Contrasting habitat and landscape effects on the fitness of a long-lived grassland plant under forest encroachment: do they provide evidence for extinction debt?

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Summary

1. Habitat loss, fragmentation and transformation threaten the persistence of many species worldwide. Population and individual fitness are often compromised in small, degraded and isolated habitats, but extinction can be a slow process and extinction debts are common.

2. Long-lived species are prone to persist as remnant populations in low quality habitats for a long time, but the population and individual-level mechanisms of extinction debt remain poorly explored so far.

3. We here investigate the mechanisms involved in the long-term persistence of the common grassland specialist, long-lived, clonal plant *Aphyllanthes monspeliensis* L. (*Asparagaceae*) after forest encroachment into semi-natural Mediterranean calcareous grasslands in Catalonia (NE Iberian Peninsula). For this purpose we assess vegetative (aboveground and belowground) and reproductive plant performance indicators and their habitat and landscape (current and historical) drivers.

4. We confirm the existence of an extinction debt for this species, since current plant frequency is related to historical but not current connectivity, and we also find a positive effect of historical connectivity on seed set. In addition, current tree cover negatively affects individual size and aboveground/belowground biomass ratio, and biotic soil acidification leads to a reduction in the flowering probability of individuals and stems.

5. However, we also find that current connectivity negatively affects flowering and that tree cover enhances seed set. The forestation process, thus, also exerts a positive effect on some fitness traits, probably by providing a moister environment.

6. *Synthesis*. Habitat loss and deterioration result in a decreased vegetative performance of *Aphyllanthes monspeliensis*, a grassland specialist, but show contrasting effects on its reproductive performance. This suggests that the species would perform better in open forests than grasslands in a context of climate change. However, further forest encroachment would increase light competition and soil acidification, threatening its persistence and promoting the payment of the extinction debt if no conservation measures are taken, like opening gaps in forests and enhancing grassland connectivity.

Key-words: Biomass, clonal plant, flowering, grassland specialist, habitat fragmentation, land-use change, Mediterranean, seed set

Introduction

Habitat loss and transformation are major threats for biodiversity all over the world (Fahrig 2003; Stockwell, Hendry & Kinnison 2003; Ouborg, Vergeer & Mix 2006). Transformation or deterioration of the suitable habitat of a species threatens survival and/or reproduction of individuals, reducing fitness (Lienert 2004; Mortelliti, Amori & Boitani 2010). In addition, altered habitat conditions due to edge effects become more important after fragmentation, which increases the transitional area between habitats (Lande 1988; Lienert 2004). Another threat to population viability is the reduced habitat area and increased isolation, which result in decreased population size and restricted individual and gene flows, respectively (Thrall, Burdon & Murray 2000; Honnay *et al.* 2005). But species can persist for a long time in small, degraded and isolated habitats. This especially happens when number, size and spatial configuration of habitat fragments are not much below their extinction thresholds for metapopulation functioning (Hanski & Ovaskainen 2002). However, for metapopulations that are not in equilibrium with current habitat, a number of local populations are expected to become extinct by deterministic or stochastic processes. During the time until the equilibrium is reached (relaxation time), the metapopulation shows an extinction debt, computed as the number or proportion of populations predicted to become extinct (Tilman *et al.* 1994; Hanski, Moilanen & Gyllenberg 1996; Bulman *et al.* 2007; Kuussaari *et al.* 2009). These populations can be precariously maintained by metapopulation, population and individual-level mechanisms (Hylander & Ehrlén 2013). For species with good dispersal ability, populations from source habitats might act as propagule sources that rescue sink populations with otherwise limited recruitment (Hanski 1999; Leibold *et al.* 2004). On the other hand, plant biological characteristics that make individuals resistant to decreased habitat quality in particular life-cycle stages also enhance species persistence (Kuussaari *et al.* 2009; Hylander & Ehrlén 2013). For example, long-lived species may show biological inertia (Summerfield 1972), i.e., they may persist for a long time as remnant populations that, without recruitment, decline slowly over time (Eriksson 1996). Thus, both traits related with competitive ability and dispersal are important for the persistence of a species in a landscape (Jacquemyn, Butaye & Hermy 2003).

So far, the population and individual-level mechanisms behind extinction debt have been much less explored than metapopulation processes (Hylander & Ehrlén 2013). Due to extended life-span and long generation times, populations of clonal plants are usually more persistent than short-lived ones, even if they consist of few individuals (Young, Boyle & Brown 1996; Honnay et al. 2005; Saar et al. 2012; but see Lindborg et al. 2012; Bagaria et al. 2012). As a consequence, these species with low extinction rates might constitute the main part of the extinction debt (Vellend *et al.* 2006; Lindborg 2007). This probably occurs because their survival and reproduction are influenced not only by the present environmental conditions but also by past ones through, for instance, the resources accumulated in perennial tissues (Stephenson 1981; Mehrhoff 1989; Lienert 2004). Although population and individual performance might also show time-lagged responses to habitat change (Ewers & Didham 2006; Takkis *et al.* 2013), they proved useful to confirm population decay in an extinction debt context (Takkis *et al.* 2013). Soil moisture (Colling, Matthies & Reckinger 2002), nutrients (Oostermeijer *et al.* 1998; Colling *et al.* 2002), vegetation cover (Oostermeijer, Van't Veer & Den Nijs 1994; Hutchings, Mendoza & Havers 1998), and also population size (Oostermeijer *et al.* 1998; Jacquemyn, Brys & Hermy 2002) have been identified as drivers of population decay for long-lived species, through effects on population structure and plant fitness. Clonal plants may change their architecture under limited resource availability (light or nutrients) as an expression of foraging behaviour to place ramets in more favourable microhabitats (Slade & Hutchings 1987; Sutherland & Stillman 1988). In response to shading many plants show etiolation, and rhizomatous species tend to reduce branching intensity, but contrary to stoloniferous species, no clear internode elongation has been found (De Kroon & Hutchings 1995). These architectural changes might be useful to assess plant performance under suboptimal conditions.

European semi-natural grasslands underwent an important reduction and fragmentation during the last century, and especially over the last 70 years, as a consequence of agricultural intensification or abandonment of traditional practices (Eriksson, Cousins & Bruun 2002; Adriaens, Honnay & Hermy 2006). Although richness patterns in these communities have been widely studied and delayed species extinctions have been reported at the community level (e.g. Helm, Hanski & Pärtel 2006; Krauss et al. 2010; Bagaria et al. 2015; but see Adriaens et al. 2006), few species-specific extinction debts have been studied (but see Herben et al. 2006), and indicators of forthcoming extinctions are still needed (Helm *et al.* 2009). The few works investigating the consequences of habitat and connectivity loss for the fitness of plants in these semi-natural systems found either that current connectivity was the main predictor of genetic diversity (Helm *et al.* 2009), which in turn enhanced reproductive effort and plant height (Takkis *et al.* 2013), or that tree cover negatively affected recruitment (Schleuning *et al.* 2009) or flower production and fruit set (Adriaens *et al.* 2009). However, some fitness traits, such as plant height and germination, were still related with historical factors (Takkis *et al.* 2013). So, connectivity loss and habitat deterioration might threaten long-term population persistence long before changes in abundance are found, especially for long-lived plants.

In the Mediterranean Basin, an important forest encroachment resulting in the loss and fragmentation of semi-natural grasslands occurred during the 20th century, which is expected to cause extinctions of grassland specialists and colonisations of forest specialists (Debussche, Lepart & Dervieux 1999). These biodiversity changes have partly occurred, but a deficit of forest specialists and a surplus of grassland specialists do still occur even after 50 years of forest encroachment and grassland area reduction (Guardiola, Pino & Rodà 2013; Bagaria *et al.* 2015). The predominance of long-lived species (hemicryptophytes and chamaephytes) in these grasslands might delay species extinctions, thus enhancing extinction debt (but see Bagaria et al. 2012). Nevertheless, little is known about the individual and population-level mechanisms causing extinction debts for long-lived plants in these systems.

