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 related to 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 in 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...
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 (Médaïl 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 Wilems, 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, 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 scaphiophilous (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
orchid book. Appearance thus accounted for observed changes between 1998 and 2005 (i.e. 7-year time interval) for all orchid species. In the analysis, we excluded 31 orchid species that were recently described scientifically, to avoid biases of ‘false appearances’ resulting from the absence of information at the former date before taxonomic description. Taxonomic inconsistency could not affect the analysis of disappearances because changes in scientific names were taken into account in the second edition of the reference book (Bournéniás and Prat, 2005).

Bioclimatic preferences (i.e. Mediterranean vs. Euro-Siberian), light requirements (i.e. heliophilous vs. shade-tolerant vs. sciaphilous) and habitat types (i.e. dry grassland vs. shrubland vs. forest vs. humid grassland vs. wetland) of orchid species were taken from the literature (Bournéniás and Prat, 2005). Red lists and protection lists were exclusively based on France, to avoid taking into account lists of different countries that are not established in the same way. The red list status ascribed to each orchid species in France was either ‘least concern’, ‘near threatened’ or ‘vulnerable’, according to the IUCN nomenclature (IUCN et al., 2010). We also noted the protection status in France (including two levels of protection, regional or national) for each orchid species, based on the 1982 French list at national level, and based on the lists established between 1986 and 2005 at regional level (Bournéniás and Prat, 2005). National level protection lists were thus ascribed earlier than regional lists and match the first sampling period. In this regard, we could test the effectiveness of national protection on species dynamics and whether protection leads to fewer declines.

2.2. Land cover

We studied recent distribution changes and analyzed whether and how these changes were related to land cover at the end of the studied period. We selected Corine Land Cover (CLC) layers from 2006 (http://www.eea.europa.eu/data-and-maps/clc-2006-vector-data-version), as they are relevant in regard to the most recent (2005) occurrence used. These layers were used to calculate the proportion of urban, agricultural and natural areas (i.e. open grassland habitats and closed forest habitats) within each administrative unit by merging CLC categories (see Supplementary material B1). We used the QGIS software to calculate the proportional area of each of these three categories within each administrative unit (Quantum GIS Development Team, 2013).

2.3. Null model-based analysis of distribution changes

We designed two null models in order to address complementary issues on orchid disappearance and appearance in the study area (see Connor and Simberloff, 1983; Gotelli, 2001). Null model 1 allowed the assessment of whether each administrative unit displayed more or fewer disappearances and/or appearances than expected by chance. This null model permuted the stable/disappeared/appeared labels of each species across administrative units, so that the number of units where a given species was stable, had disappeared or had appeared was held constant, but the number of species that were stable, disappeared or appeared in each administrative unit could vary (Supplementary material A2). The null hypothesis represented by this model stated that the administrative units where orchid species were stable, had disappeared or had appeared was independent from one species to another. The alternative hypothesis considered that some administrative units could experience more or fewer disappearances or new appearances than expected by chance due to some specific context. Because spatial patterns of disappearance/appearance could result from short-distance species dispersal and from the autocorrelation of the environment (Legendre, 1993), we constrained the permutations of species labels to be more likely between neighboring units than between distant units. Distances were calculated based on the centroids of geographical coordinates of units (Hardy, 2008; function resamp.3t of SpacodiR package in R). Therefore, any deviation from the null model was not an artifact of these sources of autocorrelation. Furthermore, the distribution of species over the period was fixed, i.e., the permutations concerned only the administrative units where species were present at least once during the investigated period. The permutations were repeated 999 times. We compared the actual number of disappearances/appearances per administrative unit to the reference null situation of null model 1. We assessed the significance of excess disappearances and appearances in an administrative unit based on the proportion of null values that fell below the observed value, which provided the P-value of the test. We also assessed whether there were fewer disappearances/appearances than expected by chance, based on the proportion of null values that fell above the observed value. Based on null model 1, we assessed the significance of species range changes. The average geographical positions of species were calculated by averaging the latitudes and longitudes of administrative units where they were present at each period. The difference of position between the periods measures the species range change in regard to the four cardinal directions. We then compared the observed range change to the corresponding null distribution predicted by null model 1.

