Biological Conservation 157 (2013) 172–177

Contents lists available at SciVerse ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Perspective

Using assisted colonisation to conserve biodiversity and restore ecosystem function under climate change

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ARTICLE INFO

Article history:
Received 15 April 2012
Received in revised form 6 August 2012
Accepted 24 August 2012

Keywords:
Ecological replacement
Managed relocation
Climate change adaptation
Ecosystem management
Restoration
Translocation

ABSTRACT

Assisted colonisation has received considerable attention recently, and the risks and benefits of introducing taxa to sites beyond their historical range have been vigorously debated. The debate has primarily focused on using assisted colonization to enhance the persistence of taxa that would otherwise be stranded in unsuitable habitat as a consequence of anthropogenic climate change and habitat fragmentation. However, a complementary motivation for assisted colonisation could be to relocate taxa to restore declining ecosystem processes that support biodiversity in recipient sites. We compare the benefits and risks of species introductions motivated by either goal, which we respectively term 'push' versus 'pull' strategies for introductions to preserve single species or for restoration of ecological processes. We highlight that, by focusing on push and neglecting pull options, ecologists have greatly under-estimated potential benefits and risks that may result from assisted colonisation. Assisted colonisation may receive higher priority in climate change adaptation strategies if relocated taxa perform valuable ecological functions (pull) rather than have little collateral benefit (push). Potential roles include enhancing resistance to invasion by undesired species, supporting co-dependent species, performing keystone functions, providing temporally critical resources, replacing taxa of low ecological redundancy, and avoiding time lags in the provisioning of desired functions.

Contents

1. Introduction

Assisted colonisation (also known as assisted migration or managed relocation) is one option that has been proposed to conserve biodiversity under anticipated climate change (McLachlan et al.,

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http://dx.doi.org/10.1016/j.biocon.2012.08.034

2007; Hoegh-Guldberg et al., 2008; Richardson et al., 2009). Assisted colonisation involves the planned introduction of a population or species beyond its current distribution where the climate is expected to become unsuitable into new localities where the taxon is expected to persist under future climatic conditions (Seddon, 2010). Management under climate change will require steps after colonisation (*sensu* managed relocation, Richardson et al., 2009), but introduction is the first step in helping species relocate as the climate changes.

The concept of assisted colonisation has generated intense debate over the relative benefits and risks of moving taxa beyond their historical range (Hoegh-Guldberg et al., 2008; Mueller and Hellmann, 2008; Ricciardi and Simberloff, 2009; Richardson et al., 2009; Vitt et al., 2009, 2010; Hewitt et al., 2011). The potential benefit is the retention of biodiversity that is threatened by climate change, but introduced populations could cause unanticipated ecological or economic damage (Mueller and Hellmann, 2008; Ricciardi and Simberloff, 2009; Sandler, 2010). To date, the assisted colonisation literature has focused primarily on a single rationale: to enhance the survival prospects of the taxon being moved, or small numbers of inter-dependent taxa, such as butterflies and host plants (Hellmann, 2002). However, here we suggest that assisted colonisation could also be undertaken to achieve a very different conservation goal – to maintain declining ecosystem processes. Adopting the terminology of Seddon (2010), this type of assisted colonisation would be classified as ecological replacement – the release of 'a species outside its historic range in order to fill an ecological niche left vacant by the extirpation of a native species', and is akin to the 'anticipatory restoration' activities proposed by Manning et al. (2009). This goal may become prominent in future climate change adaptation programs as the impacts of climate change become more severe, but the juxtaposition of goals has not been considered in the assisted colonisation literature and demands benefit–risk evaluation.

In addition to direct physiological effects on organisms and associated changes to fitness, climate change will affect many species through indirect impacts on ecosystem structure, functions and processes (Diaz and Cabido, 1997; Petchey et al., 1999; Dale et al., 2001; Gilman et al., 2010). Changes in the abundance of dominant, foundation and keystone species will alter ecosystem processes that will, in turn, affect many associated organisms. Declines in dominant forest trees, for example, lead to changes in micro-climatic conditions, nutrient and water cycles, habitat structure, and disturbances such as fire regimes (Cochrane, 2003; Foley et al., 2007; Van Mantgem et al., 2009).

