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Reductions in connectivity and habitat quality drive local extinctions in a plant diversity hotspot

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Abstract

It is well documented that habitat loss is a major cause of biodiversity decline. However, the roles of the different aspects of habitat loss in local extinctions are less understood. Anthropogenic destruction of an area of habitat causes *immediate* local extinction but subsequently three additional gradual drivers influence the likelihood of *delayed* extinction: decreased habitat patch size, lower connectivity and habitat deterioration. We investigated the role of these drivers in local extinctions of 82 declining species in a UK biodiversity hotspot. We combined a unique set of ≈ 7000 vegetation surveys and habitat maps from the 1930s with contemporary species' occurrences. We extrapolated from these surveys to the whole 2500-km² study area using habitat suitability surfaces. The strengths of drivers in explaining local extinctions over this 70 year period were determined by contrasting connectivity, patch size and habitat quality loss for locations at which a species went extinct and those with persisting occurrences. Species' occurrences declined on average by 60%, with half of local extinctions attributable to immediate habitat loss and half to the gradual processes causing delayed extinctions. On average, locations where a species persisted had a 73% higher contemporary connectivity than those suffering extinctions, but showed no differences in historical connectivity. Furthermore, locations with extinctions experienced a 37% greater decline in suitability associated with changes in habitat type. The strength of the drivers and the proportion of extinctions depended on the species' habitat specialism, but were affected only minimally by life-history characteristics. In conclusion, we identified a hierarchy of drivers influencing local extinction: with connectivity loss being the strongest, suitability change being moderately important, but changes in habitat patch size having only weak effects. We suggest conservation efforts could be most effective by strengthening connectivity along with reducing habitat deterioration, which would benefit a wide range of species.

Introduction

While it is well documented that habitat loss is a major cause of biodiversity declines in terrestrial ecosystems (Sala et al. 2000, Staddon et al. 2010), the roles of the different aspects of habitat loss in individual population extinctions are not well understood (Fahrig 2003, Dornier and Cheptou 2012). Destruction of an area of habitat causes *immediate* local extinction (Honnay et al. 2005), but there are three additional, interacting drivers that can act gradually over time to influence the likelihood of *delayed* local extinction: habitat shrinkage, lower connectivity and habitat deterioration (inferred from Fahrig 2003, Ewers and Didham 2006, Ibáñez et al. 2014). Empirical studies of the processes governing population extinctions are imperative to inform successful mitigation strategies against biodiversity loss (Pereira et al. 2010). The goal of this paper is to investigate the contributions of these individual drivers to local extinctions, using a large set of declining plant species in a well-studied UK biodiversity hotspot.

Partial habitat loss leads to diminished size of the remaining habitat patches. Both meta-population theory and many empirical studies suggest that plant populations in smaller habitats have a higher likelihood of local extinction (Fahrig 2003, Lindborg et al. 2012). Smaller patch sizes force populations to become smaller, making them more prone to genetic deterioration. Such populations are more prone to disappear through environmental and demographic stochasticity (Keller and Waller 2002, Leimu et al. 2006).

Increasing isolation by distance among plant populations – i.e., decreased connectivity – affects the potential for gene flow. As long as smaller populations are connected by flow of seeds and pollen, they may be able to maintain adaptive variation over multiple populations, which provides “genetic rescue” against fitness loss and extinction risk (Richards 2000, Keller and Waller 2002). Immigration from connected populations can also have a rescue effect by supplementing local recruitment (Brown and Kodric-Brown 1977, Ibáñez et al. 2014).

The habitat patches that remain may have reduced environmental quality for resident species (Brys et al. 2005), either directly due to processes such as agricultural intensification (Hodgson et al. 2005) or indirectly due to increased edge effects from the surrounding converted landscape (Ewers and Didham 2006). For example, changes in the plant communities of extant heathland, woodland, grassland and hedgerow patches in our study area can be related to changed local management (Keith et al. 2009,

Newton et al. 2012, Diaz et al. 2013, Staley *et al* 2013). We will refer to this process affecting species occurrences as suitability loss or habitat deterioration.

Despite the substantial body of research into individual drivers, the relative importance of each driver has not been studied in relation to local extinctions – i.e., at the scale of individual occurrences– across multiple species within a landscape. A pre-requisite for such an analysis is the availability of both historical and contemporary data describing species' occurrences as well as the landscape matrix (Kuussaari et al. 2009). Historical data are an important element in studying drivers of extinction: firstly to provide information on actual historical occurrences; and secondly because extinctions cannot be inferred directly from habitat loss data. Since population decline can be a gradual process (Keller and Waller 2002, Leimu et al. 2006), there may be a time-lag in local species' losses. Indeed, carry-over signals from historic landscapes may still be detectable, sometimes for up to 100 years (Cousins 2009, Kuussaari et al. 2009). Unfortunately, most studies by necessity lack certain historical data, such as those describing species' actual occurrences or landscape characteristics. For this study, we were able to access detailed species' occurrence data for two periods, 70 years apart. To estimate the spatial pattern of, and thus connectivity among, historical species' occurrences using historical vegetation surveys we developed a Monte-Carlo simulation framework, which extrapolated from a partial landscape coverage to the whole study area. We combined these with habitat maps of this ≈ 2500 km² area covering the same period (Hooftman and Bullock 2012, Jiang et al. 2013). These data and the framework allowed us to study both historical and contemporary drivers of local extinctions, going beyond most studies to extinctions that do not include a full matrix of historical and contemporary landscape and species occurrences (Kuussaari et al. 2009).

We studied local extinction drivers for 82 plant species, which are of regional or wider conservation concern and have undergone declines in the region. By studying numerous species we were able to assess how plants differ in their sensitivities to the different drivers of habitat loss. The ability of a species to persist in habitats of decreasing size or quality or to disperse among patches is often seen as being related to life-history traits and other characteristics (Saar et al. 2012). For example, perenniality, clonal growth and survival in the seed bank may affect the ability of plant populations to persist at a given location (Honnay and Bossuyt 2005, Lindborg et al. 2012), and the type of pollen and seed vectors may affect the ability to disperse among habitat patches and so the response to reduced connectivity (Tamme et al.

2014). Furthermore, because habitat types in this landscape –e.g., woodland vs. calcareous grassland– differ in patterns of loss and community change over time (Keith et al. 2011, Hooftman and Bullock 2012, Newton et al. 2012), one might also expect extinction processes to be affected by a species’ habitat preference.

