Global change, global trade, and the next wave of plant invasions

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Many non-native plants in the US have become problematic invaders of native and managed ecosystems, but a new generation of invasive species may be at our doorstep. Here, we review trends in the horticultural trade and invasion patterns of previously introduced species and show that novel species introductions from emerging horticultural trade partners are likely to rapidly increase invasion risk. At the same time, climate change and water restrictions are increasing demand for new types of species adapted to warm and dry environments. This confluence of forces could expose the US to a range of new invasive species, including many from tropical and semiarid Africa as well as the Middle East. Risk assessment strategies have proven successful elsewhere at identifying and preventing invasions, although some modifications are needed to address emerging threats. Now is the time to implement horticulture import screening measures to prevent this new wave of plant invasions.

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One need only peruse a nursery catalog or visit a local gardening center to realize the enormous array of plant choices available to the everyday American gardener. Unfortunately, this wealth of consumer choices comes at a steep cost. Non-native plants introduced through the horticulture trade often become invasive (Mack and Lonsdale 2001; Reichard and White 2001), which we define here as introduced species whose populations are surviving and reproducing beyond the location of introduction (sensu Blackburn *et al.* 2011). Although only a portion of species that become invasive cause ecological damage (Williamson and Fitter 1996; Sax *et al.* 2002), and some have benefited biodiversity (Davis *et al.* 2011; Schlaepfer *et al.* 2011), invasive plants as a whole substantially reduce native species abundance and diversity (Vilà *et al.* 2011) and alter ecosystem function (Ehrenfeld 2010; Vilà *et al.* 2011). Several well-known invasive plants in the US were deliberately introduced, including kudzu (*Pueraria lobata*; planted to stabilize soil), oriental bittersweet (*Celastrus orbiculatus*; planted for aesthetics), purple loosestrife (*Lythrum salicaria*; planted for aesthetics), and tamarisk (*Tamarix* spp; first planted for aesthetics and later to act as wind breaks). Indeed, Mack and Erneberg (2002) estimated that over 60% of established, non-native species in the US were deliberately introduced. Moreover, the introduction process can select for species more likely to become invasive, because traits useful in horticulture – such as rapid establishment, broad climatic tolerance, and high resource allocation to flowers – can also increase invasiveness (Mack 2005). Global change is already aiding the spread of invasive species and increasing their ecological impacts (Dukes and Mooney 1999; Bradley *et al.* 2010a). As global change proceeds, however, it will influence not just the success of introduced plants but the introduction process itself (Hellmann *et al.* 2008). Gardeners are poised to plant new species from warmer regions, as earlier onset of spring (Schwartz *et al.* 2006) and warmer temperatures decrease the requirement for winter-hardiness in ornamental plants (Arbor Day Foundation 2006). Similarly, as human populations increase in the arid and semiarid regions of the world, such as the American Southwest (Mackun and Wilson 2011), demand for drought-tolerant plants is expanding – a trend likely to accelerate in areas where climate change exacerbates drought (eg Seager and Vecchi 2010). At the same time, economic globalization offers opportunities to import new types of plants from previously untapped parts of the world. Here, we review how global changes in trade and climate could influence supply and demand for introduced ornamental plants. We predict the consequences for future plant invasions in

In a nutshell:

- New horticultural trading partners supply novel species that may become invasive
- Increasing demand for drought-tolerant species promotes the introduction of invasive species in dryland regions
- Gardeners are likely to plant new species as soon as rising temperatures allow, favoring the assisted migration of introduced species relative to non-horticultural natives
- Emerging trade supply coupled with shifting demand due to climate change makes the US susceptible to a new array of invasive plants

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the conterminous US and conclude with a review of policy changes that could mitigate this new generation of invasions.

■ Supply: identifying emerging trading partners

There is a clear link between increasing amounts of trade and abundance of invasive plant species (Westphal *et al.* 2008; Hulme 2009). In Europe and North Africa, monetary values of imports were one of the best predictors of invasive plant abundance (Vilà and Pujadas 2001), and in the UK, plants more widely available in 20th-century nurseries were more likely to be invasive today (Dehnen-Schmutz *et al.* 2007). As the number of horticultural trading partners with the US ("source" countries) continues to rise, so too will the number of introductions of non-natives that will later become invasive and potentially problematic (Hulme 2009). Moreover, the rate of introduction of future invasive species is steepest in the early stages of new trade partnerships, due to the sheer volume of novel introductions (Figure 1; Levine and D'Antonio 2003), and may contribute to an "invasion debt" that will be realized decades in the future (Essl *et al.* 2011). As trade partners become established and novel introductions slow, the number of invasive plants emerging from the trading partnership may still rise, but largely as a result of the persistent increase in propagule pressure (Lockwood *et al.* 2005) as more and more individuals of a given species are planted throughout the landscape. The greatest risk of new invasive plants arriving in the US is therefore likely to come from emerging trade partners.

We identified emerging and established sources of nursery plant imports to the US using the US Department of Agriculture's (USDA's) global agricultural trade system online database (USDA 2011). Nursery product categories assessed included bulbs and roots, trees and shrubs, herbaceous perennials, unrooted vines, and mosses and lichens, but excluded any plant identified by name (eg azaleas). We compiled import dollar value by country from 1989 (the first year of record) through 2010 (all dollar amounts hereafter are in US$). We defined "emerging" trade partners as countries with an increasing trend during the period of record, but an average import value of less than $100 000 per year from 2000–2010. "Established" trade partners had an average import value of greater than $100 000 per year from 2000–2010. This threshold divided the pool of nursery plant trade partners roughly in half. We then determined whether invasive plants have arrived from predominantly emerging or established trade partners by assessing the countries comprising the native ranges for 2608 invasive plants in the US as documented by the USDA (USDA ARS 2011; USDA NRCS 2011).

