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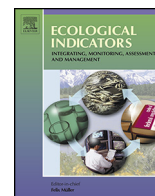
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Building relevant ecological indicators with basic data: Species and community specialization indices derived from atlas data



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ABSTRACT

Species and community specialization have become popular indicators to track the spatial and temporal changes of species and community dynamics during current global changes. However, measuring specialization requires detailed and quantitative descriptions of habitat requirements or resource use, which are difficult to obtain for many species. Here, we propose and test a new method to quantify and map the relative composition of specialist and generalist species in local plots compatible with very basic ecological data, typically used for atlases. We used co-occurrence patterns of 1090 plant species recorded in the French Mediterranean region of Languedoc-Roussillon in a systematic grid of 1225 5 × 5 km atlas cells to estimate species specialization. We then calculated the averaged specialization of each cell and tested several expected relationships of these indices. In particular, we tested the relationship between species richness and average specialization and the relationship between community specialization and landscape disturbance induced by land use. As expected from studies conducted on fine-scale data, we found that specialist species were those with more restricted distributions and occurring in richer species assemblages. We also found that community specialization was maximized at an intermediate level of landscape disturbance. These results suggest that aggregating specialization at large spatial scales provides useful species and community level indicators. Estimating specialization level with co-occurrence data is a good complementary approach to traditional estimations of diversity indices for conservation and landscape planning.

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1. Introduction

Finding the best indicator of species and community responses to landscape degradation is an ongoing challenge for ecologists. Consequently, ecological indicators based on “species diversity” are very popular; although their relevance was questioned at an early stage, when species diversity was considered a non-concept (Hurlbert, 1971). New indices (accounting for ecological, phylogenetic, or functional differences among species) have, thus, been recurrently proposed to complement species diversity metrics (Monnet et al., 2014). Developing more relevant biodiversity indicators has become, however, a scientific, political, and societal issue of great importance (Frederiksen and Gudmundsson, 2013). But rather than searching for the “best” indicator, authors have now recognized that indicators are not “good” or “bad” but that

their relevance depends on the question asked and on the data available (Feest et al., 2010).

To assess the large-scale impacts of landscape degradation on communities, ecological metrics reflecting the dynamics of “losers” versus “winners” within species assemblages were proposed as a promising approach in conservation biogeography (Devictor and Robert, 2009). In particular, the replacement rate of habitat specialist species by generalists was viewed as a direct signature of a community response to large-scale habitat degradation for animals and plants (Clavel et al., 2010; Abadie et al., 2011). In fact, it is generally expected that habitat specialists will benefit from stable and undisturbed habitats whereas, generalists should respond positively to habitat variability (Colles et al., 2009). These expectations have been widely tested and ecological indicators built upon the temporal trends of specialist species have been considered relevant official indicators of sustainable development for use at national and international levels (Gregory et al., 2005).

Ideally, the spatial or temporal replacement of specialists by generalists can be estimated using large-scale and standardized community monitoring programs (Devictor et al., 2007). With such

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data, the specialization of species and communities can be derived from the statistical relationships reflecting species distribution along habitat gradients, both monitored by standardized schemes. In practice, however, large-scale monitoring data for national or regional surveys are currently being collected for only a few groups (mostly birds, butterflies, and mammals) and are based on presence–absence data. Moreover, measuring species specialization is often impaired by the lack of high enough resolution data on habitat requirements or by the difficulty of defining habitat selection accurately (Podani and Csányi, 2010). Consequently, two main approaches have been used to quantify change in community composition following landscape disturbance: (i) at global or national scales, some authors have used crude classifications of species into specialist versus generalist groups. For instance, indicators for the state of the European avifauna rely on the average trend of some species, classified as being specialized for a given habitat type (e.g., farmland bird specialists) (Gregory et al., 2005), (ii) in contrast, others have used high-resolution data on detailed species requirements. In this case, continuous and species-specific levels of ecological specialization was derived from standardized protocols, in which habitat or resource preferences could be precisely assessed (Devictor et al., 2007; Correa and Winemiller, 2014). However, methods to estimate the specialization level of species and communities using classic ecological data (i.e., the presence or absence of species across sites) are lacking; although, they could help to track the fate of species and communities in many contexts.

