4-1-2017

Climate Change, Managed Relocation, and the Risk of Intra-Continental Plant Invasions: A Theoretical and Empirical Exploration Relative to the Flora of New England

Jesse Bellemare
jbellema@smith.edu

Bryan Connolly
Framingham State University

Dov F. Sax
Brown University

Recommended Citation
Bellemare, Jesse; Connolly, Bryan; and Sax, Dov F., "Climate Change, Managed Relocation, and the Risk of Intra-Continental Plant Invasions: A Theoretical and Empirical Exploration Relative to the Flora of New England" (2017). Biological Sciences: Faculty Publications, Smith College, Northampton, MA.
https://scholarworks.smith.edu/bio_facpubs/211

RHODORA, Vol. 119, No. 978, pp. 73–109, 2017

doi: 10.3119/16-10; first published on-line June 9, 2017.

FEATURED REVIEW

CLIMATE CHANGE, MANAGED RELOCATION, AND THE RISK OF INTRA-CONTINENTAL PLANT INVASIONS: A THEORETICAL AND EMPIRICAL EXPLORATION RELATIVE TO THE FLORA OF NEW ENGLAND

Jesse Bellemare

Department of Biological Sciences, 44 College Lane, Smith College,
Northampton, MA 01063
e-mail: jbellema@smith.edu

Bryan Connolly

Department of Biology, 100 State St., Framingham State University,
Framingham, MA 01702

Dov F. Sax

Department of Ecology and Evolutionary Biology, 80 Waterman St.,
Brown University, Providence RI 02912

ABSTRACT. The high rate of anthropogenic climate change projected for coming decades and evidence of low migration ability for many species have led researchers to warn of a looming extinction crisis. This threat is expected to be most acute for small-ranged endemic species, which could see novel climatic conditions develop rapidly across the entirety of their limited geographic ranges. To avoid extinctions, some conservationists have proposed that climate-imperiled species might be candidates for "assisted colonization" or "managed relocation" to new regions, outside their historical ranges. One major concern related to managed relocation is the possibility that some relocated species could later become problematic invasives where they are introduced. In this review, we consider how these emerging conservation challenges might unfold for the flora of New England. A range of evidence suggests that most plant species native to New England might be resilient to immediate extinction risk from climate change, as these species typically have broad geographic ranges and have migrated long distances in response to past climate change. In contrast, regions to the south, particularly hotspots of plant endemism in the southeastern US, harbor numerous small-ranged species whose current climatic niches could rapidly shift beyond their native ranges, leaving them vulnerable to extinction unless they colonize new regions to the north. Consequently, debates surrounding managed relocation in New England are likely to be focused primarily on the ecological risks versus conservation benefits of accepting climate-threatened endemic plant species from the southeastern US, and to hinge on concerns about the invasive potential of these species. To provide an empirically-grounded estimate of invasion risk from the introduction of US native plant species to New England, we reviewed invasive species lists for New England and tallied those species that are native to other parts of the contiguous US (versus other regions and continents). Between four and ten "invasive" or "potentially invasive" plant species reported from New England are from other regions of the contiguous US, depending in part on how issues of native versus exotic genotypes within taxa are resolved. A review of current floristic data from New England shows that these 4–10 problematic species are drawn from a larger pool of ~374 US native plant species reported as exotic in the region, suggesting that only 1.1–2.7% of species appearing spontaneously as adventives in the region are viewed as invasive. In light of this analysis, we suggest that managed relocation is not likely to spawn large numbers of new invasives, and might therefore be judiciously evaluated alongside other conservation options for climate-threatened plant species. We propose a collaborative effort among field botanists, land managers, conservationists, and academics in New England, partnering with botanists in the southeastern US, to initiate fundamental research to experimentally test the viability and ecological effects of climate-threatened endemic plant species from the southeastern US in the New England region.

Key Words: climate change, managed relocation, assisted colonization, migration, dispersal, invasions, extinction, endemic plants, exotic plants, conservation

Together with habitat destruction and the spread of invasive species, rapid climate change is predicted to be one of the top threats to biodiversity in the 21st century (Malcolm et al. 2006; Parmesan and Yohe 2003; Thomas et al. 2004; Urban 2015). Indeed, some studies have estimated that a million or more species might be at risk of extinction in coming decades due to anthropogenic climate change (Malcolm et al. 2006; Thomas et al. 2004). A key biological factor linked to species' projected extinction risks is dispersal ability (Thomas et al. 2004). Rapid climate change may outstrip the migration abilities of many slowly dispersing species, leaving their populations exposed to new climatic conditions that might not support continued survival. This high rate of climate change "velocity" (Loarie et al. 2009; Sandel et al. 2011), likely requiring species to migrate at rates approaching 10–80 km per decade to keep up, is predicted to exceed the natural dispersal and migration capacities of many species (Corlett and Westcott 2013; McLachlan et al. 2005). Although numerous species have migrated successfully in response to past episodes of rapid climate change, e.g., during Pleistocene glacial cycles, the high rate of anthropogenic climate change, combined with the widespread fragmentation of the modern landscape by human development, agriculture, and other barriers to natural dispersal, is predicted to trigger a major extinction crisis in coming decades (Thomas et al. 2004; Urban 2015).

Given the pivotal role that dispersal and colonization of new regions is likely to play in allowing species to avoid climate change-driven extinction, some researchers and conservationists have proposed that humans should directly intervene to "assist" poorly-dispersing species in tracking their habitat as it shifts pole-ward (Barlow and Martin 2004; Bellemare and Moeller 2014; Thomas 2011). This new conservation strategy has variously been termed "assisted migration," "assisted colonization," and "managed relocation" (Barlow and Martin 2004; McLachlan et al. 2007; Richardson et al. 2009). Most strikingly, the approach would involve moving climate-threatened species beyond their native ranges into new geographic regions where they have not occurred historically, but where they are predicted to survive in the future as climate changes (McLachlan et al. 2007).

Not surprisingly, this novel strategy of "managed relocation," although still largely hypothetical, has been highly controversial (e.g., Ricciardi and Simberloff 2009; Sax et al. 2009; Schwartz 2004). The possibility of using managed relocation as a conservation tool has run headlong into several decades of intense focus on the ecological and economic threats posed by exotic species and biological invasions (Lockwood et al. 2013; Ricciardi and Simberloff 2009). Critics of managed relocation have cited several concerns, including the risk that relocated species might become invasive in their new ranges, or that they might hybridize with related native species where they are introduced (Mueller and Hellmann 2008; Ricciardi and Simberloff 2009). In addition, it is conceivable that managed relocation might be seen as an "easy fix" that could undermine direct efforts to slow climate change and save threatened species within their native ranges. Even so, as the rate and magnitude of climate change becomes clearer (IPCC 2014), it appears that an increasing number of scientists, conservationists, and land managers are taking the possibility of managed relocation seriously and beginning to evaluate its potential risks and opportunities (Bellemare and Moeller 2014; Dumroese et al. 2015; Hoegh-Guldberg et al. 2008; Javeline et al. 2015; Loarie et al. 2009; National Fish, Wildlife and Plants Climate Adaptation Partnership 2012; New England Wildflower Society 2015; Thomas 2011; Weeks et al. 2011).

