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Inconsistent detection of extinction debts using different methods

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The extinction debt, delayed species extinctions following landscape degradation, is a widely discussed concept. But a consensus about the prevalence of extinctions debts is hindered by a multiplicity of methods and a lack of comparisons among habitats. We applied three contrasting species–area relationship methods to test for plant community extinction debts in three habitats which had different degradation histories over the last century: calcareous grassland, heathland and woodland. These methods differ in their data requirements, with the first two using information on past and current habitat area alongside current species richness, whilst the last method also requires data on past species richness. The most data-intensive, and hence arguably most reliable method, identified extinction debts across all habitats for specialist species, whilst the other methods did not. All methods detected an extinction debt in calcareous grassland, which had undergone the most severe degradation. We conclude that some methods failed to detect an extinction debt, particularly in habitats that have undergone moderate degradation. Data on past species numbers are required for the most reliable method; as such data are rare, extinction debts may be under-reported.

Keywords: calcareous grassland, extinction debt, habitat, heathland, landscape, plants, species–area relationship, species richness, woodland

Introduction

Habitat destruction is one of the main drivers of biodiversity declines worldwide (Tittensor et al. 2014). Loss and fragmentation of natural and semi-natural areas reduces the habitat available to associated plant and animal species. Even within the remaining habitat patches, environmental degradation and poor connectivity can lead to ongoing species loss (Hooftman et al. 2016). Population extinction may be immediate for some species, while others can show a delayed response. In a community context, this latter phenomenon is known as extinction debt, whereby some species persist for a time in a habitat patch following landscape-level degradation yet this degradation eventually drives their patch-level extinction (Tilman et al. 1994). Extinction debt is an important consideration for conservation planning because without active

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intervention, even protected areas will continue to lose species (Kuussaari et al. 2009). The debt means current inventories of species may mask the full effects of habitat destruction. Yet while these species persist, there may still be time to employ actions such as habitat restoration that could prevent these extinctions.

While the extinction debt is a simple concept and is widely accepted (Halley et al. 2016, Thompson et al. 2019, Watts et al. 2020), testing for it in the field is not straightforward (Kuussaari et al. 2009, Figueiredo et al. 2019). Although empirical studies of the extinction debt have increased in recent years, research in this area is still limited and conclusions are varied (Figueiredo et al. 2019). For example, Adriaens et al. (2006) found no evidence of a plant extinction debt in Belgian grasslands, yet Saar et al. (2012) identified a debt within the same habitat type in Estonia. Similarly, evidence for the existence of an extinction debt in Swedish semi-natural grasslands is conflicting (Lindborg and Eriksson 2004, Oster et al. 2007). Disparities between such studies could be due to differences in the methodology employed, which is often limited by the availability of high quality historical data.

Kuussaari et al. (2009) identified five methods to detect an extinction debt. Three of these – past habitat, past communities and stable habitats (Box 1; our nomenclature) – use species–area relationships (SAR), which relate species numbers in habitat patches to habitat area. These SAR methods have the advantage of considering the whole community rather than single species approaches (Halley et al. 2016). These methods differ, however, in their assumptions and the amount of data used. Where more comprehensive data on past and current biodiversity patterns and landscape structure are available, a more reliable evaluation of the extinction debt will be possible (Kuussaari et al. 2009). Of the SAR approaches, the 'past habitat' method is probably the least reliable, as no information on past species complements is used, nor can the magnitude of extinction debt be calculated. This method also assumes communities in past landscapes were at equilibrium. Despite this shortcoming, a review by Figueiredo et al. (2019) revealed that this was one of the most commonly employed methods to test for extinction debt; probably, we suggest, because of the relatively modest data requirements. The 'stable habitats' method can be considered more reliable as it uses much the same information as for the past habitat method but adds a contrast between putatively stable and unstable landscapes. However, stable landscapes are assumed to be at equilibrium and further assumptions are required for defining a stable landscape. The 'past communities' method on the other hand might be considered the most reliable of the three, since the relationship between the past species richness and habitat area can be used to calculate the expected species richness in the current landscape. However, past biodiversity estimates are scarce, and thus very few studies have employed this method (Cowlishaw 1999, MacHunter et al. 2006). Of the 58 extinction debt studies published between 2009 and 2017 examined in Figueiredo et al. (2019), none used the past communities method.

If a study fails to detect an extinction debt, it is important to understand whether there is an issue with the method used or whether there really is no extinction debt. However, empirical studies that have used SAR methods rarely compare methods to determine whether they give similar conclusions (Figueiredo et al. 2019). Of the few studies that have done so, all compared the past habitat and stable habitats methods

Box 1. SAR methods to evaluate extinction debts (adapted from Kuussaari et al. 2009)

'Past habitat' method: detection of extinction debt using past and present habitat characteristics

This relates the current species richness to habitat patch characteristics in past versus present landscapes, though the magnitude of the extinction debt cannot be estimated. An extinction debt is detected if the current species richness is better explained by the past landscapes compared with present landscape variables. For example, Cousins et al. (2007) examined past and present areas of semi-natural grassland patches in Sweden, but found no relationship between current species richness and habitat area from 100 years ago, suggesting no extinction debt was present.