In this paper we address these issues by asking the following questions concerning local species’ extinctions:

1. What proportions of species’ extinctions occurred immediately due to habitat destruction compared to gradual extinction processes?
2. Which is the most important driver of delayed extinctions for each species: connectivity loss, decreased patch size or habitat deterioration?
3. Are extinction patterns related only to the contemporary landscape configuration or is there a detectable signal from the past landscape?
4. Do extinction rates and the relative importance of extinction drivers differ among species according to habitat specialism and characteristics related to persistence and dispersal ability?

Methods and materials

Study area, species and land use maps

We studied the county of Dorset on the south coast of England, encompassing 2,422 km². Dorset is a UK plant diversity hotspot (Preston et al. 2002), and is also representative of many Western European landscapes, as it originally contained extensive semi-natural habitats, such as calcareous grasslands and heathlands. Much of these habitats were converted during the 20th century to arable land, underwent agricultural improvement to intensive grassland, were built upon, etc. (Hooftman and Bullock 2012, Newton et al. 2012, Diaz et al. 2013). Extended descriptions of the semi-natural habitats in Dorset and the changes between the 1930s and 2000 are given in Hooftman and Bullock (2012).

We focused on local extinctions of 82 plant species of regional conservation interest, which are all species known to have undergone declines over the last few decades. To ensure statistical power, we analysed only species that were present in at least 30 historical vegetation surveys (see below and Supplementary material Appendix 1) and are known from at least 30 contemporary occurrences. This criterion excluded the rarest species, and the selected species comprise mostly ‘Dorset Notable’ species of moderate

conservation concern (Dorset Wildlife Trust 2011), but also 12 rare or scarce species listed in the Dorset Rare Plants Register (Edwards and Pearman 2004). A list of the selected species, their habitat preferences and life history characteristics is provided as Supplementary material (Appendix 2, Table A1).

Historical species' occurrences were taken from systematic vegetation surveys that were carried out in Dorset in the 1930s at over 7,500 sites (Good 1948, Supplementary material Appendix 1). The location of each survey site has been digitised, rectified and vectorised by the Dorset Environmental Records Centre (DERC). An electronic version of this database, with over 285,000 entries, is kept by DERC (<www.derc.org.uk/projects/good.htm>). For this paper, we used 6,998 of these surveys; which gave us complete spatial overlap between historical data, contemporary data and all GIS layers. Most of the coastal areas were not fully covered by the BioClim data (see below): as a consequence coastal habitats and coastal specialist species are not considered in this study. These vegetation surveys cover 177 km², 7.2% of the study area. A small number of these historical surveys have been repeated in recent years to assess community changes in woodlands (Keith et al. 2009, 2011), calcareous grasslands (Newton et al. 2012), hedgerows (Staley et al. 2013), and heathlands (Diaz et al. 2014). This historical survey data-set was complemented with habitat maps from the same period, at a 25 x 25 m scale, taken from Hooftman and Bullock (2012).

Contemporary data on species' occurrences were derived from the DERC data-base of plant distributions (see Bowen 2000) over the period 1985-2009, which has coordinates describing occurrences at a 100 x 100 metre resolution. For these species of conservation interest, all contemporary occurrences are thought to be known in this floristically well documented area. Contemporary habitat data were based on the UK land cover map for 2000 at a 25 x 25 metre scale (Hooftman and Bullock 2012).

Both historical and contemporary species' occurrences were converted into 1-ha gridcells using ArcGIS 10.1. The polygons with historical data were converted to gridded occurrences when a gridcell overlapped more than 50% with the polygon that contained the target species. Contemporary occurrence point locations were gridded. The habitats, certainly in the 1930s, would have been more heterogeneous than suggested by our habitat map. It is thus very likely that habitat patches would have contained multiple

distinct occurrences rather than one continuous population. For this reason we analysed our data on a *per* gridcell basis (“occurrence”) and did not join neighbouring occurrences.

Statistical framework

The main aims of the analysis were to investigate: i) the proportion of occurrences lost (i.e. extinctions) to *immediate* habitat destruction; and ii) for those extinctions in surviving habitat patches, the strengths of the three putative drivers of *delayed* local extinctions, through estimating the marginal differences between extinct and persisting occurrences for these drivers. Our rationale is that this difference is directly related to the strength of the driver, in which “marginal” indicates that the driver’s strength has been corrected with the variation explained by the other two drivers.

Our calculation included estimation of the locations of historical occurrences by extrapolating from the historical data-set. Such extrapolation was necessary since the historical survey only partially covered the region. Calculation of historical connectivity and the potential connectivity of extinct occurrences requires information on all past occurrences. The Good (1948) data-set was collected using a sampling design intended to represent species’ distributions across Dorset but the data-set does not necessarily represent the density of individual species occurrences within the region. To reconstruct and analyse complete distributions of occurrences we developed a 6-step statistical framework using the data of Good (1948). This spatial, Monte-Carlo simulation-based framework is depicted in Figure 1 and uses probability scores to generate multiple, independent maps of species’ occurrences. Because this procedure is probabilistic, no single simulation generates a true distribution of occurrences across the landscape. Therefore, we run many simulations, and these multiple simulations give a good spatial representation of probable occurrences.

Step 1: Using the known occurrences of species to calculate suitability layers

The first step was to use the survey data to create habitat suitability maps for each species for both the 1930s and the contemporary landscapes. This was done with the MaxEnt v3.3.3 software (Phillips et al. 2006), which is a widely-used approach to species distribution modelling based on Bayesian maximum entropy estimation (Harte and Newman 2014). The important assumption we made is that habitat suitability maps are a suitable proxy for the likelihood of identifying species’ occurrences, with an

identical surveyor sampling bias in the extrapolated area. Sampling biases are important considerations in species distribution modelling (Phillips et al. 2009). Here, the historical surveys were all done by a single trained observer, making potential underestimates or errors in identifying species' occurrences identical across the whole data-set. We provide full details of the data layers and techniques in the Supplementary Materials (Appendix 3); below we provide a summary.

We used a set of twelve standard environmental data layers to describe the niche of each species (Engler et al. 2004, Philips et al. 2006).