What plant species might be candidates for managed relocation? Small-ranged or "endemic" species are thought to be at greatest immediate risk from climate change (Bellemare and Moeller 2014; Malcolm et al. 2006; Thomas et al. 2004). This is because these species' small geographic ranges and their biogeographic distributions suggest that many have limited long-term, large-scale dispersal ability (Bellemare and Moeller 2014; Van der Veken et al. 2007). Further, because climate conditions are likely to change rapidly and completely across the whole of their small native ranges, endemic species could be exposed to entirely novel climatic conditions in a relatively short period of time (Bellemare and Moeller 2014; Malcolm et al. 2006; Thomas et al. 2004). In contrast, species with larger ranges have, to some extent, already demonstrated the potential for substantial dispersal ability by expanding their distributions over broad geographic areas in the past (Bellemare and Moeller 2014; Van der Veken et al. 2007). More importantly, it is probable that some portions of these large-ranged species' distributions will remain climatically-suitable into the future, even as other portions might become unsuitable. For example, while the southern margins of many widespread tree species' geographic ranges have been forecast to decline or retreat in the eastern US due to warming climate, it is likely that more northerly portions of these species' ranges might remain suitable for a considerable time (e.g., Morin et al. 2008). Such species might be able to persist for centuries, even in the absence of any northward shift in their distributions. This type of "no-dispersal" scenario would not be a viable option for a small-ranged endemic species restricted to just a few counties within its native distribution.

In a recent biogeographic study, Bellemare and Moeller (2014) investigated where small-ranged endemic forest herb species occur within the eastern US. Consistent with the prediction that small-ranged species might also be dispersal-limited (e.g., Rossetto et al. 2008; Van der Veken et al. 2007), this research found that almost all forest herb endemics native to the eastern US are concentrated in the southeastern US, with a pronounced drop-off in diversity starting ~200–300 km south of the Last Glacial Maximum (LGM) boundary and northward (Bellemare and Moeller 2014; Figure 1). Like other formerly glaciated northern areas, such as the upper Midwest, New England harbors very few small-ranged forest plants. This trend in plant range size and endemic diversity relative to past climate change and glaciation appears to be a general biogeographic pattern repeated in other regions of the world as well (e.g., Jansson 2003; Médail and Diadema 2009; Morueta-Holme et al. 2013). Interestingly, many of these same endemic forest plants are grown in horticulture far to the north of their native ranges, at places like the Garden in the Woods or the Arnold Arboretum in Massachusetts. This suggests that climatically-suitable habitat might already exist far to the north of their small native ranges in the

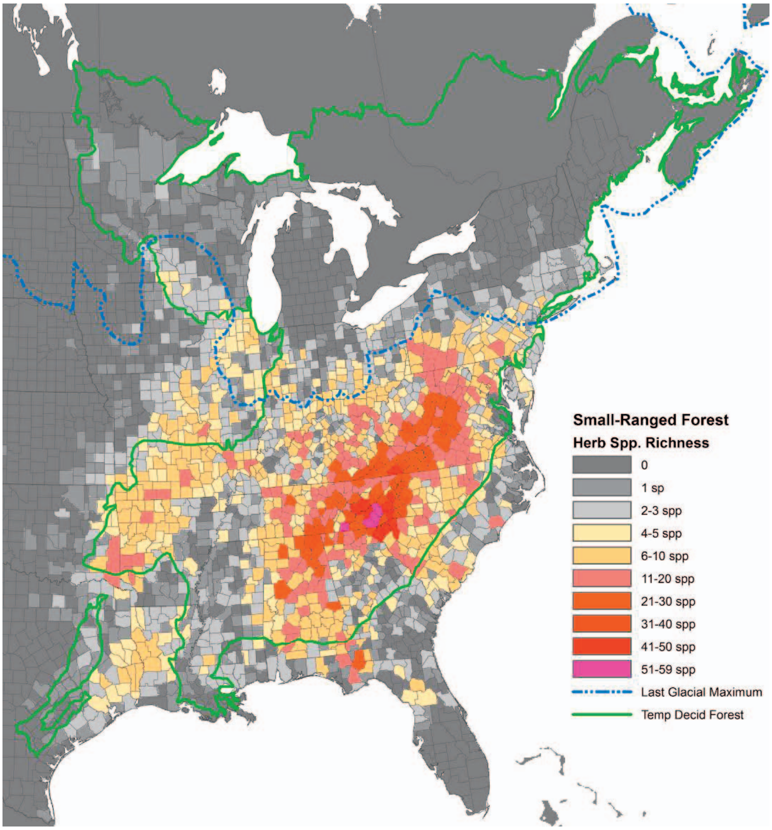

Figure 1. County-level richness of small-ranged endemic forest herb species in the eastern United States, adapted from Bellemare and Moeller (2014). Herbaceous plant species associated with deciduous forest habitats and occupying 70 or fewer US counties were compiled in a Geographic Information System (GIS) analysis to identify hotspots of diversity and trends in the density of small-ranged species across the study area. The outer boundary of the Temperate Deciduous Forest biome is indicated in green, and the southernmost extent of the Laurentide Ice Sheet at the Last Glacial Maximum is marked by a blue line. Biogeographic patterns in the distribution and diversity of small-ranged forest herbs within the biome appear to be strongly associated with aspects of past climate change, such as the position of the ice sheet. See Bellemare and Moeller (2014) for further details.

southeastern US, a pattern that is consistent with dispersal rather than climate limitation of these species' geographic distributions in areas poleward of their native ranges (Bellemare and Moeller 2014; Sax et al. 2013).

Overall, it appears that some plant species, like small-ranged endemics, have exhibited little potential for northward migration in response to past climate warming, even over the thousands of years since the late Pleistocene. Although these endemic species concentrated in the southeastern US would probably have been geographically well-positioned to survive the climatic cooling of another ice age cycle, as occurred repeatedly in the Pleistocene, the current trend toward rapid and long-term climatic warming seems to place many on the "wrong side" of climate history. Recent studies suggest the impacts of anthropogenic warming might stretch for tens of thousands of years or more (Ganopolski et al. 2016; IPCC 2014), potentially exposing temperate zone endemics marginalized in the south to considerable extinction risk (Bellemare and Moeller 2014).

Although some attention has been focused on the biogeographical dynamics of forest plant endemics in the eastern US (e.g., Bellemare and Moeller 2014), less is known about the paleoecological history and potential value of managed relocation for small-ranged endemic species associated with non-forest habitats in the region. In addition to the hotspots of forest plant endemism described in Bellemare and Moeller (2014), other studies have highlighted additional habitats with high rates of endemism in the southeastern US (Estill and Cruzan 2001), including rock outcrop communities, limestone glades, and sand hills (e.g., Baskin and Baskin 1988; Baskin et al. 1995; Estill and Cruzan 2001). The distributions of many of these non-forest plant endemics appear to be tightly linked to distinctive bedrock and soil types (e.g., serpentine, limestone, granite) that support open vegetation and reduced above-ground competition. It is unclear how decisive climatic factors might be in determining these species' distributions. For example, research suggests that local determinants of persistence for outcrop endemics are often related to biotic interactions (e.g., escape from competition, avoidance of shading by larger-statured plant species, and forest encroachment; Baskin and Baskin 1988). As such, it is conceivable that some endemic plants that have evolved to occupy open, low fertility environments (e.g., outcrops and barrens) might already be pre-adapted for coping with a wide range of abiotic environmental stresses, lessening their sensitivity to climate change (Grime et al. 2008; Harrison et al. 2015).

Whether a similar dynamic of climate resilience among rare plants associated with stressful abiotic environments might apply to alpine and coastal habitats in the northeastern US is not yet clear. However, research has found slower rates of phenological change in alpine zone plants relative to those at lower elevations during recent decades of climate change in the northeastern US (Kimball et al. 2014). Similarly, longer-term paleoecological records indicate modest responses of tree line and alpine zone plants to past episodes of climate change in the Holocene (Spear 1989; Spear et al. 1994), suggesting some level of climate resilience among these communities and the possibility that other environmental factors might play a strong role in structuring vegetation. Some field botanists in the New England region have also recently reported a surprising lack of visible change in stations for rare alpine plants in the past ∼50–100 years, running counter to the general assumption that climate change is rapidly impacting alpine communities (Cogbill 2015; Popp 2015; but see Capers and Stone 2011). Similarly, a recent meta-analysis by Chen et al. (2011), drawing data from many regions around the globe, found evidence that elevational shifts associated with climate change were less than expected, suggesting complex ecological processes influencing these habitats and their boundaries.

