time. Evaluating effects of time since introduction need not be restricted to native enemies. The increased colonisation of native symbionts, such as mycorrhizal fungi, over time (Van der Putten 2012; Mei et al. 2014) may help us understand how invasive plants, such as Russian olive, thrive in their invaded range (Fitter 2005; Lee et al. 2014).

Furthermore, I do not know how many of these plantings exist to date, however, conducting a survey of remaining plantings could fill many gaps of knowledge regarding Russian olive's invasion in Canadian ecosystems. For example, determining what plantings exist or do not exist to date will provide information about Russian olive's habitat requirements across the prairies. Additionally, if a Russian olive plant has been intentionally removed by a land owner, determining the reason for removal will provide information about how the public perceives Russian olive. These plantings may also provide a baseline for assessing potential naturalization by surveying for Russian olive in habitats surrounding plantings (existing or non-existing), especially within 1 km of a water body (see Chapter 1).

In general, very few studies have compared arthropod communities associated with exotic plants in their invaded and native ranges (Spafford et al. 2013). Furthermore, none have been conducted on Russian olive. While I conducted the first survey of insects associated with Russian olive in Canada, contrasting the insect community on Russian olive in its invaded range with that in its native range could be used to test the ERH and may potentially improve our understanding of why Russian olive has become invasive.

To account for Russian olive's ability to establish under canopies, future ENMs could include canopy cover as a predictor. Canopy cover data at 1 km<sup>2</sup> resolution covering Russian olive's entire invaded range is freely available online (e.g. Global Forest Canopy Density data from <u>http://edc2.usgs.gov/glcc/fao/index.php</u>) and could therefore be easily incorporated in future ENMs.

The effects of projected climate change on Russian olive's northward distribution is something that could be incorporated into future ENMs. Several studies have suggested that

Russian olive's southward distribution in the US could be limited under climate change scenarios (Friedman et al. 2005; Guilbault et al. 2012), yet no studies have focused on the effects of climate change on its northward expansion. Determining future Russian olive distribution is just as important as determining current potential distribution, and would be an important tool in supressing the establishment of future Russian olive populations.

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## Appendices

## Appendix A – Supplementary figures and tables for Russian olive ecological niche modeling

**Table A1** Pearson correlation coefficient (r) matrix of all predictors considered for ENM modeling. Final predictors used in modeling (highlighted in blue) were chosen based on  $|\mathbf{r}| < 0.7$  and biological relevance. Strong correlation between predictors ( $|\mathbf{r}| > 0.7$ ) is indicated by r values highlighted in orange. Topsoil USDA soil texture class was not included in the correlation analysis as it is a categorical variable but was chosen as one of the final predictors used for modeling.