In this study we investigate the population and individual-level persistence mechanisms of the clonal plant *Aphyllanthes monspeliensis* L. (*Asparagaceae*) after more than 50 years of forest encroachment into semi-natural Mediterranean grasslands. This species is preferably found in calcareous dry grasslands, stony soils and clearings in shrublands or forests of the western Mediterranean, from 0 to 1600 m a.s.l. (Rico 2014). It is a grassland specialist able to persist along forest encroachment gradients (authors' observation), and it potentially shows an extinction debt in encroached grasslands. In order to seek indicators of individual and population decay for this clonal plant, we assess vegetative and reproductive performance in relation to environmental and landscape proxies of habitat loss and transformation.

We hypothesise that: i) *Aphyllanthes monspeliensis* will show an extinction debt in the encroached sites, with its abundance depending more on past than current connectivity, since extinction debt was identified for the set of grassland specialists in the same area (Bagaria *et al.* 2015); ii) vegetative performance and flower production (and consequently seed production) will decrease under forest encroachment and canopy closure, as a result of resource limitation (Peri, Lucas & Moot 2007; Adriaens *et al.* 2009); iii) seed set will decrease with decreasing grassland connectivity, due to population isolation that can limit pollination and gene flow (Honnay *et al.* 2005), and iv) rhizome branching intensity will decrease and aboveground/belowground biomass ratio and internode length might increase under canopy closure, as a consequence of foraging behaviour and because shade-dependent etiolation commonly occurs at the expense of underground growth (Kephart & Buxton 1993).

Materials and methods

Study area and system

The study was conducted in semi-natural Mediterranean calcareous grasslands in southern Catalonia (NE Iberian Peninsula; 41º14'-41º23'N, 0º56'-1º10'E), between 800 and 1200 m a.s.l. The mean temperature in this area is around 11 ºC, and the mean precipitation around 750 mm, with a marked summer drought (Digital Climatic Atlas of Catalonia; www.opengis.uab.cat/acdc). The predominating life-forms in the studied grasslands are chamaephytes and hemicryptophytes, which usually do not grow higher than 0.5 m, and vegetation cover ranges from 50 to 80% (see Guardiola et al. 2013 for details). A historically open landscape, widely grazed by sheep and goats, was maintained until the decade of 1940s, and was dominated by semi-natural grasslands with small forest areas. However, great grazing reduction during the second half of the 20th century led to generalized grassland reduction and natural forest encroachment (Guardiola *et al.* 2013), which resulted in relatively open forests dominated by holm oak (*Quercus ilex* L.) and Scots pine (*Pinus sylvestris* L.). After more than 50 years of grassland loss and habitat transformation, a plant richness decline at small scale was detected, leading to a rarefaction of grassland specialists (Guardiola *et al.* 2013). However, a community-level extinction debt is still present at patch and sub-patch scales (Guardiola *et al.* 2013; Bagaria *et al.* 2015).

Study species

Aphyllanthes monspeliensis is a rhizomatous, tussock-forming, evergreen graminoid plant. Its leaves are reduced to basal sheaths and its junciform, photosynthetic stems arise in groups from its horizontal and highly branched rhizome (Fig. 1). Flowers develop alone or in groups of 2 or 3 at the stem apex; they are hermaphroditic, narrow at their base, insect pollinated, and show 6 tepals of 15-20 x 4-5 mm. The fruit is a trilocular capsule, which produces a maximum of one seed of 2-2.2 x 1.8-2 mm per locule (Rico 2014). We selected *Aphyllanthes monspeliensis* as our study species because it is an abundant calcareous grassland specialist in the area, but it is still present in rather closed-canopy forests even after more than 50 years since forest encroachment. Hence, it is a good model to study early indicators of decreased plant performance that would eventually trigger local species extinction in the mid or long term.

Sampling design

In order to study the changes in *Aphyllanthes monspeliensis* performance along a habitat and landscape change gradient, we selected 20 sites of 200 m of diameter, which covered a wide range in historical (19-96%) and current (16-70%) grassland proportion. These sites experienced natural reforestation to varying degrees, did not contain any crop field neither in the past nor nowadays, were not burned at least in the 25 last years, and were separated at least 1 km to ensure data independence (see Fig. 2b for a map of site locations). A preferential selection was made on basis of historical (1956) and current (2009) orthophotomaps and preliminary fieldwork, in order to cover a wide range of habitat change situations.

At each of the 20 sites, the flowering state (flowering/non-flowering) of around 50 randomly selected individuals (whenever possible, with a minimum of 37) was assessed in June-August 2012. Plant individualisation is feasible because each individual forms a well-delimited tussock that is easily distinguishable. Alongside, up to 20 flowering individuals distributed throughout the site were sampled at each site in order to obtain stem number, individual size (area of an ellipse taking length and width of the tussock), flowers per stem and seeds per flower (seed set), as measures of plant performance in response to habitat and connectivity changes (see Fig. 2c for a map showing the location of individual plants in a site). Stem number, individual size, and number of flowers per stem were log-transformed in order to improve normality and homoscedasticity. Only flowering individuals were sampled to assess plant performance to ensure enough individuals per site were available for the analyses. The proportion of flowering individuals was generally high, but it showed variability (0.83 ± 0.13; mean ± SD). One of the 20 sites was discarded because most plants showed a completely dead aerial part, probably as the combined result of low late-spring and summer precipitation (May - July) in 2012 (45 mm, while the climatic mean was 136.6 ± 79.7; mean ± SD; see Ogaya et al. 2014 for details on meteorological data) and shallow soil (12 cm). A total of 329 flowering individuals of *Aphyllanthes monspeliensis* were sampled across the 19 sites, but since some capsules were partly eaten or broken, for 9 individuals without complete capsules available seed set could not be estimated and they were excluded from the analysis of this variable.

In addition to the measures of plant performance, in 13 plots of 3 m of diameter distributed in a regular grid at each site (see Fig. 2d), the presence or absence of *Aphyllanthes monspeliensis* was recorded in the previous year (see Bagaria et al. 2015), and the frequency for each site was calculated, from 0 to 13, in order to test for the existence of an extinction debt for this species. Moreover, with the aim of investigating belowground changes in plant performance, five individuals per site were taken from the field in six of the 19 sites, and cleaned in the laboratory. The selection of these plants was preferential, in order to encompass a wide range of tree cover at each site. Rhizome branching intensity (number of ramifications per node) and internode length were taken as the mean of 20 measurements in each of these collected plants. Then, aerial (stems) and belowground (rhizome and roots) structures of these plants were separated and oven-dried at 80ºC during 24 h, and vegetative aboveground (stems after removing flowers)/belowground dry weight ratio was then obtained for each plant. All three plant measures were log-transformed in order to improve normality.

Environmental variables

In order to investigate the effect of forest encroachment and connectivity loss on the vegetative, flowering and fructification performance of *Aphyllanthes monspeliensis*, several landscape and habitat drivers were calculated. Tree cover was obtained for individual plants (in a 10 m radius), while soil measures, grazing and habitat (grassland) amount in the landscape were obtained at site scale. No measure of tree cover at site scale was used when the focus were not individuals, because it showed a high negative correlation with grassland connectivity ($r < -0.7$).

