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Research

Evolution of marginal populations of an invasive vine increases the likelihood of future spread

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Summary

- The prediction of invasion patterns may require an understanding of intraspecific differentiation in invasive species and its interaction with climate change. We compare Japanese honeysuckle (*Lonicera japonica*) plants from the core (100–150 yr old) and northern margin (< 65 yr old) of their North American invaded range to determine whether evolution during invasion increases the probability of future expansion.
- Plants from populations in the core and margin were compared in two sites beyond the northern range edge to assess their potential to invade novel areas. Data were compared with previous work to assess the effect of latitudinal climate on *L. japonica* spread. Winter survival in current climates was modeled and projected for future climates to predict future spread.
- Margin plants were larger and had 60% greater survival than core plants at sites beyond the northern range edge. Overall, winter survival decreased with increasing latitude and decreasing temperature, and was greater in margin plants than core plants.
- Models suggested that greater winter tolerance in margin populations has increased *L. japonica*'s northward spread by 76 km, and that this survival advantage will persist under future climates. These results demonstrate that evolution during invasion may increase spread beyond predictions using increasing global temperatures alone.

Introduction

By the end of the century, global temperatures are expected to rise by 2–7°C (Stott & Kettleborough, 2002). Changing climates may favor the spread of invasive species (Dukes & Mooney, 1999; Blumenthal, 2005; Bellard *et al.*, 2013) because successful invaders tend to have traits favored in disturbed habitats, such as high dispersal rates, rapid reproduction and establishment, and/or high levels of plasticity (Rejmánek & Richardson, 1996; Daehler, 2003; Anderson *et al.*, 2012). In addition, successful invaders usually have large range sizes in both their native and invaded habitats, suggesting pre-adaptation to a broad range of environmental conditions (Goodwin *et al.*, 1999; Duncan *et al.*, 2001; Kolar & Lodge, 2001; Qian & Ricklefs, 2006). The risk that changing environmental conditions will augment invasions should vary with location. Higher latitudes are expected to experience greater increases in temperature than the global average, particularly in winter (Houghton *et al.*, 1996). Rapidly warming winters may increase the amount of land open to invasions, because many invasive species are limited by extreme cold temperatures (Hellmann *et al.*, 2008; Chapman *et al.*, 2014). Thus, range expansions into higher latitudes are particularly ripe for study.

Invasive species frequently evolve when they enter novel habitats (Mooney & Cleland, 2001; Lee, 2002; Parker *et al.*, 2003), and rapid adaptation to environmental clines in invaded ranges has been demonstrated in several taxa (Thomas *et al.*, 2001; Maron *et al.*, 2004; Colautti & Barrett, 2013; Novy *et al.*, 2013; Zenni *et al.*, 2014). In addition, theory predicts that invasions will favor traits that enhance colonization success at the expanding margin (Phillips *et al.*, 2010; Shine *et al.*, 2011). Colonization success can occur through enhanced dispersal (Simmons & Thomas, 2004; Phillips *et al.*, 2006; Lombaert *et al.*, 2014) or establishment (Lankau *et al.*, 2009; Kilkenny & Galloway, 2013). Although the importance of this phenomenon to ongoing invasions is still unclear, selection on colonization success appears to have occurred repeatedly in some taxa (Van Bocxlaer *et al.*, 2010). Adaptation to environmental conditions in the invaded range and selection for traits that enhance dispersal and colonization success can interact with climate change to alter the invasion dynamics of introduced species (Travis & Dytham, 2002; Wolkovich *et al.*, 2013). Therefore, it is critical that invasion studies take both evolution and global environmental change into account.

The transplantation of invasive plants beyond the edge of the invaded range and comparison of their performance with plants within the invaded area is a powerful tool for the assessment of the potential for further spread when appropriate precautions are taken (Andersen *et al.*, 1985; Gaston, 2009; Hargreaves *et al.*, 2014). Reduced fitness of plants grown beyond the range edge suggests decreased probability of population persistence without adaptation under these novel environmental conditions (Geber

& Eckhart, 2005; Griffith & Watson, 2006; Stanton-Geddes *et al.*, 2012). Transplantation studies that compare fitness between edge and interior populations at interior, edge and beyond-edge sites can help to determine whether edge populations, the most probable sources for continued range expansion, are likely to have the capacity for further expansion, and whether this capacity is associated with adaptation during range expansion (Hargreaves *et al.*, 2014). Alternatively, interior populations that outperform edge populations at and beyond the range edge are indicative of edge populations with reduced genetic quality, probably as a result of isolation and genetic drift (Hargreaves *et al.*, 2014), or habitat-associated reductions in maternal provisioning (Dyer *et al.*, 2010). For invasive species, transplant studies may reveal evolution during invasion that could play a role in further expansion, and suggest whether further adaptation is likely to occur.

