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Spatial mismatches between plant biodiversity facets and evolutionary legacy in the vicinity of a major Mediterranean city

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ABSTRACT

The analyses of congruencies among biodiversity components address the issue of conservation priorities, but previously they have been done at coarse scales with limited relevance for conservation actions. Moreover, these former studies consider only the species level components of biodiversity and not the intra-specific evolutionary legacy that influences future biodiversity. This study represents the first assessment of congruencies between various components of plant biodiversity and the evolutionary legacy of a narrow endemic taxon (*Arenaria provincialis*, Caryophyllaceae). Assessment is conducted in the vicinity of a Mediterranean big city (Marseille, S.E. France) where habitats and flora are threatened by mass tourism and urban sprawl. Our analyses reveal that the different plant biodiversity facets assessed are spatially mismatched and unequally protected. Moreover, by using only species-level components of biodiversity as conservation targets we ignore crucial areas for the evolutionary legacy of this narrow endemic plant. Our results highlight the crucial role of phylogeography as a criterion to target the genetic precursors of future biodiversity in conservation planning.

1. Introduction

Conservation biology aims to conserve all components of biodiversity as well as the ecological and evolutionary processes that sustain them (Moritz, 2002; Lankau et al., 2011). To date, conservation strategies have largely focused on taxonomic diversity to protect species or areas at various scales. Evolutionary assessments of biodiversity may reveal serious weaknesses in the network of protected areas, especially where areas with high species richness are not cradles of diversification (Becerra and Venable, 2008) or hotspots of genetic diversity or uniqueness (Taberlet et al., 2012). For example, Davis et al. (2008), who investigated mammal

diversity, and Kraft et al. (2010), who focused on plant diversity, demonstrate some spatial discrepancies between simple counts of endemic species richness and ongoing diversification within the California biodiversity hotspot. Other recent studies report robust links between the genetic and specific components of biodiversity (e.g., He et al., 2008; Papadopoulou et al., 2011; Lamy et al., 2013) and support the existence of surrogates of genetic diversity under certain conditions and scales. These results emphasise that, for system-based conservation planning (Whittaker et al., 2005; Rodrigues and Brooks, 2007), and to better understand the future of biodiversity under global change (Lee and Jetz, 2008), we need to improve our knowledge of the relevance and consistency of putative links between the different components of biodiversity. These links question the existence and value of biological and ecological surrogates.

The inclusion of the evolutionary history of populations in conservation planning is an important issue for long-term management of biodiversity (Moritz, 2002; Sechrest et al., 2002; Tucker et al., 2012; Moritz and Potter, 2013). Historically isolated sets of populations are likely to have distinct evolutionary potential (Moritz, 1994): their existence is the consequence of past evolutionary processes that occurred within populations, shaping

genome diversity and structuring genetic variation as well as a response to selection in case of environmental change (Lankau et al., 2011). The evolutionary legacy of populations is mostly examined through phylogeographical studies (Avice, 2009) and concerns the structure of distinct evolutionary lineages at the intraspecific level or between closely related species. Their recognition led to the adoption of a dynamic view of biodiversity constituting continuously evolving lineages (e.g., Sgro et al., 2011; Hoffmann et al., 2015) sustaining the potential of future evolution to face environmental changes. As such, giving priority to areas that maximise only species-level diversity may have detrimental consequences for future biodiversity due to the inability to recognise the evolutionary legacy of population histories.

Dealing with pattern and history, biogeography has attached great importance to macrorefugia and microrefugia (Avice, 2009; Mosblech et al., 2011; Hampe and Jump, 2011; Keppel et al., 2012; Mee and Moore, 2013) because of their role in the persistence of the genetic and specific components of biodiversity, notably species endemism (Sandel et al., 2014). In the Mediterranean region, a positive association has been observed between hotspots of plant endemism and phylogeographically defined refugia, designating them as areas requiring special attention for conservation (Médail and Diadema, 2009). More recently several studies have focused on the geographical congruence between the different facets of biodiversity and analysed it at coarse spatial scales (e.g., Kraft et al., 2010; Devictor et al., 2010; Mouquet et al., 2012; Taberlet et al., 2012; Zupan et al., 2014). For example, Devictor et al. (2010) found for bird biodiversity that high taxonomic diversity is better represented in French protected areas than phylogenetic or functional diversities. However, conservation strategies need to consider multiple scales, and assessment of biodiversity components at smaller scales deserves more attention because it represents the practical scale for efficient conservation planning (Schwartz, 1999). Conservation strategies have to deal with human settlement issues and give attention to places where people live (Miller and Hobbs, 2002). Even small protected areas can be impacted by human activities such as mass tourism which can have strong effect on endangered species (Ballantyne and Pickering, 2013). Biodiversity studies focusing on large scale (e.g., Devictor et al., 2010; Zupan et al., 2014) are therefore not sufficient to deal with the difficult issue of conservation planning.

To address the issue of congruence among different components of biodiversity, including evolutionary legacy, at a practical scale for conservation planning, we have used an extensive vegetation survey coupled with phylogeographic knowledge of a Mediterranean narrow endemic threatened plant, *Arenaria provincialis* Chater & Hallid. (Caryophyllaceae). *A. provincialis* occurs on limestone outcrops in Provence (south-eastern France) surrounding the big city of Marseille, and its habitats are threatened by severe urban sprawl, recreation and trampling leading to habitat degradation. Like many other endemic species of the Mediterranean region, *A. provincialis* is high in conservation priorities (Thompson et al., 2005; Hobohm and Tucker, 2014), but seriously threatened by human activities (Hoekstra et al., 2005; Underwood et al., 2009) and particularly by urban sprawl along Mediterranean coastlines in the vicinity of major cities (Médail and Diadema, 2006; Vimal et al., 2012).