We identified a total of 42 emerging trade partners, clustered mainly across tropical regions, the Middle East, and Eastern Europe (Figure 2a). Global imports of unnamed (ie non-varietal) nursery plants were valued at more than $250 million in 2010; only $4 million of those imports were from emerging trade partners. However, imports from emerging trade partners are on the rise as compared with those from established partners: trade value from emerging sources rose by 69% from 2000–2010, while imports from established sources declined by 9% over the same period.

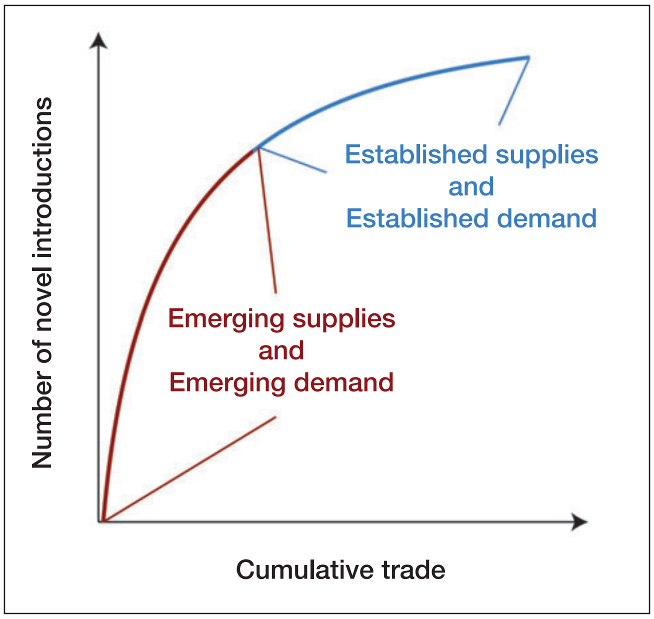


Figure 1. *New influxes of non-native invasive species are most prominent in the early stages of new trade partnerships. With established trade partners, invasions continue to rise with increase in trade, but at a slower rate. Adapted from Levine and D'Antonio (2003).*

The average invasive plant in the US had only 29% of its native range in emerging countries (Figure 2b) versus 54% in established countries (Figure 2c), supporting previous findings that more trade leads to more invasive species (Vilà and Pujadas 2001; Levine and D'Antonio 2003; Westphal *et al.* 2008). In addition, more than a quarter of invasive plants in the US have native ranges that do not include any emerging trade partners (Figure 2b). The low contribution of emerging trade partners to the current complement of invasive plants in the US implies that there is considerable scope for further invasive species introductions from these countries.

■ Demand: xeriscaping and invasion of dryland regions

Although drylands can be heavily impacted by invasive species, the number of species that have invaded such systems is low when compared with that in more mesic regions (Figure 3a). Furthermore, within dryland regions, many invasive species are restricted to relatively wet areas (Stohlgren *et al.* 1998). The limited number of invasive species established in dryland regions is probably due to a combination of historically low human population density – and therefore lower propagule pressure (Lockwood *et al.* 2005) – and historical preferences for species from

