


Unpaid extinction debts for endemic plants and invertebrates as a legacy of habitat loss on oceanic islands

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Abstract

Aim: The majority of documented extinctions world-wide in the last four centuries are of species endemic to islands. However, the phenomenon of delayed extinctions as a result of habitat loss has rarely been assessed on oceanic islands. In this study, we tested whether extinction debt (ED), in general, occurs on islands and for which taxonomical groups this phenomenon is most pronounced by assessing ED for multiple endemic taxa and for each of the main altitudinal ecosystems in a well-studied oceanic archipelago.

Location: Canary Islands.

Methods: We characterized habitat preferences for all endemic species of several taxonomic groups (vascular plants, ground and darkling beetles, flies and land snails). Using generalized linear mixed models and available data about habitat distributions, we tested for all taxa and habitat types to determine whether past habitat area better explained current richness of habitat specialists than current habitat area. If so, an extinction debt can be assumed.

Results: For all five major habitat types and five taxonomic groups studied, present-day richness of habitat specialists fitted better with past than current habitat area, evidencing habitat- and taxon-specific extinction debts. This pattern was consistent for both long-lived vascular plants and short-lived invertebrates. Single island endemics in each taxonomic group showed steeper slopes of the species–area relationship (SAR) compared to archipelago endemics indicating higher sensitivity to habitat loss which might increase sizes of ED.

Conclusion: Despite differences in species' generation times, plants and invertebrates showed delayed extinctions after habitat destruction in the Canary Islands. Our SAR approach suggests that a considerable number of Canary Island endemics will eventually become extinct in the future without further habitat loss. The case of the Canary archipelago is probably not unique. Hence, we interpret our results as a warning for island conservationists that the worst of the extinction crisis on oceanic islands might be yet to come. Conservation actions should focus on habitat restoration to attenuate or reverse current extinction processes.

KEYWORDS

Canary Islands, conservation, endemic species, extinction debt, habitat loss, relaxation time, species–area relationship

1 | INTRODUCTION

Habitat destruction is one primary cause of species extinctions from the local to the global scale (Brooks et al., 2002). Extinction processes might also be influenced by other factors such as the invasion of alien species, climate change and extinction cascades (Sax & Gaines, 2008). Species can become extinct almost immediately after habitat destruction due to the loss of all their local populations, or species might initially survive habitat change, but later become extinct without further habitat conversion as a result of deterministic and stochastic processes related to demography or genetic and environmental variability, creating an extinction debt (hereafter ED; Tilman, May, Lehmann, & Nowak, 1994).

The concept of ED includes two aspects: the time needed (relaxation time) by the ecological community to reach a new equilibrium state with equal extinction and colonization rates after habitat change, and the magnitude or size of the ED, that is the number or proportion of species typical of the focal habitat committed to extinction during this process (Kuussaari et al., 2009). The phenomenon of delayed extinctions in response to habitat loss has received more attention and has been evidenced by empirical data for different taxonomic groups and habitat types only in the last decade (Bommarco, Lindborg, Marini, & Öckinger, 2014; Halley, Monokrousos, Mazaris, Newmark, & Vokou, 2016; Helm, Hanski, & Pärtel, 2006; Krauss et al., 2010; Lindborg & Eriksson, 2004; Olivier, van Aarde, & Lombard, 2013; Vellend et al., 2006; Wearn, Reuman, & Ewers, 2012).

Nevertheless, our knowledge about the occurrence and the underlying processes of delayed extinctions across ecosystems and taxonomic groups is very limited (Halley, Sgardeli, & Triantis, 2014; Kuussaari et al., 2009). ED has rarely been assessed on oceanic islands and mostly for animals (Brooks, Pimm, & Collar, 1997; Triantis et al., 2010), despite the fact that the majority of the extinctions documented in the last four centuries are of species endemic to oceanic islands (Whittaker & Fernández-Palacios, 2007). However, such islands seem to be ideal model systems to study extinction processes, as they have been intensively, but mostly recently disturbed by human activities and generally represent global biodiversity hotspots harbouring a high number of endemic and rare species prone to extinction (Brooks et al., 2002). Endemic species on islands have mostly evolved in environments without human disturbances. They are often geographically restricted to small areas (especially single island endemics, SIEs) and ecologically constrained to specific native habitat types and are not expected to have the capacity to adapt to anthropogenic habitats under land use changes (Triantis et al., 2010). Small population sizes of habitat specialists could actually reduce the likelihood of time-lags before extinction and, at the same time, the chances of detecting EDs, because equilibrium could quickly be reached. Hence, we might ask whether ED, in general, occurs on islands and for which taxonomical group and which habitat type it is most pronounced.

Different taxonomic groups are expected to respond differently to habitat loss, depending on species traits such as generation time, trophic level or dispersal and colonization capacity (Kuussaari et al., 2009; Saar, Takkis, Pärtel, & Helm, 2012). Longer generation times

should increase the chances of finding EDs. For instance, plants have been reported to experience delayed extinctions even decades or centuries after habitat destruction (Lindborg & Eriksson, 2004; Vellend et al., 2006) due to the capacity to persist in fragmented landscapes. On the other hand, some insect groups with short generation times and high mobility such as bees and butterflies might respond more rapidly to habitat loss and reach a new equilibrium distribution in the remnant habitat patches within a few years (Bommarco et al., 2014; Krauss et al., 2010). Poor dispersal capacity or mobility might increase the size of an ED initially, but could also lead to metapopulations to relax more quickly to equilibrium.

