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Recent declines and range changes of orchids in Western Europe (France, Belgium and Luxembourg)

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ABSTRACT

In recent decades, many studies have documented local declines of orchid species due to environmental changes. However, few data are available about the changes of orchid species' distributions at large spatial and temporal scales. We aimed to characterize the recent dynamics of orchid distributions in Western Europe, in regard to (i) climate and land-cover changes and (ii) species' ecology (i.e. bioclimatic preferences and light requirements). We based our analysis on surveys made by the French Orchid Society on 134 orchid taxa in France, Belgium and Luxembourg over 20 years (i.e. before 1985 until 2005). We designed null models to assess the nature and significance of recorded changes within each administrative unit and for each orchid taxa. We found sharp declines of most orchids in the Northern part of the study area (i.e. Northern France, Belgium and Luxembourg) and many new appearances in the Central and South Western part of the study area. Heliophilous (shade-intolerant) species declined more than sciaphilous (shade-requiring) species, possibly due to the loss of open habitats in the Northern highly urbanized regions. No significant differences in appearance or disappearance were detected between Mediterranean and Euro-Siberian species. Our results suggest that climate change is not a primary driver of distribution changes over the period considered, compared to land-cover changes. Further declines in the Northern part of the study area will exacerbate the already existing contrast in species richness and related conservation priorities between the North and South of the study area.

1. Introduction

A major issue in ecology is to understand the drivers of temporal changes in the spatial distribution of species. Species can occur and persist in space under specific environmental conditions depending on the biological requirements making their ecological niche (see Chase and Leibold, 2003 for a review). Specifically, abiotic preferences (based on the physical environment) and biotic preferences (e.g. based on the open vs. closed vegetation context) are expected to influence the response of species to climate and land-cover change, respectively. Changes in climate and land cover thus imply shifts of species' distributions depending on these requirements and on species' dispersal abilities. Species with a narrow niche and low dispersal ability are expected to be more vulnerable due to their lower ability to respond to rapid environmental change (Thuiller et al., 2005a; Devictor et al., 2008; Zhu et al., 2012). Numerous studies have pinpointed the effect of global changes on biodiversity (Sala et al., 2000) in showing latitudinal/altitudinal displacements and range reductions of species (Hughes, 2000; Parmesan and Yohe, 2003; Thuiller et al., 2005b). It is thus crucial to investigate the combined effects of climate and land-cover changes on the distribution of biodiversity and to rank priorities for conservation planning (Margules and Pressey, 2000; Bottrill et al., 2008).

The territory comprising the geographical range of a species is divided into administrative units. A key task is to take this administrative dimension into account in devising conservation policies. Some species may require protection throughout their distribution (across units), while others may be highly threatened in only part of their distribution and thus require protection only in that part (Pfeifer et al., 2010; Schatz et al., 2014). Indeed, the nature and amplitude of past and current environmental changes vary spatially depending on biogeography and history of the regions (Walther et al., 2002; Reidsma et al., 2006). In consequence, species will be impacted differently across their distribution, with most

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significant distribution changes expected for species from regions prone to greater climate warming (Thuiller et al., 2005b; Chen et al., 2011). In order to investigate the current dynamics of species distributions in the face of global changes, datasets over large geographical scales are needed. Such data should cover broad environmental gradients in order to address species' responses under various regimes of environmental change (Pearson and Dawson, 2003). To date, studies of distribution change at large spatial scale and including vulnerable ecosystems are scarce. Among the world's biogeographic regions, the Mediterranean basin is a biodiversity hotspot that has experienced profound land-cover changes (Blondel et al., 2010; Sirami et al., 2010) and is now facing strong climatic changes including increasing dry periods (IPCC, 2013). Marked changes in plant distributions in these areas have already been shown (Médail and Quézel, 2003; Thuiller et al., 2005b).

Our objective here is to address the response to global changes of orchids in contrasted environmental contexts from the Mediterranean area to temperate Northern regions. Orchids are a particularly interesting group for studying changes in the distribution of species, for the following three major reasons. First, orchids are highly diverse particularly in the Mediterranean region (Schatz et al., 2014); some species are widely distributed, whereas others are more or less narrowly endemic (Bournérias and Prat, 2005). Secondly, orchid niches are segregated over broad abiotic environmental gradients in Europe (e.g. continental, alpine and Mediterranean bioclimatic contexts, Munoz, 2010). Third, orchids are particularly vulnerable to climate and land-cover changes (Wotavova et al., 2004; Pfeifer et al., 2006) due to their narrow ecological preferences. Declines in occurrence and population size of many orchid species have already been observed in Europe (Jacquemyn et al., 2005; Kull and Hutchings, 2006; Schatz et al., 2014), as well as in other continents (Whigham and Willems, 2003; Duncan et al., 2011). It is thus crucial to understand the drivers of distribution changes of orchids.

