



Short communication

The burden of genetic diversity

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ABSTRACT

In general, species with large ecological amplitudes are equipped with high genetic diversities. In contrast, more specialised species with narrow ecological amplitudes show low levels of genetic diversity. Generalist species are mostly rather marginally affected by recent land-use changes; specialist can be supported by specific conservation measures. We argue that, in the light of Conservation Genetics, species being ecologically intermediate between these two extremes are the most seriously affected ones by recent environmental changes. Such species which formerly occurred in large population networks have to sustain their high level of genetic variability via gene flow. Today, species from the latter group are negatively affected by rapid habitat collapses causing sudden lacks of population interconnectivity. Therefore, species with intermediate habitat demands and originally high genetic diversity might be at highest risk due to inbreeding depressions.

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1. Introduction

Since the development of the fundamentals of population genetics by its primary founders Fisher, Haldane and Wright and completion by studies of Dobzhansky (reviewed in Li, 1955), population genetic structures have been more and more frequently interpreted in the light of species conservation. The new and innovative scientific field of *Conservation Genetics* became a highly relevant and independent research field, highlighted by the book of Frankham (1995) and the foundation of the scientific journal *Conservation Genetics* in the year 2000.

In various studies, the maintenance of a high level of genetic diversity is assumed as an indispensable prerequisite for the conservation of viable populations (e.g. Hansson and Westerberg, 2002; Reed and Frankham, 2003; Leimu et al., 2006). More specifically, high genetic diversity has often been shown to be positively correlated with indicator values of the individuals' fitness, such as the mating success in animals (e.g. Joron and Brakefield, 2003), the adaptability on changing environmental conditions (Booy et al., 2000 with references therein) or the seed production and their quality in plants (e.g. Oostermeijer et al., 1994, 1996; Hensen and Oberprieler, 2005). Consequently, genetic bottlenecking and subsequent impoverishment can have detrimental consequences on the fitness of once genetically diverse populations (e.g. Keller et al., 1994; Saccheri et al., 1996, 1998; Madsen et al., 1999;

Bijlsma et al., 2000; Keller and Waller, 2002; Újvári et al., 2002), as for example reduced fecundity (Roff and DeRose, 2001) and/or reduced body size (Whitlock, 1993).

However, this perception of Conservation Genetics is so far mostly restricted to the intraspecific level and, therefore, has to be completed by the interspecific level for a more comprehensive understanding of the importance of genetic diversity and differentiation. In general, genetic diversity levels differ considerably among species and particularly along the gradient from specialists (i.e. narrow ecological amplitude) to generalists (i.e. wide ecological amplitude) (e.g. Brouat et al., 2004; Louy et al., 2007; Habel and Schmitt, 2009). The extent of the ecological amplitude and the dispersal behaviour of species strongly influences the abundance of a species in a landscape and, hence, the genetic composition of populations. In this generalist–specialist continuum, the more generalist species often tend to have high genetic diversities of their populations and low genetic differentiation among them (Schmitt et al., 2005; Besold et al., 2008b; Habel et al., 2010) (Fig. 1). This is the consequence of the absence of genetic bottlenecks in populations and strong gene flow among them resulting in the maintenance of high genetic diversities of populations without differentiation among them. More specialist species are affected by isolation of their populations. This causes stronger genetic differentiation among populations and genetic impoverishment within them due to small or fluctuating population sizes accompanied by high frequencies of genetic bottlenecks (e.g. Hughes et al., 1999) (see below). On the long run, this is resulting in lower genetic diversities in specialist species than in generalists (Habel et al., 2009a).

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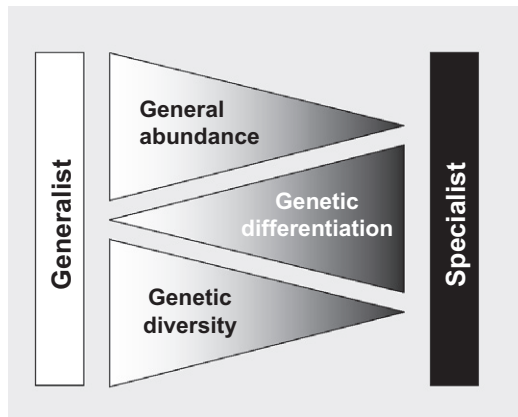


Fig. 1. Contrasting relations between general abundance, genetic differentiation and diversity of specialist and generalist species.

The dualism of generalist and specialist is currently subject of controversial discussion, and Loxdale et al. (2011) question the existence of ecological generalists with the argument that all species show ecological preferences and thus specialisation. In their answer to this article, Dennis et al. (2012) give strong ecological support for the existence of this dualism. In this article, we enlarge this debate for the genetic view.