Null model 2 allowed the assessment of the significance of disappearances and appearances across their distribution for each orchid species. The stable/disappeared/appeared labels were then shuffled within administrative units between species. In this case, the number of species that were stable, disappeared or appeared was held constant in each administrative unit, but the number of units where a species was stable, had disappeared or had newly appeared could vary (Supplementary material A2). This model thereby allowed the testing of whether orchid species showed more or fewer disappearances and/or appearances across the study area than expected by chance. An appealing aspect of this model is that it is based on fixed trends in administrative units, so that the effect of their specific land-cover and climatic trajectories on the numbers of species disappearances/appearances was kept constant, and the deviation from the null model was due to dynamics varying across orchid species. As in model 1, permutations of model 2 concerned only the administrative units where species were present at least once during the investigated period. The permutations were repeated 999 times. For the specific analysis of disappearance/appearance according to the protection status of species, the stable/disappeared/appeared labels were permuted among administrative units from France only, as we used here exclusively the French protection lists. In the case of regionally protected species, stable/disappeared/appeared labels were only permuted among administrative units (i.e. départements in France) belonging to regions where a given species has been accorded ‘protected’ status.

We adjusted the P-values for multiple comparisons among administrative units or species to avoid artificial inflation of type I error. P-values were adjusted by the ‘fdm’ method (false discovery rates, Benjamini and Hochberg, 1995) designed to control the expected proportion of incorrect rejections of the null hypothesis (see Pike, 2011 for more information).

2.4. Drivers of orchid distribution changes

To further investigate the nature of departures from the null models and to relate these departures to hypothesized drivers, we calculated a standardized effect size (SES) value of disappearance, appearance and range change. SES values of disappearance (SES app), appearance (SES app) and range change (SES range) were calculated as follows:
where $x$ is the observed value, $\mu$ is the mean of the permuted values given by the null model, and $\sigma$ is the standard deviation of the permuted values given by the null model. In regard to SES variation across orchid species, we selected species that were present in at least 10 administrative units ($n = 78$ orchid species) in order to avoid possible statistical biases in the analysis of restricted distributions.

Based on null model 1, we performed a linear model of the disappearance/appearance SES values as a function of the geographical coordinates. In addition, we related the SES$_{\text{disp}}$ and SES$_{\text{app}}$ to the proportion of urban, agricultural and natural areas (i.e. closed forest and open grassland habitats) in 2006 of the administrative units, with a generalized least squares (gls) model. This model incorporates the spatial structure of land covers in the error term of the regression model. Different models of spatial structure (i.e. spherical, exponential, Gaussian structure, see Legendre and Legendre, 1998) were tested, and the best-fit model was defined using the Akaike information criterion (AIC). In our case, the exponential correlation structure was the most appropriate (lowest value of AIC). Due to extreme values of the proportion of urban areas for both Brussels (i.e. 86%, based on CLC in 2006) and ‘Ile-de-France’ (i.e. 87% based on CLC in 2006), we excluded these administrative units from this analysis.

Based on null model 2, we performed a linear model of the disappearance/appearance and range change SES values according to orchid bioclimatic preferences (Mediterranean vs. Euro-Siberian), light requirements (heliophilous vs. shade-tolerant vs. sciaphilous) and habitat types (dry grassland vs. shrubland vs. forest vs. humid grassland vs. wetland), on the one hand, and according to the protection status (unprotected vs. regionally protected vs. nationally protected) on the other hand. We then used a Tukey post hoc test based on this linear model in order to compare SES$_{\text{app}}$, SES$_{\text{disp}}$, and SES$_{\text{range}}$ amongst these above mentioned characteristics. The Student test was used to compare the averaged SES$_{\text{range}}$ among species to the null value, i.e. to test whether the overall range of species was displaced significantly or not toward a given cardinal direction.

