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Review

Assisted colonization: Integrating conservation strategies in the face of climate change

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ABSTRACT

Global climate change poses an immense challenge for conservation biologists seeking to mitigate impacts to species and ecosystems. Species persistence will depend on geographic range shifts or adaptation in response to warming patterns as novel climates and community assemblages arise. Assisted colonization has been proposed as a method for addressing these challenges. This technique, which consists of transporting species to a new range that is predicted to be favorable for persistence under future climate scenarios, has become the subject of controversy and discussion in the conservation community due to its highly manipulative nature, questions about widespread feasibility, and uncertainty associated with the likelihood of translocated species becoming invasive. We reviewed the discussion and criticism associated with assisted colonization and sought to identify other conservation techniques that also display potential to promote the colonization and adaptation of species in response to climate change. We propose an integrated conservation strategy that includes management for habitat connectivity, conservation genetics, and when necessary, assisted colonization of species that are still unable to shift their ranges even given implementation of the above standard conservation approaches. We argue that this integrated approach will facilitate persistence for a larger proportion of species than is possible by solely using assisted colonization. Furthermore, a multi-faceted approach will likely reduce the uncertainty of conservation outcomes and will become increasingly necessary for conservation of biodiversity in a changing climate.

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1. Introduction

The impacts of climate change on species and ecological systems have already become evident (Parmesan, 2006; Williams et al., 2007). Plant and animal range shifts are consistent with climate change predictions, and phenological events are changing in response to seasonal warming patterns (Parmesan and Yohe, 2003; Root et al., 2003). Similar range shifts have occurred in response to historical changes in climate over geological time scales (Petit et al., 2008), and previous climate change rates during glacial periods have occasionally matched or exceeded the current fluctuations; however, the current and predicted rates of human-induced climate change greatly exceed the vast majority of fluctuations observed in the past 420,000 years (Hoegh-Guldberg et al., 2007; Petit et al., 1999), and they are occurring during an inter-glacial period expected to be relatively stable (NRC, 2002, 2006). These changes pose a challenge to species persistence, occurring on temporal scales that require species to rapidly shift their ranges and/or adapt (McLachlan et al., 2005; Root and Schneider, 2006) as existing environmental conditions are replaced by novel climate regimes (Williams et al., 2007). Additional stressors, such as destruction of habitat, invasive species, diseases, and alteration of disturbance regimes, also pose major threats to biodiversity and may be intensified by a changing climate (Frelich and Reich, 2009; Parmesan and Yohe, 2003).

Conservation strategies that incorporate uncertainty associated with climate change impacts will be necessary to minimize biodiversity loss (Coenen et al., 2008; Lawler et al., 2010; Root and Schneider, 2006). Key components of these "climate change-integrated conservation strategies" (Hannah et al., 2002) include predictive models of species responses to climate change (Hannah et al., 2002; Pearson and Dawson, 2003), an adaptive rather than static approach to management (Lawler et al., 2010), and conservation planning for alternative future climate scenarios (Brooke, 2008). There is also increasing recognition that a dynamic view of community composition may need to be adopted, since differential responses of species to climate change will likely result in novel or "no-analog communities" (Williams and Jackson, 2007).

Assisted colonization – also referred to as assisted migration, assisted translocation, and managed relocation (hereafter, assisted colonization) – is a conservation strategy that has been proposed to mitigate the effects of climate change on biodiversity (Hoegh-Guldberg et al., 2008a; McLachlan et al., 2007). Assisted colonization refers to the physical relocation of a species to a location outside its existing or historical range that is predicted to be favorable for persistence under future climate projections. While much uncertainty exists about assisted colonization, the strategy is thought to be most applicable for species characterized by small populations, restricted dispersal ability and adaptive potential (Ozinga et al., 2009; Petit et al., 2008; Primack and Mao, 1992), and inhabiting low-connectivity landscapes (Trakhtenbrot et al., 2005).