Predictor	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
1 Annual Mean Temperature	1																								
2 Mean Diurnal Range	0.77895	1																							
3 Isothermality	0.89607	0.84587	1																						
4 Temperature Seasonality	-0.79861	-0.51793	-0.86603	1																					
5 Max Temperature of Warmest Month	0.94629	0.87777	0.83337	-0.59536	1																				
6 Min Temperature of Coldest Month	0.95639	0.66576	0.91654	-0.92484	0.83161	1																			
7 Temperature Annual Range	-0.54664	-0.12289	-0.61029	0.90464	-0.26693	-0.75719	1																		
8 Mean Temperature of Wettest Quarter	0.67083	0.59139	0.45872	-0.22838	0.7456	0.49574	0.0167	1																	
9 Mean Temperature of Driest Quarter	0.91187	0.71799	0.90818	-0.86353	0.81953	0.93509	-0.65876	0.41968	1																
10 Mean Temperature of Warmest Quarter	0.96081	0.80042	0.80312	-0.60683	0.98574	0.85343	-0.32157	0.77643	0.81764	1															
11 Mean Temperature of Coldest Quarter	0.97815	0.72878	0.93296	-0.90225	0.8751	0.99406	-0.69573	0.55092	0.93898	0.8898	1														
12 Annual Precipitation	0.60922	0.19778	0.48345	-0.64123	0.43394	0.65011	-0.61774	0.26006	0.60805	0.49994	0.63421	1													
13 Precipitation of Wettest Month	0.57068	0.19398	0.47784	-0.60986	0.40277	0.61299	-0.59001	0.27121	0.57149	0.46189	0.59701	0.93841	1												
14 Precipitation of Driest Month	0.52381	0.13711	0.38002	-0.55359	0.36004	0.56057	-0.54929	0.19547	0.53956	0.4296	0.54559	0.89416	0.72045	1											
15 Precipitation Seasonality	-0.43995	-0.2246	-0.33099	0.44118	-0.34704	-0.44376	0.36188	-0.12899	-0.46475	-0.36839	-0.44533	-0.6033	-0.35269	-0.77479	1										
16 Precipitation of Wettest Quarter	0.56595	0.18811	0.47129	-0.60661	0.39841	0.60716	-0.58501	0.25879	0.56509	0.4562	0.59154	0.95183	0.99278	0.73393	-0.38371	1									
17 Precipitation of Driest Quarter	0.55126	0.15901	0.41083	-0.581	0.3845	0.58934	-0.57044	0.21067	0.56732	0.45356	0.57436	0.91538	0.74768	0.99398	-0.7749	0.76124	1								
18 Precipitation of Warmest Quarter	0.55692	0.23359	0.33697	-0.41373	0.44861	0.49332	-0.32843	0.52032	0.43272	0.52141	0.51231	0.81493	0.74308	0.78904	-0.54848	0.75127	0.79924	1							
19 Precipitation of Coldest Quarter	0.50191	0.14438	0.49326	-0.65388	0.31814	0.60342	-0.67292	0.01968	0.61246	0.3607	0.5693	0.90714	0.8816	0.76258	-0.48368	0.89801	0.78766	0.52651	1						
20 Elevation	0.13923	0.47897	0.43763	-0.34077	0.1455	0.19349	-0.16464	-0.11609	0.26696	0.03808	0.21351	-0.09446	-0.07819	-0.1045	-0.12959	-0.07994	-0.09464	-0.15443	-0.0027	1					
21 Length of regulated water per grid cell	0.17701	0.14374	0.15129	-0.12681	0.17843	0.16733	-0.0805	0.12689	0.14532	0.18131	0.17082	0.09002	0.07358	0.08733	-0.07005	0.07178	0.09068	0.07828	0.06458	-0.00266	1				
22 Length of all water per grid cell	0.2769	0.20646	0.28785	-0.28178	0.2453	0.29317	-0.22022	0.09335	0.27818	0.23877	0.29181	0.21411	0.19985	0.16316	-0.13913	0.20432	0.17446	0.09503	0.24147	0.06649	0.24708	1			
23 Length of major road per grid cell	0.17924	0.1024	0.1455	-0.13884	0.16327	0.1786	-0.11789	0.12609	0.15064	0.17831	0.1766	0.13531	0.10293	0.14567	-0.10816	0.10554	0.1482	0.12431	0.10567	-0.03493	0.07074	0.04173	1		
24 Topsoil pH	0.07541	0.23066	0.18962	-0.14284	0.09722	0.1045	-0.06699	0.03393	0.09936	0.04714	0.11085	-0.31755	-0.26995	-0.33634	0.18969	-0.2872	-0.3315	-0.32083	-0.26608	0.36395	0.02993	0.03759	-0.01662	1	
25 Topsoil Salinity	0.14981	0.19806	0.16993	-0.11206	0.17237	0.13935	-0.03908	0.10661	0.14311	0.15401	0.14802	-0.07505	-0.0646	-0.07416	0.01388	-0.07066	-0.07188	-0.08702	-0.05718	0.13824	0.03278	0.01997	0.01013	0.2407	1



**Figure A1** Marginal response curves for the five most important predictors used in the US and total dataset models. These curves show how varying a single variable while keeping all other variables at their average value changes the logistic prediction. Shaded areas show the 95% confidence intervals around the mean.



