

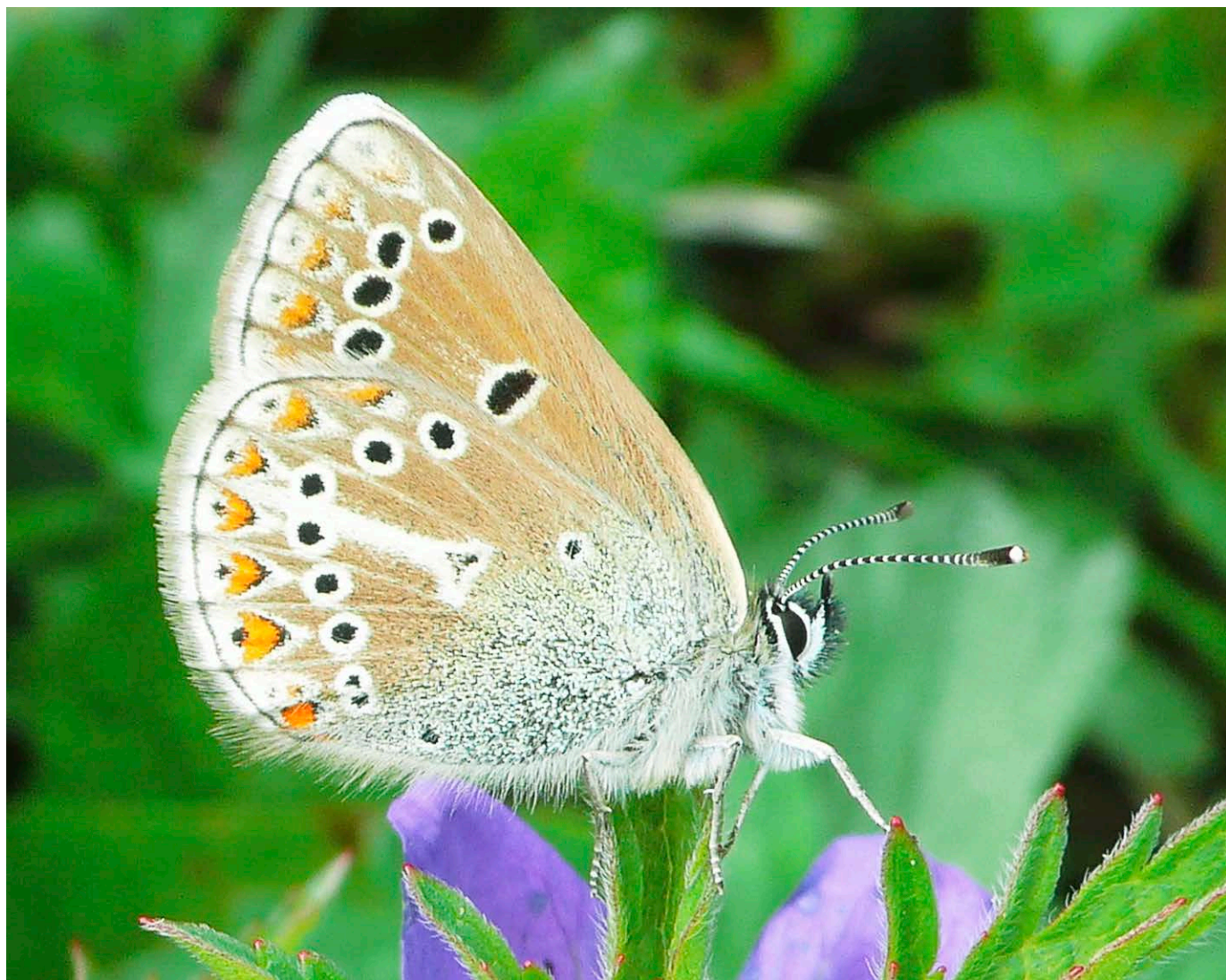
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Extinction cascades partially estimate herbivore losses in a complete Lepidoptera–plant food web

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Abstract. The loss of species from an ecological community can have cascading effects leading to the extinction of other species. Specialist herbivores are highly diverse and may be particularly susceptible to extinction due to host plant loss. We used a bipartite food web of 900 Lepidoptera (butterfly and moth) herbivores and 2403 plant species from Central Europe to simulate the cascading effect of plant extinctions on Lepidoptera extinctions. Realistic extinction sequences of plants, incorporating red-list status, range size, and native status, altered subsequent Lepidoptera extinctions. We compared simulated Lepidoptera extinctions to the number of actual regional Lepidoptera extinctions and found that all predicted scenarios underestimated total observed extinctions but accurately predicted observed extinctions attributed to host loss ($n = 8$, 14%). Likely, many regional Lepidoptera extinctions occurred for reasons other than loss of host plant alone, such as climate change and habitat loss. Ecological networks can be useful in assessing a component of extinction risk to herbivores based on host loss, but further factors may be equally important.

Key words: butterflies and moths; cascading extinctions; food webs; herbivory; plant–insect interactions.

INTRODUCTION

One of the primary goals of conservation is to preserve the Earth's biodiversity by reducing the number of human-induced global and regional extinctions of organisms. As such, we often invest heavily in direct and indirect conservation practices that benefit those organisms that are most at risk of going extinct (IUCN 2001). Assessing extinction risk, however, is difficult, and several recent predictive methods have been proposed to identify which organisms suffer the greatest risk of extinction (Purvis et al. 2000).