- (i) Historical and contemporary habitat types from Hooftman and Bullock (2012)
- (ii-v) Soil characteristics derived from the 1:250,000 vector-based National Soil Map of England, i.e., soil pH; the soil drainage capacity; texture and fertility (www.landis.org.uk/downloads/downloads/soil_classification.pdf).
- (vi-vii) Historical and contemporary average minimum and maximum rainfall, based on a Voronoi interpolation of UK Met Office rain gauge data for Dorset (www.ceh.ac.uk/data/nrfa/data/monthly_catchment.html).
- (vii-viii) The average monthly maximum and minimum temperatures using the BioClim data-base (www.worldclim.org/bioclim).
- (x-xii) Terrain characteristics derived from a 50 x 50 m Digital Elevation Map (Morris and Flavin 1990; www.ceh.ac.uk/products/integrated-hydrological-digital-terrain-model.html). We used ArcGIS 10.1 to estimate the average slope, aspect and total solar influx for each gridcell.

All layers were translated into 1-ha gridcells in ArcGIS 10.1, either by using the most frequent value when up-scaling (e.g., from the 25 x 25 m land-use maps) or by splitting into gridcells with identical values when down-scaling (e.g., from the 1-km² climate maps). Model selection among the twelve layers was done with a manual backward elimination approach, maximising the model training gain whilst minimising the layers included (details in Supplementary material Appendix 3). Training gain was estimated based on a split sample approach using a randomly selected set of 70% of the data points for model training, with the remaining 30% as test data. Note that model gain is inversely related to deviance as used in generalized additive and generalized linear models (Phillips et al. 2006). Subsequently, the selected model for each species was run with 25 replicates. Area Under the Curve (AUC) results were averaged and *per* gridcell suitability scores were cross-validated among runs. We elevated the number of background points to 100,000. We had no reason to deviate from other default parameter settings such as

the regulation multiplier (=1), maximum iterations (500) and convergence threshold (0.0001). Suitability maps for contemporary conditions were created by projecting the 1930s species' niche over the respective layers for 2000, in which the land-use and rainfall layers were different between the periods.

We report on the results of the habitat suitability mapping in Supplementary material (Appendix 2, Table A2). The AUC statistic represents the probability that a randomly chosen occurrence site will be ranked above a randomly chosen absence site (Elith 2002). The models for 61 species had $AUC > 0.85$, and all except 2 species had $AUC > 0.75$ (*Cirsium acaule* and *Plantago media*, with $AUC > 0.72$).

Step 2: Generating species' occurrences in the 1930s

We used the suitability maps to generate maps of probable species occurrences. To provide a spatial average which took account of variation among realisations of occurrences from a probability surface, we conducted 5000 independent simulations *per* species, i.e., creating thousands of realisations of maps of probable occurrences. This process was set up as a Monte-Carlo (MC) simulation loop. Median parameter values and significance levels were calculated over all simulations. The MC algorithm was written in Matlab v7.8.0.739, see Supplementary material (Appendix 4).

In generating a probable occurrence in a simulation we took three factors into account: the suitability of a gridcell according to the MaxEnt calculations, the presence/absence ratio of species in landscape and the potential autocorrelation among occurrences.

The presence/absence ratio used known presences and absences in the 1930s vegetation surveys to correct for the fact that not all suitable habitats will be occupied in a landscape at a point in time.

Presence/absence ratios were derived from a linear regression between historical occurrences in the Good data-set (1948) and habitat suitability (see step 1) and was defined as the expected presence/absence ratio at suitability = 100% (Supplementary material Appendix 2, Table A3). Given that a habitat patch close to an occupied patch may be more likely to be occupied itself than is one that is further away (Pocock et al. 2006, Dormann et al. 2007), we allowed for possible autocorrelation between occurrences (Supplementary material Appendix 5). Based on these three factors we calculated the likelihood of species occurrence ($P_{occurrence}$):

$$P_{occurrence} = suitability \times \langle presence/absence \text{ ratio} \rangle \times \text{habitat autocorrelation.} \quad \text{Eq. 1}$$

In each simulation and for each of the 241,740 gridcells independently, $P_{occurrence}$ was compared to a random draw between 0-1 from a uniform distribution; a draw lower than $P_{occurrence}$ resulted in a species' "occurrence" for that gridcell. For example, a gridcell with an 80% suitability, an overall 20% species' presence/absence ratio and an above average habitat autocorrelation (e.g., 125%) has a $P_{occurrence}$ of 0.20 (0.8 x 0.2 x 1.25). This would translate as 20 expected occurrences per 100 simulation runs for that specific gridcell. To avoid highly unlikely species' occurrences, we set a minimum threshold for occurrences at 50% suitability. In the Supplementary material (Appendix 5 and 6) we show that excluding the autocorrelation correction and altering the suitability threshold would not alter our general findings.

Step 3. Compare 1930's occurrences to contemporary occurrences

Generated occurrences in the 1930s *per* simulation were compared to contemporary occurrences. "Persisting" occurrences were defined as having a contemporary occurrence within two gridcells of the location of the simulated historical occurrence. This buffer allows for a 200 metres mapping noise and location error among data-sets. All other 1930s occurrences were regarded as "extinct". Known contemporary occurrences were designated as persisting occurrences. This included contemporary occurrences in habitats deemed destroyed (see below), since these might be in field margins and other smaller land-features that would not be represented in the vegetation maps. In total an average of 22% of all contemporary occurrences per species were found in destroyed grid cells. Given that our focus is on drivers for local species' extinctions, new colonisations in historically unoccupied habitat were not investigated further. Since we used species which have shown strong declines in Dorset, we would not expect range expansions to have occurred. We explore potential colonisation events further in the Supplementary material (Appendix 7), where we show that destruction-corrected extinction rates in these sites were double those of potential new occurrences. As a consequence, presence/absence ratios in the contemporary landscape declined compared to the 1930s.

Step 4. Calculating the strength of the drivers

For each simulation, we separated *immediate* and *delayed* extinctions. *Immediate* local extinctions are considered to be caused by anthropogenic habitat destruction. Habitat destruction was defined as a

conversion of a gridcell to urban, bare ground or arable use (Supplementary material Appendix 8). Local extinctions in these habitats were considered to be immediate through physical removal of the plants and severe soil disturbance. Within surviving habitat more gradual processes could then lead to *delayed* extinctions. To reflect this temporal sequence, our analysis of the delayed extinction drivers excluded the immediate extinctions. We considered conversion to intensive grassland –35% of the 1930s area of semi-natural habitat– as resulting in a substantial suitability loss (according to the niche requirements of each species), but not in full habitat destruction since species might be able to persist and so extinctions are not immediate (e.g., Diaz et al. 2013).