Population differentiation across an invaded range may be key to the prediction of how invasive species will respond to future climate change. Researchers have used regression equations, called response functions, to model the relationship between traits and climate, and to predict performance across a specified geographic area under both current and future climatic scenarios (Matyas, 1994; Rehfeldt *et al.*, 1999; Wang *et al.*, 2006). This technique has generally been used to predict the effect of climate change on forest trees, but can be broadly applied to any data from common garden experiments in which genetically differentiated types are grown in a series of environments. Response functions can provide insight into how the distribution of adaptive genetic variation in invasive species has been influenced by past spread, and how this distribution might influence continued spread under future climatic conditions. Thus, response functions can inform predictions of future invasion potential.

To determine whether evolution during invasion can affect future expansion, we compared Japanese honeysuckle (*Lonicera japonica*) plants from the core (established 100–150 yr ago) and margin (established within the last 65 yr) of the invaded range. Previous work has found that, although the genetic composition and diversity of populations from these two areas are comparable (Kilkenny, 2011; Kilkenny & Galloway, 2013), plants from the northern margin of the invaded range grow more rapidly and show greater survival than plants from the core of the range, regardless of whether they are planted in the core or at the margin (Kilkenny & Galloway, 2013). Plants from margin populations also show intraspecific competitive and reproductive advantages over core plants when grown under favorable conditions (Evans *et al.*, 2013). Here, we test whether this evolution during invasion increases the potential for future invasion. In particular, whether plants from the range margin may be more successful than those from the core in environments beyond the current northern range edge. To test this, we planted core and margin populations in two sites beyond the northern range edge. We also compared the first 2 yr of winter survival at the sites beyond the range edge with data on the first 2 yr of winter survival at sites in the core and at the margin of the range from the earlier study (Kilkenny & Galloway, 2013) to determine the effect of winter temperature on survival across the range. Lastly, we developed a survival response function based on winter temperature for populations from the core and margin of the invaded range to evaluate the degree to which evolution during invasion has affected range expansion and to predict the potential for further spread.

Materials and Methods

Lonicera japonica Thunb. (Caprifoliaceae) is a woody vine native to Japan, China and Korea, which invades habitats throughout the USA and worldwide (Schierenbeck, 2004). Throughout the 19th century, several horticultural varieties were introduced and widely planted in gardens across the USA (Leatherman, 1955; Nuzzo, 1997). The species has since become widespread throughout eastern North America, particularly in the south-eastern states, where the first major invasions occurred (Nuzzo, 1997; Schierenbeck, 2004; Beans *et al.*, 2012). *Lonicera japonica* has continued to spread northward in the last half century (Fig. 1). *Lonicera japonica* is considered to be a strong competitor because of its highly plastic growth form (Larson, 2000). Plants can develop roots and shoots at any node, allowing for complex architectures and clonal spread. Once established, *L. japonica* clones can persist for many decades (Kilkenny, 2011). In addition, large clones tend to produce a high number of flowers and fruits, and may do so for up to 9 months of the year in warmer habitats (Schierenbeck, 2004). Fruits are berries and are often eaten by birds (Schierenbeck, 2004), which provide a conduit for long-distance dispersal, although specific dispersal distances are unknown. Freezing temperatures during colder months have been linked to lower survival (Kilkenny & Galloway, 2013) and reproduction (Leatherman, 1955), and niche models suggest that winter temperatures limit the northern range edge in North America (Beans *et al.*, 2012).