**Figure A2** Single variable response curves for the five most important predictors used in the US and total dataset models. These curves are created by modeling with only 1 variable and determining how varying that single variable changes the logistic prediction. Shaded areas show the 95% confidence intervals around the mean.



**Figure A3** Thresholded map of US and total dataset models showing a large, continuous area in central to northern Washington where the total dataset model predicts suitable habitat but the US dataset model does not. Area enclosed by the dashed ellipse represents an area the total dataset model predicted as suitable but the Jarnevich and Reynolds (2011) models did not. For a complete explanation on the meaning of the colours in the map, see Figure 2.9. Projection: North America Albers Equal Area Conic.



**Figure A4** Suitable habitat depicted by the thresholded total dataset model in southern BC and northern Washington with Russian olive and common carp occurrences overlaid. Common carp data was obtained from FishBase (http://www.fishbase.org, accessed 25 March 2014). Projection: NAD 1983 UTM Zone 10.



**Figure A5** Location of Prairie Shelterbelt Program Russian olive plantings overlaid on the predictive potential distribution map of the total dataset model. Projection: NAD 1983 UTM Zone 13.

## Appendix B – Insect assemblages on Russian olive, Rose, and Saskatoon

Plant type	Insect order	Insect family	Number captured
		Chrysomelidae	3
		Bruchidae	1
	Coleoptera	Buprestidae	1
		Dermestidae	1
		Eucnemidae	1
	Dintoro	lerInsect familyNChrysomelidaeBruchidaeBruchidaeBuprestidaeDermestidaeEucnemidaeAcroceridaeAnthomyiidaeAleyrodidaeNabidaeCynipidaeIchneumonidaeraMymaridaeTenthredinidaeTrichogrammatidaeraHeliozelidaeaGlossosomatidaeaPhilopotamidaeaMordellidaeTrixoscelididaeaPhilopotamidaeaAdelgidaepteraEphemeridaeaAdelgidaePilapidaeAdelgidaeChloropidaeMuscidaeTrixoscelididaeBephecidaeAdelgidaeChloropidaeMuscidaeTrixoscelididaeEupelmidaeAdelgidaeAdelgidaeAdelgidaeAdelgidaeBethylidaeAntenbrionidaeAntoboridaeSyrphidaeBethylidaeBethylidaeBraconidae	1
	Diptera	Anthomyiidae	1
	Haminton	Aleyrodidae	2
	Heimptera	Nabidae	1
Rose		Cynipidae	6
		Ichneumonidae	1
	Hymenoptera	Mymaridae	1
		Tenthredinidae	1
		Trichogrammatidae	1
	Thysanoptera	Stenopsocidae	1
	Lanidantana	Heliozelidae	1
	Lepidoptera	Hesperiidae	1
	TT 1 /	Glossosomatidae	1
	Irichoptera	Philopotamidae	1
	Coleoptera	Mordellidae	1
	•	Chloropidae	4
	Diptera	Muscidae	1
	*	Trixoscelididae	2
	<b>D</b> 1	Ephemeridae	1
<b>D</b> .	Ephemeroptera	Heptageniidae	1
Russian	TT : /	Adelgidae	1
olive	Hemiptera	Pseudococcidae	1
		Eupelmidae	1
	Hymenoptera	Perilampidae	1
		Sphecidae	1
	Orthoptera	Gryllidae	2
	Psocoptera	Psocidae	1
-	Coleoptera	Tenebrionidae	1
		Culicidae	1
		Chaoboridae	1
PseudPseudHymenopteraEupeHymenopteraPeriliSpheOrthopteraOrthopteraGryllPsocopteraPsocColeopteraTeneCulioCulioDipteraSurp	Symbidae	1	
Saskatoon		Tachinidae	rainityrunible (aptiliedomelidae3idae1stidae1stidae1midae1eridae1myiidae1odidae2ae1idae6monidae1redinidae1opsocidae1zelidae1opsocidae1otamidae1opidae4dae1octamidae1octamidae1octamidae1octamidae1octamidae1octamidae1octamidae1opidae4dae1ococcidae1idae<
Lepidon Trichop Coleoph Diptera Ephema Russian olive Hemipt Orthoph Psocoph Coleoph Diptera Saskatoon Hemipt		Friesometidee	1
	Hemiptera	Discusting	1
		Bruchidae 1 Bruchidae 1 Dermestidae 1 Eucnemidae 1 Acroceridae 1 Aleyrodidae 2 Nabidae 1 Cynipidae 6 Ichneumonidae 1 Tenthredinidae 1 Trichogrammatidae 1 optera Stenopsocidae 1 optera Heliozelidae 1 ptera Mordellidae 1 ptera Mordellidae 1 Trixoscelididae 2 Chloropidae 4 a Muscidae 1 Trixoscelididae 1 Derena Ephemeridae 1 Derena Pseudococcidae 1 Eupelmidae 1 Derena Perilampidae 1 Synphidae 1 Tachinidae 1 Eriosomatidae 1 Bethylidae 1 Bethylidae 1 Braconidae 1	2
	Hymenoptera	Bethylidae	1
	- <i>j</i> op •••••	Braconidae	1