Evidence for an ED can be assumed when past habitat area explains current species richness better than current habitat area, applying the species–area relationship (SAR; Diamond, 1972; Rosenzweig, 2001; Kuussaari et al., 2009). Following this traditional approach, ED has been assessed for one species group and one habitat type (Cowlshaw, 1999; Helm et al., 2006), or for multiple taxa living in the same habitat type (Krauss et al., 2010; Lindborg & Eriksson, 2004). However, there is a lack of studies that simultaneously compare EDs for multiple taxa and multiple habitats on oceanic archipelagos. In a recent meta-analysis, Halley et al. (2016) found that the time for the ED to be paid off increases with habitat area in a similar way for different taxonomic groups. One of the few studies carried out on oceanic islands predicted possible future extinctions of more than 85% of endemic species in some arthropod groups as a result of a dramatic deforestation within the last six centuries in the Azores Islands (Triantis et al., 2010). They found differences in EDs between taxa and distribution status, classified as archipelago endemics or single island endemics (SIE), indicating that SIEs might be at greater risk of extinction.

Natural vegetation types on the Canary Islands have dramatically transformed and reduced in area following the Castilian settlement in the 15th century, showing habitat losses up to 95%. Nowadays, only remnants of the major Canary ecosystems can be found in a semi-natural state (del Arco et al., 2006). As a consequence, these endemic-rich ecosystems are likely to suffer from deterministic long-term decline of habitat specialist species, eventually resulting in an ED. The long list of threatened plant species on the Canary Islands, especially for SIEs (48% considered as threatened), which reflects the extinctions risk based on criteria such as a reduction in population size and range, may indicate the existence of delayed extinctions. Threatened species can be interpreted as those species that have come close to extinction and represent part of the ED. Therefore, they have been used to evaluate predictive models of extinction dynamics (Brooks et al., 2002; Olivier et al., 2013). Hence, the number of threatened species should be positively related to the degree of habitat loss.

Here, we present the first study that assesses simultaneously EDs for multiple endemic taxa (plants, ground beetles and darkling beetles, land snails and flies, in the last case only natives) and for each of the main altitudinal ecosystem types in an oceanic archipelago, the Canary Islands. Using the most accurate and recent maps of vegetation distribution comparing the current situation with the estimated potential distribution before human disturbances (del Arco, González-González, Garzón-Machado, & Pizarro-Hernández, 2010; del Arco et al., 2006),

we tested for ED in all five species groups which differ in their individual longevity and mobility and in five habitat types applying the species–area relationship. We hypothesized that evidence for ED should be stronger for endemic plants, mostly woody in the Canaries, than for endemic invertebrates due to longer generation times of plants. Furthermore, we expected SIEs to be more sensitive to habitat loss than archipelago endemics due to reduced distribution ranges of SIEs often dwelling only in small parts of an island. Additionally, we tested whether the number of current threatened plant species responds to loss of habitat area.

2 | METHODS

2.1 | Study area

The Canary archipelago (27°37', 29°25'N and 13°20', 18°10'W), consisting of seven major islands and occupying a total area of 7,447 km², is located in the North Atlantic Ocean close to the north-west coast of Africa. The hotspot or mantle-plume hypothesis has been considered as the most plausible explanation for the origin of Canary volcanism (Carracedo, 2011) corresponding to an age progression from the youngest western islands of El Hierro and La Palma (1.1–1.7 Ma) to the oldest eastern most islands of Fuerteventura and Lanzarote (20.6–15.5 Ma). During long periods of the Pleistocene, Fuerteventura and Lanzarote together with the surrounding islets were merged into a single large palaeo-island called “Mahan” as a result of periodically sea level changes (Rijsdijk et al., 2014). Therefore, we treat them here as a single unit.

Five of the Canary Islands are higher than 1,450 m a.s.l. and show steep climatic gradients, especially on the northern more humid slopes, whereas the eastern islands exhibit much lower altitudes (<850 m a.s.l.) and less environmental variation. Six major terrestrial ecosystem types, here also called habitats, can be distinguished in the Canary Islands from coast to high mountain (del Arco et al., 2010): coastal vegetation (found on all seven islands); *Euphorbia* scrub (seven islands); thermophilous forest (seven islands); laurel forest (five islands); pine forest (five islands); and summit scrub (two islands). A short description of each ecosystem can be found in Zobel et al. (2011) and del Arco et al. (2010).