Previous studies (Youssef et al., 2011; Imbert et al., 2011; Pouget et al., 2013) have demonstrated that *A. provincialis* evolved throughout the Pleistocene, acquiring very specific adaptations to persist in its highly stressful habitats. A recent phylogeographical study demonstrated highly structured genetic diversity from the centre towards the margins of its distribution and a high distinctness of its populations at the genetic and ecological levels (Pouget et al., 2013). One of the main striking points of the phylogeography of *A. provincialis*, revealed by the study of Pouget et al. (2013), is that the core area of its distribution has the highest level of genetic

diversity. Any efficient conservation planning of *A. provincialis* should, at least, target this core area. Here, we use our knowledge on *A. provincialis* as a natural experiment to test the efficiency of various biodiversity components as indicators for conservation planning. The theoretical threshold of 17% of areas to be designated as protected areas (proposed by the “2020” goal of the Convention for Biological Diversity, CBD, 2012), was used to compare the capacity of the various components of biodiversity and environmental heterogeneity to be surrogates of the evolutionary legacy of *A. provincialis*.

Our aims were: (i) to examine the congruencies between different components of plant biodiversity (species and phylogenetic diversity), and the evolutionary legacy of *A. provincialis*. (ii) To compare the relevance of the various components of biodiversity to be surrogates of the evolutionary legacy of *A. provincialis* and to recognise the core area of the distribution of *A. provincialis* as a prime conservation goal.

2. Materials and methods

2.1. Study area, ecological and floristic data

The study area is located in Southern Provence (South-East of France: see Fig. 1) with a strongly seasonal Mediterranean climate, in an area characterised by several limestone outcrops (up to 1150 m above sea level). The landscapes of these outcrops are characterised by a mosaic of low matorrals (“garrigues”) mainly dominated by *Quercus coccifera* with open rocky spaces and a low vegetation cover formed by herbaceous plants. Along with an increase in the human population density occurring in Mediterranean lowlands near the coast, the naturally open habitats of Provence are affected by a combination of urban sprawl, habitat fragmentation, trampling and direct or indirect pollution (Barbero et al., 1990; Médail and Vidal, 1998; Taton et al., 2004; Dumas et al., 2008; Baumberger et al., 2012; Vimal et al., 2012). In parallel, the rocky habitats of Southern Provence shelter many rare or endemic plant taxa that make this area a priority for biodiversity conservation assessment and management. Since 2012, the southern part of the focus area and the islands between Marseille and La Ciotat have been included into the National Park of Calanques (NPCal: see Fig. 1). This study focused on the rocky open habitats of these outcrops situated at the periphery of Marseille, which also encompasses the small islands and islets situated less than five kilometres off the coast (Fig. 1).

2.2. Assessment of the different components of biodiversity

2.2.1. Assessment of species taxonomic and phylogenetic diversity

The study area has been surveyed by the Mediterranean Institute for Biodiversity and Ecology (IMBE), resulting in a database of 1132 floristic and mesologic relevés established for 100 m² circular areas. This method is relevant when comparing the ecology of plants inhabiting rocky habitats in southern Provence (Youssef et al., 2010, 2011; Baumberger et al., 2012). Plant diversity was measured at the taxonomic and phylogenetic levels. Five indices of biodiversity were computed: the alpha species diversity (ASD), the beta species diversity (BSD), the floristic dissimilarity between relevés (FD), the gamma species diversity (GSD) and the phylogenetic species diversity (PSD). ASD, BSD and GSD were computed according to Jost (2007) using the “H” function of the “vegetarian” package in R (R Development Core Team, 2012). The floristic dissimilarity (FD) was measured according to the Jaccard distance (“dist.binary” function and “ade4” package in R).

The phylogeny of the 565 plant species encountered inside the 1132 relevés was constructed in two steps. A preliminary