Calculations of null models and the related statistical analyses were performed using the R software (R Development Core Team, 2013, version 2.15.0, package ‘spacodiR’, ‘nlme’, ‘fields’).

### 3. Results

#### 3.1. Global trends in orchid dynamics in Western Europe

Null model 1 yielded the highest SES values of disappearances (SES$_{\text{disp}}$) in the Northern part of the study area (i.e. Luxembourg and several neighboring administrative units from North Western to North Eastern France and in Belgium, Fig. 1A). The administrative unit ‘Walloon Brabant’ (Belgium) showed significantly more disappearances than in the null model ($P < 0.05$, Fig. 1A). A significant and positive linear relationship between SES$_{\text{disp}}$ and the latitude of administrative units was found (linear model, $P < 0.001$, $R^2 = 0.30$), but no linear relationship was detected with longitude. Null model 1 further revealed more frequent appearances of orchid species in Central and South Western France (Fig. 1B). The number of appearances was significantly higher than expected in the null model 1 in the French administrative units ‘Ile-de-France’ and ‘Landes’ ($P < 0.05$, Fig. 1B). Local disparities were observed between administrative units with numerous appearances (e.g. ‘Ile-de-France’) compared to neighboring administrative units with few appearances (Fig. 1B). A significant and negative linear relationship between SES$_{\text{app}}$ and the longitude of administrative units was shown (linear model, $P < 0.001$, $R^2 = 0.20$), but no linear relationship was detected with latitude.

#### 3.2. Orchid dynamics related to land cover

There were contrasted trends in current proportions of urban, forest and grassland areas along a North–South gradient in our study area (Supplementary material A3). When relating observed orchid dynamics to these current land covers, we found a significant positive linear relationship between SES$_{\text{disp}}$ in each administrative unit and the corresponding proportion of urban area ($P < 0.001$, Table 1) but not with agricultural and natural areas ($P > 0.05$, Table 1). In regard to appearances, SES$_{\text{app}}$ was negatively related to urban area ($P < 0.05$, Table 1) and positively related to agricultural area ($P < 0.05$, Table 1).

#### 3.3. Range changes related to orchid ecology

Based on null model 1, we further analyzed the cardinal directions of orchid range changes across the study area. The SES$_{\text{range}}$ averaged across species was significantly negative in regard to latitude, indicating an overall tendency of range change to the South of the study area (Student test, $P < 0.01$, Fig. 2). No significant differences in range change across latitude were found between habitat types (Tukey test, $P > 0.05$). A significant southward displacement was detected for Serapias cordigera (dry grassland) and Anacamptis papilionacea subsp. papilionacea (shrubland) while a significant northward displacement was detected for Neotinea maculata (shrubland) (Fig. 2). The SES$_{\text{range}}$ averaged across species was significantly negative in regard to longitude, indicating an overall tendency of range change to the West of the study area (Student test, $P < 0.01$, Fig. 2). No significant differences in range change across longitude were found between habitat types (Tukey test, $P > 0.05$). A significant westward displacement was detected for Orchis pallens (shrubland) and Dactylorhiza elata (wetland), while a significant eastward displacement was detected for S. cordigera (dry grassland) (Fig. 2).

Concerning bioclimatic preferences, we found no significant difference in mean SES$_{\text{range}}$ along longitude or latitude between Mediterranean and Euro-Siberian species (Tukey test, $P > 0.05$).