Due to its highly manipulative nature, assisted colonization has been the subject of recent discussion and criticism within the conservation community (Fazey and Fischer, 2009; Ricciardi and Simberloff, 2009; Sax et al., 2009; Schwartz et al., 2009; Seddon et al., 2009; Vitt et al., 2009). Central to this discussion is the risk that a species will become invasive, causing adverse ecological or economic impacts when introduced to a new range. While much research has attempted to identify factors pre-disposing a species to be invasive, traits of invasiveness can remain difficult to predict (Kolar and Lodge, 2001; Ricciardi and Simberloff, 2009). Social and political resistance associated with this ecological uncertainty, as well as economic constraints related to implementation, are expected to complicate decision-making about when and to what extent assisted colonization should be implemented (Hoegh-Guldberg et al., 2008a; Hunter, 2007; McLachlan et al., 2007). Richardson et al. (2009) demonstrate how biologists can begin to incorporate these complex social and economic factors into assisted colonization risk assessment and decision-making. Nonetheless, there remains much controversy and uncertainty about the widespread applicability of assisted colonization as a tool for conserving biodiversity in response to climate change.

Given the uncertainty and criticism surrounding assisted colonization, we sought to identify management practices that have the potential to contribute to an integrated conservation strategy of climate change mitigation and include assisted colonization as one option. In addition to physical movement of species, other traditional conservation actions, such as management for increased habitat connectivity, have been proposed as alternatives for indirectly facilitating natural range shifts (Hunter, 2007; Vitt et al., 2009). We expand upon this idea to examine in detail the conservation strategies that have the potential to mitigate climate change impacts. In the remainder of this paper, we (1) provide a detailed summary of current discussion and criticism of assisted colonization, focusing on factors that influence whether this method is broadly applicable to a wide range of species, (2) examine whether the existing conservation practices of management for habitat connectivity and conservation genetics have the potential to assist the colonization and adaptation of species in response to climate change, and (3) outline an integrated strategy of conservation that has potential to address a larger range of climate change impacts than is possible by focusing solely on assisted colonization.

The primary focus of this paper is on ecological concerns. Although decision-makers should take account of the social, political, and economic contexts of assisted colonization and climate change (Richardson et al., 2009), an in-depth examination of these factors is beyond the scope of this paper.

2. Discussion surrounding assisted colonization

The recent increased attention to assisted colonization within the conservation community results from the perception that moving populations of a species from one region and introducing them outside the species' native or historical range is highly manipulative (Hoegh-Guldberg et al., 2008a,b; McLachlan et al., 2007), and therefore undesirable compared to less intrusive approaches. Nonetheless, the desired outcomes of assisted colonization efforts are aligned with the broader goals of conservation biology, namely extinction prevention and biodiversity preservation (Soule, 1985). Thus, by simultaneously challenging and aligning with different principles of conservation biology, the topic of assisted colonization has sparked widespread discussion among those seeking to conserve species in the face of climate change.

2.1. Benefits and risks of assisted colonization

It is generally accepted that for at least some species and situations, and with significant precautions taken, assisted colonization has the potential to be a beneficial conservation tool (but see Ricciardi and Simberloff, 2009). Currently existing conservation practices may not be sufficient to prevent extinction of some highly-threatened species (Hoegh-Guldberg et al., 2008a,b; Hulme, 2005). Species characterized by small, isolated, and non-mobile or low-dispersing populations, and inhabiting highly fragmented landscapes, are often limited in their genetic adaptive potential and may be unlikely to naturally shift their ranges in response to changing environmental conditions. For example, range shifts of species inhabiting isolated habitat patches in an otherwise

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human-dominated landscape (e.g. agricultural or urban areas; Opdam and Wascher, 2004) may be impeded. Altitudinal range shifts of montane species including alpine plants (Grabbher et al., 1994), butterflies (Parmesan, 1998), and birds, reptiles, and amphibians (Pounds et al., 1999) will eventually be limited by the maximum elevation of the mountains they inhabit. Inaction may result in extinction for species experiencing the above conditions; therefore, they are thought to be prime candidates for assisted colonization (Etterson, 2008; Hoegh-Guldberg et al., 2008a; McLachlan et al., 2007).

Significant risks of assisted colonization may include alteration of species composition and genetic disruption of closely-related species in the recipient community (Etterson, 2008; Hoegh-Guldberg et al., 2008a). Potential mechanisms for these risks include predation, competition, gene flow, and impacts to primary production, decomposition, or other ecosystem functions. For example, hybridization between an invasive species and native species can cause genetic introgression and population decreases of native species (e.g. ducks in New Zealand, Rhymer and Simberloff, 1996; pupfish in Texas, Echelle and Echelle, 1997; and numerous plants in Britain, Abbott, 1992). Introduced species can also disrupt native populations and communities through competitive interactions (e.g. larval frogs, Kupferberg, 1997; reviewed by Sakai et al., 2001).