Reviews of climate change adaptation strategies include a wide range of approaches for maintaining ecological processes such as nutrient cycling, hydrology, species interactions, habitat provision, dispersal and disturbances (Millar et al., 2007; Bennett et al., 2009; Mawdsley et al., 2009; Steffen et al., 2009; Lindenmayer et al., 2010). Additionally, landscape and restoration ecologists have proposed that vegetation be established and restored across local and regional scales to enhance ecological processes and functions that may in turn maintain biodiversity (Hobbs and Harris, 2001; Millar et al., 2007; Manning et al., 2009; Seddon, 2010). Proposals to use assisted colonisation for ecosystem benefit are not widely encompassed by the existing literature and its decision frameworks (Sandler, 2010). We suggest that acknowledgement of a broader array of motivations for assisted colonisation will enhance our ability to contribute to the development of national and regional climate change adaptation strategies.

Therefore, we contrast two rationales for introductions of species outside their historical ranges: (1) direct conservation of one or more species diminished in their native range and (2) restoration or maintenance of a declining ecosystem function, and consider how these rationales could be combined. We restrict our attention to introductions for conservation purposes, but our framework could also encompass a wider range of goals, including utilitarian services such as timber production (McKenney et al., 2009).

2. Push versus pull assisted colonisation

For simplicity, we characterize these two contrasting rationales for assisted colonisation as 'push' and 'pull' strategies (Fig. 1). Push strategies that focus on conserving individual taxa or small groups of inter-dependent taxa are already widely discussed in the assisted colonisation literature. In these cases, issues such as rarity and threat guide the selection of target taxa, and populations are 'pushed' into one or more localities where it is expected that they will maintain viable populations for an extended period under climate change (e.g. Willis et al., 2009). Risk assessments are required to ensure that informed decisions are made to relocate taxa such that there is minimal impact on other species where they are introduced (Burbidge et al., 2011).

In contrast, assisted colonisation that is also motivated by a desire to restore ecosystem function should expect to have an appreciable impact at the recipient site. In such 'pull' scenarios, desired ecosystem functions and potential recipient sites would first be identified, and appropriate candidate species would then be 'pulled' into recipient sites to maintain or restore the specified function (Fig. 1). Relocation of taxa may be undertaken to deliver ecological functions that are directly affected by climate change, or where climate change exacerbates other causes of decline, such as fragmentation or salinisation. For example, consider a tree species that is declining (directly or indirectly) due to climate change and provides nest holes to a bird community. Pull assisted colonisation would ask which species of tree might persist regionally in the future to provide nesting habitat for birds, and could include the option to introduce multiple species, if a range of species are capable of performing the desired function. Indeed, bet-hedging approaches that relocate multiple taxa and genotypes may be prudent given uncertainties about future species performances under climate change (Beale et al., 2008). Relocation of multiple taxa will also be important for co-dependent species, such as insects and their host plants or species and their parasites.

In push + pull assisted colonisation, selection of species would be guided by the function to be performed in the recipient site, as well as the conservation status of the relocated species. Opportunities for push + pull assisted colonisation may be limited where rare taxa have restricted distributions due to biological constraints because they are unlikely to have the capacity to influence ecosystem processes strongly in recipient sites. However, there may be greater opportunities to maximize conservation outcomes using 'push + pull' assisted colonisation in landscapes where historical stochasticity has been a major driver of rarity (Yates et al., 2007).

While further research is required to develop decision support tools to guide pull assisted colonisation strategies, this approach may receive high priority where relocated taxa: (1) perform 'keystone' functions that generate a cascade of ecological services (e.g. ecosystem engineers); (2) provide ecosystem services that are unique or have low levels of ecological redundancy; (3) provide functions that take long periods to become effective, e.g. hollow-bearing trees; (4) enhance resistance to invasion by undesired species; (5) fill temporal resource gaps driven by climate-driven phenological shifts; and (6) maintain valued species that are highly dependent on other species. Descriptions and examples of these functions are provided in Table 1.

