

Avian succession along ecological gradients: Insight from species-poor and species-rich communities of *Sylvia* warblers

Alban GUILLAUMET^{1,2*}, Roger PRODON¹

¹ EPHE, CEFE-CNRS UMR 5175, 1919 route de Mende, 34293 Montpellier cedex 5, France

² Department of Wildlife, Fisheries & Aquaculture, Mail Stop 9690, Mississippi State University, Mississippi, MS 39762, USA

Abstract The mechanisms responsible for species replacement during ecological successions is a long-standing and open debate. In this study, we examined the distribution of the Sardinian warbler *Sylvia melanocephala* along two grassland-to-forest gradients, one in a high-diversity area (Albera-Aspres chain in Catalonia: eight *Sylvia* warbler species) and one in a low-diversity area (Mount Hymittos in Greece: four species). In Catalonia, distribution models suggested that the apparent exclusion of *S. melanocephala* from the open and forest ends of the gradient may be explained entirely by the preference of *S. melanocephala* for mid-successional shrublands. However, a joint analysis of both data sets revealed that: 1) *S. melanocephala* was more evenly distributed along the vegetation gradient in Greece, suggesting ecological release in the low-diversity area; and 2) a distribution model assuming interspecific competition (based on the distribution of *Sylvia* species showing a negative co-occurrence pattern with *S. melanocephala*) had a significantly higher predictive ability than a distribution model based on habitat variables alone. Our study supports the view that species turnover along ecological gradients generally results from a combination of intrinsic preferences and interspecific competition [*Current Zoology* 57 (3): 307–317, 2011].

Keywords Avian succession, Cross-validation, Diffuse competition, Ecological release, GLM, Habitat selection, Niche widening, Species distribution model

The mechanisms of species replacement during the course of primary and secondary succession is a long-standing (Halpern et al., 1997) and open debate (Sara et al., 2006; Wright and Fridley, 2010). This debate is also relevant because of renewed interest in the role of interspecific interactions in habitat selection and range limits, especially along ecological gradients (Cadena, 2007). The hypothesis that interspecific competition plays a prominent role in species turnover along ecological gradients has a long tradition in the literature in addition to recent theoretical support (Case et al., 2005; Price and Kirkpatrick 2009). Using territory mapping and heterospecific playback experiments, Robinson and Terborgh (1995) suggested that asymmetric interspecific aggression restricted species pairs of over twenty bird genera to either the early or late end of a primary successional gradient generated by the meandering action of the Manu river in Peru. Herzog and Kessler (2006) found that the historical loss of habitat specialists in small dry-island Bolivian forests coincided with an increase in the number of humid forest species in the same guild, suggesting that the latter are normally excluded by the former in dry forests. However, the

majority of studies have been conducted along elevational gradients. Evidence of ecological release in the absence of putative competitors has been found for avian groups in temperate (Noon, 1981) and tropical mountains (Diamond, 1973; Terborgh and Weske, 1975). In western Montana, a recent range expansion by the western bluebird displaced the less aggressive mountain bluebird to areas of higher elevation (Duckworth and Badyaev, 2007). Conversely, the hypothesis that interspecific competition plays a prominent role in species turnover along ecological gradients was recently challenged by Romdal and Rahbek (2009). They studied the elevational zonation of afro-tropical forest bird communities and argued that no study has convincingly demonstrated the role of interspecific competition on the elevational distribution of tropical organisms (see also Hofer et al., 1999). Hence, the causes of zonation and succession patterns are still not well understood despite decades of research, highlighting the need for studies addressing the interplay between species distributions, species richness, and environmental factors (Romdal and Rahbek, 2009; Wright and Fridley, 2010).

Here, we examine the relative roles of habitat pre-

Received June 17, 2010; accepted Dec. 14, 2010.

* Corresponding author. E-mail: aguillaumet@cfr.msstate.edu

© 2011 *Current Zoology*

ference and interspecific competition in the distribution of the Sardinian warbler *Sylvia melanocephala* along two grassland-to-forest gradients, one in a high-diversity area (Albera-Aspres chain in Catalonia: eight *Sylvia* warbler species) and the other in a low-diversity area (Mount Hymittos in Greece: four species). *Sylvia* are often the dominant species in shrubby formations in the Mediterranean region, with up to eight species sharing to various extent the habitats, from low and open shrublands to closed forests, which characterize the succession-disturbance dynamics of the region (Shirihai et al., 2001; Millington et al., 2009). The *Sylvia* genus can be considered a guild within which interactions between species are likely (Shirihai et al., 2001). While it is generally agreed that coexistence between species is facilitated by subtle ecological differences in habitat use such as nesting site, foraging substrate, foraging height, and diet (Martin and Thibault, 1996), there is considerable ecological overlap between sympatric *Sylvia* warbler species on the vegetation gradient (Prodon and Lebreton, 1981; Shirihai et al., 2001). In addition, the question remains whether these are intrinsic autoecological differences between species, as suggested by Schaefer and Barkow (2004) and Pons et al. (2008), or an adaptive response to the local presence or absence of congeners. For instance, Garcia (1983) showed that the late-arriving garden warbler *S. borin* could be excluded from otherwise suitable habitats by the blackcap *S. atricapilla*.

Ecological release from potential competitors in species-poor habitats such as oceanic islands can lead to an increase in niche width (niche expansion), which is indicative of the role of interspecific competition (Bolnick et al., 2010). The possibility of ecological release for *Sylvia* warblers is raised in the literature, although evidence is still lacking. Hazevoet (1995) suggested that the spectacled warbler *S. conspicillata* widened its niche on Cape Verde islands to the extent that it overlapped broadly with *S. atricapilla*. Blondel et al. (1988) compared habitat selection on the mainland (French Provence, six species) and under insular conditions (Corsica, five species). However, species impoverishment in Corsica was limited because the addition of the species *S. sarda* partially compensated for the loss of *S. hortensis* and *S. conspicillata*. The results were therefore mitigated: of the four *Sylvia* species present in both areas, at least one showed evidence of niche expansion and an increase of population density in Corsica, but two did not expand their niche and had lower population densities in Corsica. Here, our objective was to test the

niche expansion hypothesis in *Sylvia* warblers by comparing habitat selection in two areas with a higher contrast in *Sylvia* diversity. Cross validated distribution models of *S. melanocephala* were implemented to further test the role of interspecific competition.

