Received: 9 July 2021 | Revised: 29 November 2021 | Accepted: 21 December 2021
DOI: 10.1002/eap.2608

ECOLOGICAL APPLICATIONS
ECOLOGICAL SOCIETY OF AMERICA

ARTICLE

Extinction of biotic interactions due to habitat loss could accelerate the current biodiversity crisis

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Funding information
Audubon Connecticut Important Bird Area Small Matching Grants Program; Center for Conservation and Biodiversity Award (University of Connecticut); National Science Foundation, Grant/Award Number: DEB 1701858; Ronald Bamford Fund (Department of Ecology and Evolutionary Biology, University of Connecticut); University of California Eastern Sierra Nevada Student Research Award; Zoology Award (Department of Ecology and Evolutionary Biology, University of Connecticut)

Handling Editor: Juan C. Corley

Abstract

Habitat loss disrupts species interactions through local extinctions, potentially orphaning species that depend on interacting partners, via mutualisms or commensalisms, and increasing secondary extinction risk. Orphaned species may become functionally or secondarily extinct, increasing the severity of the current biodiversity crisis. While habitat destruction is a major cause of biodiversity loss, the number of secondary extinctions is largely unknown. We investigate the relationship between habitat loss, orphaned species, and bipartite network properties. Using a real seed dispersal network, we simulate habitat loss to estimate the rate at which species are orphaned. To be able to draw general conclusions, we also simulate habitat loss in synthetic networks to quantify how changes in network properties affect orphan rates across broader parameter space. Both real and synthetic network simulations show that even small amounts of habitat loss can cause up to 10% of species to be orphaned. More area loss, less connected networks, and a greater disparity in the species richness of the network's trophic levels generally result in more orphaned species. As habitat is lost to land-use conversion and climate change, more orphaned species increase the loss of community-level and ecosystem functions. However, the potential severity of repercussions ranges from minimal (no species orphaned) to catastrophic (up to 60% of species within a network orphaned). Severity of repercussions also depends on how much the interaction richness and intactness of the community affects the degree of redundancy within networks. Orphaned species could add substantially to the loss of ecosystem function and secondary extinction worldwide.

KEYWORDS
bipartite network, co-extinction, ecological interaction, mutualism, orphaned species, secondary extinction

INTRODUCTION

The world faces an extinction crisis arising from habitat destruction, invasive species, resource extraction, pollution,

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Morgan W. Tingley and Chris S. Elphick contributed equally to the work reported here.

and climate change (Ceballos et al., 2015). Accelerating species loss has raised concern over the implications for species with which the lost species interact (e.g., Bellard et al., 2012; Dunn et al., 2009; Urban et al., 2013). If enough species are extirpated from an area, the remaining species can lose all interaction partners, leading to secondary extinctions (Brodie et al., 2014; Dunne et al., 2002; Tylianakis et al., 2010). Secondary extinction, however, may be an infrequent result of the loss of biotic interactions (Fricke et al., 2017; Kiers et al., 2010; Valiente-Banuet et al., 2015) due to processes that slow losses within communities and mutualistic networks over the short-term such as extinction debt (e.g., Guardiola et al., 2018) and mitigate losses over the longer term such as rewiring (e.g., Kaiser-Bunbury et al., 2010). Better understanding the repercussions of interaction loss is especially pressing for mutualists that rely on each other for a critical part of their life history (Aslan et al., 2013; Christian, 2001; Figueiredo et al., 2019; Kiers et al., 2010).

Most mutualist species have multiple partner species, ensuring ecological redundancy if one partner is lost (Aizen et al., 2012; Koh et al., 2004). As redundancy declines, populations can be harmed via reduced fecundity or increased mortality, even if secondary extinctions are rare or delayed (Aslan et al., 2013; Guardiola et al., 2018). Island examples demonstrate that the loss of pollinators can significantly reduce fecundity in plant species without frequent self-fertilization (Anderson et al., 2011; Mortensen et al., 2008). Similarly, the loss of vertebrate seed dispersers can cause plant population declines and range contractions due to increased seedling mortality, reduced seedling establishment, or both (Rogers et al., 2017; Traveset et al., 2012). Animal species that rely on pollen, nectar, or fruit for nourishment can also suffer increased mortality with the loss of resources that their partner species provided (van Schaik et al., 1993). Even if some individuals of a species that has lost all mutualistic interactions persist, the loss of interactions will likely render the "orphaned" species functionally extinct, that is, no longer significantly contributing to ecosystem function and facing inevitable future extinction (Cronk, 2016; Hooper & Ashton, 2020; Säterberg et al., 2013; "orphaned" species modified from Federman et al., 2016). Previous studies have assumed that a species losing all interactions within a network leads to the secondary extinction of that species (e.g., Dunne et al., 2002; Evans et al., 2013; Fortuna & Bascompte, 2006; Memmott et al., 2004; Solé & Montoya, 2001; Vidal et al., 2019; Vieira & Almeida-Neto, 2015). We distinguish orphaned species from secondary extinctions because loss of all interactions may, but does not always, lead to secondary extinctions (Fricke et al., 2017; Valiente-Banuet et al., 2015).

Interactions among plant–animal mutualists are often portrayed as a network (Bascompte et al., 2003), and the effects of species extinctions on a network have been simulated with random or ordered species removal (Cai & Liu, 2016; Dunne et al., 2002; Memmott et al., 2004; Rezende et al., 2007; Solé & Montoya, 2001; Srinivasan et al., 2007; Vieira & Almeida-Neto, 2015). Species do not go extinct randomly, however, and the order or number of primary extinctions depends on the driver of extinction. Here, we address this problem by studying the effects of the largest contemporary driver of global species extinctions: habitat loss (Ceballos et al., 2015).

Several previous studies have addressed how spatial processes affect secondary extinctions within networks (e.g., Evans et al., 2013; Fortuna & Bascompte, 2006; Häussler et al., 2020; Srinivasan et al., 2007; Vidal et al., 2019). While these studies elucidate the influence of spatial processes such as metacommunities and the value of a habitat patch, the amount of habitat loss could have additional repercussions via its effect on the number of primary extinctions (Pimm & Askins, 1995; Pimm & Raven, 2000; Simberloff, 1991). The novelty of our study lies in asking how the amount of habitat lost affects the number of orphaned species, and how amount of habitat lost compares to network properties as a source of orphaned species.

We simulated loss of habitat via (1) observed species occurrences and (2) the species–area relationship to quantify how the number of extinctions caused by habitat loss affects network structure, and thus creates orphaned species. The species–area relationship is widely used to predict species loss as habitat area declines (Pimm & Askins, 1995; Pimm & Raven, 2000; Rybicki & Hanski, 2013; Simberloff, 1991), and takes the general form $S = cA^z$, where S is the number of species, A is the area of a habitat patch, and c and z are constants describing the intercept and slope, respectively (Connor & McCoy, 1979). Since z can vary among taxonomic groups, species losses may differ between the two groups of organisms forming a mutualistic network (e.g., pollinators and pollinated plants, or seed dispersers and the plants dispersed). By modeling differences in z (hereafter z-differences) between the two taxonomic groups, we modify the network property web asymmetry (Blüthgen et al., 2007) to be area specific. Larger z-differences will translate into larger differences in S at all but the very smallest area sizes. The taxonomic group within the network that has fewer species will have more connections per species on average, meaning that species loss from this group is expected to have a disproportionate effect on the other group (e.g., Albrecht et al., 2018; Dunne et al., 2002; Memmott et al., 2004; Palacio et al., 2016, Figure 1). A loss of functional diversity in this taxonomic

