The conservation challenge of sustaining spatially dependent evolution

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Maintaining evolutionary processes is a fundamental tenet of biodiversity conservation. Dispersal in the guise of range expansion may take place over many generations and is a key evolutionary process. Range expansion enables evolutionarily novel gene combinations in single populations to become widespread taxonomic units, it enables homogeneous populations to reach refuges which may later become isolated and diverge, and range expansion may enable species to track their environmental niche as climates change. Land management practices that impede permeability also inhibit range expansion. Land clearing, grazing, inappropriate fire regimes and introduced species have the potential to block dispersal, preventing range expansion and eliminating spatially-dependent evolutionary processes. To achieve the goal of maintaining natural processes of evolution, landscape permeability needs to be understood and re-established in the many places where it has likely been lost.

Key words: Biodiversity conservation, Speciation, Range expansion, Habitat destruction, Livestock grazing, Fire, Introduced species, Australia.

INTRODUCTION

A PRIMARY goal of conservation efforts has long been to maintain evolutionary processes (Frankel and Soulé 1981; Allendorf and Leary 1986; Woodruff 1989). Papers espousing the conservation of evolutionary processes have often emphasized that conserving genetic variation within and between populations is needed to maintain a species' evolutionary potential (e.g., Soulé 1980; Moritz 1994). However, in this brief review I argue that maintaining a species ability to expand its range across the landscape is just as important for conserving evolutionary processes as maintaining genetic variation. Soulé *et al.* (2004) introduced the problems faced by long-term range expansion in the human-dominated world, where barriers to range expansion prevent natural evolutionary processes from operating. In this paper I expand on Soulé *et al.* (2004) to argue: 1) geographic range expansions play a critical role in ongoing evolutionary processes; 2) human use of the landscape can prevent range expansion and; 3) to maintain natural evolutionary processes, we need connectivity or permeability at a continental scale.

Role of range expansion in ongoing evolutionary processes

"whether we look to the allied forms of life which have changed during successive ages, or to those which have changed after having migrated into distant quarters . . . in both cases . . . modifications have been accumulated by the same means of natural selection."

Charles Darwin, Origin of Species 1859.

Darwin emphasized the importance of range expansion in the evolution of new species. He

was particularly interested in climatic-driven range expansions that allowed cold-loving species to swarm around the bases of mountains during cold periods, only to be driven up to isolated peaks as the climate became warmer where they would subsequently diverge (the classic dumb-bell model of speciation, Mayr 1982).

More recent research has accumulated a vast store of evidence demonstrating the important role of range expansions in the evolution of biodiversity. For example, pairs of sister species or subspecies in southwestern and southeastern Australia testify to the role of range expansion in delivering a species to areas which subsequently become isolated and diverge. Examples include trees (Wright and Ladiges 1997), birds (Schodde and Mason 1991), frogs (Roberts and Maxson 1985), and reptiles (Jennings *et al.* 2003). Other evidence comes from species with widely disjunct populations that may represent recently isolated populations of formerly widespread species. For example, Davis *et al.* (1993) reported that the southern Australian beetle *Sclerocyphon fuscus* also occurred in a disjunct population in the central Australian ranges. *S. fuscus* has low dispersal powers implying that range expansion during a period of higher rainfall allowed this species to reach central Australia. In the same streams in central Australia, Davis *et al.* (1993) also found recently evolved species, a result of divergence after isolation in the ranges. The central Australian ranges now harbor a unique aquatic invertebrate fauna of high conservation value (Davis *et al.* 1993), the evolution of which was dependent on long-distance range expansion which delivered the ancestral populations.

