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Integrating demographic and genetic effects of connections on the viability of an endangered plant in a highly fragmented habitat

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ABSTRACT

Classical ecological theories state that the viability of small metapopulations is critically related to: (1) the correlation of local population dynamics, (2) the possibility of extinct patch re-colonisation, and (3) the effects of genetic deterioration. Recent works suggested that these factors are not independent because dispersal might affect both re-colonisation and genetic rescue processes and because connectivity between habitat patches may be related to their environmental synchrony. Close patches may exhibit both high connectivity and synchronisation of their environments.

Here, we examined these effects in the endangered plant *Ranunculus nodiflorus* that inhabits temporary water puddles, where water corridors constitute the vector (1) allowing seed dispersal throughout puddle networks and (2) leading to synchrony of local environmental factors. We utilised a demo-genetic metapopulation model to show how the antagonistic effects of connectivity and synchrony lead to complex interactions between the species' biology and network configuration. We specifically demonstrated that (1) when an effective seed bank occurs, viability is maximised either for systems of numerous small independent networks (not connected and not synchronised), or for one single large network, while intermediate situations lead to a dramatic increase of the extinction risk; (2) genetic deterioration has notable negative effects on viability only in situations where environmentally driven extinction is buffered by the presence of a seed bank and network configuration; and (3) temporary connections among networks lead to a dramatic reduction of the extinction risk. The implementation of such connections is an efficient management option for the species.

1. Introduction

The spatial structure and configuration of habitats affects the dynamics and persistence of species living in naturally or artificially fragmented landscapes (Hanski, 1997; Hanski and Simberloff, 1997). According to metapopulation theories, persistence depends on both the demography of each sub-unit or patch and the connection or dispersal among the patches (Levins, 1969). Habitat fragmentation may strongly influence metapopulation persistence through its impact on the quality (e.g., size) and number of available connected patches (Thomas et al., 2001; Young et al., 1996). While connection has multiple positive effects on the viabilities of metapopulations, including (re)colonisation, demographic and genetic rescue effects (see, e.g., Brown and Kodric-Brown, 1977; Casagrandi and Gatto, 2002; Fahrig and Merriam, 1985; Noël et al., 2006), studies have noted that the connectivity between habitat patches may be related to the pattern of environmental disturbances or environmental stochasticity at the metapopulation scale, another important process that drives the risk of extinction (Lande, 1993). The connectivity between patches is generally related to the average distance between them (e.g., Goodwin and Fahrig, 2002; Vos et al., 2001). Yet, the distance between two suitable habitat patches partly determines the correlation of their environments and the subsequent synchrony of their dynamics (the so-called Moran effect, see Ranta et al., 1997). The average distance among patches may affect local population synchrony and connectivity. These two processes have antagonistic impacts on population viability that may lead to complex and counter–intuitive relationships between the average distances among patches within a metapopulation and actual viability (McCarthy and Lindenmayer, 2000; Robert, 2009).

Global metapopulation dynamics depend on the connection among patches and the growth rate within each patch, which is influenced by genetic deterioration processes in small and/or genetically isolated populations (Glémin et al., 2006; Keller and Waller, 2002; Lynch et al., 1995). Theoretical and empirical studies have demonstrated that a metapopulation structure, habitat fragmentation and environmental stochasticity can greatly accelerate

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the accumulation of slightly deleterious mutations and increase the metapopulation extinction probability (Higgins and Lynch, 2001; Saccheri et al., 1998). In this context, patch connection is expected to decrease both genetic drift and the rate of inbreeding (Couvet, 2002; Mills and Allendorf, 1996; Richards, 2000) with subsequent positive effects on viability (Higgins and Lynch, 2001).

Most authors now agree that genetic and ecological mechanisms act in synergy; their integration constitutes the best approach to accurately evaluate population and metapopulation extinction risks and understand the underlying processes (Robert, 2011a). An increasing number of studies investigated the combined impact of stochastic mechanisms (both demographic stochasticity and genetic deterioration) on species extinction risks (Oostermeijer et al. (2003), but see Higgins and Lynch (2001), Lynch et al. (1995), Theodorou et al. (2009), Robert (2006, 2011a,b) for general treatments and Bjorklund and Arrendal (2008), Burton et al. (2012), Kirchner et al. (2006), Noël et al. (2010), Schueller and Hayes (2011) for study cases). Population Viability Analysis (PVA, Beissinger and McCullough, 2002) is a powerful tool to study the combined effects of demographic, environmental and genetic stochasticities on extinction probabilities (Kirchner et al., 2006; Mace et al., 2008; Morris and Doak, 2002) and to compare management options to improve population viability.