Interestingly, Fridley et al. (2007) proposed a method to estimate species specialization that only requires presence–absence data. It assumes that species co-occurring with similar species are usually those found in similar habitats and could, thus, be considered specialists. Conversely, generalists should be widely distributed across habitats and thus co-occur with many different species. In other words, for a given species, the similarity in the identity of species co-occurring with that species can be considered, according to this approach, a continuous proxy for species habitat specialization. From this assumption, and providing that co-occurrence data are available, a species specialization index (SSI) can be simply deduced for each given species using the identity of the species co-occurring with that species. This approach can be applied to any dataset providing that different species assemblages have been recorded in different locations (Abadie et al., 2011; Boulangeat et al., 2012). Using this approach, specialization was equated to niche breadth to test a specific hypothesis on the role played by competition (Manthey et al., 2011), or specific functional traits (Albert et al., 2010) in species distribution. Although originally developed for plants, this approach has also been successfully used for amphibians (Rannap et al., 2009), and fishes (Munroe et al., 2013).

This approach does not a priori tell whether ecological specialization can be relevant when measured for data collected at coarse spatial grain. Indeed, co-occurrence patterns are expected to yield different types of specialization when estimated at the quadrat, landscape, or regional scale. In this respect, although Fridley's method has been applied to various organisms in different contexts, its relevance for co-occurrence data obtained from species lists recorded across large spatial scales has not been explored (but see Boulangeat et al., 2012). Furthermore, it remains unclear whether specialization is still relevant and sensitive when defined at spatial scales different from those most likely to capture habitat selection and species interactions.

Once the specialization levels of species are estimated and are sensitive enough to habitat disturbance, the distribution of species and assemblages according to their specialization level can be investigated. In particular, specialist species are expected to be more numerous and to concentrate more individuals in less

fragmented landscapes (Devictor et al., 2007). At the community level, a community specialization index (CSI) of species assemblages can be calculated as the average of each species SSI present in the assemblage (Devictor et al., 2008). The CSI is expected to be higher for species assemblages mostly composed of specialist species. It can then be used as an interesting ecological indicator complementary to more traditional indicators based on diversity (Filippi-Codaccioni et al., 2010; Abadie et al., 2011). Mapping the CSI can thus provide a picture of spatial variation in the specialization level of communities, which can be related to independent sources of disturbance or used as a spatial guideline to identify sites of conservation interest (Devictor et al., 2008). Yet whether such a community specialization index can be used as a relevant ecological indicator with basic ecological data has never been explored.

Here, we used a large-scale co-occurrence dataset on plants to estimate a species specialization index (SSI) for each species and a community specialization index (CSI) for each grid cell. We then specifically tested several hypotheses on SSI and CSI derived from studies on specialization conducted with higher resolution data and at finer spatial resolution. In particular, we investigated (i) whether and how the species distribution was dependent on their SSI. At the assemblage level, we tested (ii) the relationship between CSI and species richness, and (iii) the relationships between these two metrics and landscape disturbance.

2. Methods

2.1. The study region

The study was carried out in the Languedoc-Roussillon region (27,376 km²) in southern France, which encompasses most of the Mediterranean region west of the Rhône valley (Fig. 1). The main landscape types occurring here are coastal landscapes with