Recent tools for assessing extinction risk to individual species or robustness of biological communities to individual extinctions incorporate the position of an organism in an ecological network, as the decline or extinction of other organisms may have cascading effects throughout the network (Sole and Montoya 2001, Dunne et al. 2002, Dunne and Williams 2009, Thebault and Fontaine 2010, Heleno et al. 2012). Such work documented the vulnerability of trophically unique species to extinction cascades (Petchey et al. 2008). As one example, many herbivorous insects feed on one or a few plant species, and the loss of those plants will almost certainly impact the extinction risk of the herbivore (Fonseca 2009). This has led to the observation that organisms with specialized trophic relationships (such as specialist herbivores) suffer a greater extinction risk

based on cascading effects of other losses throughout the community (Mattila et al. 2008).

Concern for the role of cascading effects of extinction is timely, as plant communities are changing dramatically, and this will likely have large effects on higher trophic levels (McKinney and Lockwood 1999). For example, tree species, such as elm (*Ulmus* sp.), oak (*Quercus* sp.), or pine (*Pinus* sp.), are dying off in Europe as well as in North America on a landscape scale due to the spread of introduced pathogens, habitat loss or degradation, and climate change (e.g., Rizzo and Garbelotto 2003, Breshears et al. 2009). Such trees are very important host plants for a high number of generalist and specialist insects, and subsequent extinctions of a diverse herbivorous insect community is thus a realistic scenario (Fonseca 2009). As another example, about 1800 nonnative plant species have invaded the California floristic province within less than a few centuries, where they now make up 30% of the flora, and have brought hundreds of native plant species to the brink of extinction (Cal-IPC 2006). While these novel hosts may be a new food source for some herbivore species (Pearse and Hipp 2009), the corresponding loss of native plants is problematic for specialist herbivores, whose destiny may be tightly linked to their host plants (Graves and Shapiro 2003).

While there are numerous examples of cascading effects of plant extinctions (e.g., Fonseca 2009), there have been few extensive efforts to model the predicted loss of herbivore species based on the loss of plant resources over a large geographic region. Additionally,

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factors that may alter or mitigate herbivore extinctions have only recently been considered in the context of ecological networks (Dunne and Williams 2009). For example, the identity of plant extinctions may be important and is likely related to factors such as range size, life history traits, or independent assessments of extinction risk (like red-list status). So, herbivore loss should take into account realistic models of host-loss (Srinivasan et al. 2007, de Visser et al. 2011). Another factor that could decrease extinction risk in the face of host loss is the ability to evolve novel host associations when the population of their ancestral host declines (Kleijn and Raemakers 2008). Host-switching or the evolution of novel host associations has often been observed in herbivores, and could certainly affect the likelihood of herbivore extinction in the face of host-loss (Singer et al. 1993).

The validity of extinction cascade models can be difficult to assess empirically, as extinctions are often not recorded or are misidentified. Understanding the validity of extinction cascade models is critical in order to use these models to target conservation efforts. For example, the persistence of even the most specialized herbivore likely requires other factors than its host alone (such as abiotic climate, mating ground, and adult nectaring resources). Indeed, the environmental and biotic factors that potentially affect the occurrence of a species are almost endless. Moreover, these models are static (i.e., do not contemplate population dynamics), so it is possible that they do not account for those aspects of host-use that matter to higher trophic levels. With the use of large-scale surveys of herbivore–host–plant interactions and a retrospective analysis of extinctions that have already occurred within that system, we assessed the validity and relative importance of extinction cascades vs. other factors that drive herbivores to extinction.

In this study, we used a large, virtually complete bipartite food web of Lepidoptera–plant interactions in Baden-Württemberg (Central Europe) to ask how well models of cascading extinctions can predict extinction risks to herbivores following the extinction of their host plants. First, we considered whether rates of Lepidoptera extinction differ under several realistic scenarios of plant extinction (i.e., when plants with small ranges or current red-list status are the first to go extinct vs. random extinctions). We did so by only considering direct effects of plant loss on herbivore loss, but are aware that plant loss could also trigger herbivore extinction via indirect effects (e.g., by increasing apparent competition) and thus result in more complex or more pronounced extinction scenario. We further assessed whether Lepidoptera extinction is less likely in models that allow Lepidoptera to switch hosts to closely related plants (Kondoh 2003). Finally, we compared these models of predicted herbivore loss to the 59 butterfly and moth species that have actually gone regionally extinct from Baden-Württemberg in the last

150 years. Specifically, we asked whether Lepidoptera species with greater diet breadth are less likely to face extinction than more specialized Lepidoptera. We used the information on actual Lepidoptera extinctions to assess what additional factors besides host loss might affect extinction risk of European Lepidoptera species.

MATERIAL AND METHODS

Study area

Our study area is the German state of Baden-Württemberg in Central Europe (center coordinates, 48°32'16" N, 9°2'28" E). Baden-Württemberg is in the southwestern part of Germany to the east of the Upper Rhine, and covers an area of 35 752 km².

