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Review

Assisted migration of plants: Changes in latitudes, changes in attitudes

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ABSTRACT

Rapid climate change has the potential to alter the location of bioclimatic envelopes for a significant portion of the world's flora. Plant species will respond variously via phenotypic plasticity, evolutionary adaptation, migration, or extinction. When fragmentation limits migration potential of many species or when natural migration rates are outstripped by the pace of climate change, some propose purposeful, human-mediated migration (assisted migration) as a solution. Here, we join the debate on assisted migration, and while recognizing the potential negative impacts, present a strategy to collect and bank seeds of plant species at risk of extinction in the face of rapid climate change to ensure that emerging habitats are as species-diverse as possible. We outline the framework currently being used by the Dixon National Tallgrass Prairie Seed Bank to prioritize species for seed banking, both for restoration purposes and for potential assisted migration in the future. We propose a strategy for collecting across the entirety of a species range, while targeting populations likely to go extinct under climate change, determined by application of species distribution models. Finally, we discuss current international efforts to collect and bank the global flora, as well as the research needs necessary to fully undertake the strategy presented.

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1. Introduction

Faced with a changing climate, plant species will respond plastically by changing their phenology or physiological responses, adapt to new climatic conditions via selection, migrate to a more suitable climate, or go extinct (Davis and Shaw, 2001). Species that succeed in a rapidly changing climate are likely to have ample genetic variation for traits important in the new environment, broad ecological amplitudes, highly plastic phenotypes, short generation times, or adaptations for long distance seed dispersal. However, climate change is rapidly shifting climate envelopes for plants poleward (Walther et al., 2002; Hampe and Petit, 2005) and to higher elevations (Kelly and Goulden, 2008; Lenoir et al., 2008; Trivedi

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et al., 2008) to such an extent that human-mediated movement of species may become necessary for more conservative species that are less mobile or adaptable. Such movement of species has been variously termed ''assisted migration,'' ''assisted colonization,'' and ''managed relocation.'' (http://www.nd.edu/~hellmann//Managed_relocation.html). In this paper, we limit the definition of assisted migration to the purposeful movement of species to facilitate or mimic natural range expansion, as a direct management response to climate change.

Translocating plants is nothing new. Humans have been moving plants, particularly edible, medicinal, and more recently ornamental, species throughout our history (Mack, 1999; Mack and Lonsdale, 2001). Modern horticultural and agricultural industries are responsible for wide scale translocations. This includes intra-continental plant transport, as in Europe where 73% of commercially available plant species have commercial northern range limits that exceed natural northern range limits by an average of 1000 km (Van der Veken et al., 2008). Restoration ecologists have been moving species from site to site for decades in attempts to revegetate marginal or highly impacted areas, or in response to large disturbances such as wildfire. Conservation biologists around the world have been translocating and reintroducing populations for decades. For example, in the United States the federally threatened *Cirsium pitcheri* (Pitcher's thistle), extirpated from the state of Illinois since the early 1900s, was reintroduced back to the state in 1991 (Bowles and McBride, 1996).

Intra-continental translocation has also proven an important conservation tool to help species escape diseases driving them to extinction in their native range. This includes numerous Australian species like *Lambertia orbifolia* (roundleaf honeysuckle), declining due to the devastating effects of *Phytophthora cinnamomi* (root rot fungus disease). For these species, translocation has been employed as a conservation measure since the mid-1990s (Cochrane, 2004), and in the United States, the formerly abundant Florida Torreya (*Torreya taxifolia*) has lost at least 98.5% of its former population size since the 1900s due largely to disease (Schwarz et al., 2000). Since 1989, ex situ collection and propagation, as well as translocation, have become key modes of conservation for the species. The Torreya Guardians, a group of citizens undertaking the translocation of the Florida torreya, now cite climate change as an additional rationale for movement of the species outside its historic range (Barlow and Martin, 2005), though the practice is not universally accepted (Schwartz, 2005; Ricciardi and Simberloff, in press).

Translocating plants is not without risk, the most problematic is the potential for a species to become invasive in its introduced range. Intercontinental movement of species has indeed resulted in problems with invasive species, but the vast majority of introduced species do not become invasive. It is estimated that less than 1% of species become invasive when imported to a new range (Williamson and Fitter, 1996), and only a small percentage of those (7.5% of invasives in the US) are a result of intra-continental introductions (Mueller and Hellmann, 2008). Most discussions of assisted migration in the context of climate change involve moving species relatively short distances poleward or higher in elevation within a continent, and many focus on species with limited dispersal ability which are less likely to become weedy (Rejmanek and Richardson, 1996). In many anthropogenically fragmented habitats, migration assistance in the form of short distance jump dispersal or corridor creation may be necessary for species to survive. These types of dispersal pathways are less likely to result in enemy release and biological invasion than are long distance and mass dispersal (Wilson et al., 2009).

When introducing species to novel ranges, there may be genetic consequences to existing populations that overlap with human-migrated ones. These include moving maladapted genotypes into the target zone and interbreeding of native and translocated populations leading to the disruption of co-adapted gene complexes. Species translocations may also result in cryptic invasions or genetic swamping, where a single genotype becomes dominantly representative (e.g. *Phragmites australis*), although this generally arises from intercontinental movements that cause closely related taxa, without reproductive barriers, to meet anew (Hufford and Mazer, 2003). Many of the scenarios cited as providing evidence for the detrimental consequences of assisted migration (Ricciardi and Simberloff, in press) involve intercontinental introductions or long-range translocation of species beyond the framework of assisted migration we describe here.