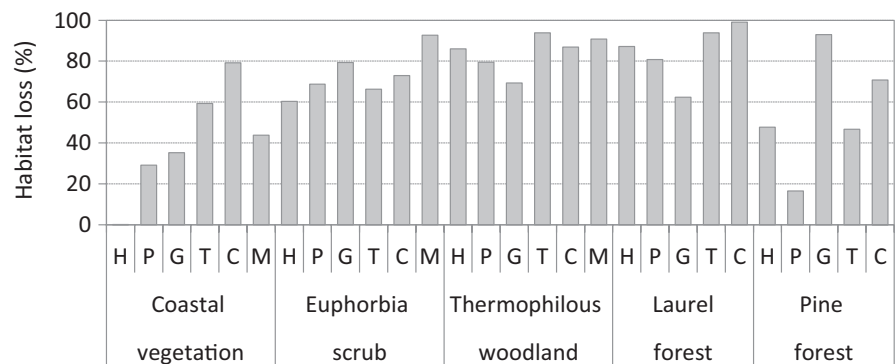
Archaeological and palaeoecological studies point to a date around 2,900 yr BP for the first human colonization of the Canary archipelago

(Atoche, 2008). Even though first settlers, most probably Berber tribes from North Africa, undoubtedly modified ecosystems to a certain extent, natural vegetation was severely disturbed after the Castilian settlement in the 15th century. Following del Arco et al. (2010, Figure 1), at the archipelago level, laurel forest and thermophilous woodlands were destroyed by 85% (range between individual islands 62% and 99%), while 73% of *Euphorbia* scrub (range 60%–93%) was lost due to human activities. The degree of habitat loss for pine forest (mean value 55%, range 17%–93%) and coastal vegetation (mean value 41%, range 0–79%) is less dramatic. We used these published data about the current habitat area and the estimated original or potential habitat area before human disturbance to analyse a possible ED. The potential habitat extension was reconstructed from bioclimatic data and current distributions of habitat indicator species (for details see del Arco et al., 2010). In our study, potential and current island habitats refer to the sum of all patches of a certain ecosystem type on a particular island in the assumed original state and in the current situation, respectively. Unfortunately, detailed reliable information about the dynamics of habitat loss for each habitat and island is not available for the Canary Islands. Hence, we were not able to include the time since habitat loss as an additional explanatory variable in our statistical models, although it would be desirable.

2.2 | Species data

We compiled species pools (not considering subspecies) for higher vascular plants (Spermatophyta), beetles (Coleoptera: Carabidae and Tenebrionidae), land snails (Gastropoda) and flies (Diptera, families) for each habitat type and island by assigning all Canary endemics (in the case of Diptera all Canary natives due to their low level of endemism) to at least one habitat type (Appendix S1, Table S1). Species list and distribution data followed Arechavaleta, Rodríguez, Zurita, and García (2010) and were updated by expert knowledge (unpublished data). The following sources were used to extract information for habitat classification: Spermatophyta (Zobel et al., 2011 and unpublished data), Carabidae (Machado, 1992), Tenebrionidae (Oromí, 1982 and unpublished data), Gastropoda (M. Ibáñez, unpublished data) and Diptera (M. Báez, unpublished data). We simplified descriptions of habitat preferences of the different sources using our approach of broad climatic ecosystem types. Species living preferably in environments such as rocks, freshwater or sand dunes were assigned to

FIGURE 1 Loss of major ecosystems on each of the Canary Islands comparing current with potential habitat area (28 island habitats). H = El Hierro, P = La Palma, G = La Gomera, T = Tenerife, C = Gran Canaria, M = Mahan, (Fuerteventura and Lanzarote are merged as they formed a single palaeo-island called Mahan during long periods of the Pleistocene)



the corresponding climatic vegetation zones where species were also cited. Cave-dwelling species were not considered in the analysis.

On the whole, we characterized habitat preferences for 1,061 species (see Table S1): 544 endemic higher vascular plants (300 SIE, 55%), 129 endemic ground beetles (94 SIE, 73%), 92 endemic darkling beetles (71 SIE, 77%), 223 land snails (163 SIE, 73%) and 73 flies (no SIE). Considering all taxonomic groups, 59% (range 45%–76%) of endemic species can be associated with a single habitat and 88% (range 69%–97%) with two habitat types. Hence, the vast majority of analysed endemics show a rather restricted environmental niche. We decided to extend the definition of habitat specialist (*sensu lato*) in this analysis to species also present in a second habitat type for two reasons: (1) the lack of knowledge about species abundance, especially for invertebrates, made it difficult even for experts to restrict preferences to one habitat in many of these cases, even though species might show a clear abundance optima in one habitat type while being only sporadically present in a second habitat; and (2) the number of true habitat specialists (*sensu stricto*, endemics present in only one habitat) is too low, in case of darkling beetles and flies, to run the statistical analysis. However, results of the global multimodel ED assessment on endemic species restricted to one or two habitat types were very similar for plants, ground beetles and land snails (compare Tables S2 and S3), indicating that the definition of habitat specialist does not affect our results.

Furthermore, we defined the subgroup of single islands endemic species (SIEs) within the larger group of Canary endemics (CEs) to test whether SIEs respond differently to habitat loss compared to CEs. To test for a significant relationship between the number of threatened species and habitat area loss, we compiled information about the current number of threatened endemic vascular plant species per island habitat. This taxon was selected for being the most extensively studied, with quality and detailed information available on threatened species (critically endangered, endangered and vulnerable) classified following the IUCN Red List (Marrero Rodríguez et al., 2007; Martín, Arechavaleta, Borges, & Faria, 2008; Moreno, 2008).