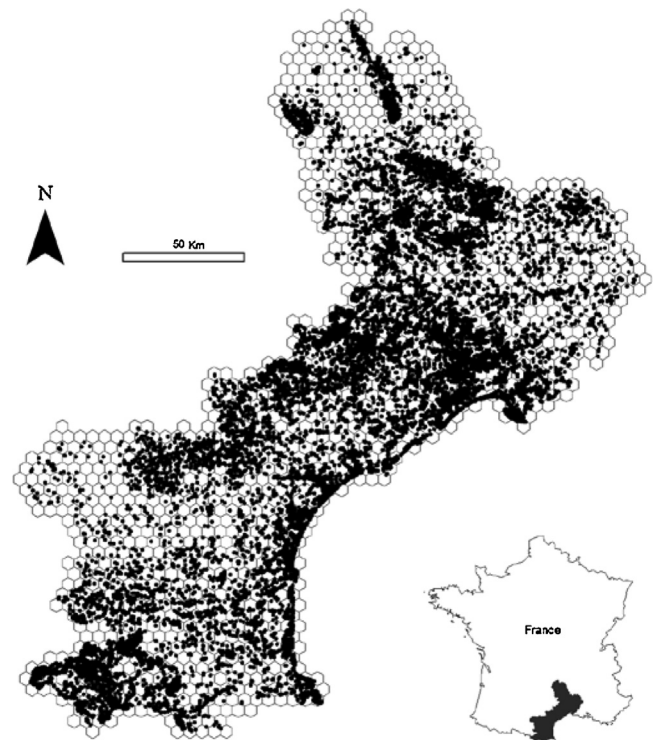


Fig. 1. The study region and the distribution of occurrence data. Each dot represents a species list recorded in the database. The grid cells of 5 × 5 km used for the aggregation are delineated.

lagoons, marshes, cliffs and dunes, and lowland garrigues. These habitats are often included in mosaic landscapes with cultivated areas, vast areas of vines, extensive upland limestone plateau areas, and hilly or mountainous landscapes on granite and schist in the southern tip of the Massif Central and the south-eastern Pyrenees. In the last 50 years, these landscapes have been profoundly modified by human activities so that heavily disturbed habitats coexist with stable ones (Thompson, 2005; Blondel et al., 2010). First, extensive and rapid urbanization spread around towns and villages across the lowland plains in conjunction with massive proliferation of coastal tourist resorts. Second, human population decline in many rural areas was accompanied by the abandonment of vineyards and grazing activity, which was followed by rapid natural reforestation of agricultural fields (IFEN, 2003).

2.2. Species data

Plant species data were compiled by the Conservatoire Botanique National Méditerranéen de Porquerolles (CBNMP), which is in charge of the regional database of all plant species present in this region. Original data were collected between the years 1611 and 2009 and correspond to the combination of all the naturalist inventories, herbariums, bibliographies, reports, and atlases available in the region. For the purpose of this study, only data on vascular plant species collected since the year 1980 were used. A database of 3667 species with 420,659 occurrences was obtained. All data were then combined and aggregated in a systematic grid of 1227 5×5 km cells to define a standardized spatial scale resolution (Fig. 1). Each grid cell was considered a site of species co-occurrence. The robustness of our results to changes in the scale of aggregation was also tested with 2×2 km and 10×10 km grids.

In large-scale biodiversity inventories, spatial, and temporal variation in sampling can introduce significant biases into the representation of species distribution. Here, species have been sampled by different observers using several methodologies. Although this variability in the protocol represents a lack of standardization, the species selection to estimate specialization (see below) further ensured that it is estimated, for each species, with the same sample size.

2.3. Measuring species and community specialization indices

First, the algorithm proposed from Fridley et al. (2007) was used to measure a species specialization index (SSI) for each plant species. This approach has recently been shown to be a suitable method for measuring plant specialization using large samples across very heterogeneous environments (Boulangeat et al., 2012). For each given species, a random combination of sites (50 sites) in which this species occurs is selected. A similarity index is then calculated between each pair of sites to reflect the degree of between sites species turnover in the 50 sites. This is repeated 100 times for each species. For each of the 100 repetitions, a new random set of 50 sites is thus selected and a corresponding SSI is calculated. The overall SSI of the given species is calculated as the average of the 100 SSI obtained (see Fridley et al., 2007). Note that species occurring in fewer than 50 sites are not considered, as it would be unreliable to measure their specialization level from co-occurring species. Among the 3667 species, 1090 were present in enough sites to provide an SSI so all analyses were conducted on these species. Note also that, in this approach, the SSI is always calculated for each species from a fixed number of sites (50). In each combination, the sites are selected randomly across the species range within the studied area. Thus, specialization of rare and common species is derived from combinations of species assemblages of equal size. This approach provides an increasing SSI

