PROCEEDINGS B

royalsocietypublishing.org/journal/rspb

Research

Cite this article: Santos M, Vázquez DP, Resasco J. 2025 Extinction debt of species and ecological interactions in a fragmented landscape. *Proc. R. Soc. B* **292**: 20251640.
https://doi.org/10.1098/rspb.2025.1640

Received: 23 June 2025
Accepted: 22 August 2025

Subject Category:
Ecology

Subject Area:
ecology

Keywords:
immigration credit, biodiversity loss, habitat fragmentation, fragment connectivity, metacommunity, fragmentation time

Author for correspondence:
Micaela Santos
e-mail: msantos@mendoza-conicet.gob.ar

Electronic supplementary material is available online at https://doi.org/10.6084/m9.figshare.c.8003574.

THE ROYAL SOCIETY
PUBLISHING

Extinction debt of species and ecological interactions in a fragmented landscape

Micaela Santos[1], Diego P. Vázquez[1,2] and Julian Resasco[3]

[1]Instituto Argentino de Investigaciones de las Zonas Aridas, Mendoza, Argentina
[2]Universidad Nacional de Cuyo Facultad de Ciencias Exactas y Naturales, Mendoza, Mendoza, Argentina
[3]University of Colorado Boulder Department of Ecology and Evolutionary Biology, Boulder, CO, USA

MS, 0000-0003-4728-3653; DPV, 0000-0002-3449-5748; JR, 0000-0003-1605-3038

Addressing the worldwide biodiversity crisis in fragmented landscapes requires considering both immediate and delayed extinctions—the extinction debt. This debt arises from the gradual loss of species following habitat fragmentation. Additionally, species interactions may also experience an extinction debt, affecting ecosystem structure and function. However, the extinction debt for species interactions has received little attention. We studied the lasting effects of habitat fragmentation on plants, herbivore insects of four trophic guilds, parasitoids and their trophic interactions in a dryland landscape in central-western Argentina. Assuming a paid debt in long-fragmented habitats, we examined the potentially unpaid debt in recently fragmented habitats as the difference between the current richness of species and interactions and their expected richness based on area and connectivity from long-fragmented habitats. We found a higher extinction debt for herbivores and plant–herbivore interactions in small, isolated habitats and a lower extinction debt for plants only in small habitats. By contrast, the extinction debt of parasitoids was higher in large, well-connected habitats, while there was no extinction debt detected for herbivore-parasitoid interactions. Understanding the magnitude of extinction debts for species and interactions offers guidance for mitigating future extinctions of species and interactions to curb the degradation of ecosystems and preserve their long-term function.

1. Introduction

Understanding the drivers of the current biodiversity crisis is among the most urgent challenges for ecologists. Most of the evidence identifies habitat loss owing to land use changes as the main driver of biodiversity loss, while the effects of habitat fragmentation *per se* have stirred debate [1,2]. Habitat destruction involves both habitat loss and fragmentation operating simultaneously, resulting in progressively smaller, more isolated habitat fragments [3]. As a result of decreased fragment area and connectivity, local species extinctions can be either immediate or delayed [4]. Delayed extinctions result in an apparent excess of richness in local communities that have experienced habitat fragmentation in the past—the extinction debt, defined as the difference between current and expected species richness after the delayed extinctions have occurred [5]. However, empirical quantification of the delayed extinctions of ecological interactions themselves have received little attention. Thus, the extinction debt implies that some extant species and their interactions will go extinct owing to past habitat destruction, even without new habitat loss or fragmentation. Therefore, quantifying the extinction debt of species and their interactions in fragmented landscapes would help to address both current and future biodiversity loss and its potential consequences for ecosystems [6].

The future loss of species interactions could influence ecosystem dynamics and stability, as they support crucial ecological functions such as herbivory, predation and pollination [7]. Although several studies suggest that species interactions are often lost before the interacting species themselves [8], implying a shorter extinction debt for interactions, it remains unclear how delayed extinctions of ecological interactions occur in fragmented habitats [9]. If interaction extinctions precede species extinctions, the extinction debt of interactions could be paid faster than the extinction debt of species, accelerating ecosystem decline by co-extinction cascades and loss of ecosystem functions [10]. Therefore, assessing the extinction debt of interactions in recently fragmented habitats would help prevent future co-extinction cascades and mitigate the lasting effects of habitat loss and fragmentation on ecological communities.

Estimating extinction debts of both species and interactions requires assessing the time elapsed since the beginning of habitat loss and fragmentation [11]. Once habitats have been fragmented, local communities typically experience a relaxation process over time governed by colonization–extinction dynamics [12]. During this process, species (especially habitat specialists) [13] become gradually extinct until the community reaches a new colonization–extinction equilibrium corresponding to the current fragment area and connectivity, leading to a lower species richness. Thus, in recently fragmented habitats, the number of delayed extinctions will be proportionally higher than in long-fragmented habitats, where the relaxation process probably has already occurred [14]. Likewise, the extinction debt will initially be larger just after the habitat loss in small, isolated habitats than in large, well-connected habitats that have lost a lower proportion of area and connectivity. However, over time, small and isolated fragments should lose species faster than larger, well-connected fragments because they have a higher extinction risk and lower recolonization rates [15], so they will pay the extinction debt first. Therefore, both fragmentation history at a landscape scale and changes in area and connectivity at the fragment scale could affect community dynamics [16,17].

In addition to time since the beginning of fragmentation, and changes in fragment area and connectivity, the magnitude of the extinction debt will depend on trophic level and species traits [4,18]. This variation in time to extinction results from traits influencing the persistence abilities of species, such as longevity and clonality in plants [19], and traits related to dispersal ability in both plants and animals, which probably promote rescue effects of small threatened populations contributing to metapopulation persistence [20,21]. However, thresholds for functional connectivity are considerably different for mobile and less mobile species, suggesting that rescue effects could be faster for the former. Therefore, a particular fragment may have an extinction debt of a certain trophic level or guild, but not of another [22]. Few studies have compared the extinction debt across different trophic levels or guilds [23]; instead, most studies have focused on a particular guild, especially plant communities in European grasslands [24]. These studies have shown that delayed extinctions may range from decades to hundreds of years for plants [25] and animal taxa [15,26], and usually a shorter time for microorganisms in microcosms [27]. These generalizations are especially valid for habitat specialist species, as habitat fragmentation can result in the immigration of generalist and ruderal species into fragments [2].

