

Extinction debt of a common shrub in a fragmented landscape

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Summary

1. Environmental stochasticity and low demographic rates may cause delayed extinctions of habitat-specialist species that were initially retained within remnant patches after habitat loss and fragmentation. Detecting such extinction debts opens opportunities to counteract future biodiversity loss, yet knowing the underlying causes of population declines is a basic need for targeting specific guidelines for conservation and restoration (e.g. habitat quantity, quality or connectivity).

2. Here, we examine the extinction debt in the common Mediterranean shrub *Myrtus communis* (myrtle) occurring in woodland patches of a highly fragmented region that has lost nearly half of the remnant woodland cover during the last 50 years (1956–2002).

3. We sampled myrtle occurrence in 304 woodland patches and modelled its probability of occurrence in relation to patch size, patch disturbance and woodland cover in the surrounding landscape. In order to test for extinction debt evidence, we tested whether myrtle occurrence is better predicted by past (1956) than by present (2002) woodland cover.

4. We found that the probability of myrtle occurrence is associated with present patch features (size and disturbance) that are linked to causes of individual mortality and/or recruitment collapse. However, it was associated with past – rather than present – woodland cover in the surrounding landscape, proving a still unpaid extinction debt. Specifically, myrtle occurrence is very unlikely in small and highly disturbed patches located in long-term deforested landscapes.

5. *Synthesis and applications.* Individual longevity of the Mediterranean shrub *Myrtus communis* (myrtle) can delay local extinctions, but *paying the debt* is a matter of time, especially considering the elevated susceptibility of small and disturbed populations to environmental stochasticity. However, these populations still offer management opportunities, and reducing disturbances and improving habitat quality, especially within small woodland patches, should be a top priority for conservation and restoration.

Key-words: delayed extinctions, habitat disturbance, habitat fragmentation, habitat loss, long-lived species, *Myrtus communis*, occurrence probability, woodland

Introduction

Habitat loss is one of the main components of current anthropogenic global change and is considered to be a major threat to global biodiversity of terrestrial ecosystems (Sala *et al.* 2000; Dirzo & Raven 2003). The fragmentation of natural habitats reduces the size of remnant

patches, increases their degree of isolation and deteriorates their quality through edge effects and increasing disturbance. All these factors can jeopardize the long-term persistence of many taxa (McIntyre & Hobbs 1999; Fahrig 2003; Ewers & Didham 2006; Lindenmayer & Fischer 2006), particularly of habitat-specialist species (Helm, Hanski & Pärtel 2006; Fahrig *et al.* 2011).

Two key questions with direct implications for biodiversity conservation and restoration arise from the theoretical

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framework of habitat fragmentation. (i) Do current habitat patches harbour species samples more impoverished than those expected by species–area relationships observed in larger and/or continuous habitats? (ii) Is the persistence of a species currently observed in remnant habitat patches ensured in the long term? (Tilman *et al.* 1994; Fahrig 2003; Ewers & Didham 2006; Lindenmayer & Fischer 2006; Kuussaari *et al.* 2009) Both questions are in fact interconnected by species–area relationships and the concepts of delayed extinctions, extinction debt and relaxation time (Diamond 1972; Tilman *et al.* 1994; Kuussaari *et al.* 2009; Wearn, Reuman & Ewers 2012). Low demographic rates owing to the effects of small population sizes (Lamont, Klinkhamer & Witkowski 1993), isolation (McEuen & Curran 2006) and/or reduced habitat quality (abiotic factors: González-Varo, Nora & Aparicio 2012; biotic interactions: Vögeli *et al.* 2011) may cause delayed extinctions of species that were initially retained by remnant patches, particularly within the smallest ones (Helm, Hanski & Pärtel 2006; Krauss *et al.* 2010). The extinction debt represents the number of habitat-specialist species – or populations from a single-species metapopulation perspective – expected to eventually become extinct after habitat loss and fragmentation (reviewed by Kuussaari *et al.* 2009), while relaxation time represents the time necessary to reach a new (quasi-) equilibrium after habitat destruction.

Delayed extinctions are more likely in long-lived species with low turnover rates, which are expected to show longer relaxation times than short-lived species (Kuussaari *et al.* 2009; Krauss *et al.* 2010). On the other hand, extinction debts are more likely in those landscapes where large-scale habitat destruction has occurred recently (Cousins 2009). Since past information on species distribution is generally lacking, extinction debts can be assessed by comparing the explanatory power of past vs. present landscape variables: extinction debts can be assumed if current species occurrences are better predicted by past than present landscape features (Kuussaari *et al.* 2009). The importance of identifying extinction debts is that there are still opportunities to counteract future biodiversity loss (Wearn, Reuman & Ewers 2012), but knowledge about the causal mechanisms (disruptors of demographic processes) that constrain the distribution of species in fragmented areas is essential for developing effective management plans for conservation and restoration (see Hylander & Ehrlén 2013). Surprisingly, there is a lack of studies at a single-species level for which underlying causes of population declines are known (Hylander & Ehrlén 2013).

