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FORUM

Clarifying climate change adaptation responses for scattered trees in modified landscapes

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Summary

1. Many studies have investigated adaptation to climate change. However, the term 'adaptation' has been used ambiguously and sometimes included parts of both classic evolutionary processes and conservation planning measures (i.e. human-mediated adaptation).

2. To reduce ambiguity, we define three classes of evolutionary processes involved in adaptation – migrational, novel-variant and plasticity. Migrational adaptation describes the process of redistribution of standing genetic variation among populations. Novel-variant adaptation describes the increase in frequency of beneficial, new genetic variants. Plasticity adaptation refers to adaptive plastic responses of organisms to environmental stressors. Quite separately, human-mediated adaptation aims to maintain these evolutionary processes.

3. Whilst the role of scattered trees in migrational adaptation of fauna may have been neglected in the past, their capacity to assist migrational adaptation of trees has been previously documented. However, their role in novel-variant and plasticity adaptation is generally unrecognised, and warrants further attention.

4. *Synthesis and applications*. By defining different aspects of adaptation carefully, we show that scattered trees should not be cleared since they may facilitate gene flow across fragmented landscapes. However, they should be avoided as dominant seed sources since their stock may be of poor quality.

Key-words: adaptation, climate change, gene flow, inbreeding, landscape management, revegetation, scattered trees, seed sourcing

Introduction

To avoid extinction, organisms must successfully adapt to changing environments. Evolutionary biology needs to be incorporated into conservation planning to augment successful adaptation of species that are vulnerable to climate change. However, the definition of evolutionary adaptation appears to have changed in recent years to include not only the classic evolutionary process of genetic improvement of populations through generations (Wright 1932), but also adaptive plastic responses of organisms (Nussay, Wilson & Brommer 2007; Visser 2008; Chevin, Lande & Mace 2010). In the literature, it is common for these processes to be merged together as 'adaptation' and, in the field of landscape management, 'adaptation to climate change' is now frequently also used to refer to human-mediated management approaches (Manning, Gibbons & Lindenmayer 2009) such as assisted colonisation. These multiple definitions are confusing and may potentially lead to erroneous conclusions about the ability of organisms to adapt to climate change.

Adaptation should be carefully defined, in particular with regard to the evolutionary processes that can facilitate species' adaptation to climate change. Using a case study involving scattered trees and their dependant flora and fauna in modified landscapes, we aim to demonstrate the value of incorporating information on evolutionary processes into conservation decision-making and landscape management.

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Defining climate change adaptation

The classic definition of evolutionary adaptation involves two components: the process involving standing genetic variants and the process based on new genetic variants (See glossary of terms in Appendix S1 and adaptation literature search guide in Appendix S2 Supporting information). We separate these two components since they are different in process, although we acknowledge that they are interdependent (Wright 1932). (i) We use the term 'migrational adaptation' to describe the process by which standing genetic variation is redistributed by gene flow and selection among populations. This results in allele frequency shifts within species, and includes species' range shifts (Wright 1932); (ii) we use the term 'novel-variant adaptation' to describe the process of increase in frequency and possibly fixation of new, beneficial genetic variants that are generated by mutation, recombination or other genetic processes. Novel-variant adaptation has well-recognised theory (Maynard Smith 1978; González & Petrov 2009) but has received limited attention with reference to adaptation to climate change and (iii) we use the term 'plasticity adaptation' to refer to adaptive plastic responses of organisms to environmental stressors. This includes both one-off trait shifts (e.g. timing of metamorphosis) and lifetime trait shifts (e.g. flowering time) (*sensu* Nussay, Wilson & Brommer 2007). This interpretation of adaptation to include phenotypic plasticity is useful for applied researchers since plasticity may allow species' survival under climate change (Nussay, Wilson & Brommer 2007; Visser 2008; Chevin, Lande & Mace 2010) and it is sometimes implied in adaptation to climate change (Manning, Gibbons & Lindenmayer 2009) or explicitly stated as part of adaptive processes (Visser 2008; Chevin, Lande & Mace 2010).

We define landscape management actions that may contribute to the process of evolutionary adaptation as 'human-mediated adaptation' (e.g. assisted colonisation, Hoegh-Guldberg *et al.* 2008; Vitt *et al.* 2010; Appendix S1, S2 Supporting information). The use of 'adaptation' in this context should be considered separate from evolutionary adaptation since it is not an adaptive response by organisms to their changing environments, but rather it involves actions performed by humans to help augment evolutionary adaptation of species. Its success relies on evolutionary adaptation, since this is the process that determines whether species will go extinct or not (Moritz 2002; Willi, Van Buskirk & Hoffmann 2006; Mace & Purvis 2008; Visser 2008; Chevin, Lande & Mace 2010).

