



The short-term impact of wetland restoration on the genetic diversity of a predominantly clonal plant species



J. Oudot-Canaff^{a,*}, G. Bornette^a, M.R. Viricel^a, F. Piola^a, S. Mousset^b, E. Martel^a

^a Université de Lyon, UMR5023 LEHNA, Université Lyon 1, CNRS, ENTPE, F-69622 Villeurbanne, France

^b Université de Lyon, Université Lyon 1, CNRS, UMR5558 Laboratoire de Biométrie et Biologie Evolutive, F-69622 Villeurbanne, France

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ABSTRACT

Genetic diversity plays a major role in ensuring the adaptive capacity and long-term viability of populations. Recent studies have shown that evaluations of the ecological benefits of ecosystem restoration should incorporate the impact of restoration on population genetic variability to accurately guide restoration priorities. This study aimed to analyse the population genetic diversity of an aquatic plant, *Berula erecta*, in wetlands restored by sediment dredging using natural local wetlands as a reference to assess the impact of ecological restoration on genetic diversity. The analyses were performed using microsatellite markers. Restoration led to a considerable increase in the open water surface area at the site, and the restored areas were efficiently colonised by *B. erecta*. The populations exhibited a high level of genetic diversity, even though clonal propagation is the major reproductive mode of this species. Two years after restoration, population genetic diversity (A_R allelic richness, F_{IS} and P_C) was very similar between the restored and natural wetlands. For one restored wetland, the individuals in the restored area of the wetland showed greater allelic richness than those in the unrestored areas of the same wetland. In addition, most of the multilocus genotypes observed in the restored wetlands only occurred as single individuals, suggesting that clonal propagation is not the only mode of recolonisation after restoration. The source of the new genotypes that appeared after restoration may have been a local relict population, seeds remaining in the seed bank after restoration (cryptic genetic diversity), or propagules (seed or vegetative fragments) that migrated into the wetland. These results suggest that the benefits of restoration may depend strongly on the genetic diversity of established relict and dormant populations. Population diversity, in turn, may partly depend on the ecological characteristics of the site (i.e., connectivity of the water body to the surrounding wetlands, successional stage and site history).

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1. Introduction

Human activities affect climate and the environment, and these alterations are particularly important in aquatic ecosystems (e.g., [Millenium Ecosystem Assessment, 2005](#)). Wetlands are among the most threatened ecosystems worldwide, and half of the world's existing wetlands are expected to disappear within the next 50 years ([Millenium Ecosystem Assessment, 2005](#)). These ecosystems are threatened both quantitatively (e.g., through the loss of area by drainage and river regulation) and qualitatively (e.g., through a decrease in connectivity or through eutrophication) ([Lasne et al., 2007](#); [Geist, 2011](#)). In floodplains, river regulation and other anthropogenic pressures lead to the collapse of fluvial dynamics and

the degradation of water quality and quantity, reducing the number, area, and quality of wetlands and their connectivity with streams and groundwater ([Bornette and Heiler, 1994](#); [Bornette et al., 1998b](#)). Organisms cope with these changes in different ways, through natural selection at medium or long time scales and through migration or morphological and/or physiological plasticity at shorter time scales ([Price et al., 2003](#); [Rice and Emery, 2003](#)). The rate and magnitude of anthropogenic alterations can, however, exceed the capacity of the developmental, genetic and demographic mechanisms that populations have developed over evolutionary time to survive environmental variation ([Harris et al., 2006](#); [Chevin et al., 2010](#); [Salamin et al., 2010](#)). Freshwater communities may be lost because aquatic ecosystems are hotspots of human use and alteration ([Dudgeon et al., 2006](#)) and because the remaining ecosystems are subject to succession and the related process of terrestrialisation ([Bornette and Heiler, 1994](#); [Bravard et al., 1997](#); [Keddy, 2010](#)). During these processes, populations may encounter differential selective pressures and/or experience genetic drift, leading to strong genetic erosion ([Amos and Harwood,](#)

* Corresponding author. Present address: Université de Lyon, UMR5023 LEHNA, Université Lyon 1, CNRS, ENTPE, F-69622 Villeurbanne Cedex, France.
Tel.: +33 4 72 43 29 57; fax: +33 4 72 43 11 41.

E-mail address: joudotcanaff@gmail.com (J. Oudot-Canaff).

1998). Consequently, there is a need to implement and promote the preservation, restoration, maintenance and improved management of aquatic ecosystems.