Data on Lepidoptera

Our study focuses on all 1167 Lepidoptera (i.e., butterfly and moth) species traditionally classified as Macrolepidoptera that have ever been recorded in Baden-Württemberg (Ebert 1991–2005). Based on traditional taxonomic classifications, this comprises the clades of Bombycoidea, Cossoidea, Drepanoidea, Geometroidea, Hepialoidea, Lasiocampoidea, Noctuoidea, Papilionoidea (including Hesperidae), Psychoidea, Sesioidea, Thyridoidea, and Zygaenoidea. For each of these Lepidoptera species, we collected their red-list status in Baden-Württemberg (Ebert 1991–2005), which classifies them into least concern, near threatened, vulnerable, endangered, critically endangered, and extinct (the latter meaning extinct in Baden-Württemberg). Of the 1167 Lepidoptera species, 59 went extinct in Baden-Württemberg over the last 150 years, and 91 are critically endangered. We collected published observations of food plants used by these Lepidoptera species during their larval stage (Ebert 1991–2005). The data set is based on 2.3 million larval individuals recorded under natural, un-manipulated field situations. In total, it contains 4983 species-specific insect–plant interactions (Ebert 1991–2005). The data set is the result of a coordinated, >50-year effort to get a virtually complete matrix of larval host plants of Lepidoptera in Baden-Württemberg (Ebert [1991–2005]; for data set details, see Appendix A and Altermatt [2010a, b]). To describe the diet of the larva, we used the number of plant species that have been used by a Lepidoptera species within Baden-Württemberg. Furthermore, we also used an independent diet breadth classification from a geographically broad European study (Koch and Heinicke 1991).

We collected species-specific information on the most likely reason of extinction in Baden-Württemberg for all 59 extinct Lepidoptera species. Highly detailed information on the biology, distribution, and extinction of Macrolepidoptera in Baden-Württemberg is summarized in the ten volumes of the monograph of Ebert (1991–2005), and we used that as the basic source of information. The original publications, some of which date back into the mid-19th century, on extinctions attributed to host plant loss were consulted. Detailed

description of the reasons of extinction and references thereto are given in Appendix C:Table C1. We also consulted literature from surrounding countries, especially northern Switzerland, to complement and confirm the suggested reasons of extinction (Altermatt 2010a, b).

Data on plants

We included all terrestrial vascular plant species found in Baden-Württemberg, based on the plant database Floraweb (*available online*).⁴ For each of the 2403 plant species, we extracted information on their red-list status (Breunig and Demuth 1999), using the same categories as for the Lepidoptera. Furthermore, we describe each plant's biogeographic status, using the categories native, ancient nonnative (archaeophyte), recent nonnative (neophyte), or ornamental. The latter refers to nonnative plants that generally do not reproduce in the wild. Finally, we compiled information on the range size of all plants within Baden-Württemberg, based on presence-absence data of, in total, 403 raster cells covering the whole area (Bundesamt für Naturschutz 2010).

Statistical analyses and extinction models

First, we calculated descriptive statistics of the plant–Lepidoptera food web. We assessed the distribution of host breadth of herbivores and the herbivore communities on plants by comparison to a log-normal distribution with a Lillifors test. We assessed the nestedness of the network using the NODF algorithm (Almeida-Neto et al. 2008) and tested for significance against a completely randomized network that retains only species richness and total number of interactions (“nestednodf” and “r00” null model) as implemented in vegan (Oksanen et al. 2010).

Next, we bootstrapped extinctions of plant species and recorded the subsequent number of Lepidoptera extinctions. In our models, the extinction of a Lepidoptera species was purely based on the dependency of an insect on its host plants. A Lepidoptera species thus went extinct when all of its food plants had become extinct. The number of plant species that went extinct increased in our simulations in a stepwise process, from 1 to 2403 (all) plants. After each step of plant extinctions, we summed up the number of Lepidoptera extinctions. The availability of specific food plants was the ultimate condition for the occurrence of an herbivore, and the results of our model can be compared with naturally observed extinction rates. In the most basic scenario, each plant species had the same likelihood to become extinct (random extinction scenario). We bootstrapped each step 1000 times using resampled “extinctions.” Additionally, we bootstrapped Lepidoptera extinctions at the observed rate of plant extinctions (100 plants of the total 2403 plants) 10 000

times, and compared it with the observed number of Lepidoptera extinctions (59). We used the probability of ≥ 59 predicted Lepidoptera extinctions as a significance test for all four plant extinction scenarios.

We compared our random extinction scenario to three other possible patterns of plant diversity loss. In the first scenario, the likelihood of extinction was proportionate to the plant's red-list status (red-list-first extinction scenario), using the IUCN criteria (IUCN 2001). We arbitrarily assigned plants of the class of least concern an extinction risk that was two orders of magnitude smaller than the lowest IUCN class (near threatened), and each ascending class was given an extinction risk two orders of magnitude higher than the previous. In the second scenario of biased plant extinction, the likelihood of extinction was proportional to a plant's biogeographic status (natives-first extinction scenario). In many natural systems, native species are threatened by nonnative species (recent nonnative and ornamentals). We thus assigned the native species a 100-times-higher extinction risk compared to recent nonnative species, and ancient nonnative species a 10-times-higher extinction risk compared to the recent nonnative species. In the final scenario of biased plant extinction, the likelihood of plant extinction was inversely proportionate to the plants' range size in Baden-Württemberg (small-range-first extinction scenario).