Here, we examine extinction debt using as a case study a common long-lived shrub occurring in woodland patches of a highly fragmented region: the Guadalquivir Valley, south-west Spain. Even though most deforestation occurred during Roman times and the Middle Ages (Aparicio 2008; Valbuena-Carabaña *et al.* 2010), this region has lost nearly half of the remnant woodland cover during the last 50 years as a result of intensive

agriculture, urbanization and infrastructure development. The study species is the myrtle (*Myrtus communis*), a sclerophyllous shrub that inhabits warm areas of the Mediterranean Basin and an emblematic component of well-preserved woodlands (González-Varo, Nora & Aparicio 2012; Migliore *et al.* 2012). Its current distribution in the Guadalquivir Valley is almost restricted to just the remnant woodland patches, and it is present in approximately 30% of them (Albaladejo *et al.* 2009). Recent studies have demonstrated that the viability of myrtle populations in small patches is jeopardized by limited seedling establishment, which is impaired far more by reduced habitat quality (edge effects and disturbance) than by increasing inbreeding (González-Varo *et al.* 2010; González-Varo, Nora & Aparicio 2012).

Thus, we hypothesized that (i) besides patch size and woodland cover, patch disturbance is the dominant factor shaping the patterns of myrtle occurrence in woodland remnants and (ii) given its longevity (several decades), non-viable myrtle populations are still paying an extinction debt after recent habitat loss (i.e. in the last 50 years), and thus, occurrence must be more associated with past rather than present landscape features. To test these hypotheses, we modelled the probability of myrtle occurrence in relation to patch size, patch disturbance and landscape woodland cover. Then, we analysed whether past rather than present woodland covers better predicted extant myrtle occurrence patterns.

Materials and methods

STUDY SPECIES AND AREA

Myrtle *Myrtus communis* L. is a common sclerophyllous shrub and the sole representative of the Myrtaceae family in the flora of the Mediterranean Basin (Migliore *et al.* 2012). It grows up to 4 m in height and 6 m in diameter with a hemispherical shape and inhabits warm fertile lowlands as one of the main components of woodland understories and late successional shrublands. Its flowers are pollinated by insects, and its berries are mainly consumed by frugivorous birds, which disperse its seeds through endozoochory. Reproductive age is reached after *c.* 10 years of growth, and adult plants are known to live for decades or even centuries. Comprehensive information on the natural history of the species can be found in González-Varo (2010), González-Varo, Arroyo & Aparicio (2009) and González-Varo, Nora & Aparicio (2012). Adult myrtles are able to resprout after disturbances such as fire or grazing (Herrera 1987).

The Guadalquivir River Valley (western Andalusia, southern Spain) is a large (21 000 km²), fertile and intensively cultivated lowland in which the historical transformation of natural habitats has left just *c.* 1% of Mediterranean woodland cover distributed among about 530 patches scattered throughout its area (Aparicio 2008) (Fig. 1). Originally, the dominant vegetation in the area was sclerophyllous Mediterranean maquis mainly associated with cork (*Quercus suber*) and holm oak (*Quercus ilex* subsp. *ballota*) forests. Currently, the landscape can be described as ‘relictual’ (*sensu* McIntyre & Hobbs 1999) since the overall woodland cover is < 10% and most remnant patches are small, highly isolated

