

# The exotic invasive plant *Vincetoxicum rossicum* is a strong competitor even outside its current realized climatic temperature range

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## Abstract

Dog-strangling vine (*Vincetoxicum rossicum*) is an exotic plant originating from Central and Eastern Europe that is becoming increasingly invasive in southern Ontario, Canada. Once established, it successfully displaces local native plant species but mechanisms behind this plant's high competitive ability are not fully understood. It is unknown whether cooler temperatures will limit the range expansion of *V. rossicum*, which has demonstrated high tolerance for other environmental variables such as light and soil moisture. Furthermore, if *V. rossicum* can establish outside its current climatic limit it is unknown whether competition with native species can significantly contribute to reduce fitness and slow down invasion. We conducted an experiment to test the potential of *V. rossicum* to spread into northern areas of Ontario using a set of growth chambers to simulate southern and northern Ontario climatic temperature regimes. We also tested plant-plant competition by growing *V. rossicum* in pots with a highly abundant native species, *Solidago canadensis*, and comparing growth responses to plants grown alone. We found that the fitness of *V. rossicum* was not affected by the cooler climate despite a delay in reproductive phenology. Growing *V. rossicum* with *S. canadensis* caused a significant reduction in seedpod biomass of *V. rossicum*. However, we did not detect a temperature x competition interaction in spite of evidence for adaptation of *S. canadensis* to cooler temperature conditions. We conclude that the spread of *V. rossicum* north within the tested range is unlikely to be limited by climatic temperature but competition with an abundant native species may contribute to slow it down.

## Keywords

Dog-Strangling Vine, *Vincetoxicum rossicum*, invasive species, invasion ecology, competition, phenotypic plasticity, climatic temperature range, spread, reproductive phenology

## Introduction

Dog-strangling vine (*Vincetoxicum rossicum* (Kleopow) Barbar.; *syn. Cynanchum rossicum* (Kleopow) Borhidi) is an alien invasive plant species from the Ukraine and south-western Russia that has established in the north-eastern United States and southern Ontario. *Vincetoxicum rossicum* was first found in Toronto in 1889 (Smith et al. 2006). It is a perennial self-pollinating vine that produces pods filled with comose seeds that are wind-dispersed. *Vincetoxicum rossicum* effectively competes for light by forming large and dense stands that climb over other plants. This life-strategy results in suppression of native plant productivity and diversity (DiTommaso et al. 2005). *Vincetoxicum rossicum* has been found growing successfully in both disturbed and undisturbed areas, in open fields, forest edges and understories, parks, road edges and railway embankments. The species produces a dense and fibrous root system and demonstrates wide environmental tolerance to variations in light intensity and soil moisture (DiTommaso et al. 2005; Douglass et al. 2009).

Currently, the distribution range of *V. rossicum* in North America has temperature and precipitation limits similar to those found in its native range (Kricsfalussy and Miller 2010). This climatic distribution pattern is consistent with what occurs for many exotic invasive terrestrial plants. A recent study on Holarctic invasive plants indicates that their new invaded range matches their native realized climatic niche, and that most species do not tend to invade beyond that range (Petitpierre et al. 2012). However, given the high degree of environmental tolerance shown by *V. rossicum*, which factor(s) may be preventing its northern range expansion? Is it possible that nothing is limiting its expansion (i.e., propagules have simply not reached the north) or specific factors (e.g., climatic, edaphic, environmental disturbance, biotic interactions) are preventing establishment? Considering the large number of seeds produced and their anemochory, it is unlikely that expansion is being limited by low propagule pressure.

It is unknown the extent to which climate serves as a barrier for further spread in the introduced range. Areas of central/northern Ontario that have, on average, slightly cooler temperatures than those in the vine's current range might be at risk of invasion by this plant. As such, determining the phenology and fitness of *V. rossicum* under those conditions is required for risk assessment and to potentially adjust management practices.

Plant phenology can be influenced by abiotic and biotic factors (Pau et al. 2011) and provides invasive plants with a competitive advantage over native plants. For instance, accurate timing of budburst can allow invasive plants to outcompete native species for light and successfully timed reproductive phenology ensures higher levels of fitness (Wolkovich and Cleland 2011; Godoy et al. 2008). Analyses of long-term phenological responses of native and exotic plant species to climate change have indicated that exotic invasive species are better able than natives at adjusting their flowering time (Willis et al. 2010).

Field studies on plant phenology have indicated that temperature cues have a large influence on flowering in many species (Pau et al. 2011; Fitter et al. 1995; Vasek and Sauer 1971). If a potentially invasive plant cannot adjust its phenology to its new climate,

its chances of establishing a successful population may be drastically reduced. Therefore, environmental tolerance, phenotypic plasticity and/or adaptive evolution may be crucial factors for invader success. Since invasion by *V. rossicum* is currently restricted to areas of North America with a climate similar to that found in its native range, its potential to spread throughout the introduced range is unknown. Nevertheless, flowering is found to occur later in Ontario than in populations from the United States, indicating a potential climate-influenced phenological gradient (Douglass et al. 2009; DiTommaso et al. 2005). Species-distribution models have indicated that the northern limits of a plant's range may be strongly influenced by its inability to set mature seeds (Morin et al. 2007). Therefore, *V. rossicum* may be limited in its capacity to spread into northern climates simply because it may not be able to complete its life-cycle.

On the biotic side, interspecific competition may be a limiting factor in species distribution (Keddy et al. 1998). Therefore, understanding competitive interactions between invasive and native species is important in risk assessment and can result in novel or improved management and restoration approaches (Firn et al. 2010). In its current North American range, *V. rossicum* is able to form what are essentially monocultures (DiTommaso et al. 2005), which would suggest that it is an excellent competitor against native species. Competitive ability has been tested in regard to *V. rossicum* polyembryony (Blanchard et al. 2010) and potential allelopathy (Douglass et al. 2011); both studies incorporated native species that co-occur with *V. rossicum* and ran from periods ranging 2–15 weeks in length under static growing conditions. However, there are no data on whether *V. rossicum* responds negatively to a highly abundant native species outside its current climatic range.

The purpose of this study was two-fold. First, we investigated whether *V. rossicum* could grow under the cooler climate of northern Ontario, and whether any observed phenological changes could represent a barrier to the successful establishment of this invasive plant. Secondly, we tested the response of *V. rossicum* to the presence of a perennial abundant native plant (i.e., Canada goldenrod - *Solidago canadensis* L. var. *canadensis*) whose center distribution range is northern Ontario, and how the competitive interaction was affected by the shift in temperature. We selected *S. canadensis* as our competing species because it co-occurs with *V. rossicum* (Kricsfalussy and Miller 2010; Averill et al. 2008; Cappuccino 2004), and is prominent in both climate regimes simulated in our study. However, it is unknown if *V. rossicum* can invade *S. canadensis* populations in southern Ontario or the United States or vice-versa. *S. canadensis* is considered an invasive species in Europe and Asia (Abhilasha et al. 2008), suggesting that it may have strong competitive abilities in its native range. We hypothesised that this native plant might possess the competitive ability to withstand invasion by *V. rossicum* and produce a detrimental effect on its growth and fitness. While this ability may be out-performed by *V. rossicum* under the invasive plant's climatic range, it may exceed that of *V. rossicum* when allowed to grow under a climate that is established as suitable for *S. canadensis* but may prove challenging to *V. rossicum*. If this is the case, seeding with *S. canadensis* in areas invaded by *V. rossicum* may serve as an effective and environmentally friendly tool for management purposes on invaded sites.

## Materials and methods

Dog-strangling vine (*Vincetoxicum rossicum* (Kleopow) Barbar.) root crowns were collected in Rouge Park, Toronto, ON (43.80526°N, 79.13594°W) in early May, 2011, before the onset of the growing season. The substrate used in the experiment consisted of soil collected from an un-invaded site adjacent to one invaded by *V. rossicum*. Root crowns were planted in one side of 10 L pots that were divided in half by a nylon mesh (30 µm opening) (Sefar Nitex 03-30/18, Heiden, Switzerland), which allows water and microbes, including fungal hyphae, to cross but prevents roots. The use of this nylon mesh still allows plants to compete for water and nutrients through diffusion, mass flow and mycorrhizal networks while preventing the roots from intertwining. The pots were filled with a 13 cm layer of a 2:1 mixture of Turface (a montmorillonite clay, Turface Athletics MVP, Profile Products LLC, Buffalo Grove, IL, USA) and non-calcareous granitic sand (Hutcheson Sand and Mixes, Huntsville, ON) followed by a 10 cm layer of 1.2 kg of field soil, and an additional 3 cm of the Turface:sand mixture.

The experiment consisted of a completely randomized block design with two crossed factors; ‘plant competition’ and ‘temperature’. Specifically, for ‘plant competition’ *V. rossicum* plants were either planted alone (control) or with a Canada Golden-rod (*Solidago canadensis* L. var. *Canadensis*; seeds were collected in the north eastern United States by Ontario Seed Company, Waterloo, ON, Canada) seedling in the other half of the pot (competition group). *Solidago canadensis* seedlings were also planted alone (*S. canadensis* control). Each of these treatments comprised a total of 24 pots, which were divided evenly among six reach-in controlled environment units (Conviron, Winnipeg, MN, Canada), each representing a block; three chambers were set to Toronto (TO) growing season temperatures and three chambers set to Sault Ste. Marie (SSM) growing season temperatures for an overall total of 72 pots. To minimize any potential variability among controlled environment units all respective pots were rotated among units and re-randomized within each block every 25 days. Toronto temperatures are on average approximately 3° C warmer than SSM. We used weather records collected by Environment Canada from 1980–2010 to simulate the monthly temperature conditions throughout the growing season (Table 1). We also used these data to simulate photoperiod throughout the growing season. Since photoperiod was similar between the two locations and the main goal was to test temperature effects, it was kept the same across treatments (Table 1).

Plants were allowed to grow for five months (simulated “May” to “September”). During this time we recorded daily reproductive phenology measurements for *V. rossicum* (presence of first flower bud, first flower opening and seedpod production). Plants were watered to field capacity every second day to ensure that water deficiency was not a factor in the experiment. Since we noticed mild signs of nutrient deficiency in all plants, all pots were fertilized with Miracle-Gro 24:8:16 (The Scotts Company LLC, Mississauga, ON, Canada) (0.84 ppm P per pot) after the first month of growth. In addition all pots received a solution of 12-0-44 fertilizer (6 ppm N per pot) and

**Table 1.** Temperature regimes used to simulate Toronto (TO) and Sault Ste. Marie (SSM) growing seasons in the controlled environment units.

Location	Range <sup>†</sup>	May	June	July	August	September
Simulated temperature (°C) <sup>Δ</sup>						
TO	High	20.3	25.5	28.4	27.4	23.0
	Average	14.5	19.9	22.7	21.9	17.5
	Low	8.8	14.2	17.1	16.5	12.1
SSM	High	17.9	22.8	25.5	24.8	20.3
	Average	11.4	16.2	19.2	18.9	14.8
	Low	5.0	9.7	12.9	13.0	9.4
Simulated photoperiod (hours of light per day) <sup>‡</sup>						
		14h; 15h	15h	15h; 14h	14h; 13h	13h

<sup>†</sup> Simulated temperatures were 1.4 °C warmer than the calculated average to meet the minimum range allowed by the spell out controlled environment units (i.e., 5.0°C).

<sup>Δ</sup> Maximum and minimum temperatures were each maintained for 6 hours, with the remaining 12 hours set at average temperatures.

<sup>‡</sup> Average light intensity ranged between 350–400  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . When two values are given, this indicates the changing day length during that month.

slow-release 18-6-8, 70-day fertilizer (meaning that after 70 days, 80% of the nutrients would have been released into the soil; 0.72 ppm N per pot) (Nutricote, Plant Products Co., Brampton, ON, Canada) after the fourth month of growth. The use of low fertilizer concentrations and of a slow release fertilizer ensured that plants had sufficient nutrients to survive but that soil fertility was such that they had to compete for nutrients. In the final month of the experiment, plants experienced an outbreak of thrips in all chambers, and were sprayed with Nemasys nematode spray (50 million count, Becker Underwood, SK, Canada).

The commercial seed stock of *S. canadensis* was contaminated with other species of goldenrod and asters. This resulted in twelve pots (three alone and six in competition under TO temperatures and three in competition under SSM temperatures) containing the “wrong” plant species, which could not be differentiated until two months into the experiment. These pots have been removed from the competition data analysis, but have been kept for the *V. rossicum* phenology analysis.

At the end of the experimental period (as determined by simulated ‘first frost date’ for SSM), all plants were harvested. Roots and shoots were placed in separate bags, dried for three days at 60°C and weighed. Competitive response was calculated for both plant species according to methodology by Goldberg et al. (1999). Specifically, we calculated relative yield by dividing the total biomass of an individual plant grown with a competitor by the average total biomass for that same plant species grown alone. Competitive response was calculated by the ln of the relative yield; a negative number indicates a negative response to competition whereas a positive number indicates a positive response to competition.

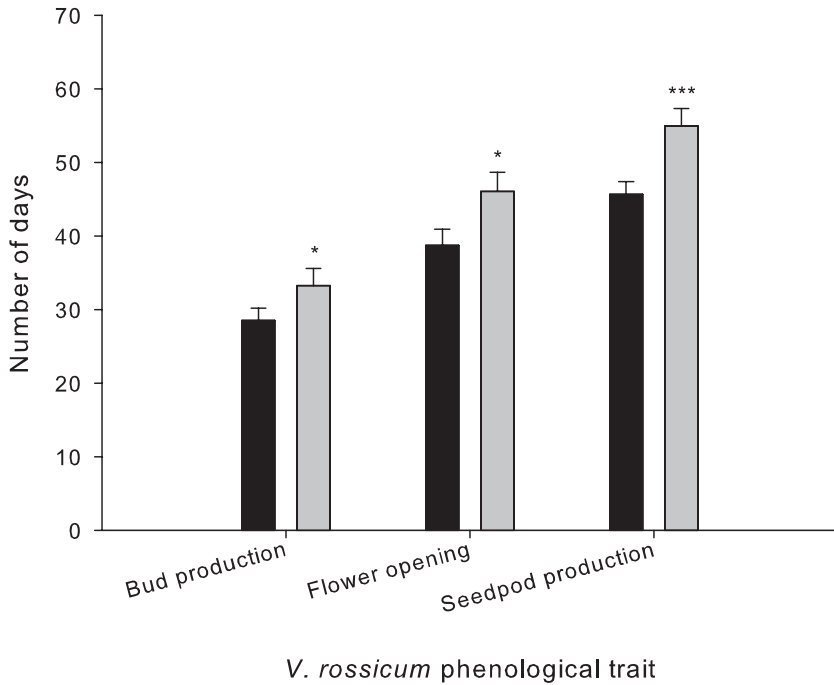
## Statistical analysis

We analysed plant responses to temperature on phenological data (i.e., flower budding, open flowering and Seedpod formation), total plant biomass, root : shoot ratio, and competitive response. Since pots were rotated and re-arranged randomly among controlled environment units as blocks to minimize the potential for chamber effects, block effects were tested first within each temperature group using one-way ANOVAs. If a block effect was not detected, factorial ANOVAs were carried out. When testing phenology, total biomass, and root : shoot ratio each plant species was tested individually with the factor 'plant competition' being comprised of two levels (i.e., either *S. canadensis* or *V. rossicum* alone or the response of that species in presence of the competitor). To test for competitive response the model included 'plant competition' and 'temperature' as factors. Data were Box-Cox transformed to meet the test's assumptions. All statistical analyses were carried out using Statsoft Inc. (2010).

## Results

There were no significant differences in the reproductive phenology (i.e., presence of first flower bud, first flower opening and seedpod production) of *V. rossicum* grown either alone or with a competitor. In addition, we did not find a significant interaction between competition and temperature for any of these response variables. Temperature, however, had a significant effect on the reproductive phenology of *V. rossicum* (Fig. 1). Plants grown under SSM temperatures took significantly longer to produce flower buds ( $F_{1,44} = 9.270$ ,  $p = 0.00392$ ), open flowers ( $F_{1,44} = 11.040$ ,  $p = 0.00180$ ), and seedpod ( $F_{1,44} = 19.778$ ,  $p = 0.00006$ ). These traits were delayed by an average of 8, 9 and 11 days, respectively, under the cooler SSM temperatures. By the end of the experimental growing season, however, all *V. rossicum* plants had produced the same biomass and number of seedpods containing mature seeds regardless of temperature treatment (Fig. 2A and C). Conversely, growing *V. rossicum* with a competitor caused significant reductions in the seedpod biomass of *V. rossicum* ( $F_{1,36} = 42.812$ ,  $p = 0.000001$ ) and in the number of seedpods produced ( $F_{1,36} = 30.73$ ,  $p = 0.000003$ ) (Fig. 2B and D). We did not detect a significant interaction between temperature and competition for seedpod biomass or number.

Depending on the species, total plant biomass was affected by either temperature or competition. The total biomass of *V. rossicum* was not influenced by temperature but it was significantly affected by competition ( $F_{1,35} = 8.3459$ ,  $p = 0.007$ ), and we did not detect a competition x temperature interaction (Table 2). *Vincetoxicum rossicum* was approximately two times more competitive than *S. canadensis* ( $F_{1,25} = 4.60392$ ,  $p = 0.042$ ) (Fig. 3). *Vincetoxicum rossicum* plants grown with *S. canadensis* were 22% smaller than plants grown alone whereas *S. canadensis*



**Figure 1.** Number of days necessary for the production of buds, flowers and seedpods under TO (black bars) and SSM (grey bars) temperatures. Significant differences between temperature regimes for each phenological trait are indicated by \* ( $p < 0.05$ ) \*\* ( $p < 0.01$ ) and \*\*\* ( $p < 0.0001$ ). Error bars represent the standard error of the mean ( $n = 24$ ).

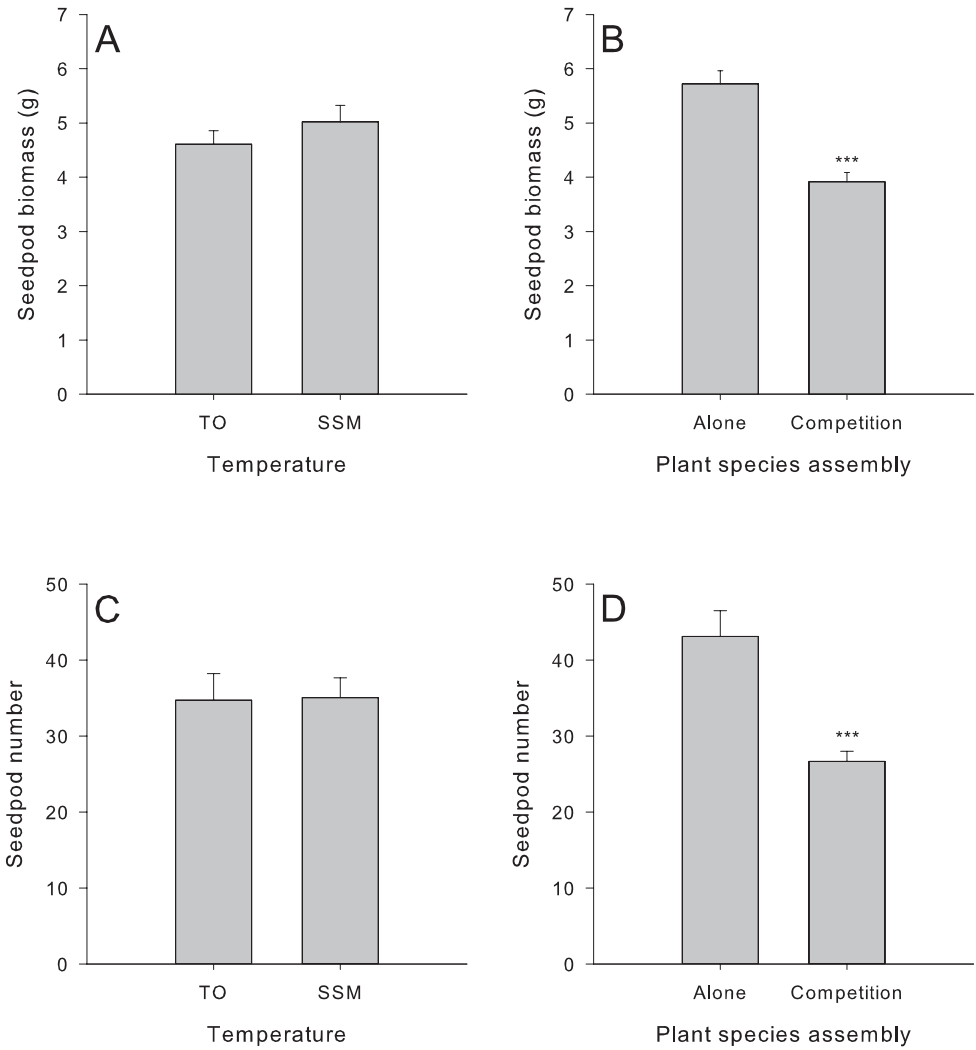
**Table 2.** Total biomass (g) and root : shoot ratio of *V. rossicum* and *S. canadensis* grown under Toronto (TO) and Sault Ste. Marie (SSM) temperature regimes and either alone or in competition with each other.

	Total biomass (g)		Root : shoot ratio	
	<i>V. rossicum</i>	<i>S. canadensis</i>	<i>V. rossicum</i>	<i>S. canadensis</i>
TO	23.56 ± 1.50	54.92 ± 4.90	2.05 ± 0.17	1.91 ± 0.18
SSM	22.75 ± 1.39	80.27 ± 8.99*	1.93 ± 0.19	2.97 ± 0.37
Alone	25.27 ± 1.39	82.46 ± 8.55	1.72 ± 0.14	2.42 ± 0.29
Competition	19.68 ± 0.86**	51.86 ± 5.23**	2.41 ± 0.20*	2.68 ± 0.42

For each species, statistically significant differences for each appropriate treatment factor are represented by \* ( $p < 0.05$ ) and \*\* ( $p < 0.001$ ). Data are presented as mean ± standard error of the mean. (*V. rossicum*, temperature:  $n = 18$  (TO),  $n = 21$  (SSM); *V. rossicum*, plant species assembly:  $n = 24$  (alone),  $n = 15$  (competition); *S. canadensis*, temperature:  $n = 15$  (TO),  $n = 21$  (SSM); *S. canadensis*, plant species assembly:  $n = 21$  (alone),  $n = 15$  (competition)).

plants were 37% smaller when competing with *V. rossicum* ( $F_{1,32} = 12.914$ ,  $p = 0.001$ ) (Table 2; Fig 3). Growing temperature influenced the total biomass of *S. canadensis*. Plants grown under the cooler SSM conditions were 1.5 fold larger than



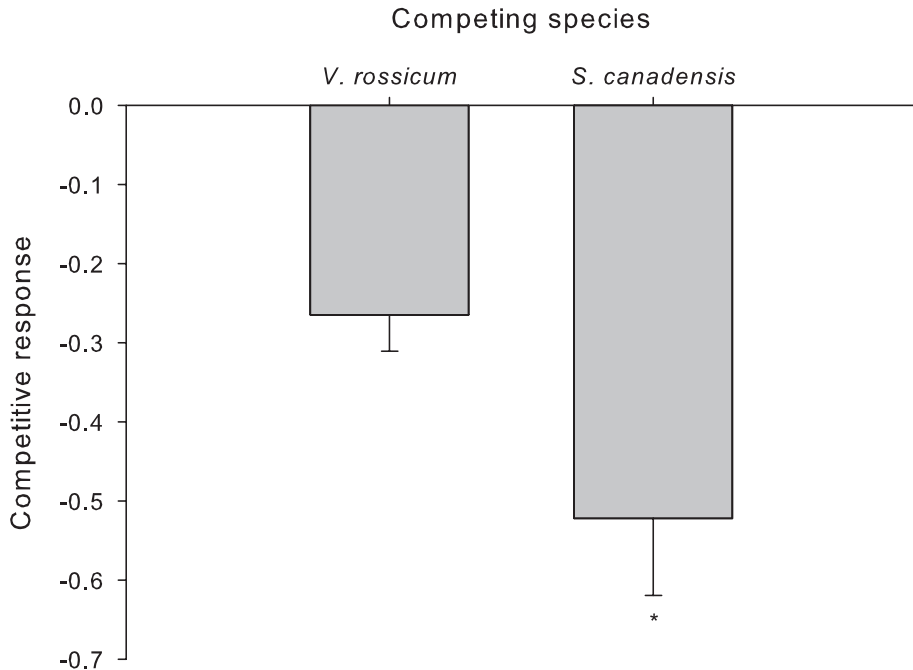


**Figure 2.** Effect of climatic temperature (i.e., Toronto (TO) and Sault Ste. Marie (SSM) and plant-plant competition (i.e., *V. rossicum* grown either alone or with *S. canadensis* (competition)) on seedpod biomass (A and B) and number (C and D) of *V. rossicum* at the end of the experiment. Significant differences between treatments are represented by \*\*\* ( $p < 0.00001$ ). Error bars represent the standard error of the mean ( $n = 24$ ).

those grown in the warmer temperature ( $F_{1,32} = 6.1587$ ,  $p = 0.018$ ). There was no significant temperature x competition interaction.

Root : shoot ratio of *V. rossicum* was 1.4-fold higher in plants competing with *S. canadensis* as opposed to those grown alone ( $F_{1,35} = 9.3602$ ,  $p = 0.004$ ) (Table 2). This ratio was not affected by temperature (Table 2) or the combination of temperature and competition (data not shown). Conversely, the root : shoot ratio of *S. canadensis* was not affected by any factor or their interaction.