Here, we studied the response of plants, herbivore insects of four trophic guilds, parasitoids and their trophic interactions to lasting effects of habitat loss and fragmentation in 14 dryland habitat fragments surrounded by an agricultural matrix in central-western Argentina. We hypothesized that: (1) as time since fragmentation decreases and the magnitude of fragmentation increases, the extinction debt in a habitat fragment increases, such that the extinction debt is greatest in recently fragmented habitats that have lost more area and connectivity (figure 1); (2) the magnitude of the extinction debt differs among trophic levels because long-lived species (perennial plants) require a longer time to become extinct than short-lived species (insects and annual plants), and higher trophic levels (parasitoids) are more sensitive to habitat changes than lower trophic levels (plants and herbivores) so they should become extinct first [28]; (3) if hypothesis 2 is supported, the extinction debt should be paid faster for herbivore–parasitoid interactions than for plant–herbivore interactions. Assuming a paid extinction debt in long-fragmented habitats, we examined the potentially unpaid extinction debt in recently fragmented habitats, as the difference between the observed current richness of species and trophic interactions in recently fragmented habitats and the expected richness for area and connectivity relationships in long-fragmented habitats. In this context, we expected: (i) for both species and trophic interactions, weaker or strongly negative current richness-area and richness-connectivity relationships in recently than in long-fragmented habitats, especially for recently fragmented habitats with higher proportion of area and connectivity loss (differences in current and past area and connectivity); (ii) a greater extinction debt in current small, isolated habitats with higher proportion of area and connectivity loss than large, well-connected habitats with lower proportion of area and connectivity loss exhibiting a greater proportion of extinction debt for insects than for plants, and a greater proportion of extinction debt for herbivores than for parasitoids; and finally (iii), a greater proportion of extinction debt for plant-herbivore interactions than for herbivore–parasitoid interactions.

2. Methods

(a) Study area

To assess the extinction debt of species and trophic interactions, we selected 14 remnant habitat fragments of Monte Desert in an agricultural region of central-western Argentina (Valle de Uco, Mendoza Province) within an area of approximately 50 000 ha (electronic supplementary material, figure S1 [29]). This ecoregion is characterized by a semi-arid climate with precipitation dominating during spring and summer, and mean annual precipitation around 150–350 mm [30]. Monte native vegetation is predominantly xerophytic, constituted by shrubs (e.g. *Larrea* spp.), cacti (e.g. *Opuntia sulphurea*), perennial grasses (e.g. *Stipa* spp.) and herbs (e.g. *Oenothera odorata*) and a small proportion of annual herbs (e.g. *Gamochaeta spicata*) (electronic supplementary material, figure S2a). The matrix surrounding Monte fragments is a mostly homogeneous agricultural cover constituted by