Although risk criteria have been developed for assisted colonization, providing a necessary first step towards formal risk assessment (Hoegh-Guldberg et al., 2008a), these frameworks lack the detail needed to reflect the complexity of ecological systems and the corresponding socio-economic concerns. It is uncertain whether the existing risk frameworks will be successful in identifying and predicting risks associated with specific assisted colonization efforts. Therefore, risk criteria, including both social and economic concerns, need to be improved (Richardson et al., 2009).

A key component of the risk associated with assisted colonization is predicting whether a species will become invasive, causing significant adverse ecological or economic effects in the introduced range (Davidson and Simkanin, 2008; McLachlan et al., 2007; Mack et al., 2000; Mueller and Hellmann, 2008; Ricciardi and Simberloff, 2009). Candidate species for assisted colonization programs are usually characterized by small populations and low dispersal and population growth rates, traits not commonly associated with invasive species. Climate change will require different species to disperse different distances, and species such as long-distance latitudinal colonizers, may pose a greater threat as invasives due to their dispersal efficiency compared to short distance elevational or latitudinal dispersers (Wilson et al., 2009). For example, when considering climate change impacts alone, the distance of range shifts required for species persistence will range from hundreds of meters for montane species to much greater distances (e.g. 100 to > 1000 km) for species inhabiting flat temperate and tropical regions. Range shifts will for the most part be more readily achieved by mobile animals or wind-dispersed plants than by species with short-range dispersal.

Given the above complexity, it will be difficult to predict the risk of a species' invasiveness, especially since it may not always hold true that small, short-dispersing species are unlikely to become invasive, and that regional or intra-continental translocations are less risky than inter-continental translocations (Ricciardi and Simberloff, 2009). The field of invasion biology has progressed greatly in identification of general traits that can be used to predict invasiveness, such as past history of invasion success (Kolar and Lodge, 2001), propagule pressure (Lockwood et al., 2005), climate matching between native and introduced ranges (Hayes and Barry, 2008), and taxa-specific characteristics, such as seed size, nutrient-use efficiency, and fecundity of plants (Pysek and Richardson, 2007). Assisted colonization programs can draw from this extensive literature to minimize invasion risk of translocated species while still maximizing likelihood of the species establishing successfully. Nonetheless, it will likely remain difficult to predict invasiveness with absolute certainty. Numerous examples exist where negative ecological impacts have arisen from species introductions that have been purposeful (e.g. biological control agents, Louda et al., 1997) and inadvertent (reviewed by Mack et al., 2000; Sakai et al., 2001). For the majority of situations, it does appear that well-designed programs of short-distance translocation are less likely than long-distance translocation to result in biological invasions (Wilson et al., 2009).

2.2. Potential for broad application, social acceptance, and logistic feasibility

The logistic feasibility of assisted colonization for a large number of species across diverse ecosystem types has also been a focus of discussion among conservation biologists. Assuming that some public support exists for assisted colonization, the number of candidate species that require assistance will likely always exceed the availability of funding for such strategies (Hoegh-Guldberg et al., 2008a; Hunter, 2007). Thus, in order to efficiently use limited funding in a manner that maximizes conservation results, it will be necessary to give priority to species that are not likely to persist without assisted colonization. Conflicts over who is financially responsible for these efforts, public resistance to species translocations, and logistic inefficiency of species-transport technology will likely reduce social feasibility and widespread success of assisted colonization (Hunter, 2007). To address this complexity, Richardson et al. (2009) proposed a multi-criteria evaluation strategy and decision-making framework for assisted colonization that includes biological considerations (e.g. likelihood and consequences of target and non-target impacts) and social factors (e.g. feasibility and acceptability of assisted colonization). Construction of models to understand the potential impacts of species translocations will also be necessary (Huang, 2008; McLachlan et al., 2007). Perhaps the most important factor that will determine the feasibility of assisted colonization is the ability of recipient ecosystems in the introduced range to successfully integrate the newly-introduced species (Hoegh-Guldberg et al., 2008a; Williams et al., 2007). Recipient habitats most amenable to assisted colonization are thought to include those within established habitat reserves (Hannah, 2008) and containing species similar to those in the original geographic range of the focal species (Willis et al., 2009). Assisted colonization may be less successful for systems not meeting these conditions. In such cases, preparation for future translocations should still be considered, as should collection and banking of genetic material for future use (e.g. plant seeds; Vitt et al., 2010).