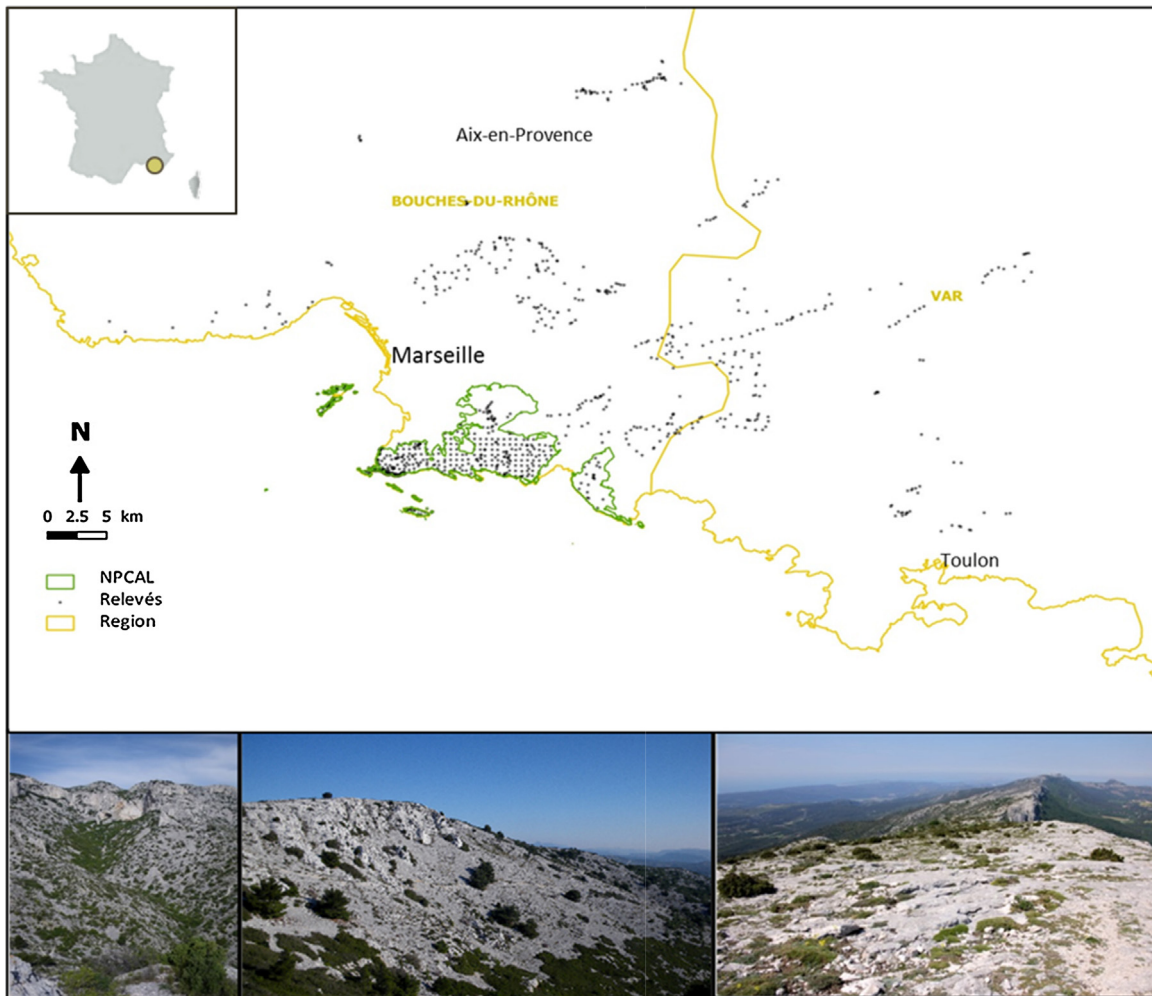


Fig. 1. Geographical distribution in south-eastern France (southern Provence) of the 1132 relevés, the limits of the National Park of Calanques (NPCal, green) and pictures of typical calcareous outcrops. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

phylogeny was established on a subset of species (*ca* 40%) using nucleotide sequence data for the *rbcl* gene extracted from the GenBank database. This phylogeny was obtained using the BEAST 1.7 software (Drummond et al., 2012) after alignment of the sequences in Mega 5.1 (Tamura et al., 2011). This first tree was compared according to APG3 to check for misidentification in published sequences. The missing taxa, *i.e.*, having no GenBank accession for *rbcl* gene, were then positioned into the phylogeny with respect to published molecular phylogenies of other markers. They have been added manually using Treegraph2 software (Stöver and Müller, 2010). When no molecular information was available, taxa have been positioned at the node of their genus, creating a polytomy that was resolved by the R function “multi2di”. It only concerned recent nodes and did not affect the results of the phylogenetic diversity measures. After corrections, the final tree was converted to a chronogram with branch lengths calibrated to millions of years (Ma) by the penalised likelihood semi-parametric method (Sanderson, 2002) using the R function “chronopl” and 26 node ages for time calibration. The phylogeny tree is provided in the supplementary material as a chronogram in newick format (Appendix 1a) with the literature used to calibrate the node ages (Appendix 1b).

The phylogenetic species diversity was calculated as the mean phylogenetic distance among all pairs of species in a relevé or a set of relevés (mean PSD, “mpd” function, “picante” package, R; Webb et al., 2002). Mean PSD represents the mean distance between two randomly chosen species in a community; this is an estimate of the

phylogenetic information occurring in a community but is independent of the number of species in the community.

2.2.2. Assessment of environmental heterogeneity

Environmental heterogeneity was also considered in these analyses because it is also often suggested as a crucial factor for biodiversity persistence in the context of metapopulation and microrefugia theories (Tamme et al., 2010; Rull, 2010; Dobrowski, 2011). The mesologic relevés were scored using 14 variables: altitude, slope, exposition, cover percentage of high and low shrubs, high and low trees, herbaceous plants and total plant cover, and the proportions of bare ground, litter, rocks, pebbles and gravel. The measurement of the environmental heterogeneity was based on the two main axes obtained through a Principal Components Analysis (PCA, 1132 relevés \times 14 variables table, “dudi.pca” function, package “ade4”, R), which accounted for 36% of the environmental variance. The results of the PCA of environmental variables are provided in the supplementary material (Appendix 2). According to the table of inertia (“inertia.dudi” function), the environmental heterogeneity (EH) is mainly represented by a gradient of the vegetation cover (first PCA axis), which ranges from a highly open habitat with a significant slope to a habitat with more trees and shrubs, and a second gradient (second PCA axis) that ranges from southern exposure to northern exposure with a more herbaceous plant cover. The environmental distance between the relevés was calculated through the Euclidean distance based on the

coordinates (latitudinal and longitudinal position) of each relevé based on the two PCA axes (function “dist”, package “stats”, R). In the correlation analyses introduced below, the environmental heterogeneity (EH) is either the pairwise distance between the relevés or determined by the mean pairwise distance within a set of relevés. A high value of EH indicates important distances within the environmental space defined by the two PCA axes between the relevés.

2.2.3. Assessment of evolutionary legacy

The results reported by Pouget et al. (2013) were used to compute the evolutionary legacy (EL) of *A. provincialis* for each of its occurrences. The EL was computed from the haplotypic diversity of four chloroplast loci (internal part of *matK* gene, *trnK* intron plus 5' part of *matK*, *trnL-trnF* spacer and *trnT-trnL* spacer). This haplotypic diversity was demonstrated to be geographically co-structured with the genomic multi-locus variation estimated by Amplified Fragment Length Polymorphism as well as the ecological distinctness of the populations (Pouget et al., 2013), and therefore we considered it a relevant indicator of the EL of *A. provincialis*.