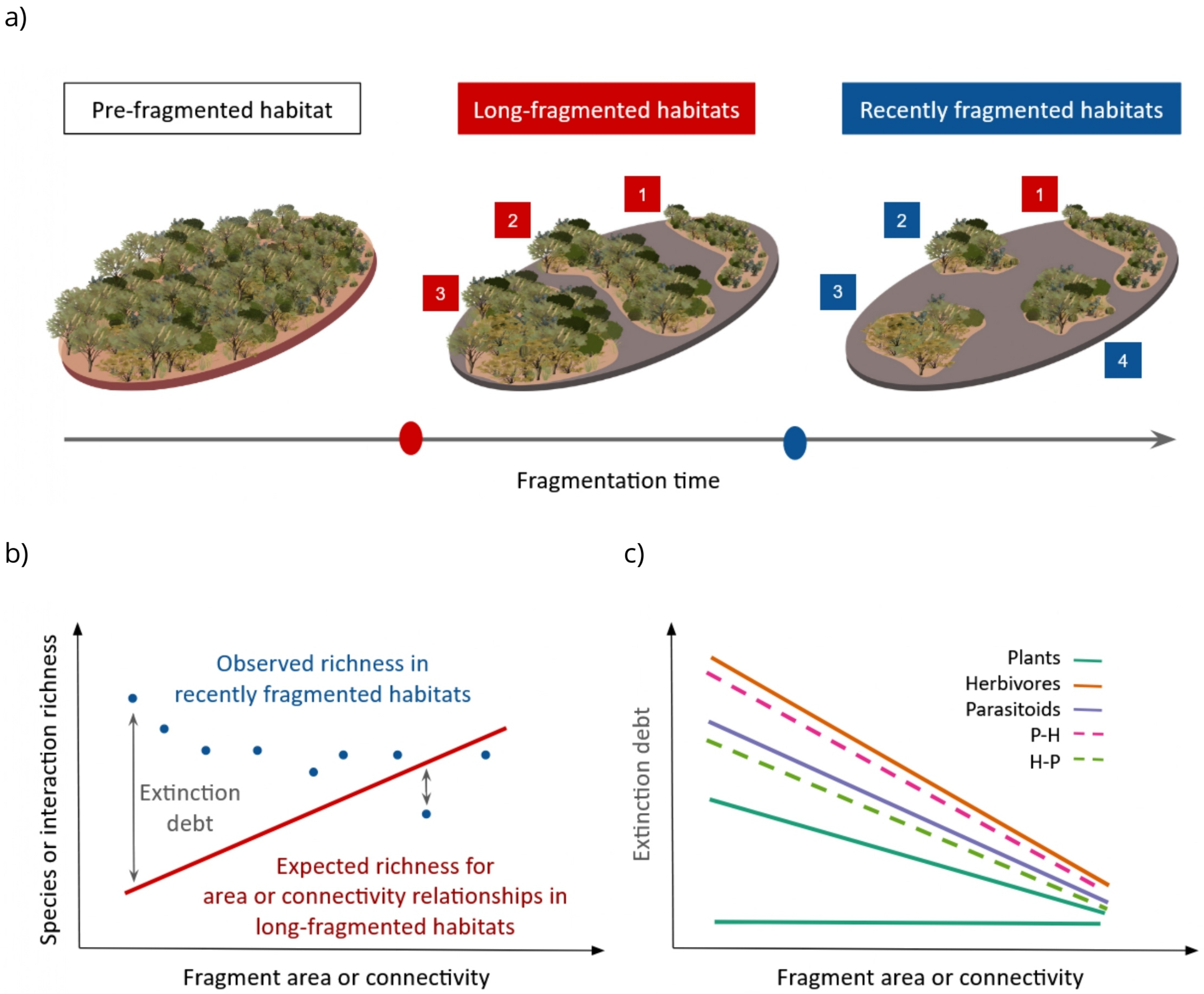

Figure 1. Conceptual representation of hypotheses and predictions evaluated in this study. (a) Schematic representation of habitat destruction over time. A hypothetical habitat undergoes an initial fragmentation event (red oval), resulting in three habitat fragments. In a subsequent fragmentation event (blue oval), fragments 2 and 3 lose area and connectivity. Fragment 2 further splits, resulting in a new fragment (habitat 4), and fragment 1 loses connectivity owing to changes in the surrounding habitat, even though its area remains unchanged. Thus, fragment 1, which remains unaltered over time, represents a long-fragmented habitat. By contrast, fragments 2–4, which have changed by the last fragmentation event, represent recently fragmented habitats. (b) Methodology used to estimate the magnitude of extinction debt in recently fragmented habitats, as the positive difference between the current richness of species and interactions and the expected richness based on area and connectivity relationships in long-fragmented habitats, while negative differences might indicate an immigration credit (c) Expected relationships between extinction debt and fragment area and connectivity for studied species and interactions in recently fragmented habitats.

vineyards and to a lesser extent by other crops (e.g. walnut orchards) or urbanized cover (e.g. roads, rural streets or human settlements; electronic supplementary material, figure S2b). Species of the Monte Desert are typically habitat specialist species, although exceptionally some species such as native herbs (e.g. *Oe. odorata*) may prosper in vineyard borders, while some ruderal and generalist species (e.g. *Portulaca oleracea*) thrive in vineyards and occasionally get into the Monte vegetation. We defined a habitat fragment as any patch of remnant native vegetation with more than 70% of its perimeter surrounded by strongly modified habitat and without indication of strong human disturbance within the fragment area. Selected fragments span 3.1–371.2 ha (s.d. = 136.2 ha), and are separated from each other by approximately 0.1–20 km (s.d. = 4.87 km) (for more details see [25]).

(b) Fragmentation time

To distinguish between long-fragmented habitats and recently fragmented habitats, we used the *timelapse* tool in GoogleEarth-Pro to track cover changes over the past approximately 30 years (1984–2017). A visual analysis of the oldest map (1984) revealed initial habitat loss and fragmentation spreading from east to west. A long-term analysis of changes in our study area showed high cropland persistence in the east between 1986 and 2018 [31], confirming that Monte desert habitats located in the east were fragmented before 1986. Therefore, the rationale of this categorization is that long-fragmented habitats have started the relaxation process earlier, regardless of how much area has been lost. The low resolution of available images prevented precise measurement of landscape features from 1984 to 2003. Consequently, we defined long-fragmented habitats as fragments that experienced significant changes before 2003, and recently fragmented habitats, after 2003 (electronic supplementary material, figure S1). This classification implies that long-fragmented habitats have remained constant in area since 2003 to the present (but they are much older), while their connectivity has changed owing to ongoing surrounding landscape changes. By contrast, recently fragmented habitats have experienced changes in both area and connectivity from 2003 to the present (figure 1a). As a result of this classification, we distinguished two subsets of five long-fragmented habitats representing the stable habitats of reference, and nine recently fragmented habitats representing the unstable habitats with a presumably unpaid debt.

(c) Area and connectivity of fragmented habitats

We measured current areas and connectivities using the 2015 map, while for past areas and connectivities we used the 2003 map (electronic supplementary material, figure S1a,b). To calculate areas and distances, we used *st_area* and *st_distance* of the *sf* package in R [32], respectively, providing a vectorized map of present and past landscape. We considered the distances edge-to-edge among both sampled and unsampled fragments in the landscape and distance to continuous habitat. In the past landscape, for habitats that currently still have an adjacent border to continuous habitat, we maintained the borders with the continuous habitat identified in the present, to avoid overestimating the past areas. To estimate fragment connectivity, we calculated the sum of the shortest geographical distances between neighbouring fragments, i.e. $\sum d_{ij}$, where d_{ij} represents the distance between fragments i and j. We used this basic structural metric instead of distance weighted by area of neighbouring fragments because, as mentioned above, in the past landscape, some of the recently fragmented habitats were connected to the continuous habitat. However, for the current landscape, we also tested connectivity considering distance weighted by area of neighbouring fragments. To estimate area loss and connectivity loss, we calculated the difference between past and current area and connectivity.