For each gridcell the proportional change in suitability for the species between the two periods was calculated by dividing the contemporary by the 1930s suitability as derived using MaxEnt for every gridcell x as:

$$\text{Suitability change}_{(x)} = \frac{\text{Suitability in 2000}_{(x)}}{\text{Suitability in 1930s}_{(x)}} \quad \text{Eq. 2}$$

This suitability change used changes in the broad habitat type and rainfall patterns; these being variables for which we had data in both time periods. We estimated the patch size of each habitat fragment in 1930 and 2000 by using the maps of Hooftman and Bullock (2012) to calculate for each gridcell the number of directly connected gridcells that contained the identical broad habitat type.

We calculated the connectivity in the 1930s and 2000 according to Hanski (1994):

$$\text{Connectivity} = \sum_{x=1}^{10} \left(e^{-d_x} \right) \times n_j(x)$$

Eq. 3

with $n_j(x)$ = the number of occurrences in concentric circles at distance x ($= d_{ij}/100x$) to the source cell i with a maximum of 1 km; and d_{ij} = the distance between the centre of the source (i) and target (j) cell in metres.

To allow for interacting effects among drivers, we carried out *per* simulation, *per* species a logistic generalized linear model of the binary variable extinct/persisting per gridcell using glmfit with a binominal distribution and logit link in Matlab v7.8.0.739. We used additive main effects with their coefficients denoted as β_x with constant ϵ , explaining variation with a Type III sum of squares:

$$P_{extinction} = \epsilon + \beta_1 \text{suitability change} + \beta_2 \text{habitat size} + \beta_3 \text{connectivity} \quad \text{Eq. 4}$$

To identify possible signals from the historic landscape structure, this analysis was done separately using patch size and connectivity in the 1930s and in 2000. Note that the contemporary connectivity for extinct occurrences should be seen as “what would have been” connectivity to persisting occurrences.

Step 5: Calculating the effect size of the drivers

To ensure comparability among the drivers the results from Eq. 4 were used to calculate marginal medians for extinct and persisting occurrences for each of the drivers, given median values of the other two drivers. Using connectivity as an example:

$$d_{connectivity,t} = \log_{10}(E_{persisting}) - \log_{10}(E_{extinct}) \quad \text{Eq. 5}$$

with:

$$E_{extinct} = (\beta'_3 \text{connectivity}_{(extinct)}) + (\epsilon' + \beta'_1 \text{suitability change} + \beta'_2 \text{habitat size})$$

$$E_{persisting} = (\beta'_3 \text{connectivity}_{(persisting)}) + (\epsilon' + \beta'_1 \text{suitability change} + \beta'_2 \text{habitat size})$$

t is either 1930s or 2000.

The effect-size (d) is generated by taking the log response ratio of the difference (Borenstein et al. 2009) of the focal driver between extinct and persisting occurrences. The significance of the difference of a driver between extinct and persisting occurrences was calculated as the 95% percentile of the p -values of Eq. 4 over all 5000-simulations; we report the coefficients of the corresponding run (denoted above as β'_x and ϵ'). The effects of the two other drivers (i.e. suitability change and patch size in the example of Eq 5) are fixed by taking the median over all runs of all occurrences for the focal period t for both nominator and denominator, while median values for the focal driver (i.e. connectivity in the example of Eq 5) are derived separately for extinct and persisting occurrences. Effect-sizes were calculated for both time periods for all three drivers. The significance level was Bonferroni corrected with the number of species analysed ($\alpha = 0.05/82$).

As well as individual occurrence statistics we calculated the *per* species extinction rate:

$$\text{Extinction rate} = \frac{\text{average estimated \#extinct occurrences among simulations}}{\text{average estimated total \# occurrences in 1930s among simulations}}$$

Eq. 6

Step 6: Grouping species based on characteristics and habitat

We grouped species according to a number of characteristics following Fitter and Peat (1994, i-v) and Kleyer et al. (2008, vi-viii), see Supplementary material (Appendix 2, Table A1). The characteristics used were: (i) Raunkiaer life-form; (ii) dominant pollen- and (iii) seed dispersal vectors; (iv) longevity of the seed bank; (v) clonal ability; (vi) seed terminal velocity; (vii) average seed mass; (viii) average seed release height. Additionally, (ix) preferred habitat of the species was assigned using Hill et al. (2004). For continuous characteristics (vi-viii) we performed a linear regression (linearmodel.fit procedure in Matlab) against the drivers and species' extinction rates. For all other, categorical, characteristics differentiation among categories was assessed with two-sided t-tests.

Results

Extinction rates

Anthropogenic destruction, causing immediate local extinctions, accounted for a 44% decline the total area of semi-natural habitat (Supplementary material Appendix 8) and resulted in an estimated 30% median local extinction rate across all species (quartiles: 22%-52%). An occurrence was defined as a single gridcell which had a species present. However, these extinction proportions varied widely among species, from 5% for *Erica ciliaris* to 90% for *Ononis spinosa* and *Cynoglossum officinale*. Grassland specialists had higher proportions of extinctions caused by habitat destruction compared to woodland and heathland specialists (Figure 2).

Delayed extinction – extinctions not caused by habitat destruction– accounted for a median 31% loss of the estimated occurrences in the 1930s (quartiles: 14%-45%). In the following we discuss delayed extinction in terms of those not caused by habitat destruction. Exclusion of these immediate extinctions results in delayed extinction rates across the remaining 1930s occurrences with a median of 48% across all species (35%-69%). Delayed extinction rates varied among species from below 10% (*Erica ciliaris* and *Hippocrepis comosa*) to over 90% (*Littorella uniflora* and *Ranunculus hederaceus*). Rates of immediate and delayed extinction for the individual species are provided in the Supplementary materials (Appendix 2, Table A3).