2.3 | Statistical analyses

To assess a possible ED for each taxonomic group, we applied a global approach using generalized linear mixed-effect models (GLMM, Bates et al. 2014) including all island habitats ($n = 28$; seven coastal vegetation habitats, seven *Euphorbia* scrub habitats, seven thermophilous woodland habitats, five laurel forest habitats and five pine forest habitats). We selected a Poisson error distribution and log link function for all richness groups as recommended for count data (Quinn & Keough, 2002). For each taxon, SIE and CE richness were introduced as response variables, whereas potential habitat area, current habitat area, habitat age (single and quadratic term) and habitat type were defined as fixed factors. Island was introduced as a random intercept to account for the spatial structure in the data and the effect of pseudoreplication. First, we performed separate GLMMs with each fixed factor as a single predictor to test for their individual predictive power. Then, we ran a combined model including all four predictors

and plotted partial residuals to visualize the independent effect of potential versus current habitat area in the models. Using a multimodel setting, we examined the Akaike information criterion corrected for small sample size (AIC_c) of all combinations of models including the four explanatory variables in order to check relative importance of predictors and to select the best model for each taxonomic group (Burnham & Anderson, 2002). Variation accounted for by each single predictor and the best GLMM was quantified using the estimated pseudo- R^2 value. We also tested for the occurrence of EDs for each habitat type and taxonomic group separately by applying generalized linear models (GLM, McCullagh & Nelder, 1989) with Poisson distribution and log link function for all richness groups. Again, we examined the AIC_c values, model coefficients and p values of models comparing combinations of predictors including potential habitat area, current habitat area and habitat age.

Potential and current habitat areas were log-transformed but not species richness, as we selected the log link function in GLMMs which relates a combination of linear predictors to the dependent variable using the natural logarithm. This leads finally to a log–log species–area relationship, the power–law model of SAR. Habitat age was defined as maximum island age, with the exception of Gran Canaria, where the centre of the island was sterilized 3.5 Ma ago by violent volcanism affecting most parts of laurel and pine forests, and speciation processes within these ecosystems (Emerson, 2003). Although Anderson, Channing, and Zamuner (2009) questioned the complete sterilization of the island presenting fossil records, we assume that forest ecosystems in the centre of Gran Canaria were severely affected causing multiple extinctions of local endemics. Therefore, these forest habitats were aged 3.5 Ma and lowland habitats 14.5 Ma (the age of the island). We have not yet sufficiently accurate data about habitat history for the other Canary Islands to distinguish between habitat age and island age. Habitat (five major ecosystem types) was included as a categorical variable.

All statistical analyses were performed in a R environment (v. 3.2.0, R Development Core Team, 2015) using the following libraries: `lme4` (v. 1.1-7) for GLMM analyses, `AICCMODAVAG` (v. 2.0-4) for best model selection, `BAYLOREDPSYCH` (v. 0.5) and `PIECEWISESEM` (v. 1.2.1) to estimate pseudo R^2 values. Overdispersion was assessed using the function `overdisp_fun` (<https://github.com>) for GLMMs and the function `dispersiontest` in the `AER` package (v. 1.2-5) for GLMs. These analyses showed that overdispersion was not a problem in the performed models.

3 | RESULTS

Evidence for EDs was found for all five taxonomic groups, and all five habitat types studied (Figures 2–4, Tables S2, S3 and S5). Species pools of endemic species (or native species in the case of Diptera) related to a certain habitat type always fitted better with potential habitat area than with current habitat area.

When considering all island habitats in a global GLMM approach, potential and not current habitat area fitted best current species richness of all taxonomic groups as revealed by the pseudo R^2 values

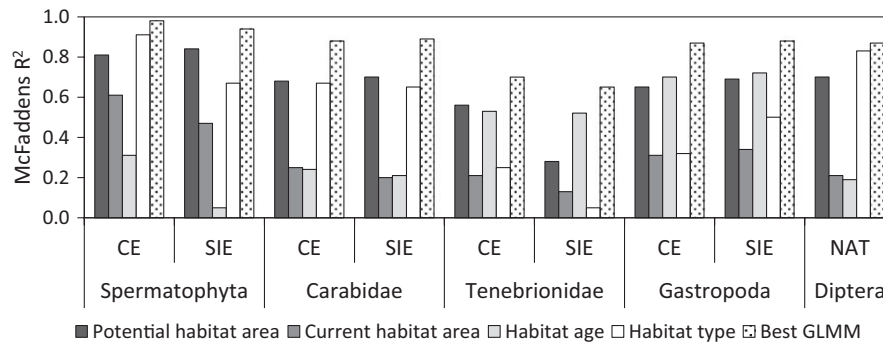


FIGURE 2 Importance of potential and current habitat area, habitat age (single and quadratic term) and habitat type as single predictors in explaining current number of Canary endemics (CE) and single island endemics (SIE) for higher vascular plants (Spermatophyta), ground and darkling beetles (Carabidae, Tenebrionidae) and land snails (Gastropoda). For flies (Diptera), only natives were considered. McFaddens R^2 indicates the deviance explained by each single predictor in generalized linear mixed models (GLMMs)

of the models, indicating the amount of deviance explained by both the individual predictors and the best combined GLMMs (Figure 2, Tables S2 and S3). However, habitat age (as single and quadratic term) and habitat type also showed a high predictive power in some taxonomic groups. Habitat age was important for darkling beetle and land snail richness. The influence of habitat type was expected due to differences in species pool sizes between habitats. For instance, coastal vegetation was generally poorer in plants, ground beetles and flies compared to the rest of ecosystems.