Range expansion not only leads to the delivery of identical individuals to new places, it can also allow evolutionary novelties in small origin

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populations, to spread and become widespread taxa. In a population genetic study of the frog *Geocrinia rosea* (Fig. 1) from south-west Western Australia, Driscoll (1998a) reported extreme genetic divergence between populations that were geographically near to each other. Populations within one river catchment (Shannon) had a fixed allozyme difference between one population and the other two which were only 4 and 7.5 km away (Driscoll 1998a). Driscoll (1998a) argued that extreme divergence in small populations was likely to be a critical part of the speciation process in the *G. rosea* species complex. However, divergence in single populations did not account for the existence of distinct genetic groups within *G. rosea*, or for the existence of four species within the species complex. Range expansion after divergence in isolation was also an essential part of the process (Driscoll 1998a,b). Driscoll (1998a) observed that the range of *G. rosea* could be divided into northern and southern groups of populations, a division well represented by the near fixed difference in the

LPP locus (Fig. 2). The most likely origin of this pattern was range expansion from two isolated and highly divergent ancestral populations (Driscoll 1998a), a process similar to Mayr's (1988) peripatric speciation mechanism. Driscoll (1998a) speculated that these range expansions were driven by climatic fluctuations, with populations expanding across the landscape under wetter climatic conditions.

Range changes driven by climatic oscillations are a global phenomenon. Dynesius and Jansson (2000) suggested that the regular Milankovitch climatic oscillations increase in magnitude with latitude, promoting increasingly large range changes and rapid speciation. They emphasized that range changes are an important component of evolutionary processes and pointed out that habitat modification is likely to inhibit habitat tracking in the future. The importance of accounting for habitat tracking in conservation plans is discussed further by Gilmore *et al.* (this volume), but over a shorter time frame than considered here.

Fig. 1. *Geocrinia rosea* call from shallow burrows in wet peaty soil near streams and in rotting logs in upland sites (Driscoll 1998b), potentially providing a mechanism for them to spread across the landscape during wet climatic periods. The permanent removal of native vegetation undermines that potential.

Fig. 2. Pie charts of the distribution of two alleles (black and grey) of the LPP enzyme locus, showing two widespread genetic groups within *G. rosea*, evidence of historic range expansion. A third rare allele occurred in a heterozygous form in one individual from one Donnelly and one Dombakup population (after Driscoll 1998).

Climate change is not the only cause of range expansion. Genetic changes within species can allow them to expand their range. In a genetic study of the gecko *Heteronotia binoei*, Moritz (1991) found that two parthenogenetic forms had evolved through hybridization of two different chromosomal races, which back-crossed giving rise to triploid individuals. The parthenogens probably evolved within the past few thousand years, and each originated in a single population in the west of Western Australia (Moritz 1991). Parthenogenetic species appeared to be at a selective advantage in the arid interior

of Australia, allowing them to expand their range into the arid zone. Moritz (1991) speculated that parthenogens might be advantaged by higher colonization rates and population growth rates than sexual species. In the harsh arid climate, local population crashes and extinctions may be frequent, so only species with good recovery and colonization rates can prosper.

Research on *H. binoei* was recently extended by Kearney *et al.* (2003), who supported Moritz's suggestion that these parthenogens might still be expanding their range (Fig. 3). Using climate models, Kearney *et al.* (2003) predicted that both

of the parthenogenetic forms could expand their ranges further to the east, potentially displacing an isolated sexual population.

Kearney and Moussalli (2003) reported that parthenogenetic taxa of stick insects (*Sipyloidea* species complex) and grasshoppers (*Warramaba virgo*) have arisen through hybridization, also in the west of Western Australia. They noted that the parthenogens have expanded their ranges to the east, like *Heteronotia*. The authors suggested that hybrids in all three groups could be explained by the same biogeographic process. Kearney and Moussalli (2003) proposed that hybrids of *Heteronotia*, *Warramamba* and *Sipyloidea* have arisen along a line running south-east from Carnarvon in Western Australia. The line marks an area of high rainfall variability and corresponds with the boundary between northern and southern taxa of each of the three species groups. Rainfall variability could cause populations to decline along the line during arid times and allow expansion during wetter times, providing ideal conditions for hybridization to occur between the northern and southern taxa (Kearney and Moussalli 2003). Not only do these taxa illustrate the important role of range expansion after new genetic forms have arisen, but they demonstrate that range expansion may also play a critical role in the initial formation of new species.