'Stable habitats' method: estimating extinction debt by comparing present-day stable and unstable habitat patches

This requires the same data inputs as the past habitat method, but quantifies the magnitude of an extinction debt by using the equilibrium species number in habitat patches which have remained more constant in area to predict the expected species number for habitat patches that have undergone a decline in area. The magnitude of the extinction debt is the difference between predicted and observed species richness. For instance, Helm et al. (2006) used species–area relationships in stable calcareous grassland sites to predict species richness in sites that had declined considerably in their habitat area (unstable sites). They found the extinction debt estimated for individual grasslands was around 40% of their current species number.

'Past communities' method: estimating extinction debt based on past and present species richness and habitat characteristics

In addition to the data for the above methods, data on past species richness is required for this method. This allows for a more precise prediction of current species richness, which is based on the relationship between past habitat area and past species richness. The expected species richness is calculated using the past SAR relationship and the difference between this and the observed species richness gives the magnitude of the extinction debt. For example, Machunter et al. (2006) used bird species richness data and land use data from both the 1980s and 2000s in south-eastern Australia and found evidence of an extinction debt.

and all found that both approaches led to the same conclusions in the specific study systems (Piqueray et al. 2011a, Guardiola et al. 2013, Soga and Koike 2013). None of these studies, however, included the possibly more reliable past communities method. Kuussaari et al. (2009) highlighted the need for comparing the performance of these three methods in the same study systems, yet to date this remains unaddressed. Such an approach can reveal whether the detection or not of extinction debts using different methods across numerous study systems is robust, and to develop best practice towards future extinction debt evaluation.

Another potential explanation for differences in the conclusions from extinction debt studies is the selection of species for analysis. Habitat specialists are expected to be more sensitive to changes in that habitat (Watts et al. 2020) and thus the inclusion of generalist species that can use other habitats in the landscape could mask any extinction debt (Kuussaari et al. 2009). For instance, butterfly specialists showed an extinction debt in urban areas in Tokyo, whereas generalists did not (Soga and Koike 2013). In contrast, some studies have detected an extinction debt for both specialist and generalist species (Cousins and Vanhoenacker 2011, Bommarco et al. 2014).

Most extinction debt studies consider communities within a single habitat type across a landscape (Vellend et al. 2006, Lira et al. 2012, Guardiola et al. 2013, Rédei et al. 2014) and the habitat types studied are not representative of the range that exist. Most extinction debt research has been in Europe (Figueiredo et al. 2019) and, even here, there has been a disproportionate research effort on calcareous grasslands (Adriaens et al. 2006, Piqueray et al. 2011a, Saar et al. 2012, Huber et al. 2017). Most likely, this is because calcareous grasslands are one of the most species-rich temperate communities (Wilson et al. 2012), and are ideal for testing for extinction debt since they are often highly fragmented and contain many specialist species. Extinction debts in other habitats which have different patterns of degradation are relatively unknown. For example, heathland extinction debt studies have been limited to Belgium, where the detection of a debt has been equivocal (Piessens and Hermy 2006, Cristofoli et al. 2010a, b). This unrepresentative sample raises the question of whether the communities within habitats focused upon may bias conclusions about the prevalence of extinction debts. If extinction debt methods are to be evaluated, this needs to be examined across multiple habitats types in the same study.

In this study, we apply and compare three SAR methods (Box 1) for the detection of an extinction debt, using vascular plant communities in three habitat types in a rural landscape in the UK: calcareous grassland, heathland and broadleaved woodland. These three habitats have experienced different trajectories of change over the last 90 years, in a landscape that has undergone profound changes (Hooftman and Bullock 2012). The greatest losses in habitat area are evident for calcareous grassland, whilst heathland also underwent decline, albeit less severely (Ridding et al. 2020a). Some small gains in woodland area occurred through planting, though this new habitat is likely not yet ecologically equivalent to what has been lost. Evaluating the SAR methods across habitats with different extents of degradation within the same study system, facilitates a reliable examination of the occurrence of extinction debts. We predict the following:

1) The three SAR methods lead to the same inferences about extinction debts.
2) Strict habitat specialists are more likely to show extinction debts than more generalist species.
3) The habitat type that has undergone the most severe decline in area – calcareous grassland – is more likely to have a large and detectable extinction debt.

Material and methods

The SAR methods require information on species richness in a number of habitat patches at the present day and also in the case of the past communities method, at some point in the past. Data are also needed on habitat area for the corresponding time periods in the past and present.

Study landscape

We conducted the study in Dorset, a predominantly rural county on the south coast of England (Fig. 1), with a historical area (pre-1974) of ca 2500 km^2 (Hooftman and Bullock 2012). In the 1930s, prior to rapid intensification of land use, semi-natural habitats, including calcareous grassland, neutral grassland, heathland and broadleaved woodland, dominated the Dorset landscape. In the decades following the Second World War, considerable proportions of these semi-natural habitats were lost, predominately to arable and agriculturally-improved grasslands. Our three habitat types differed greatly in their trajectories of change between 1930 and 2015. Calcareous grassland suffered the greatest losses (70% of sites lost), whereas over 50% of heathland sites were lost (Ridding et al. 2020a). Conversely, due to tree planting, the number of broadleaved woodland sites increased by 3% during the same 85 yr period.