In New England, coastal sandplain and coastal pond habitats also support large numbers of rare and threatened plant species (New England Wildflower Society 2015), and thus have frequently been discussed in the context of climate change threats. These habitats also include several of the few narrow endemics restricted to the region, such as *Agalinis acuta* Pennell and *Liatris novae-angliae* (Lunell) Shinners. Notably though, other state listed rare species associated with these coastal habitats tend to be common along the coastal plain further to the south, with populations in New England often representing northern, range-edge stations (e.g., *Rhexia mariana* L., *Sclerolepis uniflora* (Walt.) B.S.P.; Gleason and Cronquist 1991). As such, the broader distributions of these species suggest some existing, species-level tolerance for warmer conditions. Nevertheless, these systems certainly merit close monitoring in the face of climate change.

In the case of the distinctive coastal grassland and shrubland vegetation types found on glacial outwash and coastal plain soils, there is strong evidence that the distribution of these habitats, and many of the rare species linked to them, reflect patterns of past human disturbance and agricultural land use (e.g., Foster et al. 2002; Motzkin and Foster 2002). Indeed, it appears that the most immediate threats to these open, xeric communities come from altered disturbance regimes and residential or industrial development (Neill 2007), rather than climate change.

In the case of coastal plain ponds, which also support a suite of rare and distinctive plant species in New England, the effects of climate change are likely to be more complex, and potentially more significant. These ponds are generally "kettle holes" formed by glacial ice blocks in outwash sediment deposits, now filled by their intersection with ground water. The ponds are often characterized by widely fluctuating water levels, which limit encroachment of shrubby upland vegetation in high water years, and expose wide shorelines during droughts or draw down years. In dry years, many rare herbaceous species grow and reproduce on the exposed soil along the pond shorelines, recruiting from seed banks in the pond sediment. Research by Neill et al. (2009) investigated seed bank composition relative to elevational position within pond basins, and relative to the ephemeral versus permanent status of ponds. Their results suggested that decreased water levels, whether due to increased human water withdrawals or to climate change, might negatively impact the distinctive shoreline vegetation of permanent ponds. In particular, sediments lower in the pond basins contained fewer viable seeds and lower plant diversity (Neill et al. 2009). Further, lowered water levels might allow encroachment of upland vegetation into the species-rich areas higher in the basins (Neill et al. 2009). However, this trend was not evident for ephemeral ponds, where inputs to the seed bank were apparently more evenly distributed across the basin over time. With changing climate conditions, there is potential for these hydrologically-sensitive ecosystems to be substantially impacted (e.g., Zeilinski and Keim 2003).

Clearly, further research and monitoring is needed to better identify vulnerable plant species within the native flora of New England, and across the broader eastern US. It is likely that species' responses to climate change will be highly individualistic and idiosyncratic. Despite expectations of unpredictable responses to climate change, however, some emergent patterns regarding species risk and vulnerability are broadly suggested by biogeographical and paleoecological perspectives. In particular, as outlined above, we suspect that many of the likely candidates for managed relocation in the future will be small-ranged plant species from the southeastern US (e.g., Bellemare and Moeller 2014), rather than the wider ranging native plant species typical of New England. As such, it seems probable that much of the debate on managed relocation in a New England-specific context will be centered on the ecological risks and conservation benefits of "hosting" vulnerable species, such as narrow endemics, that might be translocated northward from the southeastern US.

Limitations on inferences of species' risk due to climate change. It is important to note that the primary sources of information used to assess species' long-term risks due to climate change tend to be indirect. For example, inferences have been drawn from biogeographical patterns, range sizes, habitat associations, and paleoecological perspectives (e.g., Bellemare and Moeller 2014). Similarly, even highly quantitative approaches, such as species distribution modeling (SDMs), are correlative in nature and provide indirect estimates of potential threats from changing climate (Dawson et al. 2011; Pearson and Dawson 2003; Sax et al. 2013). Specifically, SDM approaches typically presume that the environmental conditions seen within a species' current native range represent the full extent of its climatic requirements and tolerances (Sax et al. 2013). This "bioclimatic envelope" is then projected forward in time based on climate change scenarios to estimate where similar climatic conditions might exist in the future (Dawson et al. 2011; Franklin 2009). This widely used approach has potential shortcomings, however. For example, species might not occupy the full range of climatic conditions they can actually tolerate due to complicating factors like dispersal limitation or antagonistic biotic interactions (Dawson et al. 2011; Sax et al. 2013). In addition, small-ranged species, like endemics, tend to be difficult to model, given the close geographic clustering of their populations and the limited number of data points they provide for calibrating models (Schwartz et al. 2006). Recent work suggests that there is more inherent uncertainty in the actual climatic tolerance for species that currently occupy a narrow range of climatic conditions (Early and Sax 2014).

Ideally, the indirect approaches outlined above would be paired with direct field observations, long-term demographic studies, and experimental work exposing plant species to novel climatic conditions in order to directly quantify their vulnerability to climate change (Dawson et al. 2011; Iverson and McKenzie 2013). Unfortunately, such intensive and targeted research is lacking for the vast majority of plant species, including most endemics, as it is both time- and cost-prohibitive. Indeed, it is unlikely that such detailed efforts could ever be undertaken for the multitudes of species predicted to be at risk from climate change (e.g., Thomas et al. 2004; Urban 2015). Consequently, higher capacity approaches that can provide reasonable estimates of risk indirectly, based on distribution patterns, range sizes, habitat associations, and paleoecological inference, are crucial.

It is clear that direct evidence of demographic declines or local extinctions linked to recent environmental change would be the "gold standard" for confirming a species' vulnerability to climate change and for triggering serious discussions of unconventional conservation options, like managed relocation. Although the types of long-term demographic studies that could provide this evidence are lacking for most endemic plant species in the southeastern US, there is some field evidence of problematic trends. For example, the iconic southeastern US endemic *Torreya taxifolia* Arnott, a conifer native to a small area centered along the Apalachicola River in the Florida panhandle, has declined precipitously in recent decades and might face extinction in the wild, likely due to a combination of novel pathogens and warming climate (Schwartz et al. 2000). Anecdotal reports from field botanists suggest that other temperate forest endemics in the region, like *Magnolia ashei* Weatherby and *M. pyramidata* W. Bartram, might also be declining (J. Tobe, Ecological Resource Consultants Inc., pers. comm.). In the well-documented case of *T. taxifolia*, a private group called the Torreya Guardians has already launched unofficial managed relocation efforts aiming to naturalize the species at sites in the southern Appalachians, where the tree apparently grows more successfully than within its small native range on the coastal plain (Barlow and Martin 2004; but see Schwartz 2004). Clearly further empirical research is needed to directly document population trends in the field, and to experimentally test the performance of endemic species under novel climatic conditions.

What are the risks of managed relocation? The top concern for most biologists and land managers is the possibility that some species moved to new regions via managed relocation efforts might become problematic invasives (Mueller and Hellmann 2008; Ricciardi and Simberloff 2009). The biological invasions literature is replete with hundreds of examples from around the globe where ecosystems have been disrupted by newly introduced species (Lockwood et al. 2013; Ricciardi and Simberloff 2009; Simberloff and Rejmánek 2011). Despite years of research on invasion biology and exotic species management, it is still very challenging to predict invasion potential in plants, so a scenario where a species translocated for conservation purposes might later become a problematic invasive is almost impossible to rule out entirely, even with experimental screening efforts or trait-based predictions (Lockwood et al. 2013; Mack et al. 2000; Williamson 1996). Citing the "precautionary principle," this has led some biologists to argue against taking any management actions that could inadvertently lead to harmful biological invasions (Ricciardi and Simberloff 2009, but see Sax et al. 2009).