Human use of the landscape creates barriers to range expansion

Clearing native vegetation

Many species do not survive in landscapes that have been extensively cleared of native vegetation, causing population declines and making the cleared land an effective barrier against range

expansion. Driscoll (2004) studied reptile communities in agricultural landscapes that had been cleared of 90% of the original mallee woodland vegetation. Although the landscape was permeated by linear remnants along roadsides and around paddocks, five species showed a significant bias towards occurring in larger reserves and not in the strips, which may have isolated populations in remnant patches and prevented landscape-scale dispersal. Driscoll (2004) speculated that two species may be completely extinct in the farming landscapes, emphasizing the potential for farming practices to act as a major barrier to some species. Declines of bird species across farming landscapes are well documented (Bennett and Ford 1997; Villard *et al.* 1999; Chamberlain *et al.* 2000; Schmiegelow and Monkkonen 2002). For example, Saunders (1989) reported that in the Western Australian wheatbelt, two bird species were extinct, and that 27% were declining. Within the Kellerberrin district of the WA wheatbelt, 11% of species were extinct (Saunders 1989). The wheatbelt, and the Kellerberrin area in particular, are therefore major barriers to bird dispersal. Driscoll and Weir (2005) argued that one-fifth to one-third of the reptile, beetle, mammal and bird fauna may be prone to decline from extensively cleared landscapes.

Hill *et al.* (2001) demonstrated that natural range expansion was inhibited by habitat loss. Hill *et al.* (2001) plotted the rate of range expansion of the butterfly *Pararge aegeria* in Scotland and England over the 20th century. Although the change in climate had been more favourable for *P. aegeria* in England than in Scotland, the rate of range expansion by this widely dispersing species was significantly lower in England, where there was 24% less habitat available. Furthermore, Hill *et al.* (2001) used a

Fig. 3. Current (triangles) and predicted (shaded) distribution of two parthenogenetic races of *Heteronotia binoei* based on climatic modelling. Darker shading indicates higher probability that the species will occur there. The 3N2 race in particular is likely to be expanding its range and could extend right out through the desert regions (after Kearney *et al.* 2003).

simulation model to model these two range expansions. They parameterized the models exactly the same, but with different amounts of habitat, and the models were nearly perfect in predicting the rate of expansion in the two areas, supporting their contention that the slower rate of expansion in England was caused by the lack of habitat. Hill *et al.* (2001) argued that many butterfly species that are poorer dispersers than *P. aegeria* are currently unable to expand their range and follow their environmental niche due to habitat loss.

Grazing

Livestock grazing can impose as severe a barrier to range expansion as complete removal of native vegetation. Landsberg *et al.* (2003) examined plant communities at increasing distances from livestock watering points at eight sites across central and southern Australia. In the rangelands of Australia, grazing pressure is highest near to watering points, and decreases with increasing distance from water (James *et al.* 1999). For ground-layer plant species found only at a single site, significantly more were found at sites the greatest distance from watering points, implying that many species are excluded from most of the landscape by grazing around watering points. Approximately one quarter of species were classified as decreaser species with

14% as increasers. Landsberg *et al.* (2003) concluded that long-term grazing around watering points was detrimental to native flora and that it would prevent plant species from expanding their range. James *et al.* (1999) expanded on this research and presented a continent-wide examination of the density of watering points. They showed that vast, contiguous areas of Australia were less than 3 km from a watering point (Fig. 4). The implication is that species that are sensitive to grazing are vulnerable to decline from large areas of Australia, and that continent-scale range expansions are unlikely to occur.