 Table B1 Insect families found solely on each plant type.

Table B2 Abundance of adult insect orders and fa	milies found on each plant type	e during each sampling period (June	e, July, and
August).			

		June				July		August			
Insect order	Insect family	Rose	Russian olive	Saskatoon	Rose	Russian olive	Saskatoon	Rose	Russian olive	Saskatoon	
Coleoptera	Anthicidae	1	11	0	0	0	0	0	0	0	
Coleoptera	Bruchidae	1	0	0	0	0	0	0	0	0	
Coleoptera	Buprestidae	1	0	0	0	0	0	0	0	0	
Coleoptera	Chrysomelidae	1	0	0	2	0	0	0	0	0	
Coleoptera	Cleridae	0	3	1	0	0	0	0	0	0	
Coleoptera	Coccinellidae	2	5	1	8	2	3	17	4	4	
Coleoptera	Curculionidae	9	1	5	0	0	0	2	3	0	
Coleoptera	Dermestidae	1	0	0	0	0	0	0	0	0	
Coleoptera	Eucnemidae	1	0	0	0	0	0	0	0	0	
Coleoptera	Lathridiidae	0	1	0	1	1	0	0	3	0	
Coleoptera	Mordellidae	0	1	0	0	0	0	0	0	0	
Coleoptera	Nitidulidae	0	1	1	0	0	0	0	0	0	
Coleoptera	Scraptiidae	9	10	0	0	0	0	0	0	0	
Coleoptera	Tenebrionidae	0	0	1	0	0	0	0	0	0	
Dermaptera	Forficulidae	0	0	0	1	1	3	16	4	0	
Diptera	Acroceridae	0	0	0	0	0	0	1	0	0	
Diptera	Anthomyiidae	1	0	0	0	0	0	0	0	0	
Diptera	Chaoboridae	0	0	1	0	0	0	0	0	0	
Diptera	Chironomidae	16	11	16	9	6	1	6	9	3	
Diptera	Chloropidae	0	4	0	0	0	0	0	0	0	
Diptera	Culicidae	0	0	1	0	0	0	0	0	0	
Diptera	Hybotidae	1	0	2	0	0	0	0	0	0	
Diptera	Muscidae	0	0	0	0	1	0	0	0	0	
Diptera	Sciaridae	0	1	2	0	0	0	0	1	0	

Table B2 (cont'd) Abundance of adult insect orders and families found on each plant type during each sampling period (June,	
July, and August).	