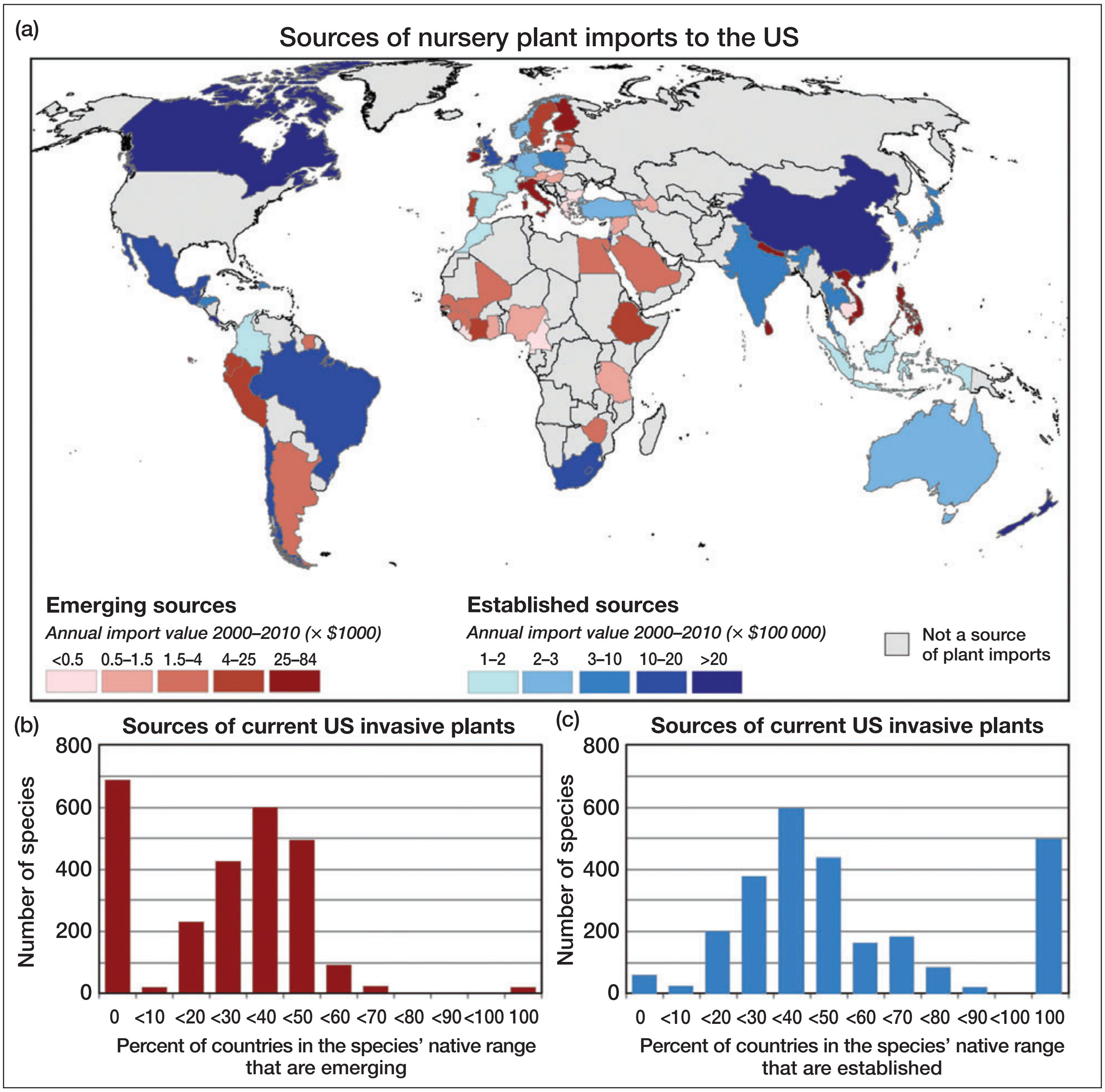
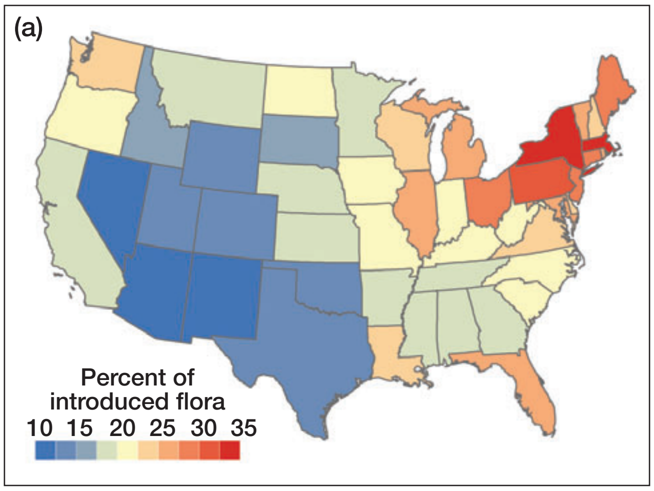


Figure 2. *Currently emerging and established horticultural trade partners, and contributions of those trade partners to US invasive plants. (a) Emerging partners (shown in red) currently average less than \$100 000 yr^{-1} in trade value, but imports are increasing. Established partners (shown in blue) currently average more than \$100 000 yr^{-1} in trade value. (b) Relatively few of the current invasive plant species in the US are native to emerging trade regions. (c) Many of the current US invasive plants are primarily native to established trade regions.*

mesic environments (Hilaire *et al.* 2008). Both of those trends are changing. Rapidly expanding human populations in dryland areas (Mackun and Wilson 2011) have not only created new gardens and planted more non-native species, but in the process have also had to contend with limited water supplies (Palmer *et al.* 2008). In many areas, particularly those at lower latitudes, climate change is expected to further reduce water available for human use (Palmer *et al.* 2008; Seager and Vecchi 2010). Water limitations have already led to restrictions on water use for gardening and greater use of drought-tolerant species for landscaping in the US (Figure 3b; Hilaire *et al.* 2008).

A large portion of residential water use in dryland regions is directed toward lawn and garden maintenance (eg 30–40% in California; Gleick 1996). Xeriscaping – the use of drought-tolerant plants in landscaping – can reduce that water use by as much as 76% (Sovocool *et al.* 2006). Furthermore, because many of the aesthetic considerations determining the appeal of xeriscapes depend