3. Contrasting risk–benefit profiles

Assisted colonisation for goals of conservation introduction or ecological replacement both share a common mechanism of

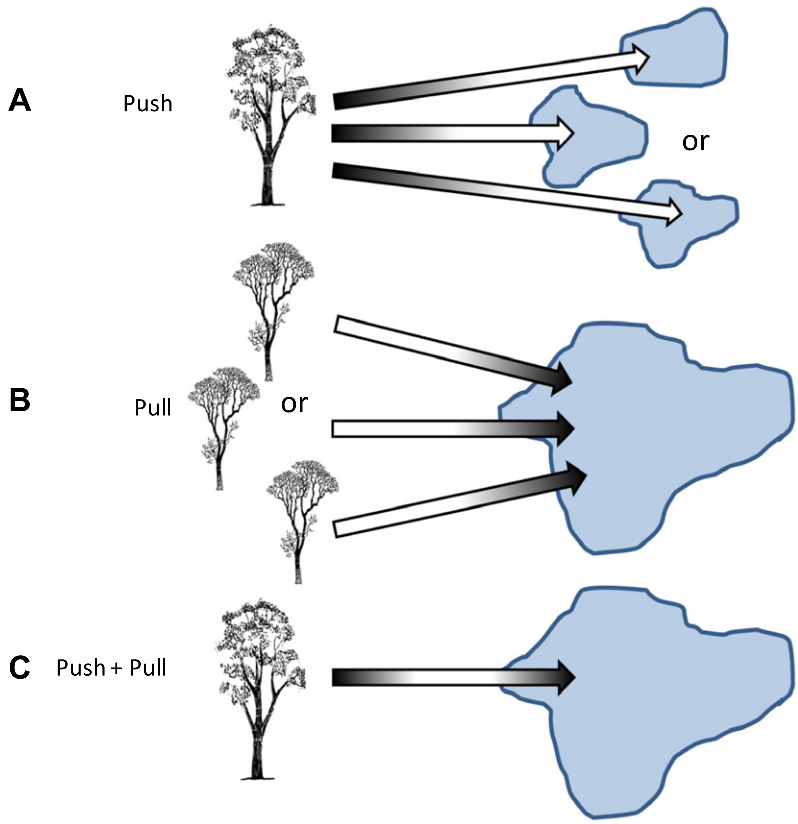

Fig. 1. Contrasting types of assisted colonisation. In (a) specific species assisted colonisation – a specified taxon threatened with decline under climate change is moved ('pushed') into one or more optional recipient sites where future persistence is predicted to be high. In (b) ecological replacement assisted colonization – one or more taxa are relocated ('pulled') to a specified recipient site to maintain or restore an ecosystem process and/or function in the recipient site that is declining due to climate change. In (c) assisted colonisation is used to 'push' a threatened taxon into a recipient site, but in so doing restores an ecosystem process and/or function that is declining due to climate change, thus achieving outcomes from options (a and b). Dark shading in arrows indicates whether the introduction is motivated by concerns about source populations (a; push), recipient sites (b; pull), or both (c; push + pull).

relocating taxa (or genotypes) beyond their historical range in order to conserve biodiversity under climate change. Nevertheless, we recognise that the two approaches have very different risk and benefit profiles.

Assisted colonisation for species conservation benefits the relocated taxon only, and minimal (if any) collateral benefits are envisaged for other taxa or processes in recipient sites. Indeed, the current assisted colonisation literature emphasizes the need to avoid relocations that may alter the composition, structure or function of recipient sites in a major way (Mueller and Hellmann, 2008; Ricciardi and Simberloff, 2009). Nevertheless, push assisted colonisation may present risks to recipient sites and ecosystems (and potentially to the broader environment and economy) if relocated taxa have negative impacts on other species and those impacts spread to additional locations (Ricciardi and Simberloff, 2009; Richardson et al., 2009). Thus, the risk–benefit profile for push assisted colonisation is one of localized benefit and potentially wide risks (akin to private benefits versus public risks in human enterprises), depending on the taxa under consideration (Hoegh-Guldberg et al., 2008; Ricciardi and Simberloff, 2009; Richardson et al., 2009; Burbidge et al., 2011).

By focusing on the conservation of threatened species as motivation for assisted colonization, ecologists may greatly under-estimate potential benefits that may arise from such introductions in providing ecosystem services. In contrast to push assisted colonisation, taxa also introduced as ecological replacements for a degraded component of an ecosystem could have multiple beneficiaries – including all taxa that benefit from the environmental functions or processes that relocated species provide. Thus, the potential biodiversity benefits provided by push + pull assisted colonisation are far greater if their impact flows broadly across an ecosystem. Because maintenance of ecosystem processes is a key component of climate change adaptation strategies (Millar et al., 2007; Mawdsley et al., 2009; Steffen et al., 2009; Lindenmayer et al., 2010), assisted colonisations that maintain ecosystem function may be prioritized above those that conserve threatened species, if relocation costs are similar, benefits are greater and risks deemed acceptable. Combined strategies that focus on threatened species conservation and maintenance of ecosystem function may also rate highly under constrained management budgets, given potential benefits to both the relocated species and recipient ecosystems.