EL was not computed directly from nucleotidic variation but from phylogenetic relationships of cpDNA haplotypes. First, a chronogram was created using the BEAST software to approximate the ages of divergence among haplotypes of *A. provincialis* (details of the methods are presented by Pouget et al. (2013)). This chronogram was used to calculate a distance matrix between the haplotypes using the function “distTips” (package “adephylo”, R). The mean pairwise distance between a precise population and all other locations was calculated for each population using this distance matrix and the “divc” function (package “ade4”, R). Second, this mean pairwise distance was collected per population (40 populations) to produce an interpolation map using the ArcGIS software version 9.1 (ESRI, Inc., Redlands, CA, USA) with the “krigage” function and an exponential variogram. Finally, the map allowed us to obtain the value of EL for all 174 populations of *A. provincialis*.

2.3. Congruency analysis between components of plant biodiversity

To set analysis of congruency we clustered all the relevés per zones computed after spatial autocorrelation analysis. The objective was to obtain several zones to compare and to map the different components of biodiversity analysed here. The spatial autocorrelations of FD, PSD and EH were evaluated by a mantelogram analysis of the correlation between each variable and the spatial distance (1000 permutations, function “mantel”, “ecodist” package, R); these analyses are provided in supplementary material (Appendix 3). According to results we decided to cluster all the relevés in zones consisting of relevés separated by a maximal distance of 2000 m. This class of distance was the best trade-off to reduce the spatial autocorrelation of the data and retain enough samples of the biodiversity components for correlation analysis. The clustering (“hclust” function, method “average”, package “stats”, R) revealed 94 local neighbourhoods named “2000 m-zones”. All 2000 m-zones with less than three relevés were removed to obtain a final number of 72 zones. The analyses (not shown) performed at the 500-m and 4000-m class distances revealed the same trends.

Pairwise correlations between the ASD, BSD, GSD, mean PSD and mean EH were analysed according to the correlation coefficient of Kendall (tau, function “cor.test”, method “kendall”, stats package, R) and a simple regression analysis (function “lm”, “stats” package, R). The five variables computed within the 2000 m-zones (ASD, BSD, GSD, PSD, EH), as well as EL, were mapped.

2.4. Surrogacy assessment based on the 17% threshold optimisation groups

The theoretical threshold of 17% of protected areas proposed by the “2020” goal of the CBD was used in this study to examine the implications of choosing a precise component of plant diversity as a conservation target for the other components, specifically, in this study, the evolutionary legacy of *A. provincialis*. After application to the dataset, the 17% threshold corresponds to a subset of 192 relevés. We chose the 192 relevés presenting the highest ASD and the highest PSD, and the 192 relevés representing at best EH range. To determine the subset representing the full EH range, we applied a *k*-means clustering method (function “kmeans”, R) on the two PCA axes of the environmental variables to obtain 192 groups of relevés. We then randomly sampled one relevé in each group for a total of 192 relevés representing at best the EH.

For each of these three sets of relevés, which were denoted conservation optimisation groups, we calculated the different indices: ASD, BSD, GSD, mean PSD, mean EH (using the distance matrix), and mean EL (calculated only for the relevés with *A. provincialis*). The differences in the mean EL according to the three conservation optimisation groups was analysed using ANOVA (“aov” function, “stats” package, R).

3. Results

3.1. Assessment of plant biodiversity

The total plant richness of the 1132 relevés included 565 species from 75 families and 33 orders with a majority of Asteraceae and Poaceae. The most frequent species was *Brachypodium retusum* followed by *Rosmarinus officinalis*. Among the tree and shrub species, *Q. coccifera* and *Pinus halepensis* were present at the highest frequencies. *A. provincialis* was ranked 54th, occurring 174 times in the dataset. The majority of the species (301) were present in less than 1% of the relevés, and 101 species were found in only one relevé. The dataset contributes to the knowledge of several rare and protected plant species, with 79 species considered rare at a regional level and 34 species protected under French laws.

The species diversity ranged from three to 68 species per relevé, with an alpha diversity (ASD) of 24.1 species per relevé. The overall species turnover between relevés, *i.e.*, beta species diversity (BSD) was 23.5, and the overall number of species (GSD) was 565. The phylogenetic species diversity (PSD) per relevé ranged from 153.8 to 422.8 mean pairwise distances with a mean of 284.6. High values of phylogenetic diversity represent relevés with few species but highly divergent species, particularly when both ferns and angiosperms are present, whereas low values are due to the presence of angiosperms belonging to closely related families. As a comparison example, the relevé with the maximum PSD (in the north of the area) has six species, including a fern, a monocotyledon and four eudicotyledons (rosids and asterids), and the relevé with the minimum PSD (in the southwest of the area) has five species, all from the Caryophyllales order.

3.2. Congruency analysis between the different components of diversity

The values of the six indices of diversity were mapped within 2000 m-zones: ASD, BSD, GSD, mean PSD, mean EH and mean EL (Fig. 2). These maps highlight a strong spatial structure for ASD, BSD, GSD and EL and a less structured pattern for PSD and EH. As previously reported by Pouget et al. (2013), the EL of *A. provincialis* is higher in the core area.