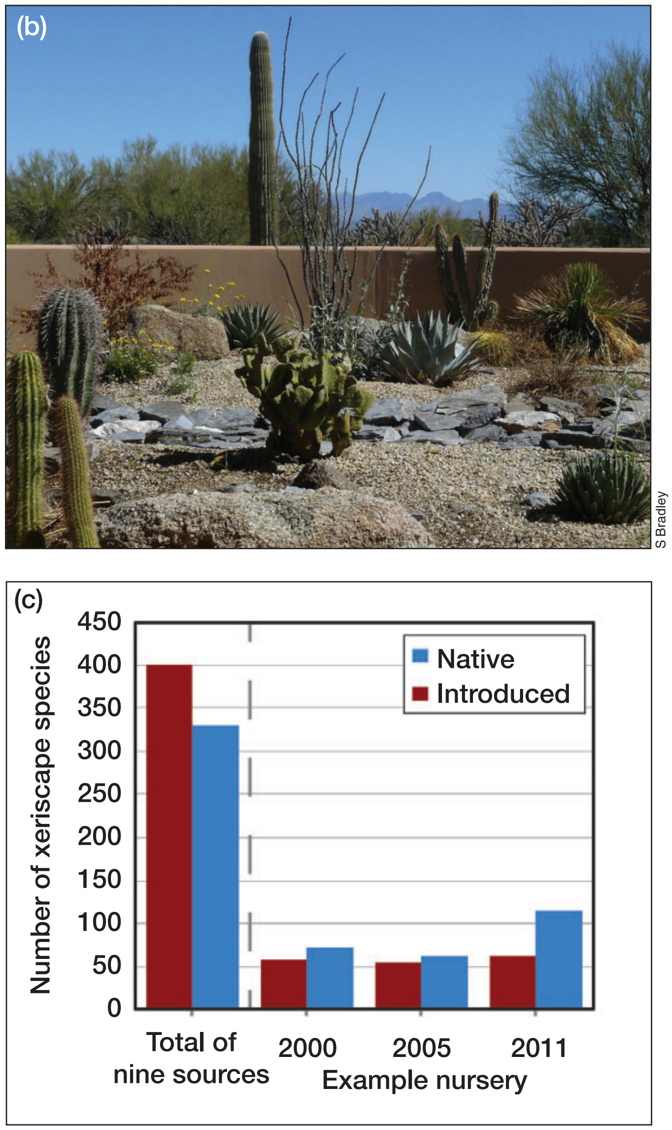


Figure 3. *Expansion of xeriscaping demand could generate new species introductions. (a) The floras of the West and Southwest deserts – the areas most likely to receive new, water-tolerant ornamental species – currently have the smallest percentages of introduced plant species. (b) A xeriscaped yard in the Sonoran Desert with predominantly introduced species native to the Chihuahuan Desert in Mexico. (c) A survey of nine nursery catalogs revealed that most species marketed as "drought-tolerant" are introduced. One nursery specializing in drought-tolerant species increased its selection of species between 2000 and 2011; encouragingly, most of the new species were natives.*

on the types of plants used (Hilaire *et al.* 2008), acceptance of xeriscaping could increase as the availability and variety of drought-tolerant species grows. Unfortunately, increasing the availability and variety of non-native, drought-tolerant species could also increase the probability of introducing species capable of invading dryland regions.

To quantify the potential of xeriscaping as a source of new invasive plants, we tabulated the number of plants being marketed for this practice. First, we identified nine nurseries in the US that advertise more than ten "xeriscape", "drought-tolerant", or "water-wise" plant species (henceforth collectively referred to as "drought-tolerant" species). Using the USDA PLANTS Database (USDA NRCS 2011) and other online sources, we then identified the origin (native or introduced) of 731 drought-tolerant species (Figure 3c). We found that more than half (401) of the drought-tolerant species were non-native, suggesting that many species that, in the future, will become invasive in dryland regions of the US may already have arrived and are increasingly being planted.

To explore how the xeriscaping industry may be changing, we requested catalogs from previous years from our nine nursery sources, but received catalogs from only one, a nursery that specializes in drought-tolerant plants. For this source, we tabulated the number of native and introduced drought-tolerant species by year. We found that while the nursery expanded its drought-tolerant species offerings by 37% between 2005 and 2011, almost all of the newly offered species were native to the US (Figure 3c). This is a somewhat encouraging trend. Together with the wide availability of native drought-tolerant plants (330) available across sources, it suggests considerable potential to supply the xeriscaping demand with US native species. Although these species may not be native to the particular US deserts in which they are planted, species introduced from one North American region to another are seldom reported as becoming problematic invaders (Mueller and Hellmann 2008). Thus, the focus on US native plants by the xeriscaping industry may help prevent detrimental intercontinental invasions.

■ Demand: shifting hardiness zones and the American gardener

In addition to the specific demands for drought-tolerant species, climate change could stimulate an overall increase in the demand for new horticultural species that thrive in new, warmer climates. Rising temperatures are already causing US "hardiness zones" (temperature isoclines defined by the USDA) to shift (Arbor Day Founda-