		June				July		August				
Insect order	Insect family	Rose	Russian olive	Saskatoon	Rose	Russian olive	Saskatoon	Rose	Russian olive	Saskatoon		
Diptera	Syrphidae	0	0	1	0	0	0	0	0	0		
Diptera	Tachinidae	0	0	1	0	0	0	0	0	0		
Diptera	Trixoscelididae	0	2	0	0	0	0	0	0	0		
Ephemeroptera	Ephemeridae	0	1	0	0	0	0	0	0	0		
Ephemeroptera	Heptageniidae	0	1	0	0	0	0	0	0	0		
Hemiptera	Adelgidae	0	0	0	0	0	0	0	1	0		
Hemiptera	Aleyrodidae	2	0	0	0	0	0	0	0	0		
Hemiptera	Anthocoridae	0	3	1	1	0	0	0	0	0		
Hemiptera	Aphididae	73	11	16	6	0	0	3	2	1		
Hemiptera	Cercopidae	1	1	0	1	2	0	3	3	1		
Hemiptera	Cicadellidae	1	0	0	0	2	0	0	3	2		
Hemiptera	Eriosomatidae	0	0	1	0	0	0	0	0	0		
Hemiptera	Miridae	3	4	0	0	0	0	0	0	0		
Hemiptera	Nabidae	0	0	0	0	0	0	1	0	0		
Hemiptera	Pentatomidae	0	1	1	0	0	0	6	1	0		
Hemiptera	Pseudococcidae	0	1	0	0	0	0	0	0	0		
Hemiptera	Psyllidae	1	0	1	0	0	0	0	0	0		
Hemiptera	Rhopalidae	0	0	0	0	0	1	0	0	1		
Hemiptera	Tingidae	0	1	21	1	1	136	1	3	221		
Hymenoptera	Aphelinidae	0	0	3	0	0	0	0	1	0		
Hymenoptera	Bethylidae	0	0	1	0	0	0	0	0	0		
Hymenoptera	Braconidae	0	0	1	0	0	0	0	0	0		
Hymenoptera	Cynipidae	1	0	0	1	0	0	4	0	0		
Hymenoptera	Encyrtidae	1	2	1	0	1	0	0	0	0		

Table B2 (cont'd) Abundance of adult inse	t orders and families found on each	h plant type during each sampling period (June,
July, and August).		

		June				July		August			
Insect order	Insect family	Rose	Russian olive	Saskatoon	Rose	Russian olive	Saskatoon	Rose	Russian olive	Saskatoon	
Hymenoptera	Eulophidae	5	62	5	0	0	0	0	0	0	
Hymenoptera	Eupelmidae	0	1	0	0	0	0	0	0	0	
Hymenoptera	Eurytomidae	1	0	2	0	0	0	0	0	0	
Hymenoptera	Formicidae	45	42	5	20	4	3	15	21	2	
Hymenoptera	Ichneumonidae	0	0	0	0	0	0	1	0	0	
Hymenoptera	Mymaridae	1	0	0	0	0	0	0	0	0	
Hymenoptera	Perilampidae	0	0	0	0	0	0	0	1	0	
Hymenoptera	Pteromalidae	1	2	0	0	0	0	0	0	0	
Hymenoptera	Sphecidae	0	0	0	0	0	0	0	1	0	
Hymenoptera	Tenthredinidae	1	0	0	0	0	0	0	0	0	
Hymenoptera	Torymidae	11	0	1	0	0	0	0	0	0	
Hymenoptera	Trichogrammatidae	1	0	0	0	0	0	0	0	0	
Lepidoptera	Heliozelidae	1	0	0	0	0	0	0	0	0	
Lepidoptera	Hesperiidae	0	0	0	0	0	0	1	0	0	
Orthoptera	Gryllidae	0	0	0	0	0	0	0	2	0	
Psocoptera	Psocidae	0	0	0	0	1	0	0	0	0	
Psocoptera	Stenopsocidae	1	0	0	0	0	0	0	0	0	
Thysanoptera	Aeolothripidae	1	1	0	1	1	1	0	0	0	
Thysanoptera	Phlaeothripidae	0	0	1	1	1	1	0	1	0	
Thysanoptera	Thripidae	33	171	13	17	28	10	1	1	2	
Trichoptera	Glossosomatidae	0	0	0	1	0	0	0	0	0	
Trichoptera	Hydroptilidae	2	2	0	0	0	0	0	0	1	
Trichoptera	Philopotamidae	0	0	0	0	0	0	1	0	0	