Examples of assisted colonization in practice are few, but in one study of the feasibility of assisted colonization in the United Kingdom, researchers assisted the colonization of two butterfly species to previously unoccupied areas (Willis et al., 2009). This example demonstrates that assisted colonization can be a logistically feasible and cost-effective response to climate change threats, particularly for cases where improving habitat connectivity would be prohibitively difficult or expensive. Nevertheless, until there is improved logistical efficiency and increased understanding of the associated risks and the factors that determine its success, assisted colonization is unlikely to be broadly applicable, widely accepted socially, or logistically feasible for most species. We argue that a wider variety of conservation methods will be necessary to preserve biodiversity in the face of climate change. In the following sections, we discuss management of habitat connectivity and the application of conservation genetics as two strategies that have the potential to aid colonization and adaptation.

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3. Improving habitat connectivity as part of an integrated conservation strategy

Habitat loss and fragmentation perforates the landscape, leaving small and discontinuous patches of habitat, thus limiting species range shifts in response to climate change. Fragmentation results in four landscape-scale effects that function as mechanisms for these limitations: (1) reduction in the amount of habitat, (2) dis-aggregation of habitat into an increasing number of disparate fragments or patches, (3) decrease in the size of fragments, and (4) increased isolation of habitat remnants (Fahrig, 2003; Laurance, 2008). Habitat fragmentation increases the probability of extinction by hindering daily and seasonal movements of species, reducing dispersal rates, and impeding the ability of species to colonize areas predicted to be favorable habitat under future climate scenarios (Coenen et al., 2008; Hunter, 2007; Peters, 1992; Trakhtenbrot et al., 2005). Landscape connectivity refers to the capacity of a landscape to facilitate species movement between fragments. For habitat to be functionally connected in the context of assisted colonization it must allow daily and seasonal movements, dispersal and gene flow, preserve ecological processes, and assist range shifts necessitated by climate change (Noss, 2007). We discuss below how management for increased connectivity, including habitat corridors and improvement of matrix habitat, has potential to contribute to an integrated strategy of assisted colonization by facilitating species' responses to climate change.

3.1. Corridors and improvement of matrix permeability to facilitate range shifts

Corridors, thin strips of habitat that connect habitat patches (Rosenberg et al., 1997; Tischendorf and Fahrig, 2000), have the potential to facilitate range shifts of species in response to climate change by improving landscape connectivity (Coenen et al., 2008). Corridors provide individuals a route for moving between patches and are thought to increase population viability (Beier and Noss, 1998; Haddad et al., 2003; Rosenberg et al., 1997; Tewksbury et al., 2002). Corridor efficacy depends on species' traits that influence their ability to cross unsuitable matrix habitat (i.e. the intervening landscape surrounding patches and corridors of habitat) and on characteristics of the corridor and matrix themselves (Debinski and Holt, 2000; Tischendorf and Fahrig, 2000). This species-specific response is illustrated by studies of songbirds in the boreal forest (Schmiegelow et al., 1997) and predatory mammals in an agricultural landscape (Gehring and Swihart, 2003) that demonstrate differential responses to habitat connectivity based on life history traits. Thus, corridors have different functions for different species, potentially serving as conduits or barriers, and should not be considered equally effective for assisting range shifts of all species (Hess and Fischer, 2001). Nonetheless, there is evidence that corridors improve landscape connectivity and have the potential to facilitate both the short-term movements and long-term range shifts required for species to respond to climate change (Hunter, 2007; Opdam and Wascher, 2004).

In addition to the presence and quality of patches and corridors, landscape connectivity also depends on the quality of matrix habitat (Dauber et al., 2003). The matrix may be inhospitable and difficult to cross (i.e. "impermeable"), resulting in increased extinction probability for species inhabiting a patchy landscape (Fischer et al., 2005; Laurance, 2008), and potentially impeding range shifts in response to climate change. The degree of permeability is determined by habitat quality in the matrix and the species' mobility and migratory behavior (Dauber et al., 2003; Gascon et al., 1999; Ricketts, 2001). For example, a study of the flowering plant *Centaurea jacea* in Germany found that numbers of bee visits to flowers was influenced by the matrix habitat, and that these matrix effects varied by bee body size, mobility, and taxon (Hirsch et al., 2003). Because matrices vary in permeability, the matrix may alter the "effective isolation" of habitat patches, causing patches to be more or less isolated than expected solely based on the distance between fragments (Ricketts, 2001). Thus, improving the quality of matrix habitat can increase connectivity and aid the colonization of new habitat or isolated patches (Fahrig, 2001).