(d) Species and interaction sampling

To estimate current richness of plants, herbivorous insects, parasitoids and their trophic interactions in the habitat fragments, we sampled at the centroid of each fragment in the austral spring and summer between 2015 and 2017 (electronic supplementary material, figure S2a). For plants, we applied the point-intercept method along four 50 m transects defining a square centred at fragment centroids, with sampling points every 2 m. For herbivorous insects and their interactions with plants, we collected galls on leaves and stems, mined leaves, aphid colonies (family Aphididae) and scale insects (superfamily Coccoidea) on all shrubs and herbs, along two 50 × 2 m transect bands. We measured interaction richness as the number of individual interactions of plant-gall, plant-mine, plant-aphid colony and plant-scale insect observed in the field. For parasitoids and their interactions with herbivores, we raised insects into galls and mines and parasitized aphids (‘mummies’) and scale insects. After 1 year, we identified all species and morphospecies emerged from galls, mines and parasitized insects, then with the help of experts, we assigned individuals to the most likely trophic guild: gall maker or mine maker, inquiline of gall or mine, or parasitoid. Finally, we measured the richness of herbivore–parasitoid interactions as the number of individual interactions of gall–parasitoid, mine–parasitoid, aphid colony–parasitoid and scale insect-parasitoid observed in the laboratory (for more details see table S1 in [29]).

(e) Statistical analyses

(i) Current richness-area and richness-connectivity relationships of species and interactions in fragmented habitats

To compare slopes of current richness-area and richness-connectivity relationships of species and interactions between recently and long-fragmented habitats, we built separate area and connectivity models for each trophic level (plants, herbivores, parasitoids) and interaction type (plant–herbivore and herbivore–parasitoid interactions) including all studied fragments. We built generalized linear models (GLMs) with the effects of current area or connectivity interacting with fragmentation time (a1 and c1), the effects of current area or connectivity loss interacting with fragmentation time (a2 and c2) and the effects of area and area loss, or connectivity and connectivity loss interacting with fragmentation time (a3 and c3, respectively). These last models test whether the proportion of area and connectivity loss intensifies the current area and connectivity effects. In all these six models, we included *fragmentation time* as a categorical variable and richness of species and interactions as a response variable. We standardized predictor variables as z-scores (mean of zero and s.d. of 1) to obtain standardized regression coefficients, which can be directly comparable to each other. In addition, we used Akaike’s information criterion (AIC) to select the best-fitting area and connectivity model, considering that models with differences of AIC values less than two have similar fits.

(ii) Extinction debt of species and interactions in recently fragmented habitats based on area and connectivity relationships in long-fragmented habitats

To estimate the extinction debt of species and interactions in recently fragmented habitats, we followed [33], who built GLMs for stable habitats (here categorized as long-fragmented habitats) to predict richness in unstable habitats (here categorized as recently fragmented habitats). We assumed that long-fragmented habitats have already paid their extinction debt or at least have started to pay it before, thus both species and interaction richness tend to be at or closer to equilibrium with current

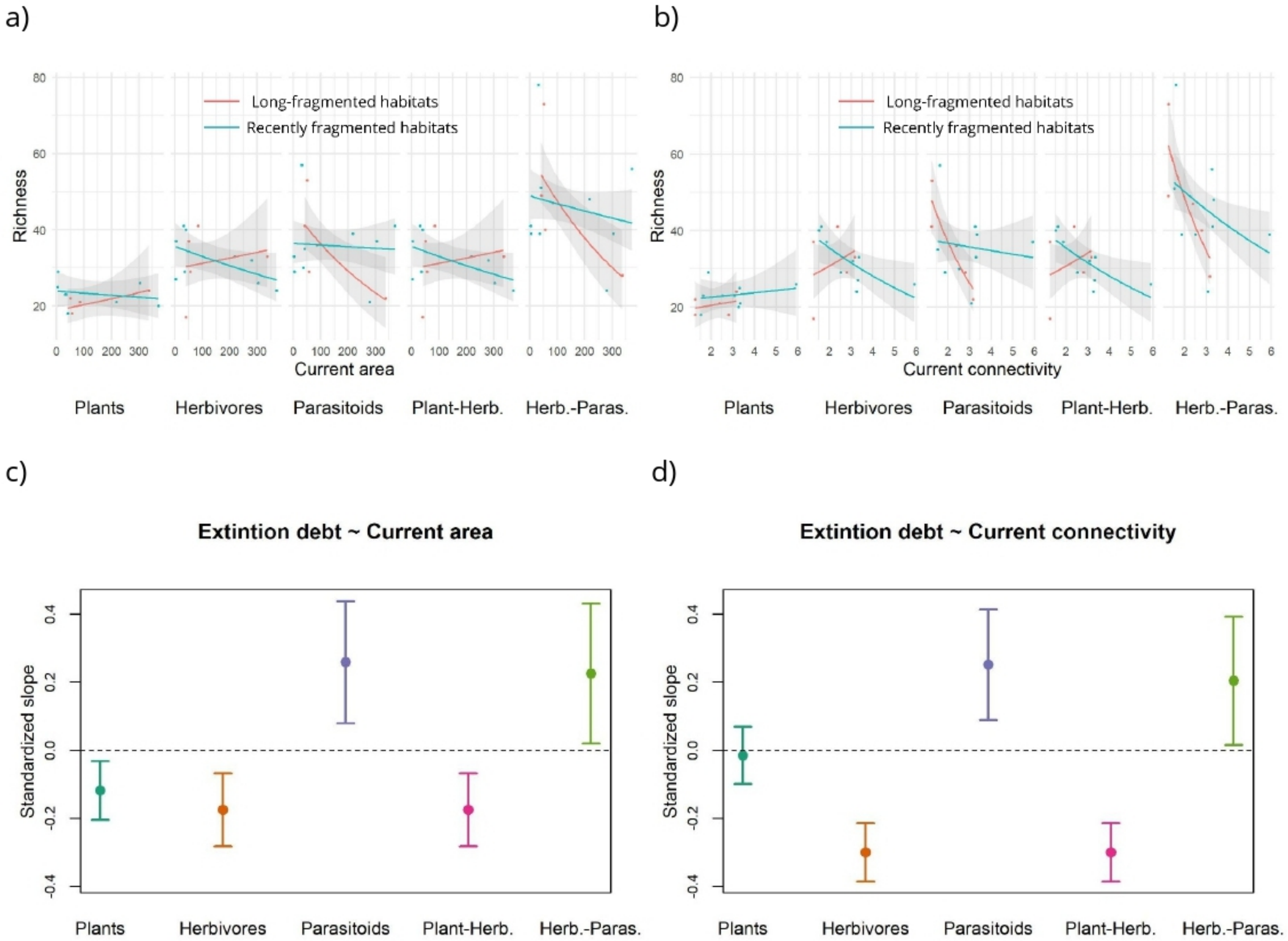

Figure 2. (a) Relationships between species and interaction richness and fragment area, and (b) fragment connectivity. (c) The strength of the relationship (standardized regression coefficient ± s.e.) between extinction debt for plants, herbivores, parasitoids, plant–herbivore interactions and herbivore–parasitoid interactions and area, or (d) connectivity in recently fragmented habitats. Labels in the abscissa match those in the same positions in the bottom panels. Extinction debt was quantified as the difference between the observed richness in recently fragmented habitats and the expected richness based on relationships observed in long-fragmented habitats.