Because many ecological processes can influence species dynamics from local to regional scale, a great current challenge in ecology is to develop adequate statistical procedures to assess the drivers of species' distributions and to predict their response to environmental changes (Thuiller et al., 2008; Munoz, 2010). Specifically, it is essential to design statistical tests that acknowledge the structure of regional species pools (Lessard et al., 2012), depending on different functional (de Bello et al., 2012) and biogeographical (Carstensen et al., 2013) properties. In the context of a large-scale biogeographical and ecological gradient of orchid richness from the Mediterranean to Northern temperate areas (Schatz et al., 2014), we expect that the significance of extinction or colonization patterns depends on the number of species likely to be locally present. Null models allow keeping constant specific features of matrices of data while randomizing others (Gotelli and Graves, 1996; Gotelli, 2001). Here we designed null models that acknowledge the variation of orchid richness in space and the overall distribution of orchid species over a 20-year period, in order to identify significant patterns of orchid disappearance and appearance in Western Europe.

We analyzed a large-scale and expert survey conducted over 20 years by the SFO (Société Française d'Orchidophilie, French Orchid Society) to investigate the dynamics of 134 orchid taxa (of which 126 species) found in France, Belgium and Luxembourg (Bournérias et al., 1998; Bournérias and Prat, 2005). The three countries we investigated encompass broad ecological and climatic gradients, including continental, alpine, Atlantic and Mediterranean bioclimatic contexts, which are affected in different ways by ongoing environmental changes. This study aimed to evaluate recent trends (disappearance/appearance/range change) in the distribution of orchid species in Western Europe, related to environmental changes and species' ecology. Firstly, we examined the general patterns of orchid temporal dynamics and range changes in response to climate and land-cover changes. We hypothesized (hypothesis 1) an overall distribution range change toward the North of the study area in response to climate warming (IPCC, 2013). Using a trait-based approach, we examined how species respond to climate change in regard to their bioclimatic preferences, and to land-cover change in regard to their light requirements. We predicted an expansion of the distribution range of Mediterranean species toward the North of the study area in response to climate warming, while Euro-Siberian species should have declined more and thus have reduced their range in the study area, as they are less tolerant of warmer temperatures (hypothesis 1a). In addition, we hypothesized that heliophilous (i.e. shade-intolerant) species have declined more than sciaphilous (i.e. shade-requiring) species due to the increase in forested area in the Southern part of our study area (Blondel et al., 2010; Sirami et al., 2010) and to the destruction of natural open habitats in the Northern part of the study area (hypothesis 1b). We expected that species that are tolerant of a broad range of light levels would be less vulnerable than species with a narrow niche along this dimension. Secondly, in regard to conservation, we examined whether protection lists effectively promote orchid protection. We predicted that protected species are better able to persist than unprotected species thanks to conservation policies (hypothesis 2). To answer these questions, we designed original null models that assess species dynamics at regional scale while taking into account the effect of richness variation over the 20- year period.

2. Material and methods

2.1. Data collection

Our analysis was based on the survey of 134 orchid taxa (i.e. 126 species and 17 subspecies) in 108 administrative units in France, Belgium and Luxembourg over 20 years (before 1985 until 2005) conducted by the French Orchid Society (SFO, http://www.sfo-asso.com/). To compare units roughly similar in area, 'administrative units' were defined in the present study as 96 'départements' in France and 11 regions in Belgium, while Luxembourg was considered as a single administrative unit of similar spatial extent (see Supplementary material A1 for details about administrative units).

This information was published in two orchid books (Bournérias et al., 1998; Bournérias and Prat, 2005) that provided for each species a map of presence in each administrative unit, except for four administrative units (numbered according to the French 'département' system), 'Paris' (75), 'Hauts de Seine' (92), 'Seine St Denis' (93) and 'Val de Marne' (94), for which the orchid presence information was combined (Supplementary material A1). We grouped these into a single unit that we term here 'Ile-de-France'. We calculated the latitude and longitude of the centroid of each administrative unit using the QGIS software (Quantum GIS Development Team, 2013).

Each species in each administrative unit was categorized as stable (presence of the species reported over 20 years), disappeared (the species was observed at least once before 1985 but had disappeared by 2005) or newly appeared (the species was not observed before 1998 but was present in 2005). Disappearance was based on the second edition of the orchid book (Bournérias and Prat, 2005) that compiled information over more than 20 years on species presence and disappearance (based on surveys conducted before 1985 until 2005) in each of the studied administrative unit. Information on new appearance was not provided in this second edition (Bournérias and Prat, 2005). We thus determined cases of new appearance when a species was reported as present in an administrative unit in the second edition (Bournérias and Prat, 2005) but not in the first edition (Bournérias et al., 1998) of our reference