To determine the potential for range expansion in *L. japonica*, plants from the core and northern margin were compared in two sites beyond the range edge. *Lonicera japonica* cuttings were collected in June and July of 2006 along two east–west geographic transects differing in latitude. One transect was in the north-eastern USA, along the range margin (40–41.3°N; Fig. 1), and the second was in the south-eastern USA in the core of the range (34.4–35.5°N; Fig. 1). Populations were sampled at *c.* 50-km intervals for a total of 14 populations from the margin and 17 populations from the core. Single individuals from seven other locations along the margin transect were included in the experiment and treated as separate populations (not shown). Within each population, cuttings from individuals were collected at a minimum sampling distance of 50 m to avoid resampling ramets of the same genet (Schierenbeck *et al.*, 1995; Larson, 2000). Between four and 10 genets were collected per population, with 211 genets collected in total. Each genet was rooted and kept under glasshouse conditions at the University of Virginia through the spring of 2008. In the summer of 2008, each genet was clonally replicated into eight cuttings with three to five nodes, treated with rooting hormone (Hormex no. 3, Maia Products Inc., Westlake Village, CA, USA) and placed in pots of perlite under intermittent mist for 1 month. Rooted cuttings were transferred to individual pots and kept in glasshouse conditions at the

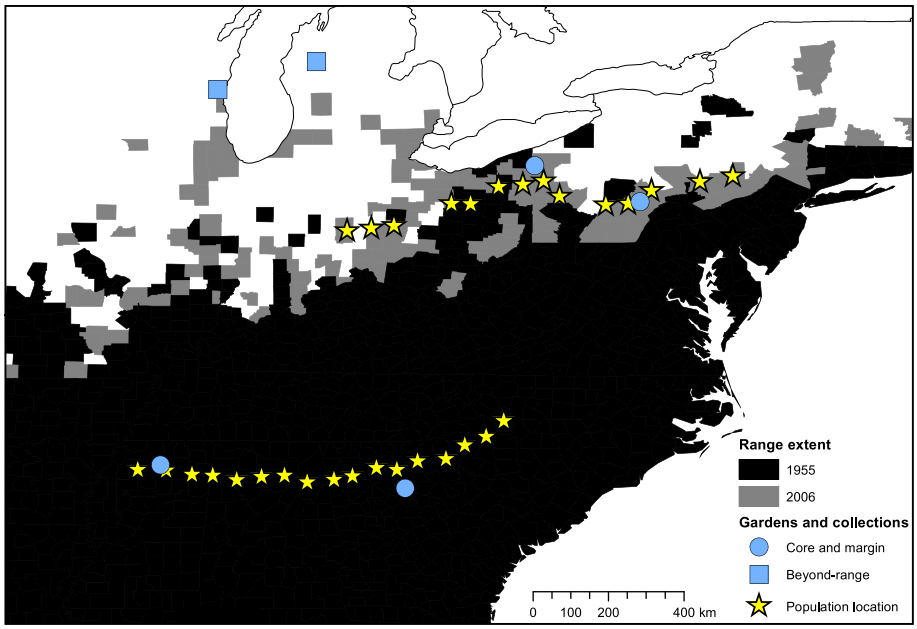

Fig. 1 Range expansion of invasive *Lonicera japonica* since 1955. 1955 range map from Leatherman (1955); 2006 range map from Beans *et al.* (2012). Stars, population collection locations; squares, beyond-range common garden sites; circles, common gardens for the earlier study at the core and margin of the range (Kilkenny & Galloway, 2013).

University of Virginia for *c.* 3 months until they were planted in the field.

Lonicera japonica clones were planted in two garden sites beyond the range edge (G. H. Gordon Biological Station run by Hillsdale College in Michigan, and University of Wisconsin at Milwaukee Field Station; Fig. 1). Each core population and each multi-genotype population from the range margin were represented by *c.* 12 plants per garden (12.03 ± 3.01 (SD); 200 core plants, 173 margin plants). Each population sample group was cloned from six genotypes per population (6.08 ± 1.38 (SD)), meaning that there were approximately two clones per genotype in each garden. In addition, 27 plants cloned from the seven single-genotype locations along the margin transect (three to five clones per genotype) were included in each garden as margin plants, bringing the total number of northern margin plants to 200 per garden. Clones were planted 1 m apart and genotypes were randomly distributed across each garden. Both gardens were located in old fields, similar to the habitat that *L. japonica* might colonize. Before planting, the longest shoot was measured as a proxy for initial plant size. Garden sites were prepared by mowing local vegetation before planting. After the initial mowing, all plants were allowed to experience natural competition. Deer fencing was present or erected at each garden site, and all experimental plants were watered once, immediately following transplant. Individuals were planted at both garden sites in late September and early October of 2008. Transplant survival was recorded in late October and early November of 2008. Only plants that survived transplant were included in the analyses (539 of the 800 planted, 67% from core populations and 67.5% from margin populations).