Fire

With the withdrawal of glaciation across Canada, boreal forests expanded northwards and now a northern limit of forest is well established (Asselin *et al.* 2003). Although Jack Pine *Pinus banksiana* generally extends to the northern limit of forest, there are several conspicuous areas where it lags behind the forest front. Jack Pine is dependent on fire for seed dispersal. Using records of past fires, Asselin *et al.* (2003) found that fire occurred with low frequency in the areas where Jack Pine had not kept up with the forest front. Absence of fire prevented this species from expanding its range (Asselin *et al.* 2003). Like habitat loss, other evidence supporting the

Fig. 4. Distance to domestic stock watering points in Australia. Vast areas of the arid and semi-arid zones are less than 3 km from water, and these contiguous zones around the country may prevent continent scale range expansion (© CSIRO, James *et al.* 1999).

potential for fire, or its absence to be a dispersal barrier comes from known species responses to fire management. Woinarksi (1999) reported that inappropriate fire regimes have contributed to two of the three bird extinctions in Australia and are a threatening process for 51 of the nationally threatened bird taxa. Generally, too frequent fire was the cause of species declines. For example in tropical woodlands and savannahs, frequent fires associated with pastoralism likely contributed to the decline of the endangered Gouldian Finch *Erythrura gouldiae* by altering the availability of grass seeds on which the finches depend (Woinarksi 1999). Complete fire suppression or frequent fires may form landscape-wide barriers to range expansion for some species.

Introduced species

In addition to the barrier effects caused by major land management practices, introduced species also create barriers to range expansion. Introduced species are well documented causes of species declines and so may form permanent barriers to range expansion. Since European colonization of Australia 16 mammal species have become extinct and the ranges of 26 other species have declined by more than 80% (Short and Smith 1994). The introduction of foxes, cats and rabbits is largely to blame for mammal extinctions and declines (Short and Smith 1994). Fox extermination and exclusion programmes have been the only way that some of the remaining vulnerable mammals have managed to expand their ranges, demonstrating the barrier effect of fox populations (e.g., Lovett 1996; Richards and Short 2003). Introduced predatory fish have caused similar range declines and are likely barriers to range expansions. Gillespie (2001) demonstrated that predation of tadpoles by the introduced Brown Trout *Salmo trutta* was the likely cause of decline of the frogs *Litoria spenceri* and *L. phyllocroa*. Fairfax and Fensham (2000) reported that the introduction of exotic pasture grasses are causing declines of native plant biodiversity, and warned that the ongoing expansion of Buffel Grass *Cenchrus ciliaris* was likely to cause continuing species declines. Buffel Grass expansion is also implicated in the decline of the skink *Egernia slateri* from central Australia (Pavey 2004). Introduced species stand as essentially permanent barriers to range expansion for many native species.

James *et al.* (1999) argued that introduced feral herbivores (goats, camels, horses etc.) may contribute to species declines near watering points, emphasizing that interactions between the categories I have discussed so far may also create barriers to range expansion. Weed invasion may alter fire regimes, increasing threats to other species (Milberg and Lamont 1995). All four processes are often cited

as possible threats in species declines (Lee 1995; Garnett and Crowley 2000), emphasizing that barriers to range expansion may be multifaceted.

DISCUSSION

It could be argued that evolution occurs at a time scale orders of magnitude longer than management actions, therefore we need not worry about maintaining options for range expansion. There are three reasons why I argue against that position. First, the time frames of range expansions may not be extremely long. Range expansions over short time periods are exemplified by parthenogens in the Australian arid zone (Moritz 1991) and by recent range expansions of some bird species, which may have been caused by environmental changes associated with grazing or climate change (James *et al.* 1999; Reid 2003).

Second, the management actions that will facilitate on-going evolution are the same management actions needed to counter two other pressing environmental problems. Providing for wildlife dispersal will help reduce impacts of habitat loss and fragmentation (Burkey 1988; Driscoll 2004) and may allow species to survive in the face of rapid climate change (Howden *et al.* 2003; Araujo *et al.* 2004; Opdam and Wascher 2004). It is a management necessity to re-establish connectivity at all spatial scales up to entire continents to facilitate evolutionary processes, to counter habitat loss and to enable species to shift their range in response to climate change.