Species data

In the 1930s Professor Ronald Good undertook a systematic survey of vascular plant species, using the 'stand' method, at 7575 sites that were evenly scattered across Dorset. Stands were considered to be '…reasonably distinct topographical and ecological entit[ies]…' (Good 1937). A subset of these sites, ranging in size from 0.04 ha to 32.24 ha were re-surveyed between 2008 and 2010. Sites that remained classifiable as the original habitat type comprised 65 heathlands (Diaz et al. 2013), 88 calcareous grasslands (Newton et al. 2012) and 86 woodlands (Keith et al. 2009). The re-surveys were designed to match Good's methodology as closely as

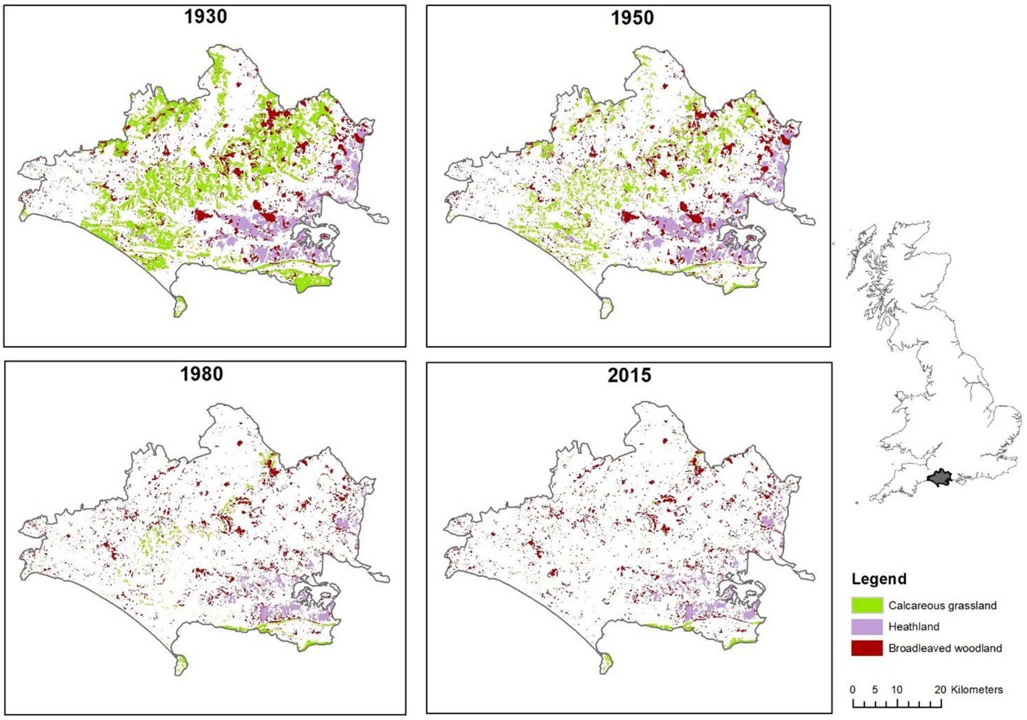

Figure 1. The extent of calcareous grassland, heathland and broadleaved woodland in Dorset, southern England in 1930 (Hooftman and Bullock 2012), 1950 (Ridding et al. 2020b), 1980 (Ridding et al. 2020b) and 2015 (Rowland et al. 2017).

possible. See Keith et al. (2009, 2011), Newton et al. (2012) and Diaz et al. (2013) for further details.

Present and past landscape composition

We determined the extent of calcareous grassland, heathland and broadleaved woodland in the past and present using a time-series of landscape maps generated by Ridding et al. (2020b). Ridding et al. (2020b) used the 1930s map produced by Hooftman and Bullock (2012) and the CEH Land Cover Map 2015 (LCM2015) (Rowland et al. 2017) to produce two intermediate maps for 1950 and 1980 at 100 m resolution, thereby generating a four-step time series for Dorset (Fig. 1). To define each habitat patch for the SAR analyses, we calculated the area of calcareous grassland, heathland and broadleaved woodland for 1930, 1950, 1980 and 2015 within a 1 km buffer around each survey site (including the site itself, where site is the area in which plant species were recorded) using ESRI ArcGIS ver. 10.4 (© ESRI, Redlands, CA). We chose the 1 km value as representing an area that would influence plant species richness at the survey site (Cousins et al. 2007, Ellis and Coppins 2007, Hooftman et al. 2016). Some calcareous grasslands were not detected by the LCM2015, since small areas of semi-natural habitat are often undetected in this dataset, which has a minimum mappable unit of 0.5 ha (Ridding et al. 2015). To address this issue, we combined the LCM2015 with calcareous grassland maps from Natural England's Priority Habitats' Inventory (Natural England 2015). Further improvements were also made to the 1950 map (Supplementary material Appendix 1). We omitted sites that did not coincide with the equivalent land cover in the landscape time-series. This procedure gave a total of 66 calcareous grassland, 62 heathland and 86 broadleaved woodland sites for further analysis.

