Received: 7 October 2025 | Accepted: 29 July 2026

DOI: 10.1111/icad.70128

ORIGINAL ARTICLE

Insect Conservation and Diversity

Dispersal mediates metapopulation response to local and regional stressors

Christopher A. Halsch[1] | Matthew L. Forister[2] | Eliza M. Grames[1]

[1]Department of Biological Sciences, Binghamton University, Binghamton, New York, USA

[2]Department of Biology, Program in Ecology, Evolution and Conservation Biology, University of Nevada, Reno, Nevada, USA

Correspondence
Christopher A. Halsch, Department of Biological Sciences, Binghamton University, Binghamton, NY, USA.
Email: chalsch@binghamton.edu

Funding information
National Institute of Food and Agriculture; Division of Environmental Biology

Editor/Associate Editor: Diana E. Bowler

Abstract

1. Many populations face multiple anthropogenic threats simultaneously; as a result, we have observed biodiversity loss worldwide. Moreover, population stressors act at different spatial scales, and understanding variation in outcomes depends on species-specific dispersal abilities.
2. In this study, we developed a source–sink metapopulation simulation to investigate how stressors that act at different spatial scales interact with landscape composition and dispersal behaviour to drive patterns of metapopulation extirpations. We are particularly interested in gaining insight into the decline of widespread species, inspired by observations of decreasing population densities of many widespread butterflies, which have challenged conventional wisdom that more dispersive species should be less vulnerable to global change.
3. We found that stressors acting at different spatial scales interact with dispersal, especially in highly developed landscapes. On average, being less dispersive results in worse outcomes because more dispersive species benefit from semi-natural habitats, which can strengthen connections between source populations. At the same time, the degradation of these types of land in particular may disproportionately impact dispersive species.
4. These findings enhance our understanding of insect biodiversity loss and demonstrate that conserving widespread insects will likely require consideration of landscape-scale connectivity.

KEYWORDS
dispersal, insect conservation, insect decline, metapopulation

INTRODUCTION

From an ecological perspective, the past century can only be characterized as a period of unprecedented change (Dirzo et al., 2014; Edwards et al., 2025; Wagner et al., 2021). Large-scale modification and destruction of natural lands have significantly reduced global habitat availability and remain the primary drivers of the global biodiversity crisis (Caro et al., 2022; Newbold et al., 2015; Raven & Wagner, 2021). Landscape-level stressors are often accompanied by, or are the cause of, additional local stressors, such as agrochemical pollutants or the introduction of non-native species, which can have further synergistic negative impacts on population vital rates (Halsch et al., 2025). As the pervasive threat of climate change continues to escalate, the potential for combinatory effects among anthropogenic

stressors is almost limitless (Harvey et al., 2023; Parmesan & Yohe, 2003; Staudt et al., 2013). Populations facing multiple stressors in increasingly fragmented landscapes are likely to suffer, but how stressors that act at different spatial and temporal scales interact to drive declines is uncertain and difficult to measure in the field (Brown et al., 2013).

An underlying factor in shaping species' responses to interactive pressures in fragmented landscapes is their rarity, which can be defined along three axes: local abundance, occupancy within a range and range extent (Crisfield et al., 2024). Local abundance influences how vulnerable a species is to demographic processes and genetic drift, while total range extent and occupancy will influence how susceptible a species is to a single, large-scale disruptive event such as a drought or large-scale land conversion (Gilpin & Soulé, 1986; Purvis et al., 2000). As a result, expectations for how widespread species (i.e., those with greater extents and occupancy rates, but not necessarily higher local abundance), respond to spatially structured threats may vary from those that are locally rare and range-limited. For example, widespread species are more likely to be dietary or habitat generalists and can occupy a greater proportion of the landscape, including degraded or suboptimal areas (Bender et al., 1998; Devictor et al., 2008). They are also more influenced by the broader landscape context, and presence and abundance at any one site can depend on processes occurring there, as well as on ecological interactions or environmental conditions far away (Pardikes et al., 2017). An extreme example of this is demonstrated by migratory animals, where presence in one location can vary by orders of magnitude from year to year, depending on conditions thousands of miles away (Hu et al., 2021; Remisiewicz & Underhill, 2020). Thus, as habitats continue to be degraded or lost, widespread species may be affected in ways different from range-restricted species, and it could be expected that species with broader geographic distributions may be just as likely to decline as those that are more isolated, although ultimate extinction probabilities could still differ.

The vulnerability of widespread and range-limited species to multiple threats is mediated by their capacity to move (Crisfield et al., 2024), and insights into this process can be found in the metapopulation literature (Vance, 1984; Vogwill et al., 2009; Wang et al., 2015). Typically, metapopulations are considered as networks of spatially separated populations connected by dispersal, with variation in the extent to which some populations act as consistent sources or sinks (Levins, 1969; Pulliam, 1988). Variation in demography and movement among populations can either stabilize the system despite temporary local losses or lead to its complete collapse (Hanski & Ovaskainen, 2002; Pulliam, 1988). For instance, increased dispersal can stabilize population networks, reduce population variability and facilitate population rescue through demographic input and the recolonization of extirpated areas. Yet, outcomes of high dispersal are not universally positive. Greater dispersal can lead to increased synchrony among populations, making the metapopulation more susceptible to large-scale disturbance (Dey & Joshi, 2006; Haynes & Walter, 2022; Heino et al., 1997). High emigration rates can also have adverse effects in areas with small populations or small habitat patches due to the direct loss of reproducing individuals (Hanski, 1998). Approaches to studying these questions have often been theoretical, though work with the Glanville fritillary butterfly has empirically confirmed a number of theoretical predictions, including the importance of patch area and connectivity (Hanski, 1998), and one meta-analysis found a negative relationship between population growth and dispersal in butterflies (Baguette & Schtickzelle, 2006). The relationship between dispersal, landscape configuration and population persistence is, however, highly context-dependent and varies among landscapes, stressors and the inherent biology of the organisms studied (Johst et al., 2002).

Recent years have seen rapid growth in the attention paid to invertebrate population trends (Althaus et al., 2021; Wagner et al., 2021). Species like the monarch butterfly (*Danaus plexippus*) and Franklin's bumblebee (*Bombus franklini*) have galvanized the public and become symbols of conservation and land stewardship (Preston et al., 2021; Thorp, 2005). The monarch in particular demonstrates a relatively under-appreciated feature of insect declines: many formerly common, widely distributed species are declining rapidly (van Dyck et al., 2009; van Klink et al., 2024; Wagner, 2020). For example, the west coast lady (*Vanessa annabella*), which has a distribution that covers the entire western United States, is the butterfly in steepest decline across that region (Forister et al., 2021; Forister, Grames, et al., 2023). Traditionally, insect conservation has focused on range-limited species, often characterized by low dispersal capabilities, with only a few populations remaining (Marschalek & Klein, 2010; Murphy & Weiss, 1988; Wagner & Van Driesche, 2010). While protecting these remnant populations remains of paramount importance for conservation, the decline of widespread species is also of great concern, particularly because the spatial scale at which conservation actions need to be taken is likely to differ from that of geographically limited species.

In this study, we employ a source–sink metapopulation framework to investigate the effects of multiple population stressors operating at different spatial scales, as well as variation in dispersal behaviour, on metapopulation dynamics. Our goal is to understand how varying intensities of local and landscape-wide stressors interact to drive population equilibria across landscapes with varying distributions of habitat quality ranging from high-quality natural sources to semi-natural transitions to developed sinks. We are particularly motivated by declines in butterflies whose ranges are large enough that they encompass both the California Central Valley, a highly converted landscape, as well as nearby mountain ranges and more natural areas (Forister et al., 2010; Halsch et al., 2020). First, we ask how metapopulations respond to landscape effects when synthetic species have different dispersal capabilities. Next, we consider whether additional stressors, acting at local and regional scales, have a greater impact on metapopulation persistence and examine how stressors interact with dispersal distance. Finally, we ask how the composition of simulated landscape conservation interacts with simulated stressors to aid in the recovery of dispersive species.

METHODS

Overview

First, a 100 × 100 cell landscape was randomly generated with varying proportions of natural, semi-natural and developed habitats, as well as different levels of patchiness. Within each time step of the simulation, the population growth rate in each cell was influenced by environmental factors, including habitat quality, landscape-wide stress, local stress, and density dependence. Individuals then dispersed, with both immigration to and emigration from a patch occurring simultaneously. At the end of each simulation, the average abundance and extinction dynamics were summarized. Parameters were varied for the magnitude of landscape-wide stress, local stress and dispersal ability, and simulations were run for all combinations of these environmental stressors and dispersal parameters. Inference is not drawn from temporal trends within a single iteration of the simulation, but rather from comparing summary statistics among iterations with different parameters. All simulations were run using R version 4.5.1 (R Core Team, 2023), and code to replicate results is publicly available (Halsch, 2026).