#### 3.4. Disappearance and appearance trends related to orchid ecology

Based on null model 2, SES$_{\text{disp}}$ was positive for 27 species and significant for 13 of them, with the highest value of disappearance for Anacamptis coriophora subsp. coriophora ($P < 0.001$, Table 2). SES$_{\text{app}}$ was found to be positive for 31 species and significant for 11 of them, with the highest value for A. papilionacea subsp. papilionacea ($P < 0.001$, Table 2). SES$_{\text{disp}}$ was significant for seven species of humid zones (wetland and humid grassland), three species of forest and shrubland, and three species of dry grassland, whereas the SES$_{\text{app}}$ was significant for nine species of forest and shrubland, and two species of humid zones (Table 2). However, no significant differences of SES$_{\text{disp}}$ and SES$_{\text{app}}$ were detected among species of different habitat types (Tukey test, $P > 0.05$). Note that three species (A. papilionacea subsp. papilionacea, A. palustris and Ophrys speculum) are concerned by both significant disappearance and appearance (Table 2).

Furthermore, the mean (± sd) of SES$_{\text{disp}}$ was significantly higher for heliophilous species (SES$_{\text{disp}} = 2.88 ± 4.53$) than for shade-tolerant (SES$_{\text{disp}} = −0.46 ± 2.08$) and sciaphilous species (SES$_{\text{disp}} = −0.31 ± 2.80$) (Tukey test, $P < 0.01$ and $P < 0.05$, respectively, Fig. 3A), but did not differ significantly among species of different bioclimatic preferences (Tukey test, $P > 0.05$, Fig. 3B). On the other hand, we found no significant differences in SES$_{\text{app}}$ between heliophilous (SES$_{\text{app}} = −0.23 ± 1.75$) and sciaphilous species
3.5. Orchid dynamics and protection status

In the French territory, the mean SES\textsubscript{disp} was significantly higher for IUCN vulnerable species (SES\textsubscript{disp} = 4.94 ± 3.93) compared to least concerned species (SES\textsubscript{disp} = −1.01 ± 1.40) (Tukey test, P < 0.001, result not shown). Therefore, the definition of IUCN status, which is posterior to our 20-year period, is consistent with species decline. Furthermore, significant differences in SES\textsubscript{disp} were detected between nationally protected species (SES\textsubscript{disp} = 3.15 ± 2.98) and both unprotected species (SES\textsubscript{disp} = −1.35 ± 1.24) (Tukey test, P < 0.001, Fig. 3C) and regionally protected species (SES\textsubscript{disp} = 0.54 ± 1.67) (Tukey test, P < 0.001, Fig. 3C). Because the protection status was defined before our 20-year period, it indicates that protected species continued declining despite their status. On the other hand, mean SES\textsubscript{app} was unrelated to protection status (Tukey test, P > 0.05, Fig. 3F).

4. Discussion

We analyzed an intensive, large-scale presence/absence database of orchid species in Western Europe, using original null models. Our results highlight a reduction of the distribution range of orchids in the highly urbanized Northern regions in our study area, resulting in a southward range change of many species. These trends were related to species’ ecology, as heliophilous species declined the most, probably because of the loss of their habitat in the Northern part of the study area. In contrast, we did not detect differential responses to environmental changes between Mediterranean and Euro-Siberian species, suggesting that the effect of land-cover change dominates over the effect of climate change on orchid species dynamics over the period considered. Consistent with IUCN red lists and protection lists, we found the highest declines for species categorized as vulnerable by the IUCN and nationally protected. However, IUCN ranking was defined after the study period, whereas the protection status was defined before. Therefore, conferring of protected status did not overcome the decline of orchids.
countries can favor orchid extension there (e.g. in Germany, the temperate in unfavorable/range edge regions in Northern European forest habitats) and (C) humid areas (humid grassland and wetland). Each point represents the SESrange of an orchid species, based on null model 1. A positive value on the ordinate represents a range change northward, while a negative value represents a range change southward. A positive value on the abscissa represents a range change eastward, while a negative value represents a range change westward. The dashed lines represent the 95% confidence interval with the lower limit of −1.96 and upper limit of +1.96. Range changes were considered as significant when the SESrange was below −1.96 and at P > 0.975, or above +1.96 and at P < 0.025. Species names are shown for species with a significant range change. Examples in disappearance were found between species with broad light requirements (sciaphilous in this case), suggesting that declines of orchids in the Northern part of our study area (i.e. 27 out of the 31 orchid genera of Europe, Bournérias et al., 2010) compared to less threatened species (e.g. least threatened species of the Mediterranean region) in the conservation priority at the national level of the Southern administrative units (notably those of the Mediterranean region) in the conservation of this plant family (Schatz et al., 2014). Conservation issues are particularly challenging in Mediterranean regions as they are already prone to marked and rapid climatic and land cover changes affecting this area.