**Figure 3.** Competitive response (i.e., calculated by the  $\ln$  of the relative yield, calculated by dividing the total biomass of an individual plant grown with a competitor by the average total biomass for that same plant species grown alone) of *V. rossicum* and *S. canadensis* relative to the presence of the competing species. Significant differences between species are indicated by an \* ( $p < 0.05$ ). Error bars represent the standard error of the mean ( $n = 15$  (*V. rossicum*; *S. canadensis*)).

## Discussion

Temperature significantly affected the reproductive phenology of *V. rossicum*. Generally, phenological reproductive events took longer to occur under the cooler growing temperature conditions. This was expected as many plant species are known to accelerate their reproductive phenology when subjected to warming (Sherry et al. 2007), especially those with flowering times that occur before the peak of summer, as is the case of *V. rossicum*. Indeed, we found that a slight reduction from the current growing temperature conditions of *V. rossicum* was sufficient to produce a significant delay in budding, flowering, and the formation of seedpods. Along with photoperiod and moisture, temperature is considered a key environmental cue for flowering (Ratchke and Lacey 1985). Since we controlled for photoperiod and moisture, changes in the phenology of *V. rossicum* were likely solely influenced by temperature in our experiment. This is consistent with data indicating that some plants require the cumulative heatsum (i.e., a sum of daily heat inputs) to reach a certain threshold before flowering occurs (Reader 1983; Vasek and Sauer 1971; Ratchke and Lacey 1985). As such, we anticipate that *V. rossicum* will take longer to reach that threshold if it can indeed establish and overwinter in field soils from northern Ontario.

A plant's northern range is determined by its capacity to overwinter and then produce viable seeds (Morin et al. 2007; Chiune 2010). In this experiment the growing season temperature limit of *V. rossicum* was not reached, as all plants planted as root crowns produced mature seeds by the end of the growing season, which was simulated to coincide with the first frost in the SSM climatic region. This suggests that, despite experiencing a delay in reproductive phenology, *V. rossicum* can successfully produce as many propagules in the northern climate simulated in this experiment as in its current climate. Plants in their northern distribution ranges shorten their phenological timing to compensate for the shorter growing season, which can be done through phenotypic plasticity (Chiune 2010). It has been suggested that rapid seed maturation may be an adaptation to a later flowering time (Vasek and Sauer 1971). *Vincetoxicum rossicum* grown at lower temperatures produced mature seeds at the same time as those grown in warmer temperatures, suggesting an increase in seed maturation rate. As such, we conclude that phenotypic plasticity may enable this species to complete its life-cycle under the cooler climate of northern Ontario. However, our study focused on the growing season and *V. rossicum* started from root crowns. Future research should consider this species' potential to rapidly evolve, including its capacity to overwinter and grow under different (a)biotic conditions, upon establishment from seeds.

The native forb *S. canadensis* is highly abundant in disturbed areas in its native range and is an exotic invader in Europe and Asia (Abhilasha et al. 2008). The species is well adapted to cold climates; the center of the distribution range of *S. canadensis* var. *canadensis* is northern Ontario (USDA NRCS, National Plant Data Team). Indeed, we did find evidence for adaptation to the colder temperature conditions of our experiment as plants grown under the cooler SSM conditions were 1.5 fold larger than those grown in the warmer temperature. These features made it a suitable candidate to potentially reduce the spread of *V. rossicum* either intentionally through seed augmentation or naturally, particularly under northern Ontario temperature conditions. There has been some discussion as to whether some native species can be considered invasive within their native range and whether they should be treated differently than exotic invasive species (Davis et al. 2011). From that perspective, using a native species that is highly abundant in disturbed areas as a means of *V. rossicum* control could be problematic. However, various factors contribute to increase the risk of invasion by exotic relative to native species (see Simberloff et al. 2012) and considering that, overall, the most problematic biological invasions are caused by exotic species, we propose that investigating interactions between abundant native competitors and invasive exotic species should be considered both as a management option and in risk assessment.

We forced *V. rossicum* to compete against *S. canadensis*, which is highly abundant across the two climatic regions considered in this study. Competition between plants has been shown to reduce biomass, including allocation of biomass to reproduction (Weiner 1988). Indeed, seedpod biomass of *V. rossicum* plants grown in competition with *S. canadensis* was significantly smaller than that of plants grown alone regardless of growing season temperature conditions to which our variety of *S. canadensis* appeared to be adapted. Likewise, the total biomass of both *V. rossicum* and *S. canadensis* were

significantly reduced in response to competition. However, even though *S. canadensis* ultimately produced more total biomass than *V. rossicum*, it was more negatively influenced by competition. This may result in *V. rossicum* populations out-competing those of *S. canadensis* over time, even though we did not determine the fitness (i.e., seed production) response of *S. canadensis* to competition. Therefore, the method of seeding *S. canadensis* in areas invaded by *V. rossicum* as a control option to reduce its fitness and spread may be an inefficient approach in the long-term. Even more so if we consider that feedback with soil biota is likely to lead to greater pathogen accumulations and growth reductions in native compared to exotic plants (Klironomos 2002).

Several factors were likely to have contributed to the competitive advantage of *V. rossicum* relative to *S. canadensis* in relation to total plant biomass. Plants were not limited by water, light or space aboveground, which suggests that most competition would occur belowground for limited nutrient resources, which were supplied in low concentrations throughout the course of the experiment. *Vincetoxicum rossicum* increased its root : shoot ratio when in competition with *S. canadensis* whereas *S. canadensis* showed no response. This response of *V. rossicum* is consistent with competitively-driven adaptive plasticity, which can be explained by the balanced resource hypothesis; plants allocate nutrients and energy for growth to the areas responsible for the acquisition of limiting resources (Brouwer 1962). Competitively-driven adaptive plasticity has been shown in other plant species especially under limited nutrient regimes (Berendse and Möller 2009). The observed differential between the two species in their capacity to shift resource allocation towards roots when in competition suggests that this may be an important factor in the success of *V. rossicum* as an invader.

Goldberg (1990) proposed that if both competitors start as seedlings, the species that is better able to acquire resources has the competitive advantage. However, if one species has an initial size advantage, which was the case in our study (*S. canadensis* seedling competing with a *V. rossicum* plant started from a mature root crown), the species that is better able to tolerate resource limitation has a competitive advantage. Our data indicate that *V. rossicum* can both tolerate and scavenge for the limiting resources present. Although the size asymmetry may have led to some initial competition bias towards *V. rossicum*, our goal was to test whether *S. canadensis* could alleviate the invasion of already established *V. rossicum*. Nevertheless, future studies on competition between these two species could start equally from seeds. Future work should also investigate whether using a greater density of *S. canadensis* may be a more effective approach to help control *V. rossicum*. However, as discussed earlier competition and possible feedbacks with biota may favour *V. rossicum* in the long-term.

*Vincetoxicum rossicum* has been shown to be dependent on the association with arbuscular mycorrhizal (AM) fungi (Smith et al. 2008) and to be more heavily colonized by AM fungi in the field than other species grown in the same area (Greips-son and DiTommaso 2006). On the other hand, there is some evidence that *S. canadensis* may not be as mycorrhizal dependent as *V. rossicum* (Dhillon and Friesse 1994). Indeed, in our experiment *V. rossicum* had lower root : shoot ratios than *S.*

*canadensis*, which is typical of more mycorrhizal plants (Oliver et al. 1983). The mesh utilized in our competition pots was designed to keep plant roots separate between species while allowing AM fungal hyphae to pass between the divided chambers. Therefore, we hypothesize that *V. rossicum*'s association with AM fungi may have facilitated access to the other half of the competition pot. Future work should focus on the role of soil biota as potential modulators of competitive interactions between native and exotic invasive species, which has not been consistently determined (Colautti et al. 2004; Levine et al. 2003).

Another possible reason for *S. canadensis* being a weaker competitor than *V. rossicum* could be that its timing for nutrient acquisition occurred later than that of *V. rossicum*'s. The two perennial species demonstrate different strategies; *V. rossicum* grows quickly early in the season whereas *S. canadensis* grows steadily over a longer period of time. A grassland study on invasion potential and resistance to invasion suggested that such resistance requires species that can establish and proliferate well, but also overlap the timing of their resource acquisition to that of the invading species (Young et al. 2008). It has also been suggested that the most accurate information about an invasive plant's competitive ability against native species comes from pairing the invasive plant with a functionally similar native species (Firn et al. 2010). Testing other competitor species that are more functionally similar to *V. rossicum* might provide further insight into the competitive ability of this invasive vine and its invasion potential when *S. canadensis* is not present.

## Conclusion

In spite of a delay in reproductive phenology, the fitness of *V. rossicum* does not appear to be limited by cooler growing season temperature regimes found outside its immediate current distribution range in North America. Competition resulted in reductions in the fitness and total biomass of *V. rossicum* regardless of climatic temperature. However, the relative reductions in total biomass were greater for the competing native species *S. canadensis*.

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# Stomach contents from invasive American bullfrogs *Rana catesbeiana* (= *Lithobates catesbeianus*) on southern Vancouver Island, British Columbia, Canada

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## Abstract

Invasive alien American bullfrog populations are commonly identified as a pernicious influence on the survival of native species due to their adaptability, proliferation and consequent ecological impacts through competition and predation. However, it has been difficult to determine conclusively their destructive influence due to the fragmentary and geographically dispersed nature of the historical database. An expanding meta-population of invasive American bullfrogs, *Rana catesbeiana* (= *Lithobates catesbeianus*), became established on southern Vancouver Island, British Columbia, Canada in the mid- to late 1980s. An on-going bullfrog control program begun in 2006 offered a unique opportunity to examine the stomach contents removed from 5,075 adult and juvenile bullfrogs collected from 60 sites throughout the active season (April to October). Of 15 classes of organisms identified in the diet, insects were numerically dominant, particularly social wasps and odonates (damselflies and dragonflies). Seasonality and site-specific habitat characteristics influenced prey occurrence and abundance. Native vertebrates in the diet included fish, frogs, salamanders, snakes, lizards, turtles, birds, and mammals, including some of conservation concern. Certain predators of bullfrog tadpoles and juveniles are commonly preyed upon by adult bullfrogs, thereby suppressing their effectiveness as biological checks to bullfrog population growth. Prey species with anti-predator defences, such as wasps and sticklebacks, were sometimes eaten in abundance. Many prey species have some type of anti-predator defence, such as wasp stingers or stickleback spines, but there was no indication of conditioned avoidance to any of these. Results from this study reinforce the conclusion that, as an invasive alien, the American bullfrog is an opportunistic and seemingly unspecialized predator that has a uniquely large and complex ecological footprint both above and below the water surface.

## Keywords

Bullfrog, *Rana catesbeiana*, *Lithobates catesbeianus*, predation, diet, invasive species

## Introduction

The American bullfrog, *Rana catesbeiana* (= *Lithobates catesbeianus*), is widely considered one of the most ecologically destructive of invasive alien vertebrate species (Lowe et al. 2000, Kraus 2009, CABI 2011). Conservation concerns arise from its adaptability to a wide variety of environmental conditions, extraordinarily rapid population growth and distributional expansion rates, and most particularly to its presumed rapacious unspecialized carnivory. However, documentation of its full impact as an invasive remains regionally fragmentary. Numerous studies from around the world have examined bullfrog stomach contents, but these have tended to sample relatively few bullfrogs from a very few sites in a narrow time frame (Table 1).

From previous studies, a number of commonalities emerge. Bullfrogs consume a large number and variety of prey species (Bury and Whelan 1984) with insects usually numerically dominant (Korschgen and Moyle 1955, Cohen and Howard 1958, McCoy 1967, Bruggers 1973, Werner et al. 1995, Hirai 2004, Laufer 2004, Barrasso et al. 2009, Hothem et al. 2009, Silva et al. 2009). Certain insect groups are eaten more frequently, and many studies have found beetles (Coleoptera) to be most often consumed (Cohen and Howard 1958, McCoy 1967, Bruggers 1973, Laufer 2004, Diaz De Pascual and Guerrero 2008, Hothem et al. 2009). Other invertebrates, such as isopods (Irwin 1994, Krupa 2002) and crayfish (Bruggers 1973, Carpenter et al. 2002, Hirai 2004) are common prey. Adult bullfrogs are known to eat larger prey (Bruneau and Magnin 1980), and this is often vertebrates—frequently frogs (Korschgen and Moyle 1955, Stuart and Painter 1993, Werner et al. 1995, Govindarajulu et al. 2006, Diaz De Pascual and Guerrero 2008).

Populations of alien, invasive bullfrogs, geographically isolated and arising independently, are scattered along the southeast coast of Vancouver Island—their origins are often obscure. However, in the mid-1980s, a population of American bullfrogs became established just north of the City of Victoria at the extreme southern end of Vancouver Island (Orchard 1999). Subsequently, the population expanded unchecked and, consequently, invaded dozens of lakes and ponds throughout regional Victoria (Saanich Peninsula). Previous studies on bullfrogs in regional Victoria have included diet (Irwin 1994, Govindarajulu et al. 2006), but the sites sampled and bullfrogs examined were limited in number (Table 1). Differences in seasonality, site variation, and age-class could not therefore be reliably inferred on either a population or regional scale. An on-going bullfrog eradication program on southern Vancouver Island got underway in 2006 (Orchard 2011) which presented a rare opportunity to thoroughly examine and compare the stomach contents of all, or a majority of, post-metamorphic size-classes from entire populations taken from a diversity of lakes and ponds and collected throughout the 6-month active season. The results presented here are derived from the stomach contents of 5,075 bullfrogs caught and euthanized during the course of the eradication program. The data explores the scope of bullfrog predation on the native fauna, as well as site and seasonal variation in prey species composition. All this is relevant to the fundamental question and discussion of whether or not control or eradication efforts are warranted for invasive alien populations of the American bullfrog.

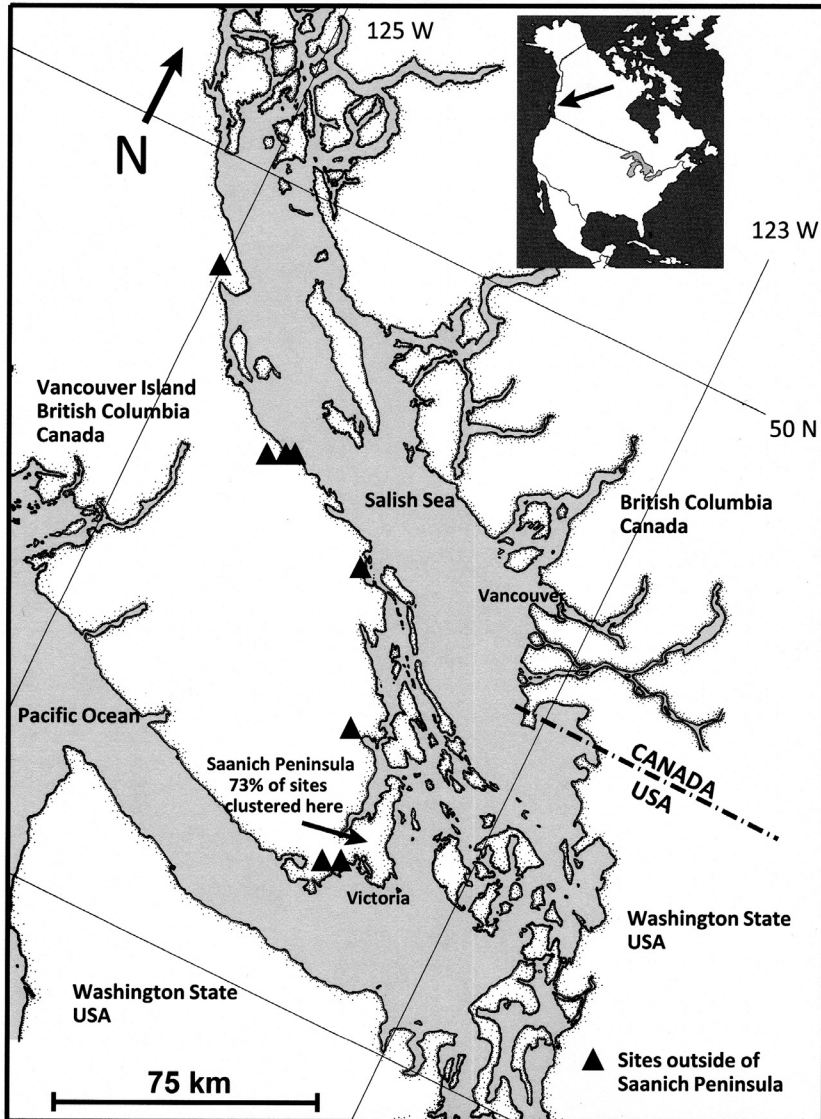
**Table 1.** Stomach contents analyses from both native and invasive alien populations.

Location	Invasive alien status	Sample size	Number of sites	Reference
Argentina: Buenos Aires	Non-native	35	3	Barrasso et al. 2009
Brazil: Minas Gerais	Non-native	113	1	Silva et al. 2009
Canada: British Columbia	Non-native	13	1	Irwin 1994
Canada: British Columbia	Non-native	150	4	Govindarajulu et al. 2006
China: Daishan Island	Non-native	121	1	Wu et al. 2005
Germany: Baden Wuerttemberg	Non-native	44	1	Laufer 2004
Japan: Kyoto	Non-native	128	1	Hirai 2004
USA: California	Non-native	5	1	Jennings and Cook 1998
USA: California	Non-native	30	1	Carpenter et al. 2002
USA: California	Non-native	107	2	Hothem et al. 2009
USA: Michigan	Native	166	2	Werner et al. 1995
USA: Missouri	Native	455	1	Korschgen and Moyle 1955
USA: Missouri	Native	4	1	Beringer and Johnson 1995
USA: Nebraska	Non-native	1	1	Bomberger Brown and Brown 2009
USA: Nevada	Non-native	28	2	Cross and Gerstenberger 2002
USA: New Mexico	Non-native	138	1	Stuart and Painter 1993
USA: New Mexico	Non-native	85	1	Krupa 2002
USA: Ohio	Native	158	1	Bruggers 1973
USA: Ohio	Native	1	1	Spetz and Spence 2009
USA: Oklahoma	Native	52	1	McCoy 1967
Venezuela	Non-native	338	1	Diaz De Pascual and Guerrero 2008
Total for all locations		2172	29	

## Methods

### Study sites

The term “site” is used here, as in Orchard (2011), to mean a discrete body of standing water—generally a lake, pond, or pool—where some or all life stages of bullfrogs are present. All bullfrogs examined came from 60 lakes and ponds spread across the coastal lowlands of southeastern Vancouver Island, 44 (73%) of which are clustered in peninsular regional Victoria (Figure 1, Table S1). All of these lakes and ponds are situated between the latitudes 49.8047 and 48.3867 (Figure 1) and range in surface area from lakes as large as 61 ha<sup>2</sup> (Langford Lake: 48.4484, -123.5296) with perimeter distances of almost 5 km down to very small ponds of less than 1 ha<sup>2</sup>. Most of the sites were florally complex with thick patches of floating aquatic and emergent vegetation, often with surrounding riparian thickets of willow (*Salix* spp.) and hardhack (*Spiraea douglasii*). Conversely, many of the smaller ponds were highly disturbed and modified habitats such as at farm ponds or golf course ponds with relatively little vegetation either in the water or around the shoreline.



**Figure 1.** Latitudinal range of study sites on southeastern Vancouver Island, British Columbia, Canada.

### Collecting and processing

All fieldwork was carried out by one 2-person team working full-time, approximately 125 nights per season (April–September). Adult and juvenile bullfrogs were captured live using a patented manual “electro-frogger” technique that stuns them momentarily in the water so that they can be netted. They were later euthanized in a two-stage process that cooled them to torpor below 2<sup>o</sup> C before being quick frozen (Orchard 2011). After at least 48 hours in a deep freeze, the bullfrogs were thawed and body lengths

measured with Vernier calipers (BL; snout to anus) recorded to the nearest 0.1 mm. The alimentary canal of each bullfrog was incised at the anterior and posterior sphincters of the stomach. All contents were removed and examined. Vegetation and other non-animal material were not included in this analysis. Size-classes were grouped according to body length and categorized as “juvenile” (< 80 mm; includes metamorphs but excludes tadpoles), “young adult” (80–120 mm), and “mature adult” (> 120 mm) (Table 2). “Metamorph” is a transitional stage whose morphology is primarily that of a juvenile but exhibiting some residual larval (tadpole) characteristics. We classed metamorphs as juveniles. Tadpoles did not figure in this study. The terms juvenile, young adult, and mature adult generally correspond to age-class cohorts, e.g. bullfrogs at this latitude spend their first year post-metamorphosis as a juvenile, their second year as a young adult, and their third year as a mature adult. Gender was determined by dissection for all specimens greater than or equal to 80 mm.

Six calendar months were available for fieldwork (April to September, inclusive) but only one site was sampled in all six calendar months (Florence Lake, 48.4589, -123.5127). This site provided 33% ( $n = 1,681$ ) of the total sample. Conversely, 58% ( $n = 35$ ) of the total sites sampled were each visited in only one calendar month of each

**Table 2. A.** Numbers of bullfrog stomachs with contents (91% of total examined), **(B)** without stomach contents (9% of total examined), and **(C)** with stomach contents as a percentage of monthly totals (with contents + without).

<b>A.</b>								
Body length (mm)	April	May	June	July	August	September	Totals	% of Total
Juveniles < 80	338	496	212	224	397	453	2120	46
Young males 80-120	70	113	182	214	313	102	994	22
Mature males > 120	7	74	95	41	53	31	301	6
Young females 80-120	110	111	111	139	242	212	925	20
Mature females > 120	3	60	61	35	67	36	262	6
Totals	528	854	661	653	1072	834	4602	100
% of Total with contents	12	19	14	14	23	18	100	
<b>B.</b>								
Body length (mm)	April	May	June	July	August	September	Totals	% of Total
Juveniles < 80	44	19	15	67	52	90	287	61
Young males 80-120	8	9	8	7	3	3	38	8
Mature males > 120	3	19	19	10	7	8	66	14
Young females 80-120	14	4	2	5	6	10	41	8.5
Mature females > 120	2	9	6	9	10	5	41	8.5
Totals	71	60	50	98	78	116	473	100
% of Total	15	13	11	21	16	24	100	
<b>C.</b>								
	April	May	June	July	August	September	Total Sample	
Total sample (with contents + without)	599	914	711	751	1150	950	5075	
% with contents	88%	93%	93%	87%	93%	88%	91%	

of the 6 months available but these collectively produced only 10% ( $n = 516$ ) of the total sample. Most of the total bullfrog sample (68%,  $n = 3,455$ ) came from 8 sites that were visited in at least 4 of the 6 months (Table S1, Table S2).

Results

The range of organisms found in the stomachs of adult and juvenile bullfrogs spans 15 taxonomic classes (Table 3). The overall sample included 350 (7%) metamorphosed bullfrogs taken between 2006 and 2008; the entire 3,835 caught in 2009 (76%); and 890 (17%) selected from a much larger sample from 2010. Contents from a total of 5,075 bullfrog stomachs, collected over a five-year span, were ultimately examined (Tables 2A, 2B). Of all stomachs, 473 were found to be empty and were removed from the subsequent analyses of the remaining 4,602 (Table 2A). A total of 18,814 identifiable individual prey remains were recovered: 15,081 (80%) of these from the 2009 series, 2,612 (14%) from the 2010 series, and the remaining 1,121 (6%) from 2006 to 2008.

Insects

Out of 18,814 instances of identifiable remains, 84% were insects. Insects were also found in 93% of bullfrog stomachs and were consumed at 95% of the 60 sites sam-

**Table 3.** Prey remains identified to class.

Class	Total number of instances	% of total prey remains	% of bullfrog stomachs with contents	% of sites
Insecta	15,827	84.1	93.0	95
Arachnida	874	4.6	12.4	51
Malacostraca	770	4.1	10.9	50
Gastropoda	644	3.4	10.3	62
Amphibia	247	1.3	4.2	72
Actinopterygii	166	0.9	2.8	32
Clitellata	107	0.6	1.4	25
Diplopoda	59	0.3	0.9	20
Mammalia	40	0.2	0.9	32
Aves	25	0.1	0.6	27
Chilopoda	20	0.1	0.3	17
Reptilia	12	0.06	0.2	15
Chelonia	12	0.06	0.2	2
Bivalvia	8	0.04	0.1	5
Gordioidea	3	0.02	0.06	2
Totals	18,814	100		



pled. The range in types of insects consumed is highly variable. Most insect parts were not identifiable to species but were at least attributable to one of 47 broader categories of variable taxonomic resolution (Table 4, Table S3).

At least 87% of adult and juvenile bullfrogs had food in their stomachs irrespective of month (Table 2C), although the species composition and densities of available prey change from month to month (Table 4). For example, dragonflies and damselflies were a dietary staple except in April, whereas social wasps were a dominant prey item but only in the late summer. Aphids were similarly important in the late summer but at only 20% of sites (Table 4). Late-summer prey also included brachyceran flies (par-

**Table 4.** Occurrence of individual prey remains identifiable as insect. The 21 most abundant insect prey categories are shown (See Table S3 for other insects identified).