In the combined models including all four explanatory variables, partial residual plots confirmed the strong independent effect of past habitat area on current species richness for all taxonomic groups, when species richness was corrected for all other explanatory variables (correlations in all cases highly significant, $r > 0.74$, $p < .001$, Figure 3). Current habitat area only showed a very weak positive, mostly not significant, or even negative independent effect on current species richness. Slopes of the SARs were much steeper for SIEs compared to CEs within the taxonomic groups of Spermatophyta, Carabidae and Tenebrionidae, indicating a higher sensitivity to habitat loss. GLMM results applying the multimodel approach revealed that the best model for each taxonomic and status group characterized by the lowest AIC_c values included potential habitat area, habitat age (as single or quadratic term) and/or habitat type but not current habitat area (Tables S2 and S3), regardless of the definition of habitat specialist (restricted to one or two habitat types). Best GLMMs showed generally high pseudo R^2 values (>0.85) and low p values (all models significant after Bonferroni correction for multiple comparison, Table S4), indicating that selected explanatory variables were important.

The results of the GLMs separately applied to each habitat type, and taxonomic group supported this trend (Figure 4, Table S2). All best habitat-specific GLMs for endemic richness groups included potential but not current habitat area and were significant at $p < .05$, but three of them at $p < .1$ (64% of GLMs were still significant after Bonferroni correction despite low number of replicates, Table S5). The differences in models' performances comparing potential and current habitat area as predictors indicated that plants among taxonomic groups and thermophilous woodland among habitat types revealed the strongest evidence for ED and flies the weakest (Tables S2 and S5). When analysing

all habitats simultaneously, we found a hump-shaped relationship between species richness and habitat age (single and quadratic term as predictor) for all taxonomic groups except for darkling beetles, which showed a linear increase (Table S2). At the habitat level, a linear relationship between species richness and habitat age was more common (Table S5).

Estimates for the predictor potential habitat area in the best fitting GLMs varied substantially between taxonomic groups, habitats and status groups (Figure 4, Table S5). These estimates that correspond to the slope or z value of the SARs ranged between 0.2 and 0.4 for Canary endemics (CE) and between 0.3 and 0.8 for single island endemics (SIE). Again, SIEs consistently showed steeper slopes of SARs when comparing with CEs of the same taxonomic group or habitat. Finally, the number of threatened endemic vascular plant species showed a highly significant exponential relationship with percentage of habitat area loss, especially when controlled for differences between habitat types ($R^2 = 0.57$, partial residuals $R^2 = 0.71$, $p < .001$, Figure 5).

4 | DISCUSSION

Our results showed that, despite the severity of habitat loss that has occurred on the Canary Islands within the last five centuries, current endemic species pools of several taxonomic groups associated with the major natural ecosystems still correspond much better to potential than to current habitat area, evidencing habitat- and taxon-specific EDs for the Canary Islands' biota. For all endemic taxonomic groups and all habitat types studied, current species richness was best explained by potential habitat extent, reflecting the pre-human conditions prior to drastic habitat loss and fragmentation. This consistent pattern suggests that a considerable number of endemic plant and invertebrate species might eventually be driven to extinction in the future without further habitat loss, which has important implications for conservation planning. However, our data did not allow the magnitude of these EDs to be estimated, as information about past species richness and imminent extinctions after habitat destruction is lacking (Halley et al., 2014; Kuussaari et al., 2009). The current number