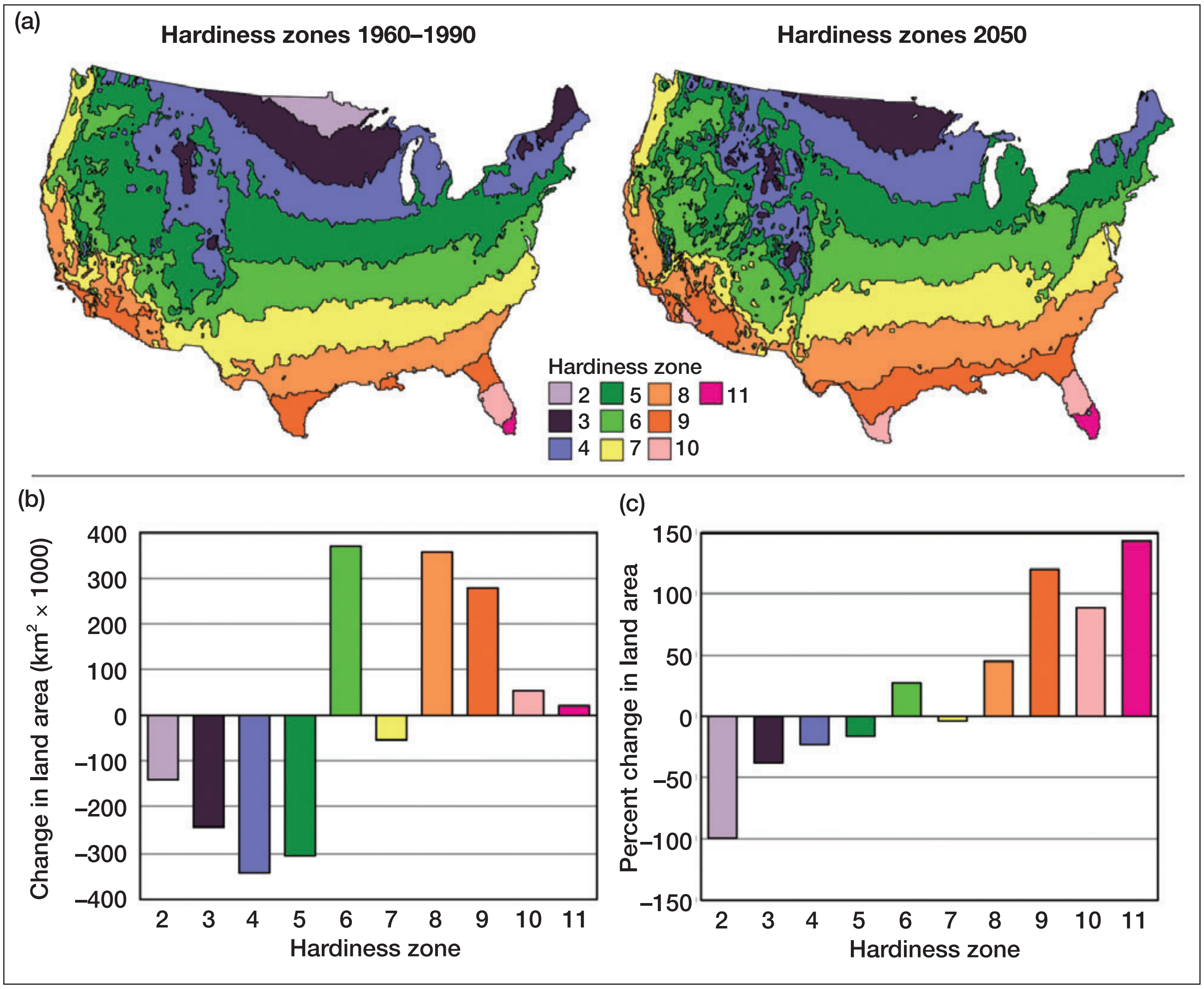


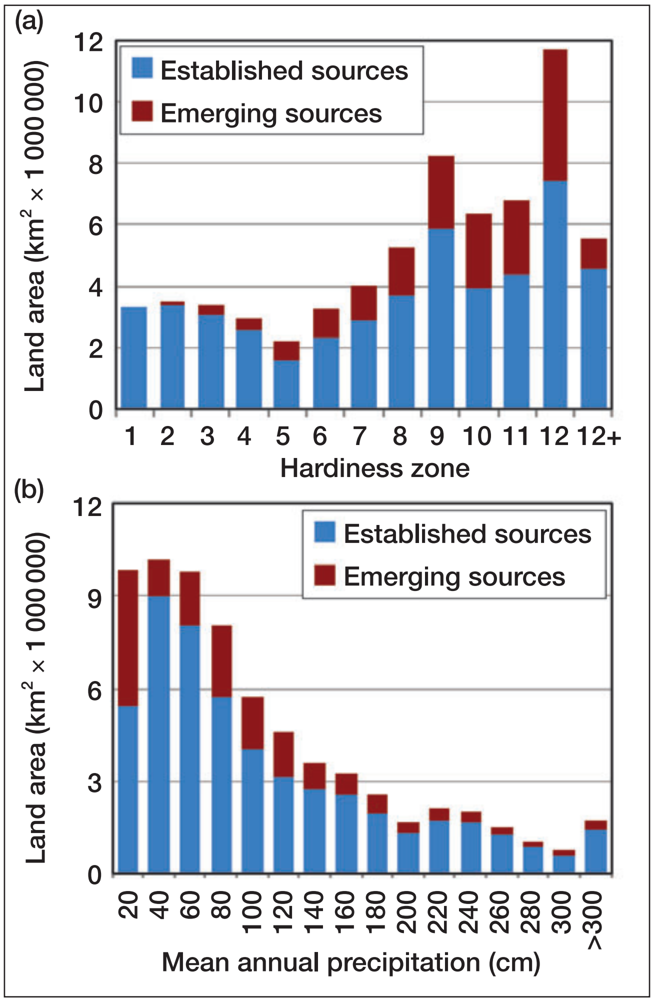
Figure 4. *Climate change is likely to shift hardiness zones northward and upward in elevation, increasing the land area in warm zones and altering demand for horticulture species. (a) Hardiness zones in the US, based on average climate from 1961–1990 and based on projected average climate from 2040–2069 (color scheme after that of Arbor Day Foundation 2006). (b) Change in land area of hardiness zones. (c) Total land area in each hardiness zone by 2040–2069.*

tion 2006) and the growing season to lengthen (Schwartz *et al.* 2006). The horticulture industry is likely to expand the array of available species in expectation of, and in response to, this new consumer demand (Figure 3c). Building on the analysis of updated hardiness zones (Arbor Day Foundation 2006), we explored how projected changes in climate will affect the distribution of plant hardiness zones over the next 40 years and how shifts in the land area of hardiness zones might influence demand.