Annual population growth rate

At the initial time step, populations were assigned sizes proportional to the habitat quality in each cell. Subsequently, the growth rate for a time step was the sum of the impact of landscape (L_t), landscape-wide stress (W_t), additional local stressors (S_t^{Local}) and density dependence ($D(N_{t-1})$) based on abundance in the previous year, as seen in the equation below (Equation 1). These effects were summed to determine the population growth for that time step (positive effects had positive values and negative effects had negative values). This sum was then exponentiated and multiplied by the previous year's population size to capture the effects of landscape, additional stressors and density dependence on population growth. Finally, the resulting value was used as the rate parameter in a single draw from a Poisson distribution, yielding the population size in the current step (before dispersal). Density dependence ($D(N_{t-1})$) was determined using an Allee effect model (Fadai & Simpson, 2020), where middle values were assigned positive population growth and high and very low values were assigned negative population growth (Figure S1). This model was parameterized with a carrying capacity (K), Allee threshold (A) and an intrinsic growth rate (r). The Allee threshold was fixed at 100, and the intrinsic growth rate was set to 0.25 across all simulation runs; we tested three different carrying capacities as a sensitivity analysis (Table 1). Results across all three carrying capacities were highly correlated ($r = 0.8$–0.9); therefore, the average was calculated across all three settings. All other effects are described in detail in subsequent sections.

$$\begin{aligned} N_t &\sim \text{Poisson}(\lambda_t) \\ \lambda_t &= N_{t-1} \cdot \exp\left(L_t + W_t + S_t^{\text{local}} + D(N_{t-1})\right) \\ D(N_{t-1}) &= r\left(1 - \frac{N_{t-1}}{K}\right)\left(\frac{N_{t-1}}{A} - 1\right) \end{aligned} \quad (1)$$

TABLE 1 Description of all experimental parameters in the simulation.

Parameter	Values	Description
Landscape composition	5%, 16%, 25%, 33%, 50%, 66%, 90% cover	The percent cover of the landscape of each habitat type.
Landscape patchiness	10, 200, 400 patches	The number of initial patches in landscape creation (Figure 1).
Local effect	0, 0.25, 0.5, 0.75, 1	The additional local stress associated with patches in semi-natural habitats.
Regional effect	0, 0.25, 0.5, 0.75, 1	The magnitude of worsening regional weather effects (Figure S1).
Dispersal distance	1, 3, 5, 8, 10 cells	The number of cells away that individuals may move to during one time step.
Carry capacity	500, 750, 1000	The carrying capacity for the density dependence function (Figure S1).
Landscape restoration	10%, 20%, 30% modified	The percent of the landscape that is changed from developed to natural. These values were used for both types of restoration simulations.

Note: Multiple iterations were run for all parameter combinations. The number of iterations for each parameter combination was determined from a preliminary analysis (described in Supporting Information).

Generating baseline habitat quality and patchiness

Landscapes were created by first generating an empty 100 × 100 matrix. Based on an input parameter, the specified number of randomly selected cells were classified into one of three land types: natural, semi-natural or developed. The more cells that were initially placed, the patchier the landscape. The landscape was then grown from these initial patches, with neighbouring cells assigned to the same class as their nearest neighbour until it reached other cells that had already been assigned to a land-use type. The final cells that bordered two different land-use types were assigned probabilistically based on the composition of the surrounding landscape. We also determined the initial proportion of cells assigned to each land-use type as another parameter of interest. The resulting landscape after this process was a matrix composed of three land-use types, with varying patchiness and proportions depending on the starting parameters. This landscape generation process is random and can result in landscapes that do not reflect the land cover proportions matching the initial parameters. Because of this, we iteratively generated landscapes and included only those in the simulation where the final percent cover of land-use types was within 1% of the target percent cover initially specified for each land-use type. We varied both patchiness and percent cover for each land cover type, as documented in Table 1.

Next, each land-use type was assigned a distinct baseline habitat quality. The quality of each natural habitat cell was drawn from a normal distribution with a mean of 0.5 and a standard deviation of 0.1. The quality of each semi-natural cell was drawn from a normal distribution with a mean of −0.25 and a standard deviation of 0.1. These values are later exponentiated as part of the process that determines annual population growth (Equation 1). Done this way, natural habitats were consistent population sources, while semi-natural habitats were, on average, sinks but could switch to sources if conditions were otherwise favourable. These values were meant to mimic landscapes of various land-use types, from high-quality natural areas to semi-natural areas, such as pollinator-friendly agriculture that may provide some resources for insects, to fully developed intensive agricultural landscapes. Cells classified as developed were assigned a value of −5, ensuring that even the best combinations of all other parameters could not render it viable. The most important aspect of the assigned habitat values was not the value itself, but rather how it compared to the other effects in the simulation. By choosing evenly divisible values and keeping all parameters within comparable ranges, we examined how land cover compared with other stressors.

Finally, each landscape was assigned edge effects, in which cells were adjusted based on the composition of the surrounding landscape. This was done by taking the mean habitat quality value of the 3×3 neighbourhood around a cell, multiplying it by 0.5 (to reduce its importance relative to the primary cell) and adding it to the cell's habitat quality value. This resulted in smoothed landscapes with varying patchiness, habitat composition and additional local stressors. We performed a preliminary analysis to assess how variation in landscape structure influences model inference (see Supporting Information; Figures S2, S3 for full details). We found that the effect of variability between landscapes was substantially greater than the effect of variability within landscapes; that is, repeated simulations on the same landscape produced much more consistent results than simulations run on different randomly generated landscapes with identical land cover proportions. Based on this, we ran simulations on five randomly generated landscapes for most parameter combinations. However, the preliminary analysis also revealed that variability increased with the proportion of semi-natural habitat, likely because additional pressures applied to these areas introduce greater stochasticity. Accordingly, we increased the number of landscapes simulated per parameter combination as the proportion of semi-natural habitat increased (see Supporting Information). Example landscapes are shown in Figure 1, and an interactive tool is described in the Supporting Information.

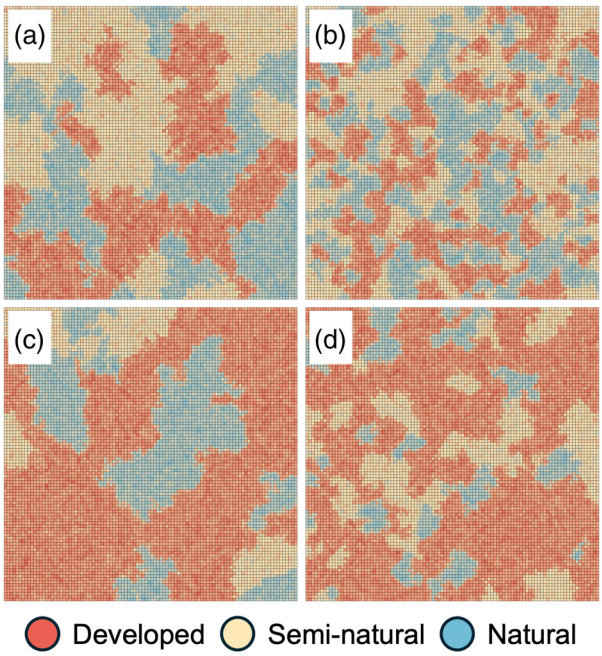

FIGURE 1 Four example simulated landscapes with different parameterizations. (a) A landscape with an even proportion of habitat types with low patchiness. (b) A landscape with an even proportion of habitat types with high patchiness. (c) A landscape with a higher proportion of developed habitat with low patchiness. (d) A landscape with a higher proportion of developed habitat with high patchiness.

Generating additional local and landscape-wide stress

The primary motivation of this simulation was not to explore the role of landscape alone, but also to examine how simulated populations respond to additional stressors across different landscape types. Additional stressors were classified by their area of impact, either local or across the entire landscape. We only added local stressors to semi-natural landscapes, and they acted at the level of the initial patch assignment, where the same negative value was applied to a patch of semi-natural cells. Local stressors are meant to mimic additional stressors associated with semi-natural land, such as pollutants or invasive species (these pressures also occur in developed land, but since these landscapes are already completely unusable, they were not applied). This design resulted in variation in the intensity of local-level stressors across semi-natural cells in one landscape. The magnitude of additional local stress for each patch was randomly drawn from a gamma distribution (and then multiplied by −1 to make it negative). The rate and shape parameters for the gamma distribution were calculated using moment matching, with the mean of the distribution as a varying parameter (Table 1).

Additional landscape-wide stress impacted all cells equally, regardless of land-use type, and was intended to represent large-scale 'good' and 'bad' weather years (such as those generated by El Nino Southern Oscillation cycles). This parameter was set up as an oscillating sine wave, with a wavelength of 6 years and an amplitude of 0.5. This effect is of the same magnitude as natural land, and thus, in this simulation, the value of a good weather year is equivalent to that of high-quality habitat. When this parameter was set to the control (of no additional landscape-wide stress), this function oscillated between 0.5 and −0.5 every 6 years. When this condition was set to worsening values, the centre of the oscillating function became increasingly negative, while the amplitude remained the same. Comparing across simulations with different landscape-wide stress

provides insight into how populations respond to worsening climates. A comprehensive description of the local and landscape-wide conditions affecting populations can be found in Table 1.