Even with the difficulties and risks involved, we maintain that there are species, sites and scenarios for which assisted migration is appropriate (Hunter, 2007; Hoegh-Guldberg et al., 2008). We believe that assisted migration may become commonplace for many species, and support efforts to create decision-making frameworks that weigh the risk of doing nothing with the risks of translocating species (Hoegh-Guldberg et al., 2008; McLachlan et al., 2007). Undoubtedly, conventional conservation measures will be sufficient for many species and may be our only choice for species where the risks associated with translocation are too high i.e. those predicted to become weedy via risk assessment procedures, (e.g. Reichard and Hamilton, 1997; Pheloung, 2001; Bradshaw et al., 2008). However, we envision a future where well-conceived translocations of species may reduce the risk of extinction, as well as increase the number of potential taxa creating new assemblages in a fluid landscape responding to broad scale changes.

We present here a strategy for seed collection and preparation for assisted migration that merges approaches from conservation biology and restoration ecology. We propose a framework in which the ecological aspects of assisted migration are evaluated using rubrics from restoration ecology, i.e. establishing or preserving functional ecosystems, while preserving the evolutionary trajectories of individual species, as most conservation biologists seek. The end goal is to preserve both the ecological roles and evolutionary potential of the greatest number of species.

2. Conservation, restoration and assisted migration

The decision framework presented by Hoegh-Guldberg et al. (2008) is a well-conceived matrix to determine the necessity of assisted migration for a particular species. We concur with the inherent prioritization of in situ conservation measures their framework creates. Allowing species to respond naturally is always the first and best option. Many species will likely evolve in situ in response to rapid climate change, especially short-lived and annual species such as *Brassica rapa* (Franks et al., 2007; Franks and Weis, 2008). There will be species, however, which may not be able to respond quickly enough. Long-lived species such as oaks and some conifers, for example, have generation times that preclude rapid adaptation (but see Morris et al., 2008), although their longevity suggests that such species may have relatively broad ecological amplitudes.

In the context of future climate change, the greatest survival limitation for many species is not their ability to adapt, nor even their intrinsic ability to migrate appropriately, given a landscape with sufficient connectivity. The most significant hurdle is that the landscapes across which they will need to move lack connectivity, and scenarios in the latter half of this century predict increasing fragmentation and decreasing effectiveness of corridors (Hannah, 2008), which will impact species differentially. Determining whether a species is at risk for extinction or decline as a result of climate change, coupled with the effects of fragmentation, requires an in-depth understanding of its biology (Hoegh-Guldberg et al., 2008). Unfortunately, population dynamics, reproductive biology, and migration rates for the vast majority of plant species, even in well-studied floras, have not been well elucidated. We simply may not know the status of many species until it is too late.

2.1. Prioritizing and banking now for the future

If the predictions regarding climate change thresholds, cascades and tipping points (e.g. Lenton et al., 2008) are even close to being correct, we may have very little time to prepare for the assisted migration of many species. Therefore, we seek to determine what is necessary to be prepared, with the goal of mitigating extinction risks for as many species as possible. We focus on plants, as concerted broad-scale conservation efforts are currently underway for many species. For example, the Millennium Seed Bank Project (MSBP) of the Royal Botanic Gardens, Kew, leads the way in terms of conserving the taxonomic breadth of the global flora. Their current goal is to collect and bank the seeds of 35% of the world's plant species. They have forged partnerships in key biodiversity hotspots, such as Australia and Madagascar, to ensure this outcome. Each partnership requires on-the-ground local participants who conduct the fieldwork. MSBP also works to build local capacity in the storage of seeds, and acts as the global repository for both primary and redundant storage of wild-collected native plant seed.

At a continental level, the European Native Seed Conservation Network (ENSCONET) consists of 24 partners in 17 countries and is focused on increasing the effectiveness of European seed conservation research, practice, and policy (Bonomi et al., 2008). ENSCONET is funded by the European Union as a means to help advance conservation practice and policy, assisting the EU in meeting its obligations to the Convention on Biological Diversity and the Global Strategy for Plant Conservation. Numerous national-level seed banking and ex situ conservation programs are also underway throughout Europe (Bonomi et al., 2008) and elsewhere.

The Australian Network for Plant Conservation produced national guidelines for seed banking and storage (ANPC, 1997) and translocation activities (Vallee et al., 2004) that are being utilized by a diversity of stakeholders, from farmers to nongovernmental organizations, as well as local and national governmental agencies (Maunder et al., 2004). Within Australia, regional work to conserve the incredibly diverse flora of the South West Australian Floristic Region has led to broad prioritization efforts at the species and landscape-level (Coates and Atkins, 2001), as well as more targeted programs to conserve the region's terrestrial orchids (Swarts and Dixon, 2009). At all levels, researchers, policy-makers and practitioners alike are working to prioritize in situ and ex situ conservation efforts while grappling with the benefits and risks of translocation as a conservation method.