Calcareous grassland specialists had lower delayed extinction rates than all other groups and non-calcareous (i.e. acid and neutral) grassland specialists had higher delayed extinction rates than all other

groups except heathland specialists (Table 1). Furthermore, species predominantly relying on self-pollination had significantly higher delayed extinction rates compared to wind and insect pollinated species (Table 1). Therophytes had higher extinction rates than the perennial hemicryptophytes and geophytes. No other differences among characteristic's groups were identified (Appendix 2, Table A4), nor did the quantitative characteristics terminal velocity, seed mass and release height explain significant variation in extinctions (all $R^2 < 0.1$, data not shown).

Drivers of delayed extinction

The median connectivity for all species decreased four-fold from 6.58 to 1.57 for locations of occurrences in the 1930s compared to the same locations in 2000, containing either surviving or extinct occurrences (quartiles: 4.9-9.5, 1.00-2.15 respectively). The habitat patch sizes for these locations also diminished greatly, from 432-ha to 5.0-ha (quartiles: 247-518 and 4.3-6.9 respectively). The habitat suitability for these locations decreased by a median of -33% across all species (quartiles: -17% and -44%). Highest suitability changes were experienced by *Succisa pratensis* (-64%), and *Ulex gallii* and *Viola canina* (-61%). Ten species experienced a positive overall suitability change, of up to +33% for *Bidens tripartita* and *B. cernua*. For a full list see Supplementary material Appendix 2 (Table A3).

Contemporary connectivity was a very strong driver of delayed extinctions (Table 1). Persisting occurrences had a 73% higher marginal contemporary connectivity compared to occurrences that went extinct (median log ratio 0.24; quartiles 0.15-0.44). For 76 of the 82 species contemporary connectivity significantly differentiated extinct and persisting occurrences (Appendix 2, Table A3). In contrast, connectivity in the 1930s was a very weak driver (Table 1), with a median 1% difference across all species between extinct and persisting occurrences (median log ratio 0.005; quartiles 4×10^{-5} -0.03). This difference between 1930's and contemporary connectivity effects was significantly different from 0 for only 21 species.

Habitat patch size was a very weak driver and did not distinguish well between extinct and persisting occurrences. Persisting occurrences had marginal medians of 2% and 1% greater habitat size for the 1930s and the contemporary period respectively (median log ratios 0.009 and 0.005; quartiles: 4×10^{-5} -0.02 and 0.002-0.02 respectively). Effect sizes were significantly different from 0 for only 16 and 8

species respectively for the 1930s and contemporary landscapes (Supplementary material Appendix 2, Table A3).

Suitability change – associated with habitat conversion and altered rainfall patterns – was a strong driver of delayed extinctions. The decrease in habitat suitability was 37% greater at locations of extinctions compared to locations of persisting occurrences (median log ratio 0.14). Effect sizes were significant for the majority of species (65). The bulk of species had log-ratios below 0.2 (\approx 58% more suitability loss for extinctions, Fig. 3) but with a long tail of up to a 10-fold difference (for *Lathyrus linifolius*).

Drivers' interactions with habitat specialism and species characteristics

The strengths of the drivers of delayed extinction differed among habitat groups (Table 1). The driver strength of contemporary connectivity ranged from relatively weak in woodland specialists – a 39% higher marginal connectivity for persisting occurrences (median log ratio 0.14) – to strong in calcareous grassland specialists (146%). Furthermore, delayed extinction rates of woodland specialists were driven more strongly by loss of habitat suitability (50 % lower suitability loss in persisting occurrences) compared to heathland and non-calcareous grassland specialists (20-30% less suitability loss). Neither connectivity in the 1930s (Table 1) nor habitat patch size (Supplementary material Appendix 2, Table A4) distinguished between extinctions and persisting occurrences in any of the habitat specialism groups.

Variation in the strength of the drivers related little to the categorisation of species according to life form, persistence and dispersal ability (Table 1; Supplementary material Appendix 2, Table A4). The only exception was a distinction according to Raunkiaer life forms showing that geophytes were more strongly driven by habitat suitability changes: a 140% greater suitability loss due to habitat type changes was associated with geophyte extinctions compared to the persisting occurrences (median log-ratio 0.38). For all the other groups suitability loss had only a 20% effect size. We found no differentiation among plant groups related to connectivity in either time period (Table 1) or habitat patch size differences (Supplementary material Appendix 2, Table A4). The quantitative characteristics terminal velocity, seed mass and release height had no significant relationship with any of the drivers (all $R^2 < 0.1$, data not shown).

Discussion

Local extinctions between the 1930s and 2000 (“contemporary”) were caused by a combination of *immediate* habitat loss through anthropogenic destruction and gradual processes leading to *delayed* local extinctions through changes in habitat suitability and the landscape structure. Both immediate and gradual processes were equally important across the 82 investigated species, with a median 30% of local extinctions caused by the former and 31% by the latter. The likelihood of delayed local extinction was strongly related to connectivity loss and decreased habitat quality.

We identified a hierarchy of drivers of delayed extinction in our large sample of declining species –with “delayed” defined as extinctions not immediately caused by habitat destruction. The effects of decreases in habitat size, connectivity and habitat quality may interact (Fahrig 2003, Dornier and Cheptou 2012) and we therefore analysed the effects of these processes by allowing for interacting additive main effects and calculating marginal medians. This hierarchy defined which drivers were most important in explaining extinctions: with connectivity loss being the strongest, suitability change being moderately important, but changes in habitat size having only weak effects. Occurrences persisting after 70 years had 73% greater contemporary connectivity compared to what would have been for those that went extinct.

Locations suffering extinctions had experienced an additional a 37% greater decline in habitat suitability, which was generally associated with grassland improvement for intensive use. Habitat deterioration could have been even more severe than detected here, since factors that are not directly related to habitat type changes or changed rainfall patterns were not included in our species’ suitability calculations due to a lack of data for the 1930s. These factors could include among-habitat or spatially varying effects of acidification, eutrophication, airborne pollutants and lowered water tables (Walker and Preston 2006), as well as conversion from broadleaved woodland to coniferous plantations (Hooftman & Bullock 2012). These findings are supported by recent re-surveys of some of the sites across the Dorset landscape. Extant habitat patches have indeed undergone community changes, which suggest decreased suitability for specialist species through eutrophication and changed management (Keith et al. 2009, Newton et al. 2012, Diaz et al. 2013, Staley et al. 2013). Furthermore, changes in beta diversity and evidence for meta-community processes (Wichmann et al. 2008, Keith et al. 2011, Newton et al. 2012) suggest large-scale spatial structuring of the communities, which support our finding of the importance of connectivity.