However, assisted colonisation intended to have a significant collateral impact also presents far greater risks, since relocated taxa are intended to have a substantial, as opposed to negligible, impact on specified ecosystem processes in recipient sites. For example, a relocated species could be structurally dominant or a keystone species, which would be unlikely to be relocated under current decision support frameworks for assisted colonisation (Hoegh-Guldberg et al., 2008; Richardson et al., 2009). Candidate taxa for assisted colonisation could now include taxa with high impact but low dispersal capacity, to minimize the potential for relocated taxa to spread to unwanted areas. In some cases, dispersal risks may be moderated by landscape context (McIntyre, 2011). For example, assisted colonisations designed to have an appreciable collateral impact might receive greater attention in degraded remnants in fragmented landscapes, where risks to existing taxa are lower and where such introductions would build upon existing interventions designed to enhance regional biodiversity (Fischer et al., 2006; Lindenmayer et al., 2010).

Table 1
Example functions potentially vulnerable to climate change that could be enhanced by assisted colonisation.

Functional issue for ecosystem	Description	Example(s)
Loss of keystone species	Keystone species interact strongly with other functions and generate a cascade of ecological services	Many forests and woodlands in Australia are dominated by long-lived *Eucalyptus* trees. These dominant, 'foundation' species control functions and processes including stand structure and micro-climate, water and nutrient cycling and fire behavior (Manning et al., 2006). Species replace each other across climatic gradients so readily lend themselves to assisted colonisation in anticipation of climate change Five species of prairie dogs *Cynomys* spp. have a strong influence on the functioning of grassland ecosystems in North America but have declined by 98% in the last 200 years (Hoogland, 2006). The existence of climate-related relictual populations (Mead et al., 2010) suggests natural dispersal has been too slow to keep up with historical climate change. There may be potential to assist movement of different prairie dog species to retain ecosystem services as future climates change
Loss of a unique ecosystem service	Provision of ecosystem services with low ecological redundancy that support the persistence of other species	Larvae of the endangered European longhorn beetle affect a profound change on the microstructure of the bark of the wild oak, enabling numerous other endangered insects to flourish in the beetle's presence (Buse et al., 2008). Assisted colonisation of the European Longhorn beetle could generate collateral benefits to invertebrate fauna at the recipient site Sheep grazing is an essential to conservation of the Chalkhill Blue butterfly *Polyommatus coridon* in the UK (Brereton et al., 2008). If conditions become too warm for existing races of sheep on the downs, there are several others that could be brought in as replacements (Gibbons and Lindenmayer, 2002)
Loss of a function that has a time lag to effectiveness	Functions that take decades or longer to establish and become effective	Tree hollows provide nesting habitat and retreat sites in almost all forest types, with approximately 10–31% of reptiles, amphibians, birds and mammals utilizing tree hollows in Australian ecosystems (Gibbons and Lindenmayer, 2002). Declining tree species could be replaced with warmer- or drier-adapted species
Biological control agent becoming increasingly ineffective in a changing climate	Species whose introduction to a recipient ecosystem could prevent or reduce the invasion of undesired species	Lesser St John's Wort beetles are effective biological control agents in cold climates but need to be replaced with Great St John's Wort beetles for effective St John's wort (*Hypericum perforatum*) control in Mediterranean climates (Schöpsa et al., 1996)
Increasing temporally mismatch of resources	Functions that fill temporal resource gaps driven by climate-driven phenological shifts	Plant species flowering at various times of the year provide resources for pollinators. *Banksia baxterii* is one of the few plants that flower in autumn in south western Australia and is major nectar resource for vertebrate pollinators, particularly honey possums, a distinct lineage of marsupials. It is vulnerable to increasing temperature (Yates et al., 2009) and may need to be replaced by other autumn flowering plants
Maintenance of co-dependence among species	Functions provided by one species that both maintain and depend on functions provided by other species	Terrestrial orchids have strong mutualistic dependence on pollinators that tends to be site specific (unlike the mutualism with fungi; Waterman et al., 2011) so that neither orchid nor pollinator could be moved without the other. Similarly many pollinators have a host of other specializations that would also need to be considered in assisted colonisation (Pemberton, 2010)