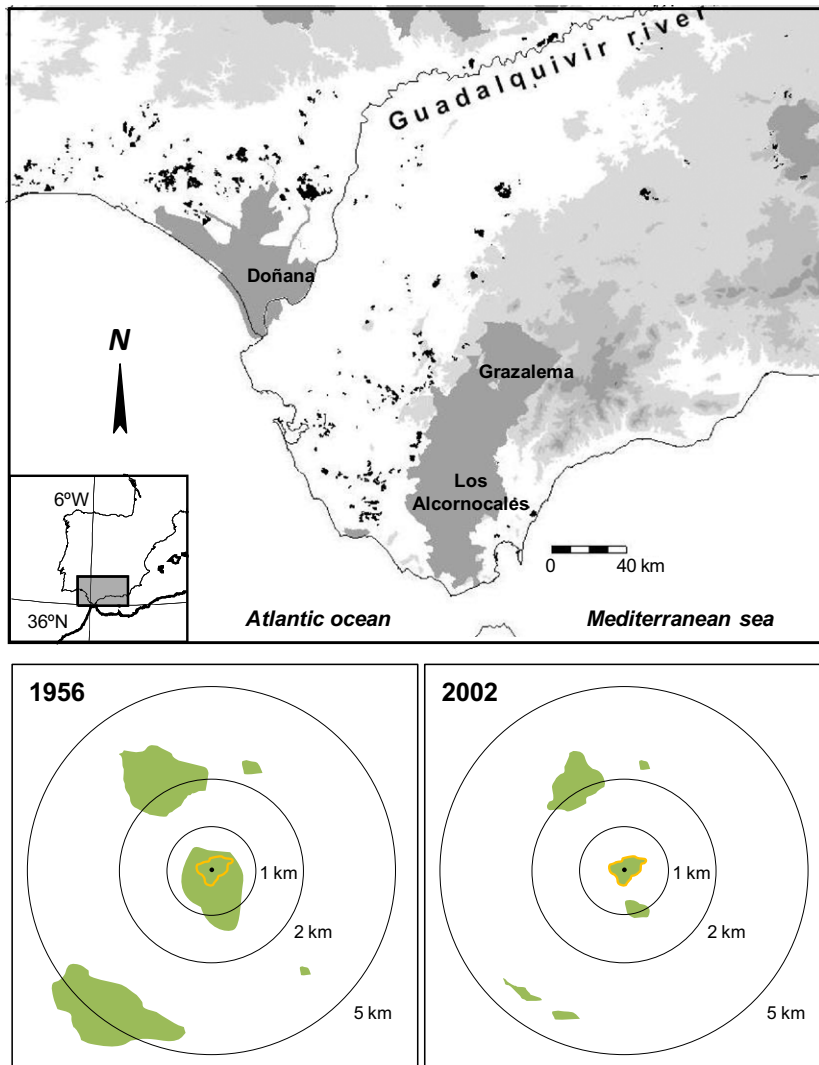


Fig. 1. Present map (2002) of the Guadalquivir Valley (south-west Spain). The unshaded area represents lowland areas (below 200 m in altitude), where the remaining woodland patches are shown in black; higher elevations and legally protected areas (the largest ones are labelled) are shown in light and dark grey, respectively. The lower panels show the three radius buffers (1-, 2- and 5-km) around the centroid of a study patch (outlined) for measuring past (1956) and present (2002) woodland cover. This example illustrates the general trend of habitat loss and fragmentation in the valley during the last 50 years (see Table 1).

and disturbed (Aparicio 2008). Table 1 and Fig. S1 (Supporting information) show the loss of woodland cover in this area in the last 50 years.

The climate in the valley is typically Mediterranean, with warm dry summers and cool humid winters; mean (range) annual precipitation is *c.* 550 mm (500–598 mm) and January and July

temperatures average (range) 10 °C (9.2–11.6 °C) and 26 °C (25.5–27.2 °C), respectively (A.E.M.E.T./I.M. 2011). The environmental variability within the valley, particularly in terms of climate and soil types (see Aparicio 2008; A.E.M.E.T./I.M. 2011), is very narrow compared to the variability across the whole distribution range of *M. communis* (see Migliore *et al.* 2012).

Table 1. Descriptive statistics of the 304 woodland patches studied in south-west Spain. Variables 1, 2 and 3 were used to model the myrtle (*Myrtus communis*) occurrence probability in relation to contemporary landscape and habitat attributes. Variables 3 and 4 were used to test for extinction debt evidence

Variable	Metric	Mean	Median	Min.	Max.
1) Patch size	Area (ha)	64.0	17.6	0.28	2024.9
2) Patch disturbance	Nitrophilous and ruderal spp. (%)	43.9	42.9	0.00	83.3
3) Present landscape (2002)					
1-km radius (R1)	Woodland cover (%)	18.3	10.8	0.20	98.5
2-km radius (R2)	Woodland cover (%)	9.9	6.6	0.05	82.6
5-km radius (R5)	Woodland cover (%)	7.2	4.0	0.03	48.6
4) Past landscape (1956)					
1-km radius (R1)	Woodland cover (%)	29.0	22.8	0.00	99.8
2-km radius (R2)	Woodland cover (%)	21.4	18.3	0.00	97.0
5-km radius (R5)	Woodland cover (%)	15.4	12.4	0.00	61.1

STUDY PATCHES AND MYRTLE OCCURRENCE

We focused our study on 304 woodland patches embedded in the agricultural matrix of the Guadalquivir Valley. The tree layer of these patches is mainly composed of stone pines (*Pinus pinea*), holm oaks (*Q. ilex* subsp. *ballota*) and/or cork oaks (*Q. suber*). The shrub layer is represented by a mixture of early successional shrubs, mainly belonging to Cistaceae, Labiatae and Leguminosae, and late successional sclerophyllous shrubs of which *Pistacia lentiscus* (Anacardiaceae), *M. communis* (Myrtaceae), *Olea europaea* var. *sylvestris* (Oleaceae) and *Quercus coccifera* (Fagaceae) are the dominant species (Aparicio 2008).

Myrtle occurrence (i.e. the presence or absence of the species) in the study patches was sampled between 1999 and 2001, within the intensive botanic surveys undertaken by the BIANDOC project (see Aparicio 2008). In such surveys, between two and three researchers walked randomly in each patch, noting all vascular plant species, with time devoted to sampling proportional to patch size and visual heterogeneity. Vouchers were collected and stored by A. Aparicio; others were deposited in the herbaria SEV, MA and MACB. Myrtle occurrence was recorded in 110 out of the 304 study patches.

CHARACTERIZATION OF CURRENT LANDSCAPE AND HABITAT FEATURES

We characterized the current habitat and landscape features of the 304 study patches using three types of predictor variables: patch size, patch disturbance and landscape woodland cover (see Table 1). From aerial digital orthophotos (available at <http://www.juntadeandalucia.es/medioambiente/site/rediam>) dating from 2002, we obtained the patch size and the percentage of woodland cover around the centroid of each patch at 1-, 2- and 5-km-radius buffers (hereafter R1, R2 and R5, respectively; see Fig. 1). These metrics can be considered as inverse estimates of habitat loss and fragmentation at the landscape scale (e.g. Steffan-Dewenter *et al.* 2002). In general, habitat cover within these buffer areas is positively correlated with the number of patches and the mean patch size and negatively with the distance between patches (see Fahrig 2003; Ewers & Didham 2006).