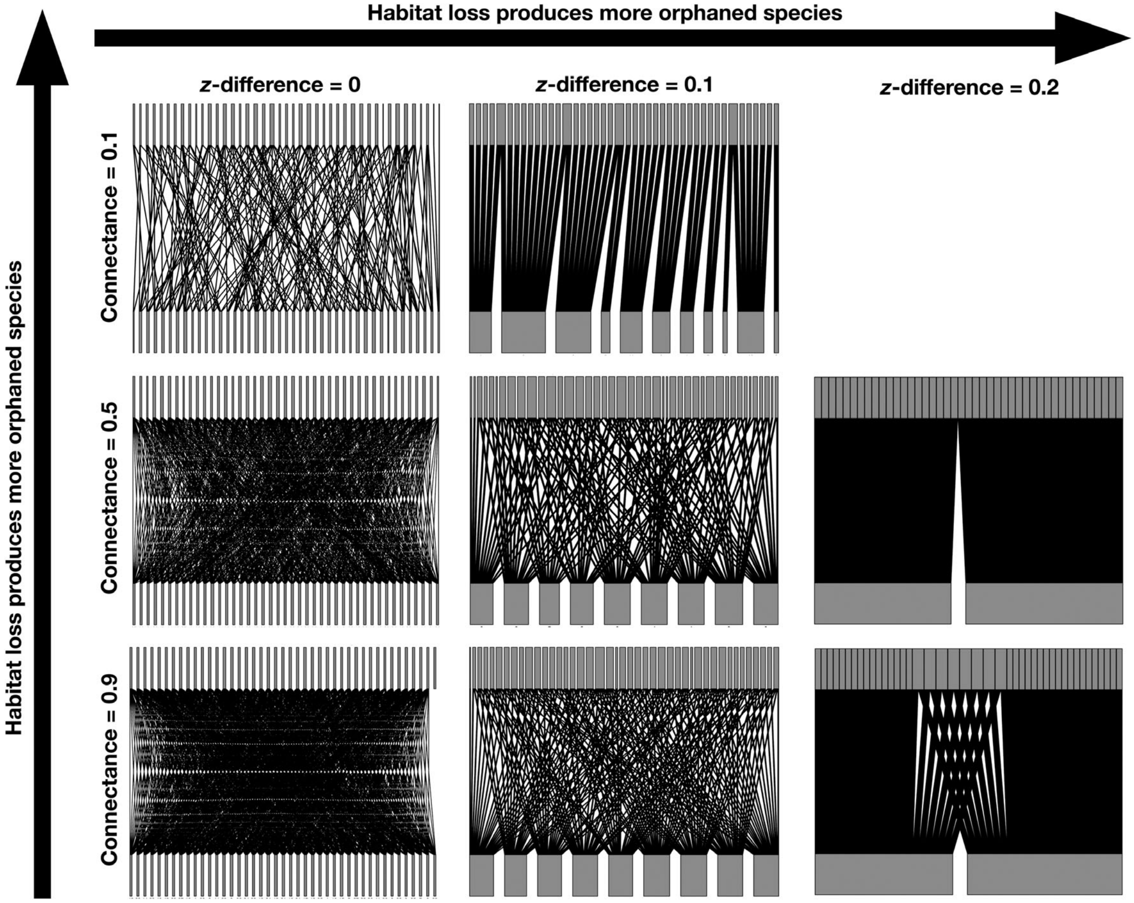

FIGURE 1 Nine synthetic plant–animal networks illustrating how *z*-differences and connectance of these networks affect the number of orphaned species produced with habitat loss (Predictions 2 and 3, respectively). For Prediction 2, greater *z*-differences (left to right) are expected to produce more orphaned species with habitat loss because the loss of more highly connected species affects a greater number of species. For Prediction 3, networks with lower connectance (bottom to top) are expected to produce more orphaned species with habitat loss because each species has fewer interactions to lose. In the network, group 1 (43 species; top of each network) and group 2 (43, 9, or 2 species; bottom of each network) species are represented by gray boxes, where the width of the box corresponds to the number of interactions with members of the other group. Black lines represent a single interaction between a species in group 1 and one in group 2. The synthetic network illustrating a connectance of 0.1 and a *z*-difference of 0.2 (top right; no network displayed) is not viable because the number of interactions required by the connectance value would result in a lower *z*-difference value than 0.2. The synthetic network illustrating a connectance of 0.1 and a *z*-difference of 0.1 (top middle) has an actual *z*-difference of 0.09 because higher values were not viable

group that is more species depauperate could drive this disproportionate effect on the other taxonomic group, which could equate to top-down or bottom-up processes within a network (Albrecht et al., 2018).

The expected number of orphans created by the loss of a random species from a network depends on connectance (Dunne et al., 2002; Dunne & Williams, 2009), a network property that describes the average number of interactions per species and ranges from 0, when there are no interactions, to 1, when each species is connected to every species in the partner group (Jordano, 1987). Networks with high connectance have many generalist species, while networks with low connectance have many species that interact with few partners. Lower connectance networks, thus, are predicted to create more orphaned species as area is lost (Memmott et al., 2004; Morán-López et al., 2020; Thébault & Fontaine, 2010; Figure 1).

To study interaction loss cascades as a function of network properties, we used data from an empirical avian seed dispersal network and simulated habitat loss to describe the frequency and patterns by which species are orphaned. The avian seed dispersal network was compiled using multiple methods of observing interactions and assumed that birds consume all species within a genus, thus reducing concerns of under-sampling due to rare interactions or temporal variation. We additionally generated synthetic bipartite networks that encompassed the full spectrum of both connectance and the empirically estimated range of z values (Drakare et al., 2006; Lomolino, 1989) and associated z-differences. These synthetic networks mimicked the full range of potential mutualistic networks, which allows us to generalize our results to any mutualistic network. We subjected each synthetic network to simulated area loss, allowing an evaluation of how network structure leads to orphaned species given different amounts of habitat loss. We modeled the resulting probability and number of orphaned species to assess their relationships with z-differences between species groups, connectance, and amount of habitat loss. We predicted that: (1) larger area losses would create more orphaned species because they cause more primary extinctions (Pimm & Askins, 1995; Pimm & Raven, 2000; Simberloff, 1991), (2) greater z-differences would produce more orphaned species because the loss of more highly connected species causes more secondary extinctions (e.g., Dunne et al., 2002;

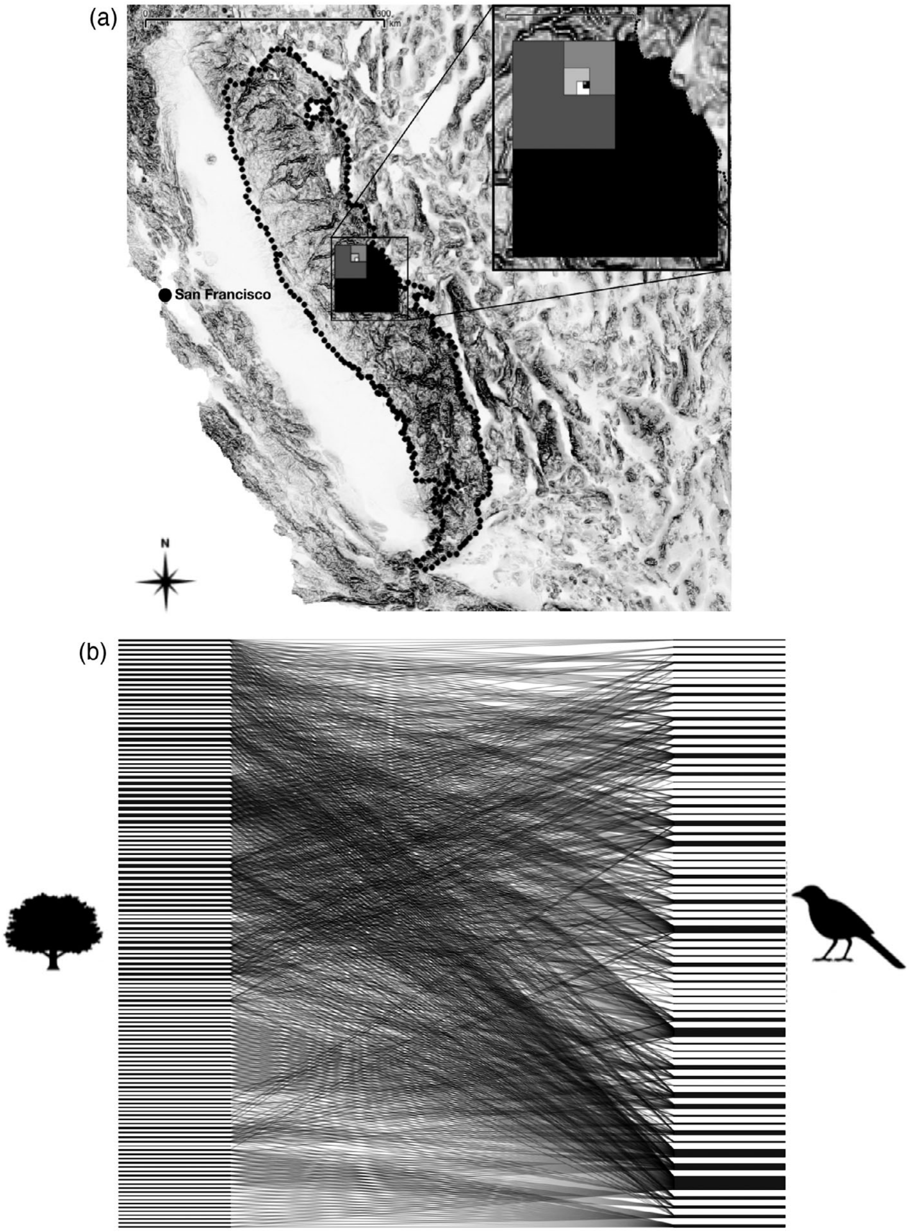

FIGURE 2 Empirical seed dispersal network within the Sierra Nevada Mountains, California, USA. (a) Overview of the Sierra Nevada Mountains study region (dotted outline) with decreasing habitat patches illustrated in black, gray, and white squares. Darker map shading indicates higher elevation. (b) Full seed dispersal network of the Sierra Nevada Mountains. Plant species are on the left and bird species are on the right. Wider species bars indicate a greater number of connections. For a larger version of the network with species labeled, see Appendix S2: Figure S1. See Appendix S1: Table S5 for details on each species

Memmott et al., 2004; Palacio et al., 2016; Figure 1); and (3) networks with lower connectance would produce more orphaned species because each species has fewer interactions to lose (Figure 1).

MATERIALS AND METHODS

Empirical network construction

To ground our work in a real ecosystem, we sampled a seed dispersal network of shrubs and small trees with fleshy or semi-fleshy bird-dispersed fruits and avian frugivores from the Sierra Nevada Mountains, California, USA, an area of high botanical diversity. Our study region covers 66,310 km^2 in the range 123°–117.5° W, 34°–43° N, and ~1000–4000 m elevation (Figure 2).

We compiled one seed dispersal network for the Sierra Nevada using data from: observations of birds consuming fruits in the western United States recorded in published literature, citizen science observations (submitted = 272), preserved stomach collections (searched = 514), camera traps (hours = 10,080), and fecal collections (collected = 300; see Appendix S3: Section S1.1). By compiling our network over multiple methods and a large area, we are ignoring processes that could affect spatially local interactions such as abundance (Guimarães, 2020; Morales & Vázquez, 2008) and temporal variation in interactions (CaraDonna et al., 2021; Chacoff et al., 2018; Chávez-González et al., 2020; Costa et al., 2020; Guimarães, 2020; Peralta, Vázquez, et al., 2020), and thus each local network represents an upper limit of the number of possible interactions. We calculated network connectance as

$$C = \frac{I}{A \times P}, \tag{1}$$

where C is connectance, I is the number of interactions, A is the total number of frugivorous animal species, and P is the total number of fruit-producing plant species (Jordano, 1987).

Scenario 1: Exponential area loss in an empirical network

Previous simulations have shown that bipartite networks are initially robust to species losses until a collapsing point is reached (Memmott et al., 2004). To determine how this resilience property is exhibited when habitat removal drives species losses, we subsampled our study region at different spatial resolutions using a series of nested grids with cell sizes 6400, 1600, 400, 100, 25, 6.25, and 1.56 km^2. Each larger grid cell contained four cells of the next finer grid resolution. We used these spatial resolutions to track sub-networks from the largest grid cell size to the smallest, thus reducing habitat area at each step (Figure 3). This approach provides a conservative estimate of species losses with reduced area because it does not account for demographic processes, habitat fragmentation, and other mechanisms that cause species to be lost from smaller patches and exacerbate the impact of habitat loss on species. This scenario, however, does account for how species' distributions across the landscape determine species–area relationships and patterns of loss with habitat destruction because we used occurrence records to build the species lists for all of the grid cells.