Survival and growth were monitored in June (spring) and October (fall) of each year for the duration of the study (fall 2008 to spring 2010). However, only survival and final size measures were used in the analyses. Size measures included the following: the number of branches > 2 cm, the length of the longest shoot and the number of nodes on the longest shoot. Because the shoots of plants occasionally died back to the root crown, the location of each plant was checked during each visit. Only 11 plants resprouted over the course of the study, and no surviving plant missed more than one census. All remaining plants were removed from each garden site in late June and early July of 2010 following 1.5 yr of growth. The removed plants were dried and the above-ground biomass was weighed. Staff at both field stations regularly mowed and monitored the garden sites to ensure that no plants escaped removal.

To determine whether plants from the core and margin performed differently beyond the range edge, final size and final survival were compared for plants from the two origins. Final size measures (biomass, branch number, branch length and node number) met the assumptions of normality and were tested for all surviving plants using MANOVA (PROC GLM; SAS Institute, 2009). Garden ('site') and region of origin ('origin') were included in the model as fixed effects, together with the site × origin interaction. Random effects of population nested in origin and site × population nested in origin, as well as initial size, were also included in the model. The canonical structure was calculated to describe the contributions of each dependent variable to the function describing differences between treatment groups. Final survival, the probability of plants that had survived transplant also surviving throughout the entire experiment, was tested using ANOVA (PROC GLIMMIX). Survival was assumed to follow a binomial distribution and was analyzed using the same mixed model structure as employed for the size traits.

To determine the effect of winter temperature on the survival of plants from the core and the margin, we tested winter survival for the first two winters after planting at sites across the invaded range. Winter survival data for the first 2 yr of growth from a previous study using the same genotypes planted at two sites in the core and two sites at the margin of the range (2006, 2007; Kilkenny & Galloway, 2013) were combined with winter survival

data from this study (2008, 2009; six total gardens). Although experiments were conducted in different years, the mean minimum over-winter temperature was similar across years (NOAA-ESRL, weather station closest to each garden, data accessed in 2010) and within the typical range for the past two decades. Survival was tested using ANOVA (PROC GLIMMIX) and was assumed to follow a binomial distribution. The latitude of the garden site and origin were included as fixed effects. The mean minimum temperature for the coldest quarter of the year at each garden site (December, January and February; NOAA-ESRL) was included as a continuous variable. The origin × site latitude and origin × temperature interactions were tested to evaluate whether the relationship between plant origin and survival differed with site latitude or temperature. The site latitude × temperature interaction accounted for differences in the effect of temperature on survival across latitudes. Population nested in origin, site latitude × population nested in origin and temperature × population nested in origin were included as random effects.

To determine the effect of adaptation of margin populations on past range expansion and to predict potential future range expansion, we developed a response function relating over-winter survival to mean minimum January temperature for both core and margin populations. Response functions are regression equations that relate traits to climatic variables, and can be constructed for populations or population groupings (Matyas, 1994; Rehfeldt *et al.*, 1999; Wang *et al.*, 2006). To develop response functions, survival data from all six gardens (Fig. 1) were compared with the mean January temperature at these gardens in both the first and second winter. Populations were pooled by region of origin, and separate functions were developed for core plants and margin plants. The response functions were then fitted with Worldclim climatic data (Hijmans *et al.*, 2005) to project expected survival gradients for both current (climate normals from 1961 to 1990) and expected future climates. The future climate was projected for the year 2050 using a consensus approach, with projections from three future climatic models (scenario A2 for CCCMA, CSIRO and HADCM3 in Worldclim; Hijmans *et al.*, 2005). The projection was limited to areas in the central and northern parts of the current North American range, as well as areas to the north of the current range, to evaluate the potential northward spread of *L. japonica*. Across the projection area, the consensus January mean temperature is expected to increase by 3.7°C by 2050. We developed both linear and quadratic versions of the response functions and found that their adjusted R^2 values were nearly identical. This makes sense given the highly directional gradient from the range core to the margin. Given their similarity, we used the simpler linear functions in this study.