Dispersal

After the effects of the environment on population growth were applied to each cell at each time step, the dispersal stage was initiated. For each cell, dispersal results from a two-step process: one step determines how many individuals will leave a reference cell, and the other determines where individuals are more likely to move. The percentage of the population emigrating from a cell was determined by a function incorporating the density-dependent effects of the current cell and its habitat quality, along with two bounding parameters that describe the asymptotes of the function. Cells with lower habitat quality (L_t) or negative density-dependent effects ($D(N_{t-1})$) promoted dispersal to other cells (total dispersal bounded by the asymptotes). Once the probability of emigration was calculated for each cell, it was normalized by the underlying dispersibility of each species, which varied throughout the simulation, as shown in Equation 2, where 0.2 and 0.6 are scaling constants that constrain dispersibility to the range explored in the simulations.

$$\%\ \text{emigrating} = \left[\frac{0.6}{1+\exp(-(D(N_{t-1})+L_t))}+0.2\right] \quad (2)$$

Once the percentage of individuals emigrating from a cell was determined, where they go depended on a dispersal-distance parameter. When this parameter was set to 1, they could only move within the 3×3 matrix with the current cell as its centre, whereas a parameter of 10 allowed them to access cells in a 21×21 area. Closer cells and those with better habitat were more likely to be moved to, with the probability (p_{ij}) inversely related to distance (d_{ij}) and positively associated with habitat quality (L_t), both assigned equal importance (Equation 3).

$$p_{ij} = \frac{1}{d_{ij}} \times L_t \quad (3)$$

Dispersal was implemented by calculating the probability that each cell receives individuals from all other cells within a defined dispersal neighbourhood (ranging from 8 neighbouring cells at the smallest radius to 441 at the largest). The dispersal process was set up as a continuous torus, where the dispersal area of cells near the edge can include cells across on the other side of the landscape. This process was represented as a three-dimensional array, where the first two dimensions (x, y) defined the spatial layout of the dispersal neighbourhood, and the third dimension (z) indexed each focal cell across the landscape. Each slice along the z-dimension, therefore, corresponded to the neighbourhood surrounding a single focal cell, with each element giving the probability of movement from a neighbouring cell to that focal cell. At the smallest dispersal distance, the neighbourhood consisted of a 3 × 3 grid, with the focal cell located at the centre and excluded from dispersal (8 cells total). For each focal cell, the expected number of immigrants was calculated by multiplying the number of emigrants from each neighbouring cell by a movement weight based on inverse distance and habitat (Equation 3) and summing across each z slice. These weights were further modified by habitat quality, favouring movement towards higher-quality habitat. The resulting sum defined the expected number of immigrants, which was used as the rate parameter for a single draw from a Poisson distribution per cell. These calculations were performed simultaneously for all focal cells. After determining the number of individuals gained by each cell, the number of individuals lost from each source cell was calculated by reallocating these movements back to their origins, generating a corresponding loss matrix. The gain and loss matrices were then applied simultaneously to the population size matrix after environmental and demographic processes. The resulting values represented the post-dispersal population sizes for that time step. Full details of the dispersal functions are provided in the supplement (Figure S5), and the complete set of parameters explored is listed in Table 1.

Simulating conservation scenarios

After developing the initial landscapes and simulation, we created two additional functions that took the generated landscapes as input and performed two types of modifications. Both functions converted land from one classification to another but differed in the spatial configurations of land modification. For this simulation, we changed land types from developed to natural to mimic land acquisition and restoration. The first function converted developed land into natural land along the edges of existing natural land, essentially expanding the edges and thus made the core habitat larger. This was done by identifying which cells in a developed patch share an edge with a natural patch and then converting a number of these cells based on an input parameter. The other function identified cells in developed patches that were furthest from the edges, then converted a number of them based on an input parameter. This scenario was intended to represent the habitat-restoration approach of creating stepping stones between natural lands (Saura et al., 2014). Examples of landscape modifications are shown in the supplement and in the online tool described therein (Figure S4). The complete set of parameters tested is presented in Table 1.

Output variables

The simulation was run a total of 175,500 times, representing the number of parameter combinations and replications. For each run, we saved the number of times a cell reached zero individuals at any point during the 50-year observation period (N_E), the number of times an extirpated cell later reached an abundance above the Allee effect threshold (N_C) and the average abundance in occupied cells. We used the extirpation and recolonization metrics to calculate the probability

that cells were extirpated (p_{ext}) and the probability that they were successfully recolonized (p_{rec}). We did not count recolonization events in which populations never reached the Allee threshold below which we imposed a negative population growth rate in the simulation (Figure S1). Our primary metric for inference was calculated using the following equation (Equation 4), which estimated the equilibrium of the number of cells extirpated (after accounting for recolonization) over 50 years of observing the simulation's behaviour. All inferences were drawn from summary statistics (mean and bootstrapped 95% confidence intervals) for each parameter combination. If an effect is presented in isolation, it was averaged across iterations, including all values of the other parameters.

$$1-\frac{(1-p_{ext})N_C+p_{rec}N_E}{N_C} \quad (4)$$

RESULTS

The number of extirpated cells in a landscape decreased when simulations included more natural habitat and increased with greater development. When the landscape was mainly composed of one of these two habitat types, the number of extirpations essentially matched the number of cells that were either developed or natural (inverse relationship) (Figure 2a,c). The relationship between extirpations and semi-natural habitat was more complex (Figure 2b). As the proportion of semi-natural habitat increased between different iterations, the number of populations quickly grew (extirpations decreased) until about one-third of the landscape was semi-natural, after which the effect plateaued and even showed a tendency to reverse with increasing extirpations at higher levels of semi-natural habitat. These effects interacted with dispersal ability. Metapopulations in simulations with more dispersive behaviour were more resilient to increased development, occupying about 20% more of the landscape until roughly one-third of it was developed, at which point population density declined rapidly (Figure 2a,c). Afterwards, the number of populations mostly tracked the amount of usable habitat (natural and semi-natural). This pattern contrasted with simulations of less dispersive dynamics, which closely followed the amount of available habitat (Figure 2b). Simulations with more semi-natural habitat (and less developed land) benefited all species, but the benefit was much greater for dispersive species. For example, when the landscape was 25% semi-natural, approximately 40% of the landscape was extirpated for non-dispersive species, but only about 25% for highly dispersive ones. We also found that species performed 15–25% better in patchier landscapes and that dispersive species fared particularly well (Figure 3).

The number of extirpations in a landscape also increased with the intensities of additional stressors, which have either local or landscape-wide effects in addition to the impact of the landscape itself (Figure 4). The relationship between additional stressors and extirpations varied with dispersal. When there was no population stress (other than the landscape itself), the more dispersive species occupied about 20% more of the landscape. As local stress increased,

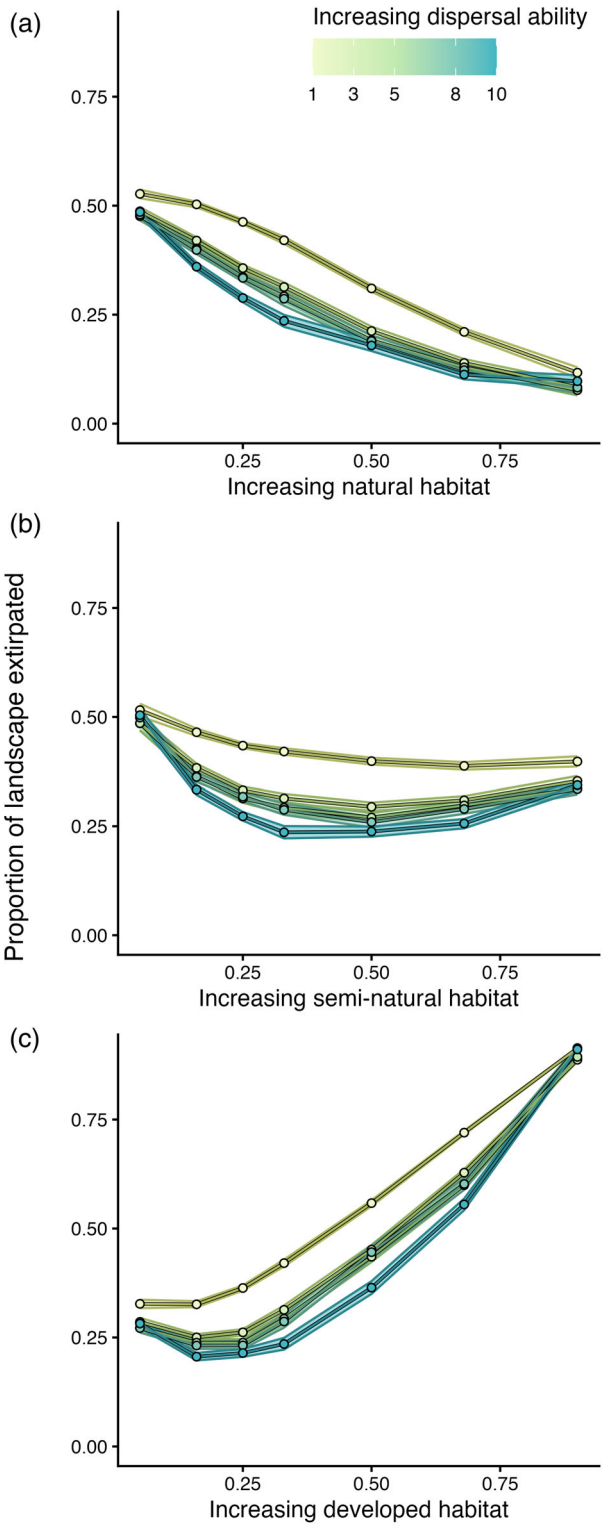

FIGURE 2 The effects of habitat quality and dispersal ability on the average number of extirpations across the simulations. Increasing values represent worsening responses. Panel a shows the impact of increasing natural habitat, Panel b shows increasing semi-natural habitat, and Panel c shows increasing developed habitat. The effects shown are the mean effects, averaged over all other effects. Points and lines represent the mean effect and are coloured by dispersal ability. The bands around the lines indicate bootstrapped 95% confidence intervals.