Existing decision support tools for assisted colonisation may be relatively easily expanded to accommodate a goal of ecosystem restoration. For example, the decision making framework developed by Richardson et al. (2009) requires the addition of diminished ecosystem function as a potential motivation for undertaking assisted colonisation, plus the expansion of the concept of 'focal impact' to include collateral benefits (not just collateral impacts). Populating these frameworks for push + pull assisted colonization will require a revised approach to the evaluation of potential impacts. For example, impacts that are generally considered as risks in assisted colonisation motivated to benefit a threatened taxon would be considered as potential benefits in movement of species to achieve ecosystem function.

In any risk evaluation, the relevant comparison is not of assisted colonisation against the *status quo*, but assisted colonisation against anticipated losses under continuing climate change (Schwartz et al., 2009). The uncertainties inherent in assessment of the scale and direction of climate change itself, and the vulnerability of species to that change, are key factors in assessment of push assisted colonisation adaptation strategies. For assisted colonisation designed to have push + pull impacts, additional uncertainties occur in relation to the potential for selected taxa to establish self-perpetuating populations that contribute to ecological function at a site within an appropriate time frame.

If assessments reveal that the benefits of undertaking either assisted colonisation option outweigh the risks, then the question becomes one of timing of implementation and monitoring of impacts. McDonald-Madden et al. (2011) present a quantitative framework to guide when to move species in push assisted colonisation activities, based on population dynamics in the source habitat, predicted dynamics in recipient sites, the cost of relocation and species recovery potential. Additional factors need to be considered to accommodate push + pull assisted colonisation, including the predicted dynamics of declining ecosystem processes, the thresholds at which major change may occur, and the need to balance the delivery of the ecological function with the climate suitability for the selected species. Development of success criteria for evaluation of push assisted colonisation is relatively straightforward (Burbidge et al., 2011). For push + pull assisted colonisation there is the added challenge of monitoring for the continued delivery of an ecological function with the potential complexities of interdependences among biotic and abiotic components of the ecosystem.

Further consideration needs to be given to the economic costs and benefits associated with all forms of assisted colonisation. This paper has emphasized the ecological value of species in sustaining ecosystem services and supporting species interactions. These services have economic value as well. For example, species that pro-

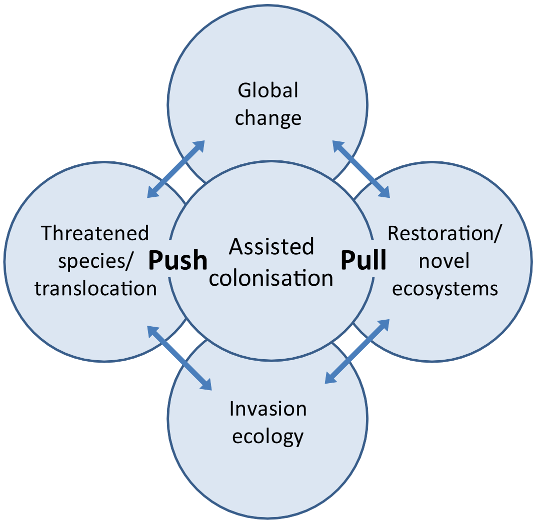

Fig. 2. Conceptual model illustrating how integration of push and pull options for assisted colonisation under global climate change integrates concepts from complementary disciplines across multiple levels of organization. In this context, assisted colonisation draws more upon the restoration and ecosystem function literature than it has previously.

mote pollination services might increase agricultural value. To our knowledge, no one has investigated economic outcomes from assisted colonization, but it may be possible for particular species and ecosystems.

This conceptual integration of push + pull motivations in assisted colonisation activities may help to reinforce synergies between the contrasting theoretical frameworks that underlie the two approaches (Fig. 2). Push assisted colonisation draws heavily on single-species population biology, invasion ecology, and an extensive literature on management of threatened species and small and declining populations (Simberloff, 1998; Parker et al., 1999; Purvis et al., 2000). By contrast, push + pull assisted colonisation has stronger theoretical foundations in landscape and restoration ecology at ecosystem scales (Noss, 1990; Fischer et al., 2006; Hobbs and Cramer, 2008; Lindenmayer et al., 2008). From an invasion ecology perspective, introduction of a high impact taxon is usually seen as inherently undesirable, whereas introduction of a functional dominant is commonly viewed as a critical component of a successful restoration strategy. Clearly, a wide range of intellectual traditions will need to be drawn upon to manage assisted colonisation effectively and safely within climate change adaptation strategies for biodiversity conservation.