value from the most generalist (i.e., those expected to co-occur with more different species and thus generate less similarity between sites) to the most specialist species (co-occurring with more similar pools of species).

Ecologists have used a large number of different measures of community dissimilarity (also called beta-diversity or turnover) with different properties and meanings (Koleff et al., 2003). Here, we measured similarity using the average of pairwise β_{sim} calculated among sites (Baselga, 2010). For two sites, β_{sim} is an index given by $\beta_{sim} = \min(b,c)/(a + \min(b,c))$ where a is the number of species common to both sites, b is the number of species that occur in the first site but not in the second and c is the number of species that occur in the second site but not in the first. This index varies between 0 (all species shared) and 1 (no specie shared). We then used $SSI = 1 - \beta_{sim}$ to measure a specialization. The SSI is, therefore, also theoretically bounded between 0 (most generalist) to 1 (most specialist).

Note that other dissimilarity indices including species abundance when available and independent of species richness can also be used (Boulangeat et al., 2012). However, other traditional ways of measuring similarity between plots (e.g., in partitioning diversity in local, regional, and among-site components (Lande, 1996)) should be used with caution. In fact, a common though unwanted property of these alternative similarity metrics is to be correlated to species richness (Koleff et al., 2003). In Fridley's algorithm, these other metrics tend to be highly sensitive to species occurring in species-poor habitats, which have strongly skewed richness distributions (Manthey and Fridley, 2009). The Simpson's pairwise index (β_{sim}) is among the less biased metric of similarity (Baselga, 2010) so we used it as a good index of beta-diversity.

Once an SSI was obtained for each species, a community specialization index (CSI) was calculated for each grid cell as the average of the SSI values belonging to the species present in this cell (Devictor et al., 2008). Only cells in which at least 10 species were present were considered. The CSI is higher for species assemblages with more specialist species (i.e., with a high SSI) and is, by construction, independent of species richness.

2.4. Measuring landscape disturbance

The indicator of spatial disturbance used was based on the compilation, for each site, of three kinds of human pressure: road density, urbanization, and agriculture. Note that disturbance is used here as a generic term without specific expectation of its negative or positive impact on plant assemblages: some of these artificial landscape modifications can be positive for some species and negative for others. For road density and urbanization, the "road" and "built-up" layers from the BD TOPO[®]/RGE GIS database (IGN Institut Géographique National) were used. For agriculture, the "arable land", "mixed agriculture", and "permanent culture" layers from the corine land cover database (Bossard et al., 2000) were used. For each site, the proportion of disturbance elements within the site was calculated. Then, a disturbance indicator was calculated for each site as the mean value of the normalized value (from 0 to 1) for each proportion. This disturbance indicator was explicitly tested in this region and was shown to provide a relevant proxy for mapping the spatial distribution of the intensity of human-induced modification of landscape composition (Vimal et al., 2011).

2.5. Data analysis

We first focused on the characteristics of more or less specialized species. We tested whether the species distribution in the area considered was related to their SSI using linear

regression. SSI was considered as a dependent variable and the number of sites occupied by the species the explanatory variable assuming independence of the observations and a Gaussian distribution of the errors. Species with lower SSI (more generalists) were expected to occur in many sites in line with the Brown hypothesis (Brown, 1984; Gaston, 2003). Indeed, niche breadth should reflect the degree to which species requirements meet environmental conditions. Niche breadth is, therefore, generally found to be positively related to species occupancy (i.e., generalist are those with broader niches, and thus with wider regional occupancy).