Third, we cannot assume the barriers to dispersal that humans have recently erected are likely to fall by themselves. It is therefore not reasonable to argue that range expansions are likely to happen long into the future, when the current features of the landscape may be long gone. In the case of introduced species, they definitely will not fall without intervention. Furthermore, our society does not plan on declining or leaving any time soon, implying that we plan to be here in perpetuity, along with our wheat-belts and livestock industries. I think we are therefore morally obliged to plan biodiversity conservation on the same time-scale: for perpetuity.

Conclusion

From Darwin through to recent genetic research, range expansion is demonstrated as essential for the continued natural evolution of species and speciation. However, human-induced barriers to range expansion mean that this important evolutionary mechanism no longer functions for many species and in many regions. The barriers include complete removal of native

vegetation, but also more subtle effects throughout uncleared landscapes, including grazing, fire and introduced species.

A quarter of a century ago, Frankel and Soulé (1981) warned that human activity was undermining natural evolutionary processes and said:

"These conclusions bode ill for the future natural production of evolutionary novelty . . . For large organisms, natural speciation requires too much space . . . For the foreseeable future, the best we can hope for is that the currently existing species will continue to survive and adapt to their changing conditions," (Frankel and Soulé 1981).

Woodruff (2001) reiterated the conclusion of Frankel and Soulé (1981), saying that evolution has essentially ended for large vertebrates. This paper concurs with their conclusions that evolutionary processes which depend on range expansion can no longer function in many species, and probably not just in large vertebrates.

Prospects

Although natural evolutionary processes involving range expansion have ended for many species through recent human actions, Soulé and Wilcox (1980) expressed optimism that it might only be a suspension rather than a permanent halt. A quarter of a century later, what grounds are there for optimism that evolutionary processes can and will be restored by removing barriers to range expansion?

We still know very little about how to restore landscapes, however, scientific knowledge about landscape restoration is rapidly expanding (Young *et al.* 2005) and is cause for optimism (Lunt 2001). There is also some social and political capacity to implement restoration (Stephens 2001), but these generally lack the geographic scope and resources to allow range expansions and dispersal on the scale that I have discussed in this paper. In contrast, in Australia the Wilderness Society's WildCountry programme (Recher 2003), and in the USA the Wildlands Project (Soulé and Terborgh 1999) have put large-scale dispersal on the conservation agenda. These programmes may provide the broad context within which existing restoration mechanisms can begin to implement landscape scale and continent scale connectivity. For example, the WildCountry programme aims to provide for dispersal at all spatial scales and is already beginning to be implemented in state based programmes including Gondwana Link in Western Australia, and NatureLinks in South Australia (Department for Environment and Heritage 2003). These programmes proclaim they are audacious and bold, but they also represent the minimum action needed for range

expansion and subsequent evolutionary processes to occur.

In a climate of inadequate funding and increasing threats to biodiversity (Williams 2001), there are calls to triage conservation management options and so achieve the best possible conservation outcome with the resources available (Possingham *et al.* 2002; Hobbs *et al.* 2003). In developing appropriate triage metrics, the contribution of range expansion to preventing species extinctions, and to facilitating the evolution of new species should be considered. One possible way of implementing this is to give a higher weighting to species saved with an intact potential to evolve through natural processes of range expansion, than to species that are saved in isolated patches only. To transform triage calculations from guesses into estimates, we need research into the likely number of species that will benefit from removing barriers to range expansion, and how best to remove them. Most importantly, we need to know about the dispersal capacity of a broad range of taxa under different levels of restoration or habitat condition so that we know what proportion of the biota can disperse across landscapes with particular habitat features. We also need distribution models that predict the amount of range change expected under realistic climate change scenarios (e.g., Araujo *et al.* 2004), so that we know how many species are likely to be dependent on moving across the landscape as the climate changes.

The long-standing conservation goal of maintaining evolutionary processes is not being achieved for many species. The further development of triage methods in biodiversity conservation, and monitoring the success of programmes like WildCountry and Wildlands will tell us if that important goal can be achieved.

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