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Semi-natural river system maintains functional connectivity and gene flow of the critically endangered gravel grasshopper (*Chorthippus pullus*)

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River engineering and the subsequent loss and fragmentation of riparian habitats during recent centuries have had serious impacts on the distribution and population size of many riverine species. Thus it is important to identify the characteristics of semi-natural river systems that still support functional connectivity for vulnerable species. *Chorthippus pullus* is a critically endangered grasshopper that inhabits patches of gravel banks along Alpine river systems. The species' distribution conceptually resembles a metapopulation. We analysed the patch occupancy and gene flow of a *C. pullus* population in a river system that had been historically drained in 1923 and improved 67 years later by allowing residual water flow. In 2010, we surveyed a total of 43 patches for occupancy, marked and recaptured 299 individuals and analysed DNA samples of 16 local populations using five microsatellite markers. We further correlated a measure of gene flow to landscape resistance matrices using least-cost-path modelling of the contemporary landscape. Our results show that occupancy patterns are positively related to habitat area and connectivity. Gene flow was restricted by forests and large river streams in the contemporary semi-natural situation. The observed high level of genetic diversity is potentially the result of the historical management over several decades. To preserve functional connectivity and gene flow among local populations of critically endangered gravel grasshoppers, habitat availability and suitability have to be maintained by ensuring appropriate temporal and spatial fluctuations in water level.

1. Introduction

During recent centuries, river systems all over the world have undergone tremendous changes. These include canalisation to avoid flooding events and the construction of reservoirs for electricity generation and drinking water which result in habitat fragmentation (Gleik, 2003; Tockner and Stanford, 2002; Ward et al., 1999), the loss of riparian habitats and species, as well as a decrease in habitat connectivity (Giller, 2005; Naiman et al., 2005). Numerous riparian and aquatic species are adapted to the dynamic nature of river systems and depend on fluctuating water levels. These species therefore encounter problems in human-modified environments and their survival may be threatened (Robinson et al., 2002; Smith et al., 2009).

Flood dynamics cause periodic disturbances that alter the location and shape of gravel banks, the vegetation that grows on them and the extent of river tributaries. Natural fluctuations and disturbances can increase habitat availability and connectivity (Robinson et al., 2002). In order to maintain populations in discontinuous landscapes, species have to be mobile among and must have the ability to cross intervening landscapes to reach habitat patches. Intervening landscapes can either impede or facilitate the dispersal of species among local populations which potentially is a disadvantage for those species with low dispersal abilities (Fahrig, 2003). For instance, terrestrial riparian invertebrates usually do not cross the river but typically migrate laterally, following the water line (Adis and Junk, 2002). The habitat fragmentation and isolation caused by channelling may lead to decreased dispersal and gene flow, increased inbreeding, higher mortality and a loss of genetic variability (Fahrig et al., 1995; Gibbs, 1998). These factors could ultimately cause local populations to become extinct (Saccheri et al., 1998).

Metapopulation biology assesses the effects of dispersal among local populations inhabiting discrete habitat patches and the requirements for regional persistence of species with non-permanent local populations (Hanski, 1991). For a functional metapopulation, local populations have to be connected by a gene flow that is not restricted to neighbouring populations, but occurs among all pairs of local populations (Pollux et al., 2009). Applying these findings to discontinuous landscapes like riparian ecosystems, species' survival can only be sustained if the extinction rate is compensated by an equal rate of colonisation (Levins, 1969; Hanski, 1991). Where landscape fragmentation is the result of natural and anthropogenic disturbances, patch area and habitat isolation are the most

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important landscape characteristics for metapopulation biology since extinction rates increase with decreasing patch area and colonisation rates decrease with increasing patch isolation (Gilpin, 1987; Hanski, 1999). If a local population has become extinct in a habitat patch, e.g. as a result of flooding of a gravel bank, recolonisation is more likely to be successful the less isolated and more connected the patches are. For example, the drying out of a river tributary can reconnect habitat patches. Metapopulation studies usually use simplified measures for connectivity (Hanski, 1998). In most cases this is the geographical distance from the nearest neighbour habitat patch occupied by the focal species. According to Wright (1943), gene flow is restricted by distance, with genetically closely related individuals or populations occurring smaller geographical distances apart.

In discontinuous riverine landscapes however, suitable and unsuitable habitats alternate and animals may not follow the shortest path. Instead, they may follow the least-cost dispersal path, i.e. the more hospitable route, so that dispersal costs can be lower even though the route may be longer (Adriaensen et al., 2003). Potentially, gene flow patterns in animals will then follow the same routes. Characterising the landscape matrix and including it in genetic analyses may help to understand metapopulation dynamics better (Pollux et al., 2009) and lead to more realistic predictions of connectivity and population dynamics than simple models of isolation by distance (Moilanen and Nieminen, 2002).