For each of the up to 20 flowering individuals sampled at each site, three variables related to tree cover were obtained: (1) current tree cover, assessed in a circle of 10 m in radius around the individual, from a combination of reclassified orthophotomaps (scale 1:5000; pixel size of 0.5 m) and land-cover layers of 2009 (see Bagaria et al. 2015 for details); (2) historical tree cover in the same circle, from a combination of reclassified orthophotomaps (scale 1:30000; pixel size of 1 m) and land-cover layers of 1956; and (3) tree cover change (current minus historical tree cover proportion). In addition, historical and current grassland proportion in the landscape (500 m in radius) was also obtained from the same maps for each site, as a proxy for habitat connectivity (see Fig. 2c,d for cover maps). Soil pH and clay proportion at each site were calculated as the mean of 13 soil samples (taken in the same plots where plant presence or absence was recorded) up to a depth of 10 cm, in accordance with plant rooting depth (see Fig. 1). Soil depth and grazing (presence of excrements) were also the mean of 13 measures per site. Grazing was assessed as absent (0), only one group of excrements (1) or more than one group (2) at each of the measure points, and taken as numeric.

Statistical analyses

To identify the existence of an extinction debt for *Aphyllanthes monspeliensis* after more than 50 years of land-use change, we related the present frequency of the species at each site with current and historical grassland connectivity in a linear model, including also potential confounding environmental factors (soil characteristics and grazing). The relative flowering frequency of the species at each of the 19 sites was investigated in relation to grassland connectivity, soil characteristics and grazing. This analysis was conducted using a generalised linear model with binomial error with historical and current area and connectivity and site environmental characteristics as predictors, in R programming language (R Core Team 2016). Since overdispersion was found, the model was constructed again using a quasi-binomial family to overcome the overdispersion problem. Then, for each of the individual-level measures (i.e. stem number, individual size, flowers/stem and seeds/flower), a linear mixed model with current and historical grassland area and connectivity, site environmental variables and historical and current tree cover as fixed factors and site as random factor was conducted using 'lme' function in the *nlme* R package (Pinheiro *et al.* 2014). For stem number, individual size was also included as a predictor to control for it. A model selection using 'dredge' function in the *MuMIn* R package (Bartoń 2014) was performed for each of the saturated models with AICc as the rank criterion (QAICc for quasi-binomial models), and for each case the best model with all the variables being significant at P=0.05 was presented. When ranking models that include random effects, the fitting method used was maximum likelihood (ML), as comparisons between models that vary in their fixed effects are not valid when they are fitted by restricted maximum likelihood (REML) (Weiss 2005). The final models, however, were fitted by restricted maximum likelihood (REML). Finally, three sets of linear mixed models with site as random factor were constructed to relate belowground measures (rhizome branching intensity, rhizome internode length and aboveground/belowground dry weight ratio) to historical tree cover, current tree cover and tree cover change. For each set, the best significant model, ranked by AICc, was chosen. Moreover, in order to estimate the variance accounted by each model, adjusted R^2, R^2_{D,γ_P} (which behaves satisfactorily when overdispersion is present; Heinzl & Mittlböck 2003), and the adjusted likelihood-ratio based pseudo-R^2 (Magee 1990) were calculated for linear models, generalised linear models and general linear mixed models, respectively. All data used for the analyses can be found in Bagaria *et al.* (2017).

Results

The model for *Aphyllanthes monspeliensis* frequency at each site accounted for 40% of the variance ($R^2 = 0.4$). The only significant predictor for the selected model was the historical grassland cover in the landscape, which was positively correlated with plant frequency (0.66 ± 0.18; standardised coefficient ± SD) (Fig. 3a). In contrast, current grassland cover was not correlated with species frequency (Fig. 3b). Hence, sites with higher grassland proportion in the landscape 50 years ago still harbour larger populations of *Aphyllanthes monspeliensis*. As for flowering frequency, the selected model accounted for 34% of the variance (R^2_{D,γ_P} = 0.34), and it only included soil pH as significant variable, that showed a positive association with flowering frequency (0.03 ± 0.01).

The model for individual size (area) accounted for a small proportion of the variance (6%), and only included current tree cover as significant variable, with a negative effect (Table 1), besides a significant site effect (random factor). The model for stem number accounted for 64% of the variance, but it only included individual size (with positive association) and none of the environmental factors as predictors, although site was significant again. The model for flowers per stem accounted, again, for a small proportion of the variation (9%), and included current connectivity, which was negatively correlated, and soil pH, which showed a positive effect. The model for seeds per flower accounted for 21% of the variance and was positively associated with current tree cover and historical connectivity, in addition to a significant site effect (random factor).

None of the tree cover measures predicted either branching intensity or internode length of *Aphyllanthes monspeliensis* rhizomes (Table 2). Nevertheless, the aboveground/belowground biomass ratio was predicted by tree cover change (with 16% of the variance explained): plants that experienced a greater increase in tree cover show lower stem biomass in relation to rhizome biomass.

All models were checked for autocorrelation of residuals using Moran's tests, and all of them met spatial independence. For details on model results and autocorrelation tests see Appendix S1 in Supporting Information.

Discussion

Our study provides evidence of an extinction debt for the long-lived common plant *Aphyllanthes monspeliensis* in Mediterranean grasslands following more than 50 years of forest encroachment, using historical and current landscape characteristics, one of the approaches suggested by Kuussaari et al. (2009): the species frequency in the study sites is significantly and positively associated to historical grassland cover in the landscape, but not with that of current grasslands (Fig. 3a,b). Similarly, previous studies found an extinction debt for grassland specialists at the community level in these encroached Mediterranean grasslands (Guardiola *et al.* 2013; Bagaria *et al.* 2015). The main contribution of our study is the focus on how vegetative and reproductive indicators of species fitness might respond to habitat and landscape factors associated to forest encroachment. Changes in these indicators, in turn, potentially affect the species demography and the likelihood of species persistence. Thus, changes in fitness associated to forest encroachment confirm the extinction risk of remnant populations showing an extinction debt (Adriaens *et al.* 2009; Takkis *et al.* 2013).

Local habitat quality (i.e. soil pH, considering that the studied species is calcicolous) affects both the relative flowering frequency and flowers per stem of flowering individuals of *Aphyllanthes monspeliensis*. Soil pH, in turn, shows a negative correlation with forest cover in the site (r = -0.58), suggesting that forest conditions that enhance the accumulation of organic matter result in soil acidification which, in turn, negatively affects fitness of this calcicolous species. Moreover, individuals are smaller under suboptimal light conditions, as found for various grassland plants (e.g. Sibbald, Griffiths & Elston 1991; Peri et al. 2007), and they show decreased stem biomass in relation to belowground biomass, contrasting with the etiolation found in other species (Kephart & Buxton 1993). Since no change in stem density was found (stem number only depends on area), it suggests a clustered necrosis of rhizome areas, which likely lose stems but persist belowground. Moreover, rhizome architecture remains fixed even in contrasting habitat conditions, contrary to what has been found in other rhizomatous species (De Kroon & Hutchings 1995), although high plasticity between genets within a species can occur (Skálová *et al.* 1997). Tree cover and a forested landscape, however, enhance seed set (mean number of seeds per flower) and flowering respectively, probably because shadow provides a moister environment than open grassland habitat (Williams, Caldwell & Richards 1993; Payne & Norton 2011), and likely promotes flower production (Akhalkatsi & Lösch 2005) and prevents the abortion of flowers and seeds in drought conditions (Stephenson 1981; Lee & Bazzaz 1982), especially in dry years. High forest cover in the landscape might also be related with generally moist conditions responsible for high flower frequency. As for other local habitat factors, no effects of grazing or soil texture or depth were found for any of the vegetative or reproductive performance traits. Grazing differences between sites are probably small and not consistent through time, because few livestock grazing occurs nowadays. Regarding soil variables, only pH appeared as an important factor. Clay proportion presents little variation between sites (0.25 ± 0.07; mean ± SE), while soil depth shows high local variability and the site mean may not correlate to water availability for the sampled individual plants.