Similarly, how specialist and generalist species were distributed in rich and poor species assemblages was tested. To do this, we used linear regression to test the relationship between SSI and the average species richness of the assemblage where the species occurs. We expected species with lower SSI to be found in species-poor assemblages following lower niche packing in these assemblages. On the contrary, we expected species-rich assemblages to favor specialist species, best able to partition the total ecological niche space (Belmaker et al., 2011).

Finally, we tested whether the richness and CSI of assemblages were related to environmental disturbance. We expected spatial dependency in observations and potential non-linearity in the relationships. We used generalized least square (GLS) models to test this relationship. GLS are specific weighted regressions in which a direct marginal variance–covariance spatial structure of the responses can be specified (Zuur et al., 2009). This structure was first investigated using different forms of semi-variograms to account for spatial dependency of the residuals. The best spatial structure (exponential) and corresponding range and nugget were then added to the model (using the function GLS and CorExp in the package nlme in R). R^2 is not well defined for GLS. Thus, to get a rough estimate of the goodness of fit for these models, we used the R^2 of linear regressions accounting for spatial gradients in which polynomial terms of the coordinates (x, y, x^2, y^2 , and xy) were added as covariates (Fortin and Dale, 2005). Community descriptors are often found to be non-linearly related to environmental variables. To test for any potential hump-shaped relationships between species richness (or CSI) and disturbance, we used the same model than above with disturbance and disturbance² as predictors. All statistical analyses were carried out using R 2.11 software and the package “nlme” for GLS models (R Development Core Team, 2014).

3. Results

At the species level, when calculated using a 5×5 km grid, the species specialization index (SSI) ranged from 0.21 to 0.43 (mean 0.32 ± 0.03 s.e.). It was robust towards change in the spatial scale considered (correlations between SSI calculated at 5 km^2 and 2 km^2 , $R^2 = 0.82$, $P < 0.001$ and between 5 km^2 and 10 km^2 , $R^2 = 0.83$, $P < 0.001$). Generalist species were more widely distributed (i.e., occurred in more sites) than specialist species ($F_{1,1088} = 244$; $P < 0.0001$; $R^2 = 0.18$; Fig. 2a). Interestingly, the shape of the relationship suggests that both specialists and generalists can have restricted distributions (i.e., occur in few sites) while, comparatively, only generalists can have wide distributions. There was also a strong positive linear relationship between specialization and the mean species richness of co-occurring species ($F_{1,1088} = 357$; $P < 0.0001$; $R^2 = 0.25$; Fig. 2b). In other words, specialist species tend to occur in richer assemblages than generalists do.

At the species assemblage level, the CSI increased linearly with species richness suggesting that rich assemblages are principally composed of specialists (GLS: $F_{1,1225} = 26.5$; $P < 0.0001$; $R^2 = 0.16$, Fig. 3). Note that the variability of CSI values was unevenly distributed along the species richness gradient: poor assemblages