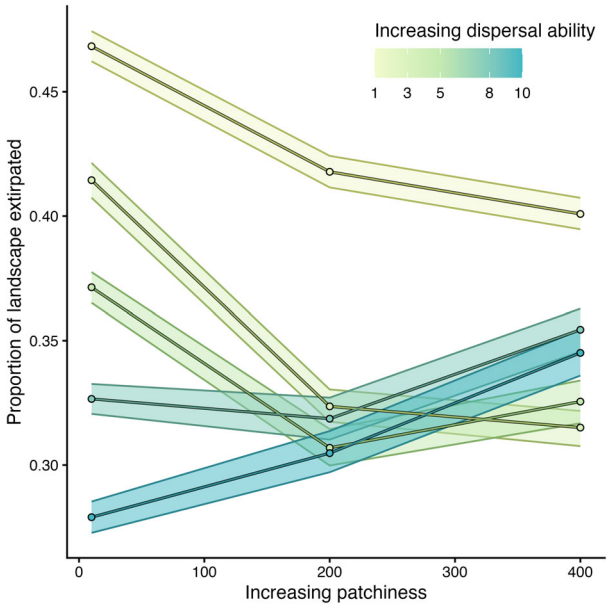

FIGURE 3 The effects of patchiness and dispersal ability on the average number of extirpations across the simulations. Increasing values represent worsening responses. The effects shown are the mean effects, averaged over all other effects. Points and lines represent the mean effect and are coloured by dispersal ability. The bands around the lines indicate bootstrapped 95% confidence intervals.

both dispersive and non-dispersive species declined linearly at approximately equal rates (Figure 4a). The opposite was true in response to landscape-wide stress (that impacted all cells), where the rate of extirpation is higher for more dispersive species (Figure 4b). Specifically, shifts from moderate to high regional stress result in a decline of 25% for non-dispersive species but a decline of over 40% for very dispersive species.

The number of extirpations across the entire simulation also revealed interactive effects among the landscape, combined local and landscape-wide stress and dispersal capability, as shown by the curved contours in Figure 5. When 50% or more of the landscape was comprised of natural habitat, most species fared well, but dispersive species were more robust to additional stressors (Figure 5a–c). Landscapes with 50% or more semi-natural habitat had more interactions, especially when the landscape comprised 50%–67% semi-natural habitat (Figure 5d,e). In these landscapes, greater dispersal ability conferred resilience to low levels of additional landscape stressors. However, as combined stress continued to increase, the dispersive species advantage decreased, and the number of extirpations was more closely related to total combined stress than to dispersal (Figure 5d–f). Landscapes that were primarily developed resulted in the most extreme interactive effects (Figure 5g–i). For instance, when the landscape was 67% developed, a non-dispersive species (on the left side of Figure 5h) declined by 35% when moving from no additional stress to the most extreme case. However, a dispersive species (on the right side of Figure 5h) declined by 80% when moving from the no additional stress condition to the extreme additional stress condition. In the most extreme simulation, where 90% of the landscape is developed, there is no difference between dispersive and non-dispersive species under high amounts of additional stress (Figure 5i).

In addition to interactions between extirpation and dispersiveness under simulated stress, we also explored metrics relevant to conservation, including recolonization rates across different land types and in simulated conservation scenarios. We observed substantial differences in recolonization rates between the two less dispersive species and the three more dispersive species in response to increasing natural and semi-natural cover. Dispersive species were much more capable of exploiting any usable habitat. For instance, when the landscape was only 25% natural or semi-natural, recolonization rates were three, four and six times higher for the three most dispersive categories, respectively, compared to the two least dispersive ones (Figure S6). These effects were nearly identical across both increasing natural and semi-natural habitats. These events seem particularly important in non-patchy landscapes, where both types of conservation (connectivity versus creation of core habitat) led to fewer extirpations, especially for dispersive species. In non-patchy landscapes, buffering existing core habitat decreased extirpation by approximately 30% while prioritizing connectivity decreased extirpations by 40% (Figure 6a,c). In patchier landscapes, we observed similar results, with less dramatic differences between groups (Figure 6d).

We also tracked the average abundance of individuals in occupied spaces (above the Allee cutoff) as an additional metric of response that may better align with monitoring programmes. Overall, this metric interacted with dispersal ability less than extirpations did; therefore, figures are primarily presented in the supplement (Figures S7, S8). We found that non-dispersive species maintained higher abundance in non-patchy landscapes with more contiguous core habitat (Figure S7). We found minor differences in average abundance between the least dispersive species and all other species in response to landscape-wide stress (Figure S8A) and no difference in response to additional local stress (Figure S8B). The variable with the most substantial impact was landscape cover, where increases in natural and semi-natural areas disproportionately benefited and increases in development land disproportionately hurt more dispersive species (Figure 7). This effect was such that, unlike patterns of extirpations, conditions were observed that are clearly worse for dispersive species than non-dispersive ones.

DISCUSSION

Many populations of wild plants and animals are facing concurrent anthropogenic threats acting at different spatial scales (Brown et al., 2013; Halsch et al., 2025), and we can expect that metapopulation outcomes will at least depend on the magnitude of stressors and species-specific variation in dispersal ability. Understanding these dependencies may, in part, explain the observed declines of common and widespread insect species, which are potentially exposed to more landscape stressors than range-restricted species (Edwards

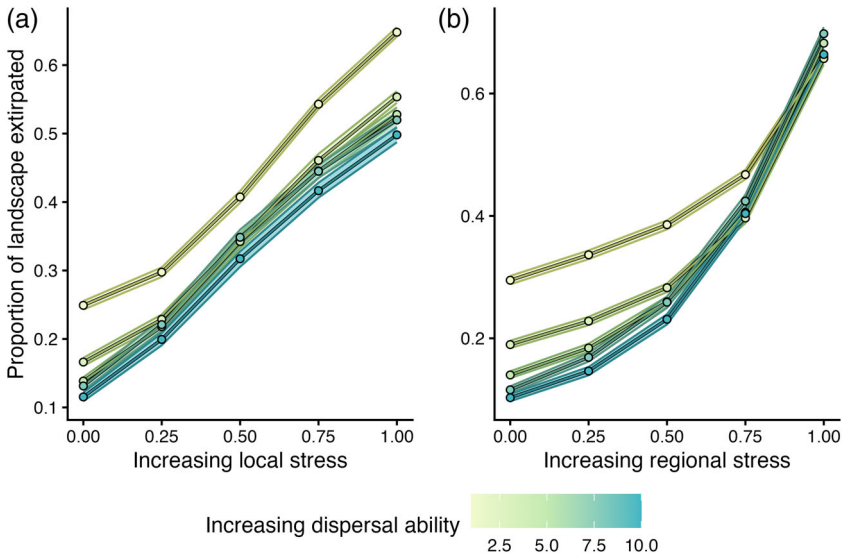

FIGURE 4 The effects of landscape stressors and dispersal ability on the average number of extirpations across the simulations. Increasing values represent worsening responses. Panel a shows the effects of local stressors associated with semi-natural habitat, and Panel b shows stressors that impact the entire landscape. The effects shown are the mean effects, averaged over all other effects. Points and lines represent the mean effect and are coloured by dispersal ability. The bands around the lines indicate bootstrapped 95% confidence intervals.

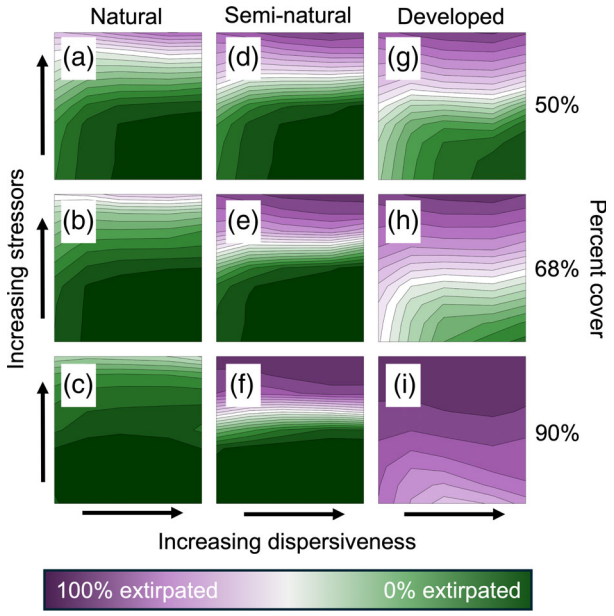

FIGURE 5 The interactive effects of habitat quality, landscape stress and dispersal ability on the average number of extirpations across the simulations. Within each panel, the *x*-axis represents increasing dispersal ability, and the *y*-axis represents increasing stressors (local and regional combined). Comparison across panels shows the effects of habitat quality. Panels in the left column show results for landscapes primarily natural, panels in the middle for landscapes predominantly semi-natural and panels on the right for landscapes primarily developed. As panels move down, the proportion of that cover type increases. Contours and colours represent the average number of extirpations across the simulations, after averaging over the effects not shown. Each contour line represents a change in 5% extirpation.

et al., 2025; van Dyck et al., 2009; van Klink et al., 2024). Here, we developed a source–sink metapopulation simulation to simultaneously explore how multiple axes of stress, from landscape composition to local and landscape-wide stressors, and dispersal behaviour, impact metapopulation persistence. We found that responses to different categories of stressors were expectedly negative and that they interacted with dispersal, suggesting that expectations for population trajectories may indeed vary with dispersal. These findings have implications for understanding patterns of insect declines, as well as for insect conservation, since strategies to help widespread insects will likely need to consider a larger scale than those for range-limited species.