1 Materials and Methods

1.1 Species and study sites

We made simultaneous comparisons of plant formations at different successional stages (Prodon and Lebreton, 1981). A total of 111 stations covering the entire grassland-to-forest gradient were surveyed in Catalonia during the breeding season (from the end of April to June) from 1975 to 1986, and 58 stations were surveyed in Greece in 1981.

The stations in Catalonia were distributed among three main sites 10–20 km apart (Fig. 1): East Albera ($n = 71$ stations), South Albera ($n = 15$) and Aspres ($n = 25$). These three sites are part of the Albera-Aspres chain which constitutes the easternmost part of the Pyrenean chain, on both sides of the France-Spain border (Fig. 1). Siliceous bedrock is covered with patches of dry grasslands dominated by *Brachypodium retusum*, shrublands dominated by *Calycotome* sp., *Cistus* and *Erica* spp. and forests dominated by *Quercus ilex* and *Q. suber*. The Greek study site is situated on Mount Hymittos in Attica (Fig. 1) and is characterized by calcareous bedrock with low and clear to high and thick shrublands, which are locally called phrygana, with *Calycotome* sp., *Cistus* and *Genista* spp. and *Quercus coccifera*, and forests dominated by *Pinus halepensis*. Both areas are frequently subjected to wildfires.

In Catalonia, 44 stations were sampled once, 64 were sampled twice, and 3 were sampled three times, for a total of 181 point counts, hereafter referred to as 181 stations. Sampling was completed with time intervals greater than five years, to ensure independency between avian surveys. *Sylvia* composition within a single station was no more similar after a five year interval than two spatially distinct stations positioned on the same part of the ecological gradient (not shown).

The landscape was prospected at ground-level to choose the stations, and stations were separated by a minimum distance of ca. 150 m. Each station was sampled by a single observer (RP) using a single-visit point-count method (Prodon and Lebreton, 1981). The *Sylvia* species were recorded from the station center as present/detected or absent/undetected by vision and hearing over 20 minutes, at a radius of 50–75 m. The habitat profile of each station was quantified by

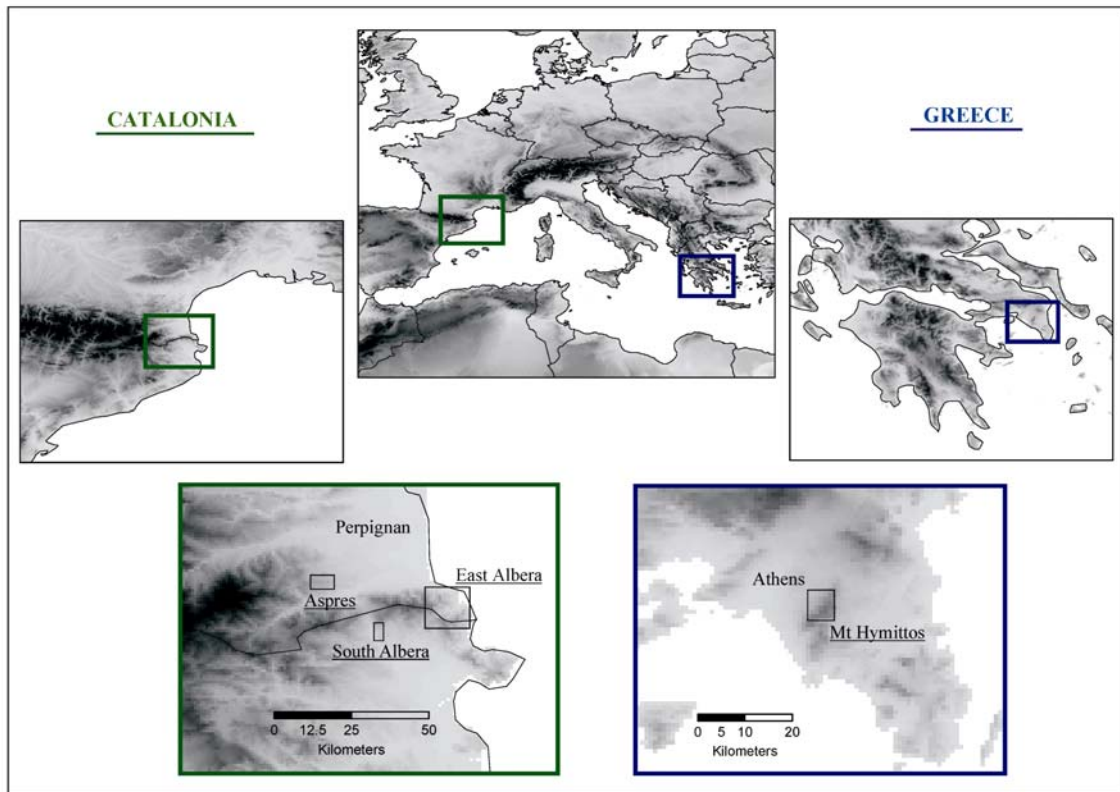


Fig. 1 Study areas

In Catalonia, stations were distributed among three main sites: East Albera ($n = 71$ stations), South Albera ($n = 15$) and Aspres ($n = 25$). The Greek study site was Mount Hymittos ($n = 58$).

estimating the relative cover of the rock (cvR), and the relative cover of the following vegetation layers: 0–0.25 m (cv0.25), 0.25–0.50 m (cv0.5), 0.50–1 m (cv1), 1–2 m (cv2), 2–4 m (cv4), 4–8 m (cv8) and 8–16 m (cv16). Radii varying from 4–8 m for the lowest layer to ca. 20 m for the highest vegetation layers were used for cover estimates. The use of a reference cover chart resulted in reliability of approximately $\pm 10\%$ for these estimates. We focused on the structural features of habitats, because habitat structure drives habitat use in birds in Mediterranean habitats of the same area more so than vegetation (Prodon and Lebreton, 1981).