Insect group (adults unless specified)	Total # of instances	% of total prey items	% of bullfrog stomachs	% of sites	Seasonality: % cases / month					
					Apr	May	June	July	Aug	Sept
Social Wasp	2,674	14.0	16.0	50	< 1	< 1	1	13	64	22
Aphid	1,982	10.0	4.9	20	1	2	1	2	71	24
Damselfly	1,947 (17% nymph)	10.0	23.0	68	2	18	35	13	25	7
Dragonfly	1,415 (27% nymph)	7.5	22.0	87	1	21	25	17	23	13
Water Strider	1,259	6.7	12.0	41	42	13	17	12	11	5
Unidentified Beetle	1,157	6.1	18.0	67	13	27	16	13	15	16
Brachycera fly	726 (61% larvae)	3.8	8.9	42	4	3	7	10	21	55
Ground Beetle	675	3.6	9.6	67	20	26	15	7	19	13
Nematocera fly (not crane flies)	472	2.5	6.9	30	8	34	7	14	24	13
Ant	415	2.2	6.3	42	7	16	11	21	39	6
Predaceous diving beetle	399	2.1	6.8	67	12	31	18	9	23	7
Butterfly/ Moth	365 (55% larvae)	1.9	5.4	55	5	14	36	12	28	5
Weevil	324	1.7	4.6	28	6	12	4	13	18	47
Other bee	257	1.4	3.4	18	4	2	7	50	18	19
Honey bee	254	1.4	2.5	11	1	< 1	8	70	16	5
Unidentified insect	234	1.2	4.6	47	13	19	16	11	20	21
Back-swimmer	225	1.2	3.4	50	2	30	25	9	8	26
Caddisfly	206 (10% larvae)	1.1	2.8	28	38	45	6	1	5	5
Non-social wasp	124	0.7	2.4	31	3	6	13	22	41	15
Click beetle	108	0.6	2.0	27	23	52	19	3	3	0
Giant water bug	96	0.5	1.9	37	1	43	24	9	14	9
Ladybird beetle	87	0.5	1.6	18	3	5	3	12	33	44

ticularly hoverfly larvae) (September), honey bees and other bees (July), and ladybird beetles (August–September) (Table 4). Water striders were especially significant at the start of the active season in mid-April (Table 4). They peaked in the diet of bullfrogs 60–70 mm in body length and then gradually dropped to zero in those over 140 mm. Giant water bugs were found in 27% of stomachs from one site (Filberg Marsh, May 27, 2010) but were relatively uncommon at most other sites.

**Non-insect invertebrates**

Collectively, non-insect invertebrates made up just over 13% of prey remains with spiders and mites (Arachnida) at 4.6%, isopods and crayfish (Malacostraca) at 4.1%, and snails and slugs (Gastropoda) at 3.4% (Table 5). These three non-insect invertebrate classes all follow immediately behind Insecta (84%) in number of prey instances (Table 3). Gastropods had been eaten at 62% of sites, followed by Arachnida (52%), and Malacostraca (50%) (Table 3).

Spiders (Arachnida) were the most frequently encountered non-insect invertebrate group (Table 5) but still ranked seventh overall behind the six dominant categories of insect. Unlike the seasonal and transient nature of many of the insect groups, spiders remained common prey throughout the active season (Table 5). After spiders, the next arthropod groups were isopods, in eleventh place overall, and crayfish (Malacostraca) in twenty-second. Crayfish figured in the diet at only 22%, of sites and their importance varied from site to site. For example, at one site they were found in 62% of stomachs, but these were taken from a relatively small series of only 16 bullfrogs. Aquatic snails ranked tenth in overall frequency while terrestrial slugs were in twenty-fifth place and found in 1.6% of bullfrog stomachs (Table 5).

**Table 5.** Non-insect invertebrate prey remains.

Non-insect invertebrate group	Total # of cases	% of total prey remains	% of bullfrog stomachs	% of sites	Seasonality: % of cases / month					
					Apr	May	June	July	Aug	Sept
Spiders	873	4.6	8.9	52	7	24	24	25	10	10
Snails	533	2.8	8.1	58	12	12	12	11	15	20
Isopods	481	2.6	5.3	40	22	17	17	6	9	26
Crayfish	174	0.92	2.8	22	2	17	17	18	52	6
Amphipods	115	0.61	0.24	2	0	62	62	9	1	0
Slugs	108	0.57	1.60	38	22	10	10	20	23	3
Earthworms	83	0.44	0.37	12	76	0	0	0	2	2
Millipedes	59	0.31	0.91	20	22	5	5	5	10	12
Leeches	24	0.13	0.48	20	17	8	8	0	13	37
Centipedes	20	0.11	0.33	17	0	33	33	20	7	7
Clams	8	0.04	0.11	5	0	25	25	0	0	12
Mites	1	0.01	0.02	2	0	0	0	100	0	0

Vertebrates

Fish (Actinopterygii) and amphibians (Amphibia) were the dominant vertebrate prey, occurring in 2.8% and 4.2% of the stomachs, respectively (Table 3). Three-spined stickleback fish (*Gasterosteus aculeatus*) was the most common vertebrate prey species, but found in only 1.5% of bullfrogs stomachs and at just 27% of sites (Table 6). Their frequency in the diet varied from place to place, but at one site they were found in 26% of stomachs.

Cannibalism of bullfrog juveniles and tadpoles collectively made up only 0.43% of total prey remains (Table 6). In one extraordinary instance, they were found in 48% of bullfrog stomachs from a single site. However, when all other records of amphibian predation [Pacific treefrogs, red-legged frogs, rough-skinned newts, ambystomatid salamanders (2 species), and plethodontid salamanders (2 species)] are combined ( $n = 159$ ), they amount to almost exactly twice the number of instances of bullfrog cannibalism ( $n = 81$ ) (Table 6, Table S4). Individual bullfrog stomachs were found to contain as many as 4 adult Pacific treefrogs and 3 adult rough-skinned newts. At one location, treefrogs were in the stomachs of 31% of bullfrogs sampled.

**Table 6.** The top 14 vertebrate prey categories in the bullfrog diet (See Table S4 for other vertebrates identified).

Vertebrate Group or Species	Total # of cases	% of total prey remains	% of bullfrog stomachs	% of sites	Seasonality: % instances/month					
					Apr	May	June	July	Aug	Sept
Three-spined stickleback ( <i>Gasterosteus aculeatus</i> )	97	0.52	1.5	27	3	30	19	11	6	31
Pacific treefrog ( <i>Hyla regilla</i> )—including tadpoles	74	0.39	1.2	33	12	39	19	25	4	1
Bullfrog juveniles ( <i>Rana catesbeiana</i> )	51	0.27	0.96	33	2	6	2	10	10	70
Rough-skinned newt ( <i>Tarhchica granulosa</i> )	50	0.26	0.87	21	0	36	18	8	26	12
Bullfrog tadpoles	30	0.16	0.43	15	0	7	33	30	27	3
Sculpin ( <i>Cottus</i> sp.)	25	0.13	0.46	3	20	8	8	0	40	24
Shrew ( <i>Sorex</i> sp.)	24	0.13	0.48	18	4	17	17	4	54	4
Unidentified fish	18	0.10	0.39	6	28	11	6	22	22	11
Townsend’s vole ( <i>Microtus townsendi</i> )	16	0.08	0.35	13	0	25	31	0	25	19
Pumpkinseed sunfish ( <i>Lepomis gibbosus</i> )	14	0.07	0.30	18	0	21	29	14	29	7
Western painted turtle ( <i>Chrysemys picta</i> )	12	0.06	0.17	2	81	19	0	0	0	0
Red-legged frog ( <i>Rana aurora</i> )	10	0.05	0.21	9	0	10	10	20	60	0
Northwestern salamander ( <i>Ambystoma gracile</i> )	10	0.05	0.20	5	0	60	40	0	0	0
Coho salmon ( <i>Oncorhynchus kisutch</i> )	9	0.05	0.13	2	0	0	0	100	0	0

The majority (60%) of the 40 individual mammals consumed were shrews, while the rest were all Townsend's voles (Table 6). There were eight passerine bird species represented by 25 records from 27% of the sites (Table S4). Of reptiles, three species of garter snakes (11 total snakes) were found in the diet along with a single northern alligator lizard (Table S4). Of special conservation concern were the 12 western painted turtle hatchlings (Class Chelonia) that equaled all reptile species combined as a percentage of total bullfrog prey (0.06%, Table 6, Table S4).

## Discussion

The approach used here is to focus primarily on instances of predation rather than on ingested volume or nutritional quality in the diet. We accept that one vertebrate is the nutritional equivalent of many insects or other invertebrates, but quantifying and analyzing the relative nutritional significance of each prey instance was beyond the scope of this study.

### Insects are the main prey group

Insects were found in 93% of the 4,602 bullfrog stomachs with contents, which is consistent with Korschgen and Moyle's (1955) 83.5% from a much smaller sample ( $n = 455$ ). Of total identifiable remains 84% were insects, whereas Cohen and Howard (1958) found only about 67% insects in a sample of 300 from California's San Joaquin Valley. The differences in these figures likely reflect lower latitude, seasonality, sample size, and size-class mix; however, the conclusions are all fundamentally the same, e.g. insects are consistently the most numerous organisms in the bullfrog diet. Certain insect groups, such as odonates and beetles, have frequently been identified as predominate (Bruggers 1973, Werner et al. 1995, Hothem et al. 2009).

This study found that early in the bullfrog active season, Odonata (dragonflies and damselflies; May: 45% adults; June: 81% adults) were a consistently important prey for all size-classes of bullfrogs, and this has also been reported by Werner et al. (1995). Water striders (Gerridae) were most frequently consumed by juvenile bullfrogs and were of particular importance during the first few weeks after spring emergence. On the other hand, Hothem et al. (2009) found a greater frequency of water striders in adult bullfrogs (21.5%) than in juveniles (6.5%), but from a much smaller series of only 107 bullfrogs (11 had no stomach contents), 31 of which were juveniles.

### Immunity from various natural defenses

Bullfrogs are seemingly immune to many natural predator defenses. Previous studies have alluded to the toxic or potentially repellent effects of natural prey defense mecha-

nisms on predatory bullfrogs. For example, Brodie (1968) found that northern rough-skinned newts from Oregon were lethally toxic to bullfrogs. Later, it was determined that newts from Vancouver Island were at least 1,000 times less toxic than those from Oregon (Brodie and Brodie 1991). Of the 50 northern rough-skinned newts removed from bullfrogs, we recovered as many as three partially to well-digested newts from a single bullfrog stomach. It appears, therefore, that bullfrogs routinely ingest and safely digest rough-skinned newts on southern Vancouver Island with no apparent lethal effects. This situation likely makes northern rough-skinned newts on Vancouver Island exceptionally vulnerable to bullfrog predation.

Krupa (2002) examined bullfrog stomach contents from New Mexico and noted that wasps were commonly consumed. He posed the question: Are bullfrogs immune to the effects of wasp stings or do individuals consume wasps until they develop a conditioned avoidance? For example, in our results 35 bullfrogs had each eaten at least 10 social wasps and as many as 19 without any apparent conditioned avoidance to the wasp sting. Wasps and bees were eaten throughout the active season. Govindarajulu et al. (2006), in examining a small sample of stomach contents from Vancouver Island, also reported wasps as being important in sub-adult bullfrogs. Similarly, Diaz De Pascual and Guerrero (2008) discovered hymenopterans to be the most important dietary item for juvenile bullfrogs in Venezuela; however, it is not stated what type of hymenopterans. Interestingly, the bullfrog's close relative, the green frog (*Rana clamitans*), showed the same seasonal pattern in terms of wasp and bee consumption in Michigan (Werner et al. 1995).

Sticklebacks were the most numerous vertebrate prey and were also one of the most defensively armed. Bullfrogs, however, were seemingly immune to the discomfort of stickleback spines, and we recovered as many as five of these fish from a single stomach. Bullfrogs are reported to have eaten both scorpions and rattlesnakes along the lower Colorado River (Clarkson and de Vos 1986), so their powers of overcoming or withstanding highly evolved, mechanical and chemical, prey defenses are known to be impressive.

### **Bullfrog survival may be facilitated by bullfrog predation**

Dragonfly nymphs are known to prey on bullfrog tadpoles (Hunter et al. 1992), but, conversely, adult and juvenile bullfrogs are major predators of adult and nymphal dragonflies (Table 4). It is fair to speculate that increasing densities of invasive predatory bullfrogs could create a corresponding decline in the densities of dragonfly nymphs. In some previous studies, dragonflies and damselflies are spoken of collectively as odonates (Korschgen and Moyle 1955, Werner et al 1995, Diaz De Pascual and Guerrero 2008), whereas in this study the two groups are reliably separated. Of damselflies, 83% consumed were adult; and of dragonflies, 73% were adult (Table 4). Other studies have found adult odonates to be important in the bullfrog diet (Werner et al 1995),

but Hothem et al. (2009) in California and Korschgen and Moyle (1955) in Missouri found that the nymphal stage was more frequently consumed.

In 2011, we observed an adult common garter snake (*Thamnophis sirtalis*) eating a juvenile bullfrog, and this aquatic-foraging snake when at full adult size should be easily able to eat at least half-grown bullfrogs. Smith (1977) considered larger *T. sirtalis* as a likely bullfrog predator but also reported smaller *T. sirtalis* in bullfrog stomachs. All three native garter snake species found on Vancouver Island (*T. elegans*, *T. ordinoides*, *T. sirtalis*) were recorded in the bullfrog diet (Table S4). Taken together, the 11 garter snakes of three species reported here would rank just above red-legged frogs in total number of instances. It seems unlikely that the two aquatic foragers, *T. sirtalis* and *T. elegans*, would be able to avoid falling prey to adult bullfrogs. Seigel (1994) found that *Thamnophis atratus*, not native to British Columbia, is an ineffective predator of bullfrog tadpoles, and only the largest snakes can eat them.

A giant water bug (Belostomatidae) was observed killing a bullfrog tadpole in captivity (K. Jancowski, personal observation), and they are known predators of other anurans including ranids (Toledo 2005). At one site, Filberg Marsh (49.8047, -125.0594; May 27, 2010), 43% of the 44 adult bullfrogs captured had consumed one or more giant water bugs. Consequently, predation of giant water bugs by adult bullfrogs may be just one more example of adult bullfrog predation facilitating the survival of bullfrog tadpoles.

Another organism found in the adult bullfrog diet, and also a predator of bullfrogs (Hunter et al. 1992) is the predacious diving beetle, which was found in almost 7% of bullfrog stomachs and had been consumed at 67% of sites (Table 4).

## Terrestrial prey

Bullfrogs routinely leave the water and migrate overland as adults and juveniles, presumably feeding as they travel. This may account for species turning up in the bullfrog diet that are strictly terrestrial, e.g. Townsend's voles, terrestrial shrews, northern alligator lizards, western red-backed salamanders (*Plethodon vehiculum*), and Oregon ensatina salamanders (*Ensatina eschscholtzii*).

## Indirect predation?

Aphids, because they are tiny, would seem to be an unlikely temptation to bullfrogs. However, aphids ranked second only to social wasps in number of instances of insect predation (Table 4). One probable explanation for this is that in late-summer aphids aggregate in large numbers to feed on the floating leaves of the yellow pond-lily (*Nuphar polysepalum*). The aphids, in turn, attract the attention of predatory wasps, dragonflies, damselflies, brachyceran flies, lacewings, and ladybird beetles, which also attract the interest of predatory bullfrogs. In the process of catching or attempting to

catch these larger insects, bullfrogs are inadvertently picking up aphids on their sticky tongues. Approximately 55% of bullfrogs containing aphids had also eaten one or more of these associated species. Consequently, pond-lily leaves can be important feeding stations for bullfrogs as aphids gather on them in late summer.

## Cannibalism

Cannibalism, though well known to occur in bullfrogs, has not been very comprehensively studied (Bury and Whelan 1984). Cannibalism in this study was of minor significance overall (0.43% of total prey remains) on south Vancouver Island, with 80% consumed in August and September (Table 6). Similarly, in Brazil, Silva et al. (2009) sampled 79 “adult bullfrogs” but found only one case of cannibalism in 49 cases of anuran predation. By contrast, Govindarajulu et al (2006) reported bullfrogs in the stomachs of almost half (44%) of a sample of 68 “large” ( $\geq 130$  mm) bullfrogs from southern Vancouver Island. One study from New Mexico (Stuart and Painter 1993) found evidence of cannibalism in 56 (40.6%) of 138 stomachs examined. In Venezuela, another study looked at 338 bullfrogs and reported cannibalism in 5% of sub-adults and 32% in adults (Diaz De Pascual and Guerrero 2008).

We sampled 448 bullfrogs that were greater than or equal to 130 mm in body length, or comparable in body size to the “large” category in Govindarajulu et al (2006). Of our 448, only 35 (7.8%) had conspecifics in their stomachs. We sampled throughout the bullfrog active season (April to September) rather than just in the latter half of summer and we sampled 56 more sites than Govindarajulu et al (2006). The smallest cannibalistic bullfrog that we found was 85 mm in body length, one of 25 cases involving bullfrogs less than 130 mm body length. Overall, we recorded 240 instances of bullfrog predation on amphibians with cannibalism accounting for only 34%.

In the absence of alternative prey, cannibalism remains an option for this species that would be of variable importance from site to site, season to season, and year to year. In the long-term, unmanaged bullfrog populations might conceivably drive down native species numbers to the point where cannibalism becomes increasingly important to bullfrog population sustainability.

## Phenology and its relation to diet and sampling

Of native amphibians, the Pacific treefrog was the most frequently eaten by bullfrogs (Table 6). Treefrogs peaked in the bullfrog diet in May (39%) as male treefrogs migrate into the water to set up a mating chorus closely followed by females. At least 30% of treefrogs eaten in April and May were females, and 53% of these were gravid. Although bullfrogs are eating more adult males than adult females during this spawning period, the numerical loss of eggs to persistent (April to July) bullfrog predation could be substantial. Male treefrogs are likely in the water for a much longer interval than



the females and they are making themselves more conspicuous by vocalizing (Smith 1977), which may account for their higher rate of mortality. Mid-summer predation of treefrogs is primarily attributable to the mass transformation of treefrog tadpoles and their subsequent migration to land (Table 6).

Second to treefrogs are rough-skinned newts. Predation on newts peaked in May (36%) and then rose again in August (26%) (Table 6). These peaks coincide with the May migration of gravid adult female newts to the water to reproduce and the late-summer transformation of larval newts into terrestrial juveniles migrating away from the water (Oliver and McCurdy 1974).

Krupa (2002) has also noted a mid-summer increase in the consumption of social wasps, rising steeply in August then dropping slightly in September (Table 4). Social wasps (Vespidae) become more accessible to bullfrogs in August as the wasps prey upon aphids that aggregate on pond-lily leaves. This wasp-aphid association is an annually recurring phenomenon that may account for the extraordinary abundance of aphids in the bullfrog diet.

Included in this study were the four sites sampled over 5 years by Govindarajulu et al. (2006). We documented more species overall, which included additional vertebrate species. Our early-spring sampling of Beaver Lake Pond (48.5102, -123.3991) on April 24 and May 5, 2010 undoubtedly accounts for our records of recently hatched red-listed western painted turtles. This species would have certainly been missed entirely if fieldwork had been carried out at any other time. Similarly, timing may have been a factor in our discovery of coho salmon at Prior Lake (48.4764, -123.4672) on July 3, 2010.

## Sites and sampling

The bullfrogs that figured in this study were not collected primarily for the purpose of examining their stomach contents. They were captured and euthanized as part of a research and development program exploring the feasibility and practicality of bullfrog eradication. This was carried out while testing and refining the electro-frogger technique on a regional scale. Most of the 60 sites included in this study (86%) were only visited in three or less of the six months available within the bullfrog's active season, resulting in only 32% of the overall sample (Table S2). This is because, for the most part, they were smaller ponds where all of the adult and juvenile bullfrogs present could be removed in one or two evenings. In addition, there were a few single-evening reconnaissance missions to sites of interest. The remaining 14% of sites were the larger and more difficult ones where bullfrog densities, immigration rates, and problematical habitats required more effort to bring bullfrog numbers down. The most demanding (Florence Lake, 48.4589, -123.5127) was the only site visited in each of all six months (April to September) and produced 33% of the overall sample (Table S1, Table S2). Consequently, stomach contents from most sites are snapshots of what bullfrogs were eating at that particular site on a specific evening or over a few nights. The database

compiled for this analysis is, therefore, a blend of a few sites sampled many times throughout the summer coupled with many sites visited only a few times each in a much more restricted time-frame. The regional database is comprehensive in terms of including samples collected nightly during the entire field season, but is fragmentary in terms of providing seasonally comparative datasets for most of the sites.

### Prey species of special concern

American bullfrogs have been identified as, or are suspected to be, a threat to the survival of various vertebrates world-wide, including native fish (Mueller et al. 2006), amphibians (Fisher and Shaffer 1996, Hecnar and M'Closkey 1997, Adams 2000, Kats and Ferrer 2003, Lannoo et al. 1994, Moyle 1973, Hammerson 1982), aquatic turtles (Spetz and Spence 2009), and island endemic birds (Pitt et al. 2005).

In British Columbia, three species of conservation concern relate to this study: the red-listed western painted turtle (*Chrysemys picta bellii*), the blue-listed northern red-legged frog (*Rana (Lithobates) aurora*), and, the aquatic-foraging and red-listed, American water shrew (*Sorex palustris brooksi*). Bullfrogs were found to be consuming hatchling western painted turtles as they entered the water. This was clear from the average carapace length of only 3 cm and the timing of these instances in late April and early May (Table 6). Any loss of hatchling painted turtles is a serious threat to turtle survival because the females produce few eggs and survivorship to recruitment is low (Gregory and Campbell 1996). Hatchling painted turtles are easily swallowed by bullfrogs and will remain vulnerable for at least the first few weeks post-hatching until their shell dimensions exceed a bullfrog's maximum gape. Red-legged frogs were consumed primarily as fully metamorphosed juveniles and eaten mostly in the month of August (Table 6). American water shrews have not been recorded in the bullfrog diet, but they are flagged because the historical database for this shrew lists localities, such as Hamilton Marsh on Vancouver Island (49.3159, -124.4625), that are now thoroughly invaded by bullfrogs. The presence of shrews (at least some were *S. vagrans*), as well as the larger Townsend's voles, demonstrate that bullfrogs will take small mammals, and the habits and habitat preferences of the American water shrew should make them especially vulnerable to bullfrog predation. The Pacific water shrew (*Sorex bedirii*) has also been recorded in the bullfrog diet (Campbell and Ryder 2004).

It is of economic interest that coho salmon (*O. kisutch*) juveniles were found in 16% of bullfrogs sampled from Prior Lake in early July (Table 6, Table S1). Most of these were about 8 cm long, though bullfrogs have been documented eating trout up to 15 cm in length (Bury and Whelan 1984). It is not known whether coho salmon are being preyed upon locally in lotic habitats. However, many streams on southern Vancouver Island become intermittent in late summer and in shallow isolated pools salmon fry could be more vulnerable to bullfrog predation. Garwood et al. (2010) recently documented an adult bullfrog from a stream in California with an 11.6 cm long coho salmon in its stomach. Lotic habitats were not sampled in our study because

bullfrogs aggregate and reproduce locally only in the warmer standing water of lakes and ponds. Salmonids, such as coho salmon, tend to prefer cooler and better oxygenated flowing waterways.

### Empty stomachs

An organism that lies dormant for almost six months of the year must replenish its fat reserves during the relatively brief six-month active season. Mature adults, in particular, should have the life experience to be proficient hunters. They also have energy demanding roles that include vocalizations, territorial defense, egg production, spawning, and may include overland migrations. Then they must end the season with sufficient reserves to overwinter for another six months. The percentage of mature adults of both genders with empty stomachs was, therefore, remarkably high (Table 2B).

Govindarajulu et al. (2006) also found empty stomachs but only in mature males and newly metamorphosed bullfrogs. The so-called “metamorph” is a brief transitional stage at the end of the tadpole stage and at the very beginning of the juvenile stage. During this interval, the frog displays combined morphological characteristics of a larva and a juvenile. Feeding in juveniles is not possible until the mouth and internal organs of the tadpole stage are fully resorbed and reformed into a completely metamorphosed morphology. An indeterminate number of the juveniles with empty stomachs (Table 2B) exhibited tail vestiges and so their empty stomachs may be attributed to this transitional “metamorph” morphology that is not yet fully, or has only just become, operational in the predator mode.

### Conclusions

- 1 As an “invasive alien” the American bullfrog is a highly adaptable, opportunistic, and seemingly unspecialized predator that has a uniquely large and complex ecological footprint both above and below the water surface.
- 2 Insects were the dominate prey group found in 84% of prey instances and 93% of stomachs with food, but seasonality influenced the relative importance of any one insect group over another at any given time period.
- 3 Cannibalism was found to be a minor component of the diet in terms of relative instances and accounted for approximately 34% of all instances of predation on amphibians.
- 4 Bullfrog control measures should be routinely factored into management plans for rare and endangered species, such as the western painted turtle on southern Vancouver Island, which are particularly vulnerable to bullfrog predation.

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## Appendix

Supplementary tables. (doi: 10.3897/neobiota.16.3806.app) File format: Microsoft Excel Document (xls).

**Explanation note:** **Table S1:** Sites where bullfrogs were collected on Vancouver Island, British Columbia, Canada. **Table S2:** Sampling frequency by month per site and its relation to catch. **Table S3:** Occurrence of individual prey remains identifiable as insect. The remaining 26 insect prey categories not given in Table 4. **Table S4:** The remaining 19 vertebrate prey groups in the bullfrog diet not shown in Table 6.

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# Can *Daphnia lumholtzi* invade European lakes?

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## Abstract

The cladoceran *Daphnia lumholtzi* is a subtropical and tropical zooplankter, and an invasive species in North America. Thus far, *D. lumholtzi* has not been detected in Europe. Here we investigated whether a hypothetical introduction to Europe could result in a successful invasion, either now or in the near future when facilitated by climate change. In laboratory experiments, we tested whether different clones of *D. lumholtzi* can invade a resident community consisting of native *Daphnia* from lake Klostersee, Germany, and how invasion success depends on temperature and the presence or absence of planktivorous fish. In some treatments, invasion success was consistently high, and *D. lumholtzi* reached densities similar to the native competitors by the end of the experiment. The presence of a planktivorous fish reduced the invasion success of *D. lumholtzi*, and a clone with an inducible defense against fish predation was a more successful invader than a permanently defended clone. Of the three temperatures tested in this study (15, 20, and 24 °C), invasion success was highest at 20 °C. To understand the competitive interaction between native and introduced *Daphnia*, we fit a Lotka-Volterra-type competition model to the population dynamics. Our experimental and modeling results suggest that *D. lumholtzi* can invade European lakes and can cause substantial declines in the population size of native *Daphnia*, with potential consequences for higher trophic levels.