Data analysis

We tested for extinction debt signals between 1930 and 2015 using the three methods. In addition, where the method enabled additional time periods to be included – 1950 and 1980 for past habitat and 1950 for stable habitats – we used these periods to assess if extinction debt was still detected, and therefore not just associated with a single arbitrary time period (Supplementary material Appendix 1). There was a slight time difference between our contemporary species richness within sites (2008–2010) and contemporary landscape (2015) datasets. However, it is very unlikely that there were any significant changes to habitat areas during 2008 and 2015, given that little change was detected in the areas of semi-natural habitats between 1990 and 2015 in Dorset (Ridding et al. 2020a). We undertook these analyses for three species groups, classified using the habitat associations of Hill et al. (2004). Where a plant species was associated with the relevant habitat (calcareous grassland, heathland, broadleaved woodland) it was defined as a 'habitat specialist', whereas if the species was associated with the relevant habitat and that habitat only it was a considered a 'strict habitat specialist'. Thus the latter group is more specialised. These two specialist groupings were exclusive. The final target group for the analysis included all plant species (i.e. the two specialist groups plus all other species), to mirror analyses that simply consider all species (Guardiola et al. 2013, Soga and Koike 2013).

Past habitat

We applied the past habitat method using the log 10 of past and contemporary areas of each habitat patch (area within 1 km buffer – see present and past landscape composition) and the log 10 of site area (area of the good site in which plant species were surveyed – see species data) as the independent variables to explain the contemporary species richness at each site. Site area was included to account for the differences among sites in the area that was surveyed for plant species (according to how good defined the stand in the 1930s). Site area was not strongly correlated with habitat patch area for any of the habitat types ($r < 0.60$). We generated generalized linear models (GLMs) with a Poisson distribution and log link (Zuur et al. 2009) in R (R Core Team). As in many other extinction debt analyses, the independent variables i.e. the area of habitat in 1930, 1950, 1980 and 2015 were all strongly correlated ($r > 0.60$), so we analysed each variable in a separate model. We selected the best of those models, and thus the time period which best predicted contemporary species richness, as that with the lowest second-order Akaike information criterion for small sample sizes (AICc), with a difference greater than 2 indicating a better fit (Burnham and Anderson 2002). AICc was calculated using the 'AICcmodavg' package (Mazerolle 2020), whilst McFadden's Pseudo-R^2 was computed using the 'pscl' package (Jackman 2015).

Stable habitats

We compared the contemporary plant species richness of 'stable' (less than 40% loss in area since the historical date) and 'unstable' habitat patches (more than 40% loss in area since the historical date (1930 or 1950). Other authors have classified stable versus unstable patches using thresholds of from 10 to 40% (Fahrig 2003, Helm et al. 2006, Guardiola et al. 2013). For Dorset, a 40% threshold ensured a more even and consistent sample size for stable and unstable patches across the three habitats. Where the sample size allowed, further analysis using a threshold of 20% was also undertaken (Supplementary material Appendix 2). For each habitat type we generated two separate GLMs with a Poisson distribution using the log of patch and site areas as independent variables to estimate species richness in stable patches in 2015. The first GLM used the past patch area, whilst the second model used the contemporary patch area. Next, we used the resulting parameter estimates from the two models for stable patches to predict species richness in 2015 in the unstable patches, using their contemporary area as the predictor variable. The extinction debt is the excess of observed species in comparison with the predicted number of species. The two models (one using the past patch area, and one using the current patch area) bracket the magnitude of the extinction debt, where the model based on past landscape structure probably gives an overestimate of extinction debt, whilst the model based on the contemporary landscape probably gives an underestimate (Helm et al. 2006). The significance of the extinction debt (i.e. observed number of species – predicted number of species) was determined using a Wilcoxon signed-rank test, since parametric assumptions were not met, as also seen in Soga and Koike (2013).

Past communities

We generated GLMs with a Poisson distribution to determine the relationship between the log of past habitat area and the past species richness for each habitat type, using species richness from each site in the 1930s and the corresponding habitat patch (area within 1 km buffer) as individual sampling points. Again, the log of site area was also included to account for differences in the area surveyed for plants. This relationship was then used to predict current species richness, using the contemporary area as the explanatory variable. As for the stable habitats method, the extinction debt is the excess of observed species in comparison with the predicted number of species, with the significance determined by a Wilcoxon signed-rank test.

Results

We identified a total of 309 species in the calcareous grasslands (82 habitat specialists and 43 single-habitat specialists), 352 in the heathlands (29, 7) and 443 (132, 54) in the broadleaved woodlands across the 1930 and 2008–2010 surveys. The respective habitat area within the 1 km buffer around the study site had declined by a mean of 73% in calcareous grassland and 46% in heathland, but increased by a mean of 2% in woodland.