3.2. Increasing landscape connectivity in the context of assisted colonization

We suggest that improvement of matrix habitat, in combination with the maintenance of habitat corridors, increases habitat connectivity and may assist colonization. While corridors have the potential to assist species in shifting their ranges in response to changing climatic conditions, there is some concern that they may also facilitate the spread of invasive species and pathogens that are already present in the landscape (Beier and Noss, 1998; Proches et al., 2005). However, it has been suggested that the traits pre-disposing a species to invasiveness, including high dispersal ability, are unlikely to be exacerbated by corridors, and thus the potential risk of corridors as a conduit for invasive species remains mostly speculative (Levey et al., 2005). Another potential limitation of providing corridors is that the spatial scale of corridors required for some species' range shifts is likely to be prohibitively large. For example, some species may require hundreds to thousands of kilometers of corridors at a regional or continental scale, rendering the needed connectivity improvements intractable. Nevertheless, regional efforts to increase functional habitat connectivity will likely benefit a large number of species. Examples of such efforts include the use of corridors or habitat reserves that provide "stepping stones" for species ranges to naturally track climate change.

Large regional and continental-scale programs of landscape connectivity have already been developed with the goals of providing population connectivity and/or buffering against climate change. Examples include the Yellowstone to Yukon Conservation Initiative in North America (http://www.y2y.net/) and the Jaguar Conservation Initiative in Latin America (Rabinowitz and Zeller, 2010). These programs can provide a blueprint for future efforts to increase connectivity in the context of climate change.

Finally, management of corridor and matrix habitat may prove less useful for some species, making them candidates for assisted colonization. Species with slow natural dispersal rates and long generation times may be unable to track climate change, even given sufficient habitat connectivity. Corridor research typically assumes climatic stability (but see Opdam and Wascher, 2004). It is unclear how successful species will be at using corridors for climate-driven range shifts especially if range shifts are limited by species interactions in the colonized location.

Despite the above limitations and complexities, management for corridors and increased matrix permeability are already widely-applied conservation techniques that have the potential to facilitate the movement of individuals of many species in response to rapid climate change, and to increase the quality and availability of habitat for both target and non-target species. Implicit in these efforts to improve habitat connectivity is the need to slow or halt current habitat fragmentation, especially in regions with small amounts of remaining natural habitat and those with species that require contiguous blocks of habitat. Together these measures show promise for improving connectivity between current species ranges and those predicted to be favorable under climate change projections, thus reducing the need for assisted colonization.

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4. Conservation genetics as part of an integrated conservation strategy

In addition to geographic range shifts, genetic plasticity and in situ adaptation also play important roles in persistence of species facing climate change (Bradshaw and Holzapfel, 2006; Davis and Shaw, 2001; Davis et al., 2005; Parmesan, 2006). Modeling studies highlight the importance of population genetic variation and the rate of adaptation for determining times to extinction and range shifts in response to climate change (Burger and Lynch, 1995; Pease et al., 1989), while numerous field studies provide evidence of a genetic basis for phenology shifts in plant and animal populations (Both and Visser, 2005; Bradshaw and Holzapfel, 2006; Reale et al., 2003; reviewed by Parmesan and Yohe, 2003).

Given the importance of genetic factors for influencing species responses to climate change, we argue that the field of conservation genetics can contribute to an integrated strategy of conservation in the face of climate change. The primary issues of concern in conservation genetics, including loss of genetic diversity, inbreeding depression, and fragmentation of populations (Frankham, 1995), are important factors for determining species responses to climate change (Etterson, 2008). In the remainder of this section, we describe how consideration of genetic issues can assist adaptation and colonization of species in response to climate change. Specifically, we discuss genetic diversity, the role of peripheral versus interior populations, and genetic correlation as a constraint to adaptation.

4.1. Genetic diversity as a source for adaptation

Just as species diversity is thought to play an important role for improving ecosystem productivity and resilience (Loreau et al., 2001), genetic diversity of populations and species has been suggested to improve resilience and recovery of ecosystems experiencing climate extremes (Reusch et al., 2005). Genetic diversity provides the raw material by which adaptation through natural selection occurs. Reduced genetic variation limits the rate of adaptation to novel climatic conditions, thus necessitating range shifts or resulting in extinction (Frankham, 2004). For example, low genetic variability of reef-building corals off the coast of Australia is thought to have reduced the corals' adaptive potential in response to climate change and has therefore increased the probability of extinction (Ayre and Hughes, 2004).