Results

Plants from populations originating from the northern margin of the range reached a greater size and showed 60% greater final survival than populations from the core of the range when grown at sites beyond the range edge (Tables 1, 2; Fig. 2). These differences were not caused by differences in the initial size of the plants. Branch number had a substantially greater canonical value than the rest of the size characters, indicating that it made the greatest contribution to origin-based size differences. Margin plants had 36% more branches than core plants. Although the other measures exhibited lower contributions to the effect of origin, the patterns were all in the same direction, showing that margin plants were larger than core plants (Fig. 2).

At the beyond-range sites, survival was low for both core and margin plants in the first winter (42% for core and 45% for margin), but diverged substantially in the second winter (45% for core and 65% for margin). Winter survival across the invaded range was predicted by latitude of the garden site, temperature and origin (Table 2), but not by the origin × site latitude or origin × temperature interactions. In general, winter survival

Table 1 Multivariate analysis of variance of four size characters of *Lonicera japonica* originating from the core and margin of the invaded range and grown at two sites beyond the range edge

Source	df	Wilks' λ	*F* ratio	*P*
Initial size	4, 24	0.76	1.93	0.14
Site	4, 24	0.88	0.85	0.51
Origin	4, 27	0.69	3.09	0.03
Site × origin	4, 11	0.90	0.30	0.87
Population (origin)	120, 99	0.06	0.81	0.87
Site × population (origin)	56, 96	0.31	0.59	0.98

Trait	Canonical structure of origin[a]
Biomass	0.12
Branch number	0.88
Shoot length	0.09
Node number	0.22

[a]Canonical structure illustrates the contribution of size traits to the origin effect.

Table 2 Analysis of variance for (a) final survival of *Lonicera japonica* originating from the core and margin of the range and grown at two sites beyond the range edge; and (b) winter survival for the first 2 yr of growth of *L. japonica* originating from the core and margin of the invaded range and grown at six sites with differing latitude (combines data from (a) with an earlier study (see text for details))

Source[a]	df	χ^2/F[b]
(a) Final survival beyond the range edge		
Site	1	0.48
Origin	1	3.90*
Site × origin	1	0.16
(b) Across-range winter survival		
Site latitude	5, 175	6.69***
Temperature	1, 37	5.56*
Origin	1, 37	4.52*
Origin × site latitude	5, 175	0.31
Origin × temperature	1, 37	1.38
Site latitude × temperature	5, 2058	13.38***

[a]Random factors in the analyses were not significant and are not reported here.
[b]*, $P < 0.05$; ***, $P < 0.001$.