Hardiness zones are regions delineated by average minimum annual temperatures that provide gardeners and landscape designers with guidance on which plants can be grown in which parts of the US (Cathey 1990). We mapped current hardiness zones using the PRISM (Parameter-elevation Regressions on Independent Slopes Model) 4-km resolution average temperature dataset from 1961–1990 (Daly *et al.* 2004) classified into 5.6°C bins defined by the USDA (Cathey 1990). To match the spatial resolution of projected future climate, we aggregated the PRISM data to 0.125° spatial resolution (approximately 12 km^2 in the US). We mapped potential future hardiness zones using averaged projections from 16 different general circulation models run for a mid–high (Special Report on Emissions Scenarios [SRES] A2) greenhouse-gas emissions scenario for the period from 2040–2069. Statistically downscaled climate projections at 0.125° resolution were provided by the Climate Wizard project (Girvetz *et al.* 2009). For mapping both the current and projected future hardiness zones, we calculated annual minimum temperatures using average temperature of the coldest month based on an empirical relationship between the two (Prentice *et al.* 1992).

Hardiness zones in the US are likely to shift substantially northward over the next 40 years (Figure 4a). This will result in an expansion of the warmer zones (particularly zones 6 and 8–11), a contraction of some of the

Figure 5. *Supplies of novel species from emerging trade partners could meet increasing demand for species adapted to warm and dry environments. (a) Current hardiness zones of emerging source countries are skewed toward warmer climates. (b) Current mean annual precipitation of emerging source countries includes some of the driest areas on Earth.*



cooler zones (zones 3–5), and the near-complete loss of zone 2, currently the coldest zone in the conterminous US (Figure 4b). With concerted planting efforts, gardeners are already helping garden plants to shift their geographic distributions into newly suitable climatic regions ahead of non-propagated species (Van der Veken *et al.* 2008). Many invasive species are unintentionally taken along for the ride (Maki and Galatowitsch 2004), whereas others are actively planted in regions forecast to become suitable for invasion with climate change (eg Bradley *et al.* 2010b). Unless assisted migration is also used for native species (Richardson *et al.* 2009), these trends raise the prospect that both existing and new invasive species may be better able to shift their ranges to align with new climatic conditions, pre-empting and possibly precluding the establishment of native species. Of further concern for invasive species biologists and managers are the novel sets of species that could be introduced in response to increasing demand for heat-tolerant species: warm hardiness zones 8 and 9 are projected to expand by 45% and 120%, respectively, and are likely to cover a substantial portion of US land area by 2050 (Figure 4c). In regions such as these, the performance of many native species will be compromised as the climate warms beyond species' current tolerance (Walther 2004). Introducing non-native species that are pre-adapted to the new climatic conditions in these regions, and can thus outperform native species, further increases the odds of invasion.

■ The intersection of supply and demand

The intersection of emerging supply and demand forces creates considerable motivation for novel species introductions and poses the greatest risk for a new wave of plant invasions into the US (Figure 1). Emerging trade partners (and sources of novel species) included clusters of nations in warm tropical regions and several arid regions of the Middle East and Africa (Figure 2). At the same time, demand for new species is increasing in dryland regions and is also likely to expand in warmer US hardiness zones (Figure 4).

To test how emerging supply and demand might overlap, we created a map of global hardiness zones at 10-arc-minute resolution using the same criteria as for the US hardiness zones. Species are generally expected to become naturalized in areas with similar climatic conditions to that of their native range (eg Thuiller *et al.* 2005). Indeed, the hardiness zones where non-native species have become naturalized in the US have historically tended to match their native hardiness zones (see WebPanel 1 and WebFigure 1), so it is reasonable to expect this trend to continue in the future. We therefore explored the degree of matching between future climatic conditions in the US (2050, represented by mean conditions between 2040 and 2069) and historical conditions in established and emerging trade partners (represented by mean conditions between 1961 and 1990). We used historical conditions in source countries based on the assumption that plants selected for the horticulture trade are adapted to historical climatic conditions in their source countries. The hardiness zones of emerging trade partners are strongly skewed toward warmer climates (higher hardiness zone numbers; Figure 5a), even more so than those of established trade partners. The land area of source countries in zones 6–10, which collectively represent the greatest increase in future US land area, increases by 31% with the addition of emerging trade partners. These emerging partners also tend to be in drier parts of the world (Figure 5b). Although established trading partners already include large areas with relatively low precipitation, source-country land area receiving less than 20 cm of precipitation per year – equivalent to climates such as those of Las Vegas, Nevada and Phoenix, Arizona – increases by 44% with the addition of emerging trade partners. These patterns suggest that emerging plant trade partners are well poised to supply the very drought- and heat-tolerant species that nurseries in the US are, or will soon be, looking to sell. We predict that the strong overlap of emerging supply and emerging demand could lead to a sharp rise in introductions of new invasive species (Figure 1).

