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The use of habitat and dispersal models in protecting European black poplar (*Populus nigra* L.) from genetic introgression in Slovenia

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ABSTRACT

European black poplar (*Populus nigra* L.) has become threatened by the widespread disappearance of riparian forests in Europe. Gene introgression through hybridization with related, non-indigenous poplar taxa may additionally reduce the population size and genetic diversity of native black poplar. We assessed the exposure of native black poplar in Slovenia to genetic introgression using a combination of habitat and gene flow models. The habitat model was built with data mining on forest inventory data employing classification decision trees. Dispersion distances for pollen, seeds and vegetative parts at 0.9% and 0.001% of adventitious presence threshold were assessed using modified gene flow models. To protect native black poplar, protection zones around native black poplar stands were proposed. Since the population of native black poplar may be exposed to various introgression pressures (e.g., the vicinity of exotic, genetically compatible poplar plantations, or feral populations potentially initiated along transport corridors or rivers), we assessed the intensity of introgression pressure by intersecting the occupied and potential habitat with the introgression pressure areas. In 2010, native black poplar occurred on 43,756 ha (2.2% of the total Slovenian territory), while the suitable habitat extended up to 108,724 ha (5.4%). The protection zones were 0.5–4.6 times larger than the occupied and potential habitat depending on the selected threshold and the type of dispersion vector. In the worst case scenario, 45.1% of protection zones would be exposed to high hybridization pressure. We recommend extending the proposed methodological approach to other regions with endangered black poplar.

1. Introduction

Natural populations of forest tree species are increasingly exposed to various influences that could reduce their genetic variation and jeopardize their life cycle processes and adaptability. Besides atmospheric pollution and overall environmental changes, a series of factors affect the conservation and management of forest genetic resources. These include intensive management, regeneration by planting including wide-scale transfer of forest reproductive material, decreased population sizes, especially due to forest fragmentation, creation of new transport corridors and introduction of exotic forest tree species and their hybrids, and genetically modified trees (Geburek and Turok, 2005). These factors can lead to a loss or to an alteration of the genetic identity of autochthonous tree populations. It has been estimated that up to 99% of European riparian forests have disappeared (Lefèvre et al., 1998; Hughes and Rood, 2003), threatening European black poplar (*Populus nigra* L.) (hereafter referred to as black poplar), which is an important tree species of these forests.

Black poplar is a dioecious species, which results in high pollen migration between male and female trees (Legionnet and Lefévre, 1996). Its light pollen and seeds are dispersed by wind and its seeds also by water, which enables the exchange of genes and seeds between poplar populations (Vanden Broeck, 2003) and enriches the gene pool (Lefévre et al., 2001). High levels of genetic diversity, which are promoted by sexual reproduction, are very important for the survival of black poplar (Fossati et al., 2003), but there are concerns that the wide scale introduction of genes from foreign species or hybrids with a very narrow genetic base could lower the effective population size and influence the gene complex of native black poplar that have evolved and that will evolve during time in response to environmental conditions (Cagelli and Lefèvre, 1995; Vanden Broeck et al., 2004). Gene introgression through hybridization with related, non-indigenous poplar taxa further endangers natural black poplar populations and potentially threatens their conservation.

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In general, hybridization in the genus *Populus* is successful between species from the same section, but occasionally species from different sections also produce viable seeds (Rajora, 1989; Barrett et al., 1993). *P. nigra* (L.) and *Populus deltoides* Bartr. ex Marsh. that belong to the section *Aigeiros* are genetically compatible, and their hybrid *Populus* × *canadensis* Moench (Erhardt et al., 2000) has been widely planted across Europe. There is great concern about massive introgression of genes from *Populus* × *canadensis* or *Populus deltoides* F_1 hybrids into the native *P. nigra* gene pool (Vanden Broeck et al., 2005) and low diversity of F_1 hybrid poplars is considered to pose a very important threat to black poplar genetic diversity (Cagelli and Leféyre, 1995). The potential hazard from natural hybridization with cultivated poplars is the loss of *P. nigra* as a pure species that may result from genetic assimilation by the more numerous cultivated poplars or from outbreeding depression (Vanden Broeck et al., 2012). Some studies (e.g. Benetka et al., 1999; Fossati et al., 2003; Tabbener and Cottrell, 2003) could not confirm introgression of *Populus* × *canadensis* or *Populus deltoides* into the progeny of *P. nigra*, but Vanden Broeck et al. (2004, 2012) and Ziegenhagen et al. (2008) presented evidence for spontaneous backcrossing between male *Populus* × *canadensis* and female *P. nigra*. Introgression of *Populus deltoides* genes to *P. nigra* was also confirmed by the presence of seedlings descending from a *Populus* × *canadensis* female (Pospíšková and Šálková, 2006). Once hybridization has begun, it is in general difficult to stop, especially if hybrids are fertile and produce progeny among themselves and with the parental species (Allendorf et al., 2001). Bialozyt et al. (2012) have detected F2 hybrids between *P. nigra* and *P.* × *canadensis* in the seeds, while first generation backcrosses occurred in seeds as well as in juveniles. High levels of introgression from *Populus* × *canadensis* can be expected in the situations where isolated female black poplar trees are surrounded by interspecific hybrid males (Vanden Broeck et al., 2004, 2005). Introgression of *P. nigra* 'Italica' is also theoretically possible but has not been confirmed for a long time, possibly due to non-simultaneous flowering (Imbert and Lefévre, 2003; Tabbener and Cottrell, 2003; Vanden Broeck et al., 2004). However, Chenault et al. (2011) recently found five trees which they consider as probable F1 hybrids between *P. nigra* and *P. nigra* 'Italica'. Since the plantations of *P. nigra* 'Italica' represent only one (male) genotype, introgression of its pollen may also result in a severe reduction of genetic diversity of wild black poplar populations. Theoretically, introgression of genetically modified (GM) poplar clones is also possible if these are eventually used in the vicinity of black poplar stands. At present time there are no commercial GM poplar plantations in Europe. However, this situation might theoretically change in the future. Flowering periods of poplars are extremely variable, not only between species or growing sites, but also between years (Vanden Broeck et al., 2003), and changes in flowering periods cannot be ruled out in the coming decades of global climatic change. In conclusion, most of present or future commercial poplar clones can theoretically be genetically compatible with domestic *P. nigra*.