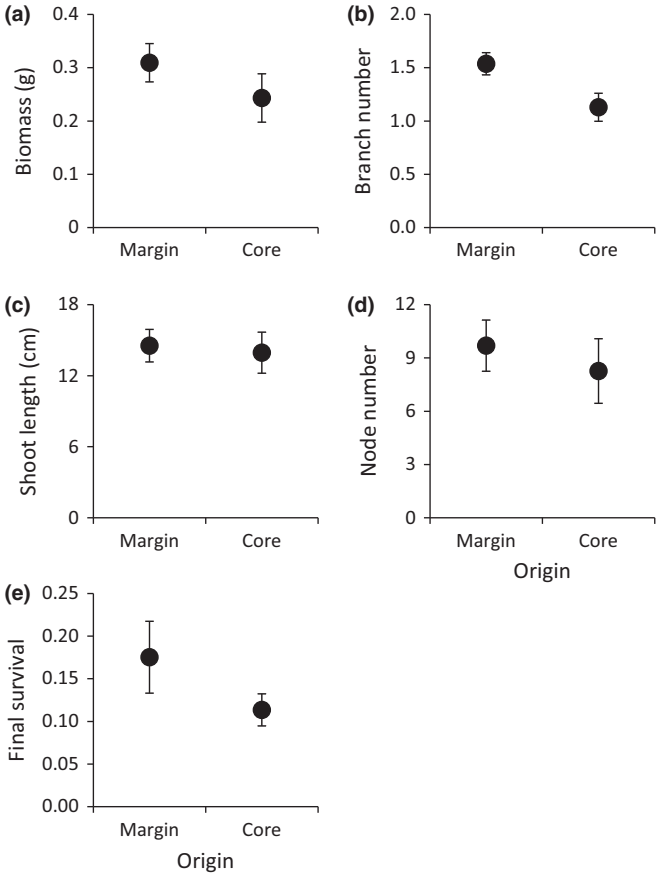

Fig. 2 Final size and survival of *Lonicera japonica* originating from the core and margin of the invaded range and grown at two sites beyond the range edge. (a) Biomass, (b) branch number, (c) shoot length, (d) node number and (e) final survival. All values are reported as least-square means. Error bars for final survival were generated by taking the standard error of proportion survival by population.

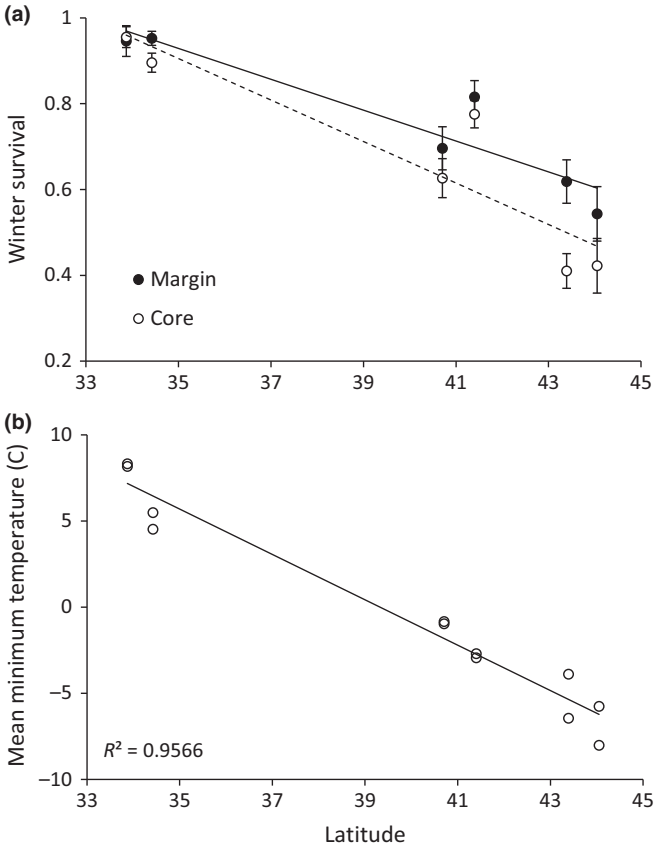

Fig. 3 Winter survival (a) for the first 2 yr for *Lonicera japonica* originating from the core and margin of the invaded range and grown at two sites within the core of the range (latitude *c.* 34°N), two sites at the margin of the range (latitude *c.* 41°N) and two sites beyond the range edge (latitude *c.* 44°N) plotted by latitude of site; and (b) the mean minimum temperature at each garden site for the coldest month in the years in which survival was measured, plotted by latitude of site. Error bars for survival were generated by taking the standard error of proportion survival by population.

decreased with increasing site latitude (Fig. 3a) and, across the range, margin plants showed 26% greater winter survival than core plants. The mean minimum temperature of the coldest month dropped with increasing latitude of the garden site (Fig. 3b). The mean difference in minimum temperature between the core and the beyond-range sites was 12.6°C and between the margin and beyond-range sites was 4.2°C.

Projections of the response function using current climatic data suggest that the adaptation of margin populations to colder conditions has shifted the current range an average of 76 ± 38 km (distance $\pm$ SD) further northwards (Fig. 4), when differences in survival from all latitudes are taken into account. The consensus projections of future climate scenarios indicate that these differences in survival between plants from core and margin populations will persist, with an average 75 ± 42 km difference in potential northward spread between core and margin populations by 2050 (Fig. 4).