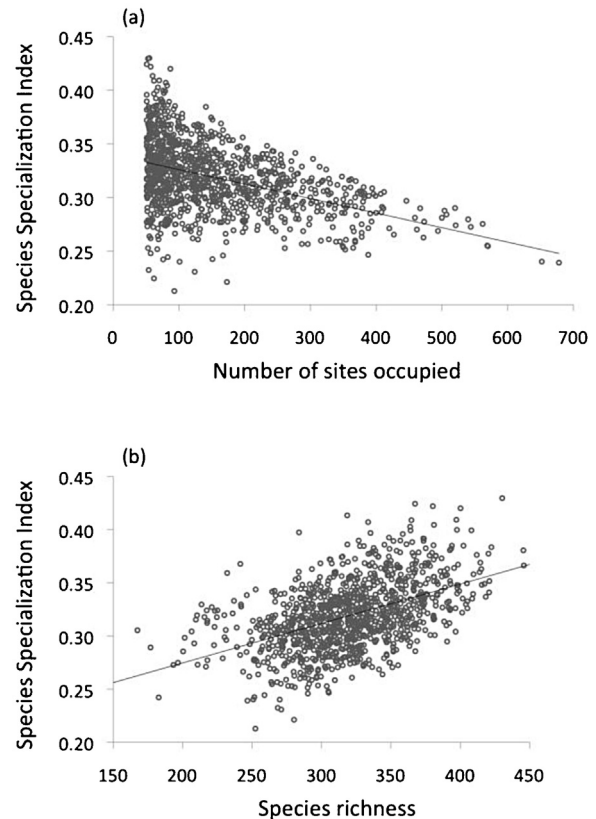


Fig. 2. Relationships between the species specialization index (SSI) and (a) the number of sites where the species occurs and (b) the average site species richness where the species occurs.

included assemblages with high and low CSI values while rich assemblages mostly consisted of specialists.

The relationships between CSI or species richness and disturbance were poorly described using linear models (not significant for CSI, $P = 0.23$, nor for species richness, $P = 0.84$). However, there were curvilinear relationships between species richness and disturbance (complete quadratic model: $R^2 = 0.16$; $P < 0.0001$; quadratic term $b = -0.0024$, $P = 0.007$). As part of the relationship between CSI and disturbance could potentially be driven by the relationship between CSI and species richness, the effect of disturbance on CSI was tested while controlling for species richness by adding it as a covariate. When variation in CSI was adjusted for variation in species richness, there was still a

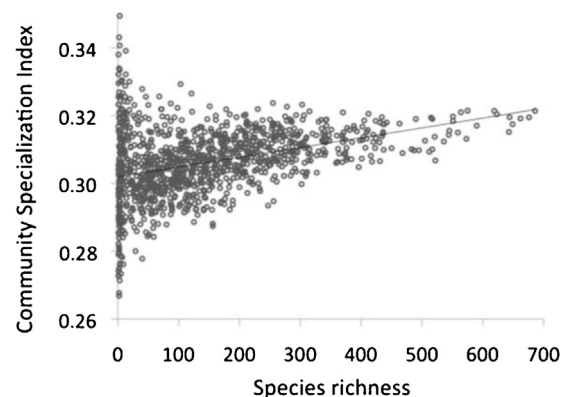


Fig. 3. Relationship between the community specialization index (CSI) of species assemblages and their species richness.