We created scenarios in which Lepidoptera species could evolve novel host affiliations at the onset of loss of their current host. In this scenario, we extended the plant–insect interaction matrix to a “maximum genus matrix,” which included all plants within the genus/genera of plants (occurring in Baden-Württemberg) that were used by the Lepidoptera. For example, when a Lepidoptera has been observed to use *Alnus glutinosa* as its larval host plant, the extended plant–insect interaction matrix would also include the two other species of alder (*A. incana* and *A. alnobetula*) as potential food plants. Each time a Lepidoptera species faced extinction due to the loss of the last of its known food plant, it could switch to use another food plant based on the “maximum genus matrix.” Since the opportunity to switch to other food plants should not only depend on the number of plants within a genus, but also on the insect's ability to include further plants, we used Koch's (Koch and Heinicke 1991) diet breadth classification as an independent factor determining the likelihood of a host switch. We assigned descending probabilities (1, 0.5, 0.1, and 0) to switch to another food plant for polyphagous, oligophagous, strictly oligophagous, and monophagous Lepidoptera species respectively. We intentionally use high probabilities for a species to switch, since the ability to switch host plants may not only be due to evolution of host plant range in the strict genetic sense, but also due to phenotypic plasticity. Also, the selective pressure to switch host plants once the only host plant becomes extinct, should be relatively high.

⁴ <http://www.floraweb.de/>

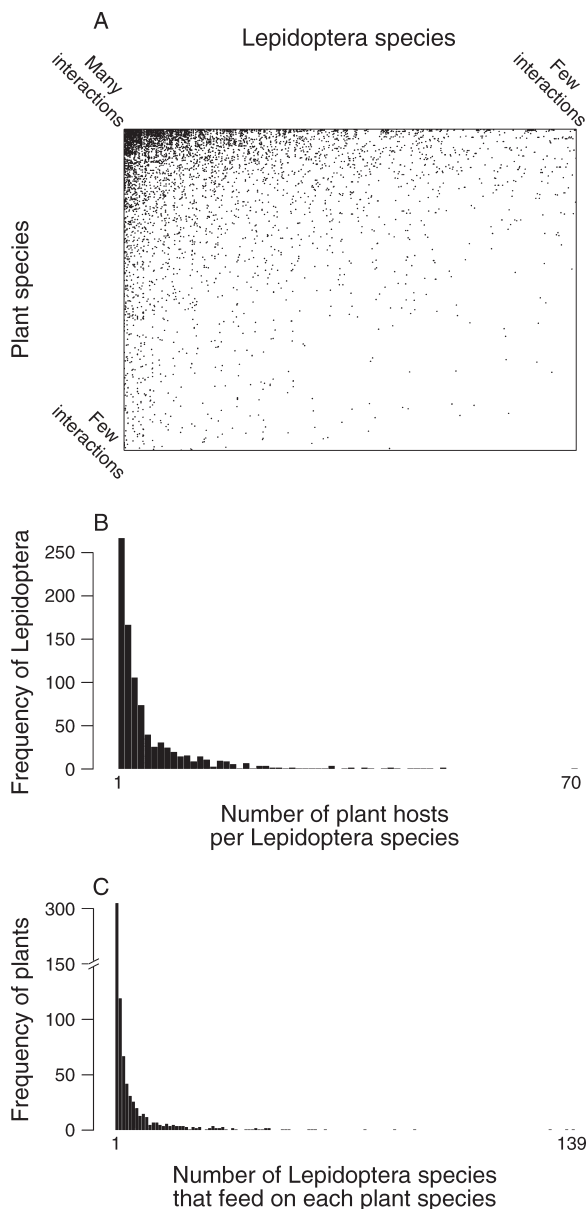


FIG. 1. Description of a network of 900 Lepidoptera species that interact with 759 plant species (within a total potential pool of 2403 plant species) in Baden-Württemberg, Germany. (A) A depiction of interactions where each dark spot indicates an observed trophic interaction between a plant species ($n = 759$ species) and larval Lepidoptera species ($n = 900$ species). Both plant and Lepidoptera species are ordered by their number of interactions. (B) Most Lepidoptera species include few plant species in their diet, but a few Lepidoptera species are widely polyphagous. (C) Most plant species are preyed upon by few Lepidoptera species, but a few are host to >100 Lepidoptera species.

It is known that measures of host use can be sensitive to sampling efforts (e.g., different sampling efforts for larval and adult stages, or for diurnal vs. nocturnal species). Thus, the recorded diet breadth might increase with sample size within a species. Even though such a

bias cannot totally be excluded, it has been shown by Altermatt and Pearse (2011) that the current data set is robust and there is no bias indicated. Specifically, Altermatt and Pearse (2011) showed that there is no systematic bias in the number of individuals recorded between diurnal and nocturnal species nor is the number of adult individuals recorded correlated with the number of larval individuals recorded. Still, we ran additional, individual simulations on three taxonomic groups of Lepidoptera (based on recent phylogenetic classifications, see Altermatt and Pearse [2011]) to see if the results were consistent for the groups with the best sampling record (e.g., butterflies and families of large, charismatic moths).

Finally, we compared the host-breadth of Lepidoptera species that fall into different red-list categories. First, we compared the proportion of Lepidoptera that fall into different predefined host breadths (monophagous, strictly oligophagous, and so on) among levels of red-list status. We used a generalized linear model (GLM) with Poisson error distribution and absolute counts of species in the different classes, and used the interaction terms to test for differences in the host breadth of Lepidoptera that are not threatened (least concern) and Lepidoptera that are either critically endangered or already extinct (Crawley 2002). We conducted an additional, comparable analysis where we compared the absolute number of host plants used by each Lepidoptera species and the Lepidoptera's red-list status.