Species composition differs between the two study areas. *S. conspicillata* and *S. undata* are present in Catalonia but not in Greece, while *S. rueppelli* is only found in Greece. Additionally, *S. borin*, *S. atricapilla*, and *S. communis*, which are predominantly non-Mediterranean Palearctic species, do not breed in the Mount Hymittos area, so are only found in Catalonia (Cramp, 1992). Their presence in Catalonia may be partly explained by the continuity of the study site with higher altitude habitats of the Pyrenean chain, including some unbroken forests (Fig. 1). *S. melanocephala*, *S. cantil-*

lans and *S. hortensis* are present in both areas, although the eastern populations of *S. hortensis* are now treated as a distinct species, *S. crassirostris*. *S. cantillans* and *S. crassirostris* were rare in Hymittos samples, so the niche expansion hypothesis test was based on the pattern of habitat use for *S. melanocephala* only.

1.2 Description of gradients

Avifauna and vegetation gradients were illustrated by Canonical Correspondence Analyses using $\log(x+1)$ -transformed habitat variables (Terbraak, 1986). One CCA was completed for each country. These analyses revealed that the grassland-to-forest gradients could be reduced to a single axis (CCA1, see Results) that correlated to the amount of vegetation. We therefore used the biologically meaningful variable biovolume in further analyses, as it is common to the gradients in both Catalonia and Greece. Biovolume corresponds to the logarithm of the Index of foliage volume (I_{FV}) as defined by Prodon and Lebreton (1981): $biovolume = \ln(0.25 \times cv0.25 + 0.25 \times cv0.5 + 0.5 \times cv1 + 1 \times cv2 + 2 \times cv4 + 4 \times cv8 + 8 \times cv16)$.

1.3 Exclusion at the station-level ?

We investigated evidence of exclusion at the station

level between *S. melanocephala* and other *Sylvia* species for the two countries. For each pairwise comparison of species (e.g., *S. melanocephala* vs. *S. borin*), we only considered the stations in the region of ecological overlap, referred hereafter as the “syntopy range”. This was because by definition no association is possible outside the syntopy range, as that region is only used by one species. Biovolume and CCA1 scores were used in two independent tests to measure ecological gradient and syntopy range. However, we also performed the test with all stations included, in case the absence of one species outside the syntopy range was driven by competition (realized niche), resulting in a too conservative test.

We tested whether the number of stations where the two species were observed together was compatible with the null hypothesis of random association. The statistic used for this test was *Nab*: the number of stations where the target species *S. melanocephala* (species A, present in *Na* stations within the syntopy range of *N* stations) co-occur with species B (present in *Nb* stations). The distribution of this statistic under H_0 ($Nab|H_0$) was obtained by independently drawing *Na* and *Nb* samples at random within *N*, and then counting the number of stations in common. This procedure is repeated *n* times, and here $n = 10000$. The *P*-value of the test corresponds to the number of times $Nab|H_0 \leq Nab$ divided by *n*. Positive co-occurrence pattern is indicated by $P > 0.5$ (*Nab* is larger than $Nab|H_0$ in more than half of the randomizations), negative co-occurrence pattern is indicated by $P < 0.5$, and $P < 0.05$ indicates significant exclusion.

1.4 Test of ecological release

The habitats and ecological gradients available to *S. melanocephala* needed to be similar across study areas for testing ecological release. We controlled for similar vegetation structure by comparing the distributions of biovolume in the two areas. We used a Wilcoxon rank-sum test, as a surrogate for non-normal distributions of a *T* test, to test for equal mean, and a Levene's test to test for equal variance. We then used the previous tests to test ecological release by comparing the distributions of biovolume in the set of stations used by *S. melanocephala*. For instance, ecological release in both directions of the ecological gradient would result in no significant difference in the “mean” from the Wilcoxon rank-sum test, but would result in a significantly larger variance in Greece using Levene's test. We also tested whether the frequency of *S. melanocephala* in Greek stations was higher than in Catalonia using a χ^2 test of

equal proportion.

1.5 Distribution modelling

Using the method described by Araujo and Luoto (2007), detailed below, we tested the predictive ability of distribution models based on habitat factors and the distribution of other *Sylvia* species. We did not consider the potential interactions between explanatory variables in this study because of sample size limitations (but see also discussion).

We fitted generalized linear models (GLM), in this case logistic regressions, to assess the relationships between the presence or absence of *S. melanocephala* and the following factors: 1) the habitat variables (relative cover of the rock and vegetation layers) and their quadratic terms (GLM habitat); 2) presence or absence of all other *Sylvia* (GLM congenetics); 3) only other *Sylvia* showing a negative co-occurrence pattern with *S. melanocephala* (GLM competition); in practice, we included species with both $P(\text{biovolume}) < 0.5$ and $P(\text{CCA1}) < 0.5$ (Table 1). These were *S. conspicillata*, *S. communis*, *S. atricapilla* and *S. borin* in Catalonia, and *S. rueppelli* in Greece; 4) both habitat (and their quadratic terms) and competition variables (GLM both).

Each of the four GLM was calibrated using a 70% random sample from the data. The best model was selected using a backward plus forward selection procedure and AIC criterion. These models were evaluated against the remaining 30% of the data for validation. The modeled probabilities of occurrence for *S. melanocephala* were transformed into presence and absence records using a cut-off defined by its prevalence in the calibration data. The agreement between observed and

Table 1 Exclusion at the station level

Other species	Catalonia		Greece	
	<i>P</i> (Bv)	<i>P</i> (CCA1)	<i>P</i> (Bv)	<i>P</i> (CCA1)
<i>S. conspicillata</i>	0.040	0.14	/	/
<i>S. communis</i>	0.28	0.27	/	/
<i>S. undata</i>	0.98	0.84	/	/
<i>S. hortensis-crassirostris</i>	1.00	0.99	0.30	0.66
<i>S. cantillans</i>	0.88	0.98	1.00	1.00
<i>S. atricapilla</i>	0.35	0.038	/	/
<i>S. borin</i>	0.002	0.029	/	/
<i>S. rueppelli</i>	/	/	<0.001	0.018