4.2. Conservation issues

Mediterranean ecosystems host the highest species richness in Europe (i.e. 27 out of the 31 orchid genera of Europe, Bournérias and Prat, 2005; Schatz et al., 2014). Their species richness is related to (i) great ecological diversity, (ii) contrasted land-cover histories (Médail and Quézel, 1999; Blondel et al., 2010) and (iii) biogeographical and evolutionary processes that have affected the region (e.g. role of glacial refugia, Médail and Diadema, 2009). The higher declines of orchids in the Northern part of the study area demonstrated in this study (Fig. 1) will strengthen the already existing North–South gradient in species richness reinforcing the responsibility at the national level of the Southern administrative units in the conservation of this plant family (Schatz et al., 2014). Conservation issues are particularly significant in Mediterranean regions as they are already prone to marked and rapid climatic and land cover changes affecting this area.

We also demonstrated significantly greater declines of threatened (i.e. vulnerable in regard to IUCN red list criteria, IUCN et al., 2010) compared to less threatened species (e.g. least

![Fig. 2. Species range changes across the study area in regard to their habitat types. (A) open natural area (dry grassland), (B) mid-open and closed area (shrubland and forest habitats) and (C) humid areas (humid grassland and wetland). Each point represents the SESrange of an orchid species, based on null model 1. A positive value on the ordinate represents a range change northward, while a negative value represents a range change southward. A positive value on the abscissa represents a range change eastward, while a negative value represents a range change westward. The dashed lines represent the 95% confidence interval with the lower limit of −1.96 and upper limit of +1.96. Range changes were considered as significant when the SESrange was below −1.96 and at P > 0.975, or above +1.96 and at P < 0.025. Species names are shown for species with a significant range change. Examples in disappearance were found between species with broad light requirements (sciaphilous in this case), suggesting that declines of orchids in the Northern part of our study area (i.e. 27 out of the 31 orchid genera of Europe, Bournérias et al., 2010) compared to less threatened species (e.g. least threatened species of the Mediterranean region) in the conservation priority at the national level of the Southern administrative units (notably those of the Mediterranean region) in the conservation of this plant family (Schatz et al., 2014). Conservation issues are particularly challenging in Mediterranean regions as they are already prone to marked and rapid climatic and land cover changes affecting this area.

4.1. The North–South gradient of species decline

Species occurring in Mediterranean ecosystems, especially in mountainous dry areas are considered to be the most vulnerable to climate change (Thullier et al., 2005b). In contrast, warmer temperature in unfavorable/range edge regions in Northern European countries can favor orchid extension there (e.g. in Germany, Hornemann et al., 2012). Therefore, we hypothesized a northward displacement of species in our study area related to increasing temperature (Parmesan and Yohe, 2003; IPCC, 2013). In contrast to this expectation, our study showed significantly more frequent declines of orchids in the Northern part of our study area (i.e. Northern France, Belgium and Luxembourg) than in the Southern part (i.e. the French Mediterranean area, Fig. 1), resulting in subsequent southward range change. In addition, no significant differences in appearances, disappearances and range changes were found between Mediterranean and Euro-Siberian species (Fig. 3). According to our results, species presence seems to be maintained in the Mediterranean region despite increasing drought stress (IPCC, 2013), in contrast to our hypothesis 1a.