area and connectivity. We first performed two separate GLMs for long-fragmented habitats using either current area and connectivity as predictors and the observed current richness as the response. Then, we calculated the difference between the current observed richness in recently fragmented habitats and the predicted richness using the estimated parameters based on area and connectivity models in long-fragmented habitats, and divided by observed richness. Therefore, a richness difference greater than zero indicates an extinction debt in a habitat fragment. To calculate predicted richness in recently fragmented habitats, we used the *predict* function from the *stats* package in R. As we aimed to compare the magnitude of extinction debt among trophic levels and interaction types, we calculated the proportion of species and interactions that will go extinct, divided by total richness at each trophic level and interaction type. Thus, to assess whether all recently fragmented habitats exhibited an extinction debt, we tested the departure of the extinction debt mean from zero using Student's *t*-test after checking the fit of the data to the normal distribution. Finally, to assess whether the extinction debt in recently fragmented habitats increases as the magnitude of habitat fragmentation increases, we built alternative GLMs using current area or connectivity, and area or connectivity loss as standardized variables. We built individual models to maintain simplicity, to interpret separately each predictor and to avoid issues arising from the potential collinearity among variables. Finally, to compare the strength of the relationships, we employed standardized regression coefficients (±s.e.). We carried out all statistical analysis with R software.

3. Results

(a) Current richness-area and richness-connectivity relationships for species and interactions in fragmented habitats

Our first hypothesis posits that as time since fragmentation decreases and the magnitude of fragmentation increases, the extinction debt in a habitat fragment increases, such that the extinction debt is greatest in recently fragmented habitats that have lost more area and connectivity. Thus, we predicted for both species and trophic interactions in recently fragmented habitats, weaker or strongly negative current richness-area and richness-connectivity relationships than in long-fragmented habitats, especially for recently fragmented habitats with a higher proportion of area and connectivity loss. According to the best-fitting models detailed below, we observed strongly negative richness-area and richness-connectivity relationships in recently fragmented habitats than in long-fragmented habitats for herbivores and plant-herbivore interactions (figure 2a,b). Furthermore, we observed weaker richness-area and richness-connectivity relationships in recently fragmented habitats than in long-fragmented habitats for parasitoids and herbivore–parasitoid interactions, regardless of negative relationships. However, for plants, we observed no differences between slopes of recently and long-fragmented habitats for richness-area and richness-connectivity relationships (electronic supplementary material, table S1). Annual plant species represented only 15% species and were recorded in low abundances.

The best-fitting area model for both plant–herbivore interaction richness and herbivore richness, included the triple interaction between the variables *area loss* that intensified the effect of *current area* and *fragmentation time*, leading to increased richness in smaller recently fragmented habitats which have lost more area (electronic supplementary material, table S1; triple interaction intercept = −1.423, *p*-value = 0.004). Similarly, for the same trophic level and interaction type, the best-fitting connectivity model included the triple interaction among the variables *connectivity loss*, *current connectivity and fragmentation time*, but it was not significant (electronic supplementary material, table S1; triple interaction = −0.3599, *p*-value = 0.1757); instead, the effect of current connectivity was more strongly positive as connectivity loss increased regardless of fragmentation time.

In addition, the best fitting area model for parasitoids included the interaction between *area loss* and *current area* (electronic supplementary material, table S1; parasitoids, model c3), but we selected the model including only *current area* because it includes significant predictors and clearer interpretability, while the best fitting connectivity model included only *current connectivity* (electronic supplementary material, table S1; parasitoids, model a1 and c1). Furthermore, the same selected models were observed for herbivore–parasitoid interactions, leading to a more negative effect with connectivity loss (electronic supplementary material, table S1; herbivore–parasitoid interactions, model c3).

(b) Extinction debt of species and interactions in recently fragmented habitats

Mean extinction debt in recently fragmented habitats overlapped with zero, which indicates that not all fragments had an extinction debt (electronic supplementary material, figure S3). In fact, the extinction debt of herbivores and plant–herbivore interactions decreased with current area, and current and past connectivity, while for plants it decreased only with current area (figure 2c,d; electronic supplementary material, figure S4). Furthermore, the magnitude of extinction debt was higher for herbivores and plant–herbivore interactions than for plants (figure 2c,d). In addition, the extinction debt of parasitoids increased with current area and current and past connectivity, while the extinction debt of herbivore–parasitoid interactions marginally increased with current area and connectivity (figure 2c,d; electronic supplementary material, figure S4).

4. Discussion

In this study, we found that richness-area and richness-connectivity relationships for species and trophic interactions were weaker or strongly negative in recently fragmented habitats than in long-fragmented habitats. This finding suggests delayed extinctions—an extinction debt for species and interactions. However, these relationships did not differ significantly between recently and long-fragmented habitats for plants, suggesting that delayed extinctions will still occur in long-fragmented habitats. Additionally, we observed that area loss and connectivity loss in the last 30 years intensified effects of current area and connectivity for plant–herbivore interactions, meaning that greater historical habitat loss leads to a greater current habitat effect. Specifically, we found a higher extinction debt of herbivorous insects and plant–herbivore interactions in small, isolated fragments, than for plants, which occurred only in small fragments. Conversely, large, well-connected fragments exhibited an extinction debt for parasitoids, but not for herbivore–parasitoid interactions, which may have already been paid. Overall, our findings reveal that current and historical area and connectivity drive the extinction debt in recently fragmented habitats differently across trophic levels and interaction types.