Ecological restoration is defined as “the process of assisting the recovery of an ecosystem that has been degraded, damaged or destroyed” (SER, 2004). One goal of population restoration is to increase species population sizes to a level that is sufficient for ensuring long-term species persistence on the landscape (Liu et al., 2008). Ecosystem restoration is usually associated with a scientific monitoring programme that determines the restoration method to be used, the goal of the restoration project in terms of biodiversity and function, and the criteria for assessing the success of the restoration process (Jungwirth et al., 2002; Woolsey et al., 2007). These criteria are usually related to physical functioning (Palmer et al., 2005), the maintenance or recovery of rare or endangered species, and species richness (Cristofoli and Mahy, 2010). However, the criteria rarely address genetic diversity explicitly, even less so in aquatic ecosystems (Geist, 2010). When they do, it is usually for conservation purposes (Galeuchet et al., 2005). In such cases, the objective is often the reintroduction of species (Henry and Amoros, 1995; Williams and Davis, 1996; Buijse et al., 2002; Travis et al., 2002; Uesugi et al., 2007; Liu et al., 2008; Lloyd et al., 2012). The impact of restoration on population genetic diversity is, however, of particular interest for accurately assessing the ecological benefits of restoration (Geist, 2010). Indeed, genetic diversity is a crucial parameter of the health and long-term viability of the populations that constitute ecological communities and is critical for the maintenance of biodiversity and related ecosystem functions (Amos and Harwood, 1998; Falk, 2001; Travis et al., 2002). Among other human impacts to ecosystems, landscape fragmentation strongly affects gene flow between populations (Lange et al., 2010; Horreo et al., 2011). As a result, species dispersal may be insufficient to offset local extinctions, leading to the erosion of local genetic diversity and an unbalanced metapopulation. If this genetic erosion is associated with a reduction in fitness components, positive feedback between population size and genetic diversity may increase the probability of population extinction. When a population is isolated from the immigration of new breeding individuals that offsets the consequences of a small population size (Richards et al., 2003), species can disappear from the landscape (Amos and Harwood, 1998).

The extinction risk for local populations may be reduced by increasing the surface area of isolated sites, restoring degraded sites, or increasing the connectivity between sites (McEachern and Bowles, 1994). Many wetland restoration schemes designed to increase water depth use substrate digging (Buijse et al., 2002), which can cause biodiversity losses by eliminating (1) existing plant communities and (2) the seed bank, which could provide genetic resources to rescuing for the past diversity (Ottewell et al., 2011). Therefore, such restoration schemes may negatively affect the recovery of plant genetic diversity. Furthermore, in the case of clonal plants, restoration may lead to the fragmentation, dispersal and establishment of ramets sharing the same multilocus genotypes, potentially leading to recolonisation of a site by only a few genotypes. Conversely, the recolonisation of restored habitats by several poorly fertile clonal genotypes may protect the population from inbreeding (Travis et al., 2004).

Therefore, it remains unclear whether wetland restoration projects may favour or reduce genetic diversity. This study aimed to address this issue by comparing the genetic diversity of a stoloniferous aquatic plant species, *Berula erecta* (Hudson) Coville (Apiaceae), among four riverine wetlands (two restored sites and two natural sites). Prior to the implementation of the restoration project, the two restored sites were largely terrestrial and free of aquatic species, although aquatic species were still present in some small relictual pools. The process of restoration consisted of preserving

these pools and dredging the dry parts of the wetlands to restore aquatic conditions.

The hypotheses tested in this study are as follows: (1) on a short time scale, restoration does not lead to genetic diversity equivalent to that of natural local sites; and (2) the genets that colonise the sites after restoration represents a subset of the genets present in the remaining water bodies.

B. erecta is a good model because this species is broadly distributed along calcareous rivers and streams where it reproduces mainly by clonal growth (Combroux et al., 2001). Furthermore, *B. erecta* extensively colonises restored wetlands after restoration, thereby ensuring large populations on which the hypotheses can be accurately tested. The genetic diversity of *B. erecta* populations is studied using microsatellites markers, which are valuable tools for analysing migration and founder events (Esfeld et al., 2008).

2. Materials and methods

2.1. Study species

B. erecta is an aquatic perennial plant species that is able to spread by sexual reproduction and vegetative means (stolons or fragments). This species is widely distributed in alkaline floodplains and is frequently associated with pioneer plant communities in flood-disturbed habitats (Bornette et al., 1998a). The plant is common at the wetland sites chosen for this study (Bornette et al., 2001). *B. erecta* is only rarely found in seed banks (Thompson and Grime, 1979; Combroux et al., 2001; Combroux and Bornette, 2004) and propagates very efficiently by vegetative means (Puijalon et al., 2008). These patterns suggest that this species may be characterised by relatively low genetic diversity, in spite of its broad distribution.

2.2. Study sites and plant collection

Four wetlands located in the Ain floodplain (Brotteaux, Villette, Bellegarde, and Gourdans) were surveyed. Two of them (Brotteaux and Bellegarde) were restored during the winter of 2005–2006. These two wetlands differ in their connectivity to the river. The Brotteaux wetland is permanently connected to the river downstream, whereas the Bellegarde wetland is disconnected during times of average streamflow and is only connected to the river during high discharge floods (floods with a return-time of 10 years on average). The restoration was justified because these wetlands changed rather rapidly (on a 10-year scale) from pools and riffles slowly flowing in a former channel to, after the deepening of the groundwater table, alternating coarse-grained vegetated dry zones and aquatic zones. *B. erecta* was absent from the terrestrial parts of the sites before restoration but remained in the aquatic zones. The restoration involved preserving the existing water bodies (called ‘preserved zones’ below) and dredging the dry areas (called ‘restored zones’) of the wetlands to reach the groundwater table and establishing a continuous aquatic channel (Fig. 1). No supplemental plant material was added to the sites after they were dredged. The recolonisation of the restored sites was thus dependent entirely on natural plant dispersal, propagation, seed bank expression, or seed germination. Two unrestored wetlands (Villette and Gourdans) were used as reference sites. These wetlands function as phreatic temporary flowing streams and are floristically stable because of groundwater inputs and periodic scouring floods. They were selected as reference sites because they are permanently aquatic and are located near the restoration sites (Villette is close to Bellegarde, and Gourdans is close to Brotteaux). A total of 159 individuals of *B. erecta* were sampled for molecular analyses during the second summer following the restoration (summer 2007).

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