The primary objective of this study was to gain insight into the nature of the decline of widespread insect species, which include the monarch butterfly and other species in North America that have been reported to have declining populations despite, in many cases, geographic ranges that span multiple broad geographic regions (Edwards et al., 2025; Forister, Grames, et al., 2023). We hypothesized that widespread species sample more of the landscape and, as a result, are exposed to more cumulative stress in a heavily modified landscape than non-dispersive species. For most combinations of conditions we explored, cumulative exposure did not have a disproportionately negative effect on dispersive species. In nearly all combinations of land-use compositions and additional stressors, we found that non-dispersive species performed worse or, in extreme cases, about as well as dispersive ones. This does not mean that dispersive species are not at risk, as long-term data indicate that many are in decline (Forister et al., 2021; van Dyck et al., 2009); instead, it invites consideration of the areas in our simulated world that most closely reflect the patterns of decline of both non-dispersive and dispersive species.

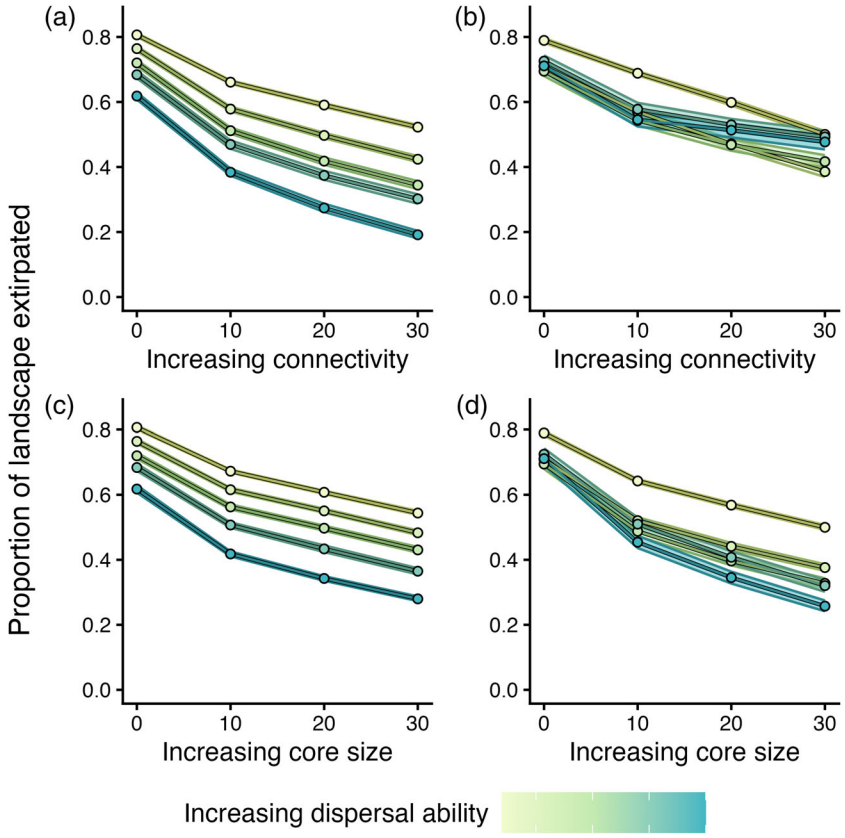

FIGURE 6 The effects of landscape restoration and dispersal ability on the average number of extirpations across the simulations. Increasing values represent worsening responses. Panel a shows the effects of enhancing connectivity between existing patches in a non-patchy landscape. Panel b shows the impact of enhancing connectivity between existing patches in a patchy landscape. Panel c shows the effects of increasing existing natural habitat in a non-patchy landscape. Panel d shows the effects of increasing existing natural habitat in a patchy landscape. The bands around the lines indicate bootstrapped 95% confidence intervals.

The conditions in which this was observed were in highly developed landscapes, where most of the landscape offers no opportunities for local population growth or persistence. It is in these landscapes that dispersive species are reduced to levels of occupancy similar to those of non-dispersive species. This pattern is likely due to reduced connectivity. Connections between source populations reduce distances to other high-quality patches and can stabilize the network through the effects of long-range dispersal and recolonization (Bowler & Benton, 2009; Howe et al., 1991; Johst et al., 2002). In primarily developed landscapes, the semi-natural spaces become fewer and more critical, recolonization rates decline, and as additional pressures increase in these spaces, this is especially detrimental to dispersive species that previously relied heavily on connectivity and recolonization.

This result may provide some insight into the contemporary loss of butterflies in highly converted landscapes (Edwards et al., 2025; Forister et al., 2010; van Dyck et al., 2009; van Klink et al., 2024; Warren et al., 2021). We were initially motivated by the butterflies in the Central Valley of California as an example of such a landscape; however, the results apply to other similarly modified landscapes. The Central Valley is a highly converted landscape, where the legacy of centuries of land-use change is now being compounded by additional factors such as invasive species, disease, pesticides and climate change (Forister et al., 2010; Halsch et al., 2020; MacLean et al., 2018). This is precisely the type of landscape where, based on our results, we should expect comparable rates of decline regardless of dispersal range. It may be that the historical loss of habitat in previous decades had greater impacts on non-dispersive species (as predicted by the simulation) and that contemporary dispersive insects are only now in significant decline in response to additional stressors such as climate change, introduced species (and pathogens) and pesticide exposure. In other words, the decline of many range-restricted species may have occurred before their geographic distributions and habitat preferences were documented (Fattorini, 2011; Forister, Black, et al., 2023; Habel et al., 2016).

While extreme landscapes yield extreme results for dispersive species, it remains true that this simulation demonstrates that being dispersive is mostly beneficial, even if it means being exposed to additional threats in a semi-natural landscape. One likely contributing factor to this finding is the landscape generation process itself. The initial patches from which each landscape was built were placed randomly, which, on average, results in well-connected and stable landscapes (Grilli et al., 2015). For instance, even if a landscape is two-thirds developed, the remaining one-third will be more evenly distributed

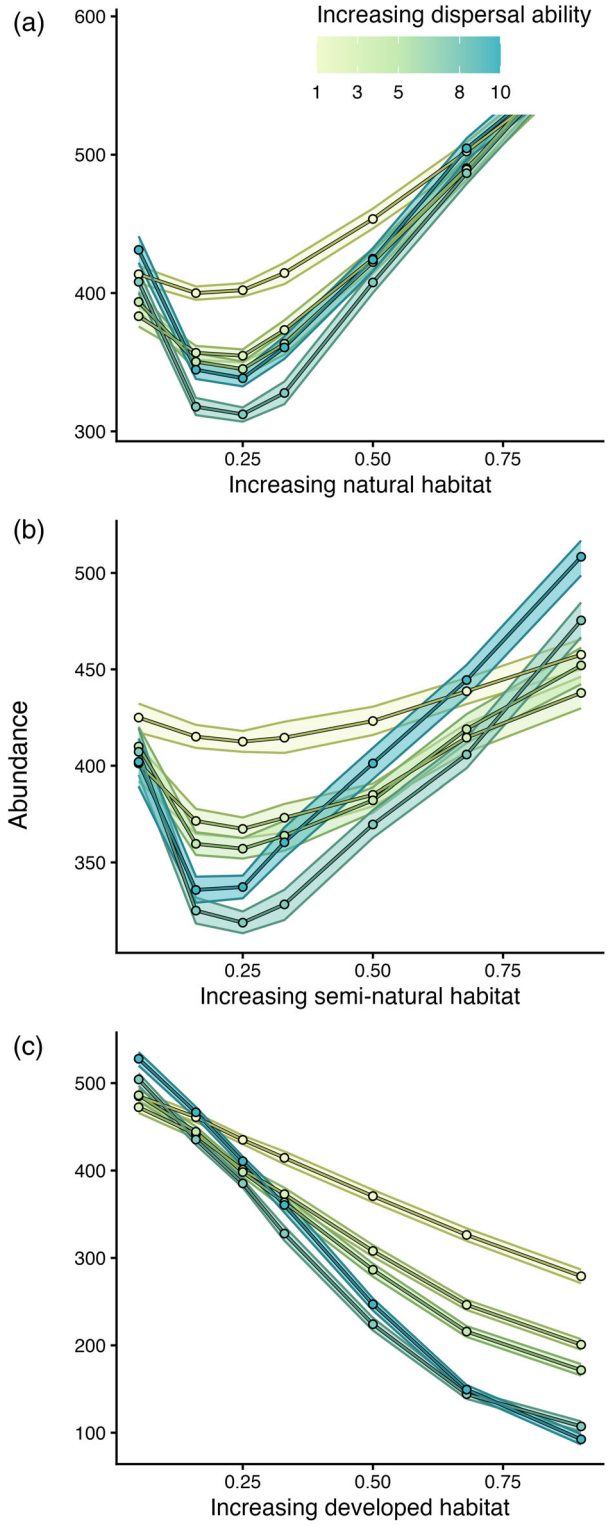

FIGURE 7 The effects of habitat quality and dispersal ability on the average abundance in semi-natural cells across the simulations. Panel a shows the impact of increasing natural habitat, Panel b shows increasing semi-natural habitat and Panel c shows increasing developed habitat. The effects shown are the mean effects, averaged over all other effects. Points and lines represent the mean effect and are coloured by dispersal ability. The bands around the lines indicate bootstrapped 95% confidence intervals.

across the matrix, resulting in a landscape that may benefit dispersive species (Howe et al., 1991). The distribution of natural land in human-modified landscapes is not random, and it is possible that specific landscape configurations can harm dispersive species more than non-dispersive ones. Such a study would be an excellent follow-up to these results, especially if it were designed based on the landscape compositions of real focal landscapes. Another way in which dispersive species may benefit from the simulated landscapes is due to a lack of interaction between land-use types and landscape-wide stress. As large-scale stress increases, it affects all land types equally; it is likely that the impacts of climate change will interact with land types. If natural areas are more resilient to the impacts of climate change, these refuges may benefit non-dispersive species more than widespread species. Still, this simulation demonstrates that under many conditions, a general expectation is that dispersive species are more stable as a metapopulation network than non-dispersive species.