Detection of extinction debts varied between the methods employed and within the different habitat types (Table 1). We employed a significance threshold of $p \leq 0.05$ but give exact p values and effect sizes from each of the GLMs for the three methods in Table 2–4. Using the past habitat method, past habitat area explained contemporary species richness better than the current habitat area for calcareous grassland, as indicated by the lower AICc for 1930 compared with 2015, across both specialist groups and all species, suggesting extinction debts exist (Table 2). This was still evident when habitat areas in 1950 and 1980 were used, but the effects were weaker (Supplementary material Appendix 1). The past habitat method suggested a heathland extinction debt only for all species, whereas for woodland current habitat area explained contemporary species richness better for all species, implying no extinction debt present. There was little difference between the 1930 and 2015 models for woodland and heathland specialists groups.

For the stable habitats method we divided habitat patches into stable and unstable patches of calcareous grassland (12 stable and 54 unstable), heathland (43 stable and 19 unstable) and woodland (79 stable and 7 unstable). The mean area retained between 1930 and 2015 in stable and unstable sites

Table 1. Summary table to show which methods (Box 1) showed an extinction debt ('Yes') or no evidence of an extinction debt ('No') for the three species group classifications (strict habitat specialist, habitat specialist and all species) in the three habitat types (calcareous grassland, heathland and woodland) between 1930 and 2015. For the 'past habitat' method if the AICc was lower for 1930 compared with 2015, an extinction debt was concluded. Extinction debt for the 'stable habitats' and 'past communities' methods, was indicated by a significantly greater observed species richness compared with the predicted species richness.

		Past habitat	Stable habitats	Past communities
Calcareous	Strict habitat specialist	Yes	Yes	Yes
	Habitat specialist	Yes	Yes	Yes
	All species	Yes	Yes	Yes
Heathland	Strict habitat specialist	No	No	Yes
	Habitat specialist	No	No	No
	All species	Yes	No	No
Woodland	Strict habitat specialist	No	No	Yes
	Habitat specialist	No	No	Yes
	All species	No	No	No

was respectively 69% and 17% for calcareous grassland, 67% and 25% for heathland and 108% and 27% for woodland. Extinction debts were identified for calcareous grassland using the stable habitats method, whereby the observed plant species richness values were significantly higher than predicted (Fig. 2, Table 3) for all three species groups. An extinction debt was also suggested using the past model within the stable habitats method for all species in heathland, though this was not consistent with the current model, where contemporary habitat area was used a predictor variable rather than past habitat area. The opposite pattern, whereby the current model revealed an extinction debt but not the past, was found when using habitat area in 1950 for all heathland species (Supplementary material Appendix 1). There were no other significant differences between observed and predicted species richness for the other heathland species groups or woodland (Table 1).

By contrast to the other methods, the past communities method showed similar results across all three habitat types for the specialist species groups (Fig. 2, Table 1), whereby extinction debts were detected for both habitat and strict habitat specialists in calcareous grassland and woodland, albeit only for strict habitat specialists in heathland. The mean total species extinction debt was similar for strict habitat specialists in calcareous grassland (3.13 species) and woodland (3.28 species) but much lower in heathland (0.35 species) (Fig. 2). An extinction debt was also evident across all species in calcareous grassland using this method, however habitat patch area explained very little of the variance in the regression model (Table 4), which was used to predict species richness in the present. For heathland and woodland however, the predicted species richness for the all species group was greater than the observed richness, which suggests no extinction debt (Table 4).

In summary, calcareous grassland was the only habitat in which an extinction debt was detected between 1930 and 2015 using all three methods (Table 1). The greatest mean extinction debt of 14.89 species was detected for all species using the past communities method for this habitat between 1930 and 2015 (Fig. 2). An extinction debt was detected for heathland using two of the methods, whereas only the past communities detected an extinction debt for woodland.

Table 2. Extinction debt evaluated using the 'past habitat' method for calcareous grassland, heathland and broadleaved woodland sites, for the three species groups (strict habitat specialist, habitat specialist and all species) between 1930 and 2015 in Dorset. The coefficient and standard error have been exponentiated for each regression model and are presented along with the p-value for the patch variable, AICc and R^2 value.

	Species groups	Year	Coefficient	SE	p	AICc	R^2
Calcareous grassland	Strict habitat specialist	1930	1.29	1.07	< 0.001	544.22	0.044
	Strict habitat specialist	2015	1.05	1.04	0.183	556.90	0.022
	Habitat specialist	1930	1.25	1.05	< 0.001	661.87	0.047
	Habitat specialist	2015	1.01	1.03	0.662	682.62	0.017
	All species	1930	1.08	1.03	0.029	709.16	0.025
	All species	2015	0.98	1.02	0.312	713.00	0.019
Heathland	Strict habitat specialist	1930	1.34	1.26	0.204	183.31	0.120
	Strict habitat specialist	2015	1.28	1.15	0.080	181.77	0.127
	Habitat specialist	1930	1.29	1.16	0.081	259.29	0.153
	Habitat specialist	2015	1.23	1.09	0.025	257.13	0.160
	All species	1930	1.30	1.07	< 0.001	561.23	0.036
	All species	2015	1.00	1.03	0.927	579.24	0.005
Broadleaved woodland	Strict habitat specialist	1930	0.98	1.04	0.628	485.95	0.017
	Strict habitat specialist	2015	0.96	1.04	0.361	485.36	0.019
	Habitat specialist	1930	0.96	1.02	0.054	626.85	0.021
	Habitat specialist	2015	0.94	1.03	0.018	625.90	0.024
	All species	1930	0.94	1.01	0.001	780.09	0.102
	All species	2015	0.92	1.02	< 0.001	775.28	0.107