We tested whether the number of stations where *S. melanocephala* and other species co-occur in their shared fraction of the ecological gradient (as measured by the biovolume = Bv, or the first axis of a Canonical Correspondence Analysis = CCA1) is lower than expected at random; *P* = *P*-value, negative co-occurrence pattern is indicated by $P < 0.5$, and significant exclusion by $P < 0.05$ (see text for details).

modeled distributions was estimated using the True Skill Statistic, defined by $TSS = \text{sensitivity} + \text{specificity} - 1$, where *sensitivity* is the probability that the model will correctly classify a presence, and *specificity* is the probability that the model will correctly classify an absence (Allouche et al., 2006). Hence, TSS quantifies the ability of a model to accurately predict presences and absences; it varies from -1 to $+1$, with larger values corresponding to better predictions. Our procedure of cross validation (calibration and validation) was repeated 500 times, yielding a distribution of 500 TSS for each of the four GLMs which were compared using Wilcoxon signed-rank tests for related samples.

The procedure listed above was repeated three times: for Catalonia alone, for Greece alone, and for both study sites together. For the latter, calibration data consisted of a 70% random sample of the Catalonian dataset augmented by a 70% random sample of the Greek dataset; the validation data consisted in the remaining 30% of the data (Catalonia and Greece pooled together).

1.6 Control for study site size, sample size and spatial autocorrelation

Study areas and sample size differed noticeably between the three Catalonian sites and the Greek study site, so all analyses (sections 1.2 to 1.5) were performed again, using only the East Albera site in Catalonia, and only the first point count for each station. This resulted in a reduced total of 71 stations for Catalonia, down from 181, compared with 58 in Greece.

Because the sampling occurred before spatial autocorrelation being accounted for became common practice in ecological studies (e.g., Lennon, 2000), geographic coordinates were not recorded for some stations in Catalonia, and were not recorded for any of the stations in Greece. Spatial autocorrelation may be an issue for distribution modeling. While habitat and thus occupancy may be spatially correlated, sampling units should be independent within habitat types (Mackenzie et al., 2009). We tested the null hypothesis (H_0) that geographic proximity does not induce positive spatial autocorrelation using the 100 stations of the original 111 stations in Catalonia that had geographic coordinates. The same process was completed for 64 of the 71 East Albera stations. We tested the Catalonia and East Albera subsets as follows: 1) the difference between the focal station i and its nearest neighbor station j was scored as 0 if *S. melanocephala* was present or absent in both stations, and as 1 if presence/absence differed. This calculation was performed for all stations, yielding the actual distribution of differences at close range (D_{close}); 2) we

repeated the procedure, this time scoring the difference between the focal station i and the most distant station k chosen among the set of stations $\neq \{i, j\}$ with a vegetation, as measured by the biovolume value, as close as possible to the vegetation of the nearest neighbor j . This calculation yielded a distribution of differences expected between the station i and a station ecologically equivalent to j , once the effect of geographic proximity has been removed (D_{distant}); 3) If H_0 is false (positive spatial autocorrelation due to geographic proximity), then we predicted that $D_{\text{close}} < D_{\text{distant}}$. D_{close} and D_{distant} were compared using a (one-tailed) Wilcoxon signed-rank test for related samples.

All statistical analyses were performed using R version 2.7.2 (R Development Core Team, 2008).

2 Results

2.1 Description of gradients

The grassland-to-forest gradient is summarized by the first axis of the canonical correspondence analysis (CCA1), which represents 60% of total variation in Catalonia and 55% in Greece (Fig. 2). Spearman's rank correlation coefficients indicate that the axis correlates with the amount of vegetation measured by the biovolume ($\rho = 0.97$, $P < 0.001$ in Catalonia and $\rho = 0.42$, $P < 0.001$ in Greece). This axis corresponds to a succession of species on the structure gradient, from *S. conspicillata* in the open-end of the gradient to *S. borin* at the forest-end in Catalonia, and from *S. rueppelli* to *S. melanocephala* in Greece. The second axis, uncorrelated to the first, corresponds to some variations of cover in the shrub layers (from cv0.25 to cv2), with no apparent effect on *S. melanocephala*. In Catalonia the variability of vegetation is essentially unidimensional, as shown by the fact that the second axis is an artificial quadratic function of the first axis (arch, or Guttman, effect). An arch effect was not detected in Greece, but the scores on the second axis for the stations with *S. melanocephala* do not differ from the scores of stations without *S. melanocephala* (Wilcoxon rank-sum test, $W = 273$, $P = 0.43$).

2.2 Exclusion at the station level ?

The role of competition is suggested by significant exclusion at the station level between *S. melanocephala* and other *Sylvia* species in their shared fraction of the ecological gradient (Table 1): *S. borin*, *S. conspicillata* (for biovolume only) and *S. atricapilla* (for CCA1 only) in Catalonia, and *S. rueppelli* in Greece. Exclusion did not reach significance for additional species when all stations were considered (not shown).