However, ecological data are emerging to suggest that the types of intra-continental movements proposed in the context of managed relocation might not be as risky as they would first appear (Mueller and Hellmann 2008; Simberloff et al. 2012). In particular, most exotic plants viewed as problematic invasives have been introduced from other continents, not from other parts of the US. In fact, only a small proportion of plant species considered invasive somewhere within the continental US are native to other parts of the US, rather, almost all problematic invasive plants are introductions from other continents (Simberloff et al. 2012). At a national scale, Simberloff et al. (2012) found that exotic plant species from other continents were about 40 times more likely to be considered invasive compared to US native species that had been introduced beyond their native ranges elsewhere in the US. In the limited number of cases where US native species were deemed invasive, Simberloff et al. (2012) noted evidence of underlying disruptions to the ecosystems involved, including fire suppression and overgrazing.

Despite growing evidence that intra-continental movements of plants probably represent a modest risk for invasions, concerns about managed relocation persist, and these concerns have focused attention on some alternative approaches to climate adaptation. For example, one proposed alternative is "assisted gene flow (AGF)" to facilitate plant adaptation to rapidly changing climate (Aitken and Whitlock 2013; Aitken and Bemmels 2016; New England Wildflower Society 2015). Assisted gene flow would involve transferring gametes (e.g., via pollen) or individual plants to distant populations in order to introduce novel genotypes that could enhance the adaptive capacity of the target population (Aitken and Whitlock 2013). This might include, for example, AGF from southern populations of a species into more northern populations with the long-term goal of increasing the latter's ability to evolve in response to warming climate. This approach would be best suited to widespread species, where populations already occur under differing climatic regimes, and, to be effective, would require that a store of locally climatically adapted genotypes exist across the range to serve as sources (Aitken and Whitlock 2013). Most importantly, in contrast to managed relocation, AGF does not involve transferring species beyond their historical range boundaries: a population needs to exist in the target area to accept incoming AGF. Although fascinating, and likely to become an important management tool for widespread and ecologically-important foundation species, AGF does not provide a safer, alternative solution for the conservation challenge of preserving narrow-ranged endemics that might confront unsuitable climatic conditions across the entirety of their small ranges.

Invasion risk from US native plants in New England. To provide more precise quantitative insight into patterns of intra-continental plant naturalization and invasion within New England, we undertook two reviews of floristic information. First, we reviewed the plant species currently listed as invasive or potentially invasive by the Invasive Plant Atlas of New England (IPANE; www.eddmaps.org/ipane/) to determine which of these problematic taxa were introduced from other parts of the contiguous US versus other regions of the globe. Second, we reviewed current data on the flora of New England (Haines 2011) to determine the underlying total number of naturalized and adventive plant species present in the region that are native to other parts of the contiguous US, regardless of their status as invasive or non-invasive within New England. Taken together, these data provide a direct empirical estimate of the rates of invasiveness seen among US native plants that have been reported as adventive or naturalized in New England.

In terms of invasive plant species in New England, as of Fall 2015, IPANE listed 111 plant taxa as invasive or potentially invasive in the region. Of those, 10 species (9%) are possibly US native plant species, and the remaining 91% are from regions outside the contiguous US (see Table 1 for US natives; IPANE website for full list). Even among the 10 taxa considered US native invaders of New England, several might be excluded on closer examination, either because their native status is in question or because they are invasive in only a limited ecological setting. For example, with both *Phragmites australis* (Cav.) Trin. ex Steud. and *Phalaris arundinacea* L. it is suspected that these taxa include a mix of North American and European genotypes, with the latter genotypes likely being most associated with problematic invasive behavior (e.g., Saltonstall 2002 for *P. australis*). Indeed, some recent treatments recognize the native taxon, *P. amercanus* (Saltonstall, P.M. Peterson & Soreng) A. Haines, as distinct from the exotic *P. australis* (Haines 2011). The case of *P. arundinacea* is not yet fully resolved, but multiple European genotypes have been widely introduced for animal forage and are likely responsible for many of the problematic populations of this species (Lavergne and Molofsky 2004, 2007). Removing these two invasive grasses from the list brings the number down to eight invasive plant species originating from within the contiguous US (7% of total species on IPANE list). Among these taxa, *Pistia stratiotes* L. and *Hypericum prolificum* L. are considered species of interest to IPANE, but review of the individual New England states' invasive plant lists indicates that neither species is yet listed as invasive at the state level, suggesting that these two species have shown limited invasive behavior in the field to date.

This revised tabulation leaves six US native plant species that are deemed invasive in parts of New England (marked by asterisk in Table 1), or about 5% of the total invasive plant species formally reported for the region by IPANE. Two of these are considered invasive only in Connecticut, *Froelichia gracilis* (Hook.) Moq. and *Silphium perfoliatum* L., and are not considered problematic in other parts of New England. The remaining four species, *Amorpha fruticosa* L., *Cabomba caroliana* A. Gray, *Myriophyllum heterophyllum* Michx., and *Robinia pseudoacacia* L., are the only US native plant species that appear on four or more New England states' invasive species lists and are conclusively invasive in the region (3.6% of total IPANE list). Notably though, *Amorpha fruticosa* appears on the lists for NH, CT, RI, and ME, but is only considered potentially invasive or a watch list species for those states; it has not been classified as highly invasive. Invasions by taxa recognized as *Myriophyllum heterophyllum* might actually be caused by a hybrid taxon resulting from crosses between *M. heterophyllum* and *M. pinnatum* (Walt.) B.S.P., another North American species (Moody and Les 2002). This instance of two North American taxa hybridizing and giving rise to an invasive hybrid taxon does raise some concerns related to managed relocation, as will be discussed below. Finally, to be thorough, the IPANE list does not yet include *Nelumbo lutea* Willd., another US native aquatic plant species that is occasionally problematic in New England (e.g., in river impoundments in Concord, Massachusetts) and is listed on the Connecticut invasive species list. However, even including *Nelumbo lutea*, this would result in only five US native plant species being considered invasive in New England, or about 4.5% of the 111 species on the current IPANE list.

Of the US native invasives discussed above for New England, only *Robinia pseudoacacia* and *Cabomba caroliana* are considered highly invasive across the region. Humans have widely, and often intentionally, dispersed both species, with invasions likely resulting from repeated introductions. For example, *Robinia pseudoacacia* was originally introduced from the southern US for its hard, rot-resistant wood (EDDMaps 2015), while *C. caroliana* is common in the aquarium trade and has been secondarily spread by recreational boating (EDDMaps 2015). Notably, this pattern of widespread, repeated, and unmonitored introduction is probably unlike anything that would be proposed in the context of a planned managed relocation effort, where

Table 1. Ten plant species native to the contiguous United States but reported as invasive or potentially invasive exotics in New England. Drawn from the full list of 111 invasive plant species developed by the Invasive Plant Atlas of New England (IPANE), accessed in November 2015 (www.eddmaps.org/ipane/), supplemented with information from state-level invasive species watch lists for the New England states (Connecticut: http://cipwg.uconn.edu/invasive_plant_list/ ; Maine: http://www.maine.gov/dacf/mnap/features/invasive_plants/invasives.htm ; Massachusetts: http://www.massnrc.org/mipag/index.htm ; New Hampshire: http://agriculture.nh.gov/publications-forms/documents/prohibited-invasive-species.pdf ; Rhode Island: http://rinhs.org/wp-content/uploads/2011/10/RIISC_2001list_wlogos.pdf ; Vermont: http://agriculture.vermont.gov/plant_pest/plant_weed/invasive_noxious_weeds/noxious_weeds_list). Habitat information was drawn from Gleason and Cronquist (1991) and other sources. Native range information was adapted from http://www.eddmaps.org/ipane/ . The six species marked with an asterisk (*) constitute the subset of species with clearest evidence of US native status and problematic invasive behavior within New England (see text for full explanation).