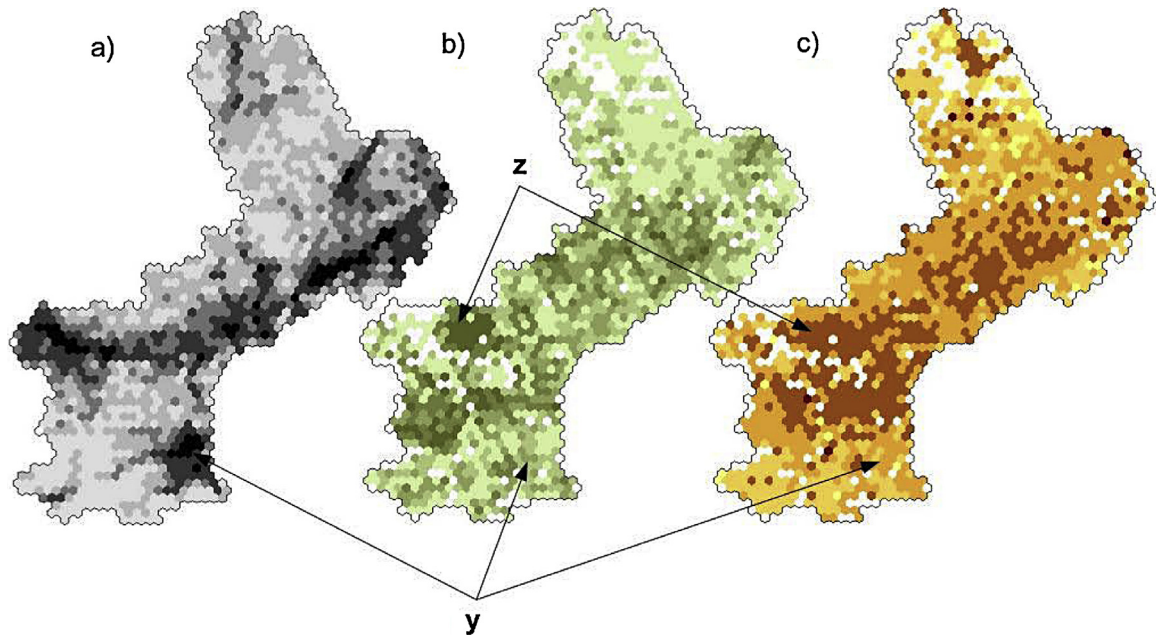


Fig. 4. The spatial distribution of (a) disturbance (b) species richness (c) community specialization index (the value increases from pale to dark colors. The missing values are in white). As examples, *y* is a zone of relatively high disturbance but with low richness and CSI. In contrast, *z* is an area of low disturbance but high CSI and richness. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

curvilinear effect of disturbance on CSI ($R^2 = 16$; $P < 0.0001$; quadratic term $b = -0.25$; $P = 0.003$).

Finally, mapping species richness, landscape disturbance, and community specialization revealed specific areas of congruencies and mismatches (Fig. 4). For instance, zone *z* illustrates an area in which richness and CSI are both of high value. These areas are of high conservation interest, yielding many specialist species. Comparatively, in zone *y* where landscape disturbance is high, richness, and CSI are relatively low, suggesting that these are areas where plant communities have been strongly impacted by disturbance leading to poor assemblages mainly composed of generalists.

4. Discussion

Using very basic co-occurrence data, we were able to segregate species along a continuous gradient of specialization. Obviously, in this approach, “specialization” is not equivalent to niche breadth as generally estimated using fine species responses to environmental conditions or specific functional traits. In our study, specialization rather reflects the tendency of species to occur in different landscapes composed of different species. Instead of providing a traditional niche breadth index, this approach gives an operational and quantitative metric for measuring the similarity of co-occurring species, relevant to large-scale occurrence data.

The ecological meaning of this species-specific attribute is scale-dependent. While plant species interact at very local scales, the co-occurrence patterns at larger scales will be more influenced by regional and dispersal processes. In other words, a species can be considered specialist at a landscape level although the same species could be a generalist for specific habitats within landscapes (Devictor et al., 2010; Boulangeat et al., 2012).

Nevertheless, our species specialization index (SSI) estimated with atlas data was robust towards changes in the scale considered (2×2 km, 5×5 km, or 10×10 km) which suggests weak variations in landscape composition between such scales. It is therefore, likely that the SSI calculated at 5×5 km already captures relevant variability in the composition of species assemblages in the region

considered. This first result also suggests that large-scale specialization estimated with atlas data reflects an interesting and robust characteristic of species. Moreover, co-occurrence-based indices of specialization were shown to be correlated with more detailed and commonly used metrics of niche breadth as well as with specialization metrics derived from multivariate analysis including habitat variables more explicitly (see Boulangeat et al., 2012 for comparison of indices).

Other results further suggest that estimating specialization with atlas data provides relevant results, in harmony with those found with finer estimations of niche breadth. First, when specialization is measured for specific habitats or resources, specialist species are generally found to be those with smaller ranges (Gaston, 2003). Here, we found that species co-occurring with many different species (i.e., with low SSI) are also those with larger distributions in the region considered (Fig. 2a), a pattern already documented for the regional flora of the French Alps (Boulangeat et al., 2012). At fine scales, greater niche partitioning is also expected when species richness (and possibly competition) increases (Mason et al., 2008). Here, we also found that specialist species tend to occur in richer assemblages (Fig. 2b). The relationship between CSI and species richness was also positive (Fig. 3) showing that richer assemblages were those concentrating more specialist species and that, inversely, poorer assemblages were those concentrating more generalist species. These results support those derived from fine-scale communities in which species interact (Belmaker et al., 2011).