In the United States, a coalition of botanic gardens and zoos has joined with the Plant Conservation Alliance and the Bureau of Land Management to undertake the Seeds of Success Program, which began in 2001 to collect and conserve geographically appropriate native plant materials (Byrne and Olwell, 2008). This involves collecting and banking seeds, which can be undertaken in a decentralized, but networked, manner, for restoration use and as an insurance policy against local extinction. Increasingly, curated seed collections accompanied by detailed provenance data like GPS coordinates, soil type and plant community structure are providing broad, long-term value given the growing threat of climate change (see Table 1). Given this foundation, we advocate for a natural extension of these efforts into a unified seed banking strategy to prioritize, collect, curate, and ultimately use seeds from a diverse array of plant species for restoration and research purposes in the context of rapid climate change. We highlight our efforts to create a seed banking program for the tallgrass prairie to identify the strengths of our approach and to provide a framework for application in other habitat types.

The Dixon National Tallgrass Prairie Seed Bank is currently banking seeds of native plants across several Midwestern and Great Plains ecoregions to insure against loss of plant diversity in the wild, while maintaining germplasm for research and restoration. We collect seeds, seeking to bank between 3000 and 30,000

Table 1
Seed collection protocols.

- Collect from a minimum of 50 maternal plants to capture 95% of the genetic diversity
- Collect no more than 10–20% available seed on any given day, to ensure that collection efforts do not impact vital rates of the target populations
- Collect across any obvious environmental gradients
- Collect both from within the center of population density AND from the periphery to ensure the greatest genetic diversity and to ensure collection from individuals that may perform better in marginal portions of the habitat
- Search out and collect even the smallest plants, because they may contain quantitative trait variation that would pre-adapt them to an alternate site
- In general, collections are bulked within a population, but maternal lines may be stored separately in some target species
  - to facilitate research efforts
  - in species with naturally low fecundity
  - to ensure equalization of founders
  - when collecting from small or marginal populations
  - when collecting species known to be self-incompatible
- Collect a minimum of 3000 seeds, with an optimal target of 30,000. It may be necessary to collect across years in the same populations. If so
  - collect no more than 10% of seeds
  - consider maternal-line collections versus bulked
  - separate years should be accessioned individually
- Collect at peak seed maturity, recognizing that some phenotypes (and sires) will be excluded, or collect on multiple days
- Collect from within the entire inflorescence, recognizing that proximal patterns of maternal plant development as well as patterns of embryo development might be influenced by genetic makeup of the embryos, and therefore skew genetic contributions
- Collect voucher specimens
  - herbarium vouchers allow expert confirmation of species identification
  - a leaf tissue sample can ultimately become a DNA voucher
- Collection information is critical to establish provenance of each accession. Standard collection protocols that include collectors name, locality information (particularly GPS coordinates), property ownership, terms of the collecting permit if it limits the use of the seeds, etc., are essential. Information on the habitat that might be critical for habitat matching includes basic soil type, description of the terrain and hydrologic qualities of the site, as well as community dominants and other associated plant species. Additional information on the status of the target population should include an estimate of population size, percentage of reproductive plants, and the number of plants from which the seeds were collected, which is particularly important when the seeds are not separated by maternal line

Seed collection protocols presented here are a synthesis of those developed for the Millennium Seed Bank; Brown and Briggs, 1991; Vitt and Havens, 2004; Guerrant et al., 2004.

seeds from more than 50 maternal plants which is sufficient to capture a high proportion of the genetic diversity present (Brown and Briggs, 1991; Guerrant et al., 2004) from a single, naturally-occurring (i.e. not restored) population. Our current accessions represent over 800 unique species. While capturing taxonomic breadth, banking a single representative sample does not provide a reasonable conservation collection. Therefore, we are in the process of expanding our efforts, with additional collections of approximately 100 species of restoration importance, with an emphasis on those considered likely to require assisted migration. We will obtain seeds from multiple populations across each species' range (minimum of 20 populations, at least one from each ecoregion in which the species occurs) to conserve genetic diversity. Once met, this target will be expanded to include additional species and additional collections from ecoregions defined at a finer scale.

This endeavor encompasses a widespread geographic area, numerous target species and sites. Given the limited resources for this work, this approach demands effective prioritization of collection efforts. We present a framework to determine collection priorities of seed-bearing species, which includes a literature-based determination of their potential to require some form of assisted migration (Fig. 1). We outline our strategy to prioritize species and collection sites as a case study. Prioritizing species with high restoration potential, while incorporating models of current and future ranges under climate change, can provide the foundation necessary to undertake targeted collection strategies across species' ranges (Fig. 2). Breeding system and data on genetic diversity and structure (e.g. is genetic diversity greatest within or among populations of a target species?) can be added to the rubric to determine the optimal strategy to retain evolutionary potential.

Using NatureServe's comprehensive list of plant species by ecoregion (Omernik, 1987), we compiled species lists for ecoregions which encompassed the grasslands of the Midwestern United States, with a focus on tallgrass prairie. We conducted a literature search for floristic surveys that documented the relative importance of species in plant communities. Further, we eliminated non-vascular species, non-native species and species with known recalcitrant seeds (i.e. those that are not amenable to seed banking procedures). A subset of important taxa for restoration was described including conservative species (i.e. those with low tolerances to disturbance and high fidelity to habitat integrity) and non-aggressive native pioneer species frequently used in restorations. We also selected native species that reached their range limits in this region, because populations at the edge of a species' range may contain traits particularly important in a changing climate (e.g. Darling et al., 2008; Dytham, 2009). Further refinement gave higher priority to rare, threatened or endangered species, narrow endemics, species that are highly conservative, or species with life history traits that might limit their migration potential, such as large, gravity dispersed seeds.