Habitat disturbance is a multidimensional feature involving different disturbance types (Ross, Fox & Fox 2002; Neal, Hardner & Grossa 2010), including those currently affecting the woodland patches of the Guadalquivir Valley (e.g. fire, forestry practices, grazing, trampling, rubbish dumping, recreation; Aparicio 2008). Here, we used the proportion of nitrophilous and ruderal herbaceous species in each patch as an integrative proxy of habitat disturbance. This species group is recognized as an indicator of anthropogenic disturbances in woodland habitats (e.g. Dzwonko & Loster 1997; Van Calster *et al.* 2007). We used detailed plant samplings carried out between 1999 and 2001 (see above) and characterized each herbaceous plant species in the study patches as nitrophilous and/or ruderal or not according to habitat description provided in regional floras (Castroviejo *et al.* 1986; Valdés *et al.* 1987).

CHARACTERIZATION OF THE PAST LANDSCAPE

We characterized the past landscape (c. 50 years ago) using aerial digital orthophotos (available at <http://www.juntadeandalucia.es/medioambiente/site/rediam>) dating from 1956 (Aparicio *et al.*

2012). We measured the percentage of past woodland cover around the centroid of each current patch at the same three spatial scales used for present woodland cover (i.e. 1-, 2- and 5-km-radius buffers, see Fig. 1). On average, past woodland cover was nearly twice as large as present cover at the three spatial scales (see Table 1 and Fig. S1). Scenarios of woodland cover expansion were the exception, particularly within the largest radius buffers (Fig. S1).

STATISTICAL ANALYSES

Myrtle occurrence in relation to current landscape features

We analysed the response of myrtle occurrence to the predictor variables (patch size, patch disturbance and woodland cover in the landscape) by means of multiple logistic regressions to account for the Bernoulli-distributed response variable (1 = presence, 0 = absence). We built generalized linear models (GLMs) with binomial distribution and a logit link function. Prior to statistical analyses, patch size was transformed as ' $\log_{10}(x + 1)$ ' to improve linearity. Prior to GLMs, Pearson correlation matrices were built to avoid the inclusion of highly correlated predictor variables in the models (see Table S1). Owing to collinearity among the three buffers (R1, R2 and R5) and patch size, we included only R5 as independent variable in all GLMs because it resulted to be the one that best predicted myrtle occurrence independent of focal patch size (see details in Appendix S1); moreover, R5 was barely correlated with patch size ($r = 0.15$; Table S1). At the end, variables included in the models (patch size, % nitrophilous and ruderal species, and R5) were in general weakly correlated ($r < |0.41|$ in all cases; Table S1). We evaluated the resulting GLMs on the basis of the Akaike's information criterion (AIC; Burnham & Anderson 2002). We selected all equivalent models with a ΔAIC (i.e. the difference between the AIC of each model and the minimum AIC value obtained among all models) values ≤ 2 . For the best models selected, we also show statistical significance ($P \leq 0.05$) of both models and coefficients and logistic R^2 -values (likelihood ratio tests). Finally, we performed a deviance-partitioning analysis to quantify the percentage of the total explained deviance accounted by each predictor variable independently (unique effects) and in combination with other predictors (i.e. joint effects) (e.g. Vögeli *et al.* 2010; González-Moreno *et al.* 2013). Analyses were conducted using R version 3.0.2 (R-Development Core Team 2012). We used the code developed by González-Moreno *et al.* (2013) based on the package 'vegan' (ver. 2.0–10; Oksanen *et al.* 2013) for deviance partitioning.

The probability of Type I error may increase when residuals of regressions between the response variable and the predictors are spatially structured (Legendre *et al.* 2002). We checked spatial structure in myrtle occurrence by means of join-count correlograms (based on the Z_{1-1} statistic: presence–presence) and in the residuals of logistic models by means of Moran's I correlograms (Fortin, Dale & Ver Hoef 2002). Correlograms were made with the software SAM 4.0 (Rangel, Diniz-Filho & Bini 2010) by constructing 16 distance classes so as to keep constant sample sizes per class. While myrtle occurrence was spatially autocorrelated, the residuals of our best-fit GLMs were not, as indicated by their very low ($I_{\text{maximum}} = |0.04-0.10|$) and statistically non-significant Moran's I -values at all distance classes, and the lack of spatial

trend with increasing distance (see details in Fig. S2). This indicates that the predictor variables included in the models accounted for all existing spatially structured variability in myrtle occurrence and, hence, that the computed *P*-values were robust and not affected by spatial autocorrelation (Kühn & Dormann 2012).

Tests for extinction debt evidences

We tested whether myrtle occurrence in woodland patches is better predicted by past than by present landscape features, which can be interpreted as evidence of an extinction debt. For this purpose, we performed two sets of complementary analyses. In the first set, we built GLMs as described above incorporating the past woodland cover within a 5-km-radius buffer (R5) together with the present attributes of patches (size and disturbance). The three predictors included in these models were also weakly correlated ($r < |0.46|$ in all cases; Table S1). In the second set, we performed simple logistic regressions between myrtle occurrence and the buffers measuring either past or present woodland cover at three spatial scales (i.e. R1, R2 and R5).