We conducted all analyses in R 2.12.1 (R Development Core Team 2010) using the vegan package (Oksanen et al. 2010) for nestedness calculations. We have submitted a list of all moths and plants used in this study to Dryad (see Supplemental Material).

RESULTS

Description of the Lepidoptera–host-plant food web

We analyzed a database containing a total of 4983 realized trophic interactions between 2403 plant and 900 Lepidoptera species (Fig. 1A). The realized interactions account for only 0.23% of all possible interactions, where each Lepidoptera species feeding on all plants would result in 2 162 700 interactions. If a Lepidoptera species can extend its larval diet to all plant species of the genus that is in its observed diet breadth, this extends to 34 694 insect–plant interactions (this is used for the maximum genus matrix in the simulations), which would account for 1.6% of all possible interactions. The diet breadth of Lepidoptera species ranged from 1 to 70 host plants, and was skewed toward more specialization (i.e., fewer hosts), and the average Lepidoptera species included 5.5 plant species in its diet (Fig. 1B). Excluding the 1644 plant species that did not interact with any Lepidoptera herbivores, the distribution of herbivore interactions with each plant species was left skewed, plants interacted with 1–139 Lepidoptera species, and the average plant species interacted with 6.5 Lepidoptera

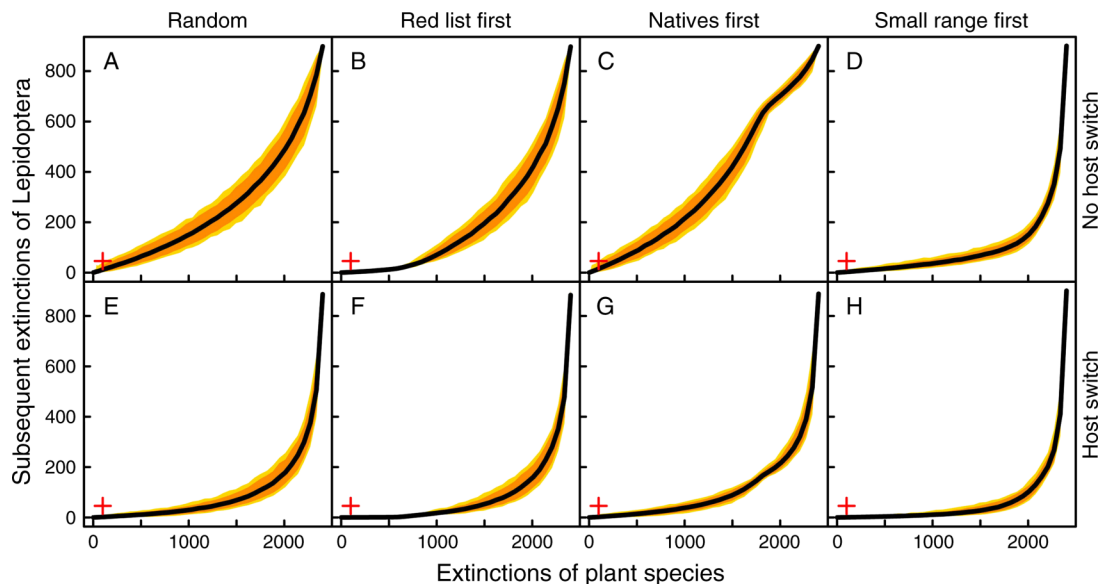


FIG. 2. Bootstrapped extinctions of plant species and subsequent number of Lepidoptera extinctions (mean, black line; 95% and 99% percentile, orange and yellow areas, respectively). Panels in the top row refer to an extinction scenario without the possibility of host switching, and panels in the bottom row refer to a scenario in which a lepidopteran species may expand its host range to its host's congeners. The simulated plant extinctions are either (A, E) random, (B, F) red list first, (C, G) natives first, or (D, H) small range first. The intersection of the actual number of regional plant extinctions (100 species) and Lepidoptera extinctions (59 species) is indicated by the red cross.

herbivores (Fig. 1C). Both the distribution of plant interactions with herbivores and herbivore interaction numbers with plants were more skewed than a log-normal distribution (Lilliefors test; $P < 0.001$ for both distributions). The network had an NODF nestedness value of 4.64, which was higher (i.e., more nested) than the NODF value of a completely randomized network that retained species richness and number of interactions (randomization test, mean = 0.81, $P < 0.01$, 100 simulations). In this case, high nestedness indicates that specialized herbivores tend to feed upon a set of plants that are also used by generalists, and plants with few herbivores are typically fed upon by generalist herbivores.

Plants with a greater range size tend to be fed upon by a greater number of Lepidoptera species (nonlinear least square fit, $t = 4.6$, $P < 0.0001$; Appendix B: Fig. B1). Plants with a large range size and large herbivore community tend to be host to a greater proportion of monophagous Lepidoptera species (Fig. B1).