Habitat and population fragmentation and the resulting geographic isolation of populations within a species' range are often underlying causes for reduced genetic variation (Ayre and Hughes, 2004). Therefore, maintenance of existing natural habitats and management for increased habitat connectivity (see Section 3) may provide the best option for promoting genetic diversity within a species. A more hands-on approach of species translocations may be necessary for increasing genetic diversity of extremely small and isolated populations in already degraded habitats (e.g. Westemeier et al., 1998). Nonetheless, management for increased genetic diversity may facilitate adaptation, especially if the future changes in climate occur in a uni-directional or cyclical manner (Lande and Shannon, 1996). Further empirical research is needed to clarify exactly how large populations need to be to have sufficient genetic variation to substantially lowers the risk of extinction from climate change. Genetic diversity has long been recognized as a primary component of biological diversity (McNeely et al., 1990), and empirical research suggests the need to manage for genetic diversity, irrespective of the potential impacts of climate change (Reed and Frankham, 2003).

4.2. Peripheral, core, leading edge, and trailing edge sub-populations

Understanding the genetics of populations at the periphery of a species' range is important for determining whether a species will adapt or shift its range in response to changing climatic conditions (Bridle and Vines, 2007; Thomas et al., 2004). Sub-populations at both the periphery and center of species' ranges differentiate and adapt to local conditions, resulting in clinal genetic variation. All sub-populations throughout a range will therefore be subject to selection under novel climate conditions (Davis and Shaw, 2001; Etterson, 2004a, 2008; Harte et al., 2004). Peripheral or leading edge (i.e. high-latitude or altitude) populations are often the focus of attention for conservation and assisted colonization. Yet, peripheral populations may not always display the potential needed to adapt to a changing climate (Hoffman et al., 2003; Pellini et al., 2009), and rear edge (i.e. low-latitude or altitude) and core populations also contribute to increasing genetic diversity and long-term persistence of a species (Hampe and Petit, 2005).

A mechanism for the interaction between core and peripheral populations that illustrates their inseparable nature is gene flow, which can either result in genetic isolation of peripheral populations if it occurs at low levels (Ayre and Hughes, 2004) or "swamping" of local adaptive potential if it occurs at excessive levels (Garcia-Ramos and Kirkpatrick, 1997; Lenormand, 2002). For species that are unable to shift their ranges fast enough to track climate change and those whose sub-populations experience sub-optimal gene flow, assisted gene flow efforts may be beneficial. As illustrated by the above tradeoff, species persistence in these cases will benefit from increased understanding of the optimal levels of gene flow that maintain genetic variation and facilitate adaptation without swamping local adaptations (Alleaume-Benharira et al., 2006). Examples of managed gene flow in practice are found in the conservation genetics literature (Westemeier et al., 1998) and can provide direction for such efforts. For example, adaptation of high-latitude or high-elevation populations receiving little gene flow, such as those occurring in isolated habitat reserves (e.g. grassland species inhabiting the highly fragmented tallgrass prairies of the Midwestern US and alpine species inhabiting mountaintop "islands"), may be assisted by importing individuals from low-latitude or low-elevation parts of the species' range. The benefits and risks of assisted gene flow are likely to vary between populations and species. Assisted gene flow, just like assisted colonization, will be a relatively risky method that may be most useful as a last resort for species that are highly threatened by lack of genetic diversity.

To successfully mitigate the impacts of climate change, an integrated climate change conservation strategy will need to shift from focusing solely on peripheral or high-latitude/altitude populations to a more holistic view of the entire range, incorporating managed gene flow among sub-populations in some cases. As with management for genetic diversity, prevention of further habitat degradation and increased habitat connectivity will aid in maintaining the links between sub-populations of a species.

4.3. Genetic correlation as a potential constraint to adaptation

Even given abundant genetic variation, genetic correlations can impede adaptation of species experiencing novel conditions (Etterson, 2004a,b; Etterson and Shaw, 2001; Hellman and Pineda-Krch, 2007; Schluter, 1996). Correlation among genes arises as a result of either linkage disequilibrium, or pleiotropy, the influence of a single gene on two or more phenotypic traits. While correlations among traits that coincide with the joint direction of selection may facilitate a rapid response of multiple traits to selection pressures imposed by environmental change, antagonistic correlation among traits may prevent simultaneous adaptation in more than one trait, making local extirpation more likely and forcing range shifts or extinction (Etterson, 2004a; Etterson and Shaw, 2001; Hellman and Pineda-Krch, 2007).