Species	New England States Where Listed as Invasive	Region of Origin within Contiguous US	Habitat Association
Amorpha fruticosa L.*	CT, ME,	From further south and west of New England	Riverbanks, flood plains, tidal zones and other areas associated with water
Cabomba caroliana A. Gray*	CT, MA, RI, VT	Southeastern United States	Lakes, ponds, slow-moving rivers and streams
Froelichia gracilis (Hook.) Moq.*	CT	Western United States	Roadsides or railroad tracks, often in sandy soil
Hypericum prolificum L.	IPANE only	Mid-Atlantic, South, Midwest	Variety of habitats that range from the margins of swamps to cliffs and woods
Myriophyllum heterophyllum Michx.*	CT, MA, ME, RI, VT	Southern United States	Lakes, ponds, swamps, rivers and mudflats

Table 1. Continued.

Species	New England States Where Listed as Invasive	Region of Origin within Contiguous US	Habitat Association
Phalaris arundinacea L.	CT, MA	Questionable: Northern New England and north, invasive incursions likely caused by non-native genotypes	Streambanks, lakesides, marshes, ditches and moist ground
Phragmites australis (Cav.) Trin. ex Steud.	CT, MA, ME, RI, VT	Questionable: found on six continents, invasive incursions caused by non-native genotypes	Shallow water, wetlands
Pistia stratiotes L.	CT, RI	Questionable: Florida, South America or Africa	Lakes, ponds and reservoirs
Robinia pseudoacacia L.*	CT, MA, ME, RI	Appalachian and Ozark regions of eastern US	Full sun on sandy, well-drained soils
Silphium perfoliatum L.*	CT	Central and southern North America	Water courses and open meadows

a target species would likely be introduced in a much more limited and closely-managed fashion to better detect early signs of problematic behavior.

To provide a broader context for the above list of 4–10 US native plants considered invasive in New England, we also tallied the total number of naturalized and adventive US native plants reported for the region by Haines (2011), whether or not these species appeared on the IPANE invasive plant list. These species were identified by cross-referencing all the plant species listed as exotic in New England by Haines (2011) against floristic data sources to determine the subset of these exotics that were native to the contiguous US, using the USDA PLANTS database (USDA, NRCS 2016) and Kartesz and BONAP (2015), as well as various regional floristic data sources. Additionally, we characterized the native ranges of this subset of exotic species geographically within the US, distinguishing among species native to the western US (west of the 100th meridian), eastern US (east of the 100th meridian), or those whose native ranges spanned the 100th meridian. Further, given our focus in parts of this review on small-ranged endemic plant species native to the southeastern US, we also flagged those plant species with ranges entirely restricted to the southeastern US region (see Appendix 1 for states included).

In total, our review of Haines (2011) indicated that approximately 374 plant species native to the contiguous US have been reported as naturalized or adventive in New England. These include the 10 potentially invasive species highlighted above and in Table 1, but also another ~364 plant species occurring outside cultivation, with populations that are either naturalized (i.e., self-sustaining) or adventive (i.e., sporadically occurring individuals). Contrasting this tally to the US native invasive species highlighted by IPANE, whether starting with a full list of 10 potentially invasive species, or the reduced list of 4–6 more widely invasive species (Table 1), it is evident that the rate of problematic invasive behavior seen among US native plants establishing as exotics in New England is quite low (1.1–2.7% of the 374 species reported as naturalized or adventive in the region).

The preliminary estimate of ~1–3% invasive species among US native plants might be an overestimate for two reasons: First, the rate calculated above uses the total number of species already observed as spontaneous, adventive exotics ($n = 374$ species) as the starting point of our calculation; however, this estimate misses an unknown, but probably large, number of US native species that have been brought into the region, either accidentally or for horticultural purposes, that have failed to spontaneously establish as exotics, and thus be reported by Haines (2011). For example, numerous southeastern US endemics are grown at botanical and horticultural sites in the region, but have not been observed as spontaneous adventives in New England (e.g., *Clethra acuminata* Michx., *Trillium luteum* (Muhl.) Harbison, *Tsuga caroliniana* Engelm.*,* among many others). Quantifying this broader pool of potential species is not feasible, but referencing the so-called "tens rule" of biological invasions (Williamson 1996; Williamson and Fitter 1996), it has been estimated that typically only ~10% of species transported to a new region will escape and appear in the wild. The majority fail to escape or establish and are, in effect, invisible to estimates of exotic species introductions. This simple rule of thumb might suggest that the 374 species observed as US native exotics in New England represent a small subsample of a substantially larger pool of plant species that have entered the region in the past but failed to appear as adventives. Of course, the so-called tens rule is only a rough rule of thumb and many exceptions to this generalization are known (e.g., Jeschke and Strayer 2005; Moodley et al. 2016). Nevertheless, given that the broader flora of the United States probably includes about 18,000 or more plant species (Stein et al. 2000; Simberloff et al. 2012), it does not seem unreasonable to speculate that several thousand US native plants might have been accidentally or intentionally transported into New England over the decades, but the majority have failed to escape and appear spontaneously in the wild.

Most importantly, the tens rule and similar estimates suggest a broader context for the ~1–3% rate of invasiveness we have calculated for US natives observed as exotics in New England. Rather than providing a direct estimate of the rate of invasiveness that might be expected among a new set of species translocated to the region (e.g., via future managed relocation efforts), our estimate of a ~1–3% rate of invasiveness might actually be viewed as an upper bound on expected invasions, as it does not include the many species that would likely fail to establish, even if intentional introduction were attempted. Incorporating that initial step (e.g., roughly ~10% of species might spontaneously establish after introduction), a realistic estimate might be closer to a 0.1–0.3% rate of invasiveness. Nevertheless, among those species that could be established in the wild, our calculation of ~1–3% invasiveness rate is likely to be a reasonable estimate of risk for successfully introduced species. It is possible these estimates of risk could be too low if increasing temperatures associated with climate change make the region more suitable for species introduced from the south or if current adventives are still experiencing time lags in their emergence as invasives. Conversely, these estimates could be too high if habitat fragmentation and other anthropogenic impacts on the environment make it difficult for species to spread.

Beyond calculating rough estimates of the risk of invasiveness among translocated species, it is important to note that any managed relocation efforts planned in the future should include invasion risk screening based on plant traits or habitat affinity. Although imperfect, such pre-screening would likely have flagged as problematic candidate species with traits such as those exhibited by several of the US native exotics already viewed as invasive in New England. For example, among the four US native plant species we have considered clearly invasive across New England (Table 1), the legumes *Amorpha fruticosa* and *Robinia pseudoacacia* might have been excluded in advance due to their ability to symbiotically fix nitrogen and propensity for aggressive clonal spread. Likewise, six of the invasive species in Table 1 are linked to wetlands, a habitat with a history of problematic invasions, and thus likely to trigger intensive critical review prior to any translocation efforts. As such, simple filters based on plant traits and habitat affinity might have precluded intentional release of most of the US native species considered invasive in New England, had similar species been proposed for managed relocation.

Comparing among geographical source regions of the 374 US natives found as exotics in New England, we found that 119 (31.8%) were otherwise native to the eastern US (but not New England), whereas 71 (19%) were native to the western US. The largest geographical grouping was the set of species with native ranges spanning the 100th meridian (our division between eastern and western US), with 166 species (44.4%) drawn from the central US region or having large ranges spanning both the eastern and western US. Given our focus in this review on endemics from the southeastern US, we also considered the subset of species whose native ranges are entirely restricted to this region: 17 of these endemic species were reported as adventive or naturalized in New England, but none of these appeared on the IPANE watch list for the region. Of the endemics, only *Catalpa bignonioides* Walt. and *Robinia viscosa* Vent., two tree species with histories of repeated and intentional introduction, would appear to merit note as being relatively common as naturalized species in many parts of New England. In contrast, the majority of these species have been reported only sporadically as adventives (e.g., *Leucothoe fontanesiana* (Steud.) Sleumer, *Rhododendron catawbiense* Michx.).

