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# Population dynamics of *Paeonia officinalis* in relation to forest closure: From model predictions to practical conservation management

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ABSTRACT

In Europe, the abandonment of agricultural activities and traditional forest usages have led to forest spread, which eventually affects the population ecology of open habitat species. This is particularly apparent in the Mediterranean hinterland, which hosts many endemic and/or rare species. In this study we explored the effects of forest spread on the population dynamics of *Paeonia officinalis*, a long-lived perennial species protected in France. We also simulated the effects of different forest management regimes, by projecting the dynamics of populations under different sylvicultural cycle lengths. From 2003 to 2009, we monitored individual plants in four sites in Southern France, where each population occurs in a woodland and in an adjacent open habitat. We found that forest encroachment negatively impacted population dynamics, manifested by reduced reproduction and germination and a marked stasis of vegetative demographic stages. Using matrix models with demographic and environmental stochasticity, we showed that for two sites, populations were only viable in the open habitat but not in the woodland. In one site, populations were viable both habitats, whereas in one site, populations were non-viable in both habitats. Tree cuttings positively affected the four populations either by increasing population stochastic growth rate or by decreasing extinction rate. However, the effectiveness of forest management depended on local ecological conditions, such as the identity of the dominant tree species (evergreen vs deciduous) and sylvicultural system (coppice vs exotic plantation). Our study highlights the need for of tailor-made rather general management recommendations in perennial plant conservation.

## 1. Introduction

Land use changes are known to be important drivers of biodiversity loss. Although habitat loss by urbanisation, drainage of wetlands or agriculture intensification is often highlighted as a major cause of biodiversity decline (see e.g. Sala et al., 2000; Robinson and Sutherland, 2002; Tilman et al., 2002), rural depopulation since the middle of the 20th century and the abandonment of traditional agro-sylvo-pastoral activities also play an important role, particularly in low mountains and in the northern part of the Mediterranean region (Carmel and Kadmon, 1999; Debussche et al., 1999; MacDonald et al., 2000; Thompson, 2005). As a consequence, fields and grasslands have been rapidly colonised by woody species by natural succession. Open woodlands that were traditionally coppiced on a 15–20 year rotation for fire-wood or charcoal have also experienced habitat closure (Barbero et al., 1990; Andrieu et al., 2013). Beyond negative impacts on ecosystem functioning such as modifications of fire disturbance regimes or water resources (Debussche et al., 1987; Moreno et al., 1998; MacDonald et al., 2000), this can affect species population dynamics (e,g. Sirami et al., 2010; Ricouart et al., 2013; Zakkak et al., 2014).

Canopy closure has been shown to negatively affect plant performance and population dynamics in many open habitat species (e.g. Oostermeijer et al., 1994; Menges and Dolan, 1998) as well as shade tolerant species (e.g. Valverde and Silvertown, 1998; Nicole et al., 2005; Jacquemyn et al., 2008; Van Calster et al., 2008). This occurs in a variety of ways including a decrease in germination rate (Valverde and Silvertown, 1995; Batlla et al., 2000), reduced plant growth (Barkham, 1980a, 1980b; Whale, 1984; Knox, 1997; Ticktin and Nantel, 2004),

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**Table 1**
Summary of characteristics of open habitat and woodland habitat in each study site (W: woodland, O: open habitat).

| Site | Location | Elevation (asl) | Woodland habitat | Open habitat | Management history | Sample size (2003) |
|---|---|---|---|---|---|---|
| PSL | 43° 46′ N 3°46′ E | 300–350 m | Predominantly evergreen *Quercus ilex* L. coppice with scattered deciduous species. | Natural clearings dominated by *Bromus erectus Huds.* and *Buxus sempervirens* L. | Last coppice ~ 1950, grazing abandonment ~ 1970. | W: 12 plots, 150 individuals<br>O: 16 plots, 238 individuals |
| STF | 44°14′ N 4°07′ E | 450 m | Predominantly evergreen *Quercus ilex* L. coppice with scattered deciduous tree species. | Open clear-cut of small *Q. ilex* trees conducted in 1996, dominated by *B. erectus.* | Last coppice ~ 1940 in the woodland habitat, 1996 in the open habitat. | W: 12 plots, 229 individuals<br>O: 7 plots, 247 individuals |
| VIS | 43° 54′ N 03° 27′ E | 550–600 m | Predominantly deciduous: *Q. humilis Mill.* coppice. | Natural shrubby clearing dominated by *B. erectus* with a few small trees. | Last coppice before 1948, grazing abandonment probably ~ 1980. | W: 15 plots, 363 individuals<br>O: 8 plots, 271 individuals |
| TAU | 43°46′ N 3°01′ E | 720–800 m | Predominantly exotic evergreen *Pseudotsuga menziesii* Mirbel plantation interspersed with narrow stripes of deciduous *Q. petraea* Liebl. coppice. | Natural clearings (diameter < 50 m) dominated by *Mercurialis perennis* L. and *Rubus ulmifolius* Schott. with scattered small trees cut in 1999. | Plantation of *Pseudotsuga menziesii* in 1971 on former coppices and grazed moorlands. | W: 13 plots, 132 individuals<br>O: 9 plots, 79 individuals |