4. Conclusions

We emphasise that we are not promoting the adoption of any particular assisted colonisation strategy, and we advocate that all assisted colonisation activities must be subject to comprehensive risk assessments and ongoing monitoring and management. However, we encourage ecologists and managers to consider how assisted colonisation could be adopted to achieve broader goals than the persistence of a single, or just a few, threatened species.

Acknowledgements

The perspective presented in this paper was developed at a workshop on assisted colonisation supported by the Terrestrial Biodiversity Adaptation Research Network of the National Climate Change Adaptation Research Facility (NCCARF) in Australia.

References

Beale, C.M., Lennon, J.J., Gimona, A., 2008. Opening the climate envelope reveals no macroscale associations with climate in European birds. PNAS 105, 14908–14912.
Bennett, A.F., Haslem, A., Cheal, D.C., Clarke, M.F., Jones, R.N., Koehn, J.D., Lake, P.S., Lumsden, L.F., Lunt, I.D., Mackey, B.G., MacNally, R., Menkhorst, P.W., New, T.R., Newell, G.R., O'Hara, T., Quinn, G.P., Radford, J.Q., Robinson, D., Watson, J.E.M., Yen, A.L., 2009. Ecological processes: a key element in strategies for nature conservation. Ecol. Manage. Restor. 10, 192–199.
Brereton, T.M., Warren, M.S., Roy, D.B., Stewart, K., 2008. The changing status of the Chalkhill Blue butterfly *Polyommatus coridon* in the UK: the impacts of conservation policies and environmental factors. J. Insect. Conserv. 12, 629–638.
Burbidge, A.A., Byrne, M., Coates, D., Garnett, S.T., Harris, S., Hayward, M.W., Martin, T.G., McDonald-Madden, E., Mitchell, N.J., Nally, S., Setterfield, S., 2011. Is Australia ready for assisted colonisation? Policy changes required to facilitate translocations under climate change. Pac. Conserv. Biol. 17, 259–269.
Buse, J., Ranius, T., Assmann, T., 2008. An endangered longhorn beetle associated with old oaks and its possible role as an ecosystem engineer. Conserv. Biol. 22, 329–337.
Cochrane, M.A., 2003. Fire science for rainforests. Nature 421, 913–919.
Dale, V.H., Joyce, L.A., McNulty, S., Neilson, R.P., Ayres, M.P., Flannigan, M.D., Hanson, P.J., Irland, L.C., Lugo, A.E., Peterson, C.J., Simberloff, D., Swanson, F.J., Stocks, B.J., Wotton, B.M., 2001. Climate change and forest disturbances. BioScience 51, 723–734.
Diaz, S., Cabido, M., 1997. Plant functional types and ecosystem function in relation to global change. J. Veget. Sci. 8, 463–474.
FAO, 2007. The State of the World's Animal Genetic Resources for Food and Agriculture. Rischkowsky, B., Pilling, D. (Eds.), FAO, Rome.
Fischer, J., Lindenmayer, D.B., Manning, A.D., 2006. Biodiversity, ecosystem function, and resilience. Ten guiding principles for commodity production landscapes. Front. Ecol. Environ. 4, 80–86.
Foley, J.A., Asner, G.P., Costa, M.H., Coe, M.T., DeFries, R., Gibbs, H.K., Howard, E.A., Olson, S., Patz, J., Ramankutty, N., Snyder, P., 2007. Amazonia revealed: forest degradation and loss of ecosystem goods and services in the Amazon Basin. Front. Ecol. Environ. 5, 25–32.