As for landscape effects, seed set is promoted by historical grassland connectivity, which is likely to be linked to genetic diversity in this long-lived species, since population size is still dependent on historical landscape and because genetic drift acts more slowly in plants with long generation times (Young *et al.* 1996). Thus, large population size and probably high genetic diversity would enhance reproductive fitness (Leimu *et al.* 2006; Takkis *et al.* 2013). Although positive effects of current connectivity on pollinator activity and seed set have been reported (Ghazoul 2005; Schmucki & de Blois 2009), *Aphyllanthes monspeliensis* populations in currently isolated grasslands would still benefit from maintained population size to attract pollinators (Lienert 2004; but see Adriaens et al. 2009).

In this study we show a negative impact of local habitat deterioration (i.e. increased tree cover and soil acidification) on plant vegetative performance and flowering, indicating population decay and confirming that extinction debt really occurs for *Aphyllanthes monspeliensis* after forest encroachment. Moreover, the positive historical connectivity effect on current seed set suggests that genetic diversity and entomophilous pollination are still maintained thanks to large population sizes in habitats that showed high connectivity in the past. However, forestation of the current landscape also promotes flowering, and tree cover positively influences seed set. Therefore, forest encroachment into these Mediterranean grasslands might exert contrasting effects on the demography of grassland specialists. On the one hand, connectivity loss, light competition and soil acidification threaten, respectively, seed production, vegetative performance and flowering of *Aphyllanthes monspeliensis*. On the other hand, a forested landscape and increased tree cover probably reduce summer water stress for understory plants and avoid seed and flower abortion, to some extent, in very dry years. These contrasting consequences of habitat loss and deterioration suggest that open forests might benefit plant fitness more than grasslands in the study area in a context of climate change, with increased temperature and summer drought in the Mediterranean Basin (IPCC 2014). In a recent study across Europe and North America, De Frenne *et al.* (2013) found that forest canopy closure, which promotes a cooler and moister microclimate, is responsible for the persistence of plants adapted to cooler conditions after recent global warming. In a climate change context, *Aphyllanthes monspeliensis* populations might show lowered flowering and seed production in open grasslands, and they would perform better in open forests. This is reinforced by the climatic space where the species occurs. While the climatic late-spring and summer precipitation of the study area matches the optimum for the species, the precipitation value of the sampling year for the same season falls in the percentile 1.6 of the climatic records for the species (Fig. 4a). Moreover, the precipitation in the study area for this season shows a tendency to decrease in the last 38 years, with the four lowest values found between 2005 and 2012 (Fig. 4b). Hence, if very dry years become more common, open grasslands in the study region would probably no longer be optimum habitats. However, further forest encroachment would continue decreasing both solar radiation under the tree canopy and soil pH, thus threatening even more the survival and reproduction of grassland specialists as *Aphyllanthes monspeliensis*. Moreover, habitat deterioration probably limits recruitment, since the species forms a transient seed bank germinating in the first favourable season after dispersal (Paula & Pausas 2009) and seed germination rate was found to be low in similar grasslands (Ninot, Petit & Casas 2008). Other studies previously found comparable contrasting effects of habitat deterioration on different indicators of population fitness for other clonal grassland plants. Adriaens et al. (2009) detected a positive effect of shrub cover on the number of flowers per plant, while shrub removal (and production of wood debris) favoured seed set and recruitment. Moreover, de Vere et al. (2009) found that bare soil promoted plant establishment, while flowering increased in unmanaged sites with tall vegetation.

In the case of *Aphyllanthes monspeliensis* in semi-natural Mediterranean grasslands, we suggest that extinction debt does not rely on a rescue effect, but on biological inertia, owing to the low dispersal ability promoted by relatively large (~2mm) seed size (Rico 2014) and the lack of specific dispersal mechanisms (Bagaria *et al.* 2012). In addition, the proposed rhizome necrosis would indicate slow individual decay, although assessing plant recruitment and studying landscape genetics (Holderegger *et al.* 2010) would be needed to fully disentangle the role of both mechanisms, i.e., rescue effect and biological inertia. Thus, the death of individuals as a consequence of increased light competition and the likely limited recruitment would lead to a decrease in population size, and the chance of stochastic processes threatening population persistence (environmental stochasticity, demographic stochasticity and genetic drift) would increase (Shaffer 1987). Inbreeding depression, the reduction in fitness caused by the mating of related individuals, is another threat for small populations, which negatively affects flower and seed production, seed size and seed germination potential (Lienert 2004, and references therein). However, ecological factors might be as important as inbreeding affecting fitness in the short term

(Ellstrand & Elam 1993). Thus, if isolation increases and plant density diminishes, pollinator efficiency might decrease (Rathcke & Jules 1993; Ashworth *et al.* 2004; Lienert 2004), hampering reproductive success (Aguilar *et al.* 2006; Aizen & Harder 2007). Moreover, in a fragmented landscape, colonisation of new favourable habitats that could eventually appear would be limited by the low dispersal ability of *Aphyllanthes monspeliensis*. Although regressive populations of long-lived plants may persist for a long period in unsuitable habitats (Eriksson 1996), extinction debt is expected to be slowly paid if no habitat improvement occurs.

Conservation measures to allow the long-term persistence of this and likely other grassland specialists of semi-natural Mediterranean grasslands before extinction debt is paid would need to guarantee high habitat heterogeneity, by the preservation of open forests with grassland areas. This would promote light availability and high pH in gaps, but also the preservation of moisture by open forest conditions. However, since plant abundance and seed production of *Aphyllanthes monspeliensis* are likely to decrease in the future even if no further forestation occurs because they depend on landscape properties that no longer exist, grassland connectivity should be enhanced by opening gaps in forested areas near persistent grassland habitat and managing them by means of livestock grazing, to promote restoration.

Author's Contributions

GB, JP and FR conceived the ideas and designed methodology; GB and MC collected the data on the field; MC and SM processed samples at the laboratory; GB and MC analysed the data; GB led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data accessibility

Available data deposited in the Dryad Digital Repository (Bagaria *et al.* 2017) at http://dx.doi.org/10.5061/dryad.d83md.

References

Adriaens, D., Honnay, O. & Hermy, M. (2006) No evidence of a plant extinction debt in highly fragmented calcareous grasslands in Belgium. *Biological Conservation*, **133**, 212–224.

Adriaens, D., Jacquemyn, H., Honnay, O. & Hermy, M. (2009) Conservation of remnant populations of Colchicum autumnale - The relative importance of local habitat quality and habitat fragmentation. *Acta Oecologica*, **35**, 69–82.

Aguilar, R., Ashworth, L., Galetto, L. & Aizen, M.A. (2006) Plant reproductive susceptibility to habitat fragmentation: review and synthesis through a meta-analysis. *Ecology Letters*, **9**, 968–980.

Aizen, M.A. & Harder, L.D. (2007) Expanding the limits of the pollen-limitation concept: Effects of pollen quantity and quality. *Ecology*, **88**, 271–281.

Akhalkatsi, M. & Lösch, R. (2005) Water limitation effect on seed development and germination in Trigonella coerulea (Fabaceae). *Flora - Morphology, Distribution, Functional Ecology of Plants*, **200**, 493–501.

Ashworth, L., Aguilar, R., Galetto, L. & Aizen, M.A. (2004) Why do pollination generalist and specialist plant species show similar reproductive susceptibility to habitat fragmentation? *Journal of Ecology*, **92**, 717–719.

Bagaria, G., Helm, A., Rodà, F. & Pino, J. (2015) Assessing coexisting plant extinction debt and colonization credit in a grassland-forest change gradient. *Oecologia*, **179**, 823–834.

