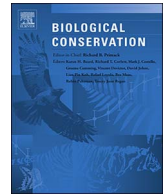




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# An ecological connectivity network maintains genetic diversity of a flagship wildflower, *Pulsatilla vulgaris*

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## ABSTRACT

Ecological connectivity networks have been proposed as an efficient way to reconnect communities in fragmented landscapes. Yet few studies have evaluated if they are successful at enhancing actual functional connectivity (i.e. realized dispersal or gene flow) of focal species, or if this enhanced connectivity is enough to maintain genetic diversity and fitness of plant populations. Here we test the efficacy of an ecological connectivity network implemented in southern Germany since 1989 to reconnect calcareous grassland fragments through rotational shepherding. We genotyped 1449 individuals from 57 populations and measured fitness-related traits in 10 populations of *Pulsatilla vulgaris*, a flagship species of calcareous grasslands in Europe. We tested if the shepherding network explained functional connectivity in *P. vulgaris* and if higher connectivity translated to higher genetic diversity and fitness of populations. We found that population-specific  $F_{st}$  was lowest in populations that had high connectivity within the shepherding network, and that well-connected populations within the network had significantly higher genetic diversity than ungrazed and more isolated grazed populations. Moreover, genetic diversity was significantly positively correlated with both seed set and seed mass. Together our results suggest that the implementation of an ecological shepherding network is an effective management measure to maintain functional connectivity and genetic diversity at the landscape scale for a calcareous grassland specialist. Populations with reduced genetic diversity would likely benefit from inclusion, or better integration into the ecological connectivity network. Our study demonstrates the often postulated but rarely tested sequence of positive associations between connectivity, genetic diversity, and fitness at the landscape scale, and provides a framework for testing the efficacy of ecological connectivity networks for focal species using molecular genetic tools.

## 1. Introduction

Habitat loss and fragmentation are major threats to the persistence of populations across nearly all taxonomic groups (Fischer and Lindenmayer, 2007). Together, these processes can lead to reductions in effective population size and gene flow among previously contiguous patches, enhancing the effects of genetic drift in small populations and accelerating the loss of genetic diversity (Frankham, 2005; Reed and Frankham, 2003). Small and isolated populations are more prone to inbreeding depression and suffer a reduced potential for adaptation (Frankham, 2005). Preserving genetic diversity is not only important for the population or species at-hand, but also plays a critical role in the functioning of communities and ecosystems, with positive influences on species diversity, disease dynamics, food-web dynamics, and ecosystem

cycling (Hughes et al., 2008; Johnson et al., 2006; Lamy et al., 2013).

Ecological connectivity networks (i.e. sets of connected suitable habitats that allow persistence of viable metapopulations for multiple species in a community), are increasingly being implemented to restore dispersal linkages between remnant patches in fragmented landscapes (Baguette et al., 2013; Boitani et al., 2007; Gilbert-Norton et al., 2010; Maiorano et al., 2015; Whitelaw and Eagles, 2007). Dispersal linkages are often structural features of the landscape, such as habitat corridors or stepping-stones that are created, protected, or maintained under the assumption that they directly support the movement of organisms and their genes, between fragments (known as functional connectivity). For plants, an alternative strategy to reconnect populations exists where vectors of seed or pollen dispersal, instead of structural aspects of the landscape, are restored for focal species. For example, rotational

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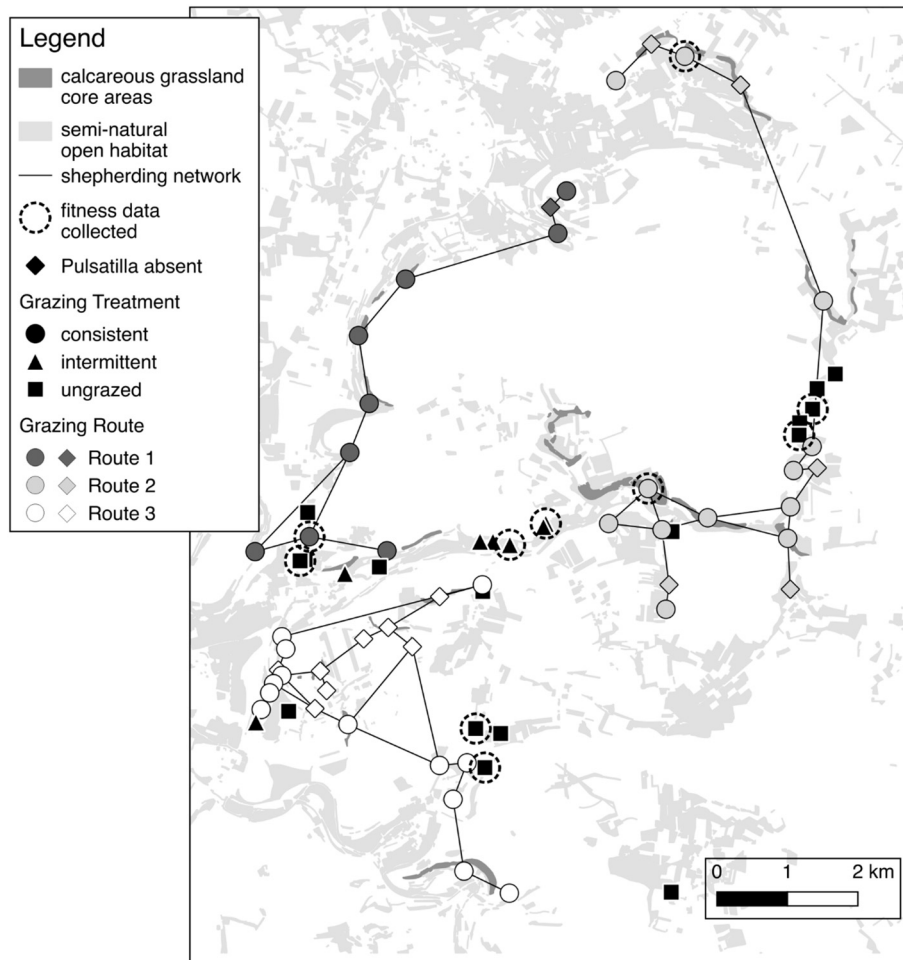