Our study suggests that land cover changes are a more important driver of orchid range dynamics than climate changes. The proportion of area affected by urbanization was indeed highly related to orchid declines (Table 1). This result is consistent with the meta-analysis conducted by Duncan et al. (2011) based on more than 8000 plant species, and that identified Orchidaceae as the plant family with the greatest extinction risk in the vicinity of cities. Urbanization can have numerous direct or indirect effects on orchid survival, such as competition with invasive species and population size reduction (Duncan et al., 2011; Meekers and Honnay, 2011). The loss of natural open habitat in the North of our study area may also induce significantly more declines in heliophilous species compared to sciaphilous species (Fig. 3), in accordance with hypothesis 1b. This is the case of S. cordigera, for example, a species whose range shifted southward because populations in North Western France disappeared (Fig. 2), and which has been described as highly vulnerable to the effect of anthropic pressure (Pellegrino and Bellusci, 2014). Few declines were found in the Mediterranean region, suggesting that forest cover increase in the South seems not to affect markedly the orchid species of this region. Some orchid species of closed habitats have indeed appeared (Table 2), probably in relation to the increase in forest areas (Sirami et al., 2010). In contrast, we showed that species with the highest declines are specialist of humid zones (Table 2). Their declines may be related to local disturbance of this habitat e.g. by drainage (Hartig et al., 1997). In addition, no significant differences in disappearance were found between species with broad light requirements (i.e. shade-tolerant) and species with narrow light requirements (sciaphilous in this case), suggesting that declines of orchids are highly linked to their distribution and to the related land-cover changes occurring in those regions.
Table 2
List of taxa occurring in at least 10 administrative units and displaying significant SESdisp and SESapp values, based on null model 2. The table includes information on: SES values based on the null model, number of administrative units for which disappearance or appearance of the species was observed (Obs. units), the total number of administrative units where the species was present (Total units), the ratio of observed number of administrative units by total number of administrative units (Ratio), and the habitat types of each species (Habitat). All information is based on Bournérias and Prat (2005). Significant values were fixed at $P < 0.05$ and adjusted by multiple comparisons.

<table>
<thead>
<tr>
<th>Taxa</th>
<th>SES value</th>
<th>Obs. units/Total units</th>
<th>Ratio (in %)</th>
<th>Habitat</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Disappearance</strong></td>
<td></td>
<td></td>
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<tr>
<td>Anacamptis coriophora subsp. coriophora</td>
<td>12.45</td>
<td>35/76</td>
<td>46</td>
<td>Humid grassland</td>
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<td>Liparis loeselii</td>
<td>9.10</td>
<td>23/43</td>
<td>53</td>
<td>Wetland</td>
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<tr>
<td>Spiranthus aestivalis</td>
<td>8.62</td>
<td>21/70</td>
<td>30</td>
<td>Humid grassland</td>
</tr>
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<td>Anacamptis palustris</td>
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<td>27</td>
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Concerned species). This result shows accordance between the dynamics we estimated for orchids (using models) and the published red list criteria. In addition, we found declines of orchid species despite their national protected status throughout the whole sampling period, in contrast to the expectation from our hypothesis 2. Similarly, a significant reduction in population size of nationally protected species was revealed in France (Feldmann and Prat, 2011), probably linked to over-collecting of some orchid species and to the loss in natural habitats. Based on our results, protection lists seem to be ineffective in promoting protection of the listed species based on changes observed over a 20-year interval. As proposed by Gauthier et al. (2010) and more specifically by Schatz et al. (2014), we suggest that vulnerability of both species and their habitats should be taken into account to protect orchids, as they are highly dependent on both their biotic and abiotic environments.