To populate grid cells with species, we compiled georeferenced herbarium records and plant observations from our study region between 1990 and 2015, using the Global Biodiversity Information Facility (GBIF, R package *rgbif*; Chamberlain, 2017) and our list of native, fleshy-fruited plant species (Appendix S1: Table S1). Georeferenced bird records came from the eBird database (downloaded 25 January 2018; Sullivan et al., 2009), restricting records to the study region, our species of interest (Appendix S1: Table S2), and the fruiting period (April–September) of 1990–2015 (Appendix S1: Table S3, see also Appendix S3: Section-S1.2). We determined species–area curves for our plant and bird communities by fitting linear regressions to observations at each scale (see Appendix S3: Section-S1.2), the fitted c parameters of which were used in our synthetic network simulations (Scenarios 2 and 3, below).

To estimate the number of orphaned species from simulated exponential area loss in an empirical network (this scenario), we created area loss "pathways." For each "pathway," habitat loss was simulated as the removal of three of the four grid cells contained by one of the cells in the largest resolution grid (one "area loss step"), cascading down to one grid cell remaining within the finest resolution grid (Figure 3; Appendix S1: Table S4). Each area loss step was designed to mimic the destruction of a large area of continuous habitat, leaving a small portion of it intact. Area loss pathways were designed to mimic an area of habitat being steadily reduced over time. Because sampling effort was not consistent from cell to cell within a single grid resolution size (which could artificially bias the primary extinction estimation), only those pathways with sufficient sampling were followed (see Appendix S3: Section S1.3). For each area loss step, we removed from the network all plant and bird species in the "destroyed" habitat, which left only those species observed in the remaining grid cell. We then calculated

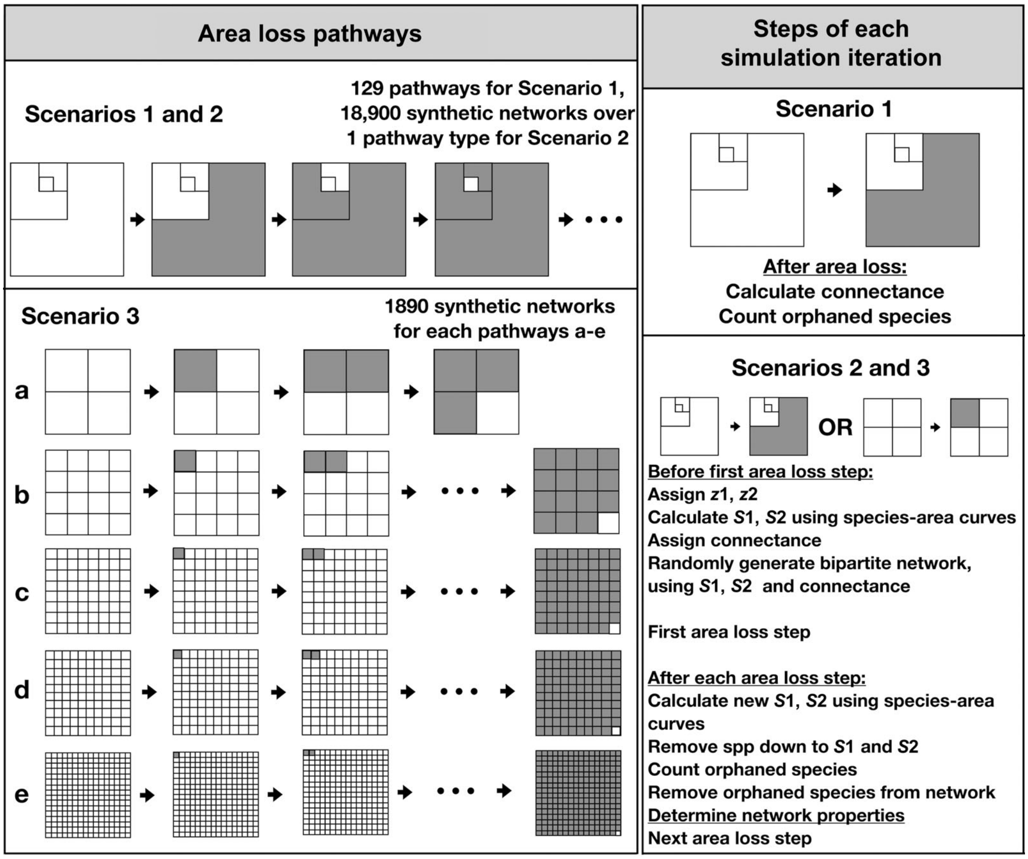

FIGURE 3 Habitat loss simulations for the exponential area loss in an empirical network scenario (Scenario 1), the exponential area loss in synthetic networks scenario (Scenario 2), and the variable linear area loss in synthetic networks scenario (Scenario 3). Left: graphical representation of area loss steps in all scenarios of habitat loss simulations, where gray squares indicate habitat destroyed. For the empirical network scenario (Scenario 1), a pathway denotes one particular series of grid cells destroyed (Appendix S1: Table S4). For the synthetic network scenarios (Scenarios 2 and 3), a pathway represents the amount of habitat destroyed at each area loss step. Top left: exponential area loss scenarios (Scenarios 1 and 2), which employ the same area lost at each step: (6400, 1600, 400, 100, 25, 6.25, and 1.56 km^2). Bottom left: area loss steps for the variable rate of linear area loss scenario (Scenario 3). Pathways a–e represent the five increments of area loss (a, 400 km^2 [three steps]; b, 100 km^2 [15]; c, 25 km^2 [63]; d, 16 km^2 [99]; e, 6.25 km^2 [255]) used. Top right: steps of each simulation iteration for the empirical network scenario (Scenario 1), which use real-world mutualistic networks from the Sierra Nevada mountains, California, USA. Bottom right: steps of each simulation iteration for the synthetic network scenarios (Scenarios 2 and 3). Parameters come from the species–area curve equation, with $z1$ and $z2$ as the slopes on a log–log scale and $S1$ and $S2$ as the number of species for a given area. The numbers 1 or 2 refer to species group 1 and species group 2 in the synthetic bipartite network. In Scenarios 2 and 3, values for $z1$ and $z2$ were assigned using values in the range 0.15–0.35 in increments of 0.01. The exponential area loss in synthetic networks scenario (Scenario 2) was used to determine general relationships, across the full parameter space, between z-difference or connectance and probability and number of orphaned species at each area loss step. The variable rates of area loss in synthetic networks scenario (Scenario 3) was used to determine the general relationship between the area lost at each step and the probability and number of orphaned species at each area loss step

connectance of the remaining network. We designated any species within the network that survived within the remaining grid cell but had lost all interaction partners due to the simulated habitat destruction as an orphaned species. We then tallied the number of orphaned species resulting from the previous area loss (Figure 3). Species that had at least one connection remained in the network. Because birds are highly mobile within continuous habitats (e.g., Neuschulz et al., 2013), we assumed interacting bird and plant species co-occurring within the same habitat patch would spatially overlap. We followed 129 pathways. Because smaller cells were nested within a few larger cells, multiple pathways used the same large cells (Figure 4; Appendix S1: Table S4), precluding formal statistical evaluation of trends in loss. We calculated percent orphaned species at each area loss step as the number of orphaned species divided by the number of species remaining within the network at the previous area loss step, and we did the same for percent extinct species.

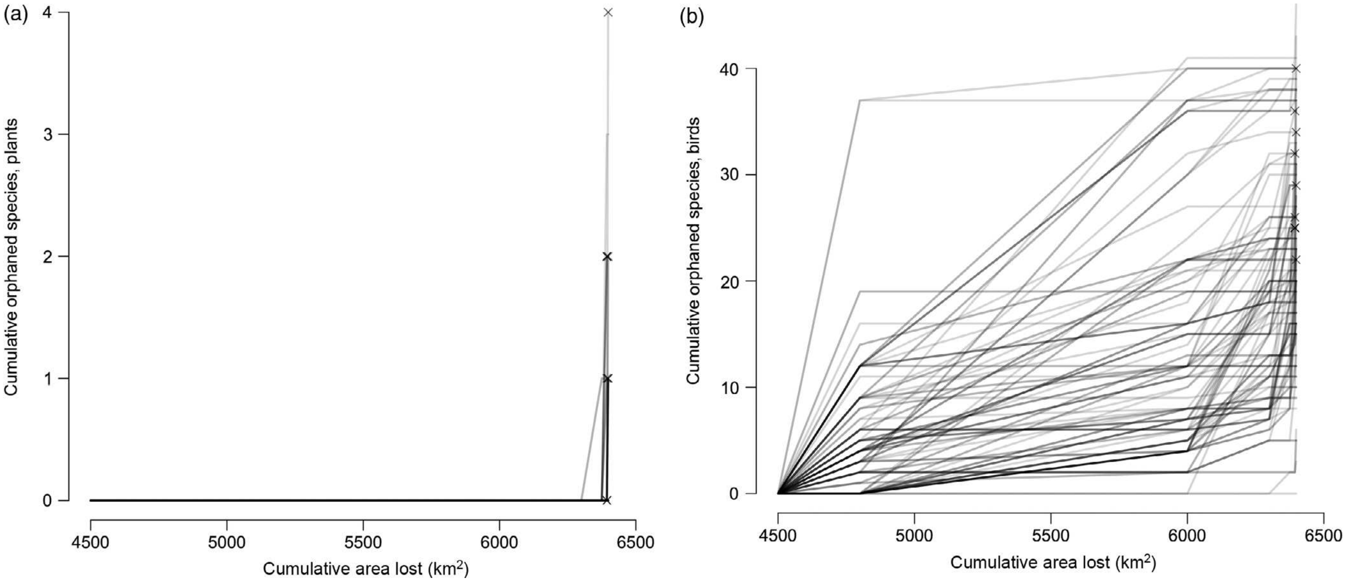

FIGURE 4 Habitat loss simulations for real seed dispersal networks within the Sierra Nevada Mountains, California, USA (Scenario 1: Exponential area loss in an empirical network). Cumulative number of orphaned (a) plant and (b) bird species as a result of simulated habitat loss and associated loss of partner species. Each line is one series of habitat patch losses ("pathway"). Habitat patches in which the seed dispersal network completely collapsed (no plant and/or bird species remaining) are denoted with ×. Network collapse can result from all species becoming extirpated, all species becoming orphaned, or a combination of the two, resulting in different numbers of cumulative orphaned species across networks. Network collapse was assessed after extirpated and orphaned species were counted