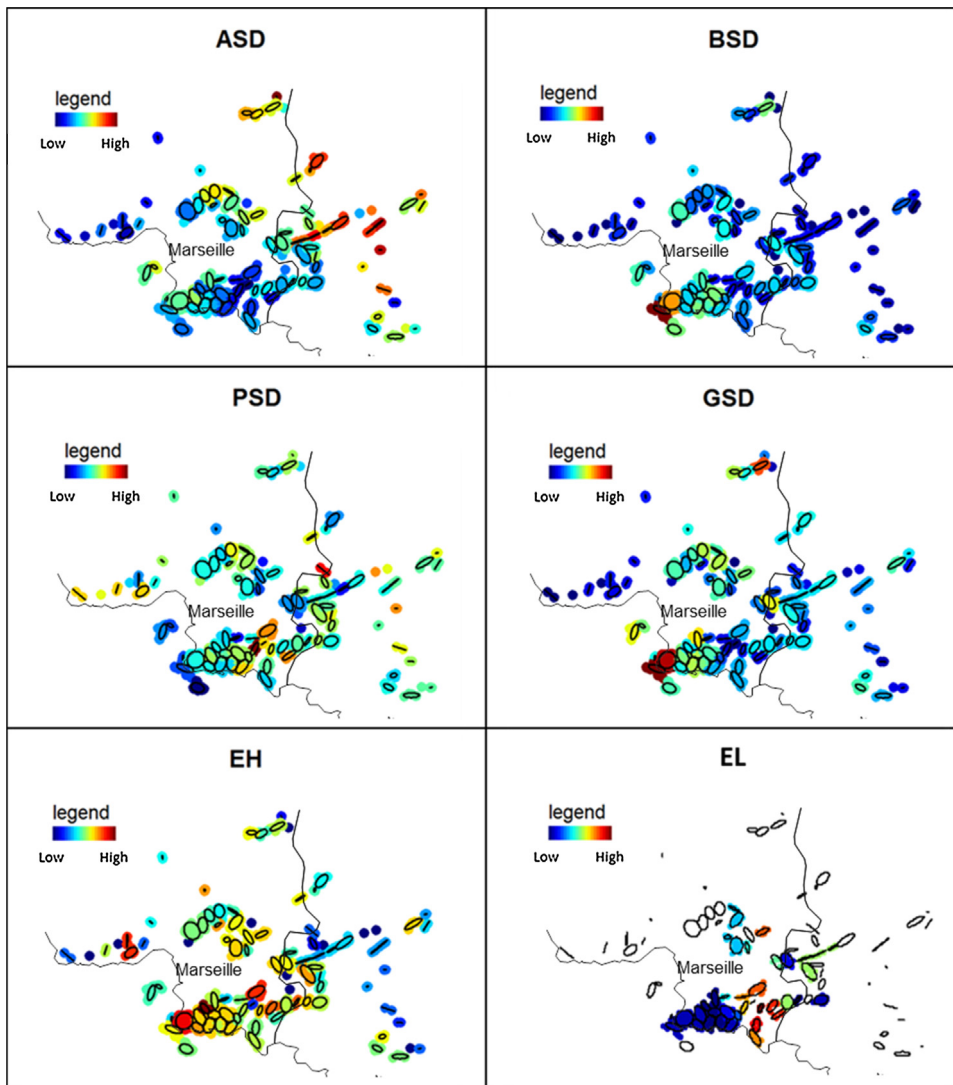


Fig. 2. Map of the alpha, beta and gamma species diversity (ASD, BSD, and GSD), mean phylogenetic diversity (PSD), mean evolutionary legacy of *A. provincialis* (EL) and mean environmental heterogeneity (EH) computed within seventy-two 2000 m-zones. The blue colours depict low values, whereas the red colours depict high values. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

The relationships between the five indices (ASD, BSD, GSD, mean PSD, and mean EH) computed in 2000 m-zones are displayed on the PCA (Fig. 3a) and on the simple linear regressions (Fig. 3b). It revealed both significant positive and negative correlations with three particular patterns of note. First, when the mean EH is increasing, the ASD is decreasing ($\tau = -0.19, p < 0.001; R^2 = 0.25, p < 0.001$), and the BSD is increasing ($\tau = 0.36, p < 0.001; R^2 = 0.16, p < 0.001$). Second, the strongest positive correlation was observed between BSD and GSD ($\tau = 0.56, p < 0.001; R^2 = 0.68, p < 0.001$). The correlation between ASD and GSD was weak. Then, in decreasing order of correlation magnitude, the overall species diversity (GSD) in a 2000 m-zone was mainly correlated to the changes in the composition between relevés (BSD), which is itself positively correlated to the mean environmental heterogeneity of this zone (mean EH). It is worth noting that the mean EH has a negative effect on ASD. Finally, the mean PSD is not correlated with the mean EH, ASD or BSD and is weakly and negatively correlated to GSD ($\tau = -0.23, p = 0.004; R^2 = 0.09, p = 0.006$). As observed previously, PSD is less geographically structured but exhibits important variations (Figs. 2 and 3b). In fact, PSD appeared to not be associated with the local species diversity or environmental heterogeneity (Fig. 3b).

3.3. Can the various components of diversity be surrogate of the *A. provincialis* evolutionary legacy?

The theoretical threshold of 17% of areas applied to the whole dataset corresponds to 192 relevés. Only eight relevés are common to the three groups of optimisation. In addition, 31 are common to ASD-17% and EH-17% only, 24 are common to ASD-17% and PSD-17%, and 27 are common to EH-17% and PSD-17%. This lack of overlap is consistent with the analyses presented above and explains that one criterion never optimises more than two targets (Table 1). There is no single optimisation criterion that matches all of the targets, *i.e.*, rejecting the existence of a single surrogate for all components of biodiversity. The evolutionary legacy of *A. provincialis* is best optimised by the PSD-17% criterion (Table 1) because it selects more relevés situated centrally (Fig. 2) with a high level of EL (Figs. 2 and 4), therefore raising the mean EL. The worse optimisation was obtained for the EH-17% criterion, which picked relevés with low values of EL. However, these results have to be nuanced by the low capacity of the three criteria to include *A. provincialis*; 13, 37 and 36 of 174 relevés were selected by one of the three criteria, namely ASD-17%, PSD-17%, and EH-17%, respectively.