Ranunculus nodiflorus L. is a rare and endangered annual species protected in France (Olivier et al., 1995). The species is restricted to specific habitats called "platière" characterised by sandstone with a thin soil layer in Europe (Arnal, 1996). Previous work has shown that Parisian populations of *R. nodiflorus* exhibit metapopulation dynamics (Kirchner et al., 2003; Noël et al., 2006, 2007). The subunit, or patch, individuals inhabit temporary water puddles that can form after rainfall. Water corridors that may form after rainfall serve as the migration/connection vector among puddles and define a network of all the puddles that may connect to each other and exchange seeds through water corridors. As in other plant species, (re)colonisations are possible via the existence of a soil seed bank, i.e., temporal migration (Kalisz et al., 1997; Levin, 1990). Water pH is an important component that defines the suitability of puddles for *R. nodiflorus*, and an overly acidic pH prevents seed germination and reduces the reproductive success of individuals (Noël et al., 2006). Demographic, genetic and ecological analyses performed between 2002 and 2006 have allowed us to access key parameters of the demography of *R. nodiflorus* populations.

Metapopulations of *R. nodiflorus* form a complex system where (1) local extinction events are frequent; (2) the dynamics of recolonisation are critically dependent on network configuration and the soil seed bank; (3) temporally variable environmental conditions underlying local extinction events are likely to be highly correlated within networks that share similar physical, chemical or biotic conditions (continuous water corridors within networks); and (4) overall population sizes are small and fragmentation is high, which raises the question of the importance of genetic aspects to the extinction risk.

To examine the less obvious effects of this combination of threats, we developed a demo-genetic model that includes a soil seed bank based on empirical data. Based on both general theoretical knowledge and specific field observations, we specifically focused on the impact of the soil seed bank and the complex role of corridors, which are associated with (1) the possibility of recolonisation of extinct local populations through seed dispersal; (2) genetic exchanges among local populations; and (3) the synchronisation of local environments through water pH variation, as described below. Through comparisons of various ecological and management scenarios, we examine how this triple role on metapopulation viability is relevant to the management of this rare species.

2. Materials and methods

2.1. Study species

R. nodiflorus L. (Ranunculaceae) is a rare and endangered annual plant restricted to wet zones in Spain, Portugal and France. In France, the species is found in Corsica, Brittany, Massif Central and the Fontainebleau forest in the Parisian region, where it has experienced a strong decline during the last century (Danton and Baffray, 1995) due to changes in forestry practises. The introduction of pine tree species, the drastic reduction of the frequency of natural fires and the draining of wetland zones have contributed to the species' decline. The species now appears as 'endangered' (E) on the French Red List of threatened species (Olivier et al., 1995). The species has strict habitat requirements and only grows in puddles with a thin soil layer and highly variable water levels. The species primarily reproduces by selfing and produces fruit-heads that contain small achenes (Kirchner et al., 2003; Noël, 2006) with a biseasonal emergence in the autumn and spring (Noël et al., 2006). Flowering and fructification occur between April and May and is followed by the rapid death of individuals. The species is unable to reproduce vegetatively or through apomixis (Noël, 2006). Previous studies (Kirchner et al., 2003; Noël et al., 2006, 2007) have shown that *R. nodiflorus* displays metapopulation dynamics. The sites where the species naturally occurs in France are characterised by a sandstone ground and the occurrence of temporary puddles that form after rainfall and last for a few days when the weather is sunny in the summer to a few weeks in the winter and autumn. Puddles are generally situated in open areas, but birch trees (*Betula pendula*) and pines (*Pinus sylvestris*) tend to naturally invade the sites (pers. obs.). Water levels are dependent on rainfall and are highly variable, which allows puddles to be transiently connected by water corridors. Although corridors usually do not form for the entire cycle of *R. nodiflorus*, they last during autumn and winter and allow the dispersal of seeds produced during late spring. Each puddle occupied by the species is considered a population of *R. nodiflorus*, and puddles are hereafter referred to as patches. Sets of puddles connected by water corridors are subsequently considered as networks or metapopulations (Noël et al., 2006).

2.2. Demographic analysis

Between October 2002 and June 2005, 224 patches were recorded at five sites in the Fontainebleau forest (≈25 000 ha, 50 km south of Paris). A total of 83 were occupied by the species, and population demography was monitored monthly using quadrats (30 cm × 30 cm, see Noël et al. (2006) for details of field monitoring). The five sites with *R. nodiflorus* consisted of 1–12 networks, containing 1–9 patches and ranging from 0.5 to 72 m^2. Patches within sites were located from a few meters to a few kilometres away for the largest sites. The detailed life-cycle of the *R. nodiflorus* was determined based on this field monitoring (Fig. 1). Three stages occur: seed, seedling and adult. The time-step between the seed and adult stage is 1 year with seasonal transitions, producing autumn and spring seedlings.

All life-cycle probabilities, that is, germination, survival and flowering probabilities, were estimated based on monthly field monitoring of populations between 2002 and 2003 unless otherwise stated, the results of laboratory experiments on the soil seed bank and the germination rates (Noël, 2006; Noël et al., 2006, 2007).

Our monthly monitoring of populations allowed us to determine most of the quantitative parameters utilised in the model, including (1) the probability for a seed to germinate the spring fol-