Scenario 2: Exponential area loss in synthetic networks and Scenario 3: Variable rates of linear area loss in synthetic networks

To generalize the relationship between reduced habitat area and the number of orphaned species in a bipartite network, and determine what affects this relationship, we used synthetic networks (randomly generated networks between two groups of unspecified species, Figure 3). These synthetic networks were designed to mimic real world networks as closely as possible by possessing properties such as nestedness and web asymmetry that arise from ecological processes like trait matching, phenological coupling, and foraging behavior (Valdovinos, 2019; see Appendix S3: Section S1.3). These networks allowed us to vary network connectance and the relative richness of the two species groups and test our predictions about how these parameters affect the number of orphaned species produced by habitat loss (Figure 1). For these simulations, we used two area loss scenarios. The exponential area loss scenario (Scenario 2) used the same six area size losses used for our real network to determine general relationships, across the full parameter space, between z-difference or connectance and probability and number of orphaned species at each area loss step. In the variable rates of linear area loss scenario (Scenario 3), we sequentially reduced an area of 1600 km^2 by one of five increments (400 km^2 [3 steps]; 100 km^2 [15]; 25 km^2 [63]; 16 km^2 [99]; 6.25 km^2 [255]) to determine the general relationships between the area lost at each step and the probability and number of orphaned species at each area loss step (Figure 3). Regardless of scenario, before the initial area loss step, and also before each subsequent area loss step, we calculated the expected number of remaining species for each group of organisms, using the species–area curve,

$$\log(S_1) = \log(c) + z_1 \log(A_i) \tag{2}$$

$$\log(S_2) = \log(c) + z_2 \log(A_i) \tag{3}$$

where S_1 and S_2 are the number of species, A_i is amount of area after area loss, c is a constant, and z_1 and z_2 are the slopes for each group of interacting species. We assigned values for z_1 and z_2 from 0.15 to 0.35 in increments of 0.01 to encompass the range generally seen in empirical studies (Drakare et al., 2006; Lomolino, 1989), ensuring the full range of likely z-difference values. We used the mean c value as determined by our species–area curves for the Sierra Nevada network (0.18), because c is variable and lacks a known set of empirical estimates (Drakare et al., 2006). Our species–area calculations resulted in each simulated taxon group having 2 to 592 species at the largest area size, depending on z.

Because we are using identical initial area sizes and *c* values for all of our networks, fewer initial species translates to slower species loss with habitat loss.

Before the initial area loss step, we generated synthetic networks for the largest grid cell, based on the number of species in each group. We varied connectance from 0.1 to 0.9, which determined the average number of binary interactions per species in the network that we randomly assigned. This range encompassed observed connectance values in mutualistic networks (Blüthgen et al., 2007; Jordano, 1987). By drawing from a normal distribution with a mean of the average number of interactions per species for that network and standard deviation of 1, we varied the number of interactions per species for each network so as to mimic the nestedness of real mutualistic networks (see Appendix S3: Section S1.3), which has been shown to confer stability in the face of primary extinctions (Fortuna & Bascompte, 2006). For the first and each subsequent area loss step, we removed species from each of the two network groups to match the predicted number of species for each group for the next smallest area size. Species from each group were removed initially without respect to their number of interactions within the network. We then counted any orphaned species. Finally, we removed orphaned species from the network and recalculated network properties under the assumptions: (1) that species would not reconnect to the network via novel interactions (i.e., no rewiring), (2) that orphaned species will be less resilient to subsequent habitat loss, and (3) that any interactions between species remaining within the habitat patch persisted. Although networks are subject to spatial heterogeneity (Guimarães, 2020), and species can become spatially disconnected at local levels (Reverté et al., 2019), our approach is conservative in that it could only result in an underestimation, rather than overestimation, of the number of orphaned species.

We repeated this process of species removal for each subsequent area loss (Figure 3, for additional details see Appendix S3: Section S1.3). The species–area relationship is a proxy for some of the spatial processes underlying species loss with habitat loss. Using the species–area relationship to remove species from the network, instead of simple random removal, has the effect of accounting for these spatial processes while also mimicking the species removal process of our empirical network scenario (Scenario 1). We calculated percent orphaned species and percent extinct species as described above for the empirical network scenario. Overall, we simulated 18,900 bipartite networks for the exponential area loss in synthetic networks scenario (100 for each combination of *z*-difference and connectance; Scenario 2), and 9450 bipartite networks for the variable rates of linear area loss in synthetic networks scenario (1890 networks for each of five pathway types, 10 for each combination of *z*-difference and connectance value within each of the pathway types; Scenario 3; Figure 3), and quantified orphaned species along each individual habitat loss simulation pathway.

We analyzed trends of orphaned species as a function of network structure by fitting regressions to simulation results. For the exponential area loss scenario (Scenario 2), combining across all simulations, we fit two models: a logistic regression with whether any species were orphaned as the response variable, and a Poisson regression with the number of orphaned species as the response variable. To control for non-independence of orphaned species within the same area loss pathway, we randomly selected a subset of the data that included only one area loss step per pathway for our analysis. We used the *z*-difference, connectance of the network before any area loss, the initial number of species, and the area remaining in the habitat patch (as a proxy for intactness of the remaining network) as independent variables in the logistic regression. We used the same independent variables in the Poisson regression, except that we used connectance of the network for the previous area loss step. All independent variables were centered on their mean and scaled to a unit standard deviation to provide standardized regression coefficients.

We also fit logistic and Poisson regressions to the variable rates of linear area loss scenario (Scenario 3) results, again for all simulations combined and with a randomly selected subset of the data that included only one area loss step per pathway. We used the same independent variables as for the exponential area loss in synthetic networks scenario, except that we used the total number of species left in the network directly before the area loss step as a proxy for intactness of the remaining network. By using the total number of species, instead of total area remaining, we modeled how the area lost affected orphaned species. For the logistic regression we used connectance of the network before any area loss and for the Poisson regression we used connectance of the network for the previous area loss step. For additional details on regression fitting in both Scenarios 2 and 3, see Appendix S3: Section S1.4.

We calculated means and 95% intervals of the marginal effects between each of our independent variables (*z*-difference, connectance, area remaining or lost, and total species or total species remaining in the network) and probability of orphaned species for both the exponential area loss scenario (Scenario 2) and the variable rates of linear area loss scenario (Scenario 3). We did the same between our independent variables and number of orphaned species for both Scenarios 2 and 3. To calculate these marginal effects, we used the posterior distributions of the fitted slopes from each regression model, logistic and Poisson, along with the means of the centered independent variables for the regression model. We used the full range of centered x-values for the independent variable of interest. For example, to calculate the marginal effects of *z*-difference on proportion of orphaned species for the exponential area loss scenario (Scenario 2), we used the means of the centered values for connectance, area remaining, and total species in the network, along with the full range of centered values for *z*-difference.

RESULTS

Full Sierra Nevada network and species–area relationships

We tallied 1022 bird–plant species interactions in our Sierra Nevada seed dispersal network comprised of 82 plant species and 65 bird species (Appendix S1: Table S5, Figure 2b; Appendix S2: Figure S1). Of this total, 96 were based on direct detections of a bird species consuming the fruit of a plant species: through researcher ($n = 11$) or citizen science ($n = 36$) observations, camera traps ($n = 3$), fecal collections ($n = 42$), or preserved stomach collections ($n = 4$). The remainder we assigned from our literature search ($n > 900$). Four linkages were duplicated across direct detection methods, and over 90 were duplicated between one of the direct detection methods and the literature search.

Our fitted z for plants was 0.19 (95% credible interval [CI]: 0.17, 0.20), with a c of 0.09 (0.07, 0.12). Our fitted z for birds was 0.24 (0.23, 0.25), with a c of 0.27 (0.23, 0.32) (Appendix S2: Figure S2). The mean *z*-difference for the network was 0.05. Connectance of our largest area networks spanned from 0.21 to 0.33.

Scenario 1: Exponential area loss in an empirical network

Nineteen of our 129 area loss pathways (15%) in Scenario 1 resulted in at least one orphaned plant species and 10 pathways (8%) had networks that collapsed to no interactions remaining within the network. In contrast, all but one of our 129 area loss pathways (99%) orphaned at least one bird species. Bird species were also orphaned with less habitat loss than plant species. The number of orphaned bird species at any area loss step on average exceeded the number of orphaned plant species (Figure 4). The maximum number of orphaned plant species occurred when area was lost from the smallest habitat patches, which occurred at the last area loss step (4 species, 11% of the plant species in the original network, Figure 4a). In comparison, the maximum number of orphaned bird species occurred in the first area loss step (4800 km^2, 37 species, 62% of the bird species in the original network, Figure 4b).

Scenario 2: Exponential area loss in synthetic networks and Scenario 3: Variable rates of linear area loss in synthetic networks

For both simulation scenarios, the minimum area lost before an orphaned species occurred was generally either two loss steps (for area sizes <100 km^2) or one loss step (for area sizes ≥ 100 km^2; Appendix S1: Table S6). The maximum number of orphaned species in the exponential area loss scenario (Scenario 2) was 40% of the original species; in the variable rates of linear area loss scenario (Scenario 3), the maximum number of orphaned species ranged between 33% and 67% of the original species (Appendix S1: Table S6). In all cases, however, there were pathways with no orphaned species, regardless of the amount of area loss. Similar to the empirical network scenario (Scenario 1), although the mean probability and number of orphaned species was low in the variable rates of linear area loss scenario (Scenario 3), the variation was high with 95% confidence intervals up to 15%–25% species orphaned, depending on the amount of area lost (Figure 5).