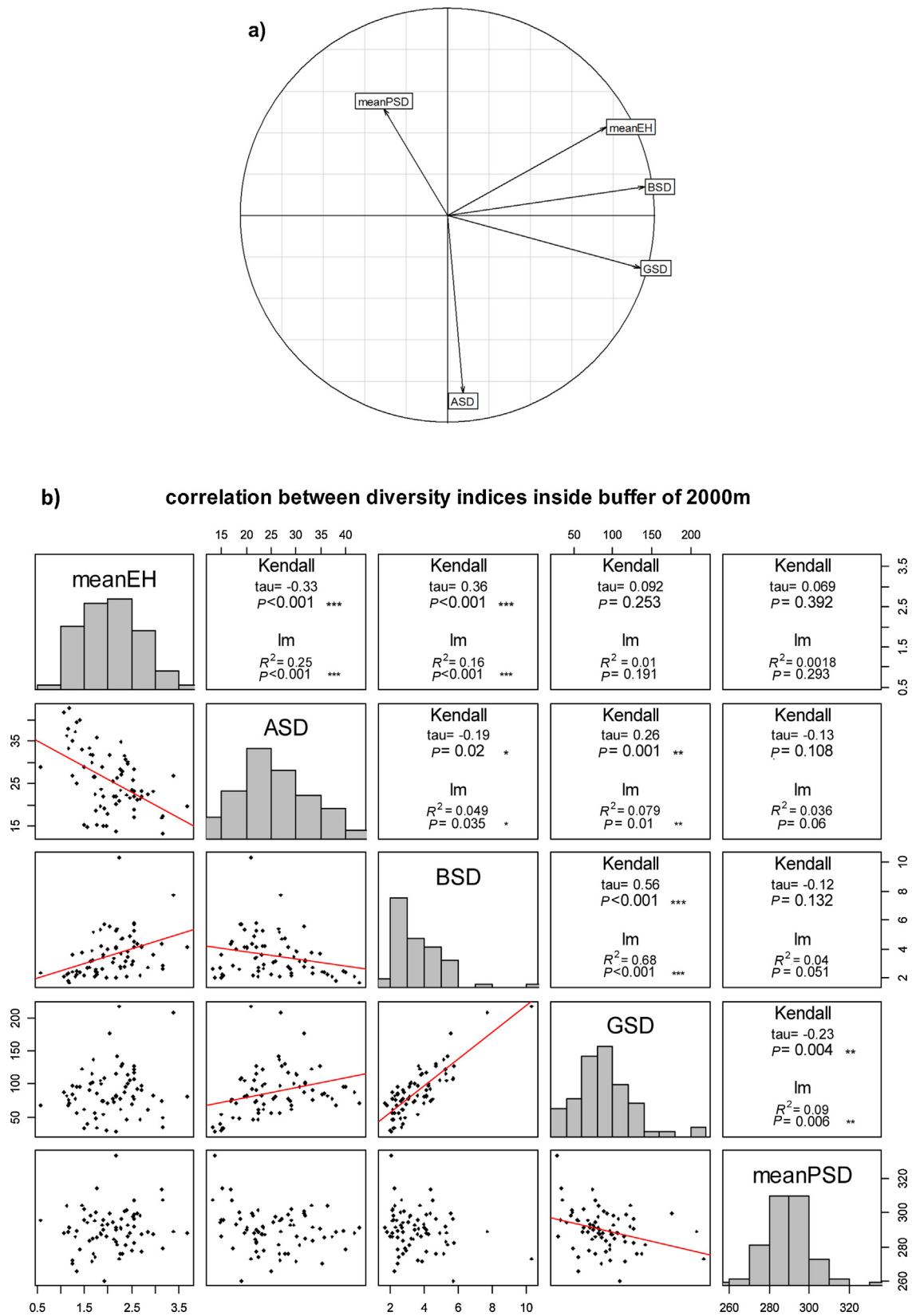


Fig. 3. (a) Principal component analysis of the relationships between the five indices of biodiversity computed for the 2000 m-zones (with more than two relevés, *i.e.*, 72) in southern Provence. (b) Plots and linear regression results of the relationships between the five indices (Kendall tau values and *p*-value of this test, *R*-squared value of the linear regression and *p*-value). ASD, BSD, GSD, mean PSD and mean EH are alpha, beta, gamma species diversity, mean phylogenetic diversity and mean environmental heterogeneity respectively, all indices were computed for the 72 zones.

Table 1
Comparison among the three criteria of surrogate capacity for different targets of biodiversity and evolutionary legacy of *A. provincialis*. Exponents ^a, ^b and ^c represent the results of the ANOVA test, and the presence of the same letter indicates no significant difference, and different letters indicate that the values are significantly different.

Criteria	Target					
	γ diversity	β diversity	α diversity (ASD)	Mean PSD	Mean HE	Mean EL
Highest ASD 17%	462	11.8	39.8	288.45	1.92	0.6 ^{a,b}
Highest PSD 17%	314	14.8	21.22	320.51	2.98	0.78 ^a
Highest HE 17%	346	17.7	19.59	293.29	3.87	0.42 ^b

4. Discussion

To the best of our knowledge, our sampling effort and analyses of diversity is the first significant study of its kind realised at a scale relevant for conservation actions in areas neighbouring a large Mediterranean city affected by the threat of mass tourism and urban sprawl. Important insights emerge from our results and involve several implications for conservation planning for the evolutionary legacy and the different components of biodiversity.