We have developed seed collection strategies for these target species using species distribution algorithms such as Maximum Entropy (MaxEnt) (Phillips et al., 2006) or BioClim (Diva-GIS) (Busby, 1991). These models use locality data of species occurrences and spatially continuous environmental and climatic layers to infer the potential niche of a species, often called the bioclimatic envelope. MaxEnt is particularly useful for species that are geographically or environmentally restricted (Elith et al., 2006), which makes it an appropriate choice for species on the priority list outlined above. Furthermore, these models can be extended by using future climate scenarios to predict range shifts under climate change (Hijmans and Graham, 2006). *C. pitcheri*, for example, is endemic to the foredune habitats of the Great Lakes, and it appears that the suitable climate envelope for this species will both contract and shift away from areas currently inhabited by the species under the model scenario (Fig. 2). While approximately 28,000 km^2 of newly available "potential suitable climate" arises in the future model, the best matching climate is predicted to occur along the southern edge of Lake Ontario outside of the species current range. The total predicted loss of suitable area is over 64,000 km^2. The predictions for this species lead us to prioritize seed collection from populations along the southern edge of Lake Michigan, where the predicted climate envelope shifts completely, as well as along its eastern shore, where the climate is likely to become unsuitable for the continued persistence of *C. pitcheri*. Climate change may already be affecting these locations, as the populations at sites along the southern edge of Lake Michigan have declined by half in the past 5 years (K. McEachern and N. Pavlovic unpublished data).

Depending upon the layers used in model development, MaxEnt identifies regions with similar environmental conditions to the known occurrence localities (Pearson et al., 2007). We included 19 climatic variables (WorldClim version 1.3 http://www.worldclim.org/bioclim.htm), elevation and land use cover data in our model, so there is likely some concordance between current and future habitat; whether or not there is appropriate foredune habitat requires further investigation. In the predicted range for *C. pitcheri* the most likely newly suitable bioclimatic envelope lies along the southern edge of Lake Ontario and is much broader than the foredune habitat required by the species (Fig. 2). MaxEnt allows us to model the potential niche on a landscape scale, but does not predict if appropriate habitat exists into which the species may expand, assisted or otherwise (Morin and Lechowicz, 2008).

Determining fine-scale habitat appropriate for species introductions might entail creating a GIS-based habitat profile, including level of site protection, edaphic characteristics, hydrological characteristics, slope, and vegetation type to determine if appropriate habitat exists in the predicted future range. This approach may be particularly important for narrow endemics and habitat specialists, and is the final stage in our assisted migration framework. Fine-scale habitat matching will determine not only potential habitat in the shifted range of species, it will further develop collection and migration strategies for species, as well as illuminate the need or potential for assisted migration. For example, if protected habitat exists in the future range, that best matches current habitat, this will increase the collection priority from populations with a predicted match.

2.2. Propagule collection and provenance

Each seed collection must be accompanied by data to fully document the occurrence, including GPS coordinates, associated species and other habitat and population data. Data such as these are essential for future restoration of these species to occur in matching habitats. The process of collection also provides an opportunity to collect baseline data on plant species distribution. Data on locality, population size, associated threats and phenology can be used over time to measure potential response to climate change, potentially providing an early warning system for the effects of climate change (Hawkins et al., 2008). In addition to providing data to monitor species responses in the short term, ex situ seed collections may provide a baseline for evolutionary changes that occur in species as they adapt to climate change over time (Franks et al., 2008).

There are legitimate concerns about collecting large amounts of seed from natural populations, as this may diminish their genetic diversity or vital rates (Sax and Williams, 2007). Over-collection has been a concern for both rare species and species commonly used in restorations. According to Menges et al. (2004), however, judicious (less than 50% of seed in 50% of years) seed collection