Number of orphaned species versus number of extinctions

Under all three scenarios, the percentage of species that went extinct was generally greater than the percentage that were orphaned, but results were highly variable among pathways. In the empirical network scenario (Scenario 1), a mean of 3%–33% of species went extinct, and a mean of 1%–4% were orphaned (Figure 5). In a few area loss pathways, the percentage orphaned was similar to the percentage that went extinct (Figure 5). The results for the exponential area loss in synthetic networks scenario (Scenario 2) were similar to the empirical network scenario in that a greater mean percentage of species went extinct than was orphaned at each area loss step (Appendix S2: Figure S3). When amount of area loss was the same at each area loss step, as in the variable rates of area loss scenario (Scenario 3), results were highly variable across all amounts of area loss and all area loss steps (Figure 5).

Prediction 1: Area loss and orphaned species

Larger area loss steps created more orphaned species, although this was only directly tested in Scenario 3. In the empirical network scenario (Scenario 1), the first area loss step nearly always resulted in at least one orphaned bird, but no plant, species (Figure 4). Similarly, in the exponential area loss in synthetic networks scenario (Scenario 2), the first area loss step often

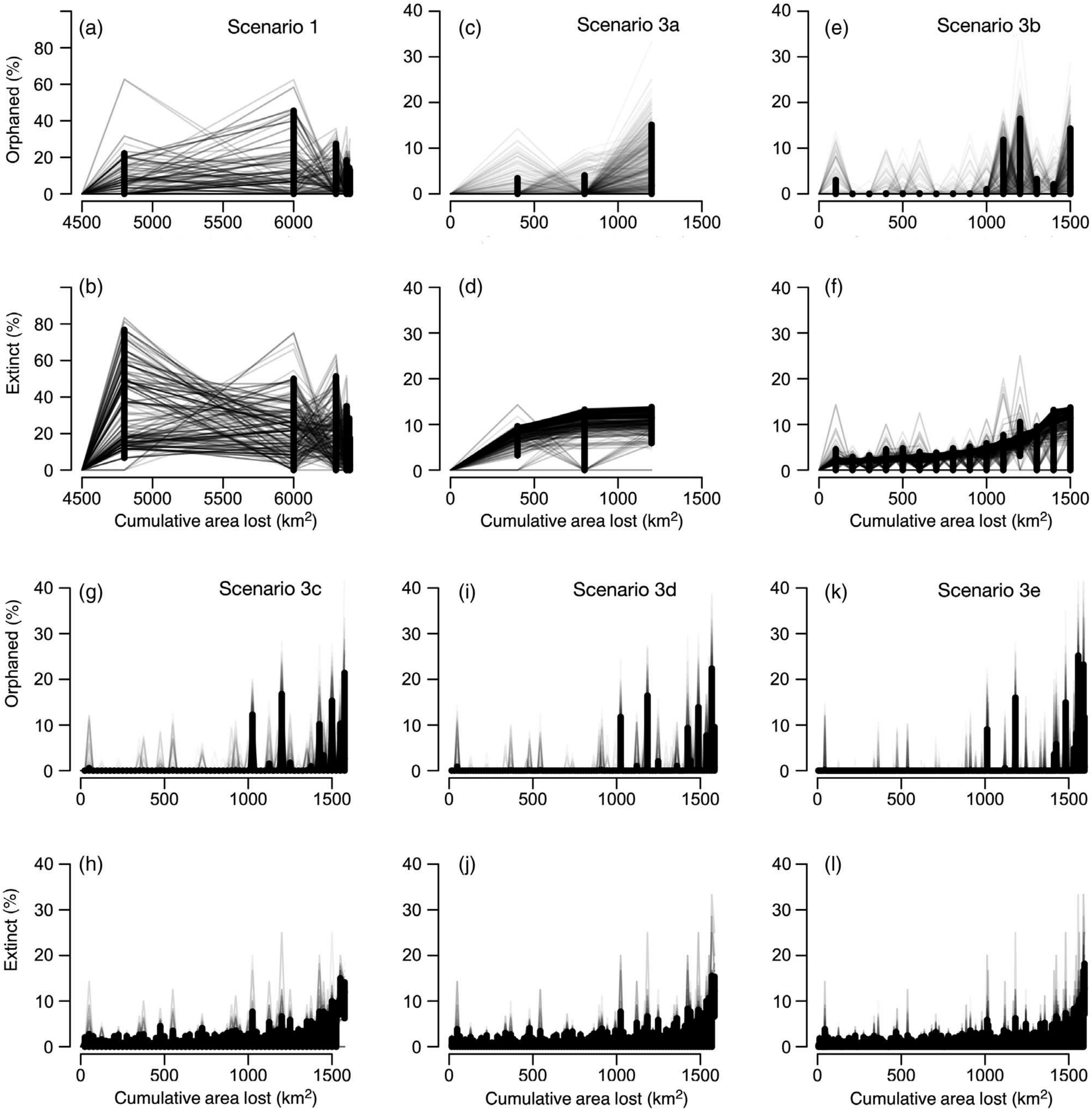

FIGURE 5 Percentage of species orphaned (a, c, e, g, i, k) and percentage of species that go extinct (b, d, f, h, j, l) at each area loss step for the exponential area loss in an empirical network scenario (Scenario 1; a, b) and the variable linear area loss in synthetic networks scenario (Scenario 3; c–l; in descending order of area lost: 400 km^2 [c, d], 100 km^2 [e, f], 25 km^2 [g, h], 16 km^2 [i, j], and 6.25 km^2 [k, l]). Bars represent the 95% confidence interval of percent species lost or orphaned at each area loss step. Lines display the underlying habitat loss simulations. Each individual line is one iteration of the habitat loss simulation for a given scenario. We calculated the percent orphaned and extinct at each area loss step by dividing the number of species orphaned or extinct by the total number of species within the network, directly before each area loss step. Mean percentages of orphaned or extinct species over all area loss steps could thus sum to >100%. The *x*-axes in (a) and (b) are abbreviated so as to show smaller area loss steps when the cumulative habitat loss is >6000 km^2

