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COMMENT

Habitat fragmentation versus fragmented habitats

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Abstract Habitats often show similar present structuring, but contrasting histories: habitats occur naturally fragmented due to abiotic or biotic factors over long time periods, but may also have become fragmented only recently through transformation from interconnected to highly fragmented habitats within short time periods. Species and populations being faced with such contrasting habitat scenarios also show contrasting responses at species and intraspecific level. Organisms and populations from naturally fragmented habitats may show a reduction in their genetic load (purging) due to purifying selection in isolation. In contrast, sudden habitat transformations from interconnected to highly fragmented structures and the resulting transition from gene flow or panmixia to strong population differentiation often have negative effects on biota; while species occur in interconnected population networks (maintaining a high proportion of genetic diversity), a sudden breakdown of gene flow may lead to a severe loss of genetic diversity and the manifestation of weakly deleterious alleles. In consequence, fragmented habitats need not have a negative impact on species per se, but the history of habitat structures, particularly fast transformation processes, may severely affect the persistence and fitness of species.

Keywords Habitat history · Habitat persistence · Habitat transformation · Genetic structure · Purging · Weakly deleterious alleles · Viability

Ecosystems frequently occur naturally fragmented due to biotic (e.g. presence of prey, hosts) and/or abiotic (e.g. climate, geology) preconditions. Simultaneously, the fragmentation of formerly interconnected habitats is one of the largest threat to global biodiversity and is a main topic in nature conservation research and policy (Debinski and Holt 2000).

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‘Fragmented habitats’ stand for the status of a specific habitat feature, while ‘habitat fragmentation’ describes the process of transformation from an interconnected into a patchy ecosystem structure. The term fragmentation has been used inconsistently (Lindenmayer and Fischer 2007). We define it as the breaking up of a formerly (more) connected habitat resulting in an increased mean isolation of habitat patches dispersed within an unfavourable matrix, with the main result being an impediment to migration among these patches and thus to gene flow. This may or may not include significant habitat loss. This point is important as the negative implications of habitat fragmentation mostly have been mixed up with those of habitat loss, and habitat loss has been shown to be much more detrimental than fragmentation per se (Lindenmayer and Fischer 2007). Indeed, a review has shown that fragmentation per se, contrary to intuitive expectations, may even have positive effects, although data are not yet conclusive and generalisations preliminary (Lindenmayer and Fischer 2007). The same holds for the assumption that fragmentation per se may be more consequential in tropical than in temperate systems (Lindenmayer and Fischer 2007). Typical examples where fragmentation is not necessarily accompanied by loss of overall habitat size is the construction of highways or dams (Wu et al. 2003). Whether or not this process occurs naturally (usually over large time scales) or not can have significantly different consequences not only on species composition (Kruess and Tscharntke 1994; Terborgh et al. 2001) but also at the intraspecific level.

Species existing in naturally fragmented habitats over long time periods often show low genetic diversity within and high differentiation among populations (Habel and Schmitt 2012). Long-term isolation and the persistence of species in remnant populations may lead to a reduction in genetic load (purging) over generations so that even continuing loss of potential habitats and existence at low effective population sizes need not necessarily have severe impacts at the intraspecific level (lower reduction of diversity and lower increase in differentiation) (Habel and Schmitt 2012). In addition, naturally fragmented habitats are more likely to be (successfully) colonised by species with higher mobility or lower genetic load. This may further mitigate the negative corollaries of isolation through gene flow or a rarer occurrence of deleterious recessive alleles responsible for inbreeding depression. At the supraspecific level, natural fragmentation may produce favourable conditions for allopatric speciation, and particularly islands and archipelagos, which may be seen as a textbook example of natural fragmentation, have long been famous for in situ radiations of birds and other taxa. Thus, naturally fragmented habitats are more likely to be inhabited by biota that are adapted to this kind of habitat-matrix mosaic.

In contrast, the transformation of naturally interconnected habitats into fragmented ones is often accompanied by a severe loss not only of species diversity (Kruess and Tscharntke 1994; Terborgh et al. 2001) but also of intraspecific diversity, and by increased homozygosity and also significant differentiation, sometimes resulting in reduced viability (inbreeding depression, e. g. Zachos et al. 2007). Those taxa are often characterised by a former relatively high genetic diversity, which was maintained by large and interconnected populations (Kruess and Tscharntke 1994). A sudden evisceration of such a panmictic population (as is often the case in human-induced fragmentation processes) would have a negative impact on the remaining, now fragmented populations. This change from panmixia or near-panmixia to disrupted gene flow can often not be compensated and finally lead to increasing genetic drift and inbreeding, ultimately resulting in a loss of adaptive potential and decline in fitness. Based on the above we conclude that (i) populations showing a similar degree of fragmentation but contrasting histories can have diverging intraspecific signatures, and (ii) fragmentation must not have a negative impact on

Fig. 1 Two fragmented forest habitats in Kenya with similar patch-matrix-ratios, but two contrasting histories: *above* the naturally fragmented forest islands in the Chyulu Hills, *below* forest patch in the Taita Hills, where 98 % of the former forest cover was destroyed and interconnected forest habitat was transformed into fragmented patches within the last few decades

populations or species per se—but the time within which habitat transformation takes place is of high relevance to the genetic outcome. This should be kept in mind when analysing the ecology of biota inhabiting disjunct habitat patches (Fig. 1).

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