## Keywords

invasive species, competition, climate change, inducible defenses

## Introduction

In their attempt to understand the determinants of invasion success, most studies focus on invasions that have already occurred. For example, many studies try to identify characteristic traits of invasive species, using data from previously successful invaders (Jeschke and Strayer 2006, van Kleunen et al. 2010). Another popular approach is to use ecological niche models, also known as species distribution models or bioclimatic models (Peterson and Vieglais 2001, Peterson 2003, Jeschke and Strayer 2008). In the latter method, presence/absence data from a species' native range, together with information on climatic and other abiotic variables, are used to build a statistical model of the species' niche. This can then be projected onto geographical regions where the species could potentially invade (Peterson and Vieglais 2001, Peterson 2003). An approach that has been less frequently applied in invasion biology is to combine experimental and modeling techniques in order to mechanistically understand biological invasions and use this understanding to predict future invasions.

We follow such a mechanistic approach here, using the example of a possible invasion by the cladoceran *Daphnia lumholtzi* Sars in Europe. This zooplankter is native to subtropical and tropical regions of Africa, Australia and Asia, where it is found up to the Middle East (Benzie 2005). *Daphnia lumholtzi* has likely been transported from Africa to North America together with fish imported to stock reservoirs (Havel and Hebert 1993). Since it was first observed in North America in 1991 (Sorensen and Sterner 1992, Havel and Hebert 1993), *D. lumholtzi* has colonized a wide variety of water bodies throughout the south-central United States and recently also the Great Lakes and the West Coast (Havel and Shurin 2004). There are many similarities in climate patterns between Europe and North America, and in the course of climate change, the European climate is expected to become more suitable for subtropical or tropical species. Hence, an important question is: Can *D. lumholtzi* also invade European lakes, now or in the near future?

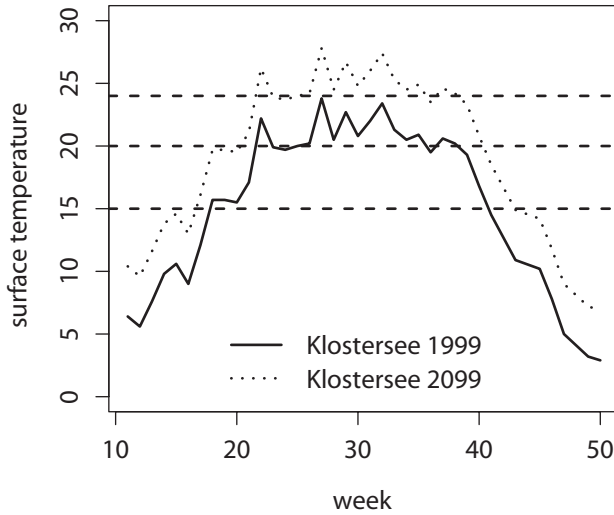
A number of studies have investigated how the invasion success of *D. lumholtzi* in North America depends on temperature, intensity of fish predation and competition with native North American zooplankton species. Since *D. lumholtzi* experiences high temperatures across its native range, it is not surprising that it is well adapted to the high summer temperatures of water bodies in the south-central US. Indeed, when temperatures rise above 25 °C in late summer and the populations of native *Daphnia* species decline, *D. lumholtzi* reaches its highest density (Lennon et al. 2001, Havel and Graham 2006). Life-table experiments indicate that *D. lumholtzi* has a positive intrinsic growth rate between 11 and 38 °C, with a temperature optimum at 24 °C (Lennon et al. 2001).

Unique characteristics of *D. lumholtzi* are the long head and tail spines that most clones form in response to chemical cues released by fish (Dzialowski et al. 2003). In this article, we will call such a clone inducibly defended, independently of whether it currently exhibits a defense or not. Some other clones are permanently defended: they carry these defenses even in the absence of predator cues. Swaffar and O'Brien (1996) and Kolar and Wahl (1998) conducted feeding experiments with bluegill sunfish (*Le-*

*pomis macrochirus*) on *D. lumholtzi* compared to other *Daphnia* species. They showed that the spines of *D. lumholtzi* make it difficult for juvenile sunfish to consume these defended *Daphnia* and strongly increase their handling time. Thus, predation pressure might be an important factor controlling the invasion success of *D. lumholtzi*. In laboratory competition experiments under predation, inducibly defended clones were more successful than a permanently defended clone (Engel and Tollrian 2009).

Temperature and predation do not only influence the growth rate of *D. lumholtzi*, but also change the way this introduced species competes with native zooplankton species, such as native North American *Daphnia*. Fey and Cottingham (2011) and Engel and Tollrian (2012) observed, in laboratory experiments, that with increasing temperature there was a shift in competitive dominance from the native *D. pulex* or *D. pulicaria* to *D. lumholtzi*. In a competition experiment, *D. pulicaria* was the superior competitor without predation, and *D. lumholtzi* the superior competitor with predation (Engel and Tollrian 2009). It is currently unclear which role competition plays for the invasion success of *D. lumholtzi* in North American reservoirs. Although *D. lumholtzi* tends to be abundant at times when native zooplankton are rare (Havel and Graham 2006), competitive effects can be weak, and it has been suggested that other factors than competition control seasonal patterns of *D. lumholtzi* abundance (Johnson and Havel 2001). However, in a mesocosm experiment conducted by Dzialowski et al. (2007), *D. lumholtzi* was only able to establish in resident communities with low densities of native zooplankton, suggesting that native communities can exhibit biotic resistance against *D. lumholtzi* invasion attempts.

In the popular statistical approaches used to predict future invasions (e.g. the ecological niche modeling approach introduced above), biotic interactions are usually neglected or assumed to be constant (Jeschke and Strayer 2008), which can be a problem if such interactions play a key role in determining under which conditions a species can persist (Davis et al. 1998). In the case of *D. lumholtzi*, the studies mentioned above indicate that invasion success does not only depend on abiotic conditions such as temperature, but also on the presence of predators and possibly interspecific competition. Therefore, we used laboratory invasion experiments that take into account the interaction of *D. lumholtzi* with the native European community and a more mechanistic competition model to examine whether and under which conditions *D. lumholtzi* would be able to invade a European lake, either now or in a warmer future. As an example scenario, we considered the potential invasion of *D. lumholtzi* to the small prealpine Lake Klostersee in southern Germany (47°58'N, 12°29'E). In our experiments, we used three temperature levels: 15, 20, and 24 °C. In 1999, 15 and 20 °C represented typical spring or summer epilimnion temperatures in Lake Klostersee, respectively (Fig. 1). While a temperature of 24 °C was an extreme event in 1999, with a predicted surface warming by 4 °C until the end of the 21st century (IPCC 2007, scenario A1FI), it is expected to be a typical summer surface temperature in 2099, whereas 20 °C might then be a typical spring surface temperature. In addition to our investigation of the establishment success of *D. lumholtzi*, we used our experimental and modeling results to consider the consequences of a potential *D. lumholtzi* invasion for competing native species.



**Figure 1.** Observed surface temperature in Lake Klostersee in 1999 (solid line) and predicted surface temperature in 2099 under climate change scenario A1FI (dotted line, see IPCC 2007). The temperature treatments used in our experiments are indicated by dashed lines.

## Methods

### Study organisms

We collected native *Daphnia* in September 2009, using plankton nets in the middle of Lake Klostersee and performing several vertical hauls. Each clone used in our experiment consisted of the descendants of a single female from this original sample. Prior to the experiments, we kept the clones at 20 °C in semiartificial *Daphnia* medium based on ultrapure water, phosphate buffer and trace elements, and regularly fed them with *Scenedesmus obliquus*, a species of green algae which is commonly found in European lakes (see e.g. John and Tsarenko 2002, Haupt et al. 2009). We used three different native *Daphnia* clones in our study: clone 1 and 3 were identified as *D. hyalina* and clone 2 as a *D. hyalina* x *cucullata* hybrid. We used clones 1 and 2 in the first invasion experiment and clones 2 and 3 in the second. As introduced organisms, we used two *D. lumholtzi* clones. The Arizona clone (AZ, from Canyon Lake, Arizona, provided by R. Tollrian and originally collected by J. Elser) is permanently defended against fish predation whereas the Texas clone (TE, from Fairfield Reservoir, Texas, provided by R. Tollrian and originally collected by K. H. Sorensen and R. W. Sterner) is inducibly defended.

The bitterling (*Rhodeus amarus*), a planktivorous fish native to Middle Europe, served as an experimental predator. The fish we used were approximately 4.5 cm long. This length compares to 2–3.5 cm for bluegill sunfish used by Swaffar and O’Brien (1996), and 1–8 cm for bluegills used by Kolar and Wahl (1998). Kolar and Wahl (1998) found that bluegills with a length of up to 5 cm had difficulty in handling *D. lumholtzi* and learned to reject them. In contrast, bluegills with a length above 5 cm

were able to ingest *D. lumholtzi*, although less efficiently than undefended *D. pulex*. Swaffar and O'Brien (1996) also found that their smaller bluegills had difficulties in handling *D. lumholtzi*. Since bitterlings differ in morphology and feeding mode from bluegills, we observed some of our experimental fish while they were exposed to adult permanently defended *D. lumholtzi*. Their behavior ranged from ingestion to rejection. In other words, the defense of *D. lumholtzi* appeared to provide partial protection against fish predation in our experiments.

### First invasion experiment

The first experiment took place from June to July 2010. The eight treatments differed in temperature (20 or 24 °C), introduced clone (TE or AZ), and predation regime (predation by a bitterling for 10 min per day or no predation) in a fully factorial design. Each treatment was replicated five times resulting in a total of 40 experimental units. The experiment was carried out in 30-L white polypropylene containers with semiartificial *Daphnia* medium which were placed in climate chambers with a 12 h:12 h light:dark cycle. We added 0.5 mg C/L of green algae (*Scenedesmus obliquus*) to each unit every second day. Algae were cultured in artificial Z medium (Zehnder and Gorham 1960) at 20 °C and a 20 h:4 h light:dark cycle.

To create the resident native communities, we divided 60 L of a culture of each of the two native clones approximately equally into 40 portions, each with on the order of magnitude of  $10^2$  individuals. The portions were assigned randomly to the 40 experimental units and used to inoculate 15 L of *Daphnia* medium in each of them. One week after inoculation, we added 10 L of fresh medium to each unit, and one bitterling to each unit in the predation treatments. For most of the time, the fish were caged in a 5-L polypropylene container floating inside the experimental container. This served to avoid elimination of the entire population while guaranteeing a permanent release of predator-borne cues. The bottom and sides of this small container were removed and replaced by a 200- $\mu$ m mesh, such that chemicals produced by the fish were exchanged through the mesh but *Daphnia* could not pass. The experimental units in the non-predation treatment had an empty 5-L container. Once a day, we released the fish for 10 min into the main compartment of the experimental unit and allowed them to feed on the *Daphnia*. After recapturing the fish, we provided them with dead defrosted red mosquito larvae (Chironomidae) as additional food.

Two weeks after inoculation (time 0), we introduced 25 *D. lumholtzi* individuals (AZ or TE, depending on the treatment) into each experimental unit. Twenty-five is a number of individuals that we expected to be large enough to make chance extinctions unlikely but that was still small compared to the size of the native population at time 0. These founding individuals had been randomly sampled from populations grown at 20 °C. To maximize the contrast between the two clones, the AZ clone had been exposed to fish kairomones during the week prior to introduction, whereas the TE clone was naive to fish at the time of introduction. We sampled 10% of the volume before the



introduction at time 0, and we sampled 5% of the volume every seven days until the end of the experiment. We filtered the sampled volume through a 125- $\mu$ m mesh and preserved the *Daphnia* retained by the mesh in 70% ethanol. At the time of sampling, we randomly redistributed the fish in the predation treatments on the experimental units within one temperature treatment.

On day 1, four fish accidentally escaped from their containers (three units in the 24 °C, AZ treatment; one unit in the 24 °C, TE treatment), so that they were able to feed on the *Daphnia* of their experimental unit for an entire night. Since this led to a strong decline in population densities, we decided to restock the respective units with approximately 500 native *Daphnia* (250 of each of the two clones) and six *D. lumholtzi*. We determined this ratio by dividing the 25 introduced *D. lumholtzi* individuals by the count of native *Daphnia* in the sample that we had taken 3 days before.

In the predation treatments, fish metabolic end products accumulated over time and apparently inhibited *Daphnia* population growth. Thus, after 21 and 28 days, we replaced one third of the volume in each unit with fresh medium. To remove the old medium, we used an aquarium pump covered by a 125- $\mu$ m mesh such that no *Daphnia* were lost from the units during medium exchange. To avoid extinction of the entire *Daphnia* community, from day 21 onward the fish were only put into their small containers for one hour per day and were not allowed to feed on the *Daphnia* anymore.

The experiment ended on day 35. At this time, we sampled 1.25 L from the units in the non-predation treatment, whereas we examined the total volume in the predation treatment due to lower numbers of remaining individuals there. We counted the complete samples under a stereomicroscope at a magnification of 16. However, in predation units that contained more than 50 individuals in the previous week's sample, we counted only 10% of the sample. Only individuals with clear contours of eye and body were counted, assuming that they were alive at the time of sampling. We distinguished native *Daphnia* and *D. lumholtzi* according to the shape of their heads and tail spines.

## Second invasion experiment

The second invasion experiment took place from March to April 2011. To better understand the observations made in the first experiment, we changed the experimental design in several points. We now chose the temperature treatments 15 °C and 20 °C in order to cover a wider range of temperatures. Because we suspected that the white container walls in the first experiment made it easy for the fish to spot *Daphnia*, we used black containers in the second experiment. We hypothesize that the light conditions in these black containers are more similar to those in natural lake environments. Because the chemical conditions in the containers had deteriorated over the course of the first experiment, we decided to regularly exchange medium in the second experi-

ment. However, large-scale medium exchange is logistically challenging, and thus we had to reduce the experimental volume to 10 L.

We inoculated native communities in 5 L medium and filled up the containers to 10 L six days later. For the first 11 days, fish were allowed to feed for only 5 minutes per day, later 10 minutes per day. To avoid the accumulation of fish chemicals, the fish were not permanently present in the experimental units, but only while feeding. For the rest of the day, we kept them together in an aquarium in 10 L of medium at the same temperature. Every day, we filtered the medium from the aquarium and used it to replace 1 L of medium from each unit in the predation treatment. In this manner, we simulated the permanent presence of fish in these units. In the other experimental units, we replaced 1 L by fresh medium every day. Among the 25 introduced *D. lumholtzi*, 5 were embryo-bearing females whereas the other 20 were randomly selected from the population. The second invasion experiment ended on day 42. Two treatment combinations (TE clone without predation at 15 °C and 20 °C), however, were continued as a long-term experiment until day 91. During this additional time, we exchanged 7 L of medium once per week. We used the following light-dark cycle: 11.5 h light: 0.5 h dusk: 11.5 h night: 0.5 h dawn. All other parameters such as food supply were identical to the first experimental setup.

## Data analysis

If *D. lumholtzi* individuals were present in the final sample from an experimental unit, we say that *D. lumholtzi* successfully established in this unit. To obtain a more quantitative measure for invasion success and the resulting change in community structure, we then analyzed the proportion of *D. lumholtzi* at the end of the experiment. We modeled this response variable and its dependence on the treatment variables using logit-link binomial generalized linear mixed models as implemented in the package lme4 (Bates et al. 2011) in R (R Development Core Team 2011). Temperature, predation regime, and the introduced clone were the fixed effects, and the experimental unit was included as a random effect. Thus, the model was of the form

$$L_i \sim \text{Bin}(L_i + N_i, p_i) \quad (1)$$

and

$$\text{logit}(p_i) = c_1 + c_2 \cdot T(i) + c_3 \cdot \mathbf{1}_{\text{predation}}(i) + c_4 \cdot \mathbf{1}_{\text{TE}}(i) + c_5 \cdot T(i) \cdot \mathbf{1}_{\text{predation}}(i) + c_6 \cdot T(i) \cdot \mathbf{1}_{\text{TE}}(i) + c_7 \cdot \mathbf{1}_{\text{predation}}(i) \cdot \mathbf{1}_{\text{TE}}(i) + c_8 \cdot T(i) \cdot \mathbf{1}_{\text{predation}}(i) \cdot \mathbf{1}_{\text{TE}}(i) + a_i \quad (2),$$

where  $L_i$  and  $N_i$  are the numbers of *D. lumholtzi* and native *Daphnia* in the last sample in unit  $i$ ,  $T(i)$  is the temperature in °C for unit  $i$ ,  $\mathbf{1}_{\text{predation}}(i)$  is 1 if unit  $i$  is in the predation treatment and 0 otherwise,  $\mathbf{1}_{\text{TE}}(i)$  is 1 if the TE clone is introduced in unit  $i$  and 0 otherwise, and

$$a_i \sim N(0, \sigma_a^2) \quad (3)$$

(see Zuur et al. 2009). For model selection, we used Akaike's information criterion (AIC). Candidate models were all possible models including subsets of the single factors as well as two and three-way interactions.

## Modeling

To better understand the competitive dynamics in the long-term experiment, we fit a  $\theta$ -logistic Lotka-Volterra competition model described by a system of ordinary differential equations

$$\frac{dN}{dt} = r_N \cdot N \cdot \left( 1 - \left( \frac{N + \alpha_{NL} \cdot L}{K_N} \right)^\theta \right) \quad (4)$$

and

$$\frac{dL}{dt} = r_L \cdot L \cdot \left( 1 - \left( \frac{L + \alpha_{LN} \cdot N}{K_L} \right)^\theta \right) \quad (5)$$

to the time series of population densities by minimizing the sum of the squared residuals with the L-BFGS-B method implemented in R's optimization function. In this model,  $N$  is the native population size,  $L$  the population size of *D. lumholtzi*,  $r_N$  and  $r_L$  are the respective intrinsic growth rates,  $K_N$  and  $K_L$  the carrying capacities,  $\alpha_{NL}$  and  $\alpha_{LN}$  the competition coefficients, and  $\theta$  a parameter that determines the strength of density regulation.

## Data resources

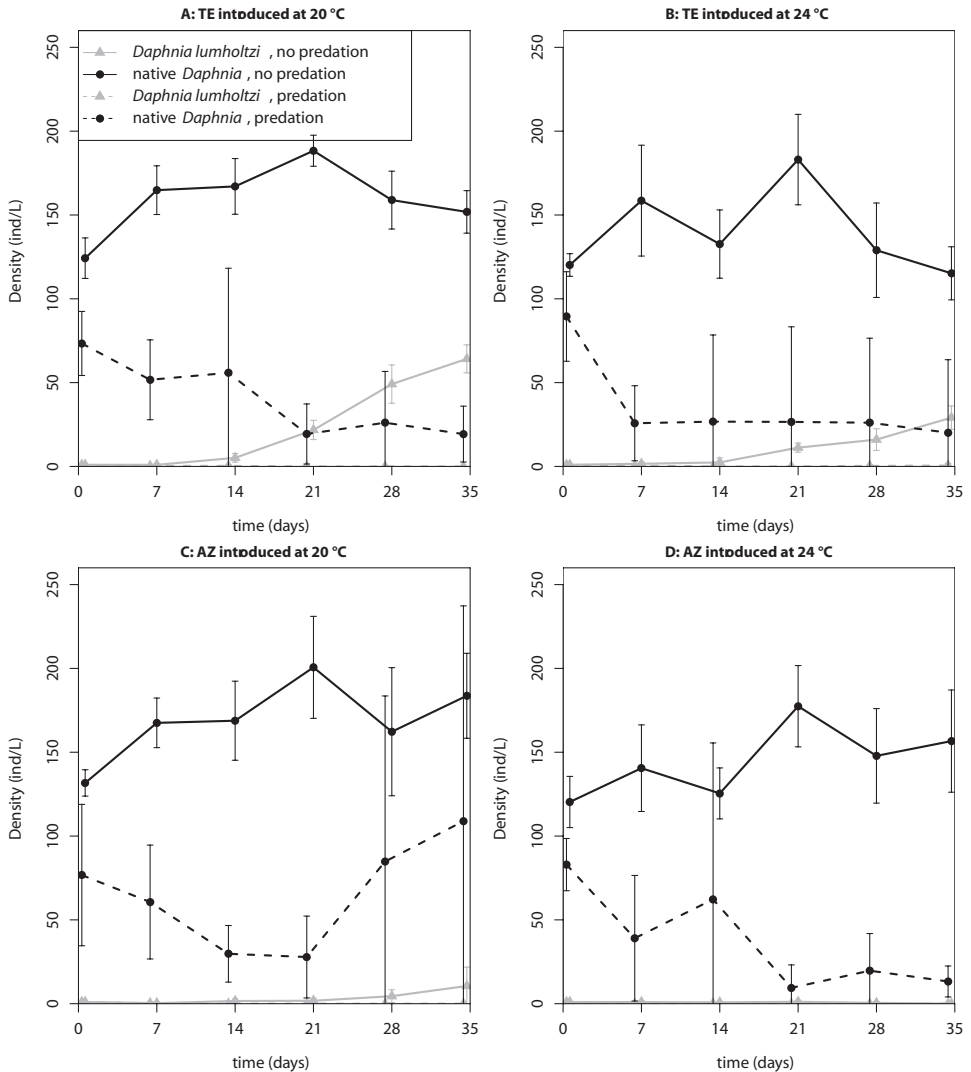
The data underpinning the analyses reported in this paper are deposited in the Dryad Data Repository at doi: 10.5061/dryad.d5c67

## Results

In both invasion experiments, the inducibly defended Texas clone established in all experimental units without predation (Tables 1 and 2). In the first invasion experiment, with one exception, all invasions in the predation treatment failed, whereas in the second experiment, the Texas clone established successfully under predation, and only the permanently defended Arizona clone failed consistently. In the absence of a predator, the Arizona clone had mixed establishment success. Temperature, predation, and the identity of the introduced clone, as well as the interactions between these factors, also strongly affected the population dynamics of introduced and native *Daphnia* (see Figs 2 and 3 for time-series plots). Consequently, the statistical models that best explained the proportion of *D. lumholtzi* at the end of the experiments (lowest AIC score) included temperature, predation and clonal identity. The selected model for the second experiment also included all three two-way interactions but not the three-way interaction. On the other hand, for the first experiment, the interaction between pre-

**Table 1.** Fraction of replicates with *D. lumholtzi* establishment for the different treatments in the first invasion experiment, and the corresponding final proportion of *D. lumholtzi*, as predicted by the selected generalized linear mixed-effects model (in parentheses).

	No predation		Predation	
	TE clone introduced	AZ clone introduced	TE clone introduced	AZ clone introduced
20 °C	5/5 (0.296)	5/5 (0.044)	0/5 (<0.001)	0/5 (<0.001)
24 °C	5/5 (0.199)	0/5 (<0.001)	1/5 (0.017)	0/5 (<0.001)



**Figure 2.** Time series of the population densities (means ± standard deviations) in the first invasion experiment.

**Table 2.** Fraction of replicates with *D. lumholtzi* establishment for the different treatments in the second invasion experiment, and the corresponding final proportion of *D. lumholtzi*, as predicted by the best generalized linear mixed-effects model (in parentheses).

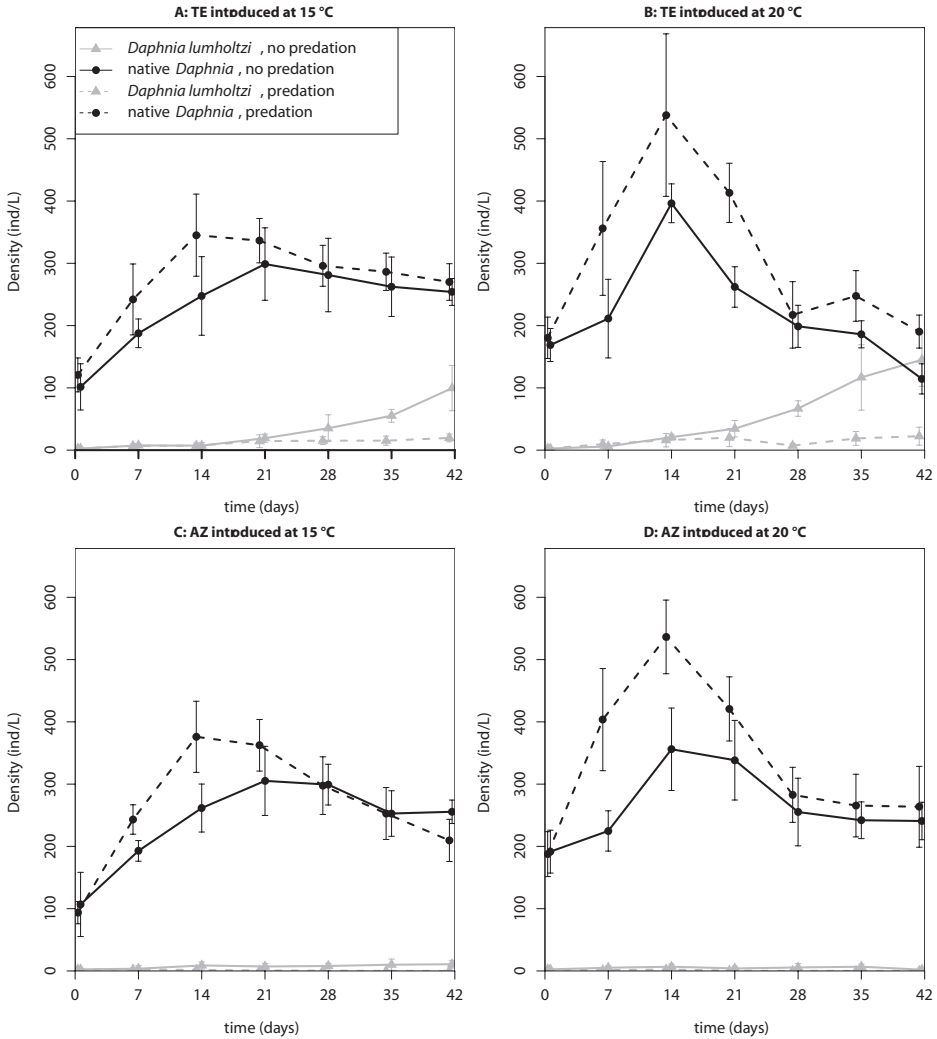
	No predation		Predation	
	TE clone introduced	AZ clone introduced	TE clone introduced	AZ clone introduced
15 °C	5/5 (0.274)	5/5 (0.039)	5/5 (0.066)	0/5 (<0.001)
20 °C	5/5 (0.557)	3/5 (0.008)	5/5 (0.101)	0/5 (<0.001)

**Table 3.** Estimated model coefficients ( $c_i$  in equation 2) for the best generalized linear mixed-effects model for the proportion of *D. lumholtzi* in the community.

	coefficient for experiment 1	coefficient for experiment 2
intercept ( $c_1$ )	102.706	1.66
temperature ( $c_2$ )	-5.289	-0.32
$\mathbf{1}_{\text{predation}}$ ( $c_3$ )	-128.150	-17.21
$\mathbf{1}_{\text{TE}}$ ( $c_4$ )	-100.945	-6.25
temperature $\cdot \mathbf{1}_{\text{predation}}$ ( $c_5$ )	5.230	-0.15
temperature $\cdot \mathbf{1}_{\text{TE}}$ ( $c_6$ )	5.157	0.57
$\mathbf{1}_{\text{predation}} \cdot \mathbf{1}_{\text{TE}}$ ( $c_7$ )	0	17.75
temperature $\cdot \mathbf{1}_{\text{predation}} \cdot \mathbf{1}_{\text{TE}}$ ( $c_8$ )	0	0
$\sigma_a$	0.46	0.28

**Table 4.** Model selection for the proportion of *D. lumholtzi* at the end of the experiment. The lowest AIC value for each experiment is highlighted in bold and indicates the respective selected model. T represents the effect of temperature, P predation, and C clonal identity;  $a_i$  is a normally distributed random variable that is independently drawn for each experimental unit  $i$ .