(a) An extinction debt for plants?

Habitat loss and fragmentation in the Monte Desert have intensified over the last 30 years in the study area, mainly owing to the expansion of agriculture towards the west, particularly vineyards [31]. However, the typical woody, xerophytic vegetation of this ecoregion exhibits a slower relaxation after habitat changes compared to the associated herbivore and parasitoid insects, driving the current weaker species-area and species-connectivity relationships. As expected, plant richness in long-fragmented habitats had steeper area and connectivity relationships than in recently fragmented habitats, although these differences were not statistically significant. This weak effect of area and connectivity on plant richness may indicate that large, well-connected long-fragmented habitats have not fully paid their extinction debt, leading to a plant richness similar to that of recently fragmented habitats of equivalent area and connectivity. Thus, we should expect that the unpaid extinction debt is actually higher for plants, because it is still running in both recently and long fragmented habitats.

However, we identified an extinction debt for plants in small, recently fragmented habitats, which makes sense given that perennial plants tend to persist for long periods in small fragments below their extinction thresholds [34]. We hypothesized that long-lived species (perennial plants) require a longer time to become extinct than short-lived species (insects and annual plants); thus after 30 years of habitat fragmentation, we expected a higher proportion of extinctions for short-lived species than for long-lived species in long-fragmented habitats, creating a larger proportion of extinction debt for short-lived than long-lived species in recently fragmented habitats. Aligning with this, we found a lower extinction debt for plants than their associated herbivore insects in small recently fragmented habitats, but instead no debt related to present connectivity. This lack of effect of current connectivity on extinction debt of plants probably results from the stronger effects of isolation on plants, which as sessile organisms should experience faster isolation effects than insects, which can often move through the landscape and colonize neighbouring habitats. Alternatively, we found a similar current connectivity effect in both long fragmented and recently fragmented habitats because of small seeded species, seeds adapted to wind or animal dispersal can be very effective dispersal agents (regardless of fragmentation time in habitats), thus maintaining the habitat fragments functionally connected; alternatively, this non-directional but effective dispersal can result in a significant loss of propagules, as they may land in habitats (e.g. arable land or sealed surfaces) unsuitable for seedling establishment. Therefore, the unpaid extinction debt in small, recently-fragmented habitats offers the opportunity to prevent future plant extinctions with efficient landscape management, such as maintaining functional connectivity.

(b) The extinction clock ticks faster for parasitoids than herbivores

Habitat loss and fragmentation affected parasitoids and their interactions with herbivores more strongly than herbivores, especially in small, isolated fragments. Surprisingly, however, richness of parasitoids and their interactions decreased with area and connectivity in both long- and recently fragmented habitats. Thus, richness may not have reached an equilibrium with current area and connectivity, allowing populations to persist in small and isolated habitats over time. One potential explanation for this observation involves the decoupling of extinctions of herbivores and parasitoids in long-fragmented habitats, followed by compensatory dynamics driving immigration credits. These immigration credits refer to immigration of new species owing to habitat loss or fragmentation [30], or to newly available habitat (e.g. reforested area, increasing connectivity between habitat fragments, environmental change such as climatic shift and so on). As higher trophic levels are more susceptible to habitat changes than lower trophic levels, this may lead to faster local parasitoid extinctions (mainly of specialists) and increased local herbivore density creating favourable new conditions to potential immigrants from the surrounding habitats. In turn, parasitoid immigration from neighbouring fragments and the non-fragmented habitat should gradually increase local richness (mainly generalists) and compensate for parasitoid extinctions [35, 36]. This scenario seems quite plausible, as this region harbours large tracts of natural vegetation in the west as a potential source of migrants (electronic supplementary material, figure S1b). As a result, this kind of metacommunity dynamics, called *mass effect* [37], may lead to flatter, or even negative, richness-area relationships in the long fragmented habitats such as we observed [38].

For herbivores and their interactions with plants, richness increased with current area and connectivity in long-fragmented habitats, suggesting that richness may have reached an equilibrium; by contrast, richness decreased with area and connectivity in recently fragmented habitats, suggesting an extinction debt. Furthermore, similar to plants, richness is no longer at equilibrium with past connectivity for long-fragmented habitats (electronic supplementary material, figure S3), suggesting a paid extinction debt. Additionally, area and connectivity loss over the last 30 years has exacerbated the current effects of area and connectivity in recently fragmented habitats, therefore, recent small fragments that have lost more area are richer than those that have lost less, and current isolated fragments that have lost little connectivity are richer than those that have lost more. This result suggests that fragments with smaller areas or lower connectivity over long periods have experienced more species and interaction extinctions. Failing to consider these interacting effects between current and historical area and connectivity may result in inconsistent evidence of an extinction debt.

(c) Do trophic interactions pay extinction debts faster than interacting species?

Based on previous studies, which suggest that species interactions are often lost before the interacting species themselves, we hypothesized that the extinction debt should be paid faster for herbivore–parasitoid interactions than for plant–herbivore interactions because higher trophic levels (parasitoids) are more sensitive to habitat changes than lower trophic levels (plants and herbivores). Our results support this hypothesis given that we found a greater extinction debt for plant–herbivore interactions than for herbivore-parasitoid interactions (which was marginally significant) in recently fragmented habitats. This finding suggests that trophic interactions involving higher trophic levels may indeed be lost more rapidly following habitat fragmentation, while interactions at lower trophic levels can persist longer, accumulating a greater extinction debt. In addition, it means there is still a time window to prevent future plant–herbivore interactions which may help to recover herbivore–parasitoid interactions.