Scattered tree adaptation to climate change

Recently, Manning, Gibbons & Lindenmayer (2009) focussed on the role that scattered trees could have in facilitating migrational and plasticity adaptation of climate-compromised tree-dependant fauna. However, whilst the potential for scattered trees to assist in faunal adaptation may not have been previously considered (Manning, Gibbons & Lindenmayer 2009), the potential for scattered trees to assist with migrational adaptation of the tree species themselves has been previously well-documented. Thus, we suggest that the recommendations of Manning, Gibbons & Lindenmayer (2009) could be integrated with data on adaptation of the tree species themselves for three reasons: (i) links exist between successful tree adaptation to climate change, particularly in relation to the future provision of tree habitat, which could then facilitate adaptation of its animal inhabitants; (ii) there is a large body of literature investigating the ability of scattered trees to contribute to migrational adaptation of the trees themselves (Hamrick 2004; Lowe *et al.* 2005; Ward *et al.* 2005; Sork & Smouse 2006) and (iii) plant–animal mutualisms lead to interdependence between successful adaptation of trees with successful adaptation of their inhabitants (Ghazoul 2005).

For trees, in contrast to animals, adaptation to climate change is limited by their inability to move across landscapes. Predictions of the migrational adaptation rates required for trees to track changing climate envelopes is thought to exceed historical rates (Aitken *et al.* 2008) and plasticity adaptation may not be capable of maintaining adaptive phenotypes under extreme environmental shifts (Nussay, Wilson & Brommer 2007; Visser 2008; Chevin, Lande & Mace 2010). Therefore, management of populations threatened by climate change should focus on maintaining, and possibly facilitating, migrational and novel-variant adaptation (Broadhurst *et al.* 2008; Sgrò, Lowe & Hoffmann in press; Vitt *et al.* 2010), so that populations have a better chance of successfully tracking this shifting adaptive peak in response to changing selection pressures due to climate change (*sensu* Wright 1932).

Positive role of scattered trees for climate adaptation

Habitat fragmentation creates small populations with increased spatial isolation, which increases the risk of extinction due to an 'extinction vortex' effect (Gilpin & Soulé 1986; Ellstrand & Elam 1993; Fagan & Holmes 2006). However, with the presence of scattered trees in the landscape providing the potential for ongoing gene flow, the severity and pace of small population genetic effects may be mitigated (Lowe *et al.* 2005; Sork & Smouse 2006). For example, many studies of scattered tree populations have shown high levels of connectivity as a result of pollen dispersal (and seed dispersal, Bacles, Lowe & Ennos 2006) amongst both scattered trees and trees in patches of remnant vegetation (Chase *et al.* 1996; Lowe *et al.* 2005; Sork & Smouse 2006). Consequently, the presence of scattered trees may facilitate migration among tree populations in response to climate change by providing gene connectivity across the landscape.

By extension, the possible adaptive roles of scattered trees for the tree populations themselves are: (i) to facilitate gene flow so that populations can undergo genetic improvements by increasing allele frequencies of genes that result in higher fitness under climate change (Wright 1932); (ii) by connecting fragments, there is a reduced probability that adaptive genetic variants may be lost by random genetic drift due to the larger effective population size (Wright 1979; Lowe *et al.* 2005); (iii) by connecting fragments, natural selection may act more efficiently due to increases in effective population size, allowing rapid loss of deleterious alleles and rapid increases in beneficial alleles (Kimura 1983; Lande 1988) and (iv) with an increased effective population size, inbreeding within each fragment is likely to be reduced, thus reducing the negative fitness consequences of inbreeding depression (Crnokrak & Roff 1999; Charlesworth & Charlesworth 2003; Lowe *et al.* 2005; Ward *et al.* 2005). This last point is of particular importance for trees since most are predominantly outcrossing, and therefore generally harbour significant genetic load (Byers & Waller 2003). Scattered trees can therefore be viewed as potential genetic connection points for forest and woodland fragments. However, their effectiveness in providing connectivity is dependent on the life-history characteristics of the species in question and, in systems with animal vectors, on the dispersal ability of pollinators and seed dispersers. Consequently, a significant management challenge is to ensure pollinator and seed disperser communities are maintained in modified landscapes.