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Several field examples highlight how genetic correlation can influence adaptive responses to environmental change. Antagonistic correlation between fitness-related traits is predicted to hinder the ability of a leguminous plant to adapt in response to the increased aridity expected to occur with climate change in the midwestern United States (Etterson, 2004b; Etterson and Shaw, 2001). In Europe, while positive genetic correlation is expected to favor adaptation of multiple life history traits in the pied flycatcher (*Ficedula hypoleuca*; Both and Visser, 2005), antagonistic correlation in the same traits may constrain adaptation in the collared flycatcher (*Ficedula albicollis*; Sheldon et al., 2003). Furthermore, the novel selective pressures associated with climate change have the potential to alter the nature of existing genetic correlations (Both and Visser, 2005).

Given evidence that genetic correlation can constrain adaptive responses to climate change, it is important to identify both positive and antagonistic correlations in species that are the focus of management and to understand how these correlations relate to adaptation in response to climate change. In practice, this process includes the collection of empirical genetic data on climate-related traits and interpreting these correlations within the context of climate change as an adaptive landscape (Hellman and Pineda-Krch, 2007). Identifying the degree to which genetic correlation impedes adaptive potential can inform decisions about whether colonization of a species should be physically assisted, or if broader management techniques, such as improvement of habitat connectivity, will be sufficient for species persistence.

To summarize, genetic diversity, the contribution of peripheral and core populations to population genetics, and correlations among climate-related traits all influence adaptation of species experiencing environmental stress. We argue that consideration and application of these factors should be a component of an integrated conservation strategy in response to climate change.

5. Discussion

We propose an integrated strategy of conservation in the face of climate change that includes management for habitat connectivity, understanding and using conservation genetics to aid adaptation, and when necessary, assisted colonization of species that still cannot shift their ranges and appear likely to go extinct. Implementing this integrated approach will be more effective than focusing solely on assisted colonization for conserving biodiversity in the face of current and future climate change (Vitt et al., 2009). Much of the assisted colonization discussion relates to widespread applicability of the method to the many current and future candidate species for translocation. In practice, assisted colonization has shown some promise as a conservation tool (Willis et al., 2009). However, due to the relatively undeveloped state of assisted colonization theory and the lack of empirical evidence for or against the success of assisted colonization, caution should be taken towards its widespread use as a conservation tool. This conclusion aligns with ethical and value-based assessments of assisted colonization that call for its use on a species-by-species basis and in only a small proportion of cases (Sandler, 2009).

We are not arguing that assisted colonization should be abandoned as a method for addressing climate change impacts, and we recognize that the strategy may prove useful for some species and cases (see Etterson, 2004b; Hoegh-Guldberg et al., 2008a). Indeed, the recent proliferation of assisted colonization literature, including development of decision-making frameworks and assessment of potential risks, is crucial for determining when and to what extent this technique is useful as biologists move to conserve species in a changing climate. Admittedly, there are many cases where the uncertainties associated with assisted colonization preclude its viability, where habitat fragmentation and matrix impermeability are intensifying (e.g. many undeveloped and developing countries), and where the implementation of corridors is prohibitively difficult or expensive. In these cases, certain stop-gap measures may still be available to “buy time” for species conservation. For example, coordinated and systematic collection and storage of plant seeds has been proposed as a means to preserve genetic material for future use in conservation programs, including assisted colonization (Vitt et al., 2010).

Further developments of assisted colonization theory and best practice that will likely increase its viability include consideration of both positive and negative inter-specific interactions in an introduced population’s new range, the likelihood of persistence of the shifted species and the species already present, and the likelihood of natural (i.e. non-assisted) colonization of the area by new species as climate conditions change. Another opportunity for assisted colonization lies in the field of restoration ecology. Instead of seeking to exclusively restore historical assemblages of species that may not necessarily be viable under future climate conditions (Seastedt et al., 2008), restoration ecologists can attempt to anticipate and establish species assemblages that are likely to occur under forecast changes (Harris et al., 2006). While much development of this newly proposed aspect of restoration is still necessary, including increased provision of specific actionable recommendations (Heller and Zavaleta, 2009), the approach provides a potential opportunity for assisting range shifts in landscapes with few other conservation options. Despite the above considerations, the holistic strategy of conservation that we propose here has potential for mitigating climate change impacts for a larger number of species than allowed by solely using assisted colonization. Some aspects of the proposed integrated strategy are already implemented for other conservation objectives (e.g. management for regional habitat connectivity; see examples in Section 3.2). Instead of requiring development of completely new conservation frameworks, it is therefore possible for the proposed strategy to “piggy-back” upon existing regional conservation efforts, resulting in more cost-effective conservation.