Table 3. Extinction debt evaluated using the ‘stable habitats’ method for calcareous grassland, heathland and broadleaved woodland sites, for the three species groups (strict habitat specialist, habitat specialist and all species) between 1930 and 2015 in Dorset. Model indicates whether past or current patch area was used to predict contemporary species richness. The exponentiated coefficient and standard error, and R^2 values are presented for each regression model. Extinction debt is calculated as the difference between the numbers of predicted and observed plant species, alongside the range and the p-value resulting from a Wilcoxon test comparing the two. Those in bold reveal where an extinction debt is suggested.

	Species groups	Model	Coefficient	SE	R^2	Extinction debt		
Calcareous grassland	Strict habitat specialist	Current	**2.62**	**1.47**	**0.123**	**8.02**	**(−4.28 ~ 25.15)**	**<0.001**
	Strict habitat specialist	Past	**1.18**	**1.20**	**0.074**	**5.60**	**(−7.42 ~ 21.01)**	**<0.001**
	Habitat specialist	Current	**2.48**	**1.32**	**0.153**	**14.25**	**(−8.00 ~ 42.15)**	**<0.001**
	Habitat specialist	Past	**1.28**	**1.15**	**0.100**	**11.44**	**(−8.89 ~ 36.50)**	**<0.001**
	All species	Current	**1.04**	**1.20**	**0.158**	**11.92**	**(−24.20 ~ 45.73)**	**<0.001**
	All species	Past	**1.00**	**1.09**	**0.158**	**10.48**	**(−25.45 ~ 43.52)**	**<0.001**
Heathland	Strict habitat specialist	Current	1.21	1.26	0.072	0.05	(−0.75 ~ 0.81)	0.623
	Strict habitat specialist	Past	1.24	1.34	0.072	0.22	(−0.61 ~ 0.99)	0.090
	Habitat specialists	Current	1.20	1.16	0.124	−0.07	(−3.12 ~ 2.16)	0.900
	Habitat specialists	Past	1.26	1.21	0.124	0.39	(−2.52 ~ 2.67)	0.241
	All species	Current	1.24	1.07	0.038	5.81	(−10.22 ~ 37.84)	0.123
	All species	Past	**1.42**	**1.10**	**0.058**	**9.58**	**(−6.44 ~ 42.11)**	**0.011**
Broadleaved woodland	Strict habitat specialist	Current	0.99	1.04	0.020	2.56	(−3.91 ~ 7.46)	0.219
	Strict habitat specialist	Past	0.98	1.04	0.021	2.48	(−3.92 ~ 7.38)	0.219
	Habitat specialists	Current	0.96	1.03	0.024	4.11	(−7.61 ~ 15.19)	0.438
	Habitat specialists	Past	0.95	1.02	0.026	3.96	(−7.80 ~ 15.12)	0.438
	All species	Current	0.94	1.02	0.115	3.66	(−9.64 ~ 21.09)	0.438
	All species	Past	0.94	1.02	0.117	3.62	(−10.15 ~ 21.25)	0.438

Discussion

Differences between three extinction debt methods

We found evidence for extinction debts in plant communities across three temperate habitats; calcareous grassland, heathland and woodland. However, our analysis showed that detecting an extinction debt is greatly dependent on the method employed, contrary to our first prediction; that the three SAR methods lead to the same inferences about extinction debts. The past communities method was the only one to suggest an extinction debt across all three habitat types. This method is used rarely owing to the extra data requirements, specifically past species richness data, but has demonstrated extinction debts in other study systems (Cowlishaw 1999, MacHunter et al. 2006). The other two methods produced different results, with the past habitat method suggesting extinction debts in calcareous grassland and heathland (for all species only), whilst the stable habitats method detected a debt only in calcareous grassland. While inconsistencies among methods have not been found in previous studies, these studies are few and they compared only the past habitat and stable habitats methods (Guardiola et al. 2013, Soga and Koike 2013), which are largely similar approaches. For example, in Belgian calcareous grasslands, Piqueray et al. (2011a) found extinction debts with both methods.

The past communities approach is likely the most powerful because data about the relationship between past species richness and past habitat area is utilised (Kuussaari et al. 2009). A SAR is constructed using historical data and this is contrasted with species data in the contemporary landscape. By contrast, the other two methods simply ask whether past landscape characteristics – habitat areas in this case – are a better predictor of contemporary species count data than

Table 4. Extinction debt evaluated using the ‘past communities’ method for calcareous grassland, heathland and broadleaved woodland sites, for the three species groups (strict habitat specialist, habitat specialist and all species) between 1930 and 2015 in Dorset. The exponentiated coefficient and standard error, and R^2 values are presented for each regression model. Extinction debt is calculated as the difference between the numbers of predicted and observed plant species, alongside the range and the p-value resulting from a Wilcoxon test comparing the two. Those in bold reveal where an extinction debt is suggested.