Another explanation for our results differing from our expectations may result from the primary metric of inference: the percent of the landscape extirpated. This metric summarized the entire landscape and, based on extirpation and recolonization rates, calculated the expected number of cells expected to be occupied at equilibrium. This metric is thus all-knowing, incorporating information from the entire landscape to assess extinction. This is not the same type of information provided by long-term monitoring programmes, which is better reflected in population abundance in one or a small number of cells in the simulation. Furthermore, many large-scale monitoring programmes are biased in their location, as they often oversample areas near development (Dunn et al., 2005; Geldmann et al., 2016). For this reason, we also tracked the average abundance of individuals in occupied cells. We found that there are indeed cases in which dispersive species decline at the same rate or faster than non-dispersive species. The factor that generated the most significant declines of dispersive species (relative to non-dispersive ones) was the development of land. This is likely a further demonstration of the previously noted importance of connectivity and availability of usable land for dispersive species (Hansson, 1991).

This result also demonstrates that while monitoring programmes may report reductions in the abundance of widespread species, it does not necessarily reflect a greater risk to the entire metapopulation relative to less dispersive species. Even in cases where dispersive species experience greater losses of individuals across the whole metapopulation, they are still at less total risk of regional extinction because of redundancy among populations. While it may be the base expectation, this finding should be taken with caution. First, many charismatic widespread insects, such as the monarch butterfly (*D. plexippus*), are not only highly dispersive but also migratory (Reppert & de Roode, 2018), and these dynamics are not captured in this simulation. For instance, we did not examine situations in which conditions in a subset of the landscape, such as overwintering grounds, disproportionately influence the entire population. Another possibility would be a widespread species in which most of the range is supported by source populations in a small but productive region, which could be

uniquely exposed to stressors if located, for example, in low-elevation areas near agriculture. In such cases, a model would need to be built to explicitly capture this dynamic, and the impacts on population growth during this one critical phase of their migration may be as crucial as the rest of the landscape (Taylor & Hall, 2011). Second, while under many conditions non-dispersive species may be at higher risk of extinction, in heavily modified landscapes under additional stressors, the role of dispersal becomes less important. Given the landscape composition of many lowland areas and the global threat of climate change, it is not unreasonable to expect that many species in such places are being pushed to their limits and that declines of both range-restricted and widespread species should be expected.

While this simulation is informative for understanding observed patterns of insect decline, it can also inform the efficacy of potential interventions. Semi-natural landscapes appear to offer considerable value for bolstering metapopulations, especially for more dispersive species (Howe et al., 1991; Reigada et al., 2015). While expanding high-quality source habitats benefits all species, increasing coverage of semi-natural habitats can have comparable effects on dispersive species (to a certain extent), likely due to improved recolonization. In the context of insects, such areas may include pollinator strips and hedgerows in agricultural areas, as well as pollinator gardens in cities, which can provide resources in otherwise substandard areas (Dilts et al., 2023; Buhk et al., 2018; Donkersley et al., 2023; von Königslöw et al., 2022). This finding is also supported by experimental work showing that open corridors that do not support populations themselves can still facilitate movement between high-quality patches (Haddad & Tewksbury, 2005). While we found that semi-natural lands as well as natural lands can facilitate recolonization for dispersive species, we also find that prioritizing connectivity is slightly more effective for preserving dispersive species than expanding core habitats. Such 'stepping stone' habitats are important for long-distance dispersal events, though they must be of adequate size or quality to be useful (Saura et al., 2014). Together, these results underscore the importance of strategically expanding and connecting semi-natural and high-quality habitats, which can amplify the persistence of dispersive species. It should be noted that expanding core habitat was also quite effective in this simulation, and any conservation action to preserve tracts of land is likely to benefit widespread species.

One of the defining features of the Anthropocene is the interconnectedness of threats imposed on natural populations (Breitburg et al., 1998; Halsch et al., 2025; Pirotta et al., 2022). Many landscapes face multiple stressors at once, which is likely crucial for understanding the decline of both range-restricted and widespread insects (Pirotta et al., 2022; Yang et al., 2021). Our findings provide additional perspective on this process and offer further insights into the decline of widespread species. All else being equal, being highly dispersive creates larger and more stable metapopulations. Still, in highly developed landscapes with a legacy of habitat loss, additional stressors (e.g., climate change) can lead to rapid declines. These results highlight the importance of marginal habitats and the role of connections in supporting mobile species (Samways, 2007). While these results are meant to be broad, further investigation of specific landscapes, especially those that are less connected, or of additional species, such as migratory species, would make excellent follow-up work. Overall, many range-limited species, or significant portions of their ranges, may already have been lost before baseline data could be established through natural history discovery and monitoring programmes; however, many widespread species, while declining, can be supported through thoughtful land conservation and management.

AUTHOR CONTRIBUTIONS

Christopher A. Halsch: Conceptualization; investigation; writing – original draft; writing – review and editing; visualization; funding acquisition; methodology; validation; software; formal analysis; project administration; data curation; supervision; resources. **Matthew L. Forister:** Conceptualization; writing – review and editing; methodology; supervision. **Eliza M. Grames:** Supervision; writing – review and editing; funding acquisition; investigation; methodology.

ACKNOWLEDGEMENTS

Christopher A. Halsch acknowledges the USDA NIFA predoctoral fellowship (2022-67011-36563) for funding this idea and the initial development. Matthew L. Forister thanks the National Science Foundation (DEB-2114793). Eliza M. Grames thanks the National Science Foundation (DEB-2225092). We also would like to thank the anonymous reviewers for their excellent feedback, which greatly improved the quality of this work.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code needed to generate landscapes and run the simulation can be found at: https://doi.org/10.6084/m9.figshare.30153277.

ORCID

Christopher A. Halsch https://orcid.org/0000-0003-1381-1905
Eliza M. Grames https://orcid.org/0000-0003-1743-6815

REFERENCES

Althaus, S.L., Berenbaum, M.R., Jordan, J. & Shalmon, D.A. (2021) No buzz for bees: media coverage of pollinator decline. *National Academy of Sciences of the United States of America*, 118(2), e2002552117. Available from: https://doi.org/10.1073/pnas.2002552117

Baguette, M. & Schtickzelle, N. (2006) Negative relationship between dispersal distance and demography in butterfly metapopulations. *Ecology*, 87(3), 648–654. Available from: https://doi.org/10.1890/04-1631

Bender, D.J., Contreras, T.A. & Fahrig, L. (1998) Habitat loss and population decline: a meta-analysis of the patch size effect. *Ecology*, 79(2), 517–533.

Bowler, D.E. & Benton, T.G. (2009) Impact of dispersal on population growth: the role of inter-patch distance. *Oikos*, 118(3), 403–412. Available from: https://doi.org/10.1111/j.1600-0706.2008.17049.x

Breitburg, D.L., Baxter, J.W., Hatfield, C.A., Howarth, R.W., Jones, C.G., Lovett, G.M. et al. (1998) Understanding effects of multiple stressors: ideas and challenges. In: Pace, M.L. & Groffman, P.M. (Eds.) *Successes, limitations, and frontiers in ecosystem science*. New York, NY:

Springer, pp. 416–431. Available from: https://doi.org/10.1007/978-1-4612-1724-4_17

Brown, C.J., Saunders, M.I., Possingham, H.P. & Richardson, A.J. (2013) Managing for interactions between local and global stressors of ecosystems. *PLoS One*, 8(6), e65765. Available from: https://doi.org/10.1371/journal.pone.0065765

Buhk, C., Oppermann, R., Schanowski, A., Bleil, R., Lüdemann, J. & Maus, C. (2018) Flower strip networks offer promising long term effects on pollinator species richness in intensively cultivated agricultural areas. *BMC Ecology*, 18(1), 55. Available from: https://doi.org/10.1186/s12898-018-0210-z

Caro, T., Rowe, Z., Berger, J., Wholey, P. & Dobson, A. (2022) An inconvenient misconception: climate change is not the principal driver of biodiversity loss. *Conservation Letters*, 15(3), e12868. Available from: https://doi.org/10.1111/conl.12868