Since hybridization and habitat reduction could threaten the existence of native black poplar in European riparian forests, several studies have been conducted in order to determine the endangerment of the species (Imbert and Lefévre, 2003; Fossati et al., 2003; Benetka et al., 1999; Tabbener and Cottrell, 2003; Vanden Broeck et al., 2004; Ziegenhagen et al., 2008; Vanden Broeck et al., 2003, 2006; Csencsics et al., 2009; Brus et al., 2010). Many European countries reported (EUFORGEN, 2007) significant reductions in populations or even complete disappearance of black poplar mostly due to habitat loss, cutting of native black poplar stands and excessive hybrid plantations, while some countries reported well-preserved populations with active regeneration in preserved riparian habitats.

The habitat of black poplar is lowland floodplain with alluvial hydromorphic sandy soil without pedogenetic processes, where a river regularly deposits sediments (Kajba, 2004). It is characterized by continuous or periodic anaerobic conditions during floods, but during normal water levels, the soil has large vertical pores which enable good soil aeration. However, black poplar avoids frequently flooded areas in the lowlands. It is a pioneer and heliophilic (i.e. sun-loving) species, which allows it to colonize also open areas on more arid sites (Brus, 2005; Vanden Broeck, 2003).

In Slovenia, forests with preserved native black poplar are found mainly in the lowlands up to 800 m.a.s.l., mostly in the Pannonian and Dinaric regions (Brus, 2005), but they are also present along the rivers Mura, Drava, Sava, Krka and Soča (Božič et al., 1999 and Božič, 2010, Fig. 1).

The aim of this paper is to propose a new methodological approach to development of conservation strategy through the following steps: (1) identification of the occupied and potential habitats of black poplar; (2) determination of the size of the protection zone using dispersal models and (3) assessment of the level of exposure of native black poplar stands to genetic introgression. The proposed approach is demonstrated for black poplar in Slovenia as a case study.

2. Materials and methods

2.1. The data

The data for identification and description of existing locations of black poplar stands and the data needed for the construction of potential habitat models were acquired from the forest information system of the Slovenia Forest Service. Forest inventory integrate attributes describing forest site and forest stand properties. Every ten years, trees with a diameter at the breast height (dbh) $\geqslant$ 10 cm are measured on permanent 500 m^2 sampling plots with a dominant sampling network size of 250 m × 250 m and 250 m × 500 m extending through all Slovenian forests regardless of their ownership. Data from the sampling network are up-scaled to forest compartments, which are distinguished by the specific environmental and stand attributes, and complemented with field stand descriptions. In our research, we used the data for forest compartments from the 2010 forest inventory (SFS, 2010). The dataset consisted of a total of 69,997 forest compartments (with an average size of 16 ha), where 1408 compartments had at least 1 m^3 of black poplar in the growing stock. For the purpose of habitat modeling, we used a set of 11 environmental attributes (Table 1) to describe poplar habitat (SFS, 2010; CPVO, 2009).

Forest compartments with at least 1 m^3 ha^{-1} of black poplar in the growing stock indicate occupied habitats. The habitat may also exist in stands where black poplar was replaced with other tree species due to economic reasons, and in non-forest areas such as agricultural land or road and railway verges. To identify the potential black poplar habitat in forests, we used the map of Slovenian forest vegetation communities (SFS, 2010), where each community is described by natural tree species composition. Based on the natural tree species composition of forest communities and forest communities in the occupied habitat we grouped all 99 described forest communities into four sets according to habitat suitability for black poplar:

(1) Black poplar is not present in the forest community (e.g. mountain forests).
(2) Presence of black poplar has a low probability: habitats with extreme environmental conditions (e.g. drought, cold climate).