Results

RELATIONSHIPS BETWEEN MYRTLE OCCURRENCE AND CURRENT LANDSCAPE FEATURES

Two significant logistic regression models were selected according to AIC values (Table 2). Both models accounted for 19–20% of the variation in myrtle occurrence and included patch size and patch disturbance with highly significant effects ($P < 0.001$). Present woodland cover was only included in one model (L₁) but produced non-significant effects (see Table 2). Myrtle occurrence was positively associated with patch size and woodland cover and negatively with patch disturbance (Table 2, Fig. 2). In both models, the strongest effects on the probability of myrtle occurrence were produced by patch disturbance (see β -values in Table 2). Indeed, patch disturbance accounted for most of the variance explained by the full model (L₁) followed by patch size, the contribution of present woodland cover being marginal (Fig. 3). Moreover, whereas most of the deviance explained by patch size and patch disturbance in model L₁ was

accounted by unique effects, most of the effects of present woodland cover were joint effects with patch disturbance (Fig. 3).

EXTINCTION DEBT

The logistic model built including past woodland cover (R5) as a predictor variable (model L₃ in Table 2) showed a better fit than the models built with or without present cover (L₁ and L₂; $\Delta\text{AIC} > 10$). In contrast to present woodland cover in L₁, past woodland cover showed a highly significant positive effect in L₃ (Table 2). Remarkably, model L₃ was also the best accounting for all existing spatially structured variability in myrtle occurrence (Fig. S2). Results of variance-partitioning analysis showed that the relative variance explained by past woodland cover in model L₃ was much higher than that accounted by present woodland cover in model L₁. Most of the effects of past woodland cover in model L₃ were also joint effects with patch disturbance; however, past woodland cover produced a higher fraction of unique effects than present woodland cover (Fig. 3). The negative joint contribution of past woodland cover and patch size indicates that this relationship between predictors is suppressive and not additive (see Chevan & Sutherland 1991). It is worth mentioning that pairwise interactions between predictors never showed significant effects and they did not improve the fitting of models L₁ and L₃ (results not shown).

We found analogous results in simple logistic models in which myrtle occurrence was better predicted by past (1956) than by present woodland cover (2002), particularly at broad spatial scales (2- and 5-km radii; Fig. 4). For example, past cover within 5 km accounted for almost twice the variance in myrtle occurrence compared to present cover (9% vs. 4%; Fig. 4).

Discussion

Environmental stochasticity and low demographic rates may cause delayed extinctions of species that were initially retained within remnant patches after habitat loss and

Table 2. Standardized coefficients (β) of best-fit ($\Delta\text{AIC} \leq 2$) logistic models (L_{1–3}) examining myrtle (*Myrtus communis*) occurrence in relation to patch size, patch disturbance (proportion of nitrophilous and ruderal spp.) and either present (a) or past (b) woodland cover within a 5-km-radius buffer ($n = 304$ patches, $P < 0.001$ for all models)

Models	Predictor variables			Model statistics		
	Patch size	Patch disturbance	Woodland cover	χ^2	AIC	R^2_L
(a) Present landscape						
Model L ₁	0.655	-0.911	0.196	78.3	327.6	0.197
Model L ₂	0.648	-0.987	–	76.4	327.6	0.192
(b) Past landscape						
Model L ₃	0.692	-0.789	0.535	89.0	316.9	0.224

Significant β -values – based on Wald chi-squared tests – are shown in bold type (all $P < 0.001$).