4.1. Spatial mismatch between different components of diversity

The general picture of our study is the lack of congruence between components of plant biodiversity (e.g., Figs. 2 and 3b) and associated spatial mismatches (Fig. 4). Various processes are con-founded in the determination of the composition and richness of plant communities (Lortie et al., 2004) and the lack of congruence between components of plant biodiversity revealed here suggest that different factors control the different components. Significant

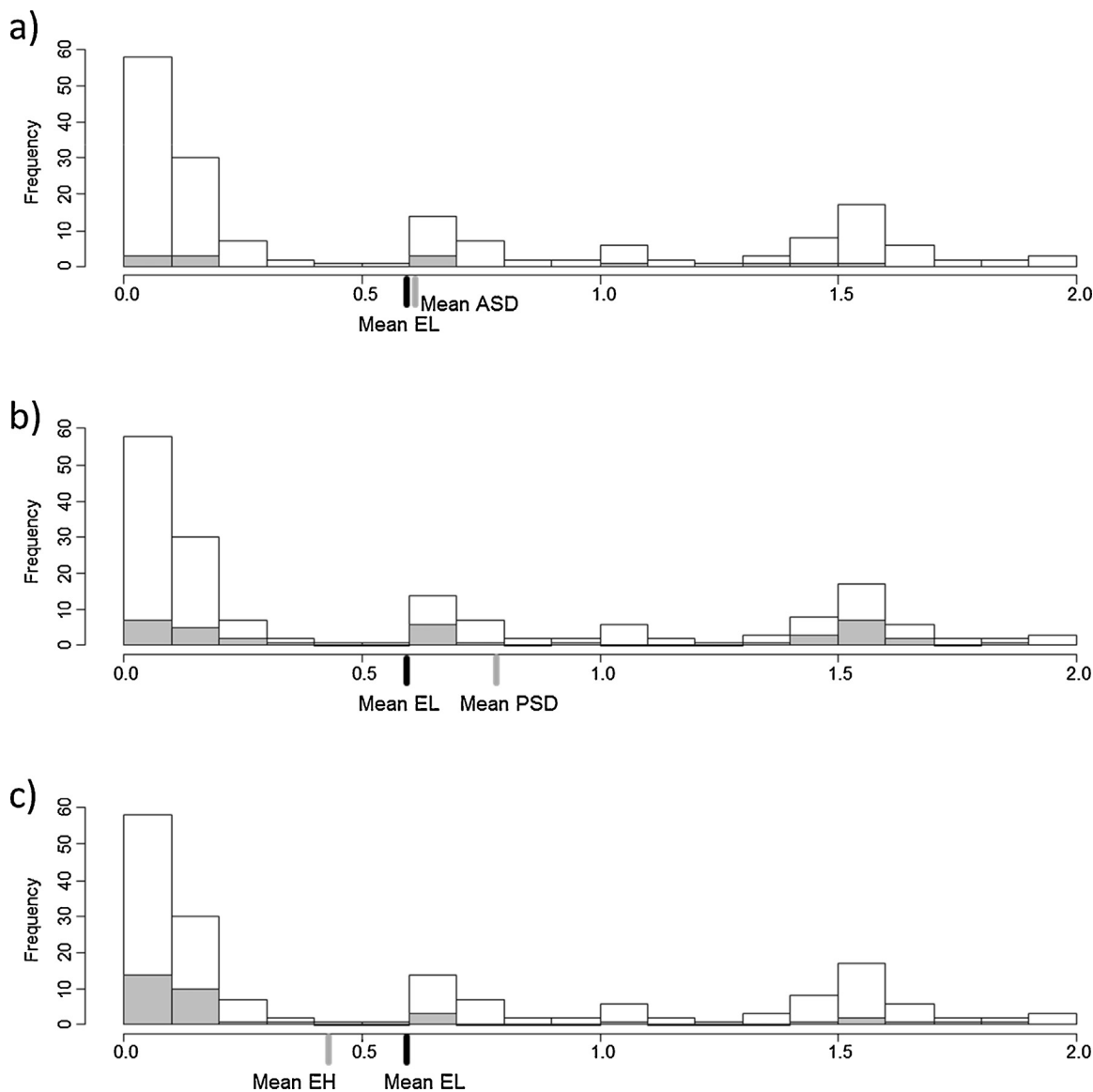


Fig. 4. *Arenaria provincialis* evolutionary legacy distribution as a function of the frequency of sites per class of EL value (white area). The grey areas represent the value for (a) the set of sites with the highest species diversity (ASD), (b) the set of sites with the highest phylogenetic species diversity (PSD), and (c) the set of sites with the highest environmental heterogeneity (EH). The overall mean value of EL is represented with a black line in (a)–(c), and the mean value of EL for each criterion is indicated by a grey line.

correlations between species and genetic diversity are more frequently observed in discrete habitats (Vellend et al., 2014); in the study area the sampling units were not isolated from similar habitats, rejecting any likely effect of patch size or isolation on diversity. Moreover, Mediterranean landscapes are also impacted by a long history of human induced disturbances (e.g., recurring fires) that may have broken the co-structures between the various components of diversity.

None of the three criteria that designate optimisation groups can match all of the conservation targets (Table 1). Contrary to the observation of Rodrigues and Brooks (2007) that review a positive surrogacy power, our key result rejects the hypothesis of a single surrogate. The spatial mismatches among biodiversity facets involve the necessity of conservation planning considering several targets in order to protect the various components of biodiversity (Margules and Pressey, 2000; Devictor et al., 2010; Mouquet et al., 2014; Zupan et al., 2014). Zupan et al. (2014) demonstrate that patterns of diversity including taxonomic, phylogenetic and functional diversity of terrestrial vertebrates strongly diverge and that evolutionary history is unequally protected. Areas with a high phylogenetic diversity are likely to harbour a great evolutionary history, which is by itself a crucial aspect of biodiversity (Faith, 1992; Webb et al., 2002; Mace et al., 2003; Mace and Purvis, 2008; Cadotte and Davies, 2010). In this study the phylogenetic species diversity, measured by mean phylogenetic pairwise distance methods (mean PSD), is less spatially structured than the other indices (Fig. 2). Reinforcing overall observation of spatial mismatches among biodiversity facets, our analyses revealed that phylogenetic species diversity (mean PSD) was poorly correlated to the taxonomic species diversities (ASD, BSD and GSD) and to the environmental heterogeneity (EH) (Fig. 3b). The mean PSD highlighted zones with the widest phylogenetic composition among vascular plants, e.g., deep phylogenetic divergence within angiosperms. Maximising protection of phylogenetic diversity may aid protecting ecosystem function (Smith et al., 2014).