2. Advantages of low genetic diversity

Highly specialised species in most of the cases are restricted to a small fraction of the available landscape in most of the cases resulting in highly isolated populations (van Dorp and Opdam, 1987; Johansson and Ehrlén, 2003). This ecological specialisation (and thus geographic restriction to local populations) is usually combined with reduced gene flow and thus leads to both, low population sizes and genetic differentiation. Consequently, such species can only survive when being adapted to low genetic diversities (e.g. Kassen, 2002; Berezcki, et al. 2005; Packer et al., 2005; Watts et al., 2006; Kawamura et al., 2007; Zachos et al., 2007; Habel et al., 2009b; Bernard and Schmitt, 2010). However, the resulting genetic make-up consisting of only few alleles has to be highly adapted to these very specific environmental conditions (Watt, 1995; Watt et al., 2003; Karl et al., 2008).

While highly adapted but showing low genetic diversity, such specialists will only marginally be affected by inbreeding, genetic bottlenecks or strong population fluctuations within local populations, as the major proportion of eventual ancient genetic diversity has already been lost (Frankham et al., 2001; Crnokrak and Barrett, 2002; Thévenon and Couvet, 2002). Due to this particularly low genetic diversity at the species level, there is no further necessity of genetic refreshment by exchange of individuals among populations. Consequently, such taxa show no negative effects of landscape fragmentation on population viability as exemplified for the Black Mangrove tree *Aegiceras corniculatum* (Ge and Sun, 1999), the San Nicolas Island fox *Urocyon littoralis dickeyi* (Aguilar et al., 2004), or a viable but genetically uniform cattle herd (Vischer et al., 2001).

As another case study, the Red Apollo butterfly *Parnassius apollo* was analysed by two molecular markers systems for a strongly isolated local relict subspecies in the Mosel valley (southwestern Germany), and both marker systems were monomorphic (Habel et al., 2009b). Also populations from the centre of its distribution showed low, but at least some genetic diversity (Napolitano et al., 1990). Interestingly, the Mosel populations after being close to extinction recovered very quickly following conservation

measures. Apparently, the low population densities had no negative influence on the population viability, as shown by the genetic constancy found over a time period of more than 100 years, and by the lack of increasing deviations of bilateral symmetries in the wing-shape (Habel et al., 2012).

The Fritillary butterfly *Melitaea aurelia*, although showing typical traits of a generalist (Table 1), is restricted to well preserved calcareous grasslands in Central Europe (Ebert and Rennwald, 1991). This species shows a quite low genetic diversity, and populations in Rhineland-Palatinate and adjoining regions exist in viable but strongly isolated populations with apparently no gene flow among neighbouring sites (Habel et al., 2009a). This capacity of surviving in isolation might be the benefit of the low genetic diversity of this species, and thus resistance against the disruptive influence of periodical population bottlenecks.

Nevertheless, these specialist species are in the most cases listed in the respective Red Data Books. However, this is most probably the consequence of the destruction of their specific habitats (and thus fewer and smaller populations which are more severely affected by environmental stochasticity, see Melbourne and Hastings, 2008) and not the result of population genetic disruption. Consequently, these species can be sustainably conserved through the maintenance of suitable habitats regardless of their degree of isolation (Fig. 2). Therefore, such low genetic diversity can be an advantage in fragmented landscapes: populations of such species can survive in isolation without any contact with other conspecifics, whereas taxa with high genetic diversity are in urgent need for gene flow and intact population networks for their survival. However, this environmental precondition is more and more disappearing in our environment being characterised by industrial agriculture (see below). This coherence of ecological niche breadths, genetic configuration and endangerment can be exemplified for a set of butterflies of Central Europe for which genetic data were performed by the same molecular method (allozyme electrophoresis) and for which ecological classifications (see Bink, 1992) are available (see Table 1).

3. Disadvantages of high genetic diversity

Up to now, we have mostly discussed about pure generalists and pure specialists. However, in the generalist–specialist-continuum, many species exhibit intermediate positions. Such species often show moderate ecological specialisation being neither pure generalists, nor pure specialists so that the transitions are fluent and therefore necessarily have to be somehow subjective if categorising species. Despite their moderate habitat specialisation, these ecologically intermediate species often do not share the phenomenon of low genetic diversity with pure specialist, but show species specific genetic diversities in the order of magnitude of generalists. Most of these intermediate species show values from 0.4 to 0.5 (some few even up to 0.511) in our specialist–generalist classification of butterflies (Table 1). However, these taxa in general are classified as much more endangered as one would think from their degree of specialisation.

Exemplarily, the hermit butterfly *Chazara briseis* shows a strongly restricted distribution in the Czech Republic today (however formerly being widespread all over the country), but vanished from the territory very quickly and without previous alarming signals except for one meta-population system. However, this last relict of a formerly wide distribution still has a remarkably high level of genetic diversity (Kadlec et al., 2010). This situation can be detrimental in the process of decreasing populations and may be one of the enhancers of extinction in this case, probably due to genetic disruption of the populations and the stochastic accumulation of deleterious genes. Another example of sudden extinction over

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