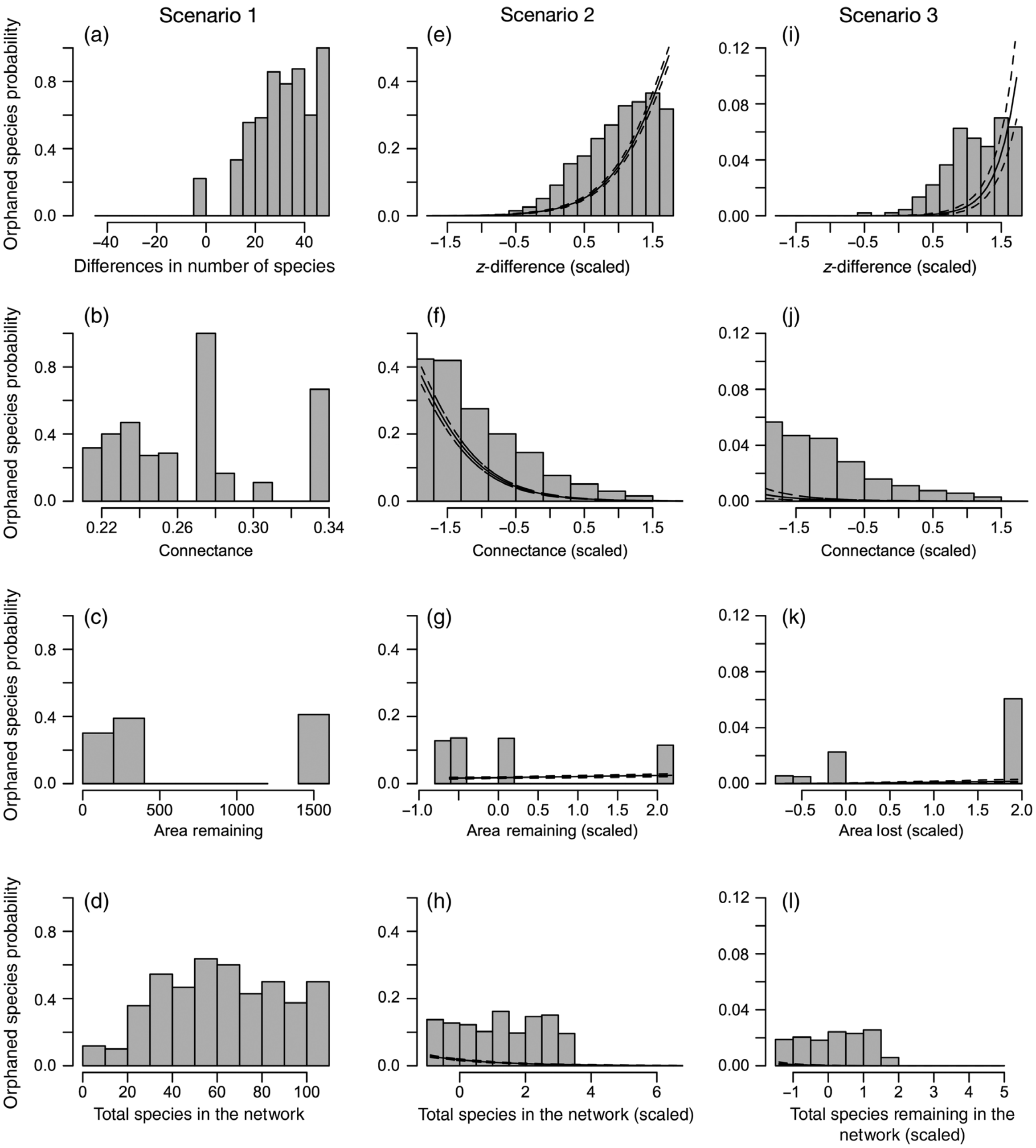

FIGURE 6 The proportion of habitat loss simulations that resulted in at least one orphaned species, at each area loss step. These results are displayed for (a–d) exponential area loss in an empirical network scenario (Scenario 1), which is composed of a real seed dispersal network within the Sierra Nevada Mountains, California, USA; (e–h) exponential area loss in synthetic networks scenario (Scenario 2); and (i–l) variable linear area loss in synthetic networks scenario (Scenario 3). More area lost (k, Prediction 1), greater *z*-differences (e and i, Prediction 2), and lower connectance (f and j, Prediction 3) resulted in an increased probability of orphaned species, in accordance with our predictions. For each scenario, the summarized proportion of the habitat patch loss iterations that resulted in at least one orphaned species is plotted against (1) the difference between the number of species in each group of the bipartite network, as measured in actual number of species (a) or *z* exponent from the species–area equation (e and i), (2) connectance of the network before habitat loss simulations (b, f, j), (3) amount of area remaining (km^2; as a proxy for network intactness) (c and g) or lost (km^2) (k), and (4) the total number of initial species within the network (d and h) or the total number of species remaining in the network at that area loss step (l; as a proxy for network intactness). For the synthetic network scenarios (Scenarios 2 and 3) the line in each panel depicts the marginal effect of the variable shown on the *x*-axis with 95% credible intervals. These are the marginal effects from the Poisson multivariate linear regressions, and as such, the apparent fit of these lines to the underlying data are dependent upon the strength of the relationship between the independent variable and the number of orphaned species. For Scenarios 2 and 3 we centered the independent variables within the linear trend (*z*-difference, connectance, area remaining or area lost, total initial species within the network or total remaining species within the network) on their mean and scaled to a unit standard deviation. The mean of each independent variable is centered on zero (*x*-axes)

resulted in at least one orphaned species (Appendix S1: Table S6, Appendix S2: Figure S3). Amount of area lost had a significant effect on both the probability and total number of orphaned species in the variable rates of linear area loss scenario (Scenario 3; Appendix S2: Figure S4). The probability of orphaned species increased from a mean of <0.1% (95% CI: <0.1, 2%) at 6.25 km^2 of area loss (the smallest unit of area loss in our simulations) to 1.7% (95% CI: 1.0, 3.0%) at 400 km^2 (the largest unit of area loss; Figure 6). Number of orphaned species increased from a mean of 4.3 (95% CI: 3.8, 4.9) species at 6.25 km^2 of area loss to a mean of 5.6 (95% CI: 5.1, 6.1) species at 400 km^2 (Figure 7). Across all simulations, as little as 12.5 km^2 (1% of the total starting area) and an average of 1090 km^2 (68% of the total starting area, Scenario 3) had to be lost before a species was orphaned (Appendix S1: Table S6).

Prediction 2: *z*-differences and orphaned species

In the empirical network scenario (Scenario 1), networks with greater differences in the number of plant and bird species generally orphaned species, usually birds, more frequently and at a higher rate (Figures 6, 7). Across both synthetic network scenarios (Scenarios 2 and 3), higher *z*-differences increased the probability of species becoming orphaned (Figure 6; Appendix S2: Figure S4), orphaned more species (Figure 7; Appendix S2: Figure S4), and had the greatest effect on the orphaning of species (Appendix S2: Figure S4).

Prediction 3: Connectance and orphaned species

Lower starting connectance, and lower connectance within a network immediately before an area loss step, both had the potential to result in a greater probability of and more orphaned species (Figures 6 and 7). Across both synthetic network scenarios (Scenarios 2 and 3), connectance was the next most important variable after *z*-difference (Figures 6 and 7; Appendix S2: Figure S4), with lower connectance causing a greater probability and number of orphaned species.

DISCUSSION

While much concern has been expressed over the role of secondary extinctions in the on-going global extinction crisis, we lack detailed understanding of how habitat loss contributes to the loss of connections in networks, orphaned species, and ultimately to secondary extinctions (Blois et al., 2013; Figueiredo et al., 2019; Gonzalez et al., 2011). Simulated habitat loss suggests that up to 60% of species from an intact network could be orphaned (Figure 5a), resulting in a loss of mutualistic function, which could ultimately lead to extinction of the orphaned species. Further, in our simulations up to 5% of species had a small probability of being orphaned at initial or early area loss steps (i.e., after an area loss of only 100 km^2 or less; Figure 5e, g, i, k). Both our empirical and synthetic networks assumed large, intact starting areas (6400 and 1600 km^2, respectively). Even small amounts of habitat loss, therefore, have potential to orphan species. Although the number of species orphaned by habitat loss was highly variable across scenarios, and the chance of an orphaned species becoming secondarily extinct is not quantified, our results suggest we could be vastly underpredicting biodiversity losses by not accounting for biotic interactions (Lewis, 2006; Vidal et al., 2019; Wood et al., 2015).

Area loss and orphaned species

Our statistical models showed a positive relationship between the amount of area lost and both the probability of orphaned species and the number of resulting orphaned species, as shown by results for Prediction 1. However, the amount of area lost did not have as large an effect on either response variable as did *z*-difference or connectance (Appendix S2: Figure S4). The comparatively small effect of amount of area lost on probability and number of orphaned species indicates that some networks, by virtue of their diversity and structure, are more stable in the face of habitat loss. Notably, large percentages of species within plant–animal networks have the potential to be orphaned by a single habitat loss incident. The percent of orphaned species occasionally equaled, or even exceeded, the percent of species that went extinct from habitat loss, particularly when smaller areas of habitat remained (Figure 5).

z-Differences, connectance, and orphaned species

As the *z*-difference between interacting groups increases, species have a greater probability of becoming orphaned from the network and more orphaned species result (Figures 6 and 7; Appendix S2: Figure S4), as shown by results for Prediction 2. Greater *z*-differences necessitate that the group with fewer species has more connections

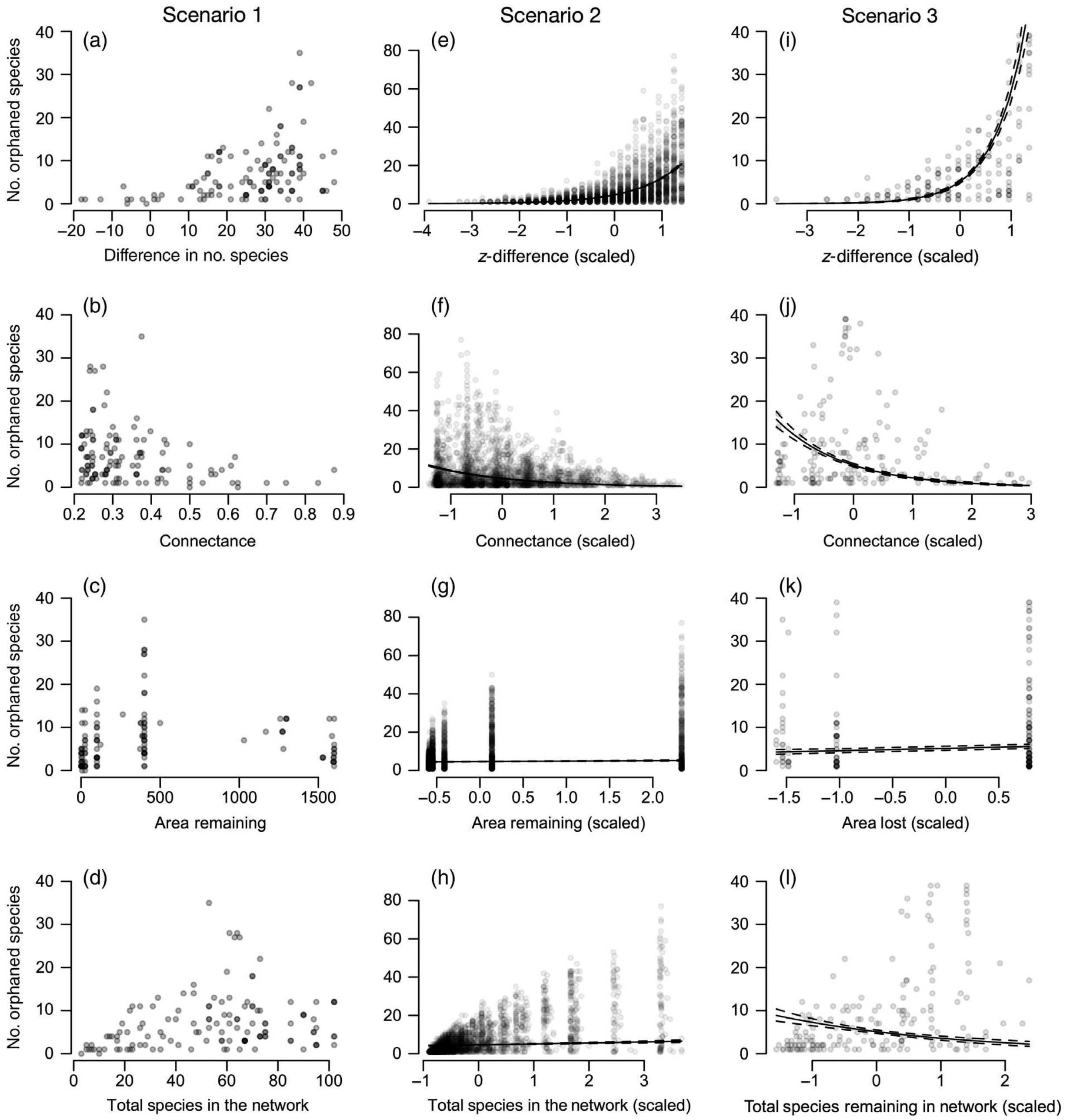

FIGURE 7 The number of orphaned species that resulted from any given habitat loss simulation step for (a–d) exponential area loss in an empirical network scenario (Scenario 1), which is composed of a real seed dispersal network within the Sierra Nevada Mountains, California, USA; (e–h) exponential area loss in synthetic networks scenario (Scenario 2); and (i–l) variable linear area loss in synthetic networks scenario (Scenario 3). More area lost (k, Prediction 1), greater *z*-differences (e and i, Prediction 2), and lower connectance (f and j, Prediction 3) resulted in an increased number of orphaned species, in accordance with our predictions. For each scenario, the number of orphaned species is plotted against (1) the difference between the number of species in each group of the bipartite network, as measured in actual number of species (a) or *z*-difference (the difference between the two *z* exponents from the species–area equations for each species group in the networks; (e and i), (2) connectance of the network before habitat loss simulations (b, f, j), (3) amount of area remaining (km^2; as a proxy for network intactness) (c and g) or lost (km^2) (k), and (4) the total number of initial species within the network (d and h) or the total number of species remaining in the network at that area loss step (l; as a proxy for network intactness). For the synthetic network scenarios (Scenarios 2 and 3) the line in each panel depicts the marginal effect of the variable shown on the *x*-axis with 95% credible intervals. These are the marginal effects from the Poisson multivariate linear regressions, and as such, the apparent fit of these lines to the underlying data are dependent upon the strength of the relationship between the independent variable and the number of orphaned species. For Scenarios 2 and 3 we centered the independent variables within the linear trend (*z*-difference, connectance, area remaining or area lost, total initial species within the network or total remaining species within the network) on their mean and scaled to a unit standard deviation. The mean of each independent variable is centered on zero (*x*-axes)