Gibbons, P., Lindenmayer, D.B., 2002. Tree Hollows and Wildlife Conservation in Australia. CSIRO Publishing, Melbourne.
Gilman, S.E., Urban, M.C., Tewksbury, J., Gilchrist, G.W., Holt, R.D., 2010. A framework for community interactions under climate change. TREE 25, 325–331.
Hellmann, J.J., 2002. The effect of an environmental change on mobile butterfly larvae and the nutritional quality of their hosts. J. Anim. Ecol. 71, 925–936.
Hewitt, N., Klenk, N., Smith, A.L., Bazely, D.R., Yan, N., Wood, S., MacLellan, J.I., Lipsig-Mumme, C., Henriques, I., 2011. Taking stock of the assisted migration debate. Biol. Conserv. 144, 2560–2572.
Hobbs, R.J., Cramer, V.A., 2008. Restoration ecology: interventionist approaches for restoring and maintaining ecosystem function in the face of rapid environmental change. Ann. Rev. Environ. Res. 33, 39–61.
Hobbs, R.J., Harris, J.A., 2001. Restoration ecology: repairing the earth's ecosystems in the new millennium. Restor. Ecol. 9, 239–246.
Hoegh-Guldberg, O., Hughes, L., McIntyre, S., Lindenmayer, D.B., Parmesan, C., Possingham, H.P., Thomas, C.D., 2008. Assisted colonisation and rapid climate change. Science 321, 345–346.
Hoogland, J.L., 2006. Conservation of the Black-tailed Prairie Dog: Conservation of North America's Western Grassland. Island Press, Washington.
Lindenmayer, D., Hobbs, R.J., Montague-Drake, R., Alexandra, J., Bennett, A., Burgman, M., Cale, P., Calhoun, A., Cramer, V., Cullen, P., Driscoll, D., Fahrig, L., Fischer, J., Franklin, J., Haila, Y., Hunter, M., Gibbons, P., Lake, S., Luck, G., MacGregor, C., McIntyre, S., MacNally, R., Manning, A., Miller, J., Mooney, H., Noss, R., Possingham, H., Saunders, D., Schmiegelow, F., Scott, M., Simberloff, D., Sisk, T., Tabor, G., Walker, B., Wiens, J., Woinarski, J., Zavaleta, E., 2008. A checklist for ecological management of landscapes for conservation. Ecol. Lett. 11, 78–91.
Lindenmayer, D.B., Steffen, W., Burbidge, A.A., Hughes, L., Kitching, R., Musgrave, W., Stafford Smith, M., Werner, P., 2010. Conservation strategies in response to rapid climate change: Australia as a case study. Biol. Conserv. 143, 1587–1593.
Manning, A.D., Fischer, J., Lindenmayer, D.B., 2006. Scattered trees are keystone structures – implications for conservation. Biol. Conserv. 132, 311–321.
Manning, A.D., Fischer, J., Felton, A., Newell, B., Steffen, W., Lindenmayer, D.B., 2009. Landscape fluidity – a unifying perspective for understanding and adapting to global change. J. Biogeo. 36, 193–199.
Mawdsley, J.R., O'Malley, R., Ojima, D.S., 2009. A review of climate-change adaptation strategies for wildlife management and biodiversity conservation. Conserv. Biol. 23, 1080–1089.
McDonald-Madden, E., Runge, M.C., Possingham, H.P., Martin, T.G., 2011. Optimal timing for managed relocation of species faced with climate change. Nat. Clim. Change. 1, 261–265.
McIntyre, S., 2011. Ecological and anthropomorphic factors permitting low-risk assisted colonization in temperate grassy woodlands. Biol. Cons. 144, 1781–1789.
McKenney, D., Pedlar, J., O'Neill, G., 2009. Climate change and forest seed zones: past trends, future prospects and challenges to ponder. For. Chron. 85, 258–266.