Overall, our review of US native plants reported as adventive or invasive in New England suggests that, consistent with other studies (e.g., Mueller and Hellmann 2008, Simberloff et al. 2012), such plant species do not pose a great threat of intra-continental invasion. Most importantly, these findings suggest that the widespread perception that a large proportion of exotic species become problematic invasives when moved to new regions is not consistent with available empirical data, particularly when the species movements occur within continental regions.

Why might US native plants have a low rate of invasiveness in New England? Several hypotheses have been proposed as to why US native plant species are not prone to high rates of invasive behavior beyond their ranges in the US. First, plant species living within a broad geographic area or biome likely have a shared ecological and evolutionary history spanning millions of years, even if they do not occur together across the entire region presently. This suggests some level of co-evolution within ecological communities that might constrain many native species from becoming too successful or invasive in regions near their native ranges (Simberloff et al. 2012). Similarly, within a broad geographic region, the natural enemies that have co-evolved with native plant species (e.g., insect herbivores, pathogens, etc.) might regulate population growth, limiting their potential for invasiveness. In contrast, plant species introduced from other continents often leave behind their natural enemies and can exhibit more rampant population growth than natives carrying a higher load of pests and pathogens (i.e., the Enemy Release Hypothesis; Elton 1958; Mitchell and Power 2003). Further, some plant species from other continents might have evolved in a setting with greater biological diversity (e.g., temperate forests of East Asia) and have been honed more finely by natural selection, providing them with fitness advantages in their introduced range, ones that make them more likely to become problematic invaders (Darwin 1859; Fridley and Sax 2014; Vermeij 2005).

Finally, within a continental region it is likely that most species prone to high population growth rates and rapid geographic spread have already done so, thousands of years ago (Simberloff et al. 2012). In fact, these types of "ancient invaders" are the common, widespread native plant species that form the post-glacial, Holocene vegetation of New England and other northern areas, having colonized these regions since deglaciation, apparently quite rapidly in some cases (Cain et al. 1998; Clark 1998; Johnson and Webb 1989). To some extent, the post-glacial Holocene period might even be viewed as a long-running natural experiment testing plant species' potential for invasiveness and spread in the eastern US. In contrast to the many native plant species that are already widespread in the northeastern US, it appears that many of the small-ranged endemic species concentrated in the southeastern US are among the species least likely to spread rapidly (Bellemare and Moeller 2014). Overall, these trends suggest that invasion risk from US native species, particularly small-ranged taxa, is probably quite small. On balance, a slight possibility of problematic invasive behavior in the future might be an acceptable risk to consider when weighed against the threat of species extinction and permanent biodiversity loss.

The issue of aquatic plants and ecosystems. As has been noted elsewhere, insular ecosystems, such as oceanic islands or freshwater wetlands, are particularly prone to biological invasions (e.g., Sax et al. 2002; Zedler and Kercher 2004). In New England we see clear evidence of this trend among the many problematic invasive plants, both US native and from other continents, associated with wetland and aquatic habitats (IPANE – EDDMapS 2015). It has been suggested that many productive and eutrophic wetland plant communities are highly structured by competition (Keddy 1990), potentially yielding dramatic community changes if new, more competitive, species are added to regional species pools. Given these patterns, there might be some general argument for avoiding translocations of aquatic and wetland plant species until any threatened species proposed for managed relocation is rigorously and extensively tested against native plants in a controlled, experimental setting (e.g., prior to field experiments or introductions).

What are the risks of hybridization and "genetic contamination?" Although less conspicuous than ecosystem invasion and dominance by new exotic species, the potential for non-native species to hybridize with native species and lead to "genetic contamination" is another concern raised about managed relocation (Ricciardi and Simberloff 2009). In particular, the intentional introduction of new plant species into a region where closely-related natives already occur would require careful consideration, as it could result in unintentional crossing and gene flow between formerly distinct taxa. Hybridization and introgression could lead to genetic swamping and the loss of the genetic distinctiveness between a New England native and the threatened species that was being moved in hopes of preserving its value for biodiversity.

It is also conceivable that hybridization between two North American taxa could lead to the formation of a new, invasive hybrid taxon (e.g., *Myriophyllum* example mentioned above). This seems unlikely for most genera, however, because plant ranges in the eastern US have been highly dynamic over the Pleistocene and Holocene, and many species, even those that are disjunct today, have likely come into contact with each other during previous times. Plant congeners with a history of sympatry often exhibit reproductive barriers and isolating mechanisms (Levin 2000; Widmer et al. 2009). For example, it has been suggested that the unusual late autumn flowering phenology of the widespread *Hamamelis virginiana* L. might have evolved in the past as a response to antagonistic, pollinator-mediated interactions with the late winter-early spring flowering *H. vernalis* Sargent, a species that is now endemic to the Ozark and Ouachita regions of southeastern US (Anderson and Hill 2002). The existence of such isolating mechanisms is also suggested by the many other eastern North American plant genera that contain numerous distinct species, but few or no regularly reported hybrids (e.g., Gleason and Cronquist 1991). Further, most well-known examples of plant hybridization leading to the formation of invasive hybrid taxa are spawned by contact between related taxa with a history of significant geographic isolation (e.g., between continents, as in the formation of *Spartina anglica* C.E. Hubb in Europe; Soltis and Soltis 2009).

Nevertheless, some examples are known of ancient hybridization between eastern North American plants that are disjunct today, but apparently had past periods of contact (e.g., Haufler et al. 1995a; Schilling et al. 2007). Even so, these hybridizations have not led to the loss of genetic distinctiveness of the species involved, nor have they spawned any invasive daughter species. Two striking examples of this phenomenon are seen in *Polypodium* L. and *Eupatorium* L. In *Polypodium*, hybridization occurred in the past between a native New England species and one found much further to the north at present. *Polypodium appalachianum* Haufler & Windham, now found in New England, hybridized with *Polypodium sibiricum* Siplivinskij, a species currently native to northern Canada, Alaska, and Greenland. This hybridization probably occurred during the Pleistocene, when *P. sibiricum* was likely pushed south during glaciation and came into contact with *P. appalachianum*, giving rise to the allopolyploid (4n) taxon *P. virginianum* L. (Haufler et al. 1995a, 1995b). The tetraploid species does occasionally backcross with *P. appalachianum*, forming a sterile triploid *P. ×incognitum* Cusik. However, *P. appalachianum*, *P. ×incognitum*, and *P. virginianum* can all currently be found in several New England states (Haines 2011), as well as co-occurring within many counties of these states (Cullina et al. 2011; Don Lubin, New England Botanical Club, pers. comm.). No one of these *Polypodium* taxa appears to be displacing another. Furthermore, *P. ×incognitum* is sterile and does not form introgressive swarms that might be capable of swamping either parent.

A second example of hybridization between a native New England plant species and another North American species is seen in the genus *Eupatorium*. It has recently been shown that *Eupatorium novae-angliae* (Fern.) V. Sullivan ex Haines & Sorrie, formerly known as *E. leucolepis* (DC.) Torr. & Gray var. *novae-angliae* Fern., is of hybrid origin. This taxon is derived from the widespread *E. perfoliatum* L., which is common in New England, and a newly-described species, *E. paludicola* E.E. Schill. & LeBlond (LeBlond et al. 2007). Amazingly, the latter species is a small-ranged endemic known today only from clay soils in the Cape Fear Arch region of North Carolina and South Carolina (Weakley 2015). The hybrid-derived *E. novae-angliae* is an apomictic polyploid and produces only sterile pollen, giving it little or no chance of introgressing into *E. perfoliatum*. Notably, *E. novae-angliae* is not invasive, and is known from only about 12 populations in Rhode Island and Massachusetts (Elliman 2001).