Discussion

When grown beyond the northern edge of the invaded range, *L. japonica* plants originating from the northern range margin grew to a larger size and showed greater survival than plants originating from the core of the range. The survival and growth advantage of margin plants are consistent with earlier work, which revealed that margin plants grew to a larger size and showed greater survival when grown both at the margin and in the core of the range (Kilkenny & Galloway, 2013). The genetic composition of populations is similar across the invaded range (Kilkenny & Galloway, 2013), indicating that local differences in which horticultural varieties were imported did not drive the observed differences in growth and survival (cf. Keller & Taylor, 2008). Therefore, the general advantage of northern *L. japonica* over core populations suggests the evolution of these traits during invasion. Several selective processes may be acting in concert to drive these broad differences in growth and survival.

First, local environmental selection may act to increase growth rates in the shorter growing seasons associated with more northern latitudes. Rapid growth leading to larger plant size may enhance over-winter survival. In earlier work, we have shown that larger plants have higher rates of survival, particularly in the

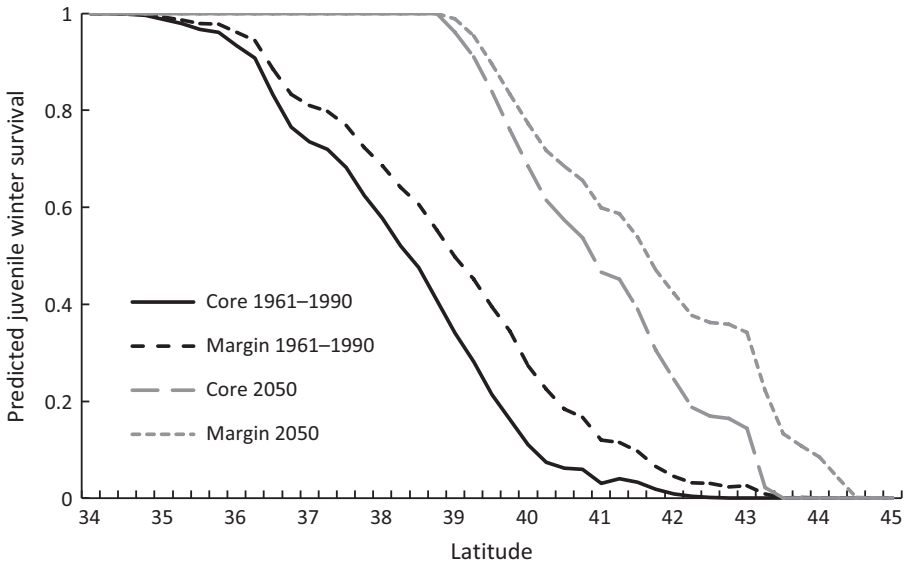

Fig. 4 Predicted juvenile winter survival of *Lonicera japonica* by latitude under recent climate normals (1961–1990) and a consensus of future climate scenarios for 2050 (scenario A2 for CCCMA, CSIRO and HADCM3) for populations sourced from the core and margin of the invaded range.

winter, at the core and at the margin of the range (Kilkenny & Galloway, 2013). This suggests that margin plants, with rapid growth rates, are more likely to reach sufficient size for winter survival than are plants from the core. The rapid growth rates and increased winter survival give margin plants an advantage over core plants throughout the range and in novel, beyond-range habitats. It may be that this rapid growth is associated with decreased competitive ability (cf. Lankau & Strauss, 2011). However, there is no evidence for fitness trade-offs in *L. japonica*'s invaded range; plants from populations in the core are not better competitors than those from the range margins (Evans *et al.*, 2013), despite enhanced intraspecific density in core habitats (Kilkenny, 2011). It may also be that periodic selective events, such as drought or pest outbreaks, were not experienced during the study period and may result in conditions that do not favor faster growing margin plants.

Second, differences between plants from the core and those from the range margin may be driven by selective processes favoring colonization success. For example, establishment selection may favor plants with higher rates of clonal spread, particularly in low-density populations, such as those found at the range margin (Kilkenny, 2011). *Lonicera japonica* reproduces clonally by rooting at nodes along runners (Larson, 2000). Therefore, the number of branches should multiply node-rooting opportunities. In addition, spatial sorting (Shine *et al.*, 2011) may favor faster growth rates, leading to greater long-distance dispersal (Phillips, 2009). *Lonicera japonica* can flower at any node, and so flower production increases with size. This could lead to increased mating opportunities and mating success, leading to an increase in the rate of propagule production. In cases in which long-distance dispersal is possible, such as for bird-dispersed plant species, such as *L. japonica*, higher propagule pressure can lead to more rapid spread (Wilson *et al.*, 2009; Ricciardi *et al.*, 2011). Although no plants flowered in the 21 months of this study in natural old-field conditions, and only four plants flowered in the 32 months of the study of Kilkenny & Galloway (2013) under comparable conditions, in more favorable conditions, the greater growth rate of margin plants leads to increased flower production (Evans *et al.*, 2013).