Bagaria, G., Pino, J., Rodà, F. & Guardiola, M. (2012) Species traits weakly involved in plant responses to landscape properties in Mediterranean grasslands. *Journal of Vegetation Science*, **23**, 432–442.

Bagaria, G., Rodà, F., Clotet, M., Míguez, S. & Pino, J. (2017) Data from: Contrasting habitat and landscape effects on the fitness of a long-lived grassland plant under forest encroachment: do they provide evidence for extinction debt? *Journal of Ecology* doi:10.5061/dryad.d83md.

Bartoń, K. (2014) MuMIn: Multi-model inference. R package version 1.10.0.

Bulman, C.R., Wilson, R.J., Holt, A.R., Bravo, L.G., Early, R.I., Warren, M.S. & Thomas, C.D. (2007) Minimum viable metapopulation size, extinction debt, and the conservation of a declining species. *Ecological Applications*, **17**, 1460–1473.

Colling, G., Matthies, D. & Reckinger, C. (2002) Population structure and establishment of the threatened long-lived perennial Scorzonera humilis in relation to environment. *Journal of Applied Ecology*, **39**, 310–320.

Debussche, M., Lepart, J. & Dervieux, A. (1999) Mediterranean landscape changes: evidence from old postcards. *Global Ecology and Biogeography*, **8**, 3–15.

Ellstrand, N.C. & Elam, D.R. (1993) Population genetic consequences of small population size: implications for plant conservation. *Annual Review of Ecology, Evolution, and Systematics*, **24**, 217–242.

Eriksson, O. (1996) Regional dynamics of plants: A review of evidence for remnant, source-sink and metapopulations. *Oikos*, **77**, 248–258.

Eriksson, O., Cousins, S.A.O. & Bruun, H.H. (2002) Land-use history and fragmentation of traditionally managed grasslands in Scandinavia. *Journal of Vegetation Science*, **13**, 743–748.

Ewers, R.M. & Didham, R.K. (2006) Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews*, **81**, 117–142.

Fahrig, L. (2003) Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, **34**, 487–515.

De Frenne, P., Rodriguez-Sanchez, F., Coomes, D.A., Baeten, L., Verstraeten, G., Vellend, M., Bernhardt-Romermann, M., Brown, C.D., Brunet, J., Cornelis, J., Decocq, G.M., Dierschke, H., Eriksson, O., Gilliam, F.S., Hedl, R., Heinken, T., Hermy, M., Hommel, P., Jenkins, M.A., Kelly, D.L., Kirby, K.J., Mitchell, F.J.G., Naaf, T., Newman, M., Peterken, G., Petrik, P., Schultz, J., Sonnier, G., Van Calster, H., Waller, D.M., Walther, G.-R., White, P.S., Woods, K.D., Wulf, M., Graae, B.J. & Verheyen, K. (2013) Microclimate moderates plant responses to macroclimate warming. *Proceedings of the National Academy of Sciences*, **110**, 18561–18565.

Ghazoul, J. (2005) Pollen and seed dispersal among dispersed plants. *Biological reviews of the*

Cambridge Philosophical Society, **80**, 413–443.

Guardiola, M., Pino, J. & Rodà, F. (2013) Patch history and spatial scale modulate local plant extinction and extinction debt in habitat patches. *Diversity and Distributions*, **19**, 825–833.

Hanski, I. (1999) *Metapopulation Ecology*. Oxford University Press, Oxford, UK.

Hanski, I., Moilanen, A. & Gyllenberg, M. (1996) Minimum viable metapopulation size. *The American Naturalist*, **147**, 527–541.

Hanski, I. & Ovaskainen, O. (2002) Extinction debt at extinction threshold. *Conservation Biology*, **16**, 666–673.

Heinzl, H. & Mittlböck, M. (2003) Pseudo R-squared measures for Poisson regression models with over- or underdispersion. *Computational Statistics & Data Analysis*, **44**, 253–271.

Helm, A., Hanski, I. & Pärtel, M. (2006) Slow response of plant species richness to habitat loss and fragmentation. *Ecology Letters*, **9**, 72–77.

Helm, A., Oja, T., Saar, L., Takkis, K., Talve, T. & Partel, M. (2009) Human influence lowers plant genetic diversity in communities with extinction debt. *Journal of Ecology*, **97**, 1329–1336.

Herben, T., Münzbergová, Z., Mildén, M., Ehrlén, J., Cousins, S.A.O. & Eriksson, O. (2006) Long-term spatial dynamics of Succisa pratensis in a changing rural landscape: Linking dynamical modelling with historical maps. *Journal of Ecology*, **94**, 131–143.

Holderegger, R., Buehler, D., Gugerli, F. & Manel, S. (2010) Landscape genetics of plants. *Trends in Plant Science*, **15**, 675–683.

Honnay, O., Jacquemyn, H., Bossuyt, B. & Hermy, M. (2005) Forest fragmentation effects on patch occupancy and population viability of herbaceous plant species. *New Phytologist*, **166**, 723–736.

Hutchings, M.J., Mendoza, A. & Havers, W. (1998) Demographic properties of an outlier population of Orchis militaris L. (Orchidaceae) in England. *Botanical Journal of the Linnean Society*, **126**, 95–107.

Hylander, K. & Ehrlén, J. (2013) The mechanisms causing extinction debts. *Trends in ecology & evolution*, **28**, 341–346.

IPCC. (2014) *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (eds VR Barros, CB Field, D. Dokken, MD Mastrandrea, KJ Mach, TE Bilir, M Chatterjee, KL Ebi, YO Estrada, RC Genova, B Girma, ES Kissel, AN Levy, S MacCracken, PR Mastrandrea, and LL White). Cambridge University Press, Cambridge, UK and New York, NY, US.

Jacquemyn, H., Brys, R. & Hermy, M. (2002) Patch occupancy, population size and reproductive success of a forest herb (Primula elatior) in a fragmented landscape. *Oecologia*, **130**, 617–625.

Jacquemyn, H., Butaye, J. & Hermy, M. (2003) Influence of environmental and spatial variables on regional distribution of forest plant species in a fragmented and changing landscape. *Ecography*, **26**, 768–776.

Kephart, K.D. & Buxton, D.R. (1993) Forage quality responses of C3 and C4 perennial grasses to shade. *Crop Science*, **33**, 831.

Krauss, J., Bommarco, R., Guardiola, M., Heikkinen, R.K., Helm, A., Kuussaari, M., Lindborg, R., Öckinger, E., Pärtel, M., Pino, J., Pöyry, J., Raatikainen, K.M., Sang, A., Stefanescu, C., Teder, T., Zobel, M. & Steffan-Dewenter, I. (2010) Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. *Ecology Letters*, **13**, 597–605.

De Kroon, H. & Hutchings, M.J. (1995) Morphological plasticity in clonal plants - the foraging concept reconsidered. *Journal of Ecology*, **83**, 143–152.

Kuussaari, M., Bommarco, R., Heikkinen, R.K., Helm, A., Krauss, J., Lindborg, R., Öckinger, E., Pärtel, M., Pino, J., Rodà, F., Stefanescu, C., Teder, T., Zobel, M. & Steffan-Dewenter, I. (2009) Extinction debt: a challenge for biodiversity conservation. *Trends in Ecology & Evolution*, **24**, 564–571.

Lande, R. (1988) Genetics and demography in biological conservation. *Science*, **241**, 1455–1460.

Lee, T.D. & Bazzaz, F.A. (1982) Regulation of fruit and seed production in an annual legume Cassia fasciculata. *Ecology*, **63**, 1363–1373.

Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., Holt, R.D., Shurin, J.B., Law, R., Tilman, D., Loreau, M. & Gonzalez, A. (2004) The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters*, **7**, 601–613.