4.3. Opportunities and challenges in using null models

In this study, we used orchid presence/absence data in Western Europe. Such a large geographical scale is needed to investigate changes in species’ distribution range in response to major environmental changes. However, spatial heterogeneity at such large scales can give rise to methodological issues. In our case, heterogeneity in species richness amongst administrative units can affect the analysis of raw appearance and disappearance patterns in administrative units, as more changes are expected in species-rich units than in species-poor units. In order to correct for the effect of richness variation and test for significance, we designed two original null models shuffling species labels of presence/disappearance/appearances amongst administrative units, while keeping constant the variation of richness among units. In addition, the null models conserved the whole distribution of each species over the period in France, Belgium and Luxembourg, and thus conserved the large-scale ecological envelope of species.

On the other hand, spatial autocorrelation, i.e. the dependency among observations in relation to their geographical proximity (Legendre, 1993), can influence the reliability of statistical tests. For instance, short-distance dispersal can affect the spatial patterns of colonization. For example, a species has a higher probability of colonizing an administrative unit neighboring one where it already exists than colonizing more distant units, while disappearance could be less likely close to sources in neighboring administrative units than in more isolated populations (Dunning et al., 1992). Moreover, spatial autocorrelation exists between land-cover proportions and land-cover changes across administrative units, as close administrative units are expected to be more similar in these respects than distant administrative units. We thus took into account the effect of spatial autocorrelation by constraining the permutations across space in the null model 1, and considered that the likelihood of permutations was greater between neighboring administrative units than between distant ones (Hardy, 2008).

A further important issue concerns the probability of detecting species. This probability can vary in space, time, and across species. In the context of our study, we did not have information on detection probabilities. However, it is noteworthy that SFO has organized the cartography of orchids in the study area with the objective of controlling and correcting as much as possible any bias and heterogeneity, based on judgement by a panel of experts at both national and local levels. Therefore, we can reasonably assume that sampling heterogeneity was controlled regarding the observer effects and regarding taxonomy. However, unavoidable heterogeneity can occur when some areas are more prospected and better known than others (Reddy and Davalos, 2003; Romo et al., 2006). Our approach is based on the difference between two surveys of orchid presence, which render it dependent on the difference of sampling efforts between the two periods and on the initial sampling effort, factors that cannot be corrected by the model. Our patterns of species appearances in ‘île-de-France’ and in South Western France are consistent with increasing...
prospection efforts in these areas over the period, and therefore should not be interpreted as real species colonization and appearance. On the other hand, such bias is unlikely to affect disappearance patterns. With increasing prospection efforts, if a species was found earlier, there is no reason to expect that it could escape detection. Such limits could be overcome in the future by regular updates of the survey and by further standardization of protocols among administrative units. Despite some limitations, mainly affecting appearances, null model-based analysis greatly enhances our ability to interpret and discuss the trends in species distribution changes at a large spatial scale.

5. Conclusion and perspectives

This study improves our understanding of spatial distribution and temporal dynamics of orchids in Western Europe. First of all, we have demonstrated that the primary driver of distribution changes for orchids, over the period considered and in our study area, is not the climate as was expected, but rather land-cover changes. The orchid species diversity that persists in Southern France could be affected by future environmental changes in this region. These include drier climate (and increasing frequency of severe drought events), increased forest cover leading to greater vulnerability of open-habitat species, and rapid urbanization.

Second, this study has revealed declines of species despite protection suggesting that protection lists were ineffective in promoting conservation over the considered time-interval. Protection and restoration of habitats, going beyond a simple species-protection approach, seem to be essential to conserve orchids. In the future, this study could be extended to other countries, with particular attention focused on the Mediterranean biodiversity hotspot, in order to evaluate at a large spatial scale how the ongoing and future changes in orchid distribution are related to their specific ecological requirements and to the rapid alteration of their habitats.

Acknowledgments

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2015.05.002.

References

Bottrell, M.C., Joseph, L.N., Carwardine, J., Bode, M., Cook, C., Game, E.T., Grantham, H., Kark, S., Linke, S., McDonald-Madden, E., Pressey, R.L., Walker, S., Wilson,