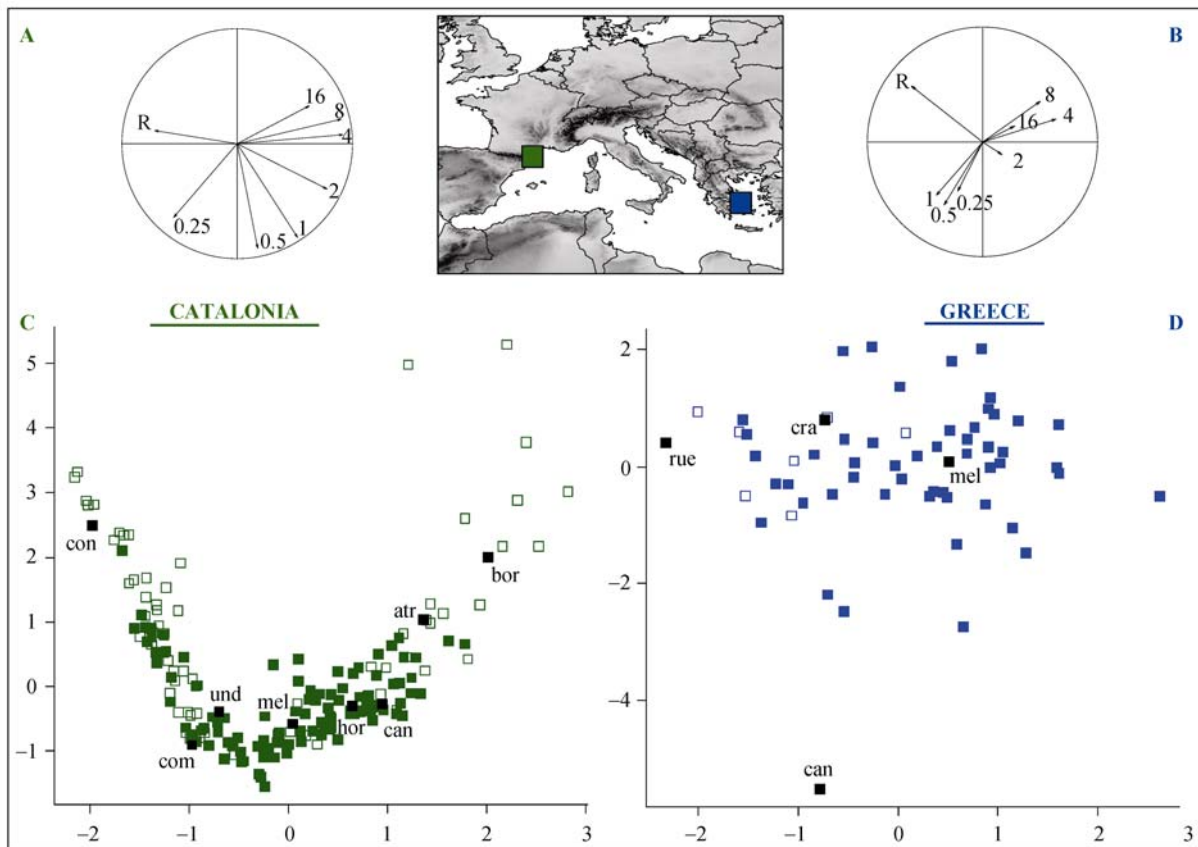


Fig. 2 Description of avifauna and vegetation gradients using Canonical Correspondence Analyses

Left: Catalonia (Albera-Aspres), right: Greece (Mt Hymittos); upper part (A-B): the correlation circles show the correlation between the two first axes (x -axis = CCA1, y -axis = CCA2) and habitat variables ($R = cvR$, $0.25 = cv0.25$, etc...; see text for details); lower part (C-D): black squares show species scores: atr = *S. atricapilla*, bor = *S. borin*, can = *S. cantillans*, con = *S. conspicillata*, com = *S. communis*, cra = *S. crassirostris*, hor = *S. hortensis*, mel = *S. melanocephala*, rue = *S. rueppelli*, und = *S. undata*; colored squares show the stations scores (green for Catalonia, blue for Greece): filled squares: stations with *S. melanocephala*.

2.3 Test of ecological release

The distributions of biovolume in both study areas were not statistically different, suggesting similar vegetation structure (Wilcoxon rank-sum test, $W = 4851$, $P = 0.39$; Levene's test, $W = 1.27$, $P = 0.26$). Our results suggest consistency in average niche selection across countries for *S. melanocephala* (Wilcoxon rank-sum test, $W = 2543$, $P = 0.35$), together with niche widening in Greece, with a variance nearly two times larger than in Catalonia (Levene's test, $W = 13.6$, $P < 0.001$). Ecological release in Greece was also suggested by the higher proportion of stations with *S. melanocephala* (86 vs 62 %, $\chi^2 = 10.82$, $P = 0.001$), that may be linked to the lower average number of other *Sylvia* species in this country: 0.26 (SD = 0.48) other *Sylvia* species in Greek stations versus 1.59 (SD = 0.86) in Catalonia (Wilcoxon rank-sum test, $W = 9369$, $P < 0.001$).

2.4 Distribution modelling

The predictive ability of GLM competition, as esti-

mated by the True Skill Statistic (TSS), was either superior to or not significantly different from GLM congenetics, indicating that the main information about *S. melanocephala* distribution is due to species with a negative co-occurrence pattern (Table 2).

For Catalonia alone, the predictive ability of GLM habitat (0.490 ± 0.112) was significantly better than GLM competition (0.400 ± 0.112) and even GLM both (0.447 ± 0.114). A strikingly different pattern was found in Greece (alone), as the predictive ability of GLM competition (0.711 ± 0.296) was significantly better than GLM habitat (0.151 ± 0.322) and GLM both (0.628 ± 0.365).

When the data from Catalonia and Greece were pooled, the predictive ability of GLM habitat (0.406 ± 0.099) was significantly worse than GLM competition (0.424 ± 0.098). However, GLM both (0.464 ± 0.105) was significantly better than GLM competition, suggesting that both habitat preference and competition

Table 2 Distribution modelling

Study area	Statistic		Results				
Catalonia	TSS	H	S	C	H+C		
		mean	0.490	0.381	0.400	0.447	
		SD	0.112	0.122	0.112	0.114	
	Wilcoxon		S	C	H+C		
		H	***	***	***		
		S		***	***		
Greece	TSS	H	S	C	H+C		
		mean	0.151	0.711	0.711	0.628	
		SD	0.322	0.296	0.296	0.365	
	Wilcoxon		S	C	H+C		
		H	***	***	***		
		S		na	**		
Catalonia + Greece	TSS	H	S	C	H+C		
		mean	0.406	0.420	0.424	0.464	
		SD	0.099	0.099	0.098	0.105	
	Wilcoxon		S	C	H+C		
		H	*	**	***		
		S		ns	***		
	C			***			

For each study area, the table gives the mean and standard deviation of the True Skill Statistic (TSS), which quantifies the ability of a model to accurately predict presence and absence of *S. melanocephala* (larger TSS values correspond to better predictions); TSS distributions were obtained by a 500-fold cross validation procedure, and TSS for different models were compared using Wilcoxon Signed-rank tests for related samples (*** = $P < 0.001$, ** = $P < 0.01$, * = $P < 0.05$, ns = $P > 0.05$, na corresponds to identical distributions): H = GLM habitat, S = GLM congenics (all other *Sylvia*), C = GLM competition (only *Sylvia* with a negative co-occurrence pattern), H+C = GLM habitat + competition or GLM both.

help explain *S. melanocephala* distribution.