Leimu, R., Mutikainen, P., Koricheva, J. & Fischer, M. (2006) How general are positive relationships between plant population size, fitness and genetic variation? *Journal of Ecology*, **94**, 942–952.

Lienert, J. (2004) Habitat fragmentation effects on fitness of plant populations – a review. *Journal for Nature Conservation*, **12**, 53–72.

Lindborg, R. (2007) Evaluating the distribution of plant life-history traits in relation to current and historical landscape configurations. *Journal of Ecology*, **95**, 555–564.

Lindborg, R., Helm, A., Bommarco, R., Heikkinen, R.K., Kühn, I., Pykälä, J. & Pärtel, M. (2012) Effect of habitat area and isolation on plant trait distribution in European forests and grasslands. *Ecography*, **35**, 356–363.

Magee, L. (1990) R^2 measures based on Wald and likelihood ratio joint significance tests. *The American Statistician*, **44**, 250–253.

Mehrhoff, L.A. (1989) The dynamics of declining populations of an endangered orchid, Isotoria medeoloides. *Ecology*, **70**, 783.

Mortelliti, A., Amori, G. & Boitani, L. (2010) The role of habitat quality in fragmented landscapes: a conceptual overview and prospectus for future research. *Oecologia*, **163**, 535–547.

Ninot, J.M., Petit, A. & Casas, C. (2008) On the role of soil seed bank of rich pasture communities in a fragmented submediterranean landscape. *Grasslands: ecology, management and restoration* (ed H. Schröder), pp. 109–132. Nova Science Publishers, Inc., New York, NY.

Ogaya, R., Llusià, J., Barbeta, A., Asensio, D., Liu, D., Alessio, G.A. & Peñuelas, J. (2014) Foliar CO2 in a holm oak forest subjected to 15 years of climate change simulation. *Plant Science*, **226**, 101–107.

Oostermeijer, J.G.B., Luijten, S.H., Krenova, Z. V & Den Nijs, H.C.M. (1998) Relationships between population and habitat characteristics and reproduction of the rare Gentiana pneumonanthe L. *Conservation Biology*, **12**, 1042–1053.

Oostermeijer, J.G.B., Van't Veer, R. & Den Nijs, J.C.M. (1994) Population structure of the rare, long-lived perennial Gentiana pneumonanthe in relation to vegetation and management in the Netherlands. *Journal of Applied Ecology*, **31**, 428–438.

Ouborg, N.J., Vergeer, P. & Mix, C. (2006) The rough edges of the conservation genetics paradigm for plants. *Journal of Ecology*, **94**, 1233–1248.

Paula, S. & Pausas, J.G. (2009) BROT: a plant trait database for Mediterranean Basin species. Version 2009.01.

Payne, T. & Norton, D. (2011) Influence of shade on soil and foliage water in a depleted short tussock grassland, Mackenzie Basin. *New Zealand Natural Sciences*, **36**, 21–31.

Peri, P.L., Lucas, R.J. & Moot, D.J. (2007) Dry matter production, morphology and nutritive value of Dactylis glomerata growing under different light regimes. *Agroforestry Systems*, **70**, 63–79.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core Team. (2014) nlme: Linear and nonlinear mixed effects models. R package version 3.1-117.

R Core Team. (2016) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, AT.

Rathcke, B.J. & Jules, E.S. (1993) Habitat fragmentation and plant-pollinator interactions. *Current Science*, **65**, 273–277.

Rico, E. (2014) Aphyllanthes L. *Flora iberica 20* (eds S. Talavera, C. Andrés, M. Arista, M.P. Fernández-Piedra, E. Rico, M.B. Crespo, A. Quintanar, A. Herrero & C. Aedo), pp. 217–219. Real Jardín Botánico, CSIC, Madrid, ES.

Saar, L., Takkis, K., Pärtel, M. & Helm, A. (2012) Which plant traits predict species loss in calcareous grasslands with extinction debt? *Diversity and Distributions*, **18**, 808–817.

Schleuning, M., Niggemann, M., Becker, U. & Matthies, D. (2009) Negative effects of habitat degradation and fragmentation on the declining grassland plant Trifolium montanum. *Basic and Applied Ecology*, **10**, 61–69.

Schmucki, R. & de Blois, S. (2009) Pollination and reproduction of a self-incompatible forest herb in hedgerow corridors and forest patches. *Oecologia*, **160**, 721–733.

Shaffer, M. (1987) Minimum viable populations: coping with uncertainty. *Viable Populations for Conservation* (ed M.E. Soulé), pp. 69–86. Cambridge University Press, Cambridge, UK.

Sibbald, A.R., Griffiths, J.H. & Elston, D.A. (1991) The effects of the presence of widely spaced conifers on under-storey herbage production in the U.K. *Forest Ecology and Management*, **45**, 71–77.

Skálová, H., Pecháčková, S., Suzuki, J., Herben, T., Hara, T., Hadincová, V. & Krahulec, F. (1997) Within population genetic differentiation in traits affecting clonal growth: Festuca rubra in a mountain grassland. *Journal of Evolutionary Biology*, **10**, 383–406.

Slade, A.J. & Hutchings, M.J. (1987) The effects of light intensity on foraging in the clonal herb Glechoma hederacea. *Journal of Ecology*, **75**, 639–650.

Stephenson, A.G. (1981) Flower and fruit abortion: proximate causes and ultimate functions. *Annual Review of Ecology and Systematics*, **12**, 253–279.

Stockwell, C.A., Hendry, A.P. & Kinnison, M.T. (2003) Contemporary evolution meets conservation biology. *Trends in Ecology & Evolution*, **18**, 94–101.

Summerfield, R.J. (1972) Biological inertia - An example. *Journal of Ecology*, **60**, 793–798.

Sutherland, W. & Stillman, R. (1988) The foraging tactics of plants. *Oikos*, **52**, 239–244.

Takkis, K., Pärtel, M., Saar, L. & Helm, A. (2013) Extinction debt in a common grassland species: immediate and delayed responses of plant and population fitness. *Plant Ecology*, **214**, 953–963.

Thrall, P.H., Burdon, J.J. & Murray, B.R. (2000) The metapopulation paradigm: a fragmented view of conservation biology. *Genetics, demography and viability of fragmented populations* (eds A.G. Young & G.M. Clarke), pp. 75–96. Cambridge University Press, Cambridge, UK.

Tilman, D., May, R., Lehman, C.L. & Nowak, M.A. (1994) Habitat destruction and the extinction debt. *Nature*, **371**, 65–66.

Vellend, M., Verheyen, K., Jacquemyn, H., Kolb, A., Van Calster, H., Peterken, G. & Hermy, M. (2006) Extinction debt of forest plants persists for more than a century following habitat fragmentation. *Ecology*, **87**, 542–548.

de Vere, N., Jongejans, E., Plowman, A. & Williams, E. (2009) Population size and habitat quality affect genetic diversity and fitness in the clonal herb Cirsium dissectum. *Oecologia*, **159**, 59–68.

Weiss, R.E. (2005) *Modeling Longitudinal Data*. Springer, New York, NY, US.

Williams, K., Caldwell, M.M. & Richards, J.H. (1993) The influence of shade and clouds on soil water potential: The buffered behavior of hydraulic lift. *Plant and Soil*, **157**, 83–95.

Young, A., Boyle, T. & Brown, T. (1996) The population genetic consequences of habitat fragmentation for plants. *Trends in Ecology & Evolution*, **11**, 413–418.

Supporting Information

Details of electronic Supporting Information are provided below.

Appendix S1. Additional information on model results.

Tables

Table 1. General linear mixed models (LMMs) for size, stem number, flowers/stem and seed set (seeds/flower) at individual level and site as random factor. Standardised coefficients and their standard error for all the selected variables and total adjusted likelihood-ratio based pseudo-R^2 of the model are presented.