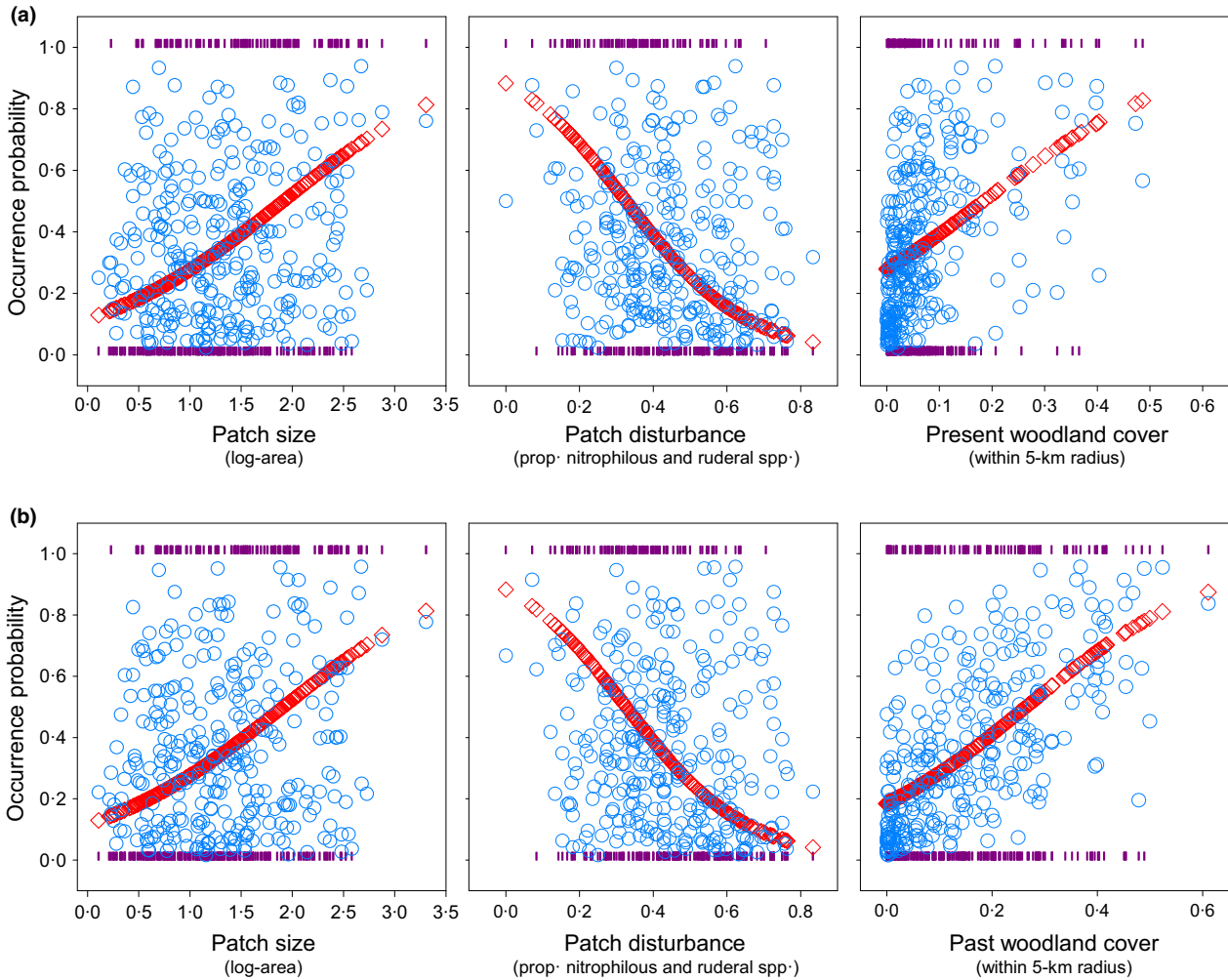


Fig. 2. Relationships between the probability of myrtle (*Myrtus communis*) occurrence in a woodland patch and the predictor variables included in the logistic models that incorporated patch size, patch disturbance and either present (a) or past (b) landscape woodland cover within a 5-km-radius buffer (models L_1 and L_3 in Table 2, respectively). Circles denote occurrence probabilities predicted by the model, diamonds denote occurrence probabilities predicted by simple logistic regressions, and vertical marks the observed presence (1) or absence (0) of the species in each patch ($n = 304$). R^2_L of simple logistic regressions (all $P < 0.001$): patch size = 0.07; patch disturbance = 0.14; present woodland cover = 0.04; past woodland cover = 0.09.

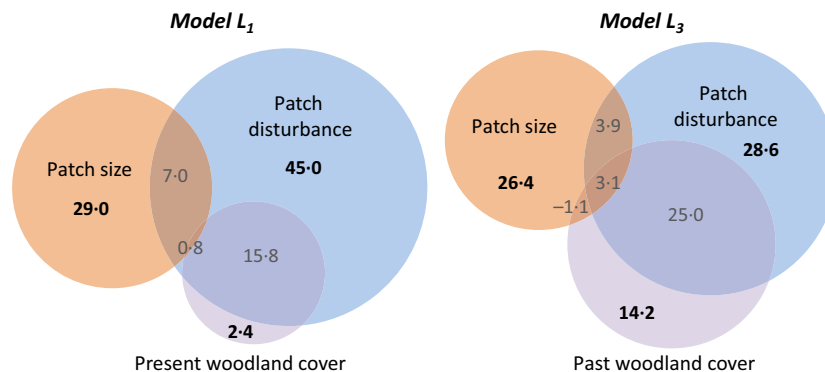


Fig. 3. Percentage of the total explained deviance in myrtle occurrence models accounted by unique and joint effects of predictor variables, represented by circles (patch size, patch disturbance and present or past woodland cover in the surrounding landscape). We present results for models L_1 (present landscape) and L_3 (past landscape) (details in Table 2). The size of circles and overlapping areas is proportional to the deviance explained. Black numbers denote unique effects; grey numbers denote joint effects between pairs of variables or between the three variables.

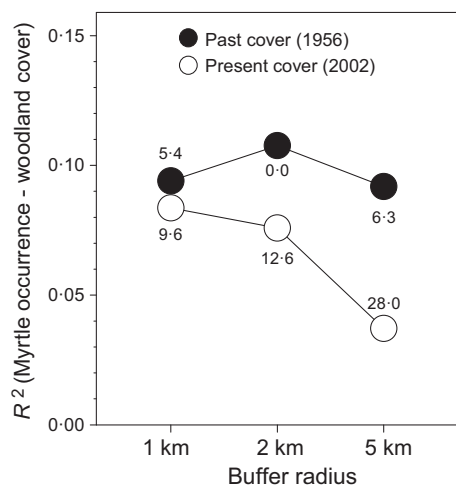


Fig. 4. Goodness of fit (circles = logistic R^2_L ; numbers = ΔAIC) of logistic regressions between myrtle (*Myrtus communis*) occurrence and woodland cover in past (1956) and present (2002) landscapes around the centroids of the studied patches ($n = 304$) at different spatial scales (1-, 2- and 5-km radius). $\Delta AIC = AIC_{\text{model}} - AIC_{\text{best-fit model}}$ (359.1). $P < 0.001$ in all cases.

fragmentation, particularly of those that are long lived (Kuussaari *et al.* 2009; Krauss *et al.* 2010). We found that the probability of myrtle occurrence in woodland remnants is associated with present patch features (size and disturbance) and also with past – rather than present – woodland cover in the surrounding landscape, supporting the expectation of an unpaid extinction debt. Specifically, myrtle occurrence is very unlikely in small and highly disturbed patches located in long-term deforested landscapes. These results are congruent with the scarce recruitment of the species found in small patches of reduced habitat quality as a consequence of edge effects and disturbance (González-Varo, Nora & Aparicio 2012). The longevity of this shrub species, together with its resprouting ability, is thus buffering the imminent extinction of several populations, which opens management opportunities for conservation.