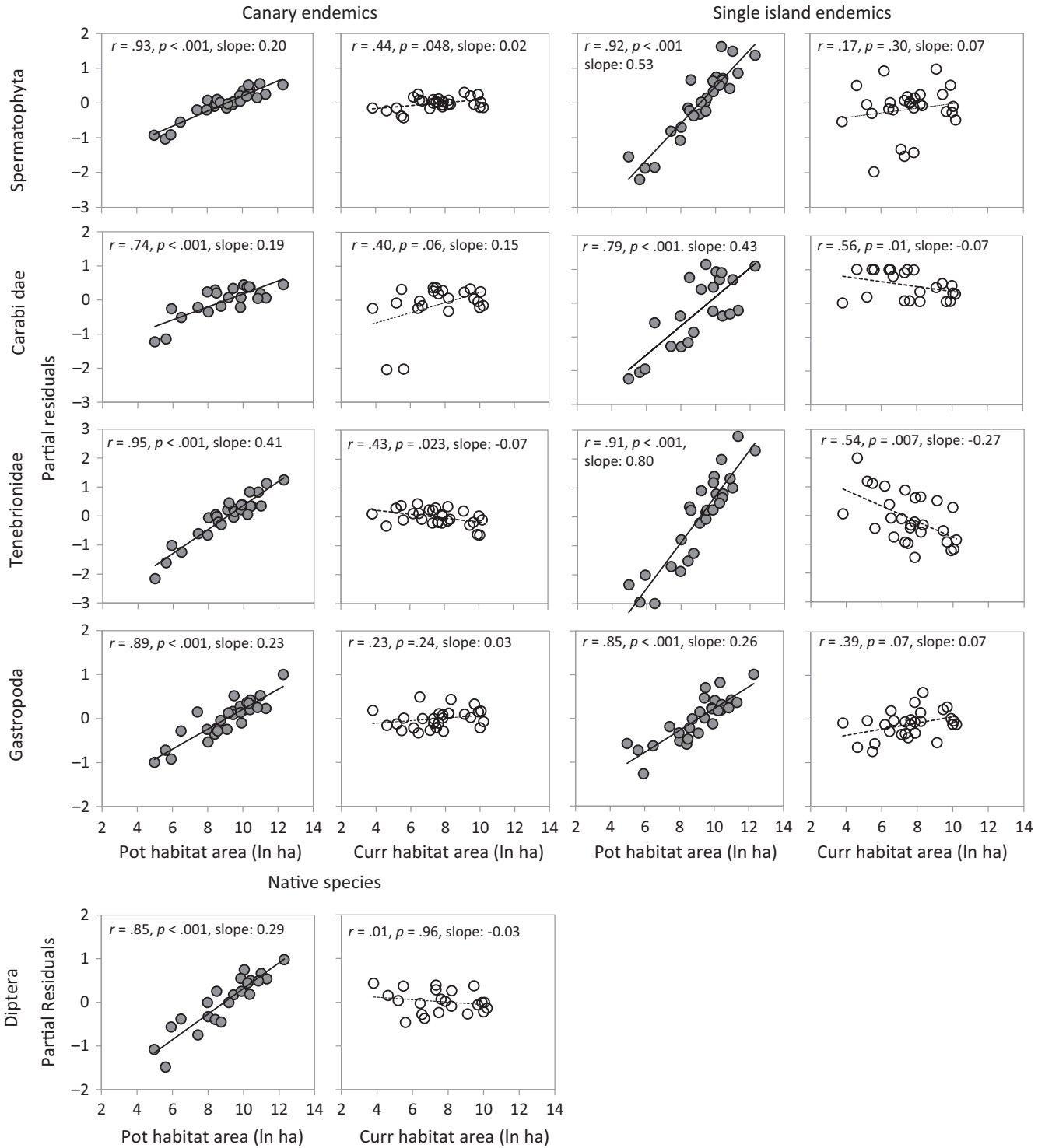


FIGURE 3 Partial residuals of multiple generalized linear models showing the independent importance of potential (pot) versus current (curr) habitat area on current number of Canary endemics and single island endemics for higher vascular plants (Spermatophyta), ground and darkling beetles (Carabidae, Tenebrionidae) and land snails (Gastropoda). For flies (Diptera), only natives were considered. Each plot shows the relationship between the focal variable and the residuals from a model without this variable but including the other explanatory variables (potential or current habitat area, habitat age as single and quadratic term, habitat type) highlighting the independent effect of the focal variable on species richness. For purposes of visual presentation, r and p values of partial regressions for potential and current habitat area are indicated. "Slope" represents the slope coefficients from a generalized linear model (logit link). Partial residual plots for habitat age and habitat type are not shown

of threatened plants per island habitat shown to strongly respond to habitat area loss might reflect the part of the ED that is close to occurring.

We found indications of EDs not only for vascular plants, the group of long-lived species, but unexpectedly also for all short-lived species such as beetles, snails and flies. A slow response of plant

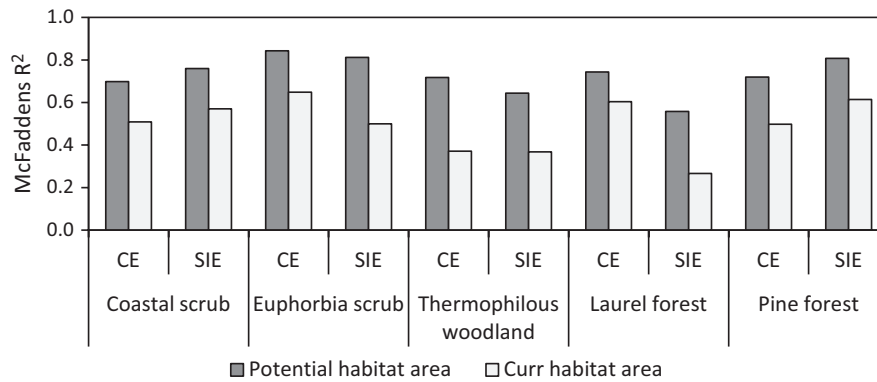


FIGURE 4 Importance of potential versus current habitat area in explaining current number of Canary endemics (CE) and single island endemics (SIE) dwelling in the five major climatic ecosystems (coastal scrub, *Euphorbia* scrub, thermophilous woodland, laurel forest and pine forest). McFaddens R^2 (mean value across taxonomic groups) indicates the deviance explained by the focal predictor in generalized linear models (GLMs) separately applied to each habitat type and taxonomic group (Spermatophyta, Carabidae, Tenebrionidae and Gastropoda)

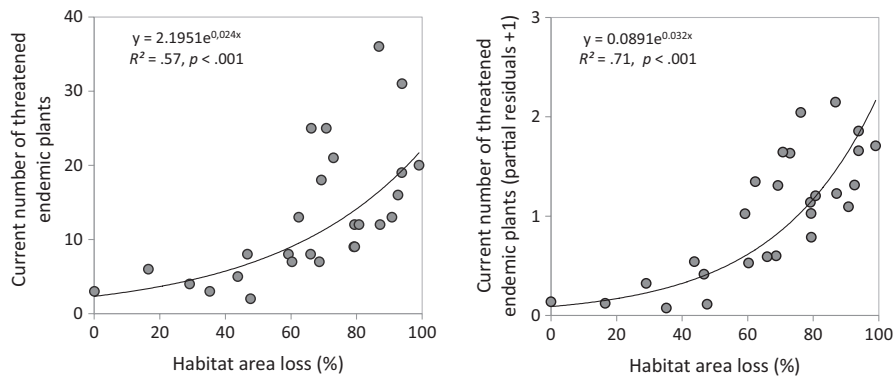


FIGURE 5 Relationship between the current number of threatened plant species endemic to the Canary Islands (IUCN classes critically endangered, endangered and vulnerable) and the percentage (%) of habitat area loss (difference between potential and current habitat area for each island habitat). Points represent the five selected habitat types on the seven Canary Islands ($n = 28$; coastal vegetation 7, *Euphorbia* scrub 7, thermophilous woodland 7, laurel forest 5 and pine forest 5). Partial residuals refer to a generalized linear model with the same variables when controlling for the differences between habitat types