More broadly, experimental data on potential for interbreeding and hybridization could also be generated to address concerns of genetic swamping or the creation of invasive hybrid taxa. Climate-threatened plant species that were being proposed for translocation into New England could first be tested in controlled environments (e.g., in common gardens with any New England congeners) to observe reproductive behavior. Species could be specifically monitored for evidence of prezygotic isolation mechanisms, such as differing flowering phenology, pollen compatibility, fertile embryo development, and also postzygotic isolation mechanisms, such as evidence of outbreeding depression or hybrid sterility. Further, certain genera where hybridization is known to occur either in nature or in cultivation, for example *Aesculus* L., *Baptisia* Vent., *Echinacea* Moench, and *Quercus* L., should be given more intense scrutiny when considered for translocation to new geographic areas where congeners occur. Other plant species, that do not have close relatives in the regional flora, such as monotypic genera or families, would pose an extremely low threat of hybridization, and might be translocated more readily without risk of genetic introgression with native species.

Why not *ex situ* conservation in seed banks and botanical gardens alone? Given persistent concerns about the potential for invasiveness or genetic contamination with managed relocation, why would we risk releasing non-native plant species into the wild in New England? It might seem that preservation of genetic material in seed banks and as representative individuals in botanical gardens would be sufficient.

However, these standard approaches to *ex situ* conservation have limitations. For example, many plant species have recalcitrant or short-lived seeds, making long-term seed banking impracticable (Baskin and Baskin 2014; Oldfield 2009). For actively growing plants in botanical gardens, there is the added challenge of space limitations, particularly for large-statured woody species, making long-term housing of multiple individuals difficult (Oldfield 2009). Further, the long-term maintenance of species in botanical collections would require considerable financial resources, and this might be unsustainable over many decades or centuries.

Finally, one of the core goals of managed relocation would be to maintain species as wild, ecologically and evolutionarily dynamic entities over time. Establishment of translocated populations in natural areas would allow climate-threatened species to maintain ecological interactions with other species in the wild, and possibly evolve and adapt to climate change (Weeks et al. 2011). Although more traditional *ex situ* options, such as seed banks and preservation in botanic gardens, have certainly played a crucial role in plant conservation efforts worldwide for many decades, such efforts cannot be viewed as a permanent substitute for wild, self-sustaining populations (Oldfield 2009). This is particularly true in the case of species whose native ranges might be compromised by altered climate, as the timescales involved extend over millennia (Ganopolski et al. 2016), and reintroductions to the species' former native ranges might never be feasible.

Geographic ranges and ecological communities are dynamic. On human timescales, most plant species appear to have relatively static geographic distributions and most ecological communities seem to maintain relatively constant species composition. For the most part, the only plant species we directly perceive as actively expanding their ranges are ecologically-threatening invasive plants with histories of recent introduction and rapid spread. However, as paleoecological and paleontological studies have clearly demonstrated, this stasis and apparent equilibrium among the native, non-invasive flora are illusory once broader timescales are considered (Davis 1983; Jackson et al. 2000; Williams et al. 2004); as Iverson and McKenzie (2013) noted: "range shifts are nothing new." Many temperate plant species have migrated widely across eastern North America during the late Pleistocene and Holocene, and their distributions at the Last Glacial Maximum (LGM; ~20,000 y ago) are likely to have been very different from where they are found today (Huntley and Webb 1989; Jackson et al. 2000; Williams et al. 2004). New England was fully glaciated at the

LGM, so our entire flora has been assembled in the recent geologic past from plant species that survived the Pleistocene in other regions (Barrington and Paris 2007; Jackson et al. 2000). Indeed, much of the New England temperate forest flora might be viewed as a subset of the broader species pool present in the unglaciated portions of the eastern US. At the community level, paleoecological evidence clearly suggests that plant species have migrated individualistically in response to past climate dynamics, not as unified communities, with members of present-day communities arriving in the region at different points in time and from different geographic sources (Davis 1976, 1983; Jackson et al. 2000; Webb 1988). Some researchers have even speculated that northern forest plant communities are still not "saturated" with species due to this slow, and potentially ongoing, history of post-glacial colonization (Bellemare and Moeller 2014; Gilbert and Lechowicz 2005).

Although many of the small-ranged endemic plant species that might be candidates for managed relocation in the future are not currently native to New England, it is probable that many have a shared ecological and evolutionary history with plant species and other organisms that are native to the region. Even today many plant species typical of Northern Hardwood forest in New England, such as *Betula alleghaniensis* Britt., *Clintonia borealis* (Ait.) Raf., *Mitchella repens* L., and *Oxalis montana* Raf., have ranges extending into the southern Appalachian Mountains where they co-occur in forest communities with a suite of small-ranged endemics unique to the southeastern US, such as *Cimicifuga americana* Pursh, *Clintonia umbellata* Michx. Morong, and *Diphylleia cymosa* Michaux (J. Bellemare, pers. observation). On longer timescales, over the multiple glacial cycles of the Pleistocene, it is probable that the temperate flora and vegetation of the eastern US has been repeatedly disassembled and reorganized, often retreating and comingling in glacial refugia in the southeastern US, then expanding to re-occupy northern areas in warmer interglacial periods, such as during the present Holocene epoch (Davis 1983).

Is unplanned managed relocation already happening and what might be the genetic consequences? Even as ecologists, conservation biologists, and land managers are debating the merits and risks of managed relocation (Ricciardi and Simberloff 2009; Richardson et al. 2009; Sax et al. 2009; Schwartz et al. 2012; Thomas 2011), it appears that some unplanned, accidental managed relocation might already be taking place via the horticultural trade (Bellemare and Deeg 2015; Van der Veken et al. 2008). For example, many plant species from the southeastern US are already present in the horticultural trade across the eastern US as commonly used landscape plants [e.g., *Aesculus parviflora* Walter, *Fothergilla gardenii* L., *Hamamelis vernalis* Sarg., *Hydrangea quercifolia* W. Bartram, *Isotrema macrophyllum* (Lam.) C.F. Reed, *Rhododendron vaseyi* Gray] or as specialty items from native plant nurseries (e.g., *Diphylleia cymosa*, *Shortia galacifolia* Torr. & Gray, various endemic *Trillium* spp.). Furthermore, there are records of numerous southern plant species occasionally escaping from horticulture and naturalizing beyond their native ranges in the north (Gleason and Cronquist 1991; Haines 2011). For example, a recent investigation by Bellemare and Deeg (2015) found *Magnolia tripetala* (L.) L., an understory tree species from the southeastern and mid-Atlantic US escaping from horticultural settings and naturalizing at multiple sites across Massachusetts, nearly 400 km beyond its native range edge in southern Pennsylvania. Similar observations have been reported for *Catalpa speciosa* (Warder) Warder ex Engelm., *Isotrema macrophylla*, and *I. tomentosa* (Sims) Huber, among others (Burk and Lauermann 1977; Burk 1984; Burk and Zebryck 2001). As such, it appears that a subset of native plants, particularly those with ornamental value, might already have had opportunities to shift their ranges northward via inadvertent human assistance (Bellemare and Deeg 2015; Van der Veken et al. 2008).