Negative role of scattered trees for climate adaptation

Forest fragmentation and vegetation clearance can have strong negative effects on plant mating systems (Lowe *et al.* 2005; Ward *et al.* 2005), and an over-reliance on scattered trees as seed sources for climate change adaptation may result in reduced progeny fitness (Broadhurst *et al.* 2008; Sgrò, Lowe & Hoffmann in press). This literature raises two issues of concern: (i) the genetic effects of spatial isolation on a tree's mating system may alter their reproductive dynamics, which can then, in turn, reduce fitness (Rocha & Aguilar 2001; Cascante *et al.* 2002). Reproductive failure could occur if insufficient compatible pollen is deposited to fertilise the ovules of the scattered trees (an Allee effect, Lamont, Klinkhamer & Witkowski 1993). Other possible impacts include reduced pollen diversity, increased breeding among close relatives and/or increased selfing in predominantly outcrossing species (Lowe *et al.* 2005; Ward *et al.* 2005). These changes generally result in reduced fitness, either due to a reduced opportunity for pollen competition (Mulcahy 1979) or reduced heterozygosity (Lowe *et al.* 2005) and (ii) reproductive dominance can lead to founder effects resulting in genetic bottlenecks, reducing genetic variation and the adaptive potential of the population (Willi, Van Buskirk & Hoffmann 2006). This is likely to occur when few trees dominate the reproductive output (Aldrich & Hamrick 1998; Sezen, Chazdon & Holsinger 2005; Davies *et al.* 2010) or when seed is collected from only a few trees for revegetation (Broadhurst *et al.* 2008). Furthermore, in cases where the trees that dominate reproduction have experienced elevated biparental inbreeding and/or selfing, effects more likely in a scattered context, the resultant founding population is likely to be genetically inbred. Reduction in genetic diversity of founding populations could result in dramatic reductions in the population's mean fitness and adaptive potential due to inbreeding depression and reduced genetic variability.

Implications for scattered tree management

Genetic factors are frequently implicated in the extinction process (Spielman, Brook & Frankham 2004; Fagan & Holmes 2006; Chevin, Lande & Mace 2010). In particular, loss of genetic diversity and inbreeding impact individual and population fitness, often leading to demographic declines and can direct species into an 'extinction vortex' (Fagan & Holmes 2006). Consequently, to minimise long-term extinction risks and maximise the adaptive potential of species to climate change, evolutionary processes should be incorporated into management by considering the genetic attributes of individuals and populations so that evolutionary processes are maintained (Moritz 2002; Mace & Purvis 2008). Evolutionary adaptation (i.e. migrational, novel-variant, plasticity) should be integrated into human-mediated adaptation (i.e. conservation management) through better communication among evolutionary biologists, managers and applied ecologists to maximise successful management.

Over-reliance on scattered trees as seed sources should be avoided since their stock is likely to be of poor quality (Lowe *et al.* 2005). Seed collecting should aim to capture a broad-range of genetically diverse seeds for plantings to improve the adaptive potential of restored communities, and therefore restoration success (Broadhurst *et al.* 2008; Sgrò, Lowe & Hoffmann in press). Even if scattered trees are the only 'local' seed sources available, they should be avoided since inbreeding and low genetic diversity are possibly as detrimental to fitness as introducing potentially suboptimally adapted genotypes (Broadhurst *et al.* 2008; Sgrò, Lowe & Hoffmann in press). However, scattered trees should not be cleared and their locations should be foci for revegetation that utilises genetically diverse seed. Managers will need to trade-off spatial isolation (i.e. increasing the numbers of trees around scattered trees and creating highly isolated pockets of vegetation), against the benefits of larger population size (i.e. having additional scattered trees in the landscape, creating many potential connection points in moderately isolated contexts). It will be important to use genetically diverse seed, since planting distant relatives of the same species around scattered trees could help to minimise inbreeding and maximise adaptive potential of the restored population, thus increasing population mean fitness and long-term survival. Recommending a specific population size or isolation distance threshold is not currently possible, but warrants additional investigation. A strategic approach could be to focus expansion towards nearby genetically diverse populations as these could provide a good resource for gene flow to the scattered trees.

Conclusion

In considering ecosystem-level adaptation and restoration activities, the potential and limitations of using scattered trees needs careful treatment. Scattered trees may facilitate gene flow across fragmented landscapes, assisting the trees to overcome small population genetic problems. However, scattered trees have also been shown to produce genetically poor stock, which may impact their adaptive potential, thus limiting their application as a source for revegetation. As such, we recommend that scattered trees should, in the absence of genetic and climate modelling data, be avoided as sources of seed, but should be the focus of revegetation to increase their population sizes and to connect them with genetically diverse fragments. This should help to maximise the chances of successful adaptation to climate change of the trees themselves and their dependant fauna.

We concur with Manning, Gibbons & Lindenmayer (2009) in that scattered trees are potentially important in facilitating adaptation of vulnerable taxa to climate change in a human-dominated landscape. There is a need for greater understanding of the processes underlying adaptive responses to climate change, in particular the role of novel genetic variants and phenotypic plasticity to climate change in fragmented systems. Teasing apart the roles of standing and new genetic variants in adaptation has proven insightful in other fields (e.g. invasive species biology, Prentis *et al.* 2008) and is likely to be useful for predicting the potential impacts of climate change in fragmented systems.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Glossary of terms.

Appendix S2. Adaptation literature search guide.

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