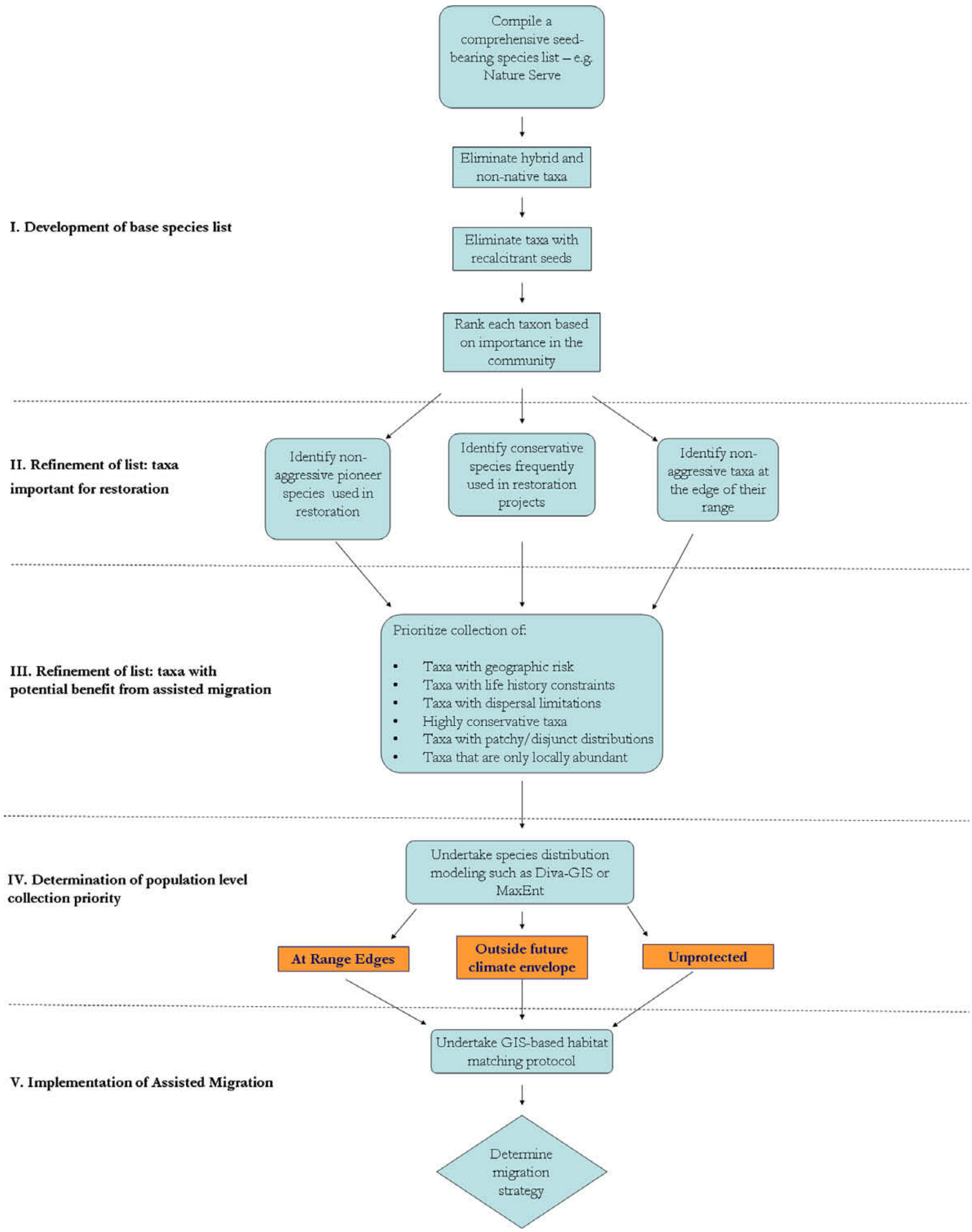

Fig. 1. Proposed framework for determining, prioritizing, and developing collection strategies for potential target species for assisted migration. (I). Using NatureServe's comprehensive list of plant species by ecoregion (Omernik, 1987), we compiled species lists for ecoregions within the grasslands of the Midwestern United States. A literature search was conducted for floristic surveys that reflect species overall importance in plant communities located within these ecoregions. (II). A more refined list of important taxa for restoration is created. (III). Refinement of target list for species that potentially benefit from assisted migration. The target list attained in level III is used with species distribution models created in Diva-GIS and/or MaxEnt software, to predict current distribution of species as well as their predicted range shifts under climate change to estimate the likelihood of extinction, particularly at the edges of their current range. (IV). Population level collection priority is determined. (V). Habitat matching protocols, within the predicted future ranges, will be used to determine if new suitable habitat is likely to be available as the climate changes, enabling determination of migration strategies for species and illuminate the need and/or potential for assisted migration.

of most taxa in large populations (over 500 plants) should not appreciably decrease their vital rates. Even relatively small populations tolerate removal of 10% of the seed crop in 10% of the years. Our collection protocols are designed to minimize this risk (see Table 2).

2.3. Timing and costs

The most recent climate change predictions suggest that the rate of change is increasing and that tipping points may soon be surpassed, leading to the general conclusion that we are past the