Although these horticultural escapes might provide insight into underlying climatic and biogeographic dynamics (Bellemare and Deeg 2015; Bellemare and Moeller 2014; Sax et al. 2013), this mode of plant migration is potentially problematic from a conservation genetics standpoint. The horticultural plants triggering these naturalizations likely represent a very small sample of the genetic diversity present among populations within these species' native ranges. In some cases, adventive populations appear to trace to single horticultural specimens (e.g., Bellemare and Deeg 2015), likely resulting in severe genetic bottlenecks and the potential for inbreeding depression as these new populations establish and spread. Although this mode of colonization and its impacts on genetic diversity might actually be somewhat analogous to the spread of species via rare long distance dispersal events (e.g., during post-glacial migration; Hewitt 2000; Excoffier et al. 2009), it is probably not the approach that would be chosen if managed relocation efforts were designed and implemented in an intentional way (Weeks et al. 2011). For example, much attention has been focused on the unique elements of genetic diversity often preserved among geographically-isolated refugial populations near species' southern range margins in the Temperate Zone, where species have likely persisted across multiple glacial cycles during the Pleistocene (Hampe and Petit 2005; Hewitt 2000; Keppel et al. 2012; Petit et al. 2003). It seems unlikely that plants in the horticultural trade derive from these distinctive, often marginal or disjunct, populations along southern range edges. If anything, horticultural selections might be biased toward material from northern populations under the assumption that cold hardiness would be increased and, hence, marketability across more of the eastern US. However, these more northern occurrences are likely to be those with reduced genetic diversity due to repeated bottlenecks during post-glacial migration (Hewitt 2000).

In contrast to the inadvertent constriction of genetic diversity that might occur during the horticultural introduction and trade of a plant species, the field of conservation genetics might recommend much broader and more intentional sampling from across the native range to preserve genetic diversity and account for potential ecotypic differences among populations (Hufford and Mazer 2003; Weeks et al. 2011). Further, considerable thought would need to be devoted to the potential for inbreeding vs. outbreeding depression in newly established populations (Charlesworth and Willis 2009; Galloway and Etterson 2005; Hufford and Mazer 2003; Weeks et al. 2011). While there might be arguments for preserving the genetic structure present among populations within the native range (e.g., via establishing a series of distinctive translocated populations), there might also be value in increasing genetic diversity within translocated populations to enhance the potential for adaptive evolution in response to new environmental conditions and changing climate (Weeks et al. 2011). These issues would need to be considered and resolved on a case-by-case basis as threatened species were selected for managed relocation intervention.

Managed relocation: The view from New England. It appears likely that the first experience New England botanists might have with proposals for managed relocation will come in the form of endemic plant "climate refugees" from outside the region. Because of New England's recent geologic history of full glaciation, the region is home to relatively few of these vulnerable small-ranged endemic species. Within the eastern US, most candidates for more intensive conservation interventions, such as managed relocation, will likely come from hotspots of botanical endemism in the southeastern US. Are New England botanists, land managers, and the broader public ready to host new plant species via intentional introductions from elsewhere? This development would certainly signal an expansion of plant conservation efforts in the region from a primary focus on local preservation of regionally-rare species to considerations of the larger biogeographical scales across which the impacts of climate change will unfold.

Importantly, there is a great need for additional study and cautious experimentation before any intentional managed relocation efforts are undertaken in the region. Empirical data from well-designed and closely-monitored field studies would be critical for developing a reasonable debate on these issues. For example, despite an intensive focus on the potential for invasive behavior by species introduced from other regions, it appears that establishing self-sustaining populations of most plant species outside their native ranges is likely to be quite difficult. The likelihood of a relatively high failure rate is consistent with some evidence from the field of reintroduction biology, where attempts to establish or reestablish populations of rare plant species also often fail (Drayton and Primack 2012). Indeed, such failures to establish are probably more common than is generally realized, as they might be underreported in the literature (Kennedy et al. 2012). We suspect that movement of most climate-threatened species into new regions would likely face similar challenges to successful establishment and long-term persistence. Rigorous field experiments would help to better understand these dynamics and hone strategies for successful introductions, should they become desirable in the future.

A proposal for field research on managed relocation. We propose that botanists, academics, and other interested volunteers in the New England region could play a crucial role in undertaking critical research for better understanding the risks and opportunities of managed relocation. Much of the exploratory work testing the establishment and performance of plant species outside their native ranges will need to be implemented at a relatively broad geographic scale, across multiple sites, and over substantial time scales. These challenging logistics make it unlikely that such research would be undertaken by individual academic researchers. This presents an exciting opportunity for a well-planned, collaborative effort across a network of botanical partners in the region and beyond. We believe that one of the best opportunities to conduct such an integrated project would be across college- and university-owned research forests and field stations, but could also include those public (e.g., US Forest Service) and private lands where there is interest in contributing to such an endeavor. In addition to providing crucial data on the performance and ecological interactions of climate-threatened plant species, such a model would provide excellent research experiences for students and present opportunities for greater connection between the regional botanical community and academic biologists.

In addition to research in the New England region, it is clear that better understanding long-term demographic trends in native populations of climate-threatened species in the southeastern US would be key to accurately gauging risk and deciding whether unconventional conservation measures, like managed relocation, might be justified. Research in the context of managed relocation might motivate much needed population monitoring, with the potential to enhance research collaborations between botanists in the southeastern and northeastern US. In particular, documenting key demographic processes (e.g., seed germination, juvenile survival, reproductive output) in native populations would provide an important baseline against which to compare performance and gauge success at experimental sites beyond species' native ranges.

Finally, we feel strongly that all research plantings undertaken in this experimental framework would need to be classified as temporary, with a clear timeline for monitoring and eventual removal. None of the research activities proposed would include permanent introduction of study species to the New England region; rather, research would be intended to inform future conservation efforts, should they be deemed necessary. Any efforts to permanently introduce climate-threatened species to the region would require further ethical consideration, legal review, and updated regulatory frameworks. These issues are beyond the scope of the present paper (but see: Camacho 2010; McLachlan et al. 2007; Schwartz et al. 2012; Shirey and Lamberti 2010).

CONCLUSIONS

Rapid anthropogenic climate change is a threat that will likely require new and unconventional approaches to biodiversity conservation. The temporal and spatial scales of the range shifts that are likely to be triggered in coming decades are difficult to conceive; however, it is becoming clear that some important subsets of plant diversity, such as endemics, might be at high risk of severe decline or extinction. Managed relocation presents one possible, though controversial, approach to lessening biodiversity losses in this mounting crisis. Although much has been written about the potential risks of managed relocation, our review of data on intra-continental plant naturalizations in New England suggests that the threat of invasion posed by US native species adventive in the region is quite low (e.g., ~1-3% of species). As such, field research on this important topic, including carefully monitored seed sowing and demographic study of experimental populations, would appear to be relatively safe and would be of high value for informing discussions of managed relocation. Because many of the endemic plant species of concern are slow-growing, long-lived perennials, the time scales necessary for even exploratory research on establishment and demography might require many years. Overall, we believe that this presents a significant opportunity for the botanical community in New England to undertake fundamental research on the feasibility and risks of managed relocation and to contribute substantially to future efforts to preserve plant biodiversity in the eastern US.

ACKNOWLEDGMENTS. We thank N. Rajakaruna for the invitation to develop this review, and two anonymous reviewers who provided valuable comments and suggestions for improving the manuscript. Discussions with W. Brumback and the New England Plant Conservation Program's (NEPCoP) Regional Advisory Council were also helpful in developing our thinking on several of the issues covered in this review. J. Bellemare and D. Sax were supported in part by funding from the U.S. Department of Defense's Strategic Environmental Research and Development Program (SERDP RC-2508).

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APPENDIX

List of US states used in identifying adventive plant species in New England as being endemic to the southeastern US in their native ranges. Only species with native ranges entirely restricted to the states listed here were placed in this category.

Alabama
Arkansas
Florida
Georgia
Kentucky
Louisiana
Mississippi
Missouri
North Carolina
South Carolina
Tennessee
Texas
Virginia
West Virginia