species richness to habitat loss has been repeatedly documented in continental regions (Bommarco et al., 2014; Helm et al., 2006; Krauss et al., 2010; Lindborg & Eriksson, 2004; Vellend et al., 2006), whereas the relatively few assessments for invertebrate groups did not reveal a clear trend. For instance, butterflies showed an ED in semi-natural grasslands in Sweden (Bommarco et al., 2014) and in Estonian alvar grasslands (Sang, Teder, Helm, & Pärtel, 2010), but not in a pan-European grassland study (Krauss et al., 2010). Delayed extinctions are also reported for hoverflies in grasslands, but not for bees (Bommarco et al., 2014). In island settings, invertebrate groups such as spiders and beetles were found to respond very slowly to habitat changes showing large ED (Triantis et al., 2010). Our results support these findings regarding beetles, despite the lack of estimates of delayed extinctions.

However, we detected differences in the strength of evidence for ED among taxonomic groups which were strongest for plants and weakest for flies, which might be explained by differences in generation time and mobility. Flies are the group with the highest dispersal ability and lowest resource selectivity, which should enable species to

adapt more quickly to new landscape configurations and resource distributions. Similar results were documented for true bugs in the Azores with lower levels of predicted extinctions compared to beetles and spiders (Triantis et al., 2010). This is also consistent with some studies on the continent, where butterflies have experienced more severe declines compared with long-lived vascular plants and birds (Thomas et al., 2004). By contrast, endemic beetles and land snails showed strong indication for ED in our study despite their shorter generation time, higher trophic level and active dispersal modes compared to plants, suggesting that they are able to persist in small habitat patches for a long period.

The indirect approach using the species–area relationship (SAR) to detect delayed extinctions has been widely applied and considered a useful tool (Kuussaari et al., 2009), but also questioned (Lewis, 2006). There are several uncertainties related to SAR-based extinction studies such as the use of default slope values ($z = 0.25$) among different taxonomic groups and geographic regions (Brooks et al., 2002) or the usually ignored role of the surrounding human-disturbed matrix of remaining habitat patches for the persistence

of threatened species (Pereira & Daily, 2006). In our approach, we generated specific SARs for each taxon and habitat revealing a high variability of *z*-values (between 0.2 and 0.8) among taxa and habitat types. Interestingly, single island endemics (SIE) consistently showed higher *z*-values compared to Canary endemics for the same taxon and habitat, supporting earlier findings that SIE–area relationships always exhibit higher *z*-values compared to indigenous species–area relationships (Triantis, Mylonas, & Whittaker, 2008). Consequently, SIEs show a higher rate of species loss per unit habitat loss compared to CEs, indicating that these mostly in situ evolved endemics are more affected by habitat area reduction. Hence, SIEs are expected to suffer from large ED.

In our broad approach, we did not analyse either the role of the contemporary landscape mosaic including human-disturbed ecosystems on the extinction process (Pereira & Daily, 2006) or the influence of other possible landscape configurations, that is intermediate stages of the habitat area reduction between the two extremes of habitat extension (Triantis et al., 2010), on the outcome of SAR models due to the lack of data. However, on the Canary Islands, strongly disturbed habitats such as abandoned fields or roadside communities usually harbour native plants with a wide geographical distribution and ecological range but not rare endemic species (Arévalo et al., 2005). Further investigation is still needed to elucidate the role of secondary habitats reflecting different levels of anthropogenic disturbance in the extinction process of threatened species in the Canary Islands.

Our results underline the need to include habitat age to improve habitat SARs for endemic species on oceanic islands (Triantis et al., 2010), even if habitat age is only roughly estimated by the geological age of the island. Despite the uncertainty about the age of the major Canarian ecosystems (Domínguez-Lozano, Price, Otto, & Fernández-Palacios, 2010), we showed that the current number of endemic species typical of a certain habitat not only depends on the spatial but also on the historical abundance of that habitat on an island (Zobel et al., 2011). This is consistent with earlier findings that diversification processes in insular ecosystems are strongly linked to an island's geological history (Borges & Hortal, 2009; Otto et al., 2016; Steinbauer, Otto, Naranjo-Cigala, Beierkuhnlein, & Fernández-Palacios, 2011; Whittaker, Triantis, & Ladle, 2008). Furthermore, changes in island and habitat areas throughout geological history related to climate change might also have influenced speciation rates and endemic species pools on oceanic islands (Fernández-Palacios, 2016; Fernández-Palacios et al., 2016; Rijdsdijk et al., 2014).