Simulation of Lepidoptera extinctions based on extinction of their host plants

The bootstrapped simulations on Lepidoptera extinction as a consequence of larval host plant extinction revealed large differences in Lepidoptera extinctions following different plant extinction scenarios (Fig. 2). Overall, a biased plant extinction scenario of natives first leads to the highest rates of subsequent Lepidoptera extinctions. At lower plant extinction rates (up to about 25% of plant species going extinct), the predicted

Lepidoptera extinction rates were similar between random plant extinctions and an extinction of natives first. The red-list-first plant extinction scenario or small-range-first plant extinction scenario resulted in lower or much lower subsequent Lepidoptera extinctions, respectively. Thus, the loss of plant species, especially rare or threatened plants, does not necessarily translate into comparable losses of herbivorous insects. The results were robust and highly comparable when running the simulations separately for the three largest taxonomic groups (based on current phylogenetic classifications; for details see Altermatt and Pearse [2011] and Fig. B2). The predicted extinction patterns of butterflies (Papilionidea; Fig. B2A), noctuid moths (Noctuidae; Fig. B2B) and geometrid moths (Geometridae; Fig. B2C) were almost identical when simulating unbiased losses of host plants, even though these taxonomic groups differ in life cycle and habitat use. Also, when comparing the observed proportion of extinct species among groups, there was no significant difference among the three largest groups (i.e., the observed proportion of extinct species relative to the extant species was not different between butterflies, Noctuidae and Geometridae; Fisher exact tests, all $P > 0.05$). Allowing Lepidoptera to evolve diet breadth strongly decreased Lepidoptera extinction rates (Fig. 2E and F). Also, the simulated extinction rates between the four different scenarios became much more similar to each other when allowed to form novel host associations. In the simulations with host switching, the extinction rate of Lepidoptera

remained relatively low (<15%) for a large range of plant extinction rates (from 0% to about 75%).

In all extinction scenarios, the observed number of regional Lepidoptera extinctions from Baden-Württemberg ($n = 59$) was significantly higher than the predicted number of Lepidoptera extinctions at the observed rate of plant extinctions ($P = 0.0012$ for a natives-first extinction scenario, $P < 0.0001$ for all other extinction scenarios, both with 10 000 simulations; Fig. 3). Interestingly, the actual number of Lepidoptera extinctions that could be independently attributed to the decline of host plants fell within the distribution of the random plant extinction and natives-first predicted plant extinction scenarios (10 000 simulations; $P = 0.66$ and $P = 0.84$, respectively), and at the margins of the red-list-first and small-range-first scenarios (10 000 simulations, $P = 0.06$ and $P = 0.05$, respectively).

Comparison of actual Lepidoptera extinctions

The database contained information on 59 regional extinctions of Lepidoptera species from Baden-Württemberg (Ebert 1991–2005) over the past 150 years (Appendix C: Table C1). Of the 59 regional Lepidoptera extinctions, the extinction of eight Lepidoptera species could clearly be attributed to host loss or decline. An additional nine Lepidoptera regional extinctions reflected broader declines throughout the southern range of these species, which are consistent with the effects of climate change. The habitat of another eight Lepidoptera species had become highly fragmented or lost due to agricultural intensification. We have good knowledge on the host plants of these 34 species, and in no case were there documented extinctions or serious population declines of their host plants in parallel of the Lepidoptera extinction. It is thus unlikely that host plant loss was a driving factor for the “unknown extinctions causes,” and it is generally agreed that many of these extinctions may be due to large scale habitat loss or habitat change (Ebert 1991–2005), though, no single factor could be clearly attributed them. Of all extinct species, 18 extirpated Lepidoptera species were at their range edge in Baden-Württemberg, and regional extinction could feasibly represent natural meta-population dynamics of extinction and recolonization in combination with one of the three other causes of extinction.

Lepidoptera species of different red-list categories have a different larval diet breadth (Fig. 4). The relative proportion of species in the four different diet breadth classes was significantly different between least concern and critically endangered species. Specifically, a significantly higher relative number of non-threatened species are polyphagous, while the relative number of species with a more narrow diet breadth (oligo-, strictly oligo-, and monophagous) is significantly smaller in the non-threatened species compared to the critically endangered species (GLM, all z values of the interaction of phagie and red-list category least concern vs. critically endangered were >2.6 , and all P values were <0.01 ; Fig. 4).

The relative proportion of species in the four different diet breadth classes did not differ between critically endangered and extinct species (GLM, all z values of the interaction of phagie and red-list category critically endangered vs. extinct were <1.5 , and P values were >0.14 ; Fig. 4). Furthermore, and consistent with the previous results, Lepidoptera species that fall into any of the red-list “threatened” categories use significantly fewer host plants in their larval diet compared to species that are not threatened (category least concern, Wilcoxon signed rank test, $W = 133\,250$, $P < 0.0001$; Fig. B3).

DISCUSSION

All network models used to predict Lepidoptera extinctions based on the loss of their larval host plant underestimated the actual number of Lepidoptera extinctions within our study region, but accurately predicted the number of Lepidoptera extinctions that could be independently attributed to larval host loss (Fig. 3). As such, network models may be a useful tool for assessing one component of herbivore extinction risk. Insect herbivores are thought to be particularly susceptible to extinction cascades, as they often have a narrow host use compared to other organisms, and Lepidoptera–plant networks should be a prime candidate for finding large cascading effects of plant extinctions (Fonseca 2009). However, there are relatively few large, comprehensive data sets of herbivore–plant interactions, so extinction risks to herbivores based on host affiliations have been poorly understood.