per species, or in other words, the species in that group have a larger niche breadth, where niche breadth is defined as the number of species in the network with which an organism interacts (Albrecht et al., 2018; Blüthgen & Klein, 2011). Loss of these more highly connected species have a disproportionate effect on the network, akin to the effect of the loss of a top predator on food webs (e.g., Paine, 1969), resulting in more orphaned species. In keeping with this pattern for individual species, lower connectance within the original network also resulted in a greater probability, and number, of orphaned species (Figures 6 and 7; Appendix S2: Figure S4), as shown by results for Prediction 3. Bipartite networks that have an even number of species in each group and high connectance result in a near-zero probability and number of orphaned species, but these situations may be uncommon given that mean connectance for mutualistic networks is generally below 0.6 and that asymmetry between the number of species in each group is common (Blüthgen et al., 2007).

Our simulations assume that *z*-differences are the result of solely spatial processes driving species richness and thus we model a large range of *z*-differences in combination with a range of connectance values. However, *z*-differences within a network might be governed by both spatial processes and network constraints, in tandem with connectance, via niche-breadth and partitioning (Albrecht et al., 2018; Peralta, Perry, et al., 2020). Niche-based processes, in turn, may be driven by trait-matching and differential environmental drivers of functional diversity across both groups, incorporating both top-down and bottom-up processes occurring simultaneously (Albrecht et al., 2018; Bender et al., 2018). Network assembly due to niche-based processes is only beginning to be investigated, and while we have shown through simulations that *z*-difference and connectance are important for orphaned species, the mechanistic link needs further research.

Extinctions and orphaned species

Previous simulations have shown that networks are resilient to species loss until a threshold number of extinctions have accumulated, at which point, secondary extinctions and higher degree extinctions through indirect paths increase and, eventually, the network collapses (Dunne et al., 2002; Fortuna & Bascompte, 2006; Memmott et al., 2004; Rezende et al., 2007; Solé & Montoya, 2001; Srinivasan et al., 2007; Vidal et al., 2019). Our simulations tested this finding in the context of area loss as the driving force behind orphaned species. Initial large amounts of habitat loss, such as in both exponential area loss scenarios (Scenarios 1 and 2), resulted in a slight deceleration of orphaned species at later habitat losses (Figure 5; Appendix S2: Figure S3), likely because most species had already gone extinct. In the variable rates of linear area loss scenario (Scenario 3), however, the accelerated rate of orphaned species occurred and was more pronounced with less area lost at each area loss step. This acceleration of orphaned species matched an acceleration of primary extinctions in the later area loss steps (Figure 5), mirroring results from other studies. Our results suggest that the number of orphaned species is directly tied to the amount of habitat loss through extinctions (Figure 7). Therefore, in circumstances where habitat of an area is lost gradually and piecemeal, small initial habitat losses may prevent species from becoming orphaned unless more habitat is lost in the future (e.g., Spiesman & Inouye, 2013), whereas large initial habitat losses may produce many orphaned species.

Alternatively, large initial habitat losses may produce fewer than expected extinctions and so fewer than predicted orphaned species, at least in the short term. Areas subjected to habitat loss accumulate extinction debt (Tilman et al., 1994) because extinctions take generations to be realized (Wearn et al., 2012), and can be mitigated by immigration or recolonization from nearby habitat patches (Hanski & Ovaskainen, 2002; Wu et al., 2020). We assumed that primary extinctions and orphaned species occurred at each area loss step with habitat destruction, but in real situations, extinctions, and associated orphaned species, could take decades to occur. Guardiola et al. (2018) showed that networks are also subject to extinction debt, through disproportionately detrimental effects of habitat loss on specialized interactions versus general ones and mitigation of interaction loss in well-connected habitat patches. These findings add further complexity to the process of predicting orphaned species, secondary extinctions, and network collapse with habitat loss, and may allow for the rescue of some orphaned species, preventing them from becoming secondary extinctions.

In situations when an acceleration of secondary extinctions does occur with incremental habitat loss, one explanation is that even if connectance within a network is high, smaller networks have fewer possible interactions. This feature makes small networks less resilient to secondary extinctions because each species lost removes, on average, a greater proportion of the network's interactions (Menge, 1995; Montoya et al., 2006; Sanders et al., 2018). In fact, we found that less intact networks, those with fewer species before habitat loss, resulted in a greater probability and higher number of orphaned species (Figure 6; Appendix S2: Figure S4). Thus, to modify previous findings of how primary extinctions affect orphaned species within a network, number of species remaining in a network and amount of area lost work in tandem to determine the probability and number of orphaned species.

Highly connected and orphaned species

Several factors suggest that information specific to a given system is needed to completely assess the severity of the network changes explored in our analysis. These include the identity, abundance, and spatial distribution of highly connected species within the network. When a well-connected species is removed from the network, many connections are lost and network collapse can occur (Bascompte & Stouffer, 2009; Memmott et al., 2004). For our empirical network (Scenario 1), well-connected bird species included American Robin (*Turdus migratorius*) and Townsend's Solitaire (*Myadestes townsendii*) (Figure 2b; Appendix S2: Figure S1), and their loss generally led to plant species being orphaned. Robins, unlike Solitaires, are widespread and ubiquitous across the landscape and their extirpations within our simulations, which happened only after much habitat had already been lost, are likely an artifact of the distribution of species observations in the underlying data. This species loss is thus unlikely in the real world, even in the face of climate change, while loss of the Solitaires due to anthropogenic disturbances, and regardless of rewiring, seems more likely (Siegel et al., 2014).

In our empirical network, highly connected species could be either widespread across the landscape (e.g., American Robin) or highly localized and only present in a small portion of our study area (e.g., Townsend's Solitaire). Likewise, species with few connections had no consistent spatial ubiquity or rarity, echoing the results of Vidal et al. (2019) that habitat specialization and mutualism specialization are not always correlated. Thus, extinctions within habitat loss simulations for our synthetic networks (Scenarios 2 and 3) were consistent with our empirical network (Scenario 1). Further research on the relationships between spatial distributions of species and their level of specialization within a mutualistic network would elucidate whether our empirical network represents global trends.

For our synthetic networks (Scenarios 2 and 3), some species were removed irrespective of their number of interactions, making it equally likely for well-connected species to go extinct at early as well as late area loss steps. Unlike previous studies with random species removals (e.g., Dunne et al., 2002; Memmott et al., 2004), our simulated extinctions included species from both partner groups and happened in batches dictated by amount of habitat loss. In this case, our simulated species loss is more like that modeled by Bayesian network models in that species with multiple interaction partners have a non-zero chance of going extinct (Häussler et al., 2020) due to habitat loss. Our analysis is unlike a Bayesian network model in that we are modeling species extinctions and becoming orphaned as separate, but related, processes. Also, unlike previous studies with random species removals, species that were orphaned in the previous area loss step went extinct in the next area loss step (synthetic networks; Scenarios 2 and 3). This resulted in each area loss step after the initial one being partially random in that orphaned species had an extinction probability of 1 and all other species, regardless of number of connections within the network, had an equal extinction probability to each other. Thus, the number of species removed from the network at any area loss step could consist of (1) entirely orphaned species, (2) only species driven to extinction by habitat loss, or (3) a mixture of both. While the loss of all partner species does not necessarily result in secondary extinctions (Fricke et al., 2017; Valiente-Banuet et al., 2015), it is reasonable to assume that species that have no remaining interaction partners would be more vulnerable to further ecosystem perturbation, like habitat loss. We checked our assumption that orphaned species would go extinct by comparing patterns of orphaned species and primary species extinctions within the exponential area loss in synthetic networks scenario (Scenario 2) to those within the exponential area loss in an empirical network scenario (Scenario 1), and the results of our habitat loss simulations were similar (Appendix S2: Figure S3).

Local interactions, behavior, rewiring, and orphaned species

We compiled our real and synthetic ecological networks at a regional level and assumed that species interactions would apply to local scales anywhere two interacting species co-occurred. Given that species co-occurrence does not necessarily translate to interactions on a local scale (but see Fortuna et al., 2020, who found that mutualists had high partner fidelity at biogeographical scales, particularly when interactions are asymmetric), our local networks could have been biased towards more interactions. Higher connectance resulted in a lower probability and number of orphaned species, meaning that our estimates for the probability and number of orphaned species with habitat loss may be conservative.

Including species-specific traits and behavioral details into applications of our habitat loss simulations would make them more realistic and allow more nuanced predictions for particular systems (Morán-López et al., 2020; Peralta, Vázquez, et al., 2020; Valdovinos, 2019). Given that our simulations of habitat loss using synthetic networks (Scenarios 2 and 3) were similar to our results for real world networks (Scenario 1; Figures 6 and 7), these additional details are not necessary for illuminating the relationship between habitat loss and network structure. Generally, resilience to orphaned species conferred by well-connected species indicates that, even in the face of large area losses, networks may persist without orphaned species, or secondary extinctions. With enough area lost, though, even these well-connected species may become extirpated, leading to orphaned species.