The lower rate of *L. japonica* survival at the beyond-range sites compared with sites within the range indicates that further northward spread may not occur without adaptation and/or environmental change (cf. Griffith & Watson, 2006). However, rising global temperatures are expected to allow *L. japonica* to invade beyond the current range edge even without additional adaptation, as limiting winter conditions shift northwards. In addition, increased over-winter survival of margin plants in the second year, but no change for core plants, suggests that margin plants adapted to cooler climates and were therefore able to persist for long periods, allowing for further growth and possible reproduction beyond the current range edge. This intraspecific adaptive advantage is likely to be maintained under future climatic conditions. Finally, we observed a linear decrease in survival with latitude, but no abrupt transition from high to low survival. This is in contrast with a recent study in a similar location of native *Chamaecrista fasciculata*, in which the population growth rate decreased abruptly beyond the range, with high fitness at the margin but very low fitness just beyond the range edge (Stanton-Geddes *et al.*, 2012). The lack of an abrupt fitness boundary in *L. japonica*, in conjunction with the greater fitness of margin plants than core plants beyond the range edge, are characteristics of taxa with expanding ranges, such as invasive species or non-expanding species whose ranges are nonetheless limited by dispersal (Hargreaves *et al.*, 2014). Further adaptation in response to cold conditions also seems possible (but see Broennimann *et al.*, 2014), because the more cold-adapted margin populations will be the likely source material for further spread, and the lack of an abrupt fitness boundary should allow opportunities for additional selection.

Species distribution models, developed from species-wide presence or presence/absence data, have been used to determine the climatic distribution niche of a species, and to predict the expansion of invasive species under both current and future conditions (Broennimann *et al.*, 2007; Beaumont *et al.*, 2009; Bellard *et al.*,

2013). Although this approach has been quite fruitful, including the prediction of the further northward spread of *L. japonica* in North America (Beans *et al.*, 2012), it does not take into account genetic and adaptive differentiation within a species. An understanding of intraspecific differentiation can be critical to the prediction of range expansions (Wang *et al.*, 2010; Oney *et al.*, 2013), because populations in proximity to changing range margins are the most likely progenitors of novel populations. Here, we adopted the approach of using response functions, which can be applied to well-designed common garden experiments (Matyas, 1994; Rehfeldt *et al.*, 1999; Wang *et al.*, 2006), to determine how differences in climatic differentiation between populations of an invasive species might affect future spread. The inclusion of intraspecific variation in such models allowed the prediction that adaptation to the northern margin increases the potential for spread, and this approach should be applied more widely in studies on invasions for which common garden data are available.

Recently, greater recognition has been given to the fact that species can evolve rapidly (Carroll *et al.*, 2007; Anderson *et al.*, 2014). One of the aspects of global change, and rising temperatures in particular, is that there are clear directional shifts away from previous environmental norms. This is likely to drive directional selection in many species (Carroll *et al.*, 2007; Kilkenny, 2015). It is possible that invasive species in the process of range expansion will have an advantage over species with more stable boundaries, particularly if invaders have evolved traits that increase dispersal, establishment and viability. Indeed, the strong climate-based directional selection may be acute in higher latitudes in which the rate of temperature increase is well above the global average. In this case, it seems likely that invasions into higher latitude environments will occur with increasing frequency. Future studies should evaluate the potential for spread of invasive species into higher latitudes using both empirical and modeling approaches. Such studies may help to develop strategies to lessen the imbalance between the migration of invasive and native taxa in changing climates.

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Author contributions

F.F.K. and L.F.G. planned and designed the research; F.F.K. carried out the field experiments, modeling and data analysis; F.F.K. and L.F.G. interpreted the results and wrote the manuscript.

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