Crisfield, V.E., Guillaume Blanchet, F., Raudsepp-Hearne, C. & Gravel, D. (2024) How and why species are rare: towards an understanding of the ecological causes of rarity. *Ecography*, 2024(2), e07037. Available from: https://doi.org/10.1111/ecog.07037

Devictor, V., Julliard, R. & Jiguet, F. (2008) Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. *Oikos*, 117(4), 507–514. Available from: https://doi.org/10.1111/j.0030-1299.2008.16215.x

Dey, S. & Joshi, A. (2006) Stability via asynchrony in drosophila metapopulations with low migration rates. *Science*, 312(5772), 434–436. Available from: https://doi.org/10.1126/science.1125317

Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B. & Collen, B. (2014) Defaunation in the anthropocene. *Science*, 345(6195), 401–406. Available from: https://doi.org/10.1126/science.1251817

Donkersley, P., Witchalls, S., Bloom, E.H. & Crowder, D.W. (2023) A little does a lot: can small-scale planting for pollinators make a difference? *Agriculture, Ecosystems & Environment*, 343, 108254. Available from: https://doi.org/10.1016/j.agee.2022.108254

Dunn, E.H., Francis, C.M., Blancher, P.J., Drennan, S.R., Howe, M.A., Lepage, D. et al. (2005) Enhancing the scientific value of the Christmas bird count. *The Auk*, 122(1), 338–346. Available from: https://doi.org/10.1093/auk/122.1.338

Dilts, T. E., Black, S. H., Hoyle, S. M., et al. (2023) Agricultural margins could enhance landscape connectivity for pollinating insects across the Central Valley of California, USA. *PLOS ONE*, 18(2), e0267263. Available from: https://doi.org/10.1371/journal.pone.0267263

Edwards, C.B., Zipkin, E.F., Henry, E.H., Haddad, N.M., Forister, M.L., Burls, K.J. et al. (2025) Rapid butterfly declines across the United States during the 21st century. *Science*, 387(6738), 1090–1094. Available from: https://doi.org/10.1126/science.adp4671

Fadai, N.T. & Simpson, M.J. (2020) Population dynamics with threshold effects give rise to a diverse family of Allee effects. *Bulletin of Mathematical Biology*, 82(6), 74. Available from: https://doi.org/10.1007/s11538-020-00756-5

Fattorini, S. (2011) Insect extinction by urbanization: a long term study in Rome. *Biological Conservation*, 144(1), 370–375. Available from: https://doi.org/10.1016/j.biocon.2010.09.014

Forister, M.L., Black, S.H., Elphick, C.S., Grames, E.M., Halsch, C.A., Schultz, C.B. et al. (2023) Missing the bigger picture: why insect monitoring programs are limited in their ability to document the effects of habitat loss. *Conservation Letters*, 16(3), e12951. Available from: https://doi.org/10.1111/conl.12951

Forister, M.L., Grames, E.M., Halsch, C.A., Burls, K.J., Carroll, C.F., Bell, K.L. et al. (2023) Assessing risk for butterflies in the context of climate change, demographic uncertainty, and heterogeneous data sources. *Ecological Monographs*, 93(3), e1584. Available from: https://doi.org/10.1002/ecm.1584

Forister, M.L., Halsch, C.A., Nice, C.C., Fordyce, J.A., Dilts, T.E., Oliver, J.C. et al. (2021) Fewer butterflies seen by community scientists across the warming and drying landscapes of the American west. *Science*, 371(6533), 1042–1045. Available from: https://doi.org/10.1126/science.abe5585

Forister, M.L., McCall, A.C., Sanders, N.J., Fordyce, J.A., Thorne, J.H., O'Brien, J. et al. (2010) Compounded effects of climate change and habitat alteration shift patterns of butterfly diversity. *Proceedings of the National Academy of Sciences of the United States of America*, 107(5), 2088–2092. Available from: https://doi.org/10.1073/pnas.0909686107

Geldmann, J., Heilmann-Clausen, J., Holm, T.E., Levinsky, I., Markussen, B., Olsen, K. et al. (2016) What determines spatial bias in citizen science? Exploring four recording schemes with different proficiency requirements. *Diversity and Distributions*, 22(11), 1139–1149. Available from: https://doi.org/10.1111/ddi.12477

Gilpin, M.E. & Soulé, M.E. (1986) Minimum viable populations: processes of species extinction. In: *Conservation biology: the science of scarcity and diversity*. Sunderland, Massachusetts: Sinauer Associates, Inc.

Grilli, J., Barabás, G. & Allesina, S. (2015) Metapopulation persistence in random fragmented landscapes. *PLoS Computational Biology*, 11(5), e1004251. Available from: https://doi.org/10.1371/journal.pcbi.1004251

Habel, J.C., Segerer, A., Ulrich, W., Torchyk, O., Weisser, W.W. & Schmitt, T. (2016) Butterfly community shifts over two centuries. *Conservation Biology*, 30(4), 754–762. Available from: https://doi.org/10.1111/cobi.12656

Haddad, N.M. & Tewksbury, J.J. (2005) Low-quality habitat corridors as movement conduits for two butterfly species. *Ecological Applications*, 15(1), 250–257. Available from: https://doi.org/10.1890/03-5327

Halsch, C.A. (2026) Dispersal mediates metapopulation response to local and regional stressors. https://doi.org/10.6084/m9.figshare.30153277

Halsch, C.A., Code, A., Hoyle, S.M., Fordyce, J.A., Baert, N. & Forister, M.L. (2020) Pesticide contamination of milkweeds across the agricultural, urban, and open spaces of low-elevation northern California. *Frontiers in Ecology and Evolution*, 8, 1–11. Available from: https://doi.org/10.3389/fevo.2020.00162

Halsch, C.A., Elphick, C.S., Bahlai, C.A., Forister, M.L., Wagner, D.L., Ware, J.L. et al. (2025) Meta-synthesis reveals interconnections among apparent drivers of insect biodiversity loss. *Bioscience*, 75(6), 448–456. Available from: https://doi.org/10.1093/biosci/biaf034

Hanski, I. (1998) Metapopulation dynamics. *Nature*, 396(6706), 41–49. Available from: https://doi.org/10.1038/23876

Hanski, I. & Ovaskainen, O. (2002) Extinction debt at extinction threshold. *Conservation Biology*, 16(3), 666–673.

Hansson, L. (1991) Dispersal and connectivity in metapopulations. *Biological Journal of the Linnean Society*, 42(1–2), 89–103. Available from: https://doi.org/10.1111/j.1095-8312.1991.tb00553.x

Harvey, J.A., Tougeron, K., Gols, R., Heinen, R., Abarca, M., Abram, P.K. et al. (2023) Scientists' warning on climate change and insects. *Ecological Monographs*, 93(1), e1553. Available from: https://doi.org/10.1002/ecm.1553

Haynes, K.J. & Walter, J.A. (2022) Advances in understanding the drivers of population spatial synchrony. *Current Opinion in Insect Science*, 53, 100959. Available from: https://doi.org/10.1016/j.cois.2022.100959

Heino, M., Kaitala, V., Ranta, E. & Lindström, J. (1997) Synchronous dynamics and rates of extinction in spatially structured populations. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 264(1381), 481–486. Available from: https://doi.org/10.1098/rspb.1997.0069

Howe, R.W., Davis, G.J. & Mosca, V. (1991) The demographic significance of 'sink' populations. *Biological Conservation*, 57(3), 239–255. Available from: https://doi.org/10.1016/0006-3207(91)90071-G

Hu, G., Stefanescu, C., Oliver, T.H., Roy, D.B., Brereton, T., van Swaay, C. et al. (2021) Environmental drivers of annual population fluctuations in a trans-Saharan insect migrant. *National Academy of Sciences of the*

United States of America, 118(26), e2102762118. Available from: https://doi.org/10.1073/pnas.2102762118

Johst, K., Brandl, R. & Eber, S. (2002) Metapopulation persistence in dynamic landscapes: the role of dispersal distance. *Oikos*, 98(2), 263–270. Available from: https://doi.org/10.1034/j.1600-0706.2002.980208.x

Levins, R. (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America*, 15(3), 237–240. Available from: https://doi.org/10.1093/besa/15.3.237

MacLean, S.A., Rios Dominguez, A.F., de Valpine, P. & Beissinger, S.R. (2018) A century of climate and land-use change cause species turnover without loss of beta diversity in California's Central Valley. *Global Change Biology*, 24(12), 5882–5894. Available from: https://doi.org/10.1111/gcb.14458

Marschalek, D.A. & Klein, M.W. (2010) Distribution, ecology, and conservation of Hermes copper (Lycaenidae: Lycaena [Hermelycaena] hermes). *Journal of Insect Conservation*, 14(6), 721–730. Available from: https://doi.org/10.1007/s10841-010-9302-6

Murphy, D.D. & Weiss, S.B. (1988) Ecological studies and the conservation of the bay checkerspot butterfly, Euphydryas editha bayensis. *Biological Conservation*, 46(3), 183–200. Available from: https://doi.org/10.1016/0006-3207(88)90067-5

Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A. et al. (2015) Global effects of land use on local terrestrial biodiversity. *Nature*, 520(7545), 45–50. Available from: https://doi.org/10.1038/nature14324

Pardikes, N.A., Harrison, J.G., Shapiro, A.M. & Forister, M.L. (2017) Synchronous population dynamics in California butterflies explained by climatic forcing. *Royal Society Open Science*, 4(7), 170190. Available from: https://doi.org/10.1098/rsos.170190

Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421(6918), 37–42. Available from: https://doi.org/10.1038/nature01286

Pirotta, E., Thomas, L., Costa, D.P., Hall, A.J., Harris, C.M., Harwood, J. et al. (2022) Understanding the combined effects of multiple stressors: a new perspective on a longstanding challenge. *Science of the Total Environment*, 821, 153322. Available from: https://doi.org/10.1016/j.scitotenv.2022.153322

Preston, S.D., Liao, J.D., Toombs, T.P., Romero-Canyas, R., Speiser, J. & Seifert, C.M. (2021) A case study of a conservation flagship species: the monarch butterfly. *Biodiversity and Conservation*, 30(7), 2057–2077. Available from: https://doi.org/10.1007/s10531-021-02183-x

Pulliam, H.R. (1988) Sources, sinks, and population regulation. *The American Naturalist*, 132(5), 652–661.