McLachlan, J.S., Hellmann, J.J., Schwartz, M.W., 2007. A framework for debate of assisted migration in an era of climate change. Conserv. Biol. 21, 297–302.
Mead, J.I., White, R.S., Baez, A., Hollenshead, M.G., Swift, S.L., Carpenter, M.C., 2010. Late Pleistocene (Rancholabrean) *Cynomys* (Rodentia, Sciuridae: prairie dog) from northwestern Sonora, Mexico. Quat. Int. 217, 138–142.
Millar, C.I., Stephenson, N.L., Stephens, S.L., 2007. Climate change and forests of the future: managing in the face of uncertainty. Ecol. Appl. 17, 2145–2151.
Mueller, J.M., Hellmann, J.J., 2008. An assessment of invasion risk from assisted migration. Conserv. Biol. 22, 562–567.
Noss, R.F., 1990. Indicators for monitoring biodiversity: a hierarchical approach. Conserv. Biol. 4, 355–364.
Parker, I.M., Simberloff, D., Lonsdale, W.M., Goodell, K., Wonham, M., Kareiva, P.M., Williamson, M.H., Von Holle, B., Moyle, P.B., Byers, J.E., Goldwasser, L., 1999. Impact: toward a framework for understanding the ecological effects of invaders. Biol. Invas. 1, 3–19.
Pemberton, R.W., 2010. Biotic resource needs of specialist orchid pollinators. Bot. Rev. 76, 275–292.
Petchey, O.L., McPhearson, P.T., Casey, T.M., Morin, P.J., 1999. Environmental warming alters food-web structure and ecosystem function. Nature 402, 69–72.
Purvis, A., Gittleman, G.L., Cowlishaw, G., Mace, G.M., 2000. Predicting extinction risk in declining species. Proc. Roy. Soc. Lond. Ser. B – Biol. Sci. 267, 1947–1952.
Ricciardi, A., Simberloff, D., 2009. Assisted colonisation is not a viable conservation strategy. TREE 24, 248–253.
Richardson, D.M., Hellmann, J.J., McLachlan, J.S., Sax, D.F., Schwartz, M.W., Gonzalez, P., Brennan, E.J., Camacho, A., Root, T.L., Sala, O., Schneider, S.H., Ashe, D.M., Clark, J.R., Early, R., Etterson, J.R., Fielder, E.D., Gill, J.L., Minteer, B.A., Polasky, S., Safford, H.D., Thompson, A.R., Vellend, M., 2009. Multidimensional evaluation of managed relocation. PNAS 106, 9721–9724.
Sandler, R., 2010. The value of species and the ethical foundations of assisted colonisation. Conserv. Biol. 24, 424–431.
Schöpsa, K., Syretta, P., Embersona, R.M., 1996. Summer diapause in *Chrysolina hyperici* and *C. quadrigemina* (Coleoptera: Chrysomelidae) in relation to biological control of St John's wort, *Hypericum perforatum* (Clusiaceae). Bull. Entom. Res. 86, 591–597.
Schwartz, M.W., Hellmann, J.J., McLachlan, J.S., 2009. The precautionary principle in managed relocation is misguided advice. TREE 24, 474.
Seddon, P.J., 2010. From reintroduction to assisted colonisation: moving along the conservation translocation spectrum. Restor. Ecol. 18, 796–802.
Simberloff, D., 1998. Flagships, umbrellas, and keystones: is single-species management passe in the landscape era. Biol. Conserv 83, 247–257.
Steffen, W., Burbidge, A.A., Hughes, L., Kitching, R., Lindenmayer, D., Musgrave, W., Stafford Smith, M., Werner, P.A., 2009. Australia's Biodiversity and Climate Change. CSIRO, Collingwood.
Van Mantgem, P.J., Stephenson, N.L., Byrne, J.C., Daniels, L.D., Franklin, J.F., Fule, P.Z., Harmon, M.E., Larson, A.J., Smith, J.M., Taylor, A.H., Veblen, T.T., 2009. Widespread increase of tree mortality rates in the western United States. Science 323, 521–524.
Vitt, P., Havens, K., Hoegh-Guldberg, O., 2009. Assisted migration: part of an integrated conservation strategy. TREE 24, 473–474.
Vitt, P., Havens, K., Kramer, A.T., Sollenberger, D., Yates, E., 2010. Assisted migration of plants: changes in latitudes, changes in attitudes. Biol. Conserv. 143, 18–27.
Waterman, R.J., Bidartondo, M.I., Stofberg, J., Combs, J.K., Gebauer, G., Savolainen, V., Barraclough, T.G., Pauw, A., 2011. The effects of above- and below ground mutualisms on orchid speciation and coexistence. Am. Nature 177, E54–E68.
Willis, S.G., Hill, J.K., Thomas, C.D., Roy, D.B., Fox, R., Blakeley, D.S., Huntley, B., 2009. Assisted colonisation in a changing climate: a test-study using two UK butterflies. Conserv. Lett. 2, 45–51.
Yates, C.J., Ladd, P.G., Coates, D.J., McArthur, S., 2007. Hierarchies of cause: understanding rarity in an endemic shrub *Verticordia staminosa* (Myrtaceae) with a highly restricted distribution. Aust. J. Bot. 55, 194–205.
Yates, C.J., McNeill, A., Elith, J., Midgley, G.F., 2009. Assessing the impacts of climate change and land transformation on *Banksia* in the South West Australian Floristic Region. Divers. Distrib. 16, 187–201.