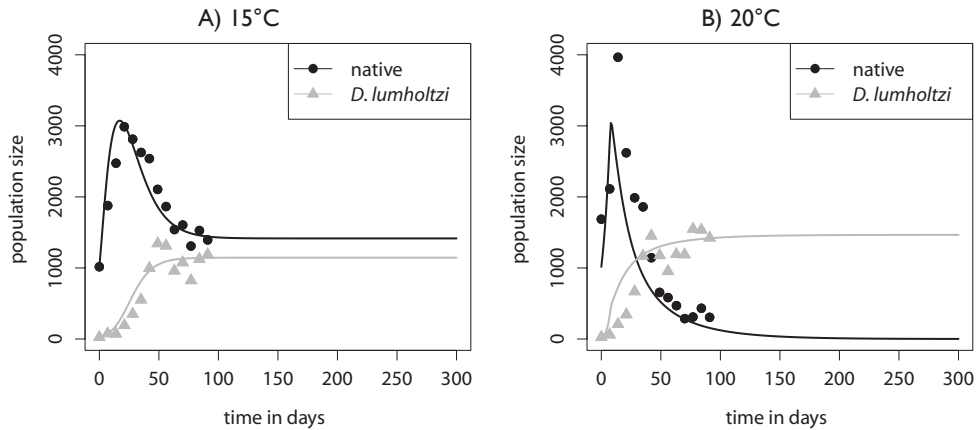
Model	AIC (experiment 1)	AIC (experiment 2)
T + P + C + T $\times$ P + T $\times$ C + P $\times$ C + T $\times$ P $\times$ C + $a_i$	63.13	71.63
T + P + C + T $\times$ P + T $\times$ C + P $\times$ C + $a_i$	61.13	<b>69.63</b>
T + P + C + T $\times$ P + T $\times$ C + $a_i$	<b>59.13</b>	75.24
T + P + C + T $\times$ P + P $\times$ C + $a_i$	81.08	92.55
T + P + C + T $\times$ C + P $\times$ C + $a_i$	77.29	71.89
T + P + C + T $\times$ P + $a_i$	80.71	96.61
T + P + C + T $\times$ C + $a_i$	77.34	75.97
T + P + C + P $\times$ C + $a_i$	96.27	90.58
T + P + C + $a_i$	94.83	94.62
T + P + $a_i$	115.83	168.04
T + C + $a_i$	131.02	134.34
P + C + $a_i$	96.16	94.10
T + $a_i$	139.681	174.83
P + $a_i$	114.83	166.04
C + $a_i$	129.90	132.35
$a_i$	138.33	172.84



**Figure 3.** Time series of the population densities (means  $\pm$  standard deviations) in the second invasion experiment.

dation and clonal identity was not part of the selected model (see Table 3 for estimated model coefficients and Table 4 for the AIC values of all candidate models). We used the estimated model coefficients to compute the final proportion of *D. lumholtzi* that the models predict for the different treatment combinations (values in parentheses in Tables 1 and 2). Throughout, the Texas clone reached higher densities than the Arizona clone. Predation prevented, or at least slowed down, the population growth of *D. lumholtzi*, especially that of the Arizona clone. In both experiments, the Texas clone at 20 °C had the highest invasion success.

The long-term experiments provided additional insights into the influence of temperature on the invasion success of the Texas clone and its interaction with the native



**Figure 4.** Time series of native and introduced *Daphnia* in the long-term experiments with the fitted and extrapolated Lotka Volterra model.

A) 15 °C with estimated model parameters:

$r_N=0.412$ ,  $r_L=0.204$ ,  $a_{NL}=1.88$ ,  $a_{LN}=0.000$ ,  $K_N=3.57 \cdot 10^3$ ,  $K_L=1.16 \cdot 10^3$ ,  $\theta=0.505$  with a residual sum of squares  $RSS=1242993$

B) 20 °C with estimated model parameters:

$r_N=0.143$ ,  $r_L=0.369$ ,  $a_{NL}=3.120$ ,  $a_{LN}=0.308$ ,  $K_N=4.53 \cdot 10^3$ ,  $K_L=1.47 \cdot 10^3$ ,  $\theta=15.3$  and  $RSS=940080$ .

*Daphnia*. The simple Lotka-Volterra model (eqs. 4 and 5) together with the set of estimated parameters produces a satisfactory fit to the competitive dynamics (Fig. 4). At the cooler temperature of 15 °C, native *Daphnia* had the higher estimated growth rate. This was reversed at 20 °C. Competition was intensified with the increase in temperature and highly asymmetric at both temperatures, with *D. lumholtzi* having much higher competitive effects on the native *Daphnia* than vice versa. The estimated carrying capacities for both species were higher at 20 °C than at 15 °C, and under both conditions, *D. lumholtzi* had a smaller estimated carrying capacity than native *Daphnia*. The difference in the estimates for the parameter  $\theta$  indicates that density dependence is stronger at 15 °C than at 20 °C. Furthermore, the Lotka-Volterra model allowed us to extrapolate the population dynamics and predict that at 20 °C, the native *Daphnia* would eventually reach a very low density or even go extinct, whereas at 15 °C coexistence with *D. lumholtzi* would be possible.

## Discussion

In our experimentally simulated introductions to European lakes, *D. lumholtzi* had a high invasion success in the absence of predators. This was particularly true for the inducibly defended Texas clone. In most successful invasions, *D. lumholtzi* reached high densities over the course of the experiment and substantially reduced the population size of native *Daphnia*.



Surprisingly and in contrast to the results of Engel and Tollrian (2009), both clones of *D. lumholtzi* performed better in our experiments without rather than with predation. Thus it seems that in our predation treatment, *D. lumholtzi* either could not derive a competitive advantage from being defended, or this advantage was not large enough to compensate for the costs of defense or other indirect negative effects associated with the presence of fish, such as a deterioration of the chemical conditions in the containers.

Additional observations that we made indicated that the defense of *D. lumholtzi* was effective against some of the fish in our experiments (see also Methods section above). However, the effect of the defense could have been counteracted by the fact that fish are visual, size-selective predators and therefore might have preferred *D. lumholtzi* over native *Daphnia*: *D. lumholtzi* are better visible than native *Daphnia*, due to their larger body size, their conspicuously colored broods, and their stronger tendency to produce ephippia. Selective predation for individuals with pigmented reproductive structures has been shown for other *Daphnia* species: Mellors (1975) demonstrated that ephippia-carrying *Daphnia galeata mendotae* are preyed upon selectively by pumpkinseed sunfish and yellow perch. Tucker and Woolpy (1984) found that *Daphnia magna* with pigmented parthenogenetic eggs could be detected by bluegill sunfish from a larger distance than *Daphnia* without parthenogenetic broods. Large differences in visibility are unlikely for our second invasion experiment, however, where we used dark containers in order to equalize the visibility of *D. lumholtzi* and native *Daphnia*.

For the inducibly defended Texas clone, the weak performance in the predation treatment compared to the predator-free treatment could be partly due to the costs of developing the defenses. Following the classification of defense costs by Tollrian and Harvell (1999), these costs may include allocation costs for the formation of head and tail spines, opportunity costs such as developmental constraints resulting from the defenses and environmental costs such as a higher risk of individuals to get entangled in algal filaments. Thus one possible scenario for the Texas clone is that individuals in the predation treatment developed defenses which gave them some protection from fish, but that the costs of the defenses reduced the population growth rate compared to the predator-free treatment.

High costs of their large defense structures could also explain why the permanently defended Arizona clone was less successful than the inducibly defended Texas clone under all experimental conditions. These costs might be outweighed by the benefits only at a predation pressure higher than the one encountered in our experiment, an explanation that has also been suggested by Engel and Tollrian (2009) who used the same permanently defended clone in their experiment. The Arizona clone could also have a higher sensitivity to some environmental conditions, such as crowding or water quality. Finally, it is possible that during the many generations the Arizona clone has been kept in the laboratory, it accumulated mutations that decrease its competitive ability. Overall, we conclude that the invasion of European lakes would be more likely with a clone similar to the inducibly defended Texas clone.

Temperature plays an important role for biological processes, from individual physiology to ecosystems. Therefore, climatic warming has the potential to affect biological invasions at all stages of the invasion process (Hellmann et al. 2008, Walther et al. 2009, Engel et al. 2011). An example where climatic warming has led to the establishment of new populations in areas that were previously not suitable is the establishment of the palm *Trachycarpus fortunei* just south of the Alps (Walther et al. 2007). A similar spread into more northern regions in Italy is predicted for the tiger mosquito *Aedes albopictus* (Roiz et al. 2011). These predictions of regions that might become suitable for establishment in the future are based on a model that combines current distribution and temperature data with climate change predictions. In our study, the inducibly defended clone of *D. lumholtzi* could establish at all temperatures we investigated. Since a vast number of European lakes have epilimnion temperatures above 15 °C for a considerable time period every year, e.g. 23 weeks in Klostersee in 1999 (see Fig. 1), we would expect the establishment of *D. lumholtzi* in Europe to be possible even before further warming.

We must consider, however, that the establishment of a self-sustaining population of *D. lumholtzi* in a European lake would also require populations to survive from year to year. Since *D. lumholtzi* populations can persist in the form of resting eggs, it is not necessary for adults to be able to survive winter temperatures. Because resting eggs are produced sexually, and the encounter rate between mating partners can be reduced in small populations, *D. lumholtzi* might be subject to an Allee effect (Stephens et al. 1999). In this case, the growing season would have to be sufficiently long and temperatures sufficiently warm to reach high population densities and to produce enough resting eggs that will hatch in the next year. Increases in temperature may thus promote *D. lumholtzi* establishment by helping them to overcome Allee effects, as has been suggested for another cyclical parthenogenetic cladoceran, *Bythotrephes longimanus* (Wittmann et al. 2011).

At later invasion stages, changes in temperature may influence the growth and spread of established populations, for example by influencing their competitive abilities compared to native species (Walther et al. 2009). Consistent with previous studies by Fey and Cottingham (2011) and Engel and Tollrian (2012), we observed shifts in competitive dominance from native *Daphnia* to *D. lumholtzi*, especially when comparing the dynamics at 15 °C and 20 °C in the long-term experiments. Such shifts in dominance from native to non-native species are predicted for many aquatic as well as terrestrial systems. Mehnert et al. (2010) compared the growth rates of native European and introduced tropical species of cyanobacteria at different temperatures and then used a model to predict a shift in dominance from native to exotic species in a future temperature scenario. In Sandel and Dangremond's (2012) study on California grass communities, native and non-native species differed in ecologically important traits, with non-native species exhibiting more traits that are favored in regions with high temperature. Stachowicz et al. (2002) monitored the onset and magnitude of recruitment for native and introduced marine invertebrates over a time period of three years, with marked fluctuations in mean winter temperatures. They showed that the introduced species, in contrast to the native species, benefited from warmer winters. Simi-

larly, our long-term experiments predict that *D. lumholtzi* would benefit more from climatic warming than native *Daphnia*. Surprisingly, however, *D. lumholtzi* proved to be a strong competitor in our experiments even at temperatures as low as 15 °C.

Since we supplied only one algal species as resource, the potential species coexistence suggested by our modeling results is surprising at first sight. One possible explanation is intraspecific interference (Vance 1984), where *Daphnia* individuals are more sensitive to crowding by conspecifics than by individuals of the other species. Coexistence between the species could also be explained by temporal resource fluctuations (Levins 1979), which in our experiment could result from the two-day feeding interval and would allow for coexistence if one species is more efficient at exploiting high algae concentrations and the other specialized on low algae concentrations. A third possible explanation is that even our small experimental containers might provide different niches. For example, one *Daphnia* species might be specialized on algae from the bottom and the sides of the containers, whereas the other species specializes on floating algae in the medium. Although it is unclear whether these mechanisms also operate under field conditions, we would expect more niche differentiation in the field, where the algal community consists of multiple species and is also subject to seasonal changes. Thus we hypothesize that coexistence would be possible under a wider range of conditions in the field than in our experiments.

This is an example for the more general problem that our native *Daphnia*, fish, and algae represent only a small subset of the actual native community in a natural lake. In other areas of ecological research, a field study would be a good way to test hypotheses in a more realistic setting. However, in a study on potential future invasions, this is obviously too hazardous. A safer but challenging avenue of future research is to use more complex food webs in laboratory experiments. The differential success of the two *D. lumholtzi* clones in our study highlights that it can even be important to include a set of genotypes within the same species. Such differences in invasion success between genotypes within one introduced species have also been reported by Vellend et al. (2010) in invasion experiments with dandelions (*Taraxacum officinale*). They also tested different genotypes of a resident species, *Poa pratensis*, and found significant differences in their resistance to invasion by the dandelions. Thus, since our experimental results are based on a small subset of the naturally occurring species and genotypes, we must be cautious in transferring conclusions to the field. Nevertheless, we believe that some general conclusions for more complex natural systems are possible.

## Conclusion

Assuming that the detrimental effects of the presence of fish detected in our study do not, or less strongly, act in the field, our experiments did not identify any obstacles to an invasion of *D. lumholtzi* in European lakes. A successful clone could be similar to the inducibly defended Texas clone, which can grow and compete for food at temperatures at least as low as 15 °C. Using our results and prior knowledge on the interaction

of *D. lumholtzi* with North American communities, what can we conclude about the potential impacts of *D. lumholtzi* in the case of an invasion into European lakes? In contrast to some studies that found only weak effects of competition and suggest that *D. lumholtzi* might be filling an empty niche in North America (Johnson and Havel 2001, Havel and Graham 2006), our results indicate that competition between *D. lumholtzi* and native European *Daphnia* may be strong, and that *D. lumholtzi* may suppress the population growth of native *Daphnia* and even outcompete them in some cases. In accordance with Dobberfuhl and Elser (2002), the carrying capacities estimated under the Lotka-Volterra model indicate that total *Daphnia* abundance and possibly also biomass may decrease with increasing *D. lumholtzi* abundance. This can have impacts on the population dynamics at higher trophic levels, such as on planktivorous fish.

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# Correlations between global and regional measures of invasiveness vary with region size

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## Abstract

We aimed to assess the utility of the Global Compendium of Weeds (GCW) as an indicator of plant invasiveness, by relating it to invasiveness at smaller scales. We correlated two global measures of invasiveness for alien plant species taken from the GCW (the total number of references for each species and the number of continental areas they are reported from), against distribution data from 18 regions (countries and continents). To investigate relationships between correlation strength and region size and spatial resolution (size of distribution units), we conducted meta-analyses. Finally, invasiveness measures were correlated against the number of habitats occupied by alien plant species and their median abundance in those habitats, in fine-scale vegetation plots in the Czech Republic and the state of Montana (USA). The

majority of Spearman's rho coefficients between GCW-derived invasiveness and regional distributions were less than 0.4. Correlation strength was positively related to region size and resolution. Correlations were weaker when the number of habitats occupied by a species, and species abundances within occupied habitats, were considered. We suggest that the use of the GCW as an invasiveness measure is most appropriate for hypotheses posed at coarse, large scales. An exhaustive synthesis of existing regional distributions should provide a more accurate index of the global invasiveness of species.

### Keywords

Abundance, alien species distribution, database, exotic plant, global invasiveness, range size

## Introduction

Rejmánek (2011) defines invasiveness as 'the degree to which a species is able to reproduce, spread from its place of introduction, and establish in new locations.' However, a clear, useable and repeatable measure of the extent to which species are invasive is still lacking. For plants, many studies employ continuous measures of invasiveness in the introduced range, which involve quantifying species distributions – how widespread species are (Stohlgren et al. 2011). Examples of such data include the number of states (van Kleunen and Johnson 2007, Winter et al. 2010), countries (Lambdon et al. 2008, van Kleunen and Fischer 2009, Winter et al. 2009) or provinces (Castro et al. 2005, Zuloaga et al. 2008) where a species is established, the number of grid cells (Williamson et al. 2009, Pyšek et al. 2011, Speek et al. 2011) or the number of habitats (Pyšek et al. 2012a, b) occupied by a species in particular countries, the number of herbarium records for species (Delisle et al. 2003, Fuentes et al. 2012), or various measures of the rates of spread derived from distribution data (Forcella 1985, Pyšek and Prach 1993, Williamson et al. 2005). These measures correspond well to the process of invasion in the strictest sense, which involves spread – at multiple scales – from initial points of introduction (Richardson et al. 2000, Rejmánek 2011).

A recent aim in invasion biology has been to synthesise across the accumulated wealth of studies, in order to elucidate any general patterns regarding both causes and consequences of invasions, across species and regions (Blackburn et al. 2011, Gurevitch et al. 2011). Building generalisations may be hampered by the often very different definitions and measures of invasiveness employed (Guo 2011, Pyšek 2011). Synthesising efforts may therefore benefit from the use of a general measure of invasiveness, which integrates information on invasion success from multiple regions and at multiple scales. Recent studies have used the Global Compendium of Weeds (GCW, Randall 2002) to obtain such a measure of invasiveness for alien plant species (Pyšek et al. 2009, Jenkins and Keller 2010, Dawson et al. 2011, Dostál et al. 2011). The 2002 version of the GCW includes nearly 300 species lists referring to over 20,000 taxa in various regions of the globe, which cite species as being a 'weed', 'casual alien', 'noxious' or 'environmental weed', and 'naturalised', among other labels (Randall 2002).

Use of the GCW as an indicator of invasion success has not gone without criticism (Richardson and Rejmánek 2004). It was not originally devised for the purpose

of quantifying invasiveness of plant species, and the representation of different regions is not equal, with a bias of more references covering North America and Australia than other continents (Pyšek et al. 2009). This is partly due to well-known geographical biases in the quality of information on invasive species globally (Pyšek et al. 2008, Jeschke et al. 2012), but reporting and survey-effort biases can also occur in regional distribution datasets (Lambdon et al. 2008), which are commonly used to quantify invasiveness despite not being originally intended for this use. Given the interest in using, and value in having a general measure of invasion success for plants, the utility of measures derived from the GCW requires validation against multiple measures that are region-specific.

Here we assess the adequacy of the GCW in providing a general indication of invasiveness, by analysing the strength of correlation between two measures of invasion success derived from the GCW, and regional distribution data for 18 regions varying both in their size (spatial extent) and spatial resolution (i.e., the grain of the distribution units used). Distributions of native plant species have been shown to be more closely correlated when the size (Thompson et al. 1998) and resolution (Hartley et al. 2004) of distributions are more similar. For alien species, we might expect the processes involved which determine invasiveness to be more closely matched to those captured by the GCW, when the region is larger (Pauchard and Shea 2006). Environmental heterogeneity changes across scales (Milne 1991) and larger areas may be more likely to contain habitats and environments allowing a species to establish and invade, which are also found elsewhere globally. Heterogeneity of smaller units nested within larger units means that occurrence in a region does not equate with species occurrence everywhere within the region. Thus, we also assess how the relationship between the GCW and regional distribution data may be scale-dependent. Whilst we do not expect relationships to be 1:1, we do expect there to be variation in how much the relationships deviate from 1:1, and we predict the correlations between the GCW and regional measures will be greater when the region is larger, and the resolution coarser.

We also assess (i) the strength of correlation between GCW-invasiveness measures and the number of habitats species occupied, and (ii) their median abundance in those habitats, derived from fine-scale vegetation-plot data in two regions for which such data are available: the Czech Republic and the state of Montana (USA). At the finest spatial resolution of vegetation plots within habitat types, environmental conditions and exposure to alien plant propagules will be strongly site-dependent. At this scale, the identity and characteristics of individual habitat types may be the most important determinant of invasions (Chytrý et al. 2008a). Thus at the finest spatial scale, we expect there to be little or no relationship between local-scale vegetation plot abundance and global invasiveness. Species' commonness can also be indicated by their level of habitat-specificity, i.e. the number of habitats which species can occur in (Rabinowitz 1981). Widespread species within a region also tend to occupy a greater range of habitats (Pyšek et al. 2009, 2011), so we also expect GCW-derived invasiveness measures to correlate well with the number of habitats occupied by a species.

## Methods

### Data collection

We obtained regional species-distribution data as regional invasiveness measures, for vascular plants for 18 regions in total, on six continents (Table 1). The regions ranged from countries to whole continents (Table 1). The data were obtained largely from online national databases, floras and published literature (see Table 1). Data for the grid-cell occupancy of species in the Czech Republic were obtained from the working database CzechFlor, held at the Institute of Botany, Academy of Sciences of the Czech Republic, Průhonice. The species included in regional datasets were considered at least to be casual (*sensu* Richardson et al. 2000, Pyšek et al. 2004), naturalised (*sensu* Richardson et al. 2000, Pyšek et al. 2004) or weed/invasive species (Table 1). For Europe, and all European countries, only species introduced after AD 1500 ('neophytes') were included.

The number of alien species per region varied from 221 (China) to 3,682 (North America; Table 1). There was no significant correlation between region area and the number of species included (Spearman's  $\rho = -0.117$ , 95% CI =  $-0.6376, 0.4615$ ,  $p = 0.644$ ). Region areas were obtained from atlas sources. For regions with non-grid cell distribution units, atlas sources were also used to calculate the mean average area of distribution unit per region, and these values were used as a measure of resolution (Table 1). The largest region was North America (USA + Canada), which also had the coarsest resolution of distribution; the smallest of the 18 regions was New Jersey (Table 1).

Data on the number of habitats/communities and the median abundances of species within those habitats were obtained from vegetation-plot data for the Czech Republic and Montana. Both datasets used originally included native and alien plant species that were present in each plot; however, we excluded the native species for our purposes and included all aliens for Montana and all neophytes for the Czech Republic. The dataset used for the Czech Republic was from Chytrý et al. (2005); it included a stratified selection of over 20,000 vegetation plots from the Czech National Phytosociological Database (Chytrý and Rafajová 2003: GIVD code EU-CZ-001, Dengler et al. 2011); these plots varied in size according to vegetation type (see Chytrý et al. 2005, for details) and contained species-cover records determined according to the Braun-Blanquet or Domin scale (van der Maarel 1979). These plots were classified into 32 habitat types based upon EUNIS Habitat Classification (Davies and Moss 2003; Chytrý et al. 2005). We calculated three metrics from this dataset: (i) the number of habitats occupied by a species, (ii) the average median cover of species across habitats occupied, and (iii) the maximum median habitat cover (i.e. the habitat with the highest median cover). Median covers per habitat were calculated using vegetation plots where a species was present and average median covers per habitat were calculated across habitats where a species was present. The median cover from the habitat with the highest median cover for a species was used as the maximum median cover. For Montana, data were downloaded from VegBank (<http://vegbank.org/vegbank/index.jsp>, accessed 03/02/2011; GIVD code NA-US-002; Dengler et al. 2011), which in-

**Table 1.** The 18 regions included in this study and the data sources for the species distributions per region. Also included is the number of species per region, the region area, the unit of distribution used, and the resolution (area of distribution units, average values given for non-grid cell units).