THE ROLE OF PRESENT PATCH FEATURES

Significant associations occurred between present patch features (size and disturbance) and myrtle occurrence. Notably, patch features explained 19% of the variance in myrtle occurrence, which accounted for most variance explained by best-fit models (Table 2). Occurrence of myrtle is less likely in small woodland patches, a pattern that can be explained by at least two non-mutually exclusive causes. First, the low probability of myrtle occurrence in small patches could reflect that such probability might also be low in small-sized plots sampled within continuous woodlands (random sample hypothesis; Haila 1983). However, it seems unlikely that this is the only or even the prevalent factor behind the patch size–myrtle occurrence association because myrtle is a relatively abundant

shrub; thus, it is easily ‘sampled’ even within small-sized plots. For example, average myrtle density in ten patches where the species occurs is 28 ind. ha⁻¹ (range = 2–67 ind. ha⁻¹; González-Varo, Nora & Aparicio 2012), and only 3% of 304 patches studied here are smaller than one hectare. The second and more plausible cause is that extinctions after habitat fragmentation are more likely in small patches where myrtle population sizes are smaller and, thus, more susceptible to demographic and environmental stochasticity (Schemske *et al.* 1994).

The probability of myrtle occurrence also decreases sharply with increasing disturbance independent of patch size. This result supports our first hypothesis, highlighting the important role of habitat quality in remnant patches for the occurrence of habitat-specialist species and, thus, for biodiversity conservation (Harrison & Bruna 1999). Disturbance can directly cause individual mortality leading to population extinction. Although adult myrtle plants are able to resprout after disturbance events, recurrent disturbance regimes can increase mortality rates of previously resprouted individuals (Paciorek *et al.* 2000). Many disturbance types (e.g. fire, forestry practices, grazing) are currently affecting the woodland patches of the Guadalquivir Valley (Aparicio 2008) and increasing myrtle mortality rates. For example, *M. communis* has been reported as the shrub species most consumed by cattle in woodlands of our study region (Mancilla-Leytón, Parejo-Farnés & Martín-Vicente 2012), and woodland patches are commonly used by cattle in the Guadalquivir Valley, affecting directly *c.* 50% of existing patches (Aparicio 2008). Disturbance can also affect myrtle occurrence by impeding colonization of unoccupied patches or impairing long-term population persistence in occupied patches. Indeed, the impoverishment of habitat quality caused by edge effects and disturbance has been claimed as the main limitation for the establishment of myrtle seedlings within small woodland patches (González-Varo, Nora & Aparicio 2012).

EXTINCTION DEBT

We found consistent evidence for an extinction debt in the results of both sets of analyses (simple and multiple logistic regressions), since myrtle occurrence was more associated with past than present woodland cover. This pattern mainly arises because the current distribution of the species still mirrors the more forested landscapes found in the region 50 years ago, which supports our second hypothesis: given the longevity of the species, non-viable myrtle populations are still paying an extinction debt after recent habitat loss. These results are consistent with previous studies working at a community level and finding evidence for extinction debt in long-lived but not in short-lived species (Kuussaari *et al.* 2009; Krauss *et al.* 2010).

Current presence of myrtles is more likely in those landscapes that harboured high woodland cover 50 years

before. In turn, woodland cover is positively correlated with patch size and negatively with patch isolation (Fahrig 2003; Ewers & Didham 2006); thus, patches in past landscapes were on average larger and more connected (e.g. Fig. 1). Hence, myrtle population sizes should have been larger and rescue effects and recolonization after local extinctions more frequent in the past (Hylander & Ehrlén 2013). The expected past ubiquity of this shrub across the valley is now mostly represented by small populations composed of adult plants in small and highly disturbed woodland patches where regeneration is negligible (González-Varo, Nora & Aparicio 2012).

Even though the predictive power of past woodland cover on myrtle occurrence is relatively low (max. *c.* 10%; Fig. 3), it is outstanding to detect an effect of the 'recent' past landscape when considering that significant deforestation in the Guadalquivir Valley started during Roman times, several centuries ago (see Aparicio 2008; Valbuena-Carabaña *et al.* 2010). Likely, the woodland remnants belonging to the past cover already differed in age, rate of habitat loss before 1956 and past disturbance regimes. Thus, it is expected that each patch already represented different snapshots along the continuum of the processes of landscape alteration (see temporal sequence of contemporary woodland destruction in Fig. S3). Indeed, the extinction debt concept could also be applied to habitat disturbance; however, its applicability is constrained by the fact that past habitat quality is hard – if not impossible – to measure, whereas past habitat quantity can be easily measured where past aerial photographs exist.