5. Conclusions

Extinction debt offers an opportunity to stem biodiversity loss before it is gone. However, understanding extinction debt remains a challenge for biodiversity conservation. In this study, we addressed three important limitations to quantifying extinction debt [14]: we focussed mainly on habitat specialists, considered both area and connectivity as lasting effects of habitat fragmentation, and used long-fragmented habitats as reference rather than continuous habitat. However, the availability of appropriate high-quality historical data from long-term monitoring of landscape changes and biodiversity remains a limiting factor for accurately estimating the extinction debt. Nevertheless, we identified an extinction debt in recently fragmented habitats whose magnitude differed across trophic levels and interaction types. Importantly, this study represents, to our knowledge, the first empirical attempt to estimate the magnitude of the extinction debt not only of species but also of species interactions in fragmented landscapes. Specifically, we found a higher extinction debt for herbivores and plant–herbivore interactions in small, isolated habitats, but a lower extinction debt for plants only in small habitats. The extinction debt of parasitoids was higher with respect to the other groups but in large, well-connected habitats, while there was no extinction debt detected for herbivore–parasitoid interactions. Our findings have implications for the conservation of plants, herbivores, and natural enemies in drylands surrounded by vineyards, which represent the main driver of land use change in the central-western of Argentina. We found that current and historical area and connectivity drive the extinction debt in recently fragmented habitats differently across trophic levels and interactions. Our results underscore the conservation value of recently fragmented small, isolated habitats which, if managed correctly, may help prevent future species and interaction extinctions, mitigating the negative effects of habitat fragmentation. Conservation actions to this end include the maintenance and restoration of functional connections among recently and long-fragmented habitats through corridors and encouragement for landowners to preserve remaining habitats.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. Data are available on Dryad [39].

Supplementary material is available online [40].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. M.S.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, visualization, writing—original draft; D.P.V.: conceptualization, funding acquisition, resources, supervision, validation, visualization, writing—review and editing; J.R.: conceptualization, funding acquisition, resources, supervision, validation, visualization, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

Funding. This work was supported by start-up funds from the University of Colorado granted to J.R., National Council for Scientific and Technical Research (CONICET) with a postdoctoral fellowship granted to M.S (no. 4122/17), and Fund for Scientific and Technological Research (FONCYT) with a Scientific and Technological Research Project granted to D.P.V. (PICT- 2014-3168).

Acknowledgements. We thank Hugo J. Marrero for helping in field work, and Juan José Martínez and M. Laura Bernaschini for helping in taxonomic identifications. We also thank the J.R. research group for hosting M.S. during a stimulating stay at the University of Colorado.

References

1. Fahrig L *et al*. 2019 Is habitat fragmentation bad for biodiversity? *Biol. Conserv*. **230**, 179–186. (doi:10.1016/j.biocon.2018.12.026)
2. Fletcher RJ *et al*. 2018 Is habitat fragmentation good for biodiversity? *Biol. Conserv.* **226**, 9–15. (doi:10.1016/j.biocon.2018.07.022)
3. Didham RK, Kapos V, Ewers RM. 2012 Rethinking the conceptual foundations of habitat fragmentation research. *Oikos* **121**, 161–170. (doi:10.1111/j.1600-0706.2011.20273.x)
4. Krauss J *et al*. 2010 Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. *Ecol. Lett*. **13**, 597–605. (doi:10.1111/j.1461-0248.2010.01457.x)
5. Tilman D, May RM, Lehman CL, Nowak MA. 1994 Habitat destruction and the extinction debt. *Nature* **371**, 65–66. (doi:10.1038/371065a0)
6. Wearn OR, Reuman DC, Ewers RM. 2012 Extinction debt and windows of conservation opportunity in the Brazilian Amazon. *Science* **337**, 228–232. (doi:10.1126/science.1219013)
7. Hagen M *et al*. 2012 Biodiversity, species interactions and ecological networks in a fragmented world. *Adv. Ecol. Res.* **46**, 89–120. (doi:10.1016/B978-0-12-396992-7.00002-2)
8. Valiente-Banuet A *et al*. 2015 Beyond species loss: the extinction of ecological interactions in a changing world. *Funct. Ecol*. **29**, 299–307. (doi:10.1111/1365-2435.12356)
9. Blanchard G, Munoz F. 2023 Revisiting extinction debt through the lens of multitrophic networks and meta-ecosystems. *Oikos* **2023**, e09435. (doi:10.1111/oik.09435)
10. Koh LP, Dunn RR, Sodhi NS, Colwell RK, Proctor HC, Smith VS. 2004 Species coextinctions and the biodiversity crisis. *Science* **305**, 1632–1634. (doi:10.1126/science.1101101)
11. Betts MG *et al*. 2019 Extinction filters mediate the global effects of habitat fragmentation on animals. *Science* **366**, 1236–1239. (doi:10.1126/science.aax9387)
12. Diamond JM. 1972 Biogeographic kinetics: estimation of relaxation times for avifaunas of southwest pacific islands. *Proc. Natl Acad. Sci. USA* **69**, 3199–3203. (doi:10.1073/pnas.69.11.3199)
13. Matthews TJ, Cottee-Jones HE, Whittaker RJ. 2014 Habitat fragmentation and the species–area relationship: a focus on total species richness obscures the impact of habitat loss on habitat specialists. *Divers. Distrib*. **20**, 1136–1146. (doi:10.1111/ddi.12227)
14. Kuussaari M *et al*. 2009 Extinction debt: a challenge for biodiversity conservation. *Trends Ecol. Evol*. **24**, 564–571. (doi:10.1016/j.tree.2009.04.011)
15. Haddad NM *et al*. 2015 Habitat fragmentation and its lasting impact on Earth's ecosystems. *Sci. Adv*. **1**, e1500052. (doi:10.1126/sciadv.1500052)
16. Guardiola M, Pino J, Rodà F. 2013 Patch history and spatial scale modulate local plant extinction and extinction debt in habitat patches. *Divers. Distrib*. **19**, 825–833. (doi:10.1111/ddi.12045)
17. Resasco J, Fletcher RJ. 2021 Accounting for connectivity alters the apparent roles of spatial and environmental processes on metacommunity assembly. *Landsc. Ecol.* **36**, 1089–1099. (doi:10.1007/s10980-021-01203-z)
18. Deák B *et al*. 2021 Different extinction debts among plants and arthropods after loss of grassland amount and connectivity. *Biol. Conserv*. **264**, 109372. (doi:10.1016/j.biocon.2021.109372)
19. Saar L, Takkis K, Pärtel M, Helm A. 2012 Which plant traits predict species loss in calcareous grasslands with extinction debt? *Divers. Distrib*. **18**, 808–817. (doi:10.1111/j.1472-4642.2012.00885.x)
20. Damschen EI, Brudvig LA, Burt MA, Fletcher RJ Jr, Haddad NM, Levey DJ, Orrock JL, Resasco J, Tewksbury JJ. 2019 Ongoing accumulation of plant diversity through habitat connectivity in an 18-year experiment. *Science* **365**, 1478–1480. (doi:10.1126/science.aax8992)
21. Hanski I, Ovaskainen O. 2003 Metapopulation theory for fragmented landscapes. *Theor. Popul. Biol*. **64**, 119–127. (doi:10.1016/s0040-5809(03)00022-4)
22. Holt RD, Lawton JH, Polis GA, Martinez ND. 1999 Trophic rank and the species–area relationship. *Ecology* **80**, 1495–1504. (doi:10.1890/0012-9658(1999)080[1495:tratsa]2.0.co;2)
23. Halley JM, Monokrousos N, Mazaris AD, Newmark WD, Vokou D. 2016 Dynamics of extinction debt across five taxonomic groups. *Nat. Commun.* **7**, 1–6. (doi:10.1038/ncomms12283)
24. Figueiredo L, Krauss J, Steffan-Dewenter I, Sarmento Cabral J. 2019 Understanding extinction debts: spatio–temporal scales, mechanisms and a roadmap for future research. *Ecography* **42**, 1973–1990. (doi:10.1111/ecog.04740)