Purvis, A., Gittleman, J.L., Cowlishaw, G. & Mace, G.M. (2000) Predicting extinction risk in declining species. *Proceedings of the Biological Sciences*, 267(1456), 1947–1952. Available from: https://doi.org/10.1098/rspb.2000.1234

R Core Team. (2023) *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/

Raven, P.H. & Wagner, D.L. (2021) Agricultural intensification and climate change are rapidly decreasing insect biodiversity. *Proceedings of the National Academy of Sciences of the United States of America*, 118(2), e2002548117. Available from: https://doi.org/10.1073/pnas.2002548117

Reigada, C., Schreiber, S.J., Altermatt, F. & Holyoak, M. (2015) Metapopulation dynamics on ephemeral patches. *The American Naturalist*, 185(2), 183–195. Available from: https://doi.org/10.1086/679502

Remisiewicz, M. & Underhill, L.G. (2020) Climatic variation in Africa and Europe has combined effects on timing of spring migration in a long-distance migrant willow warbler *Phylloscopus trochilus*. *PeerJ*, 8, e8770. Available from: https://doi.org/10.7717/peerj.8770

Reppert, S.M. & de Roode, J.C. (2018) Demystifying monarch butterfly migration. *Current Biology*, 28(17), R1009–R1022. Available from: https://doi.org/10.1016/j.cub.2018.02.067

Samways, M.J. (2007) Insect conservation: a synthetic management approach. *Annual Review of Entomology*, 52, 465–487. Available from: https://doi.org/10.1146/annurev.ento.52.110405.091317

Saura, S., Bodin, Ö. & Fortin, M.-J. (2014) EDITOR's CHOICE: stepping stones are crucial for species' long-distance dispersal and range expansion through habitat networks. *Journal of Applied Ecology*, 51(1), 171–182. Available from: https://doi.org/10.1111/1365-2664.12179

Staudt, A., Leidner, A.K., Howard, J., Brauman, K.A., Dukes, J.S., Hansen, L.J. et al. (2013) The added complications of climate change: understanding and managing biodiversity and ecosystems. *Frontiers in Ecology and the Environment*, 11(9), 494–501. Available from: https://doi.org/10.1890/120275

Taylor, C.M. & Hall, R.J. (2011) Metapopulation models for seasonally migratory animals. *Biology Letters*, 8(3), 477–480. Available from: https://doi.org/10.1098/rsbl.2011.0916

Thorp, R. (2005) *Species Profile: Bombus franklini*. Portland OR: The Xerces Society for Invertebrate Conservation Red List of Pollinator Insects of North America.

van Dyck, H., van Strien, A.J., Maes, D. & van Swaay, C.A. (2009) Declines in common, widespread butterflies in a landscape under intense human use. *Conservation Biology*, 23(4), 957–965. Available from: https://doi.org/10.1111/j.1523-1739.2009.01175.x

van Klink, R., Bowler, D.E., Gongalsky, K.B., Shen, M., Swengel, S.R. & Chase, J.M. (2024) Disproportionate declines of formerly abundant species underlie insect loss. *Nature*, 628(8007), 359–364. Available from: https://doi.org/10.1038/s41586-023-06861-4

Vance, R.R. (1984) The effect of dispersal on population stability in one-species, discrete-space population growth models. *The American Naturalist*, 123(2), 230–254. Available from: https://doi.org/10.1086/284199

Vogwill, T., Fenton, A. & Brockhurst, M.A. (2009) Dispersal and natural enemies interact to drive spatial synchrony and decrease stability in patchy populations. *Ecology Letters*, 12(11), 1194–1200. Available from: https://doi.org/10.1111/j.1461-0248.2009.01374.x

von Königslöw, V., Fornoff, F. & Klein, A.-M. (2022) Pollinator enhancement in agriculture: comparing sown flower strips, hedges and sown hedge herb layers in apple orchards. *Biodiversity and Conservation*, 31(2), 433–451. Available from: https://doi.org/10.1007/s10531-021-02338-w

Wagner, D.L. (2020) Insect declines in the Anthropocene. *Annual Review of Entomology*, 65, 457–480. Available from: https://doi.org/10.1146/annurev-ento-011019-025151

Wagner, D.L., Grames, E.M., Forister, M.L., Berenbaum, M.R. & Stopak, D. (2021) Insect decline in the Anthropocene: death by a thousand cuts. *National Academy of Sciences of the United States of America*, 118(2), e2023989118. Available from: https://doi.org/10.1073/pnas.2023989118

Wagner, D.L. & Van Driesche, R.G. (2010) Threats posed to rare or endangered insects by invasions of nonnative species. *Annual Review of Entomology*, 55(1), 547–568. Available from: https://doi.org/10.1146/annurev-ento-112408-085516

Wang, S., Haegeman, B. & Loreau, M. (2015) Dispersal and metapopulation stability. *PeerJ*, 3, e1295. Available from: https://doi.org/10.7717/peerj.1295

Warren, M.S., Maes, D., van Swaay, C.A.M., Goffart, P., van Dyck, H., Bourn, N.A.D. et al. (2021) The decline of butterflies in Europe: problems, significance, and possible solutions. *National Academy of Sciences of the United States of America*, 118(2), e2002551117. Available from: https://doi.org/10.1073/pnas.2002551117

Yang, L.H., Postema, E.G., Hayes, T.E., Lippey, M.K. & MacArthur-Waltz, D.J. (2021) The complexity of global change and its effects on

insects. *Current Opinion in Insect Science*, 47, 90–102. Available from: https://doi.org/10.1016/j.cois.2021.05.001

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Functions that determine population growth each year. A) Weather fluctuations over the simulation's length (with no trend imposed). Weather impacts all cells equally. B) The three curves for density dependence used in the simulation.

Figure S2. The reduction in error in the population estimate as the number of iterations for each parameter combination increases. Each plot shows the same relationship, but the points are coloured by the different tested variables. Points are slightly jittered horizontally to better display data.

Figure S3. Distribution of the ratios of within landscape variance to between landscape variance on when comparing landscapes of the same proportion of land types from the preliminary analysis. Values below one indicate that between landscape variation (running the same parameters on different landscapes of the same proportion) is greater than within landscape variation (running the same parameters on the same landscape additional times). The majority of variation is introduced between landscapes rather than from multiple runs on the same landscape.

Figure S4. Demonstration of the landscape modification functions. A) The original landscape before any modification. B) The function that turns borders between natural and semi-natural habitats into a natural habitat. C) The function that turns areas in the middle of semi-natural patches into natural habitat. In figures B and C the same number of cells were converted.

Figure S5. Functions that determine dispersal. A) Individuals favour moving into patches that have a higher patch quality. B) Individuals favour moving from patches with higher abundance. C) The combinations of panels A and B in a single figure.

Figure S6. The effects of habitat quality and dispersal ability on the probability of recovery in a cell across the simulations. Panel A shows natural habitat and panel B shows semi-natural habitat. The effects shown are the mean effects after averaging over all other effects. Points and lines represent the mean effect and are coloured by dispersal ability. The bands surrounding the lines indicate bootstrapped 95% confidence intervals based on bootstrapping.

Figure S7. The effects of patchiness and dispersal ability on the average abundance in semi-natural habitats across the simulations. The effects shown are the mean effects after averaging over all other effects. Points and lines represent the mean effect and are coloured by dispersal ability. The bands surrounding the lines indicate bootstrapped 95% confidence intervals based on bootstrapping.

Figure S8. The effects of landscape stressors and dispersal ability on the average abundance in semi-natural cells across the simulations. Panel A shows the effects of local stressors associated with semi-natural habitat, and Panel B shows stressors that impact the entire landscape. The effects shown are the mean effects after averaging over all other effects. Points and lines represent the mean effect and are coloured by dispersal ability. The bands surrounding the lines indicate bootstrapped 95% confidence intervals.

Table S1. The effects of different parameters in the simulation on variability in the simulated answer.

How to cite this article: Halsch, C.A., Forister, M.L. & Grames, E.M. (2026) Dispersal mediates metapopulation response to local and regional stressors. *Insect Conservation and Diversity*, 1–14. Available from: https://doi.org/10.1111/icad.70128