Surprisingly, reduced habitat patch size did not emerge as a strong driver of extinctions for these species, although other work led us to expect otherwise (Hooftman et al. 2004, Leimu et al. 2006, Dornier and Cheptou 2012). The resulting decreases in population sizes would have been substantial since semi-natural habitats patches diminished almost 100-fold in size over the study period (see also Hooftman and Bullock 2012). These size reductions would likely have decreased the viability of most populations and so elevated their overall susceptibility to extinction. Furthermore, by increasing the ratio of edge to patch area, habitat shrinkage would also have led to increased edge effects (Fahrig 2003, Ewers and Didham 2006). While we did not investigate edge effects here, such changes might have had an added role in habitat deterioration.

Shrinking patch size and resulting population decreases amplify genetic deterioration and the influence of environmental and demographic stochasticity on population fluctuations, and so increase the need for demographic and genetic rescue at the meta-population scale (Keller and Waller 2002, Dornier and Cheptou 2012). Demographic and environmental stochasticity work at different scales: the individual scale for demographic stochasticity – “random variation in the reproduction and mortality of individuals” – and the population scale for environmental stochasticity – “unpredictable variation in population growth imposed by environmental factors” (Keller & Waller 2002). However, we would need assessments of population demography and environmental variation to differentiate these mechanisms (e.g., Lande, 1993, Löfgren and Jerling 2003), which is beyond this study. We suggest that the differences in habitat size loss among individual species occurrences was not a strong predictor of extinctions in our study because pollen and/or seed flow maintained viability of the better connected ones, and allowed these to persist over 70 years, despite occurring in substantially shrunken habitat patches. The level of connectivity could have been enhanced by the existence of more temporally dynamic populations that would have acted as periodic stepping-stones forming a “regional ensemble” sensu Freckleton & Watkinson (2002). In the better connected parts of the landscape such temporally dynamic populations would have been more likely than in less connected and more modified parts of the landscape.

The strong roles of suitability and connectivity losses mean that the contemporary landscape represents the current potential for species’ occurrences. The limited strengths of these 1930s drivers –1-2%

difference between extinct and persisting species occurrences– suggests there are few carry-over effects from the historical landscape. Much stronger historical carry-over effects have been found for several other rural areas such as in Sweden (e.g., Lindborg and Eriksson 2004, Cousins and Vanhoenacker 2011), Belgium (Piqueray et al. 2011) and the UK (McGovern et al. 2011), and in these cases it has been concluded that persisting populations may be doomed to extinction. In Dorset the signal from the past landscape may be weak because of low variation in the drivers at that time, and subsequently the connectivity and habitat suitability drivers acted on extinctions at a quicker pace than the 70-years between the time points of our study.

Species' characteristics and drivers of local extinction

In line with studies showing correlations between species' characteristics and extinction rates (Piqueray et al. 2011, Lindborg et al. 2012, Saar et al. 2012), delayed extinction rates in our study were higher for short-life cycle species, such as therophytes. Short-lived species will be more at risk through demographic stochasticity and so would likely exhibit a more rapid loss of genetic variation after isolation (Leimu et al. 2006). Local extinction rates were also higher for self-pollinated species, as was also found by Saar et al. (2012). However, earlier meta-analyses have suggested that species with a high level of self-compatibility are less sensitive to fragmentation (Honnay et al. 2005, Aguilar et al. 2006). The interaction between pollination mode and extinction risk therefore remains debatable. Immediate extinctions caused by anthropogenic habitat destruction cannot be driven by species characteristics, but reflect the different levels of destruction among habitat types.

In contrast, with a few exceptions we did not find the expected variation in the roles of the gradual drivers of extinction according to species' characteristics. This suggests that species' life history characteristics are less critical in differentiating the drivers of local extinction than in determining overall extinction rates as described above. This is probably because the landscape changes were so profound that all species responded similarly to the major drivers. Indeed, a recent meta-analysis found little difference among species functional groups in their responses to habitat fragmentation (Ibáñez et al. 2014). One exception to this lack of differentiation was that species with underground survival structures (geophytes) were more sensitive to loss of habitat suitability. This might be explained by such species having low

competitive ability against the species that come to dominate as habitats become more eutrophic (Sala et al. 2007).

Habitat specialism and drivers of local extinction

The strength of the drivers differed among species according to their habitat specialisms. Calcareous grassland species were most sensitive to connectivity loss, but their delayed extinction rates were lower than the other species whilst immediate local losses were higher, reflecting the higher conversion rate of grasslands (Hooftman and Bullock 2012). Woodland specialists showed lowest loss of habitat and lowest sensitivity to decreased connectivity, but highest sensitivity to suitability change. The habitat types differed in area lost and in changes to patch size and connectivity (Hooftman and Bullock 2012), which suggests differences in spatial patterns of habitat change. This variation will have been caused by the initial distributions of habitats in the 1930s and in the patterns of anthropogenic habitat destruction, for example through targeting of sites more suitable for agriculture or which were less remote (Reitalu et al. 2010). These differences among species according to habitat specialism, but not according to species life history, dispersal and persistence characteristics, suggest that the idiosyncratic patterns of habitat change dominate in determining patterns of extinction and thus the major drivers of local species' losses. This raises the possibility that conservation activities aimed at reversing loss of habitat area, connectivity, etc. might do so based on habitat types without having to consider the detailed life history differences among specialist species that are usually incorporated into modelling strategies (e.g., Moilanen et al. 2005, Ball et al. 2009). In this case, actions to maintain and increase connectivity should benefit all species.

Constraints

Our historical data-set and the analysis it allows is unique but at the same time has its constraints. The historical land use maps have been validated with the vegetation surveys (Hooftman and Bullock 2012), but we extrapolated from a 7.2% spatial coverage of these vegetation surveys to produce species distributions over the whole landscape. This analytical framework was necessary to allow us to estimate patterns of extinctions and connectivity among the historical species' occurrences. However, we have confidence in the derived data. The MaxEnt niche models gave a good fit to the historical data. Furthermore, we examined a large number of Monte Carlo derived independent realisation maps of probable occurrences, which incorporated presence/absence rates and spatial autocorrelation. We also

explored sensitivity of our statistical models to assumptions about spatial autocorrelation and criteria for assigning species to locations. We found that altering these assumptions had little influence on our conclusions (Supplementary material Appendices 6-8).