This integrated strategy of assisted colonization is analogous to integrated pest management, which combines a variety of management techniques rather than relying on one risky or environmentally destructive method, such as pesticide application, to improve effectiveness of controlling insect pests (Dent, 1995; Kogan, 1998). In the same way, combining habitat management, conservation genetics, and when necessary, assisted colonization in an integrated strategy is likely to be less risky than relying solely on species translocations. Thus, we advocate coordinating assisted colonization, habitat management, and conservation genetics into an integrated strategy of conservation in response to the effects of climate change.

Further research is needed to maximize the efficacy of such an integrated conservation strategy. The field of conservation genetics will benefit from investigation of how genetic correlations shape adaptation of traits experiencing climate stress. Successful implementation of assisted colonization requires further development of multi-criteria evaluation strategies that consider both biological and socio-economic factors in decision-making (Richardson et al., 2009). It will also be necessary to conduct formal assessment of the magnitude of landscape management (i.e. corridor length and amount of increased matrix permeability) needed for species persistence and/or range shifts, since the efficacy and needed scale of habitat connectivity will vary by species and landscape.

Central to the success of the proposed strategy is the development and improvement of ecological risk assessment methods for assisted colonization (e.g. Hoegh-Guldberg et al., 2008a; Richardson et al., 2009). Risk assessments should thoroughly assess the potential adverse effects of moving a species to a new

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location and will benefit from improvement of models that predict what makes a species invasive. Since likelihood of invasion appears to depend at least partially on the conditions specific to the time and place of introduction (i.e. stochasticity; Ricciardi and Simberloff, 2009), these risk assessments and models need to be improved with regard to case-by-case sensitivity. Ideally, a sequence of laboratory and field tests should be conducted to identify potential non-target effects of the candidate species prior to release. These tests could follow a framework similar to that required by some national governments for biological control agents or genetically modified crops, with testing proceeding from laboratory tests (e.g. greenhouse tests for plants) to confined field tests to field release with close monitoring. Using such adaptive management techniques, the potential negative impacts of a candidate species on non-target species or the environment can be identified prior to release, and the risk of undesired effects can be minimized.

Climate change impacts extend across political boundaries and may be especially acute for undeveloped and developing countries that lack organized government systems for regulation of species translocation and risk assessment. For this reason, capacity building and coordination among governments and among non-government organizations (NGO's) working internationally will be necessary to ensure that all countries are able to benefit from integrated conservation strategies like the one we propose, and from advances in assisted colonization technology and risk assessment. In both developing and developed countries, funding limitations will often prevent simultaneous implementation of all aspects of the proposed integrated strategy. As recommended by Vitt et al. (2009), priority in these cases can be given to adapting current conservation approaches, such as management for habitat connectivity, before proceeding to more untested and risky methods, such as assisted gene flow and assisted colonization.

6. Conclusions

Given the unprecedented rate of climate change and the degree to which plant and animal range shift or adaptation is required for species to persist, conservation biologists and ecologists seeking to conserve biodiversity face an immense challenge. A key component of this challenge is the need for decision-making that minimizes risk under future climate scenarios. The success of assisted colonization is unclear, due to the difficulty of predicting responses of individuals in colonizing and recipient populations, population genetics, and community interactions. Therefore, the use of assisted colonization by itself is likely to be characterized by highly uncertain outcomes. Nevertheless, recognizing that assisted colonization is a promising strategy for some species and contexts, we argue for an integrated strategy of conservation in the face of climate change that includes careful use of assisted colonization in addition to traditional conservation strategies such as improvement of habitat connectivity and application of conservation genetics practices. This integrated approach will likely reduce risk of detrimental consequences and result in more predictable and effective conservation.

Although risks exist during the implementation of any management technique, we strongly feel that this integrated strategy of conservation will help shift focus towards understanding in what cases and in what combination conservation approaches for assisted colonization should be implemented. Biodiversity loss is inevitable but may be lessened by mitigating the impacts of climate change. We argue that the measures outlined herein provide a viable means to reduce these losses, and that such integrative strategies will become increasingly necessary for the conservation of biodiversity in a changing environment.

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