Region	Data Source	No. of species	Species included are at least:	Area (km <sup>2</sup> )	Unit of distribution (number of units)	Resolution (km <sup>2</sup> )
Argentina	Zuloaga et al. (2008)	582	Naturalised	3,744,977	Province (24)	162,825
Australia	AVH Australia Virtual Herbarium ( <a href="http://chah.gov.au/avh/">http://chah.gov.au/avh/</a> ) Australian Government weeds list ( <a href="http://www.environment.gov.au/cgi-bin/biodiversity/invasive/weeds/weedspeciesindex.pl?id=701">http://www.environment.gov.au/cgi-bin/biodiversity/invasive/weeds/weedspeciesindex.pl?id=701</a> )	416	Invasive ('Weeds')	7,617,930	Point record	NA
Chile	Fuentes et al. (2012)	688	Naturalised	757,725	Province (50)	15,155
China	Weber et al. (2008)	221	Invasive	9,677,012	Province (32)	224,621
Europe	DAISIE ( <a href="http://www.europe-alien.org/">http://www.europe-alien.org/</a> )	1,238	Naturalised	4,767,682	Country/region (23)	207,291
Czech Republic	CzechFlor Database	918	Casual	78,866	Grid cell (679)	132
Germany	FlorKart ( <a href="http://www.floraweb.de">http://www.floraweb.de</a> )	427	Casual	357,021	Grid cell (2995)	ca. 130
Great Britain	British and Irish Flora (Preston et al. 2002)	1,340	Casual	229,848	Grid cell (2886)	100
Ireland	British and Irish Flora (Preston et al. 2002)	521	Casual	84,421	Grid cell (1028)	100
Italy	Celesti-Grapow et al. (2010)	922	Naturalised	301,338	Province (21)	15,066
North America	Kartesz (2011)	3,682	Naturalised	19,811,345	State/Province (66)	303,742
Alabama	Kartesz (2011)	777	Naturalised	135,765	County (67)	1,962
California	Kartesz (2011)	1,359	Naturalised	423,970	County (58)	6,969
Florida	Kartesz (2011)	1,057	Naturalised	170,304	County (67)	2,080
Montana	Kartesz (2011)	534	Naturalised	380,838	County (56)	6,801
New Jersey	Kartesz (2011)	683	Naturalised	22,588	County (21)	915
Pennsylvania	Kartesz (2011)	1,038	Naturalised	119,283	County (66)	1,764
South Africa	Weeds and Invasive plants database ( <a href="http://www.agis.agric.za/wip/">http://www.agis.agric.za/wip/</a> )	286	Invasive	1,221,037	Grid cell (1575)	775

cluded 6,251 vegetation plots (also varying in size depending on vegetation type). The same three metrics were calculated as for the Czech plot data (except ‘number of communities’ replaced ‘number of habitats’). The community data in VegBank followed definitions outlined by the guidelines for describing associations and alliances of the US National Vegetation Classification (Jennings et al. 2009). Species cover in plots was measured as percentage of total area. A total of 175 and 158 species were included in the final datasets for the Czech Republic and Montana, respectively.

The Global Compendium of Weeds is the most comprehensive list of weedy and invasive species to date (Randall 2002), and whilst it is not exhaustive, it is still global in scale, and draws on records from all six inhabited continents, and also oceanic islands. We used the GCW to generate two invasiveness measures for species present in each regional dataset. First, all references to a species were counted. Second, the number of GCW areas was counted (11 in total) within which a species was referenced as occurring. These GCW areas were Africa, Europe, North America, Central America, South America, Australasia, Central Asia, South Asia, Middle East, South-East Asia and Pacific Islands (including Hawai’i; see Table S1 in Appendix for further details; Dawson et al. 2011). Additionally, a number of references included within the GCW only record species as ‘introduced’, which may not indicate that the species has established, or is invasive. Thus, these two invasiveness measures were recalculated, including only those references explicitly referring to species that were weedy, naturalised or invasive (i.e. species were weeds, noxious or environmental weeds, naturalised, invasive alien/exotic, exotic/alien of ecological/conservation concern; these references are hereafter referred to as ‘weed only’ references). References exclusively citing weeds of agriculture were not included as ‘weed only’ references.

## Analyses

We used Spearman’s rank correlation to assess the association between regional distribution data and GCW invasiveness measures, because (i) we did not expect relationships to be linear and (ii) data were skewed and sometimes included outliers. Whilst Spearman’s rank correlation is robust to the presence of outliers compared to the product-moment correlation, it can still be affected by heteroscedasticity, and by outliers when they are large in number (Bin Abdullah 1990). To ensure that estimates of Spearman’s rho coefficients were robust, we used a resampling-with-replacement bootstrapping procedure (with 9999 sample replicates) in order to calculate 95% confidence intervals (bias-corrected). Confidence intervals not overlapping zero indicate that the correlation between a regional distribution and GCW invasiveness measure is significantly greater than zero. However, the numbers of species within regions are large, and the precision with which one can estimate a correlation coefficient increases with sample size. Thus, even weak correlations are likely to be estimated accurately and differ significantly from zero. Therefore, the strength of the correlations themselves is of greater relevance to this study than whether or not the correlations differ significantly from zero.



Coefficients and confidence intervals were calculated for correlations between distribution data of each region and one of the two GCW-invasiveness measures: (i) the total number of GCW references, (ii) the number of GCW areas a species was recorded in. This was repeated for (iii) the number of ‘weed only’ category references, and (iv), the number of GCW areas according to ‘weed only’ category references. In all cases, to avoid non-independence of GCW-derived invasiveness and regional distribution measures, references in the GCW from the area containing the target region considered were always excluded (see Table S1 for description of GCW areas). For example, for correlations involving the German and European regional distribution data, all references of species from Europe were excluded in the calculation of the GCW measures. Similarly, for the data from China, all references from East Asia were excluded, as were all references from North America, when Canadian provinces and USA states were analysed.

We used the random effects meta-analysis approach outlined by Gurevitch and Hedges (1999) to analyse the relationship between correlation coefficient strength and region area or resolution. A Pearson’s rank correlation test of area and resolution (both log transformed) revealed that regional areas and resolution were strongly and significantly correlated (Pearson’s  $R = 0.806$ , 95% CI = 0.531, 0.927,  $df = 15$ ,  $P < 0.0001$ ), and so they were considered individually. Australia was excluded from the analyses involving resolution, as the distribution units for Australia were point records.

First, we transformed Spearman’s rho coefficients ( $\rho$ ) from the correlations between regional distributions and GCW measures, using Fisher’s Z transformation:

$$Z = \frac{1}{2} \ln \left( \frac{1 + \rho}{1 - \rho} \right)$$

The variance associated with each Z-transformed coefficient was calculated as:

$$var(Z) = \frac{1}{n - 3}$$

where  $n$  equals the sample size. This transformation has the benefit of stabilising the variance of the correlation coefficients, reducing heteroscedasticity. We wanted to analyse these transformed coefficients meta-analytically, and to do so, Gurevitch and Hedges (1999) recommend a random-effects approach, to account for random variation that occurs between effect sizes (transformed coefficients in this study). This requires estimation of not only within-region coefficient variances, but also between-region coefficient variances (Gurevitch and Hedges 1999). To achieve this, we ran a fixed effects linear regression model, with Z-transformed correlation coefficients as the effect sizes, and area or resolution (ln-transformed) as the explanatory variable. The between-region variance in coefficients was then extracted and added to the within-region variances (Gurevitch and Hedges 1999). The inverse of these summed within- and between-region variances was then used as weightings per region in a second linear regression model (the actual meta-analysis). Because of the relatively low sample size (17/18 regions), the second linear regression model was bootstrapped with 999 replicates (where the region coefficients

were randomly sampled with replacement), and bias-corrected 95% confidence intervals were inspected to assess the significance of slopes (confidence intervals containing zero indicate that the relationship between correlation strength and region area/resolution is not significantly different from zero). This meta-analytical procedure was conducted for coefficients with each of the GCW-derived invasiveness measures per region.

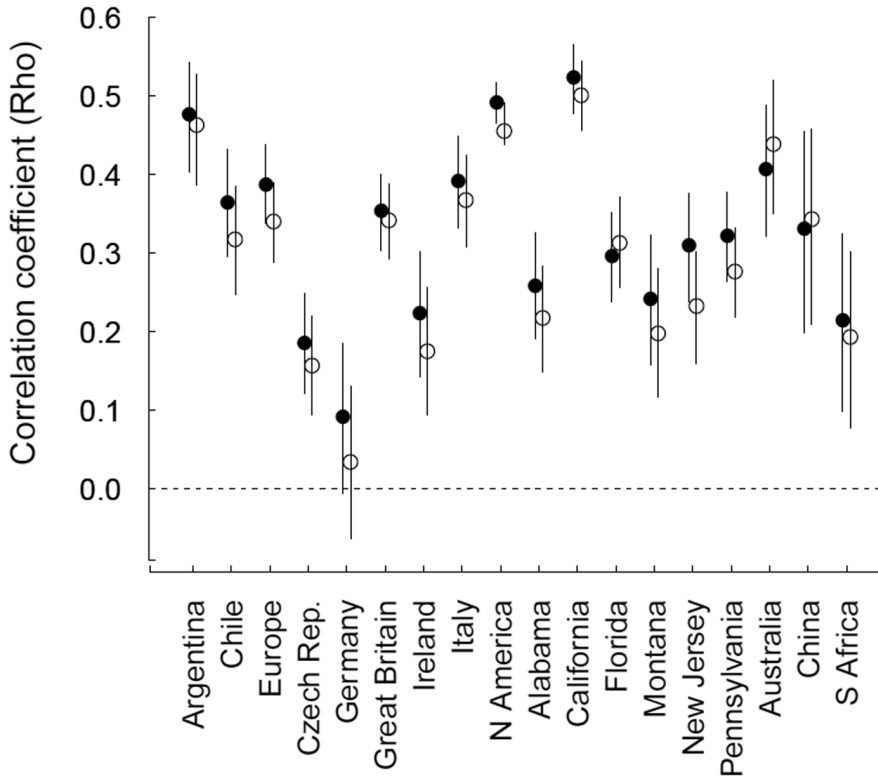
One potential reason for correlation strength varying between regions could be due to the fact that smaller regions are more likely to have dissimilar, idiosyncratic sets of species compared to the larger regions. To test this, Spearman's rho correlations were conducted between region size (area) and the proportion of species within a region with zero references from elsewhere outside the target region. A negative correlation with region area would be expected, if smaller regions tend to have more idiosyncratic species not found elsewhere. A bootstrapped, bias-corrected 95% confidence interval (9999 replicates; confidence intervals are hereafter referred to as '95% CI') was used to assess significance of the correlation, as above.

For the vegetation-plot data from the Czech Republic and Montana, the same analytical procedure was used as for the individual regional-scale distribution correlations with GCW invasiveness measures. All analyses were conducted using R 2.14.0 (R Development Core Team 2011).

## Results

### **How strongly correlated are GCW invasiveness measures and regional alien plant distributions?**

When all GCW references were considered, the correlation between the number of GCW references and regional distribution measures was significantly different from zero for all regions except Germany (Fig. 1). Spearman's rho coefficients ranged from 0.091 (Germany) to 0.523 (California). Despite the significance of the correlations, all of them were far from a 1:1 relationship. Only one region (California) had a correlation strength above 0.5 with this GCW invasiveness measure; the majority of regions (13) had correlation coefficients <0.4 (Fig. 1). When the number of GCW areas recording a species was used as the GCW invasiveness measure, the majority of regions (14) had correlation coefficients slightly (but not significantly) lower than when the number of references was used (Fig. 1). When 'weed only' category references were considered, the correlations between the number of GCW references or GCW areas and regional distributions were similar in strength overall to those obtained when all references were considered (Fig. S2). Correlation strength was also high (>0.4) for North America and Australia (Fig. 1), which are the two regions most over-represented by references in the GCW, suggesting that the GCW is a reasonable correlate of regional alien plant distribution independently of the reference bias for these two regions. The proportion of species per region with zero references outside the target region was not significantly correlated with region area ( $\rho=0.170$ ; bootstrapped, bias-corrected 95% CI= -0.4137, 0.6390).

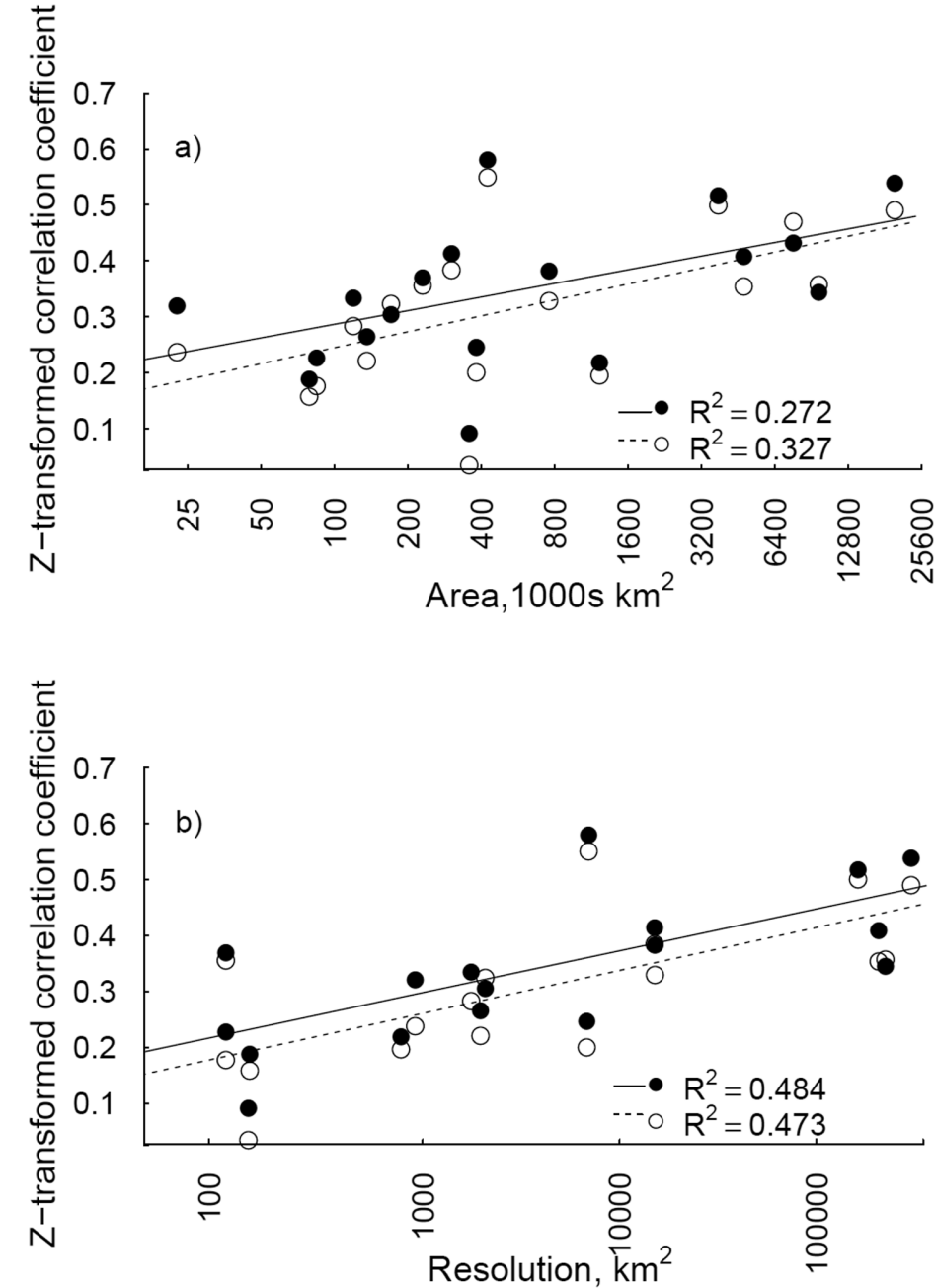


**Figure 1.** Spearman's  $\rho$  correlation coefficients of the relationship between the number of GCW references (closed circles), or the number of GCW areas occupied (open circles) and the distribution (number of units occupied) of species in 18 regions. GCW measures were calculated using all non-target region references (See Fig. S2 for coefficients using 'weed-only' references). Error bars indicate bootstrapped, bias-corrected 95% confidence intervals; the dashed line signifies  $\rho=0$ .

### Is correlation strength related to region area and resolution?

In the meta-analyses, the strength of correlation between GCW-derived invasiveness and regional distributions was significantly and positively related to the area of the target region (Fig. 2a), when the number of references was considered ( $\beta_{\ln(\text{area})}=0.035$ , 95% CI= 0.012, 0.054). A similar significant, positive relationship with area was observed for the number of GCW areas occupied ( $\beta_{\ln(\text{area})}=0.041$ , 95% CI= 0.023, 0.059; Fig. 2a).

The strength of correlation between regional distribution and GCW invasiveness was also related to resolution of distribution units; correlation strength increased with increasing average area of distribution units (Fig. 2b). The relationship between resolution and correlation strength was similar whether the number of references ( $\beta_{\ln(\text{resolution})}=0.032$ , 95% CI= 0.015, 0.048) or the number of GCW areas was used ( $\beta_{\ln(\text{resolution})}=0.033$ , 95% CI= 0.013, 0.049; Fig. 2b). The relationships between area or resolution and correlation strength were similar when 'weed only' references were used, but less variation in coefficient strength was explained by area, than when all references were used (Fig. S3).



**Figure 2.** Relationships between the correlation strength (Z-transformed Spearman's  $\rho$  coefficient) of GCW-derived invasiveness measures and regional distributions, and region area (a) and resolution (area of distribution units; b). Solid lines and circles represent the fitted models and correlation strengths per region, respectively, with number of references in the global compendium of weeds as the GCW-invasiveness measure. Dashed lines and open circles are fitted models and region correlation strengths, respectively, with the number of GCW areas as the invasiveness measure. Note the natural log scale on the x axes.

### Is invasiveness according to the GCW correlated with number of habitats and abundance at the vegetation-plot scale?

In the Czech Republic, the number of habitats occupied by a species was significantly correlated with GCW invasiveness measures, and the correlation was strongest when number of 'weed only' references was used; however, none of the coefficients were  $>0.3$  (Table 2, Table S4). In comparison, correlation strength for the same set of species was always greater (although not significantly) when the number of occupied  $11 \times 12$  km grid cells in the Czech Republic was considered (Table 2). Maximum median cover in a habitat was not significantly correlated with the number of references or the number of GCW areas occupied (Table 2). Results were similar when 'weed only' references were used, except average median cover in a habitat for the Czech Republic was significantly and negatively correlated ( $\rho = -0.15$ ) with the number of GCW areas recording a species (Table S4).

In Montana, the number of plant communities occupied by a species was significantly correlated with the number of GCW references and the number of GCW areas (Table 2). The correlation coefficients for the same set of species were not significant when the number of Montana counties occupied was considered (Table 2). Average median cover in a community was not significantly correlated with the number of

**Table 2.** Spearman's  $\rho$  correlation coefficients (and bootstrapped, bias-corrected 95% confidence intervals) of relationships between GCW-derived invasiveness measures and regional measures of species abundance and distribution from vegetation-plot data in the Czech Republic and Montana. Also given, for comparison, are correlations for the number of Czech Republic grid cells and the number of counties in Montana occupied by a species, using the subset of species occurring in the vegetation plot data for the respective regions. The values in bold are  $\rho$  coefficients, that are significantly greater than zero. GCW measures included number of references and the number of global regions according to the Global Compendium of Weeds with all non-target region references included.

	GCW invasiveness	
	References	Areas
<b>Czech Republic</b>		
<i>Grid-cell data</i>		
Number of $11 \text{ km} \times 12 \text{ km}$ squares	<b>0.382 (0.241, 0.508)</b>	<b>0.261 (0.111, 0.400)</b>
<i>Vegetation plot data</i>		
Number of habitats	<b>0.282 (0.143, 0.414)</b>	<b>0.216 (0.070, 0.349)</b>
Average median cover per habitat	-0.031 (-0.181, 0.113)	-0.093 (-0.232, 0.053)
Maximum median cover in a habitat	0.072 (-0.080, 0.214)	-0.003 (-0.150, 0.139)
<b>Montana</b>		
<i>County data</i>		
Number of counties	0.168 (-0.023, 0.339)	0.135 (-0.043, 0.309)
<i>Vegetation plot data</i>		
Number of communities	<b>0.240 (0.057, 0.403)</b>	<b>0.223 (0.048, 0.384)</b>
Average median cover per community	0.114 (-0.049, 0.270)	0.083 (-0.080, 0.241)
Maximum median cover in a community	0.160 (-0.006, 0.315)	0.120 (-0.051, 0.281)

GCW references or the number of GCW areas (Table 2). The maximum median cover of species in a habitat for Montana was significantly and positively correlated ( $\rho = 0.19$ ) with the number of ‘weed only’ references (Table S4).

## Discussion

Synthesis of information on plant invasions and risk assessment schemes across multiple studies and regions could benefit from the development of a globally applicable measure of invasion success. We have shown that the correlations between regional measures of invasiveness and measures derived from the Global Compendium of Weeds (Randall 2002) were largely significantly different from zero, but also diverged considerably from a 1:1 relationship. Correlations were stronger for larger, continental-scale regions with coarse resolution, but weaker for smaller areas with finer-scale distribution data.

The weaker correlation between the GCW and fine-scale regional distributions may reflect the incongruence in spatial distribution between scales observed elsewhere for native species (Thompson et al. 1998, Hartley et al. 2004). A shift in the dominant processes affecting species distributions may occur as one moves from fine-scale to coarse-scale distributions (Hartley et al. 2004, Pauchard and Shea 2006). Globally invasive species may have been widely introduced, but at a smaller regional scale they may not be able to establish and spread because of abiotic and biotic environmental barriers, or introduction effort in the region has not been sufficient to allow escape from cultivation. For a larger, continental-scale region, it is more likely that an invasive species will be introduced in sufficient numbers and locations, and encounter favourable conditions somewhere within the region, for establishment and spread to occur. Conversely, some species may be invasive within regions at a local scale, but may not be widespread at a larger, or even global scale due to dispersal restrictions (natural or human), or spatially restricted introduction effort. Just as with rarity in native plants (Rabinowitz 1981), an alien plant that is widespread at a coarse spatial scale can be abundant or rare in many locations throughout the range, or it can be abundant or rare in few but widely distributed locations. Thus, the coarse-scale GCW measure of invasiveness is unable to capture the more complex, fine-scale spatial structure of species distributions, but is more likely to reflect frequency of occurrence of species in larger regions with coarse distribution units. Dissimilarity in species introductions among regions is also likely to increase as the areas of the target regions decrease, leading to poorer correlations between the GCW and region measures. For example, Lloret et al. (2004) found that only one tenth of alien species on eight Mediterranean islands were found on half or more of the islands, indicating a high level of idiosyncrasy in species pools at the local (island) scale. Additionally, Chytrý et al. (2008b) showed that only few neophyte species were shared among the species present within habitats of three separate regions of Europe (see also Stohlgren et al. 2011). However, we found that smaller regions in our study did not have a greater proportion of alien species without references of being alien elsewhere outside the target region, compared to larger

regions. This, coupled with the lack of a correlation between species sample size and region size, suggests that smaller regions are not necessarily more likely to have species pools that are less representative of the global pool than larger regions.

Many of the regions considered in our study are recipients of largely European plant species (Pyšek 1998, Ugarte et al. 2010; Winter et al. 2010, Stohlgren et al. 2011, Fuentes et al. 2012). As most non-European regions considered are larger in area and coarser in distribution resolution than European regions, the relationship between global-regional correlation strength and area/resolution could be an artefact of dissimilarity in introduced species pools. However, this seems unlikely, as the GCW-regional correlation strength for the whole of Europe was still high and similar to that of North America when 'weed only' references were considered. Thus, it seems unlikely that differences in the character of the regional species pools are confounding the effects of area and resolution on GCW-regional correlation strengths. One final potential cause of the poor correlation between the GCW and regional distributions is that many neophyte species have not yet reached their full extent in invaded regions (Williamson et al. 2009, Gassó et al. 2010, 2012). Over time, species may 'fill in' more fine-scale spatial units in a region, potentially reducing the disparity between fine- and coarse-scale distributions.

GCW-derived measures of invasion success were poor correlates of species' abundance in habitats and communities within which they occur. However, the correlations between habitat breadth and GCW invasiveness measures were significant (Table 2). A relationship between range size and habitat breadth was recently reported for the Czech Republic, where the range of habitats occupied by an alien species increased with larger distribution of the species in this country (Pyšek et al. 2011). Species' range sizes may be large, either because of wide niche breadths or because they utilise a widespread resource (Thompson et al. 1998). The results of our study corroborate those of Pyšek et al. (2009) and Dostál et al. (2011), who showed that the likelihood of Central European plant species being introduced and becoming a weed in other regions globally was greater for species with a larger native range size and niche breadth, respectively. However, this does not mean that commonness of those habitats is unimportant. Chytrý et al. (2005) demonstrated that only 6% of neophyte species in the Czech Republic occurred in more than 10 habitat types, and that the highest species richness of neophyte species was in anthropogenic habitats, which are likely to be more common than those relatively undisturbed that are also rarely invaded. Separating out the roles of habitat niche breadth and commonness of optimal habitat type in determining larger scale alien plant distributions thus remains an interesting challenge.

The significant relationship between the number of habitats/communities containing a species and the GCW could potentially be created by a bias toward inclusion of already widespread and established plant species. For example, alien plant species in the Czech vegetation data may not be representative of the entire Czech neophyte flora, as many rare casual aliens will not have been recorded in vegetation plots (Chytrý et al. 2005). This would focus the data on those species clearly able to establish and spread in the region, whilst species not found in vegetation plots could be either widespread or restricted in their global invasiveness. The 347 species in only one grid cell



for the whole Czech neophyte flora had a range of 0 to 62 references in the GCW. In contrast, the subset of 16 species recorded in only one grid cell and also present in the vegetation dataset had a range of 0 to 30 references in the GCW. This may explain why the correlation strength between the GCW and the number of grid cells occupied by species for the Czech vegetation subset was slightly greater than for the entire list of Czech alien species (Table 2; Fig. 1).