2.5 Control for study site size, sample size and spatial autocorrelation

The null hypothesis that geographic proximity does not induce spatial autocorrelation could not be rejected in the East Albera subsample ($V = 210$, $P = 0.43$) or in Catalonia ($V = 405$, $P = 0.12$).

Repeating the previous analyses (2.1 to 2.4) for East Albera ($n = 71$) instead of Catalonia ($n = 181$) yielded similar results, with a few noticeable differences. The grassland-to-forest gradient was almost unchanged, with the first axis explaining 52 % of total variation, and the correlation with biovolume was $\rho = 0.95$, $P < 0.001$. However, we note that *S. borin*, which is rare in this part of the Catalonian study site, was not present in the subsample analyzed. Only *S. conspicillata* showed a negative co-occurrence pattern with *S. melanocephala*: the probability of exclusion was $P = 0.082$ when the zone of syntopy was measured by biovolume but $P < 0.001$ when all stations were considered.

Evidence for a role of interspecific competition was unaltered for ecological release, and reinforced for distribution modelling using East Albera only. While the distributions of biovolume in East Albera and Greece were not statistically different ($P > 0.25$ for both Wilcoxon rank sum and Levene's tests), ecological release in Greece was again suggested by niche widening and a higher proportion of stations with *S. melanocephala*, together with a lower average number of other *Sylvia* species (all $P < 0.009$). The predictive ability of GLM competition turned out to be significantly better than any other model, both for East Albera alone and when the data from East Albera and Greece were pooled (all pairwise comparisons between GLM competition and other models yielded $P < 0.001$).

3 Discussion

3.1 A role for interspecific competition ?

In Catalonia, habitat variables appear sufficient to explain the distribution of *S. melanocephala* (Table 2),

suggesting that the apparent exclusion of *S. melanocephala* from the open and forest ends of the gradient by species such as *S. conspicillata* and *S. borin* (Table 1) may be entirely explained by a preference of *S. melanocephala* for mid-successional formations (shrublands, Fig. 2). Of course, the role of past competition in driving such preferences, referred to as ghost of competition past, cannot be assessed here. In Greece however, *S. melanocephala* was more evenly distributed along the vegetation gradient, and competitive exclusion by *S. rueppelli* in some open-end stations provides the best distribution model of *S. melanocephala* (Fig. 2, Tables 1-2). How can we reconcile these observations?

A first possibility is that interspecific competition does not affect *S. melanocephala* distribution. For instance, we did not find a negative co-occurrence pattern between *S. melanocephala* and *S. undata* in Catalonia (Table 1). This result agrees with a recent study conducted in NE Catalonia that did not show any negative effect of the density of three warbler species (including *S. melanocephala*) on the territory size and shape of *S. undata* (Pons et al., 2008). Also consistent with this view, competition appears stronger in the species-poor Greek site, and weaker in the species-rich Catalanian region. Under this "no competition" hypothesis, the apparent exclusion of *S. melanocephala* by *S. rueppelli* in Greece would have to be due to an unrecorded important habitat variable that explains *S. melanocephala* absence in most *S. rueppelli* stations.

Alternatively, *S. rueppelli* could possibly be the only species that has a negative impact on *S. melanocephala*, with no species affecting *S. melanocephala* in Catalonia (the "Greece only" hypothesis). Finally, *S. melanocephala* may decline in the open and forest ends of the gradient in Catalonia at least partly because of some competitive exclusion by formation specialist *Sylvia* species, but this effect would be masked by the strong correlation between *S. melanocephala* distribution and habitat variables (the "competition" hypothesis). Including another transect in Greece where these specialist species are absent proved helpful in the examination of the relative role of habitat preference and interspecific competition (see also Terborgh and Weske, 1975).

The "competition" hypothesis was first supported by an apparent ecological release in Greece. Niche widening in Greece occurred despite the smaller sample size and study area, while the "no competition" hypothesis predicts no niche widening and the "Greece only" hypothesis predicts niche restriction. Higher variance in Greece could be alternatively explained by unrecorded ecologi-

cal variables for which the two areas actually differ, making the grassland and/or forest ends of the gradient in Greece more favourable to *S. melanocephala*. We consider this alternative to be less likely although it cannot be excluded using the present data. The most obvious difference between the two gradients concerns the forest end, dominated by two *Quercus* species in Catalonia and by *Pinus halepensis* in Greece. However, in Majorca where *Pinus halepensis* is the dominant tree species and where *S. melanocephala* is living sympatrically with *S. atricapilla*, *S. atricapilla* was found to occupy patches with higher vegetation height and density than *S. melanocephala* (Schaefer and Barkow, 2004), mirroring the pattern found in Catalonia (Fig. 2). This suggests that the different composition of tree species between our two study areas cannot explain why *S. melanocephala* is present in all forested stations in Greece, but not in Catalonia (Fig. 2). The absence of forest *Sylvia* species in Greece offers a parsimonious explanation to this pattern.

Our distribution modelling approach also supported the "competition" hypothesis. When the data from Catalonia and Greece were analyzed simultaneously, we found that the predictive ability of GLM habitat was significantly worse than GLM competition (Table 2). However, accounting for habitat variables significantly improved the competition model (although this was not true for the analysis based on East Alpera only), suggesting that both habitat preference and competition may explain *S. melanocephala* distribution. Considering potential interactions between habitat and competition variables may have supported this conclusion, as it could have boosted the predictive power of GLM both.