	Species groups	Coefficient	SE	R^2	Extinction debt		
Calcareous grassland	Strict habitat specialist	**1.15**	**1.07**	**0.026**	**3.13**	**(−10.00 ~ 19.26)**	**<0.001**
	Habitat specialist	**1.11**	**1.05**	**0.023**	**5.86**	**(−15.63 ~ 30.85)**	**<0.001**
	All species	**1.00**	**1.04**	**0.001**	**14.89**	**(−23.01 ~ 46.70)**	**<0.001**
Heathland	Strict habitat specialist	**0.91**	**1.26**	**0.103**	**0.35**	**(−1.74 ~ 2.89)**	**0.009**
	Habitat specialists	0.96	1.15	0.095	0.32	(−3.84 ~ 4.74)	0.242
	All species	0.84	1.05	0.089	−3.58	(−61.36 ~ 23.44)	0.070
Broadleaved woodland	Strict habitat specialist	**0.92**	**1.04**	**0.031**	**3.28**	**(−6.75 ~ 11.93)**	**<0.001**
	Habitat specialists	**0.92**	**1.03**	**0.048**	**4.25**	**(−17.45 ~ 19.16)**	**<0.001**
	All species	0.91	1.02	0.127	−5.13	(−40.85 ~ 28.96)	0.002

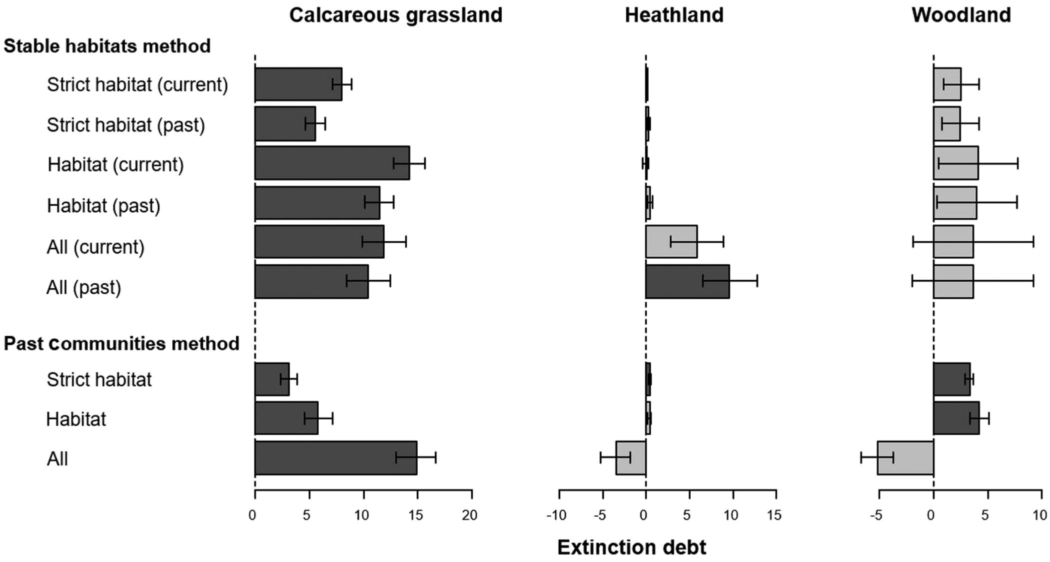

Figure 2. Extinction debt (± SE), in terms of the mean number of species across sites, as assessed using two methods between 1930 and 2015 across three habitat types; calcareous grassland, heathland and woodland (see also Table 3, 4). For the 'stable habitats' method, '(current)' and '(past)' indicate which patch area was used to predict contemporary species richness. Bars in dark grey indicate models where the observed species richness is significantly greater than the predicted species ($p < 0.05$), i.e. there is an extinction debt.

contemporary landscape characteristics. Because landscape characteristics are correlated over time, as we and other studies (Husáková and Münzbergová 2014, Rédei et al. 2014) show, these methods rely on an assumption that species richness was tightly linked to landscape characteristics at the chosen point in the past and this signal remains strong in the contemporary species record. The past communities method does not rely on finding some relationship between present species data and past landscapes, and this may explain why this suggested extinction debts where the other methods did not. Indeed, the fact that the past communities method identified extinction debts in all habitat types suggests that the use of the past habitats and stable habitats methods could increase uncertainty in the detection of extinction debts. This has important implications for conclusions about the existence and prevalence of extinction debts more broadly. This problem is further exacerbated by the fact that the past habitats and stable habitats methods are more commonly employed in the literature (Figueiredo et al. 2019), probably owing to their less demanding data requirements. The threshold used in the stable habitats method is also an important cause of uncertainty, since the magnitude of extinction debt can be very sensitive to the threshold selected (Piqueray et al. 2011b). However, the additional analysis using a threshold of 20% for calcareous grassland (Supplementary material Appendix 2), also indicated an extinction debt across the three species groups, as found when employing a 40% threshold. Another factor which may influence the detection of an extinction debt is the time period selected in the past, which is usually governed by availability of historical data rather than hypotheses about the rate at which species are lost (Bagaria et al. 2015, Neumann et al. 2017). Efforts over recent years have increased the number of historical biodiversity datasets (Vellend et al. 2013, Dornelas et al. 2014). While these vary in quality and so must be used with care (Cardinale et al. 2018), they provide the potential for a more systematic and robust analysis of extinction debts using the past communities method. Data on landscape composition for the corresponding time period is also required, which can be challenging to attain. However, recently a number of studies have utilised historical national maps to explore changes in land cover (Kaim et al. 2016, Chen et al. 2019), which could be extended to extinction debt analysis providing suitable species data are available.