Actual Lepidoptera extinctions

By observing the probable cause of Lepidoptera extinctions within our data set, we can assess the relative importance of extinction cascades as a contributor to Lepidoptera extinctions. Many of the regional Lepidoptera extinctions could not be attributed to a particular cause, but several trends emerged for the remaining extinctions. A large portion of reported Lepidoptera extinctions ($n = 18$ extinctions, 30%) were Lepidoptera species that were already at their range's edge in the study region, and thus especially vulnerable to changes in regional occurrence due to small changes in their habitat, host plant populations or climatic changes (Wilson et al. 2004, Franzen and Johannesson 2007). As such, it is unclear what priority the regional conservation of these species should have, as in many cases these Lepidoptera were abundant in nearby regions that were more central to their range. Moreover, extinction of some of these species may represent natural metapopulation dynamics of these species (Anderson et al. 2009). The remaining 41 of regional Lepidoptera extinctions (70%) reflect a true decline of a species in a central part of its range.

Overall, large biogeographic shifts of species ranges accounted for nine (15%) of regional Lepidoptera extinctions for our study area. Climate change and a poleward shift of mobile taxa have been broadly

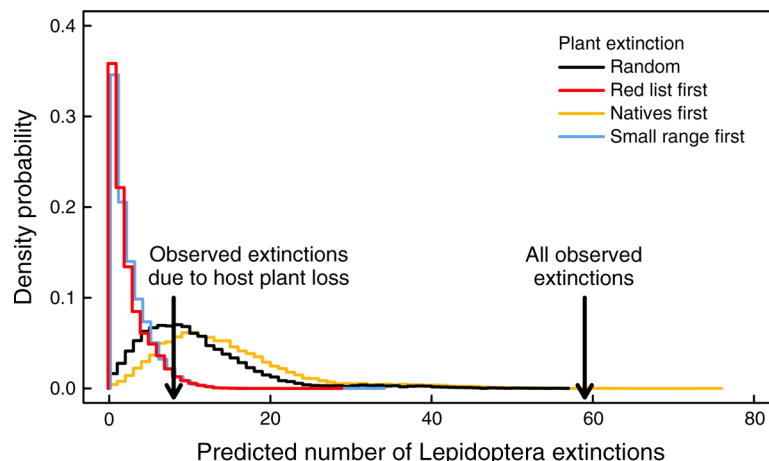


FIG. 3. Predicted density distribution of the number of Lepidoptera extinctions as a result of the simulated extinction of 100 plant species (equal to the observed number of plant extinctions). The bootstrapped plant extinctions followed different scenarios (random, red list first, natives first, and small range first; for details see *Material and methods* and Fig. 2). The arrows indicate the total observed number of Lepidoptera species that went extinct and the total number of Lepidoptera species that went extinct due to host loss. The observed number of extinct Lepidoptera species ($n = 59$) was significantly higher than predicted by any simulation scenario. For clarity, values of red list first and small range first are slightly shifted on the x-axis.

implicated in the reshuffling of Europe's biota (Parmesan et al. 1999, Walther et al. 2002). Loss of habitat due to land-use changes (especially agricultural intensification) accounts for an additional eight (14%) of regional Lepidoptera extinctions, an effect consistent to other areas of Europe that have sustained long-term land-use changes (Warren et al. 2001, Helm et al. 2006). The effects of land-use changes on Lepidoptera extinctions may in part be due to the loss of host plants, but may more broadly reflect habitat fragmentation and loss of non-larval host resources. Finally, eight (14%) of regional Lepidoptera extinctions could be attributed to the loss or decline of larval host plants, which is very consistent with modeled moth extinctions based on host loss (Fig. 3). When looking at reasons of extinctions and excluding the 18 species that are at their range edge, the absolute values change but only marginally affect the percentage change due to the following causes: extinction due to large-scale climatic changes ($n = 8$ extinctions, 20%), extinctions due to habitat change ($n = 5$, 13%), extinctions due to host plant loss changes ($n = 5$, 13%), and extinctions due to unknown factors changes ($n = 23$, 56%).

Modeling extinction cascades using realistic extinction scenarios

Network models of extinction cascades can be made more realistic by taking into account several factors governing extinctions. There has been recent interest in attempting to model the effects of a realistic sequence of extinctions on biotic communities (Dunne et al. 2002, Petchey et al. 2008, Bascompte and Stouffer 2009, Dunne and Williams 2009). In our Lepidoptera-host-plant network, we found different scenarios of plant extinctions resulted in different patterns of subsequent

Lepidoptera extinctions. When plants with a more critical red-list status or smaller range size were modeled as more likely to face extinction, subsequent Lepidoptera extinctions were delayed compared to a scenario of random plant extinctions (Fig. 2B, D). This is likely because plants with a more critical red-list status or smaller range were fed on by fewer herbivores and a smaller proportion of monophagous herbivores (Fig. 4, Appendix B: Fig. B1). Likewise, when Lepidoptera species were modeled to switch hosts onto congeners upon the decline of their ancestral host, Lepidoptera extinction was delayed (Fig. 2E–H), which is consistent with recent studies that find host plasticity increases network robustness (Ramos-Jiliberto et al. 2012). Host expansions may not be a ubiquitous feature of changing

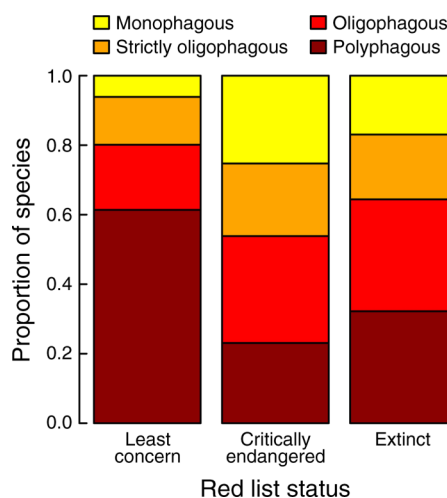


FIG. 4. Diet breadth of larval Lepidoptera relative to the Lepidoptera species' red-list status.