25. Vellend M, Verheyen K, Jacquemyn H, Kolb A, Van Calster H, Peterken G, Hermy M. 2006 Extinction debt of forest plants persists for more than a century following habitat fragmentation. *Ecology* **87**, 542–548. (doi:10.1890/05-1182)
26. Brook BW, Sodhi NS, Ng PKL. 2003 Catastrophic extinctions follow deforestation in Singapore. *Nature* **424**, 420–423. (doi:10.1038/nature01795)
27. Gonzalez A, Chaneton EJ. 2002 Heterotroph species extinction, abundance and biomass dynamics in an experimentally fragmented microecosystem. *J. Anim. Ecol*. **71**, 594–602. (doi:10.1046/j.1365-2656.2002.00625.x)
28. Wang Z, Chase JM, Xu W, Liu J, Wu D, Zhang A, Wang J, Luo Y, Yu M. 2024 Higher trophic levels and species with poorer dispersal traits are more susceptible to habitat loss on island fragments. *Ecology* **105**, e4300. (doi:10.1002/ecy.4300)
29. Santos M, Cagnolo L, Roslin T, Marrero HJ, Vázquez DP. 2019 Landscape connectivity explains interaction network patterns at multiple scales. *Ecology* **100**, 1–8. (doi:10.1002/ecy.2883)
30. Labraga JC, Villalba R. 2009 Climate in the Monte Desert: past trends, present conditions, and future projections. *J. Arid Environ*. **73**, 154–163. (doi:10.1016/j.jaridenv.2008.03.016)
31. Rojas F, Rubio C, Rizzo M, Bernabeu M, Akil N, Martín F. 2020 Land use and land cover in irrigated drylands: a long-term analysis of changes in the Mendoza and Tunuyán River Basins, Argentina (1986–2018). *Appl. Spat. Anal. Policy* **13**, 875–899. (doi:10.1007/s12061-020-09335-6)
32. Pebesma E, Bivand R. 2023 *Spatial data science: with applications in R*, p. 314. New York, NY: Chapman and Hall/CRC.
33. Helm A, Hanski I, Pärtel M. 2006 Slow response of plant species richness to habitat loss and fragmentation. *Ecol. Lett*. **9**, 72–77. (doi:10.1111/j.1461-0248.2005.00841.x)
34. Bommarco R, Lindborg R, Marini L, Öckinger E. 2014 Extinction debt for plants and flower-visiting insects in landscapes with contrasting land use history. *Divers. Distrib.* **20**, 591–599. (doi:10.1111/ddi.12187)
35. Jackson ST, Sax DF. 2010 Balancing biodiversity in a changing environment: extinction debt, immigration credit and species turnover. *Trends Ecol. Evol*. **25**, 153–160. (doi:10.1016/j.tree.2009.10.001)
36. Dunn RR, Harris NC, Colwell RK, Koh LP, Sodhi NS. 2009 The sixth mass coextinction: are most endangered species parasites and mutualists? *Proc. R. Soc. B* **276**, 3037–3045. (doi:10.1098/rspb.2009.0413)
37. Leibold MA *et al*. 2004 The metacommunity concept: a framework for multi-scale community ecology. *Ecol. Lett.* **7**, 601–613. (doi:10.1111/j.1461-0248.2004.00608.x)
38. Kamiya T, O'Dwyer K, Nakagawa S, Poulin R. 2014 Host diversity drives parasite diversity: meta-analytical insights into patterns and causal mechanisms. *Ecography* **37**, 689–697. (doi:10.1111/j.1600-0587.2013.00571.x)
39. Santos M, Vázquez D, Resasco J. 2025 Data from: Extinction debt of species and interactions in a fragmented landscape. Dryad Digital Repository (doi:10.5061/dryad.gf1vhhmzb)
40. Santos M, Vázquez DP, Resasco J. 2025 Supplementary material from: Extinction debt of species and ecological interactions in a fragmented landscape. Figshare. (doi:10.6084/m9.figshare.c.8003574)