	Size (area) (n=329)	Stem number (n=329)	Flowers/stem (n=329)	Seeds/flower (n=320)
Historical tree cover				
Current tree cover	-0.19±0.07			0.15±0.07
Proportion of historical grassland in the landscape				0.31±0.11
Proportion of current grassland in the landscape			-0.25±0.07	
Soil depth				
Soil pH			0.17±0.07	
Clay proportion				
Grazing				
Individual size[1]	-	0.75±0.03	-	-
Total pseudo-R^2	0.06	0.64	0.09	0.21

[1] Only tested for stem number, to control for area.

Table 2. General linear mixed models (LMMs) for aboveground/belowgroud biomass ratio, branching intensity and internode length at individual level and site as random factor. Standardised coefficients and their standard error for all the selected variables and total adjusted likelihood-ratio based pseudo-R^2 of the model are presented.

	Aboveground/belowground biomass ratio (n=30)	Branching intensity (n=30)	Internode length (n=30)
Current tree cover			
Tree cover change	-0.37±0.18		
Total pseudo-R^2	0.16	0	0

Figures

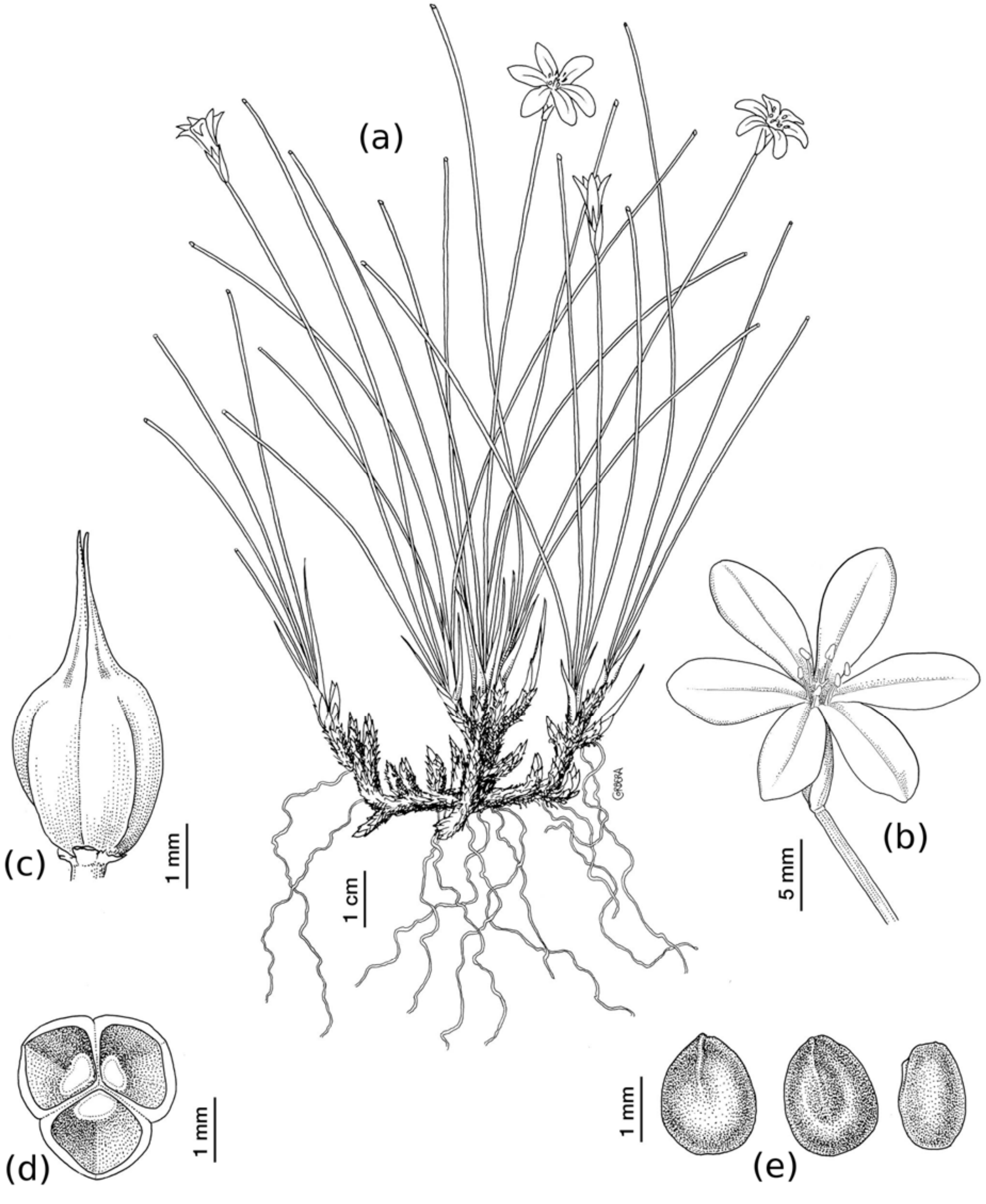

Fig. 1. *Aphyllanthes monspeliensis* morphology; a) part of an individual, showing junciform stems arising in groups from its horizontal, branched rhizome; b) flower; c) capsule; d) cross-section of a capsule, showing its three locules; e) seeds.