4.2. Species biodiversity components are not effective surrogate of evolutionary legacy

This study represents the first assessment of the congruence between plant biodiversity and evolutionary legacy of an endemic taxon. The inclusion of intra-specific genetic diversity in conservation planning is key for evolutionary resilience over the long-term (Sgro et al., 2011).

At the fine scale of the analyses conducted in this study, neither the taxonomic species diversity, i.e., alpha, gamma or beta diversity, nor the mean environmental heterogeneity are able to target the core area of the distribution of *A. provincialis* (Fig. 2). This core area is sheltering the highest level of genetic diversity of *A. provincialis* and has been at the origin of westward and eastward expansions that led to the current distribution of the species (Pouget et al., 2013).

Contrary to the congruent biogeographical patterns observed at the coarser scale in the Mediterranean area (Médail and Diadema, 2009), our analysis supports the lack of congruency between the evolutionary legacy of a narrow endemic plant and the floristic diversity of the vegetation surrounding its habitat. Giving priority to the plant taxonomic species diversity criterion does not optimise and would not protect the overall population distinctness of *A. provincialis*. The species is represented by two major phylogeographic lineages, occurring in two well-differentiated parts of the ecological niche (Pouget et al., 2013): the alpha species diversity (ASD) level is high in the northeast lineage of *A. provincialis*, whereas the beta species diversity (BSD) level is high in the southwest lineage. Similarly, the environmental heterogeneity will especially target the southwest lineage. As a result, prioritising the taxonomic

diversity (alpha or beta) or environmental heterogeneity will not optimise the conservation of the evolutionary legacy of *A. provincialis* (Table 1 and Fig. 4a and c). High levels of phylogenetic species diversity (mean PSD, Fig. 2) result in a better sampling of the evolutionary legacy of *A. provincialis* (EL) because of relevés with a high mean PSD within the core area where molecular variation of *A. provincialis* is highest. As a result, mean PSD is the “least bad” criteria among the three criteria compared (Table 1 and Fig. 4b) to target the evolutionary legacy of *A. provincialis* but we cannot exclude the possibility that this result was due to a random effect linked to the absence of spatial correlation among the mean PSD values.

As previously shown by Lamy et al. (2013) correlations analyses between species and genetic diversities should be conducted at the relevant spatial and temporal scales. Our results are demonstrating that coarse scale studies of biodiversity will overlook evolutionary legacy as well as crucial areas for long-term persistence. To our knowledge and in the current state of our analysis of biodiversity in the study area, no component of biodiversity was able to predict the area sheltering the highest evolutionary legacy of *A. provincialis*. Perspectives will be to generalise these findings to specialist plant species living with *A. provincialis* in lapiaz (e.g., *Linaria supina* or *Pimpinella tragium*) or in steep screes (e.g., *Laserpitium gallicum*) to restrict the range of processes (Manel and Holderegger, 2013).

4.3. Applied implications for conservation planning

Our analyses, conducted at a finer scale than recent studies of spatial congruency (e.g., references cited above), raise a concern regarding the difficulty of maximising the efficient use of limited conservation resources to protect all components of biodiversity (Bottrill et al., 2008). Especially, it rejects the possibility of a single surrogate of biodiversity.

For example, *A. provincialis* is protected under European Habitat Directive (annexe 2) and French laws, and therefore, its presence could have a beneficial effect on the conservation of the whole flora and surrounding habitats. However, the presence of *A. provincialis* is rarely associated with the area of strongest species richness (ASD or BSD) and this species is not a good surrogate for the preservation of floristic diversity. Furthermore, the focus area is also partially protected from urban sprawl by the recent establishment of the National Park of Calanques (NPCal, Fig. 1), which was created in 2012. NPCal protects a large number (425 species) of the 565 species within the study area and shelters several nationally protected plant species (25 species), mostly on islands and coastal plant communities. Yet, NPCal covers only partially the evolutionary legacy of *A. provincialis* and the ecological distinctness of its populations (Figs. 1 and 2). This fact is true for the evolutionary legacy of *A. provincialis* but also for the other components of biodiversity measured in this study. Indeed, the highest values of phylogenetic diversity (mean PSD) or species richness (ASD) fall outside the perimeter of the NPCal (Fig. 2), and this result should be considered for any future planning of protected areas near Marseille. The spatially mismatched and unequally protected biodiversity facets studied here are an example of the high singularity of Mediterranean biotas that have already been reported at higher scales (e.g., Nieto Feliner, 2011; Aparicio et al., 2012). Our results strengthen the need for higher consideration of the complexity of Mediterranean biodiversity in conservation planning, with more focus on intra-specific diversity, which may be high and vulnerable in the surroundings of urban areas (Araújo, 2003; Luck, 2007).

Since Avise et al. (1987), the repeated discovery of phylogeographic lineages within species has challenged the perspectives of conservation biology. The importance of intra-specific diversity for ecosystem functioning and for preserving the evolutionary potential of species demands that genetic diversity should not be neglected when designing conservation strategies (Bonin et al.,

2007; Lankau and Strauss, 2011; D'Amen et al., 2013; Smith et al., 2014) even when time and money are lacking (Ponce-Reyes et al., 2014). The strong phylogeographical structure of *A. provincialis* affords an excellent opportunity to relate the evolutionary legacy of long-term persistence to current environment and species diversity patterns. Our study highlights the crucial role of phylogeography in the evaluation of current protected areas and as a necessary criterion for future conservation planning.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolind.2015.07.017>.

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