Some plant and invertebrate species have probably already become extinct due to habitat loss as the first human settlement of the Canary Islands and before the onset of scientific research. These include all imminent extinctions due to immediate loss of all populations of an endemic species after habitat area contractions, and the first delayed extinctions after a certain time-lag (Halley et al., 2014). However, our SAR models suggest that there might be relatively few compared to the high present-day diversity of local endemics. Reports on recent extinctions of known species are extremely rare for this archipelago, up to now only five endemic and two native plants, one

endemic land snail and two endemic beetles have been considered extinct, whereas no extinctions have been confirmed for flies so far (Ibáñez & Alonso, 2001; de Nascimento, Willis, Fernández-Palacios, Criado, & Whittaker, 2009; Bañares, Blanca, Güemes, Moreno, & Ortiz, 2010; M. Báez and P. Oromí unpublished data). Drastic declines in populations and disappearances for decades have been reported for several land snails and beetles. On the other hand, nine endemic bird extinctions (six of them pre-description extinctions) probably related to negative effects on human colonization have been documented for the Canaries representing almost two-thirds of all known bird species endemic to this archipelago (Illera, Rando, Richardson, & Emerson, 2012; Illera, Spurgin, Rodríguez-Expósito, Nogales, & Rando, 2016). Most of these extinct birds were ground nesters and flightless or weak fliers showing increased susceptibility to hunting, habitat destruction and introduced alien species. Hence, in contrast to plants and invertebrates, a possible ED for endemic birds has already been paid to a great extent on the Canary Islands. In this context, we have to consider that extinctions are more difficult to prove for both invertebrates and plants than for vertebrates. Some invertebrates considered extinct have been rediscovered.

In general, our results seem comparable to the situation in the Azores where 54%–99% of the forest-dependent arthropod species might become extinct due to deforestation since pre-human conditions (Triantis et al., 2010). The temporal scale of extinction processes on both Atlantic archipelagos is similar to most habitat reduction having occurred within the last 600 years after European colonization indicating relaxation times of centuries even for short-lived species. Hence, these findings should alert conservationist to possible mass extinctions of endemic species on oceanic islands in the future if no restoration actions are taken. Restoration efforts should concentrate on areas with greatest habitat loss and ED (Wearn et al., 2012). As the number of threatened species, in our case regarding vascular plants, is assumed to represent at least part of the ED (Brooks et al., 1997; Olivier et al., 2013), our approach enables the localization of the island and the habitat type where restoration projects should be most urgently implemented. However, our analysis showed a generalized ED for single island endemics across taxonomic groups indicating the need to conserve and restore heavily destroyed habitats on all islands not only on one specific island in order to avoid possible future extinctions. Consequently, we highlight the need to restore the Canary thermophilous woodland, the worst preserved ecosystem with the highest level of threatened endemic plants but the richest in SIEs (Fernández-Palacios et al., 2008).

Additionally, we should consider that the time-lag in extinctions may not be properly reflected in the current red lists, and that red lists actually underestimate extinction risks (Dullinger et al., 2013). This means that the number of threatened species will probably increase without further habitat loss, especially for habitats that were most recently disturbed. On the Canary Islands, population growth and land use changes have increased strongly during the 20th century. Consequently, we would expect that the list of threatened Canary endemics will increase in the near future, especially for the lowland

habitats most affected by agriculture, urbanization and touristic development.

In this study, we analysed the response of overall endemic species pools to recent habitat destruction and warn of possible future extinctions due to delayed extinction processes. However, our data set, probably the largest used to test ED on oceanic islands, did not allow the calculation of the magnitude of ED or conclusions or predictions to be made for individual species (Kuussaari et al., 2009). To simplify, we identified broad habitat entities that encompass environmental variation and that could easily be subdivided into different vegetation types (del Arco et al., 2010). Therefore, our approach does not enable us to predict the extinction risks of particular species, especially for endemics with a very restricted ecological niche and geographic range and which are highly vulnerable to idiosyncratic habitat loss. Standardized monitoring projects for rare endemics are needed to obtain long-term data about population dynamics and to estimate individual extinction risks.

We conclude that both plants and invertebrates showed delayed extinctions after habitat destruction and fragmentation in the Canary Islands, although we were not able to estimate the corresponding magnitudes and time-lags with the available data. This is of great conservation interest as many island systems represent global hotspots of biodiversity (Brooks et al., 2002; Myers, Mittermeier, Mittermeier, Fonseca, & Kent, 2000). On the one hand, our results highlight the high extinction risk of different taxa of the Canary biota depending on habitat type and landscape history of each island, reflected by trends of currently threatened vascular plants. On the other hand, the existence of an unpaid ED also provides opportunities for carefully directed management and conservation projects and points to the need for habitat restoration to attenuate or even reverse current extinction processes (Wearn et al., 2012). The case of the Canary archipelago is probably not unique, and our approach to detect EDs may be applicable to many other oceanic island groups, where detailed information about dynamics of habitat loss and species richness is available. Our study might, therefore, contribute to increase the awareness of potential extinctions debts and to maintain biodiversity on islands.

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AUTHOR CONTRIBUTIONS

R.O. and V.G.-M. conceived the idea; R.O., V.G.-M., M.d.A., S.F., P.O., M.B., M.I. and M.A. compiled data; R.O. performed the statistical analyses of the data; R.O., V.G. and S.F. carried out GIS analyses; R.O. and J.M.F.-P. led the writing; and all authors contributed to the writing process.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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