The habitats, certainly in the 1930s, would surely have been more heterogeneous than suggested by our habitat maps, despite the fact that these were detailed. It is thus very likely that habitat patches would have contained multiple distinct occurrences rather than one continuous population. For these reasons we analysed our data on a *per* gridcell basis (“occurrence”) and did not lump neighbouring occurrences into assumed populations. Note that these grid cells were 1-ha in size and so lumping would have assumed very extensive populations of these uncommon species. We note as well that our analyses controlled for autocorrelation and so addressed the implicit assumption that these *per* gridcell occurrences were independent.

Conclusions

We calculated that landscape changes associated largely with agricultural intensification caused an average over 60% of occurrences of 82 vascular plant species of conservation concern in Dorset to be lost between the 1930s and the contemporary period (\approx 2000). The persisting occurrences for most species reflect strongly the structure of the contemporary landscape. We found that the likelihood of local extinction was strongly related to lower contemporary levels of connectivity and higher levels of habitat suitability loss, but not to the amount of change in patch size. Based on our findings, conservation efforts would be best focussed on strengthening connectivity by either building ecological corridors (Lawton et al. 2010, Staddon et al. 2010) or establishing new populations in restored habitats and reducing habitat deterioration, e.g., by decreasing nutrient input and reinstating appropriate management. The use of large-scale analyses over a wide variety of species and habitats, as we have done, provides the best chance of distinguishing among drivers of species extinctions and so informing the necessary balance between such activities. Of course, enhancing connectivity needs to be coupled with conserving current habitats and avoiding further losses. However, restoration –to increase future connectivity– and protection are both crucial components of a conservation strategy that aims at maximising biodiversity and both should be given emphasis (Hooftman & Bullock 2012, Possingham et al. 2015).

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Supplementary material (Appendix EXXXXX at
<www.oikosoffice.lu.se/appendix>). Appendix 1–8.

Table Legend

Table 1. Differences in the strengths of gradual drivers of local delayed extinction among species grouped by habitat specialism and life history characteristics. The among-species median logarithmic marginal effect size between persisting and extinct occurrences is given [$\log_{10}(\text{persisting}) - \log_{10}(\text{extinct})$]. Larger effect sizes indicate stronger drivers; significant among-group differences are indicated by differentiating letters ($\alpha = 0.05$). As habitat patch size did not show significant effects, the results are provided in the Supplementary materials (Appendix 2, Table A4), as are the results for the characteristics showing no significant relationship to the drivers (seed dispersal mode, seed bank type and clonal ability). The delayed extinction rate is the proportion of occurrences that went extinct by gradual processes of all occurrences averaged over all runs, excluding those lost through habitat destruction. The Coefficient of Variation (CV) within groups is provided.

	N	Contemporary connectivity		1930s Connectivity		Suitability change		Delayed extinction rate	
		Median	CV	Median	CV	Median	CV	Median	CV
All species	82	0.24	0.96	0.005	2.28	0.12	1.14	0.48	0.42
<i>Habitat specialism</i>									
Woodland specialists	14	0.14 (a)	0.56	0.01	1.40	0.30 (a)	0.67	0.46 (a)	0.30
Heathland specialists	25	0.16 (ab)	0.96	0.003	3.29	0.10 (bc)	1.34	0.61 (ac)	0.36
Calcareous grassland specialists	20	0.39 (b)	0.70	0.03	0.84	0.17 (ac)	1.07	0.32 (b)	0.50
Non-calcareous grassland specialists	23	0.26(ab)	1.07	0.01	3.08	0.03 (b)	1.35	0.61 (c)	0.28
<i>Pollen dispersal</i>									
Insect pollinated species	63	0.26	0.93	0.005	2.20	0.10	1.26	0.46 (a)	0.45
Wind pollinated species	9	0.16	0.34	<0.001	1.76	0.25	0.49	0.42 (a)	0.24
Predominantly selfing species	9	0.19	0.50	0.02	1.24	0.14	0.96	0.61 (b)	0.27
<i>Raunkiaer life form</i>									
Hemicryptophytes	48	0.23	0.85	0.003	2.01	0.14(a)	1.02	0.46 (a)	0.39
Therophytes	11	0.24	1.38	0.001	1.65	0.06 (a)	1.22	0.72 (b)	0.30
Geophytes	7	0.29	0.51	0.03	1.14	0.38 (b)	0.80	0.49 (a)	0.47

		Contemporary connectivity		1930s Connectivity		Suitability change		Delayed extinction rate	
Chamaephytes & Phanerophytes	16	0.23	0.90	0.01	2.10	0.04 (a)	1.39	0.45 (ab)	0.55

Figure Legends

Figure 1. A schematic representation of the analyses and the data included in each step. **(step 1)** For each species, we extrapolated the known 1930s occurrences of species into suitability layers using MaxEnt software. **(step 2)** We generated 5000 maps with probable 1930s occurrences *per* species based on these suitability layers (“simulations”). **(step 3)** For each of these occurrence maps we assessed local extinctions and persisting occurrences in comparison with contemporary species’ occurrences. **(step 4)** We calculated connectivity, habitat patch size and suitability loss *per* occurrence and carried out a logistic generalized linear regression of extinction (yes/no) against these drivers, estimating driver strength. **(step 5)** All simulations were collated and marginal effect sizes of the drivers were calculated *per* species. **(step 6)** We collated the data across all species, comparing species’ characteristic groups.