Fig. 1. Location of calcareous grassland patches and grazing treatment of patches in the study area in the Franconian Alb, Germany. Grazing routes connecting consistently grazed populations are indicated by black lines. Dashed circles indicate populations where fitness-related traits were measured. Semi-natural open habitat is shown in light grey and core calcareous grassland patches ('core areas', see [Methods](#) for details) are indicated in dark grey.

shepherding has the potential to disperse seeds over very long distances (e.g. > 100 km; [Fischer et al., 1996](#); [Manzano and Malo, 2006](#)) and has been used as a strategy to reconnect grassland plant populations in central Europe ([Auffret et al., 2012](#); [Butaye et al., 2005](#)).

The spatial extent of ecological connectivity networks and their large number of corridors often preclude the collection of base-line connectivity data to help inform decisions about the suitability of linkages for protection. Most often, ecological connectivity networks are designed solely based on the structural connectivity of the landscape ([Cushman et al., 2009](#)). More recently, conservation managers have considered *potential* functional connectivity when designing networks, using dispersal thresholds of focal species to select linkages for protection (e.g. [Bruinderink et al., 2003](#); [Carroll et al., 2012](#); [Cushman et al., 2009](#)). However, it is rarely tested if ecological connectivity networks are successful at maintaining *actual* functional connectivity (i.e. realized dispersal or gene flow, [Calabrese and Fagan, 2004](#), but see [Melles et al., 2012](#)), or test if the enhanced connectivity provided by the network is enough to maintain genetic diversity of populations. Consequently, there is a great need to evaluate the utility of ecological connectivity networks for supporting functional connectivity for focal species and communities ([Boitani et al., 2007](#)). Neutral genetic diversity on its own may not be a suitable conservation target as the argument to conserve diversity is made on the basis of its presumed association with fitness and potential for adaptation; for selectively neutral markers this evidence is equivocal across the plant world ([Leimu et al., 2006](#)). Thus a better evaluation of the outcomes of conservation planning involves applied targets such as fitness compo-

nents or a demonstrated link between diversity and fitness.

Here we tested the efficacy of an ecological connectivity network implemented in southern Germany since 1989 to reconnect abandoned calcareous grassland fragments through rotational shepherding. We measured genetic differentiation, genetic diversity and fitness-related traits in the perennial wildflower *Pulsatilla vulgaris* Mill. (Ranunculaceae) – a flagship and specialist species of calcareous grasslands in Europe and one of high conservation concern ([Schweizer and Hasinger, 2014](#)). We tested the hypothesis that the shepherding network maintains seed dispersal and thus gene flow of populations, and that this enhanced gene flow translates to higher genetic diversity and fitness. Previous ecological research in this system showed that shepherding connectivity is associated with increased species richness ([Wagner et al., 2013](#)), patch colonization rates ([Rico et al., 2012](#)) and patch occupancy ([Rico et al., 2014a](#)) of characteristic calcareous grassland plants. At the molecular level, research on a single species, *Dianthus carthusianorum*, indicated that shepherding decreased genetic divergence among connected populations ([Rico et al., 2014b](#)), and increased within-population neutral genetic diversity ([Rico et al., 2014a](#)). The question that remains is whether such an increase in genetic diversity is enough to make an impact on the fitness of populations, specifically for species of concern such as *P. vulgaris*. We ask: (1) Does the shepherding network explain gene flow among *P. vulgaris* populations, as quantified by population-specific genetic differentiation? (2) Does the potential enhanced gene flow provided by the shepherding network translate to higher genetic diversity in connected populations? (3) Does higher genetic diversity translate to higher

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