Although we were unable to explicitly control for the effects of spatial autocorrelation in this study due to a lack of geographic coordinates, our results should be unaffected for the following reasons: 1) while a general pattern of spatial autocorrelation can alter the predictive ability of distribution models, it cannot explain a wider ecological niche (ecological release) in Greece; 2) we compared the predictive power of habitat and competition variables, and do not expect spatial autocorrelation, if any, to modify their relative influence; 3) the null hypothesis that geographic proximity on its own does not induce spatial autocorrelation could not be rejected in the Catalanian study site. One possible reason for this result is that the landscape, a mosaic of shrubland at various successional stages, is generally favorable to *S. melanocephala*, which was present in more than 60% of

stations in Catalonia and 80% in Greece. Hence *S. melanocephala* occupancy pattern is not driven by restricted dispersal, as found in species living in patchy environments (Selmi et al., 2003).

The *Sylvia* species are characterized by a high level of ecomorphological similarity (Shirihai et al., 2001; Böhning-Gaese et al., 2003), highlighting the possibility of competition not only for prey, but also for foraging substrates between the ten species considered here. Accordingly, our observation that *S. melanocephala* widened its niche in Greece may be partly explained by the concept of diffuse competition (as modified by Pianka, 1974), which predicts that the average amount of overlap between pairs of species is negatively related to the number of competing species in the community. In Catalanian (and East Albera only) stations, the average number of *Sylvia* species (excluding *S. melanocephala*) was more than five times higher than in Greek stations. Diffuse competition could explain why *S. melanocephala* and *S. conspicillata* tended to exclude each other in the species-rich Catalanian study site (Table 1), while Shirihai et al. (2001) suggested that these species coexist with few agonistic interactions on two strongly impoverished island communities in Malta and the Canaries. Conversely, Pomeroy and Walsh (2002) discuss possible evidence of competition in Malta.

As is the rule with correlational or “natural experiment” approaches, our results do not constitute a formal demonstration of the role of competition. In particular, we do not refute the hypothesis that both ends of the gradient may be sub-optimal for *S. melanocephala*, and that the apparent exclusion with some other *Sylvia* warblers may be due to subtle differences in habitat selection, not detected using our set of ecological variables. However, as experimental approaches become impracticable for large communities, correlational approaches constitute a suitable alternative to investigate communities’ properties and reach a general understanding of the frequency and relative importance of interspecific competition in species distribution (Hofer et al., 2004). In addition, they may pave the way for experimental studies targeting the species with potentially strong negative interactions, and aiming to investigate the possible mechanisms behind exclusion.

A benchmark study was conducted on a New world warbler species pair, the orange-crowned warbler *Vermivora celata* and Virginia’s warbler *V. virginiae*. In addition to interference and possible exploitative competition, with exclusion of *V. virginiae* from preferred

nest sites through direct aggressive interference from *V. celata*, and increased feeding rates of *V. virginiae* in response to the removal of *V. celata*, the study revealed that both species experienced lower predation rates in plots where one species had been removed than in control sympatry plots (Martin and Martin, 2001). This apparent competition was strong, as both species fledged approximately 100% more young per nest on removal plots, and the competition was apparently caused by a shift in foraging behavior of nest predators in response to an increased density of their preys. Interestingly, nest predation of these two warblers was also positively related to the density of other ground-nesting passerines, including the red-faced warbler *Cardellina rubrifrons*. This suggests yet another possible mechanism by which diffuse competition may occur in *Sylvia*.

3.2 Implications for species turnover along ecological gradients

Our study adds support to the view that species distribution along ecological gradients may generally result from a combination of intrinsic habitat preferences and interspecific competition (e.g., Beckerman, 2000; Cadena and Loiselle, 2007; Herzog and Kessler, 2006), although of course some other abiotic factors such as climate and biotic factors such as predation may also play a role (Graham et al., 2009; Menge, 1976; Twomey et al., 2008).

The role of habitat preferences in the succession of *Sylvia* species is supported by the relatively consistent position of species along grassland-to-forest gradients in various regions (this study for *S. melanocephala*; see also Shirihai et al., 2001), and by the existence of species-specific habitats, evidenced by both observational and experimental studies (Elle, 2003; Garcia, 1983). The role of interspecific competition is supported by the existence of interspecific territoriality (Garcia, 1983), niche contraction (*S. melanocephala*: this study; maybe also *S. conspicillata* outside species-poor islands: Hazevoet, 1995), niche shift (as possibly exemplified by *S. undata* in Corsica, see Martin and Thibault, 1996), or even possible local population decline or extinction in response to the colonisation of another *Sylvia* species (Pomeroy and Walsh, 2002).

Acknowledgements This study is thankfully dedicated to Professor J. Matsakis, who invited one of the authors (RP) and made his field work possible. The authors are also grateful to four anonymous referees for very helpful comments on a previous draft of this manuscript.