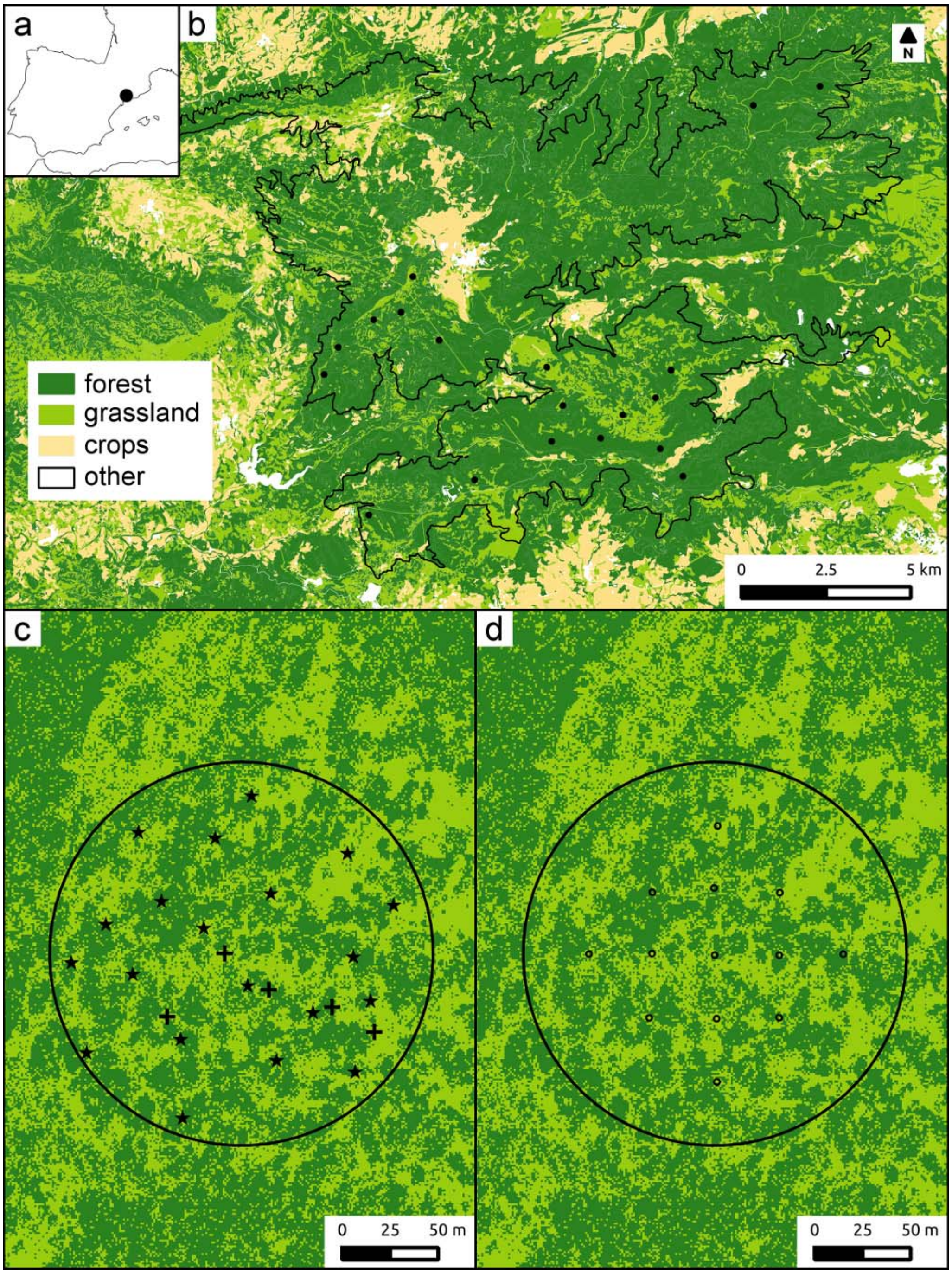

Fig. 2. Map of the study sites and sampling methodology; a) study area location in the Iberian Peninsula; b) distribution of the 19 sites in the Prades Mountains (contour line 800 m) over the 2009 land-cover map; c) location of the 20 individuals sampled for vegetative and reproductive plant performance (stars), and the 5 individuals collected for belowground measurements (crosses), within a site; d) location of the 13 plots of 3 m of diameter in a regular grid within a site, where *Aphyllanthes monspeliensis* frequency was assessed.

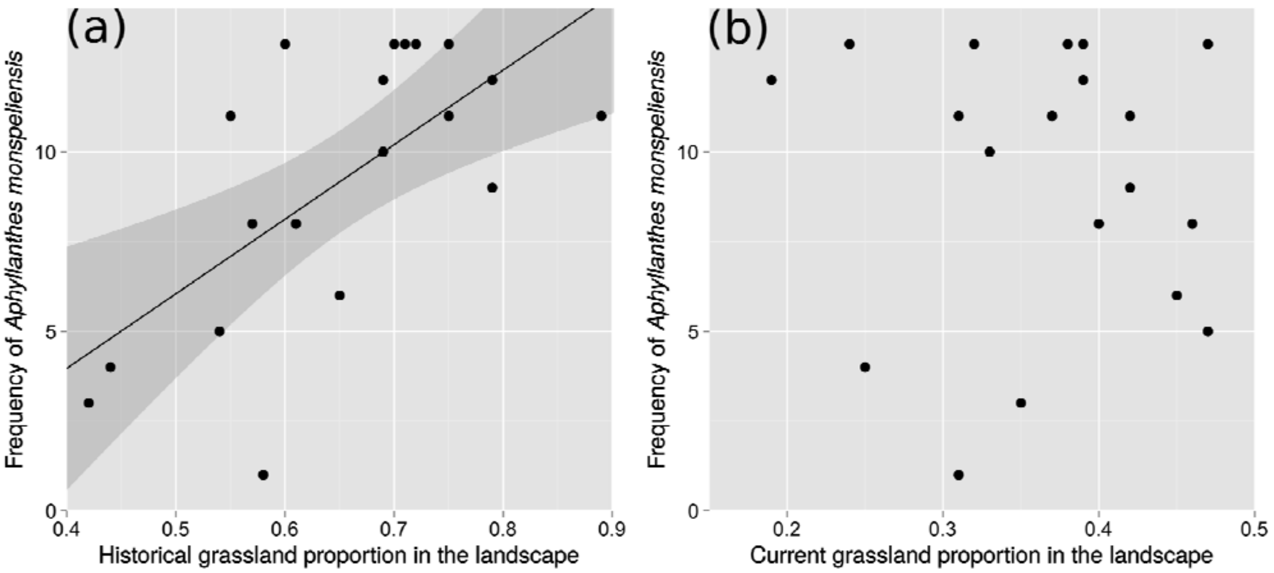

Fig. 3. Relationship between *Aphyllanthes monspeliensis* frequency at each of the 19 sites and historical (a) and current (b) grassland connectivity. Historical connectivity explains 40% of the variance in current plant frequency, while current connectivity shows no relationship with it. Regression line and confidence intervals at 95% are shown for the significant model.

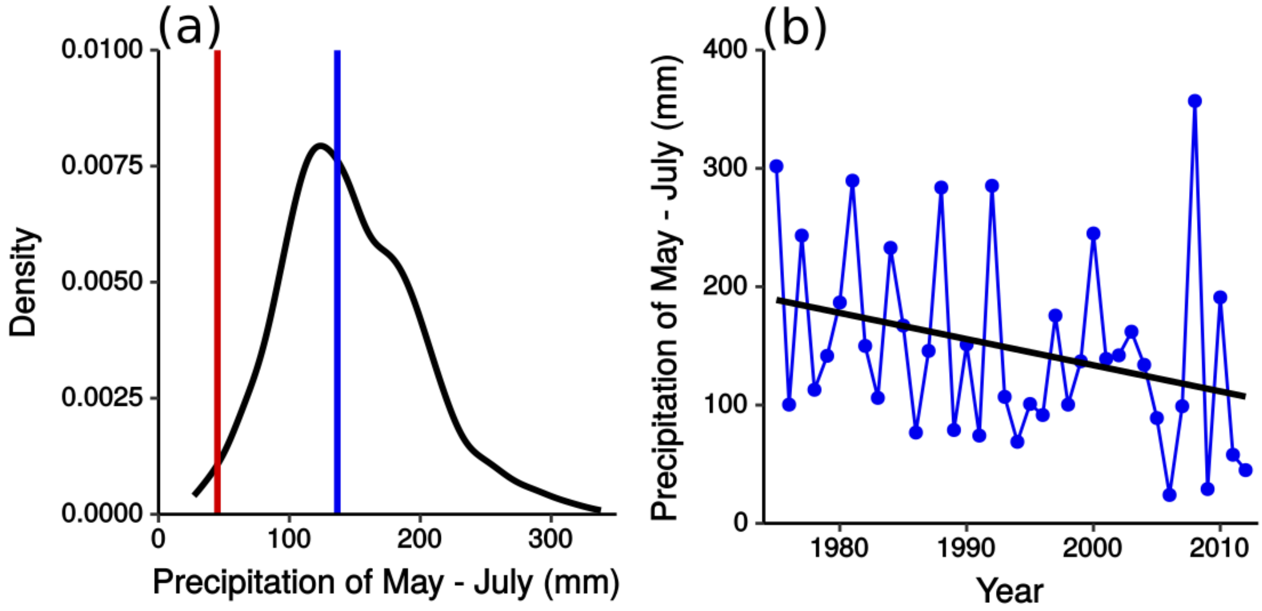

Fig. 4. (a) Climatic (blue line; 136.6 mm) and sampling year's (red line; 45 mm) late-spring and summer precipitation values on the species climatic precipitation density plot for the same season. The climatic density plot for the species was obtained extracting the WorldClim (www.worldclim.org) values of the GBIF (www.gbif.org) locations of *Aphyllanthes monspeliensis*, after reducing the density of the records to a maximum of a point every 7.5 km approximately. (b) Late-spring and summer precipitation (May - July) at the study area between 1975 and 2012. The black regression line shows a tendency to precipitation decrease over the last 38 years, with the lowest four values within the last eight years.