To what extent any member of a bipartite network depends on its partners, and to what extent the species can compensate with other resources, affects the survival of that species if all partners go extinct (e.g., Fricke et al., 2017; Liao et al., 2017; Vieira & Almeida-Neto, 2015). For example, functionality for plants in the face of pollinator loss could be maintained through self-pollination if the plant is self compatible (although this could be an inviable long-term strategy; Cheptou, 2019). In temperate ecosystems, few bird species specialize on fruit, meaning that the loss of all fruit-bearing plants may have limited repercussions for the survival of these species due to their ability to also consume seeds or insects (Barnagaud et al., 2019). Bird species that are orphaned from their fruit resources may have less chance of becoming secondarily extinct as a result. Further, those that do specialize on fruit may be able to switch to species they do not normally consume, as is seen by species that incorporate the fruit of invasive species into their diets (Barnum et al., 2015; Kiers et al., 2010; Richardson et al., 2007; Valiente-Banuet et al., 2015). In the empirical network scenario (Scenario 1), if any bird species had a probability of starting to consume new fruit species when it lost all species interactions, our habitat loss simulations would likely show fewer orphaned species over all area loss steps, a lower percent orphaned species per area loss step, and a lower probability of orphaned species at each area loss step.

Rewiring often occurs in generalists and can be a response to increased abundance of a potential partner or prey species or other resource (Hagen et al., 2012). In mutualistic networks, if rewiring occurs, the critical services that a species receives would be restored, rescuing that species from extinction (Kaiser-Bunbury et al., 2010). Rewiring may be possible but uncommon in ecological bipartite networks and food webs (Colwell et al., 2012; Dunn et al., 2009; Grass et al., 2018; Rezende et al., 2007). It is less clear whether it can affect mutualistic networks (Fricke et al., 2018 though see Burkle et al., 2013 for evidence within a pollination network and González-Varo & Traveset, 2016 for temporal variations), particularly because analyses of multiple networks have shown the existence of “forbidden links” due to phenophase and size mismatch (e.g., avian gape and fruit diameter) as well as accessibility limitations (Olesen et al., 2011; Sebastián-González, 2017). While several studies have modeled rewiring (see Valdovinos, 2019 for a review), critical decisions about how rewiring would occur within a network are based on little empirical evidence. Greater understanding about the extent and limitations of rewiring within different types of mutualistic networks would inform to what extent it confers network stability in combination with habitat loss. Based on the results of previous studies (e.g., Valdovinos et al., 2013), the inclusion of rewiring in our habitat loss simulations for synthetic networks (Scenarios 2 and 3) would likely have resulted in a lower probability of, and fewer, orphaned species at each area loss step.

Species, network, and geographic traits and orphaned species

While rewiring and the persistence of more functionally effective species could prevent secondary extinctions and extinction cascades, other ecological properties of networks could increase them. Our simulations may underestimate the impacts of ecological processes related to species abundance within, and habitat fragmentation on, networks. First, because our data set contains no abundance information, we assume throughout that species abundance has no effect on interaction strength, and that all interactions within our network have equal strength. However, functional loss of species and interactions frequently happen with even small reductions in partner abundance and interaction strength, across many types of ecological networks (Chacoff et al., 2018; Grass et al., 2018; McConkey & Drake, 2006; Säterberg et al., 2013; Vázquez et al., 2005). Second, diversity of partners may matter to the extent that species may be unable to persist within a landscape when a fraction of their partner species go extinct (Häussler et al., 2020). Third, our habitat loss simulations do not directly mimic habitat fragmentation. They do not account for demographic process, isolation, configuration, and other mechanisms that affect the rate at which species disappear from smaller patches (e.g., Grass et al., 2018; Harrison, 1991; White & Smith, 2018). Further, habitat fragmentation can negatively affect mutualistic interactions by decreasing the visits by animal partners to plants within these habitat patches (Aguilar et al., 2006; Cordeiro & Howe, 2002; Ferreira et al., 2020; Gómez-Martínez et al., 2020; Lázaro et al., 2020; Marjakangas et al., 2020; McConkey et al., 2012; Rodríguez-Cabal et al., 2007; Santamaría et al., 2018; Townsend & Levey, 2005). Fourth, we assume that any species remaining after an area loss step will spatially overlap within the remaining habitat, which ignores fine-scale spatial heterogeneity in species distributions and the potential for species not to interact at local scales (Morales & Vázquez, 2008; Reverté et al., 2019). If the mutualist species within the network display high spatial heterogeneity with a lack of overlap, species in remaining habitat patches after habitat loss may still be orphaned. Using our habitat simulation framework and adding species-specific details about traits, behavior, spatial distribution across the landscape, abundance, and, if known, rewiring would allow managers to make informed predictions about orphaned species with habitat loss.

Studies that have quantified how habitat loss affects networks and secondary extinction have found effects of network structure, geographic prevalence, habitat specialization, and habitat patch value. Fortuna and Bascompte (2006) used a metacommunity model and habitat loss simulations to demonstrate that the structure of real mutualist networks allows species to persist longer in the face of habitat loss and secondary extinctions before collapse, as compared to null model networks. Our results echo theirs in that *z*-difference and connectance, network structure measurements, were more important for determining probability and number of orphaned species than amount of habitat lost. Geographic prevalence, or how widespread a species occurs across a landscape, did not appear to be related to mutualism specialization or generalization within our empirical network, as discussed above, but we did not statistically analyze the relationship. However, Srinivasan et al. (2007) found in simulated extinctions of a freshwater food web that when extinctions were ordered by least to most prevalent geographically, more primary species had to be removed before secondary extinctions occurred.

In contrast to Srinivasan et al.'s (2007) results, but more similar to our empirical network, Vidal et al. (2019) compared habitat loss simulations in a plant–frugivore network with primary extinctions of avian frugivores and found that number of species lost had more impact on the network than order of extinctions. Lastly, metacommunity processes that lead to certain habitat patches being more valuable than others for network stability may be important. Across a heterogenous farmland landscape, Evans et al. (2013) found that certain habitat types produced more secondary extinctions within a terrestrial food web when removed. Similarly, Häussler et al. (2020) found that removing the most valuable habitat patches first, or random patch removal, produced more secondary extinctions than removing the least valuable patches first. Since we did not quantify habitat patch value, our removal of habitat is more similar to random. If habitat were to be lost with least important patches first, fewer orphaned species may result.

Conclusions

Previous studies have quantified secondary extinctions in various ways, including by using linear models (e.g., Stork & Lyal, 1993, reviewed by Moir et al., 2011), randomly chosen species eliminations (Koh et al., 2004), eliminations in order of number of connections (Memmott et al., 2004), metacommunity effects (Fortuna & Bascompte, 2006; Häussler et al., 2020), geographic prevalence (Srinivasan et al., 2007), historical precedence (Strona & Lafferty, 2016), and intrinsic dependence of one species on another (Vieira & Almeida-Neto, 2015). However, few have quantified how the amount of habitat loss affects the number of secondary extinctions within ecological networks (Figueiredo et al., 2019), nor how network properties like web asymmetry and connectance interact with amount of habitat loss. Our simulations demonstrate how area loss and network properties affect the probability and number of orphaned species, how our framework could be applied to other systems to determine the effects of habitat loss on bipartite networks, and how species extinctions alone do not encapsulate the full severity of the current biodiversity crisis.

AUTHOR CONTRIBUTIONS

Manette E. Sandor, Chris S. Elphick, and Morgan W. Tingley designed the study. Manette E. Sandor collected the data and performed simulations and analyses. Manette E. Sandor wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

ACKNOWLEDGMENTS

We thank the following people and organizations. For permission and help with mist net and camera trap work: D. Dawson, C. Thomas, K. Rose, and other Valentine Eastern Sierra Reserve staff. For collecting fecal samples: R. Siegel, L. Helton, and colleagues (Institute for Bird Populations); R. Burnett, L. Morgan-Outhisack, B. Campos, and colleagues (Point Blue Conservation Science and the Gurnsey Creek MAPS station); D. LaBerteaux and colleagues (Cranebrake Ecological Reserve); J. Brokaw (Perazzo Meadow MAPS station); F. Felix and W. Clevenger (Sagehen Creek Field Station, University of California Natural Reserve System); and M. Magnuson (Drakesbad National Park). For assistance with Louisiana State University Museum of Natural Science's extensive collections: S. W. Cardiff and J. V. Remsen. For assistance at the California Department of Food and Seed Agriculture Seed Herbarium: R. Price. For assistance in the field and lab: A. Edwards, I. Gibson, A. Mueller, B. Nahorney, J. Riley, K. Wrensford, D. Zandbergen, and E. Zhao. For helpful comments on research in progress and previous drafts: J. A. Silander,

C. S. Jones, E. L. Jockusch, M. Rubega, C. R. Field, and the UConn Ornithology Research Group. For comments that improved earlier drafts of this paper: C. Weiss-Lehman and two anonymous reviewers. For Funding: Department of Ecology and Evolutionary Biology (Ronald Bamford Fund and Zoology Award) and Center for Conservation and Biodiversity at the University of Connecticut, University of California Eastern Sierra Nevada Student Research Award, Audubon Connecticut Important Bird Area Small Matching Grants Program, and the NSF (Grant DEB 1701858). All applicable institutional and/or national guidelines for the care and use of animals were followed.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data sets utilized for this research are as follows: plant species occurrences pulled from the Global Biodiversity Information Facility (https://www.gbif.org) and bird species occurrences pulled from eBird (https://ebird.org/home) as described in Appendix S3. Data and novel code are available from Zenodo: https://doi.org/10.5281/zenodo.5865792.

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SUPPORTING INFORMATION

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How to cite this article: Sandor, Manette E., Chris S. Elphick, and Morgan W. Tingley. 2022. “Extinction of Biotic Interactions Due to Habitat Loss Could Accelerate the Current Biodiversity Crisis.” *Ecological Applications* e2608. https://doi.org/10.1002/eap.2608