Management, policy, and stakeholder solutions

Identifying invasive plants before they arrive is crucial for preventing damage to native biodiversity. Post-introduction control of established species may not repair the desired ecosystem functions because invasive species, combined with other elements of global change, may have already altered biotic interactions (Schlaepfer *et al.* 2011). Currently, under the US Plant Protection Act (Public Law 106-224), plant importation conforms to a "Black List", which labels plants as "prohibited" or "restricted" after they are proven harmful. This policy is akin to closing the barn door after the horse has bolted, however, and will prove particularly ineffective if, as we predict, changing supply and demand forces facilitate a new generation of introductions. In contrast, "Green List" (or "White List") approaches – based on weed risk assessments (WRAs) – have been used in countries such as Australia and New Zealand (Perrings *et al.* 2005). Predictors of invasive plants include whether the species has a history of invasion elsewhere, climate matching, and reproduction and dispersal strategies (Pheloung *et al.* 1999). WRA scores have repeatedly been shown to have good predictive power for separating out invasives from the array of horticultural import species (see examples in McClay *et al.* 2010) and provide a clear economic benefit (Keller *et al.* 2007). The Animal and Plant Health Inspection Service (APHIS) branch of the USDA has proposed a new rule for plant imports that would add the category "NAPPRA" ("Not authorized pending pest risk analysis") to the Plant Protection Act (USDA APHIS 2009). The NAPPRA rule would require APHIS to perform a WRA at the request of plant importers on taxa that have previously not been imported, and then determine whether the plant should be accepted or prohibited (USDA APHIS 2009). If implemented, this rule would represent a major positive step in the long-term prevention of new invasive species.

One concern with WRA efficacy – in light of emerging, novel invasives – arises because a major component of risk assessment considers whether the species has a history of invasion elsewhere (Pheloung *et al.* 1999). Emerging US trade partners are unlikely to have long-established trade relations with other parts of the world, so the invasiveness of species supplied by these partners will be unknown. This lack of information should not be mistaken for a lack of invasiveness, and WRAs will have to be adjusted accordingly for emerging trade partners. In addition, the climate-matching criteria of WRAs should be applied to both current and future climate conditions of the recipient region.

The US horticulture industry is among the most important players in the prevention of future invasions, and increasing awareness of invasive species among nursery professionals is a critical step. The St Louis Declaration (Baskin 2002) made an important contribution toward identifying ways the horticulture industry can help, but the information has reportedly not reached industry professionals (Burt *et al.* 2007). The voluntary codes of conduct in the Declaration would reduce invasions by encouraging nursery professionals to assess invasive potential of new plants before selling them and to promote native species in breeding programs. Many nursery professionals will discourage customers from planting known invasive species and will phase out plants known to be invasive but often lack information on which species are problematic (Burt *et al.* 2007). Links between invasive plant managers and the horticulture industry need to be strengthened to promote better dissemination of that information (D'Antonio *et al.* 2004; Peters *et al.* 2006). The trade in drought-tolerant species – which is ultimately driven by environmental concerns (Hilaire *et al.* 2008) but presents novel environmental risks for dryland regions (Figure 3) – may afford a particularly good opportunity for education. Preferential use of species for xeriscaping that are native to the US, and especially to the region of planting, would greatly reduce propagule pressure from non-native species. This move might be attractive to environmentally conscious gardeners and horticultural companies.

Finally, the horticulture industry can take proactive steps to aid risk assessment and prevention, such as providing needed information to WRAs based on field trials and identifying and ceasing production of plants that escape cultivation easily (Mack 2005). Furthermore, the horticulture industry can help fight range expansion of invasive plants by stopping the sale of plants known to be invasive elsewhere in the US. Collaborative groups involving representatives from the horticultural industry, nursery and landscape organizations, regulatory agencies, and non-governmental organizations are now working toward limiting the sales of invasive plants, in part by developing lists of non-invasive alternatives (eg Cal-HIP 2004).

Conclusions

Many lines of evidence suggest that global change will, on average, increase risk of plant invasion (Dukes and Mooney 1999; Bradley *et al.* 2010a). Here, we identify another risk – one that policy can effectively address. Climate change is likely to increase demand for drought- and heat-tolerant landscaping plants in the US. Emerging trade partners have warm, dry climates that are well matched to this future demand and could supply many new and potentially invasive species. This emerging threat intensifies the need for preemptive screening of nursery stock species prior to import. Although the numbers and abundance of invasive species already in the US might engender complacency, we suggest that active management of new invasion risks will remain important well into the future.

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WebPanel 1. Comparison of climate conditions in plant species' native and introduced ranges

We established how well climate-matching predicts the current distribution of species within the US using two climate variables that are thought to limit plant species distributions. Absolute minimum temperature was calculated from mean temperature of the coldest month and categorized by converting into hardiness zone (described in the main text). Mean annual precipitation (MAP) was calculated in units of millimeters per year and categorized into 200-mm bins. We analyzed the 2608 plant species introduced in the conterminous US whose native countries could be found in the USDA Germplasm Resources Information Network (USDA ARS 2011). Each species' US distribution was taken to be the US states in which they are recorded as introduced by the USDA PLANTS website (USDA NRCS 2011). If species were recorded as native to Argentina, Australia, Brazil, Chile, China, or the "Russian Federation", they were not included in the analysis, because the range of climates found in these countries was too broad to feasibly represent the climatic tolerances of a species found in them. However, the individual native country states from which species were recorded within these entities were included (and termed "country" for clarity).

We calculated average climate from 1961–1990 (New *et al*. 2002) within each species' native/US range by extracting the 10-arc-minute climate grid cells that fell within each country/US state where the species was recorded. We compared the mean hardiness zone of the coldest country in each species' (USDA NRCS 2011) native range and the coldest state in each species' US range (where "coldest" signifies the country/state of each species' range that has the coldest mean hardiness zone; WebFigure 1a). MAP of the driest country in each species' native range and the driest state in each species' US range were also compared (where "driest" signifies the country/state of each species' range that has the lowest MAP; WebFigure 1b).