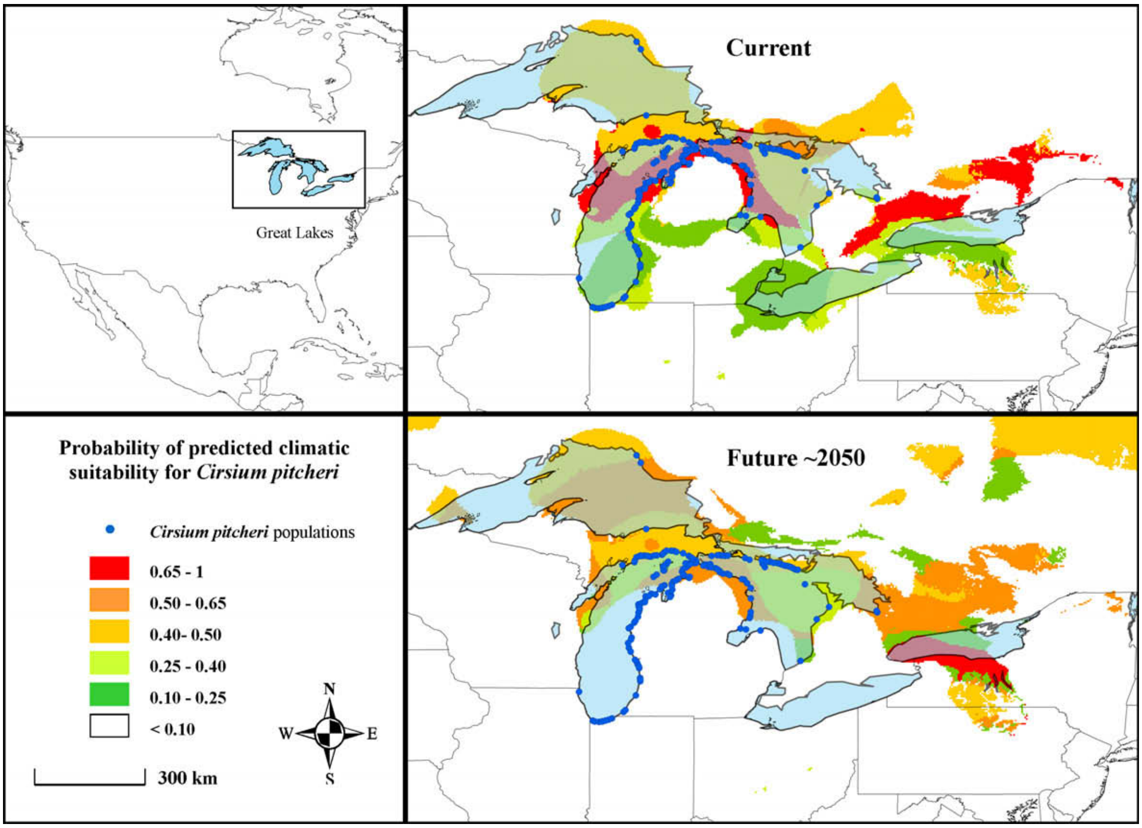

Fig. 2. Species distribution model for *Cirsium pitcheri* (Pitcher's Thistle) a threatened species that is narrowly endemic to the dune system of the Great Lakes. Future climate model shows predicted distribution under a doubling of CO^2 (CCM3 model; Govindasamy et al., 2003) predicted to occur by approximately 2050. Warmer colors indicate a high probability of appropriate bioclimatic conditions; cooler colors indicate a lower probability. A collection strategy for this species would target the edge of its range along the southeastern edge of Lake Michigan, as the bioclimatic envelope shifts completely away from this region. Assisted Migration of this species could include use of seeds collected in the southern portion of its range to augment extant populations in the northern portion to introgress potentially adaptive traits (sometimes called facilitated adaptation). Another strategy could include introduction of the species along the southern edge of Lake Ontario, outside of both its current and historic range, if suitable habitat is present there.

time when policy changes might reverse climate trends (Lenton et al., 2008). Therefore, we propose that now is the time to begin implementing the seed collection and banking strategy presented here.

Table 2

Nineteen bioclimatic variables available from WorldClim (http://www.worldclim.org/bioclim.htm) which are derived from monthly temperatures and rainfall values. They represent annual trends (e.g., mean annual temperature, annual precipitation), seasonality (e.g., annual range in temperature and precipitation), as well as extreme or limiting environmental factors (e.g., temperature of the coldest and warmest month, and precipitation of the wet and dry quarters). WorldClim.org defines a quarter as any period of three months (1/4 of the year) (Hijmans et al., 2005).

BIO1 = Annual mean temperature
BIO2 = Mean diurnal range (mean of monthly (max temp–min temp))
BIO3 = Isothermality (P2/P7) (*100)
BIO4 = Temperature seasonality (standard deviation *100)
BIO5 = Max temperature of warmest month
BIO6 = Min temperature of coldest month
BIO7 = Temperature annual range (P5–P6)
BIO8 = Mean temperature of wettest quarter
BIO9 = Mean temperature of driest quarter
BIO10 = Mean temperature of warmest quarter
BIO11 = Mean temperature of coldest quarter
BIO12 = Annual precipitation
BIO13 = Precipitation of wettest month
BIO14 = Precipitation of driest month
BIO15 = Precipitation seasonality (coefficient of variation)
BIO16 = Precipitation of wettest quarter
BIO17 = Precipitation of driest quarter
BIO18 = Precipitation of warmest quarter
BIO19 = Precipitation of coldest quarter

A comprehensive seed banking strategy has the potential to provide a safety net from both natural and human uncertainty. The national Seeds of Success (SOS) Program estimates that it will cost approximately $500 million dollars (US) and take approximately 10 years to collect and bank the entire US flora (~15,000 species) and to develop restoration protocols and bulked seed for 1000 species (P. Olwell, pers. comm.). While a large figure, these costs need to be weighed against the loss of biodiversity if we do not act. Currently, the Bureau of Land Management (BLM) invests approximately $5 million/year in seed banking and native plant materials development. Although BLM is by far the largest investor in the SOS program, it is still an order of magnitude less than what is required on a national level to accomplish the task at hand. If we approach assisted migration as an extension of current efforts in restoration, and focus on providing the seed stock, complete with proper provenance, the upfront costs become more acceptable.