PLATE 1. Scarce large blue *Maculinea teleius* whose larva is monophagous on the relatively rare plant *Sangisorba major*. The butterfly is depicted on its obligate larval host plant. As some Lepidoptera strongly depend on a few plants, extinctions of host plants could cause cascading herbivore extinctions. Photo credit: F. Altermatt.

herbivore–plant interactions, but it is still a relatively common scenario (Pearse and Hipp 2009). Cases have been reported in which herbivores expand their host range based on the relative abundance of potential hosts (Singer et al. 1993).

Some realistic plant extinction scenarios expedited the predicted extinction of Lepidoptera species. When native plants were modeled as more susceptible to extinction than nonnative plants, Lepidoptera extinctions were accelerated, likely because nonnative plants tend to interact with fewer herbivores than natives (Keane and Crawley 2002). One scenario that our study does not account for is the importance of geographic structure to plant and Lepidoptera populations. As the data come from a large geographic region, it is likely that Lepidoptera simply do not encounter all plants within that region, as those plants exist in regions with environmental conditions where the moth could not persist. In the future, it will be important to independently assess the realism of these different extinction scenarios, as each of these scenarios result in different subsequent extinctions (Srinivasan et al. 2007). Moreover, the network models used here were conservative in that they only took into account the topological structure of the herbivore–plant network, and these types of analysis may underestimate extinction risks, as they fail to account for interaction strengths between species and the resulting changes to population dynamics (Gilarranz and Bascompte 2012). Moreover, in a previous study, we showed that there is a relationship between the specificity of host plants by the larval and

adult stages of these Lepidopterans, but that the strongest specificity is in the larval stage (Altermatt and Pearse 2011). However, extinction dynamics may be more complex for those (relatively few) herbivore species that are specialists on different sets of plants at different life stages.

Host breadth and extinction risk

The nature of host affiliation is important in the decline of many Lepidoptera species (see Plate 1). A disproportionate number of Lepidoptera with a critical red-list status, an assessment of extinction risk that is independent of host affiliation, feed on only one or a few host plant species (Fig. 4, Appendix B; Fig. B3), which mirrors a global pattern of specialists being more susceptible to extinction (Forister et al. 2012). Overall, however, most monophagous Lepidoptera species feed on plants that are both geographically widespread, and also host to many other herbivore species (Fig. 1A). The particularly troubling situation is monophagous herbivores that feed on rare plants (Fig. 1A). While not particularly common within our data set, there are several noteworthy examples of such insect–plant relationships. Exemplary of this are the moths *Eublemma minutatum*, which feeds only on *Helichrysum arenarium*, *Gortyna borelii*, which feeds only on *Peucedanum officinale*, or *Chamaesphecia tenthrediniformis*, which feeds only on *Euphorbia esula*. All of these plants are rare to very rare in Baden-Württemberg, and fall into red-list categories (Breunig and Demuth 1999). In each of these cases, many local populations of the plants

(and with them the Lepidoptera) have gone extinct (Ebert 1991–2005), and the moths have been assigned a critically endangered red-list status.

Conclusions

Host loss is one of many extinction threats to herbivorous insects. Network models of extinction cascades accurately predict the number of actual moth extinctions due to host loss (Fig. 3), but there are many additional factors that lead to moth extinction as well. Other factors than host loss have caused the majority of region extinctions of Lepidoptera in our study, despite these organisms being a textbook example of host fidelity and thus susceptibility to cascading extinctions. Network analysis that models the effects of host-loss on higher trophic levels may be a useful tool for assessing the risk of host loss to many species including herbivores. Indeed, a tendency of monophagous herbivores to feed on widely distributed plant species likely results in the robustness of these herbivores to plant extinctions. As such, potentially realistic models of plant loss that assign rare plants a higher extinction risk compared to common plants, predict a lower immediate extinction risk to Lepidoptera than models of random plant extinctions. Network analysis may be a useful tool in assessing the effects of species loss on higher trophic levels, but other factors that are unrelated to trophic interactions, such as land-use change and changing climate, also account for many regional extinctions of herbivores.

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SUPPLEMENTAL MATERIAL

Appendix A

Additional methodological information ([Ecological Archives E094-162-A1](#)).

Appendix B

Figures showing results of additional simulations ([Ecological Archives E094-162-A2](#)).

Appendix C

Table giving species-specific details on observed Lepidoptera extinctions ([Ecological Archives E094-162-A3](#)).

Data Availability

Data associated with this paper have been deposited in Dryad: <http://dx.doi.org/10.5061/dryad.gv4n5>