## Conclusion

There is a need for a general measure of how invasive alien plant species are across different scales, which will facilitate synthesis of existing and on-going studies in invasion ecology. Whilst a general measure of invasion success based upon the Global Compendium of Weeds may be a good starting point as a correlate of coarse-scale distributions of alien plants in larger regions, it is unable to capture more detailed, fine-scale distributions and species abundances at a local scale. If understanding global-scale patterns of invasiveness remains an important goal in this field, efforts should be made to integrate existing distribution data in a more sophisticated manner than simply compiling lists, using common units of distribution in order to capture how widespread alien plant species are and to allow comparisons among species. In the meantime, we recommend that ecologists use the GCW with caution, as a general indicator of invasiveness limited to larger-scale questions.

## Acknowledgements

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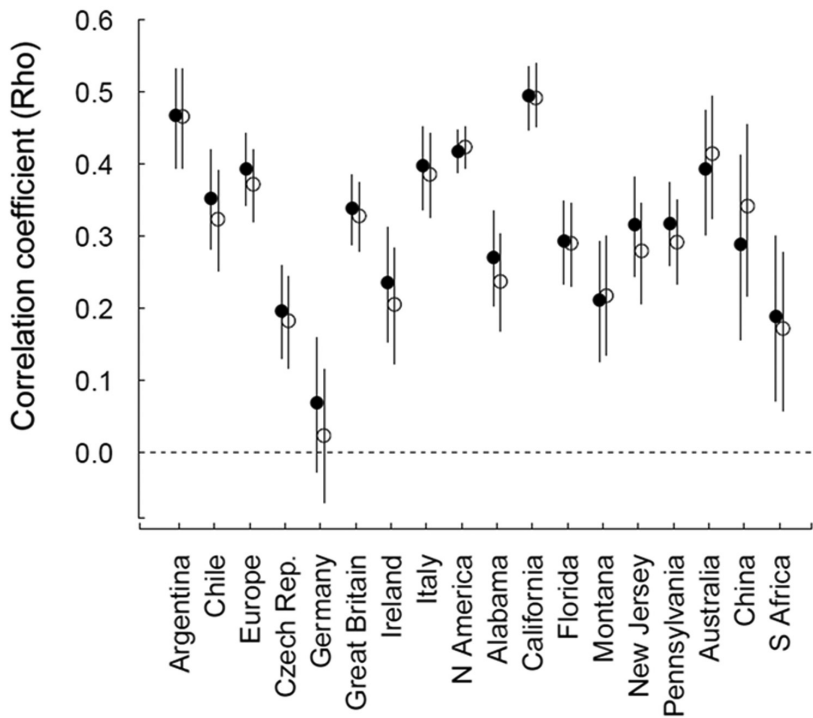
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## Appendix

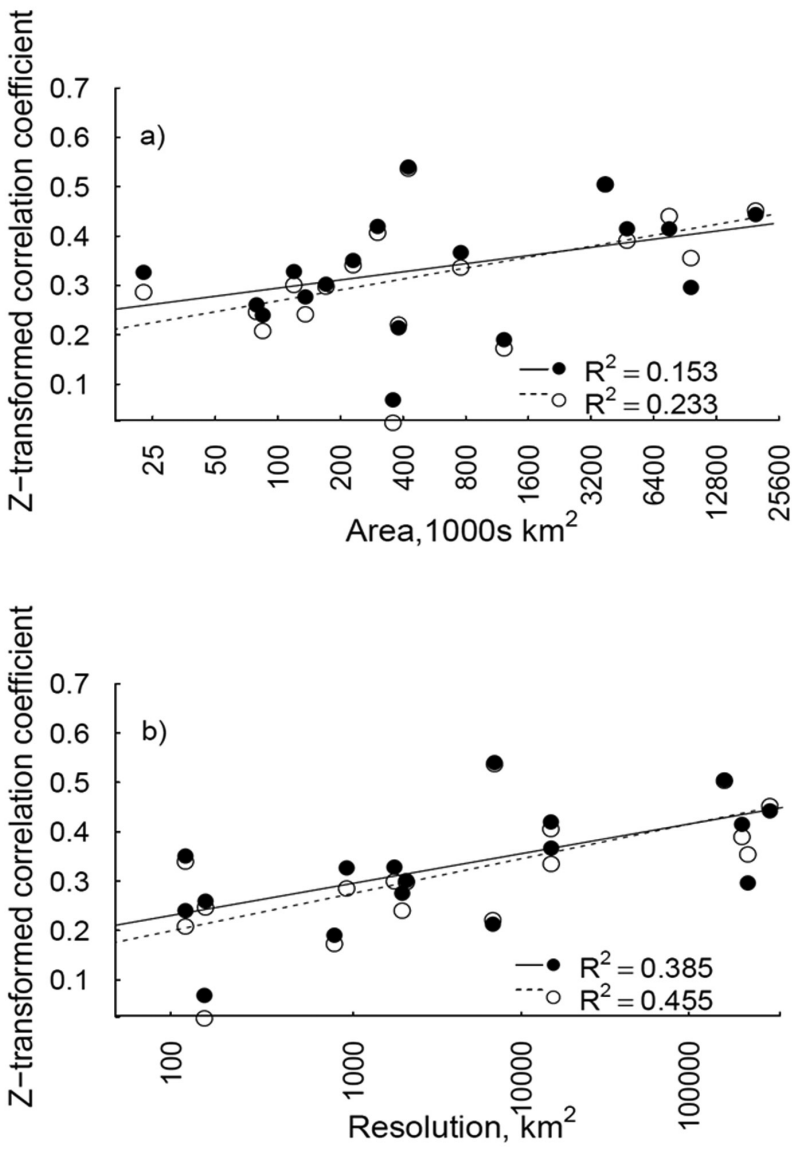
**Table SI.** Description of GCW areas used as a measure of invasiveness, based on references in the Global Compendium of Weeds recording a species in a particular global area. The number of references in the Global Compendium of Weeds referring to each global area is listed, along with the countries (or regions) covered.

Areas	Countries/regions covered	Number of references
Africa	East Africa, Egypt, Ethiopia, South Africa, Sudan, Tropical Africa, West Africa, Zimbabwe and Zambia	21
Asia, North and East	Asia (whole), China, Japan, Mongolia, Nepal, Taiwan	15
Asia, South	Bangladesh, India, Pakistan, Sri Lanka	4
Asia, South East	Indonesia, Java (Indonesia), Papua New Guinea, South East Asia (whole), Thailand, Vietnam.	11
Asia, Middle East	Iran and Iraq, Israel, Middle East (whole), Syria	4
Australasia	Australia, New Zealand	52
Central America	Central America (whole), Cuba, Guadeloupe, Jamaica, Mexico, Puerto Rico	10
Europe	Eastern Europe, Europe (whole), Finland, Italy, Mediterranean, Portugal, UK, Western Europe	14
North America	Canada, North America (whole), USA	88
Pacific	Galapagos, Hawai'i, Micronesia, Pacific (whole), Pohnpei	8
South America	Argentina, Brazil, Chile, Guyana, Suriname and French Guiana, Peru, Peru and Ecuador, South America (whole)	16



**Figure S2.** Spearman's  $\rho$  correlation coefficients of the relationship between the number of references in (closed circles), or the number of GCW areas occupied (open circles) according to the Global Compendium of Weeds (using 'weed only' references), and the distribution (number of units occupied) of species in 18 regions. GCW-invasiveness measures were calculated using all non-target region references. Error bars indicate bootstrapped, bias-corrected 95% confidence intervals; the dashed line signifies  $\rho=0$ .





**Figure S3.** Relationships between the correlation strength (Z-transformed Spearman's  $\rho$  coefficient) of GCW-derived invasiveness measures (using 'weed only references in the Global Compendium of Weeds) versus regional distributions, and region area (a) and resolution (area of distribution units; b). Solid lines and circles represent the fitted models and correlation strengths per region, respectively, with number of references in the global compendium of weeds as the GCW-invasiveness measure. Dashed lines and open circles are fitted models and region correlation strengths, respectively, with the number of GCW areas as the invasiveness measure. Note the natural log scale on the x axes.

**Table S4.** Spearman's  $\rho$  correlation coefficients (and bootstrapped, bias-corrected 95% confidence intervals) of relationships between GCW-derived invasiveness measures with 'weed-only' non-target region references included, and regional measures of species abundance and distribution from vegetation plot data in the Czech Republic and Montana. Values in bold are  $\rho$  coefficients significantly greater than zero. GCW measures included number of references and the number of areas occupied according to 'weed only' references in the Global Compendium of Weeds.

	'Weed only' references	
	References	Areas
<b>Czech Republic</b>		
<i>Grid cell data</i>		
Number of 11 km × 12 km squares	<b>0.416 (0.272, 0.542)</b>	<b>0.354 (0.204, 0.487)</b>
<i>Vegetation plot data</i>		
Number of habitats	<b>0.300 (0.162, 0.431)</b>	<b>0.263 (0.117, 0.396)</b>
Average median cover per habitat	-0.069 (-0.206, 0.079)	<b>-0.154 (-0.290, -0.005)</b>
Maximum median cover in a habitat	0.050 (-0.095, 0.193)	-0.043 (-0.187, 0.105)
<b>Montana</b>		
<i>County data</i>		
Number of counties	0.108 (-0.072, 0.291)	0.157 (-0.031, 0.335)
<i>Vegetation plot data</i>		
Number of communities	<b>0.207 (0.022, 0.375)</b>	<b>0.232 (0.049, 0.397)</b>
Average median cover per community	0.149 (-0.014, 0.304)	0.094 (-0.064, 0.248)
Maximum median cover in a community	<b>0.189 (0.023, 0.339)</b>	0.130 (-0.037, 0.285)

# A systematic review of arthropod community diversity in association with invasive plants

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## Abstract

Invasive plants represent a significant financial burden for land managers and also have the potential to severely degrade ecosystems. Arthropods interact strongly with plants, relying on them for food, shelter, and as nurseries for their young. For these reasons, the impacts of plant invasions are likely strongly reflected by arthropod community dynamics including diversity and abundances. A systematic review was conducted to ascertain the state of the literature with respect to plant invaders and their associated arthropod communities. We found that the majority of studies did not biogeographically contrast arthropod community dynamics from both the home and away ranges and that studies were typically narrow in scope, focusing only on the herbivore feeding guild, rather than assessing two or more trophic levels. Importantly, relative arthropod richness was significantly reduced on invasive plant species. Phylogenetic differences between the invasive and local plant community as well as the plant functional group impact arthropod diversity patterns. A framework highlighting some interaction mechanisms between multiple arthropod trophic levels and native and invasive plants is discussed and future research directions relating to these interactions and the findings herein are proposed.

## Keywords

Arthropod, invasive plant, multi-trophic interactions, biogeographic contrast, phylogenetic differences

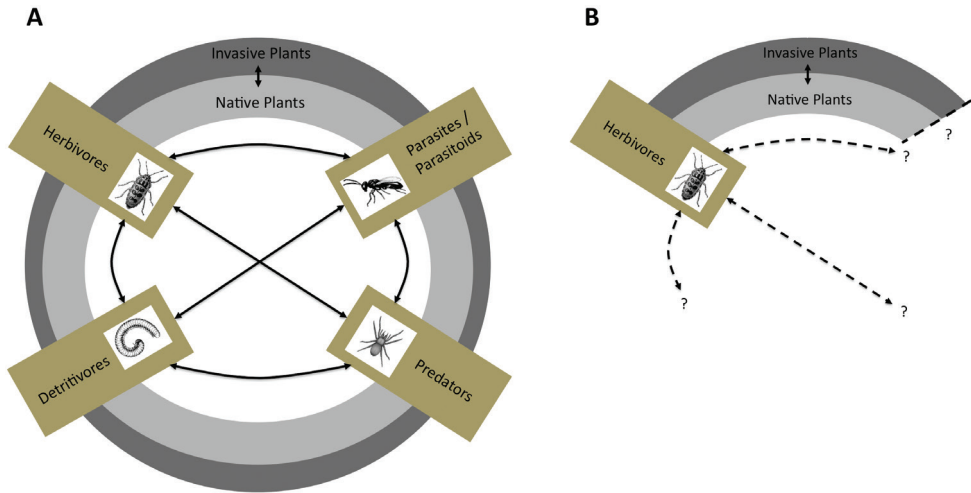
## Introduction

Invasion is a worldwide epiphenomenon as a consequence of both significant dispersal and global change, and the environmental costs are staggering (Mack et al. 2000; Pimentel et al. 2000; Pimentel et al. 2005; Colautti et al. 2006). Several hypotheses have been proposed to explain the success of invasive species typically highlighting a novel characteristic of the invader or a relative deficiency in a novel habitat that renders it susceptible to invasion (Catford et al. 2009). One of the most widely invoked explanations for the success of invasive plants is the enemy release or escape-from-enemies hypothesis (hereafter referred to as the enemy release hypothesis, ERH) that posits that natural enemies (e.g. pathogens and herbivorous arthropods) do not follow invaders from their native range into their introduced range and thus are not able to suppress their expansion (Elton 1958; Crawley 1987; Maron and Vilà 2001; Keane and Crawley 2002; Wolfe 2002). Consequently, invasive species may achieve pronounced vigour and growth in their introduced ranges (Baker 1974; Noble 1989; Blossey and Notzold 1995; but see Vilà et al. 2005) or more importantly relative numerical dominance (Barney and DiTomaso 2008; Siemann and Rogers 2006). The key assumptions of the ERH are that (1) herbivores are capable of regulating plant populations; (2) specialist herbivores endemic to the invasive species are not present in the introduced range; (3) host-switching of specialist herbivores from native congeners is rare; and (4) native plant species experience greater pressure from generalist herbivores than do invasive species (Keane and Crawley 2002; Cripps et al. 2006). Insects are assumed to be the dominant herbivores associated with invasive plants (McEvoy and Coombs 1999; McEvoy 2002).

The ecological research on native herbivore effects on invasive plants is equivocal depending on the herbivore species, plant taxa, and spatial and temporal context (Southwood 1961; Proches et al. 2008; Rohacova and Drozd 2009; Schooler et al. 2009; Fork 2010). For instance, Agrawal et al. (2005) paired 15 exotic plant species with 15 native con-familials in a common garden and allowed native arthropod fauna to colonize the plots over several years. Overall, their results indicated that there was less herbivore damage on exotic species, but this did not correlate with different patterns of herbivore richness or net abundances on native versus exotic plant species. In a similar experiment, Zuefle et al. (2008) paired 15 native plant species with 15 non-native congeners and 15 non-native species lacking congeners in the United States (termed “aliens”), and the authors allowed native arthropod fauna to colonize the plants over two years. Herbivore biomass was greater on natives than non-native congeners and aliens, but biomass did not consistently differ between congeneric pairs of plants. Additionally, aliens retained more biomass than non-native congeners but there was no difference in herbivore species richness or the number of specialist and generalist species collected among the three plant groupings in either year. Other studies have found that invasive plants experience reduced herbivory, lower herbivore species richness estimates, and little if any attack from specialist herbivore species in comparison to native plants (Costello et al. 2003; Cuda et al. 2007; Rohacva et al.

2009; Ando et al. 2010; Lieurance and Cipollini 2012). A meta-analysis conducted by Liu and Stiling (2006) provided evidence that insect herbivore fauna richness is significantly greater in the native than introduced ranges of invasive plants, and this reduction is skewed towards specialists and insects feeding on reproductive parts. Herbivore damage levels were also found to be greater on native plants than on introduced invasive congeners, however, herbivore damage levels were only marginally greater for plants in native than in introduced ranges. Direct control of some invasive plant species by arthropod herbivores is thus plausible (e.g. singular control by biological control agents, see Myers 1985), but fluctuations in herbivore pressure do not necessarily translate into meaningful differences in invasive plant performance (Hierro et al. 2005; Liu and Stiling 2006), an important assumption of the ERH. Nonetheless, the community dynamics of arthropod-plant interactions are generally overlooked as we have focused primarily on target feeding guilds (i.e. herbivores) and not on local arthropod communities within an invaded site or region. The role of arthropod diversity at the community level is thus largely unexplored and likely a very important avenue of future invasion research.

We propose that a powerful evaluation of plant invasion processes can be achieved by documenting whole arthropod community dynamics (e.g. richness, diversity, interactions) in the native and introduced range of a plant invader. Biogeographically contrasting invasion dynamics is rarely practiced (Hierro et al. 2005), either because differences between ranges are assumed to exist *a priori* and are therefore deemed unimportant, or because comparative studies across continents can be prohibitively expensive (Hinz and Schwarzlaender 2004). Further, studies that do contrast invasion dynamics biogeographically are typically limited to plant-plant interactions without quantifying the arthropods that may significantly moderate the plant invasions directly or indirectly. Therefore, studies that document invasive plants in both their native and introduced ranges *and* include measurement of more than one arthropod feeding guild (i.e. predators, parasitoids, detritivores, etc.) could provide a more comprehensive understanding of plant invasions than those documenting only herbivores on select target plants in one place. Plant-plant and plant-arthropod interactions are complex, and the capacity for herbivorous arthropods to induce damage is mediated by both higher and lower trophic levels limiting their abundance, diversity, presence, or feeding behaviour (Hairston et al 1960; Bernays 1998; Schmitz 1998). Further, predator and parasitoid efficacy is mediated by plant architecture (e.g. shrubs vs. grasses vs. trees), volatile cues, and dynamically fluctuates in response to prey and competitor abundance (Price et al. 1980; Pearson 2010). Detritivore abundances may be enhanced by plant invasions when microclimates are favourably altered (e.g. increased moisture or inputs of food matter), or when predator efficacy is reduced. A conceptual framework for potential interactions in native/invasive plant-arthropod systems illustrates the complexity of whole food-web interactions (Figure 1A) and the uncertainty introduced when only herbivores are targeted in plant invasion studies (Figure 1B). Herbivores, predators, parasitoids, and detritivores are all linked strongly to native and invasive plant community complexes (boxes embedded within concentric native/invasive plant circles).



**Figure 1. A** conceptual framework of potential interactions in native/invasive plant-arthropod systems. Herbivores, predators, parasitoids, and detritivores are all linked to native and invasive plant community complexes (boxes embedded within concentric native/invasive plant circles). Solid lines denote reciprocal interactions between arthropod feeding guilds **B** Dashed lines denote the uncertainty introduced when only herbivores are targeted in plant invasion studies. The influence of multi-trophic interactions becomes lost when studies of plant-arthropod systems are limited in scope to only the herbivorous feeding guild.

Reciprocal interactions between arthropod feeding guilds are denoted by solid lines and encompass predation, parasitisation, and intra- and interspecies competition. The influence of these interactions becomes lost (i.e. dashed lines in Figure 1B) when arthropod-plant interactions are limited in scope to enumeration of only the herbivorous feeding guild.

The purpose of this systematic review was to quantify the state of knowledge of arthropod community dynamics in the context of plant invasion, in order to examine the general hypothesis that a biogeographical and multi-trophic examination of arthropod communities enhances evaluations of plant invasions. Specifically, we explored whether: (1) biogeographical contrasts of the arthropod communities associated with invasive plants are under-utilized in the invasion biology literature; (2) arthropod sampling is biased to the herbivore feeding guild and largely ignores the arthropod community as a whole; (3) relative richness of arthropods associated with invasive plants is lower than commonly found on native plants; and (4) phylogenetic differences between the invasive plant and the local plant community and the plant functional group of the invader have the capacity to impact arthropod diversity. Exploration of the literature via quantitative systematic review provides a broad assessment of the importance of local arthropod communities as an indicator or even predictor of invasive plant species dynamics, and studies documenting the dynamics of entire arthropod communities are a logical step in future evaluations of plant invasions.

## Methods

### Literature search, description, and within-study variables recorded

A systematic review of the literature using the Web of Science was conducted in September 2011 using following keywords: “invas\* plant\* (insect OR arthropod OR herbivor\* OR natural OR phytophag\*) and (diversit\* OR abundance OR richness OR herbivory OR removal OR enem\*)”. A total of 1746 studies were retrieved. However, studies were retained for this review only if they explicitly included arthropods, i.e., studies on mammals were excluded. Aquatic systems and secondary studies not based on experimental data directly collected by the authors (i.e. review or idea articles) were also excluded. Finally, all references cited within these articles were also inspected and included to further extend scope.

A total of 53 relevant articles published in 31 different journals were selected for inclusion in this review. The first study was published in 1982, and only three studies were published prior to 2000. The majority of studies (38%) were published in 2009 and 2010. These articles have been cited a total of 759 times as of December 2011. The number of citations/article ranged from 0 to 104 (0 to 14.86 citations/year; mean = 2.23), with most articles (70%) being cited less than 10 times, indicating that perhaps literature corresponding to arthropod community dynamics on invasive plants is not highly visible. Journals contributing the highest number of articles were Biological Invasions (17%), Biological Conservation (9%), and Environmental Entomology (7%).

To characterize the literature on native arthropod communities associated with non-native plant invasions, the following parameters of each study were recorded: ecosystem type (e.g. grassland, experimental field, waste area); the country in which it took place and whether or not it was biogeographical (i.e. data on arthropod communities in association with the invasive recorded in more than one region); native plant species community richness; invasive plant species taxonomy; the plant functional group (PFG) of each invader (tree, shrub, graminoid, or herb); native arthropod community characteristics on invasive host plants/within invaded habitats (i.e. abundance, order, family, and species level richness) and; the class and number of arthropod trophic levels examined (i.e. herbivores, predators, detritivores). Studies were permitted more than one database entry if they examined more than one non-native plant species or geographic region. As this study is strictly a systematic review and not a meta-analysis, effect sizes were not calculated.

### Statistical analyses

Descriptive statistics were used to explore the first two broad patterns associated with the literature including Chi-square tests for differences in relative proportion of studies where appropriate. Generalized linear models (GLMs) were used to explore the latter two patterns that diversity of arthropods is affected by native versus invasive plants and then by PFG and phylogenetic measures of these plants (firstly, we used the entire dataset and then did a second more direct test via paired t-tests of only the studies that



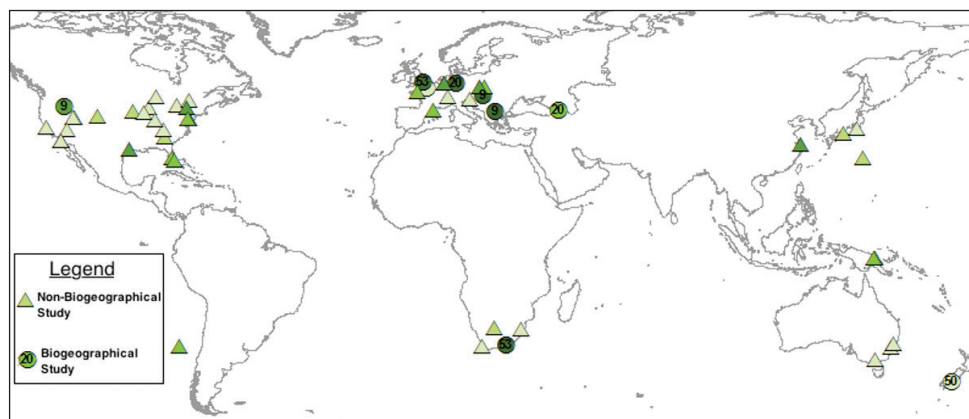
used coupled contrasts). Alpha was set at  $p < 0.05$ , and *post hoc* contrasts were applied when significant to identify specific differences if more than two levels (Nonparametric Wilcoxon signed-rank tests were used as highly conservative between-level tests). Studies were included in these analyses if more than a single trophic group was examined, arthropod richness estimates were provided, and contrasts between target (i.e. on the invasive plant) and native plants or within the community were reported in some form. A total of 4 studies reported only order-level arthropod richness whilst all others reported species-level estimates. The order-level values fell within one standard error of the mean of species-level estimates so were not excluded. The log response ratio (LRR) was also calculated to summarize the strength of the relative difference between arthropods associated with native versus invasive plants (Hedges et al. 1999) within each study (using only the studies that used a target invasive-native paired plant design directly).

Finally, phylogenetic relationships among all 1045 plant species reported were constructed by grafting published phylogenies onto a family-level backbone based on the APG3 derived megatree produced with Phylomatic (Webb and Donoghue 2005). Polytomies were present below the family level and were resolved from published clade-specific phylogenies to the genus level (see Supplementary File 1 for references and Supplementary File 2 for the Newick file). Polytomies among species within genera were randomly broken as species-level phylogenetic information was rarely available or consistent across studies. The lack of resolution at terminal nodes is likely to make subsequent tests more conservative (Swenson 2009). Dated nodes from Wikstrom et al. (2001) and TimeTree (Hedges et al. 2006) were used to restrict branch-lengths based on estimated divergence dates with undated descendant nodes evenly spaced using the *bladj* algorithm in Phylocom (Webb et al. 2008). Within a study, the mean and maximum phylogenetic distance was calculated between the invader and all other species within the community. Regression analyses were used to test whether these two phylogenetic measures impact arthropod richness. All statistics were performed with JMP 9 ver. 9.0.2 (SAS).

## Results

### Broad-scale literature characteristics and frequency and extent of biogeographical contrasts:

From the 53 studies included in this review 11 ecosystem types were censused for arthropods. In decreasing order of prevalence these were: grassland, mixed, forest, experimental field, marsh/wetland, shrubland, riparian, waste area, desert, dune, and floodplain ecosystems. Two studies did not detail the ecosystem from which data was collected. Geographically, arthropod communities were censused in 27 countries (Figure 2). Fifty three percent of all studies were conducted in North America, while 28% were conducted in Europe (Figure 2). Less than 8% of all studies (4/53) used biogeographical contrasts to record arthropod dynamics in the native and introduced ranges of invasive plant species.



**Figure 2.** A world map illustrating the geographic distribution of arthropod-invasive plant studies from the literature in this review. Darker coloured icons represent greater relative arthropod richness.