2.4. Geopolitical boundaries

The international conservation community has long recognized the need to incorporate geopolitical boundaries into conservation policy and programs to ensure that international movement of plant and animal species does not threaten their survival or produce adverse side-effects greater than their intended conservation benefit. This includes the Convention in International Trade in Endangered Species (CITES), ratified in 1975, as well as the IUCN's *Position statement on translocation of living organisms* (IUCN, 1987) and *Guidelines for re-introduction* (IUCN,1995). However, predictive climate models even under low-emission scenarios show that many plants in Europe and North Africa will be making significant moves across geopolitical borders. This border crossing may lead to serious policy and conservation concerns, including questions about when a species is considered non-native and targeted for eradication, when seed-banked material can or should be shared across borders, and how to manage the shifting roles of countries in conserving species that are moving into or out of their boundaries (Harrison et al., 2006).

It seems obvious that species ranges occur outside the context of geopolitical boundaries, yet a comprehensive conservation program ignores political and bureaucratic realities at its peril. Given that local, regional, and national governments, as well as NGOs and agencies, are all stakeholders, it is appropriate that an umbrella program at a national or even continental level be responsible for overall coordination of a comprehensive seed banking strategy, while coordinating with regional groups who are responsible for local implementation. In the United States, the Seeds of Success network functions in this manner, as members of the network are responsible for regional collections. For example, the Bureau of Land Management collects and banks the seeds of species on their lands in the western United States, and several botanical gardens collect seed in their biogeographical region. Target species lists are coordinated at the national level so that each participating group knows what species have previously been collected and banked.

To illustrate the importance of cooperation between countries, consider the case of *Platanthera leucophaea*, a geographically widespread but sparsely distributed and globally threatened species. Our future distribution model of this species suggests a severe contraction of the portion of its range in the United States under climate change (P.V. and E.Y, unpublished data), and its remaining, bioclimatically appropriate range will move northeast further into Canada. Efforts to assist in the migration of this species across national borders would run afoul of US laws on the protection of Endangered and Threatened Species, as well as the international CITES treaty, neither of which is yet designed to address this type of species protection.

3. Research needs

While there is an urgent need to adopt and implement a comprehensive strategy to collect and bank restoration collections of important species before they are lost, implementation of assisted migration requires additional time and research. Seeds can be safely banked for decades to centuries until suitable sites for their re-introduction are identified and prepared through preliminary restoration activities. To make introductions more effective, areas of research need to be addressed concomitant with collection and banking activities. We highlight a few of the most important here.

3.1. Dynamic seed transfer zones

Seeds banked today offer hope for the continued survival of plant and animal diversity in a rapidly changing climate through effective ecological restoration (Rice and Emery, 2003), but an often overlooked component of restoration practice involves the selection of seed sources. Attempts to define optimal seed sources have led to the establishment of seed transfer zones, largely based on geographic distances between seed source and restoration site. Decades of ecological genetics research has revealed that populations commonly used in ecological restoration are often adapted to their local conditions (Langlet, 1971; Hufford and Mazer, 2003). Research has documented site-specific adaptation to soil conditions (McNeilly and Antonovics, 1968; McNeilly and Bradshaw, 1968; Feist and Parker, 2001), winter temperature and length (Balduman et al., 1999), water availability, flood tolerance (Dudley, 1996a,b; Fenster, 1997), herbivory and disease resistance (Crémieux et al., 2008), photoperiod (Griffith and Watson, 2006) and numerous other factors. Additional studies have shown that local populations may perform poorly when transplanted to sites that differ greatly from their home site (Joshi et al., 2001; Montalvo and Ellstrand, 2001). Together, these studies confirm that biotic and abiotic conditions greatly affect fitness of many plant species, and affirm the validity of our approach to collect seeds from across ecologically important gradients on a broad scale.

Given this, the most appropriate material to ensure restoration success will be from sources most closely matching the climatic and edaphic factors of the restoration site. To facilitate the application of this principle, static seed transfer zones have been outlined for many species to guide the appropriate movement of seeds for restoration efforts. However, given climate change scenarios, this application must become more dynamic, as some or even most plant populations may no longer be optimally adapted to local conditions. The forestry community began to grapple with the implications of climate change on seed transfer zones for commercially valuable tree species nearly two decades ago (Billington and Pelham, 1991; Rehfeldt et al., 1999; Rehfeldt, 2004; O'Brien et al., 2007). Research has focused on ensuring the successful matching of source material to restoration and revegetation sites, leading to the development of dynamic or 'floating' seed transfer zones (Ying and Yanchuk, 2006). Continued use and modification of these seed transfer zones will be critical to the success of any future restoration efforts that may include assisted migration.

Similar seed transfer zone research for native herbaceous species has lagged significantly behind that for trees, partly because so little is known about their biology. Therefore, the movement of seeds for restoration is often circumscribed by distance from a source-site, resting on the assumption that biotic and abiotic factors are likely to be similar between populations in close proximity. This is a conservative approach to source-site matching and may not be effective in either creating successful restorations or protecting species from extinction under rapid climate change. However, research-based seed transfer zones similar to those used in the forestry community are beginning to be defined (Johnson et al., 2004; Erickson et al., 2004), and are vital to determine when, where, and how assisted migration might be a valuable restoration and conservation technique.