These relationships could, however, miss complex community responses to large-scale disturbance. For instance, non-linear (Davey et al., 2012) and negative (Filippi-Codaccioni et al., 2010) relationships between CSI and species richness have been documented in human disturbed landscapes. Here, we found similar curvilinear relationships between landscape disturbance and species richness or community specialization index, which also correspond to those widely described in the so-called intermediate disturbance hypothesis (Wilkinson, 1999). According to this hypothesis, competitive, and specialist species should dominate and exclude others at low levels of disturbance, and only

a few generalist species can thrive in highly disturbed sites. Species richness should therefore be greater at intermediate levels of disturbance, under which both specialist and generalist species can coexist. Although the mechanisms of such curvilinear relationships have been debated, our results can be explained by the Mediterranean mosaic landscapes in which human activities can contribute, up to a certain point, to increasing local species richness (Thompson, 2005; Blondel et al., 2010).

The curvilinear relationship between CSI and disturbance also suggests that the coexistence of many specialist species is maximized at an intermediate level of anthropogenic landscape modification. This pattern is probably driven by the presence, in this region, of many species co-occurring in human-dominated landscapes. This result also generalizes previous findings established with fine-scale data showing that individual specialist species can be associated with habitats disturbed by humans (Davison and Fitzpatrick, 2010; Boulangeat et al., 2012). Although many studies have shown that, following habitat disturbance, generalists should replace specialists (Devictor et al., 2008), others have documented the relative increase in specialist species in disturbed assemblages (Clavero et al., 2011). Here, we have shown that the direction of change in community composition can also be dependent on disturbance intensity. Although a more detailed analysis of the mechanisms leading to non-linear relationships is needed, these results suggest that, as already stated at a local scale, large-scale specialization and CSI will not always be a surrogate of ecosystem quality but should rather be used in conjunction with other community descriptors (Filippi-Codaccioni et al., 2010; Filippi-Codaccioni et al., 2010).

Overall, our results suggest that measuring species and community specialization (SSI and CSI) generates meaningful results compared to what is expected using more detailed and finer data on species associations with habitats. Some of our results, however, could be biased by the way data were collected. In particular, a greater sampling effort could be expected for rare, charismatic, or endemic species. However, the SSI was calculated only for those species present in at least 50 squares, thus, eliminating the effect of rare and occasional species. The randomization procedure of Fridley's algorithm also removes most of the potential non-uniform collection effort throughout the studied region. Note also that depending on the data considered, this technique could induce a link between specialization and rarity. For a given species, the index is estimated as the average (after 100 repetitions) of the similarity indices calculated from 50 sites randomly selected among the sites where this species occurs. For rare and localized species, the probability that two repetitions include more often the same sites is higher. The variability in the similarity indices generated is thus lower for rare species. Although this does not necessarily biases the index itself, it might affect the confidence in specialization estimates. A more elaborated algorithm in which the number of repetition is proportional to species rarity could be used. Finally, the objective of our analysis was not to define the local variation in SSI or CSI values precisely but rather to describe their relative variations across species or across large spatial gradients. The biases above, if any, would hardly explain the curvilinear relationship between CSI and disturbance and the positive relationship between CSI and species richness.

We believe that our approach offers an interesting tool to delineate areas of conservation interest based on the spatial variation in community composition. The CSI derived from atlas data could enable managers to implement differentiated conservation plans among ecoregions when coupled with other indicators. A similar analysis can be conducted on any group or data providing that co-occurrence-based specialization can be estimated. Moreover, the estimation of a temporal change in the CSI calculated in areas where data have been collected several

times should be a promising route to shed light on biotic homogenization.

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