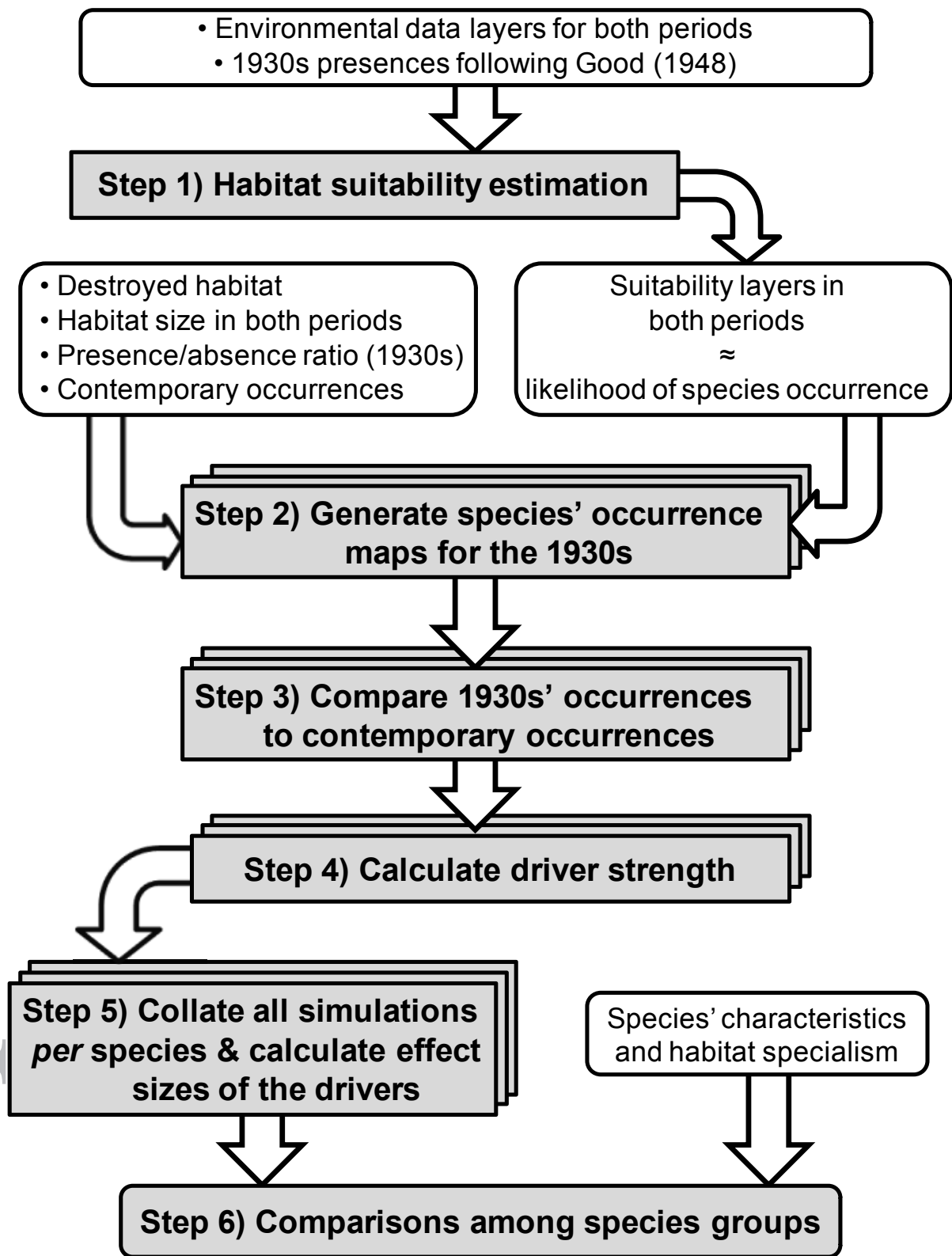


Figure 2. The proportion of occurrences going extinct immediately through anthropogenic habitat destruction according to habitat specialism across species (median \pm CV). Significant among-group differences are indicated by differentiating letters (t-test with $\alpha = 0.05$).

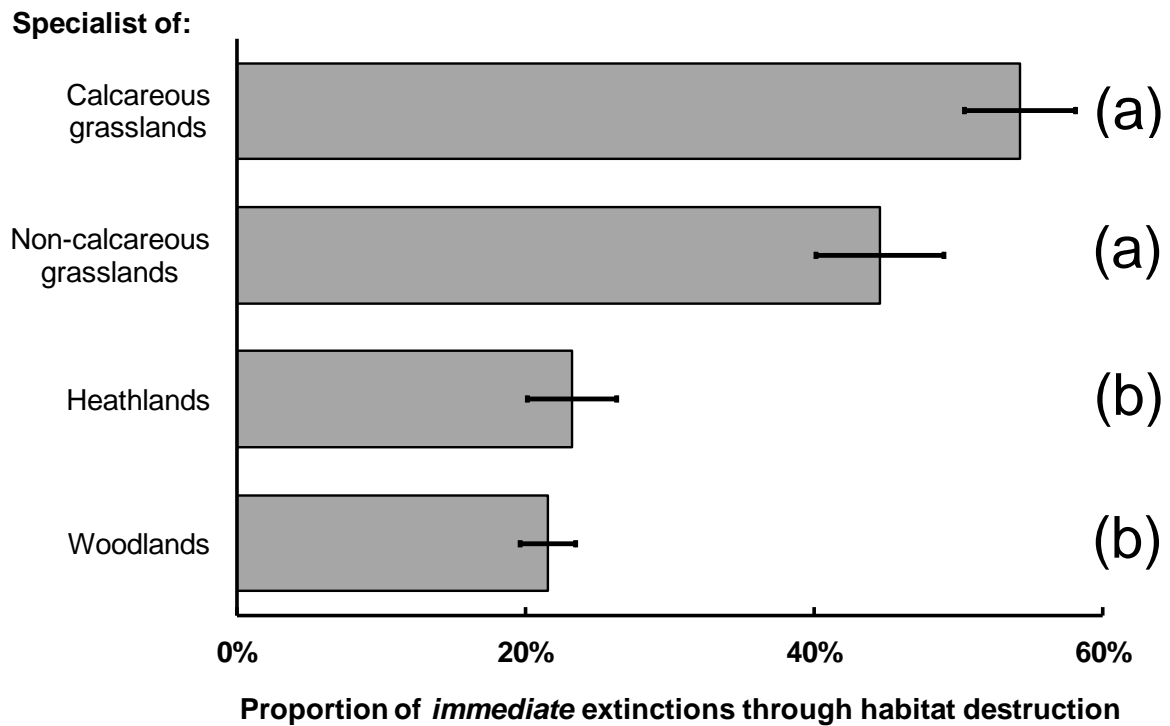


Figure 3. Histogram of the marginal effect sizes of suitability loss differences between extinct and persisting occurrences – $[\log_{10}(\text{persisting}) - \log_{10}(\text{extinct})]$ – for 82 species. The proportion of species with an effect size significantly $\neq 0$ is indicated in grey per histogram category (Bonferroni corrected with $\alpha = 0.05/82$).