As climates continue to shift, even the most dynamic seed transfer zones may be of little use when novel combinations of climatic and edaphic conditions emerge. Research to inform the careful selection of species and source material will be critical for future success. For example, native species with significant phenotypic plasticity may be an effective choice for inclusion into a restoration site; species and populations distributed in an environmentally heterogeneous metapopulation with high among-site gene flow may have more trait plasticity than those with low among-site gene flow (Sultan and Spencer, 2002). Seed source selection may benefit from incorporating distribution data, as populations found on the margins of a species' distribution may be more likely to be adapted to new conditions, and may also have a greater dispersal ability than those at the center of the species' range (Darling et al., 2008; Dytham, 2009). Assisted migration may be most successful when introductions mimic natural range expansion, when genetically variable populations are established and given time for microevolution to occur (Rice and Emery, 2003).

3.2. Producing large quantities of seeds to allow successful restoration

One of the chief obstacles of the strategy outlined here is the optimal use of seed-banked resources (Schoen and Brown, 2001), as banked germplasm does not generally exist in the quantities necessary for either restoration or assisted migration. Research into optimal germplasm multiplication methods, to retain the genetic diversity of the source population, disallow artificial selection and limit the potential of genetic drift (Havens et al., 2004), is necessary to fully implement assisted migration in the most rigorous manner possible. To limit the impact of genetic drift, for example, is it better to establish seed beds in multiple locations or just one? Or, does limiting seed production to the first generation produced by wild-collected plants preserve the genetic diversity and structure of the source population? Do we want to preserve the evolutionary trajectory of the source populations, or should we establish seed beds at the latitudes to which we are likely to be moving a species (or population) to allow a few generations to adapt to the local environment before using them for restoration? While bulking seed via traditional agricultural practices is the most expedient method to obtain large quantities of seed, these practices may not retain sufficient genetic diversity for successful restorations.

3.3. Monitoring current trends to predict future needs

Monitoring species in natural populations allows us to determine how climate change is affecting native species, as well as how are they are adapting in response. Monitoring is required to determine if and when assisted migration is necessary, to effectively prepare for assisted migration by banking seeds, and to prioritize where it is implemented based on extinction risk and/or potential loss of biodiversity. Some long-term monitoring programs are already established and well-situated to provide this data, at least for rare plant species. For example, there are several programs in Europe (Kull et al., 2008) and the United States that monitor trends in rare plant populations (e.g. New England Plant Conservation Program and Plants of Concern in Illinois). Monitoring data will provide insights into demography, habitat requirements, and other factors that will determine the success of introduced populations. There is also a need to monitor invasive species and currently common native species, as the response of these species will largely determine how habitats look and function over time.

Additional pressing questions can be answered through a combination of monitoring and evaluation. For instance, it will be important to determine experimentally if there are fundamental life history traits that make species more or less likely to need assisted migration in order to persist in a changing climate. In addition, we clearly need to understand the factors that determine which native species have the potential to be aggressive in new habitats if they are to be used in an assisted migration scenario. Using weed risk assessment methods can greatly decrease, although admittedly not eliminate, the likelihood of introducing new invaders (Groves, Panetta and Virtue, 2001). In addition, there is a tremendous wealth of knowledge resident in the restoration and horticultural communities in this regard, which needs to be formally documented so that it can inform decisions about assisted migration. For instance, many species that are likely to be migrated have already had populations restored within their native range or have been cultivated at botanic gardens and other settings both in and outside of their native range (Primack and Miller-Rushing, 2009). Several native species, particularly clonal and/or rhizomatous forbs, such as grass-leaved goldenrod (*Euthamia graminifolia*), showy sunflower (*Helianthus* x *laetiflorus*), and whorled milkweed (*Asclepias verticillata*) are known to be aggressive and these taxa are rarely used in restorations (Diboll, 1997) but can be useful for certain applications like erosion control in highly degraded sites.

4. Conclusions

Detractors of assisted migration point out that we may not be able to protect every species, particularly those whose habitats or climate zones disappear entirely as a result of climate change. Unfortunately, this is true. There will undoubtedly be species that will slip through the cracks, especially if they are cryptic or their status is difficult to determine. Additionally, we may simply run out of time, and species may go extinct without our noticing. Models of climate change predict that many non-analog, novel habitats are likely to develop (Pacala and Hurtt, 1993; Walther et al., 2002; Walther, 2003); it may prove difficult, or even impossible, to match species' habitat requirements with shifting climate envelopes as a result. However, as Rice and Emery (2003) remind us, one of the basic tenets of restoration is to consider the cost of doing nothing. Whether or not the majority of plant species adapt in place or migrate appropriately in response to future conditions is a question for the next generation(s) of ecologists and evolutionary biologists. By judiciously collecting seeds for the future we leave all options open. This includes the option of doing nothing.

While we debate about whether and how to implement assisted migration strategies, species already at risk are being further stressed by the unpredictability of the environmental changes they are experiencing. For plants, at any rate, the solution seems clear: collect and bank them now, and then plan the implementation stage when it is appropriate. As Hunter (2007) points out: implementation of an ex situ conservation strategy is far less problematic for plants, and a great deal less expensive, than for other taxa of conservation interest.

Ultimately, implementation of assisted migration, or other large scale conservation mechanisms, will require reconciliation between the hubris of being able to control nature, with the hubris that humans are somehow not a part of nature. Incorporating the newly emerging science of restoration genetics, and the lessons learned from both rare plant translocation experiments and the practice of restoration ecology will provide a road map for how to design assisted migration events. While natural communities of the future may not have current day analogs, our job is to ensure that they are as species-rich and genetically-diverse as possible.

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