### Scope of arthropod community recorded:

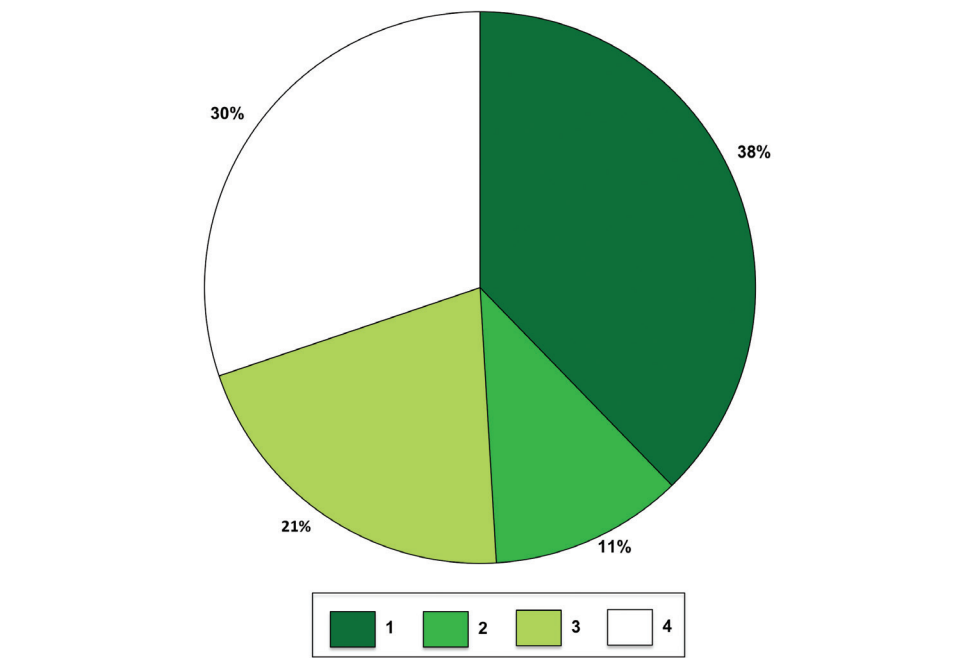
A total of 38% of studies measured only one trophic level whilst 30% of studies evaluated 4 trophic levels. Fewer studies evaluated only two or three trophic levels (Figure 3, 11% and 21%, respectively). These proportionate differences were significantly different (Chi-square,  $c^2 = 8$ ,  $p = 0.039$ ,  $n = 53$ ). A breakdown of studies based on which feeding guilds were examined indicated that the majority (92%) targeted at least herbivorous arthropods. Predators were measured in 64% of the studies, detritivores in 53%, and parasites/parasitoids in 34% (Figure 4, Chi-square,  $c^2 = 16$ ,  $p = 0.0013$ ,  $n = 129$ ).

### Arthropod diversity on invasive plants:

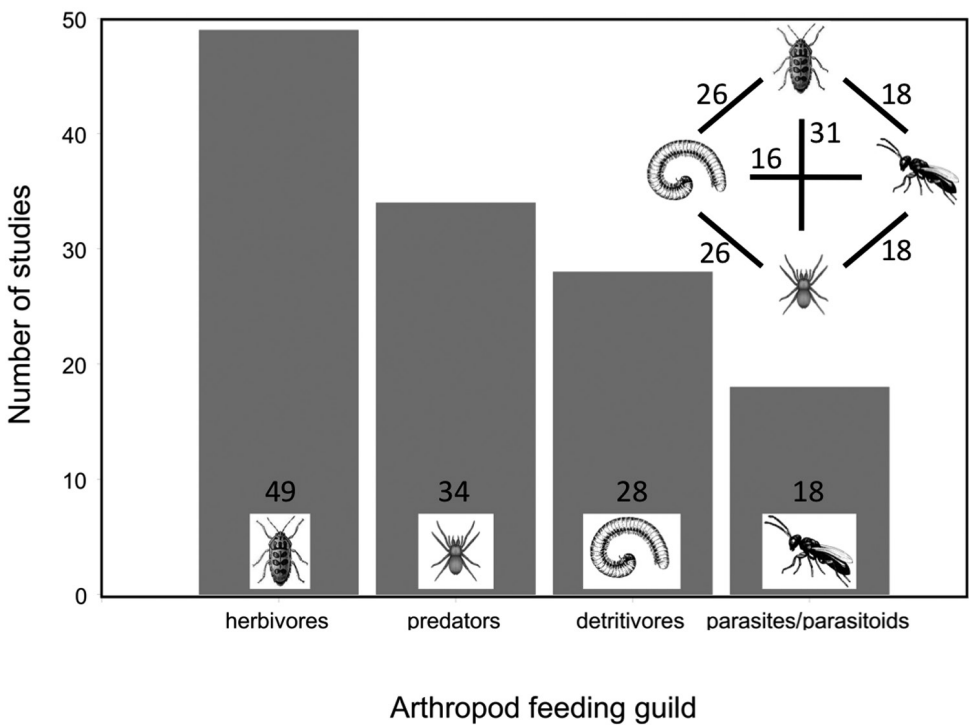
Arthropod richness estimates associated with invasive plants were significantly depressed relative to native plants or monoculture/community estimates using all cases (Figure 5, GLM, chi-square = 385,  $p < 0.0001$ ,  $n = 124$ ). Using only paired contrasts within studies, the strength of the relative depression in arthropod richness between invasive and native plants was  $-0.18 \pm 0.06$  (mean LRR with s.e.), and this estimate was significantly different from a null of 0, i.e. no difference (t-test for mean diff from 0,  $t = -2.5$ ,  $p = 0.01$ ,  $n = 62$  cases).

### Phylogenetic differences and PFG as potential mediators of diversity:

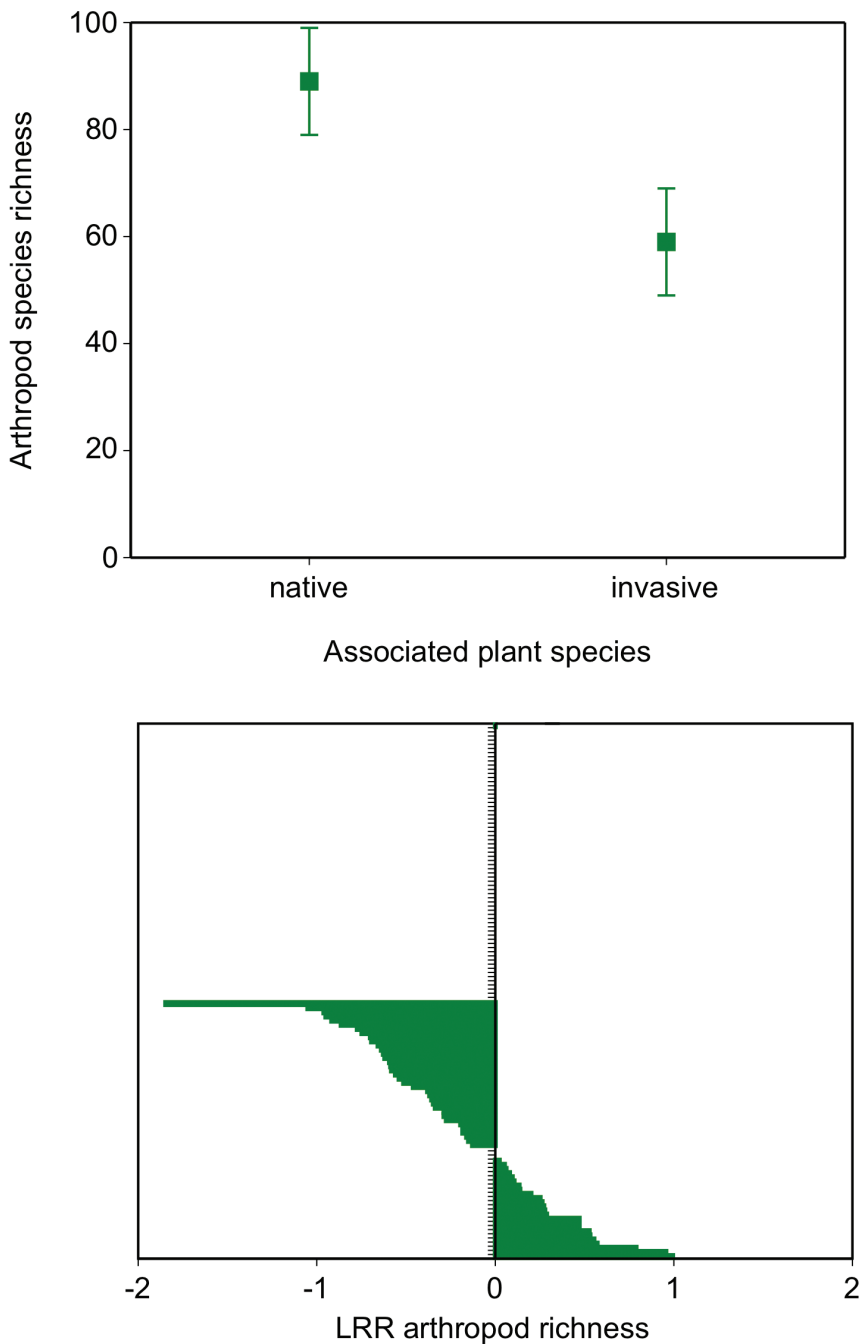
Both mean and maximum phylogenetic distances significantly predicted arthropod richness on invasive and on native plants (Figure 6, Regression analyses, all  $p < 0.0001$ ,



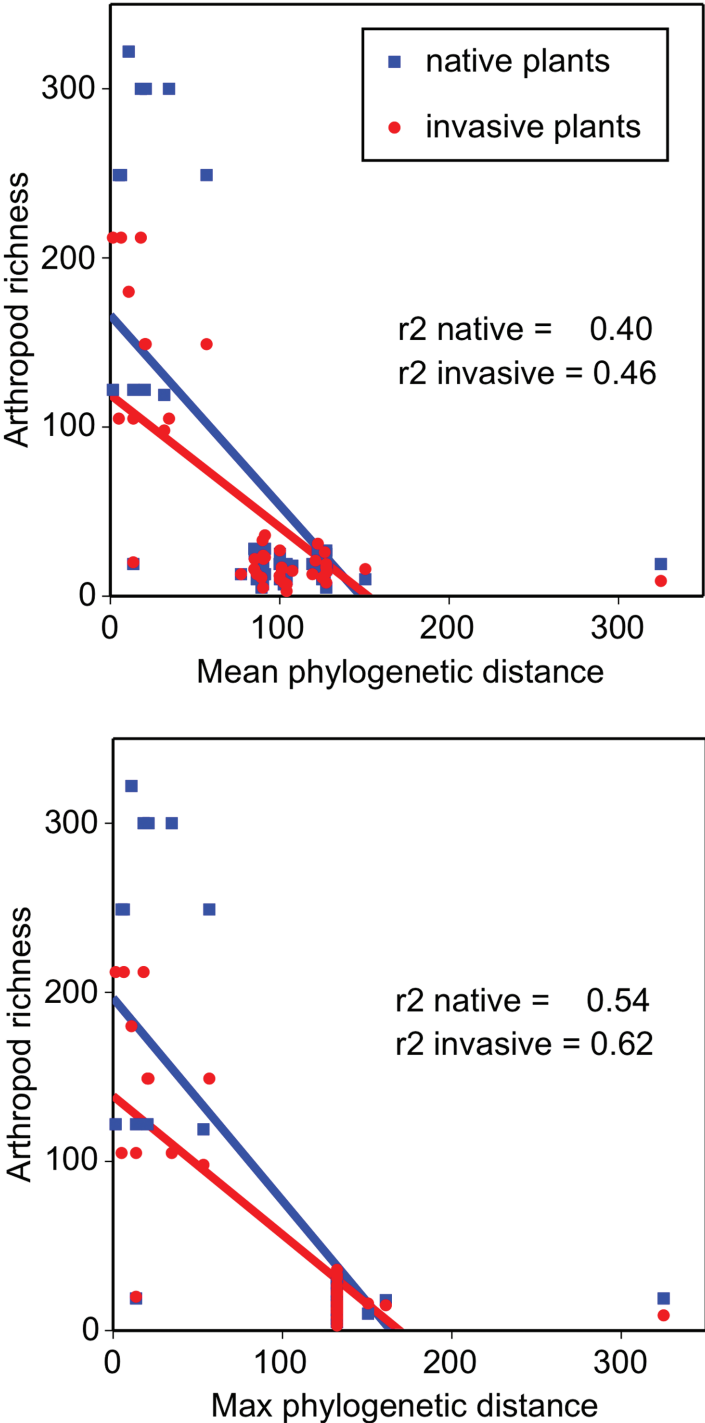
**Figure 3.** Proportion of all 53 studies in this review examining either 1, 2, 3, or 4 trophic levels.



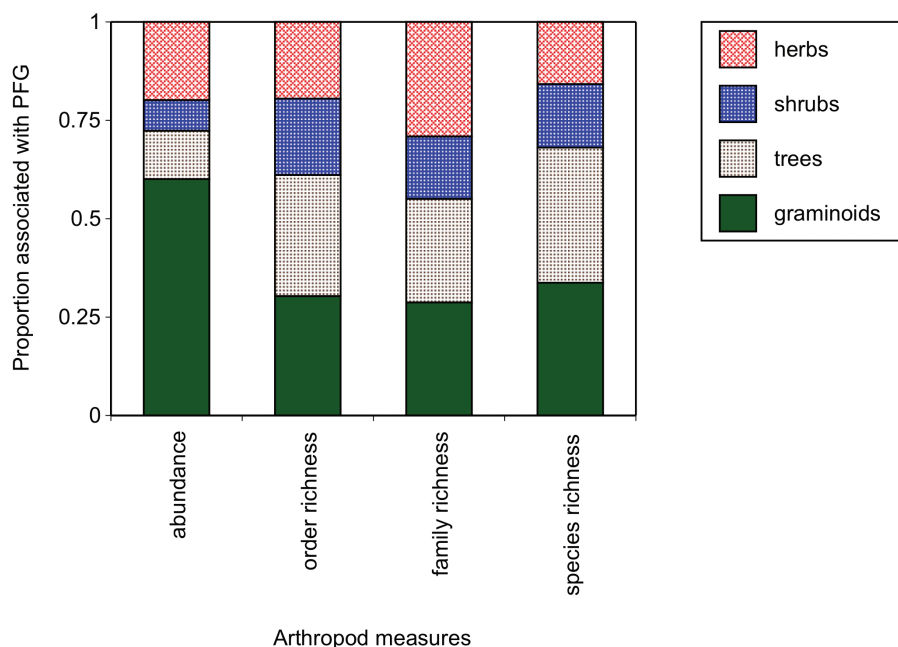
**Figure 4.** Number of all 53 studies in this review examining each of the arthropod feeding guilds.



**Figure 5.** The diversity of arthropods associated with native and invasive plant species. The top plot shows the mean number of arthropod species reported on invasive target plants and the native community  $\pm$  1 s.e. for all studies. The lower modified Forest plot shows the log response ratio (LRR) for only studies that used direct paired contrasts between an invasive and target plant species ( $n = 62$  cases, see text for details). Negative values denote a relative reduction in arthropod species richness on invasives relative to native plants.



**Figure 6.** The effect of mean and maximum phylogenetic distance estimates on arthropod species richness on invasive and native plants. Linear regressions are shown ( $p < 0.0001$ ).



**Figure 7.** The relative arthropod order richness, family richness, species richness, and abundance across PFG on invasive plant hosts. For simplification, relative proportions are plotted instead of raw data as values ranged widely.

$r^2$  values listed on plots). Increasing phylogenetic distances reduced arthropod diversity (Figure 6). Plant functional group significantly influenced arthropod richness at the species level (GLM, Chi-square = 33.8,  $p = 0.001$ ,  $df = 1$ ) but only for arthropods associated with invasive plant hosts - not native plants (GLM, Chi-square PFG\*host = 80.3,  $p = 0.0001$ ,  $df = 3$  with Wilcoxon post hoc paired contrasts,  $p > 0.05$  for all natives). Specifically, arthropod species richness differed between invasive trees and herbs (Figure 7, Wilcoxon paired contrasts,  $p = 0.02$ ), and the abundance of arthropods associated with invasive trees differed from graminoids (Wilcoxon paired contrast,  $p = 0.05$ ). Given the exploratory nature of this review, corrections for multiple comparisons were not made (Rothman 1990; Saville 1990), and importantly, inflated type I error is controlled by the overarching GLMs used to determine which pair-wise comparisons to make. In a strict two-way comparison, PFG for woody plants significantly influenced arthropod richness at the species level (Wilcoxon rank sum test,  $Z=2.27$ ,  $p = 0.023$ ). Specifically, arthropod species richness differed between invasive trees and shrubs (Figure 7).

## Discussion

The primary objective of this systematic review was to quantify the state of knowledge of arthropod community dynamics in the context of plant invasion. Results of this

review highlight some key trends in the arthropod-invasive plant literature: few studies adopt a biogeographical approach when contrasting arthropod communities associated with invasive plants in both native and invasive ranges. Sampling is also relatively simple, primarily documenting only the herbivore feeding guild and not the arthropod community as a whole. The relative richness of arthropods associated with invasive plants is lower than commonly found on native plants suggesting direct or indirect depressions of arthropods. Finally, phylogeny and plant functional grouping can be important factors influencing these reductions in diversity. Arthropod communities clearly respond differently to invasive plants than to native plants.

### **Biogeographical contrasts**

Studying invasive species from a biogeographical perspective is a powerful yet underappreciated tool in invasion ecology (Hierro et al. 2005). At different spatial scales, biogeographical contrasts can provide a direct way to infer the overall extent of invasion as well as to directly compare community dynamics between ranges. For instance, Lamarque et al. (2012) contrasted two congeneric maple species (density, relative abundance, age structure, effects on native species) between France and Canada locally and regionally and demonstrated that density is a viable and useful proxy for invasibility. A study from this review by Cripps et al. (2006) contrasted herbivore community dynamics (diversity, evenness, richness, host utilization) on *Lepidium draba* in its native, expanded, and invasive range effectively testing whether biotic restraint can be mediated through biogeography (it was). However, studies such as these remain scarce in the literature probably due to high financial costs and logistical constraints when sampling in both regions. Regardless, wider scales in sampling of arthropods will dramatically improve our understanding of the full community consequences of invasion.

### **Plant invasion, vegetation complexity, and a multi-trophic perspective**

Sampling regimes focusing on only the herbivore feeding guild comprise a large proportion of the literature (e.g. two of the four biogeographic contrasts in this review). While informative, these studies are not adequate to fully explain the mechanisms by which plant invaders are successful and may introduce uncertainty and thus false conclusions regarding observed declines in herbivores within invaded regions (i.e. Figure 1B). Herbivore declines are often attributed directly to invasive plants but they may be the product of an indirect interaction whereby an invader facilitates predacious or parasitoid species that in turn depress herbivore communities. Specialized enemies such as parasitoids use both visual and volatile cues from plant hosts and their prey items when hunting. In invaded habitats novel plants may initially mask prey presence, although novel cues can be learned after successful foraging (Vet and Dicke 1992). Pearson (2009) found that native spiders were enhanced in grasslands invaded by *Centaurea*



*maculosa* due to altered vegetation architecture for building webs, whereby formerly simple vegetation was replaced by more complex stands. This resulted in a substantial increase in invertebrate predation rates. Similarly, female condition and reproductive output of the endangered wandering spider *Arctosa fulvolineata* were enhanced in salt marsh habitats invaded by *Elymus athericus* (Pétillion 2005; 2009). These positive effects were attributed to a more complex litter layer in invaded habitats compared to uninvaded ones and food limitation was not considered a factor (Pétillion 2005). In other instances where invaders have altered litter inputs within novel habitats, micro and macrodetritivores have responded both positively and negatively to changes in detritus microclimates and food resources (Gratton and Denno 2005; Mayer et al. 2005; Kappes et al. 2007; Wolkovich et al. 2009). Within invaded systems, how shifts in detritivore communities influence predacious or parasitic arthropods, and in turn, how changes in consumer guilds may impact arthropod herbivores is not well understood. Whilst it is intuitive and convenient to limit arthropod studies to herbivores, it would be imprudent to regard invaded systems so simplistically because plant-herbivore interactions have evolved through selection pressures acting in both bottom-up and top-down directions (Hairston et al. 1960; Price et al. 1980; Bernays and Graham 1988; Agrawal 2000; Dicke 2000). Predators and parasitoids have tremendous potential to mold arthropods community structure in the context of plant architecture. In general, plants with greater architectural complexity (e.g. shrubs vs. grasses) provide more places for arthropods to hide from natural enemies (Lawton 1983). arthropods can gain spatially mediated “enemy-free space” on architecturally complex plants by modifying their distribution or behaviour in a way that eliminates or reduces their vulnerability to natural enemies (Jeffries and Lawton 1984). For example, the polyphagous tansy leaf beetle *Galeruca tanacetii* is hypothesized to gain spatial enemy-free space by ovipositing in structurally diverse habitats over simpler ones, which reduced the searching efficiency of its specialized egg parasitoid (Meiners and Obermaier 2004). Conversely, plants can also provide shelter and alternative food to predators, resulting in depauperate herbivore communities in the presence of predators (Dicke 2000).

## Plant phylogeny

Phylogenetic tools are rapidly being applied to the study of plant interactions, community dynamics, and invasion. Phylogenetic similarity between host plants can be associated with similarity in herbivory levels (Hill and Kotanen 2009; Ness et al. 2011), mutualistic interactions (Rezende et al. 2007), and overall arthropod community composition (Weiblen et al. 2006). The link between phylogenetic and ecological similarity can be attributed to the high degree of phylogenetic conservatism in relevant traits (Wiens et al. 2010); invasive plant species may often be both phylogenetically (Gerhold et al. 2011) and functionally (Godoy et al. 2011) unique from the invaded native community. We propose, and show for the first time, that these tools can be an effective means to infer or even predict relative impact on arthropods communities by novel plant species. We must

point out however that this approach was tested via a systematic review using data compiled across studies and not from single, controlled experiments. Nonetheless, this broad test showed a clear correlation between phylogenetic distance estimates and richness.

Diversity is an important response variable in ecology, a major ecosystem service, and sometimes a predictor of relative sensitivity to perturbation at larger scales. Plant invasions in general have been shown to reduce diversity of native plant species (Alvarez and Cushman 2002; Flory and Clay 2010). The impact of plant invasions on arthropods is predicted to also negatively impact diversity (Simao et al. 2010), and this finding was confirmed here in the first thorough systematic review of the topic. In general, more complex and productive habitats increase arthropod species richness - particularly that of herbivores (Murdoch et al. 1972; Root 1973; Allan et al. 1975; Siemann et al. 1998; Agrawal et al. 2006; de Groot et al. 2007; Simao et al. 2010). Aggressive plant invaders thus have the potential to drastically alter native plant communities both directly through plant competition with natives and indirectly through introduction of poor host plant material for native arthropods (Lau and Strauss 2005). The most parsimonious explanation for the depressed diversity detected here is the lack of suitable host plants. Nonetheless, it is also reasonable to extend this implication to much larger ripples including eventual collapse of arthropod communities through reduced trophic complexity or even melt-downs and additional invasions with less potential arthropod controls persisting within regions. Arthropod diversity must be incorporated into the study of plant invasion so as to effectively assess impact and resilience more broadly. Like most correlative approaches however, it is difficult to infer cause and effect or decouple drivers from passengers in the invasion literature (MacDougall and Turkington 2005). Consequently, it is important to note that whilst documentation of background arthropod community patterns in plant invasion studies effectively enhances our capacity to infer larger scale impacts of invasion, delineation of mechanism and tests of top-down control should also be nested within studies of arthropod community dynamics.

## Conclusions and future directions

The interactions between arthropods and plants are complex and reciprocal. Plant invasions offer an interesting and unique opportunity to study these dynamics not only where arthropod-plant relationships have not developed, perhaps due to a lack of evolutionary history, but also in instances where new arthropod-host plant relationships have begun to emerge (Novotny et al. 2003). The movement of invasive species globally is not expected to cease (Mack et al. 2000). As demonstrated by this systematic review, examinations of plant invasions would be enhanced by biogeographical and multi-trophic approaches, and would allow ecologists to better understand the mechanisms behind the successful establishment of invasive plant species. To remedy the research gaps detailed in this review (and echoing sentiments expressed elsewhere, Harvey et al. 2010; Harvey and Fortuna 2012), future studies should consider the following research directions:

- 1 Integrate a biogeographic contrast of invasion with even a coarse but robust community arthropod sampling regime to comprehensively assess the mechanisms surrounding plant invasions. This might entail documenting at least the proportion of predators vs. prey items, and if possible the specific feeding mode of each arthropod (e.g. specialist or generalist), to clarify the direction and mechanism by which herbivore controls are acting on invasive plants similar to what has been detailed in food web studies (Schmitz and Suttle 2001; Henry et al. 2010).
- 2 Consider the role of plant functional group and by extension the complexity (or simplicity) of the native and exotic vegetation, and how this may mediate arthropod community interactions at all trophic levels (i.e. enemy-free space; resources available to arthropods). An extension of this concept could involve plant functional groups as they relate to plant primary and secondary defense compounds against herbivores, and the role this might play in trophic interactions.
- 3 Contrast the phylogenetic distances of invaders vs. native species where possible to elucidate mechanisms by which arthropod communities interact, both arthropod-arthropod and arthropod-plant. An invader that shares relatives (i.e. same family or genus) in a receiving community might be more amenable to hosting native arthropods by nature of similar morphology and chemistry than phylogenetically distinct invaders.

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## Appendix 1

List of family-level phylogenies used to construct the master phylogeny. (doi: 10.3897/neobiota.16.4190.app1) File format: Microsoft Word Document (docx).

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## Appendix 2

Phylogenetic tree contrasting invasive and native plant species. (doi: 10.3897/neobiota.16.4190.app2) File format: Tree Files (tre).

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