References

- Allouche O, Tsoar A, Kadmon R, 2006. Assessing the accuracy of species distribution models: Prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology* 43: 1223–1232.
- Araujo MB, Luoto M, 2007. The importance of biotic interactions for modelling species distributions under climate change. *Global Ecology and Biogeography* 16: 743–753.
- Beckerman AP, 2000. Counterintuitive outcomes of interspecific competition between two grasshopper species along a resource gradient. *Ecology* 81: 948–957.
- Blondel J, Chessel D, Frochot B, 1988. Bird species impoverishment, niche expansion, and density inflation in Mediterranean island habitats. *Ecology* 69: 1899–1917.
- Böhning-Gaese K, Schuda MD, Helbig AJ, 2003. Weak phylogenetic effects on ecological niches of *Sylvia* warblers. *Journal of Evolutionary Biology* 16: 956–965.
- Bolnick DI, Ingram T, Stutz WE, Snowberg LK et al., 2010. Ecological release from interspecific competition leads to decoupled changes in population and individual niche width. *Proceedings of the Royal Society B* 277: 1789–1797.
- Cadena CD, 2007. Testing the role of interspecific competition in the evolutionary origin of elevational zonation: An example with Buarremon brush-finches (Aves, Emberizidae) in the neotropical mountains. *Evolution* 61: 1120–1136.
- Cadena CD, Loiselle BA, 2007. Limits to elevational distributions in two species of emberizine finches: Disentangling the role of interspecific competition, autoecology, and geographic variation in the environment. *Ecography* 30: 491–504.
- Case TJ, Holt RD, McPeck MA, Keitt TH, 2005. The community context of species' borders: Ecological and evolutionary perspectives. *Oikos* 108: 28–46.
- Cramp S, 1992. *Handbook of the Birds of Europe the Middle East and North Africa: The Birds of the Western Palearctic, Warblers*. Oxford: Oxford University Press.
- Diamond JM, 1973. Distributional ecology of New Guinea birds. *Science* 179: 759–769.
- Duckworth RA, Badyaev AV, 2007. Coupling of dispersal and aggression facilitates the rapid range expansion of a passerine bird. *Proceedings of the National Academy of Sciences of the United States of America* 104: 15017–15022.
- Elle O, 2003. Quantification of the integrative effect of ecotones as exemplified by the habitat choice of blackcap and white-throat (*Sylvia atricapilla* and *S. communis*, Sylviidae). *Journal für Ornithologie* 144: 271–283.
- Garcia EFJ, 1983. An experimental test of competition for space between blackcaps *Sylvia atricapilla* and garden warblers *Sylvia borin* in the breeding season. *Journal of Animal Ecology* 52: 795–805.
- Graham CH, Parra JL, Rahbek C, McGuire JA, 2009. Phylogenetic structure in tropical hummingbird communities. *Proceedings of the National Academy of Sciences of the United States of America* 106: 19673–19678.
- Halpern CB, Antos JA, Geyer MA, Olson AM, 1997. Species replacement during early secondary succession: The abrupt decline of a winter annual. *Ecology* 78: 621–631.
- Hazevoet CJ, 1995. *The Birds of the Cape Verde Islands*. BOU Check-list No 13. Tring: British Ornithologists' Union.
- Herzog SK, Kessler M, 2006. Local vs. regional control on species richness: A new approach to test for competitive exclusion at the community level. *Global Ecology and Biogeography* 15: 163–172.
- Hofer U, Bersier LF, Borcard D, 1999. Spatial organization of a herpetofauna on an elevational gradient revealed by null model tests. *Ecology* 80: 976–988.
- Hofer U, Bersier LF, Borcard D, 2004. Relating niche and spatial overlap at the community level. *Oikos* 106: 366–376.
- Lennon JJ, 2000. Red-shifts and red herrings in geographical ecology. *Ecography* 23: 101–113.
- Mackenzie DI, Nichols JD, Seamans ME, Gutierrez RJ, 2009. Modeling species occurrence dynamics with multiple states and imperfect detection. *Ecology* 90: 823–835.
- Martin JL, Thibault JC, 1996. Coexistence in Mediterranean warblers: Ecological differences or interspecific territoriality? *Journal of Biogeography* 23: 169–178.
- Martin PR, Martin TE, 2001. Ecological and fitness consequences of species coexistence: A removal experiment with wood warblers. *Ecology* 82: 189–206.
- Menge BA, 1976. Organization of the New England rocky intertidal community: Role of predation, competition, and environmental heterogeneity. *Ecological Monographs* 46: 355–393.
- Millington JDA, Wainwright J, Perry GLW, Romero-Calcerrada R, Malamud BD, 2009. Modelling Mediterranean landscape succession-disturbance dynamics: A landscape fire-succession model. *Environmental Modelling & Software* 24: 1196–1208.
- Noon BR, 1981. The distribution of an avian guild along a temperate elevational gradient: The importance and expression of competition. *Ecological Monographs* 51: 105–124.
- Pianka ER, 1974. Niche overlap and diffuse competition. *Proceedings of the National Academy of Sciences of the United States of America* 71: 2141–2145.
- Pomeroy D, Walsh F, 2002. A European endemic warbler under threat? Population changes in *Sylvia* warblers on the island of Cyprus. *Oryx* 36: 342–348.
- Pons P, Bas JM, Prodon R, Roura-Pascual N, Clavero M, 2008. Territory characteristics and coexistence with heterospecifics in the dartford warbler *Sylvia undata* across a habitat gradient. *Behavioral Ecology and Sociobiology* 62: 1217–1228.
- Price TD, Kirkpatrick M, 2009. Evolutionarily stable range limits set by interspecific competition. *Proceedings of the Royal Society B* 276: 1429–1434.
- Prodon R, Lebreton JD, 1981. Breeding avifauna of a Mediterranean succession: The holm oak and cork oak series in the Eastern Pyrenees. 1. Analysis and modeling of the structure gradient. *Oikos* 37: 21–38.
- R Development Core Team, 2008. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. URL <http://www.R-project.org>.
- Robinson SK, Terborgh J, 1995. Interspecific aggression and habitat selection by Amazonian birds. *Journal of Animal*

- Ecology 64: 1–11.
- Romdal TS, Rahbek C, 2009. Elevational zonation of afro-tropical forest bird communities along a homogeneous forest gradient. *Journal of Biogeography* 36: 327–336.
- Sara M, Bellia E, Milazzo A, 2006. Fire disturbance disrupts co-occurrence patterns of terrestrial vertebrates in Mediterranean woodlands. *Journal of Biogeography* 33: 843–852.
- Schaefer T, Barkow A, 2004. Habitat and nest site preferences of *Sylvia atricapilla* and *S. melanocephala* in Majorca. *Ardeola* 51: 445–450.
- Selmi S, Boulinier T, Faivre B, 2003. Distribution and abundance patterns of a newly colonizing species in Tunisian oases: The common blackbird *Turdus merula*. *Ibis* 145: 681–688.
- Shirihai H, Gargallo G, Helbig AJ, 2001. *Sylvia Warblers*. London: Christopher Helm.
- Terborgh J, Weske JS, 1975. The role of competition in the distribution of Andean birds. *Ecology* 56: 562–576.
- Terbraak CJF, 1986. Canonical correspondence analysis: A new eigenvector technique for multivariate direct gradient analysis. *Ecology* 1167–1179
- Twomey E, Morales V, Summers K, 2008. Evaluating condition-specific and asymmetric competition in a species-distribution context. *Oikos* 117: 1175–1184.
- Wright JP, Fridley JD, 2010. Biogeographic synthesis of secondary succession rates in eastern North America. *Journal of Biogeography* 37: 1584–1596.