Models predicting the occurrence of short-lived (average lifespan < 5 years) and habitat-specialist birds in habitat fragments have accounted for *c.* 50% of the observed variance (e.g. González-Varo, López-Bao & Guitián 2008; Vögeli *et al.* 2010). Our best model (L_3 , with past woodland cover) accounted for *c.* 23% of the variance in myrtle occurrence; the *c.* 77% unexplained variance is then expected to be mostly accounted for by differences among present patches in age, rate of habitat loss before 1956 and past disturbance regimes. We argue that this is a modest but remarkable predictive power, especially when considering the life-history traits of our target species (sessile, long-lived and with resprouting ability) and the long-term history of habitat loss and degradation of our study region. Thus, our results should be taken into consideration for management guidelines.

IMPLICATIONS FOR CONSERVATION AND RESTORATION

In this study, we uncover factors associated with landscape alteration that reveal an extinction debt for populations of Mediterranean myrtle living in the fragmented landscape of the Guadalquivir Valley. Extinction debts may be caused by mechanisms acting at the population and metapopulation levels. Knowledge about causal

mechanisms is a basic need for targeting the specific management guidelines needed for restoration, such as habitat quality, quantity or connectivity (Hylander & Ehrlén 2013). We know that extant myrtle populations are more threatened by population than by metapopulation processes. Together, a set of ecological and genetic studies (Albaladejo *et al.* 2009; González-Varo, Arroyo & Aparicio 2009; González-Varo 2010; González-Varo *et al.* 2010; González-Varo, Nora & Aparicio 2012) have demonstrated that the viability of myrtle populations in small patches is jeopardized by limited seedling establishment, which depends far more on reduced habitat quality – edge effects and disturbance – than on the genetic fitness of progenies. In agreement, we show in this study that myrtle occurrence is mostly explained by local patch attributes (size but especially disturbance) that are linked to causes of individual mortality and/or recruitment collapse. Albeit individual longevity can delay imminent local extinctions, *paying the debt* is just a matter of time, especially considering the elevated susceptibility of small and disturbed populations to environmental stochasticity and the impacts that currently threaten the remnant woodlands (e.g. Fig. S3). Consequently, reducing disturbance and improving habitat quality, especially within small woodland patches, should be a top priority for conservation and restoration. This can be achieved by avoiding disturbances such as grazing, trampling, clearings or fires, as well as promoting succession (see González-Varo, Nora & Aparicio 2012). This is not in disagreement with certain management practices. Indeed, myrtle can occur at high densities even in small woodland patches if they are not subject to disturbances (e.g. *c.* 200 ind. in a patch of 3 ha devoted to hunting; González-Varo, Nora & Aparicio 2012).

Because it is impossible to obtain demographic and genetic information on whole communities for conservation purposes, we should profit from available information on keystone or umbrella species. Particularly, myrtle is an important component of late successional woodlands across the Mediterranean Basin (Migliore *et al.* 2012), a vegetation type dominated by long-lived species susceptible to suffer an extinction debt still unpaid. Further, myrtle interacts with several mutualistic animals, such as flower-visiting insects and frugivorous birds, for whom it represents a non-redundant food source. As an example, myrtle blooms nearly in isolation during the summer, well out of the flowering peak of the entomophilous plant community, and several bee, bee-fly and hoverfly species visit its flowers for pollen (González-Varo, Arroyo & Aparicio 2009). Thus, preserving myrtles is expected to have multiple effects at the community level.

Nearly 70% of patches in our study region are on private land and 30% belong to the Andalusian Regional Government (Aparicio 2008). Exceptionally, the Regional Government monitors and manages certain patches (private or public) if they shelter endangered species. We also encourage the regional authorities to devote conservation

efforts on preserving those ‘yet’ common species that, as myrtle, serve as indicators of ecosystem functionality (Gaston 2010). Since increasing patch size or woodland cover may not be feasible considering the current land uses (mostly extensive agricultural fields and urban development), we encourage authorities to preserve certain woodland patches as microreserves (Akeroyd 1998), especially in central and eastern parts of the Valley, where deforestation is extreme and some myrtle populations still persist (Fig. S4).

To conclude, our study highlights the importance of considering past landscapes when assessing contemporary patterns of occurrence for habitat-specialist and long-lived species. Different species may differ not only in their susceptibility to local extinction, but also in the underlying causes. Hence, assessing extinction debts in functional groups based on life-history traits (e.g. longevity, dispersal ability) within species assemblages may be a useful and cost-effective approach in conservation planning.

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Data accessibility

Data available from the Dryad repository: doi: 10.5061/dryad.cs5b4 (González-Varo et al. 2015).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Selection procedure of the woodland cover variable for GLMs.

Fig. S1. Differences between 1956 and 2002 in woodland cover around the studied patches at three spatial scales (1-, 2- and 5-km-radius buffers).

Fig. S2. Spatial correlograms of myrtle occurrence and residuals of best-fit logistic models.

Fig. S3. Example of contemporary woodland destruction by road construction.

Fig. S4. Maps showing observed myrtle occurrences and predicted occurrence probabilities based on the best-fit model.

Table S1. Pearson's correlation matrices among predictor variables.