Extinction debt detection using different species groups

Using the past communities method, we detected extinction debts for the two types of specialist species in calcareous grassland and woodland, and for the strict habitat specialist in heathland, supporting our second prediction, indicating strict habitat specialists are more likely to show extinction debts than more generalist species. This result supports the suggestion that only specialist species should be included in extinction debt analyses (Kuussaari et al. 2009). While the SAR approach is valid for specialists and generalists because both will react to loss of their habitat, the inclusion of generalist species which can persist in other habitats than that focussed on is likely to obscure relationships between species number and area of the focal habitat. If generalists are persisting well in the landscape by living in other habitats, then this may lead to a conclusion of no extinction debt. Generalists may exhibit an extinction debt where the focal habitat is very different to other habitats in the landscape, meaning the generalists persist poorly elsewhere in the landscape. This may explain the extinction debt detected for generalists in calcareous grassland by all three methods. This is consistent with other studies, where the past habitat and stable habitats methods detected extinction debts for all species and for specialists in semi-natural grasslands (Cousins and Vanhoenacker 2011, Piqueray et al. 2011a).

Extinction debt within three habitat types

Calcareous grassland was the only habitat for which an extinction debt was suggested by all three methods and for all species groups. Furthermore, the debt in calcareous grassland was greater than those in woodland and heathland, estimated using the stable habitats and past communities methods. These findings support our third prediction; calcareous grassland exhibits the greatest extinction debt. Numerous other studies have also identified the presence of an extinction debt within this habitat type across Europe (Helm et al. 2006, Krauss et al. 2010, Piqueray et al. 2011a). By comparison with the other habitats, our study suggests that the extent of the extinction debt in calcareous grassland is due to the combination of a history of severe degradation with the richness of specialist species. Heathland, on the other hand, has experienced considerable, although lesser, degradation in the region but we did not find extinction debt for this habitat across all methods. Heathland specialists are generally long-lived and have a persistent seedbank (Piessens and Hermy 2006, Saar et al. 2012) like specialists in calcareous grassland, however the number of such specialist species is much lower than in calcareous grassland (we found 43 for calcareous grassland specialists only versus 7 in heathland), which may explain the weaker signal of an extinction debt for heathland. Furthermore, the differences between calcareous grassland and heathland may be linked to the colonization and connectivity of populations and metapopulations (Figueiredo et al. 2019), because heathlands are more tightly clustered in Dorset than are calcareous grasslands (Hooftman and Bullock 2012). The surrounding landscape may also be important. The SAR methods employed in this study assume that the species cannot survive outside their habitat, and this is probably true of the strict habitat specialists. Other SAR methods e.g. cSAR (Pereira et al. 2014) recognise that species may not be constrained to fragments of their habitat, which could be an important consideration in future extinction debt studies.

We detected an extinction debt in woodlands similar in magnitude to that in calcareous grassland, albeit only using the past communities method. Woodland did not suffer the severe declines in habitat area over the whole of Dorset, as seen for calcareous grassland and heathland, but instead increased over time, due to planting of new woodland, which countered losses of old woodland. The planting of new woodland seems to have been rather scattered across Dorset, and not focussed on increasing woodland around existing patches (Hooftman and Bullock 2012). As a result, of our 86 woodland patches, 52 suffered declines in woodland area from past to present. Our finding of an extinction debt for woodlands reflects the local losses and highlights the fact that to avoid the paying of the extinction debt, restoration needs to enhance the landscape around existing habitat (Newmark et al. 2017).

Conclusion

This study is the first to compare three SAR methods for detecting an extinction debt and also across multiple habitats. Considering the results from the most data intensive, and hence presumably most reliable method (past communities), all habitat types demonstrated an extinction debt. The detection and magnitude of this debt however, differed among habitats, species with different levels of habitat specialisation, and method used. This result has important implications for confidence in reported extinction debts and emphasises the need for accurate extinction debt information using the best quality data. In our study, extinction debts were most clear for the habitat which had suffered the most severe decline (calcareous grassland) using all methods. However, two of these methods (past habitat, stable habitats) did not consistently reveal a debt where the habitat loss was less severe (heathland) or where the habitat had actually increased over time (woodland). This outcome suggests that unless habitat loss is severe, the two methods that do not incorporate any past species information have a limited capacity for detecting extinction debt. This has important implications for conservation in the future, where restoration opportunities may be missed if an extinction debt is thought not to be present.

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Supplementary material (available online as Appendix ecog-05344 at <www.ecography.org/appendix/ecog-05344>). Appendix 1–2.