There was a strong relationship between the mean hardiness of the coldest portion of species' native and US introduced distributions (WebFigure 1a). A large proportion of species' native and introduced distributions extended to the same minimum hardiness conditions. However, species did appear to invade slightly colder conditions than in their native range, particularly the relatively small number of species that are native to warm regions (eg native hardiness zones > 9).

Although some correlation was found between MAP values of the driest portion of species' native and introduced distributions (WebFigure 1b), predictive power is clearly much weaker than for hardiness (WebFigure 1a). The temperature gradient runs north–south in the heavily invaded eastern US (Figures 3 and 4 of main text). The long introduction history in this region appears to have allowed species to extend to their full hardiness tolerances, accounting for the strong relationship in WebFigure 1a. However, the precipitation gradient in the conterminous US runs mainly east–west (declining toward the west). Dryland regions of the American Southwest have had lower introduction rates, providing fewer non-native species the opportunity to establish at the drier limit of their tolerance. This could artificially reduce apparent drought-tolerance in their US range for species that are actually drought-tolerant (eg WebFigure 1b shows elevated MAP values in the US for native species originating in countries with MAP of 200–400 mm). This also suggests that current non-native species in the US might be further introduced into dryland areas for xeriscaping. At the other end of the spectrum, WebFigure 1b suggests that species native to wet regions appear to be able to invade drier regions in the US. However, there are few introductions of species for which the driest portion of their range has a MAP value above 1600 mm (WebFigure 1b). This coincides with the fact that there are few areas in the US with MAP above 1600 mm (the Pacific Northwest, southern Alabama, Georgia, Louisiana, and northwestern Florida). Thus, there is insufficient sample size to test whether measured native moisture-tolerances in species from wet regions dictate their US distribution. But this deficiency might itself arise because species native to wet tropical regions are non-viable in most of the US. It is also possible that humans have modified the climates that introduced species encounter by watering in urban and agricultural areas. Species native to wet regions might naturalize in the US in places where they can take advantage of this increased water availability.

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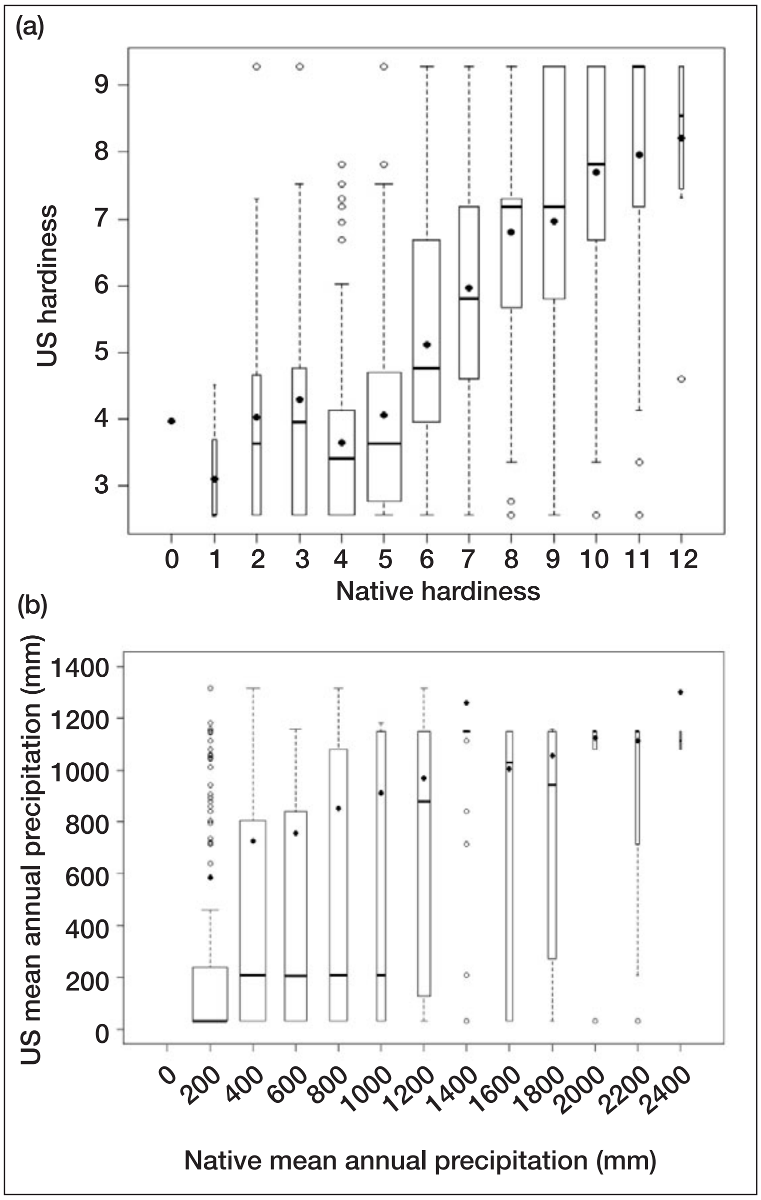

WebFigure 1. *Comparison of native and exotic climate tolerances. (a) Mean hardiness of the coldest and (b) mean annual precipitation of the wettest country/conterminous US state to which a species is native/exotic. Boxplots show medians and quartiles, whiskers extend to a distance from the box of 1.5* interquartile range. Boxplot widths are proportional to the square roots of the number of observations in each x-axis bin. Black points are the mean y-axis values for each x-axis bin.*