Depending on a particular species' life history and physiological and anatomical characteristics, certain landscape elements may act as barriers or provide benefits which in turn may influence the species' dispersal patterns and genetic exchange (Wiens, 2001). For instance, streams and forests influence the dispersal of adult individuals of riparian calopterygid damselflies, as these resources provide resting and foraging sites (Jonsen and Taylor, 2000). To develop a simplified, but ecologically relevant, representation of a real landscape that corresponds to an animal's dispersal ability, we can either depend on expert knowledge or perform experiments designed to assign resistance values to different landscape components (Verbeylen et al., 2003; Coulon et al., 2004; Rayfield et al., 2010; Spear et al., 2010).

In the present study we investigated presence-absence patterns and gene flow of a population of the gravel grasshopper (*Chorthippus pullus*). In Central Europe, *C. pullus* mainly occurs along natural Alpine river systems where disturbance dynamics create discontinuous patterns of gravel banks. The study area is on the upper part of the river Isar in Bavaria, Germany, which has one of the few remaining semi-natural river systems in the Alps with an extensive flood plain and riparian forests. The study area formed a natural river ecosystem until the Krüner dam was built in 1923 upstream of the area. This dam retained all the water from the Isar, so that the area below the dam completely dryed out. The water was collected for energy production and channelled to a reservoir called Walchensee. Only flood events where discharges were higher than 25 m^3/s induced the spillways to open and flooded the riverbed below the dam, including the study area. These human-induced disturbances led to less groundwater, so that many plants were unable to establish root systems. As a result, there were extensive open areas and low vegetation cover in the channel and along the banks (Reich et al., 2008). Since 1990, a multi-functional conservation practice has been implemented which ensures seasonal residual water flow of 4.8 m^3/s in summer and 3.0 m^3/s in winter (M. Hannweber, personal communication). Since spillways are opened during flooding events and the Isar is supplied by several tributaries downstream of the dam, variation in rainfall causes periodic disturbance events and preserves some typical traits of a riparian ecosystem.

The goal of this study was to assess how habitat occupancy, genetic diversity and genetic differentiation of local populations of *C. pullus* are influenced by a dynamic pattern of discrete habitat patches. The local populations were embedded in a matrix composed of various landscape types differing in their resistance to *C. pullus* movement, as the species is not expected to cross large river branches but to move along open areas with low vegetation cover (Baur et al., 2006; Janssen, 1993). Using a landscape genetic approach, we correlated the genetic differentiation among local populations (F_{ST}) to landscape resistance matrices using least-cost-path modelling of the contemporary landscape.

2. Methods

2.1. Study species

Chorthippus pullus is a short-horned grasshopper (Orthoptera: Caelifera, Acrididae). The species is thermophilic and mainly occurs in two different habitat types in Europe: in xeric grasslands along forest margins in Eastern Europe and along a small number of natural riverbeds in the Alps in Central Europe (Schlumprecht and Waeber, 2003; Maas et al., 2002). In Central Europe, *C. pullus* is classified as a critically endangered species (Monnerat et al., 2007; Ingrisch and Köhler, 1998), with rare occurrences in the Alps today due to the loss of riparian ecosystems. *Chorthippus pullus* is a pioneer species that colonises gravel banks and conceptually resembles a metapopulation (Fig. 1). Its preferred habitats are characterised by substrate mixtures of sand and stones with low vegetation cover of grasses, herbs and bushes (Baur et al., 2006; Janssen, 1993; Landeck et al., 1999; Schlumprecht and Waeber, 2003; Schwarz-Waubke, 1997).

Due to its shortened wings *C. pullus* is unable to fly and its dispersal is thus limited. However, some fully winged individuals have been observated (macropterous; Janssen, 1993; Schlumprecht and Waeber, 2003; personal observation at the Isar 2009/2010, Germany). Although macropterous individuals have an improved jumping ability, Janssen (1993) did not detect any differences in dispersal ranges compared to micropterous (short-winged) individuals. Therefore, this species is considered to be philopatric (Kurth, 2007), with small home ranges (below 100 m^2; Janssen, 1993; Schwarz-Waubke, 1998). Since the species lives close to the river margin and eggs are deposed in the sand, an alternative dispersal path could be the longitudinal downstream drift in the river. Stream drift is important for riparian plant species (Pollux et al., 2009), as well as for several aquatic invertebrates and amphibians (Bruce, 1985; Lambeets et al., 2010; Waters, 1972), and could also play a role in *C. pullus* movement.

Local populations of *C. pullus* are situated along the Isar in Bavaria, Germany. We investigated a section of the Isar 1.3–1.4 km long, located between river-kilometres 240.0 and 242.0 (Fig. 1). The floodplain is about 300–400 m wide. The lower boundary line to the adjacent mountain slopes defined the lateral margins of the study area, which included only flat areas influenced by the flow dynamics of the river system.

2.2. Population analysis

2.2.1. Habitat survey

To identify potential habitat patches, we conducted a habitat survey at the very beginning of the fieldwork. The extent of the study area was assumed to be appropriate for detecting ecologically meaningful environmental variables on a small scale, particularly when considering the species' small home range and short dispersal distances (Cushman and Landguth, 2010; Janssen, 1993; Schwarz-Waubke, 1998). The goal of the extensive habitat classification was to: (1) identify potential habitat patches on gravel banks and investigate their size, margins and distribution; and