and a decline or even absence of flowering and seed production (Barkham, 1980a, 1980b; Cipollini et al., 1994; Valverde and Silvertown, 1995; Knox, 1997; Petit and Thompson, 1998). Canopy closure has also been shown to alter plant-pollinator interactions and thus again reduce plant fecundity (Warren and Thomas, 1992; Cadenasso et al., 1997). Many environmental drivers have been proposed to explain such a decrease in plant performance following canopy closure, such as reduction in light intensity (Valladares et al., 2005), alteration of nutrient cycles (Barkham, 1992; Cadenasso et al., 1997) and changes in water availability (Valladares and Pearcy, 2002). However, the gap between identification of critical demographic parameters and realistic management actions can be large, particularly if population growth rate is sensitive to variation in a demographic parameter that the conservation management staff cannot act upon. For example it is unrealistic to try to restore open-grassland in the context of extensive landscape-scale habitat closure. Forest management that integrates regular coppicing may however be a promising option for the conservation of open-habitat but shade-tolerant plant species in areas affected by forest spread.

Individual monitoring coupled with matrix population models are a powerful tool to address the effects of environmental variables on demographic parameters and population growth rates and ever since the landmark publication of Schemske et al. (1994) have become very popular in plant conservation biology (see e.g. Fréville et al., 2004; Nicole et al., 2005; Andrieu et al., 2013). This allows for instance retrospective analysis (e.g. Life Table Response Analysis) that permits the identification of how past environmental variables affected demographic parameters and population growth rate. It also allows prospective analysis (e.g. elasticity analysis and simulation of population trajectories under different scenarios) predicting the demographic consequences of future management actions to be assessed (Caswell, 2000). These tools have allowed the identification of factors that influence plant population dynamics (Silvertown et al., 1993), such as plant-herbivore interactions (Bastrenta et al., 1995; Kolb et al., 2007; Jacquemyn et al., 2012) and climate variability (Marrero-Gómez et al., 2007), but also comparing different habitat management strategies (Andrello et al., 2012).

The aim of this study was to explore the effects of habitat closure on the population demography of *Paeonia officinalis* L., a rare herbaceous perennial species whose populations are affected by natural forest encroachment and reafforestation (Andrieu et al., 2007; Andrieu et al., 2013), and to identify an optimal sylvicultural regime for conservation management. First, we determined how forest encroachment affects demographic parameters and population viability under demographic and environmental stochasticity. We hypothesised that populations in woodlands would have lower population growth rates and higher extinction risk than populations in open habitats. Second, we tested whether regular coppicing may enhance population viability. To do so, we simulated population dynamics using stochastic matrix models in which the durations of open and woodland phases varied. We use the results to identify pertinent management strategies for perennial plant species occurring in open habitat which are affected by forest closure.

## 2. Materials and methods

### 2.1. Species and study sites

*Paeonia officinalis* L. occurs in the low mountains and hills of central and southern Europe (Tutin et al., 1993). It grows on rocky soils in grassland, open scrubland and woodland. This species is listed for protection by French law and its current population trend is evaluated as decreasing by the IUCN Red List (LC). In France, scattered populations are found in the Southern Alps, Southern Massif Central and locally in the eastern Pyrenees. In the southern part of the Massif Central, populations are distributed along a 200 km wide band of low mountain ranges, from the Rhône valley toward the south-west. Among 20