Ecosystem services at risk from declining taxonomic and interaction diversity in a tropical forest

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Abstract: Reports of biodiversity loss have increasingly focused on the abundance and diversity of insects, but it has been less clear if substantive losses are occurring in intact low-latitude forests. We collected 22 years of plant-caterpillar-parasitoid data in a protected tropical forest and found reductions in diversity and density of these insects that appear to be partly driven by a changing climate and weather anomalies. The decline in parasitism represents a reduction in an important ecosystem service: enemy control of primary consumers. The consequences of these changes are in many cases irreversible and will likely negatively impact surrounding agriculture. The decline of important tropical taxa and associated ecosystem function underlines the apparent threat to global insect diversity and provides additional impetus for research on tropical diversity.

One Sentence Summary: Tropical insect diversity and populations densities are declining in response to climate change, resulting in loss of ecosystem function.

Main Text: The impacts of global change are multi-faceted and ubiquitous *(1)* with ecological and evolutionary consequences *(2)* spanning aquatic and terrestrial ecosystems, and a wide

diversity of taxa and species interactions *(3)*. Much of global change research has focused on effects on single trophic levels, and despite an increased emphasis on interaction diversity in ecology *(4),* very few studies have linked global change to interactions and to effects on ecosystem stability and services. Past studies have also been geographically and taxonomically biased towards temperate ecosystems *(5)* and vertebrate taxa *(6)*. Thus, although it has been clear for some time that a sixth mass extinction event is underway *(7),* only recently have studies attempted to document declines in abundance and diversity in intact tropical forests *(8)* where the majority of biodiversity resides. Threats to insect diversity include climate change, habitat loss, fragmentation, invasive species, pesticides, and pollutants *(9-11)*. The magnitude of these global change forces and the levels of ecosystem resilience vary considerably across biogeographic regions, and there has been a long-standing expectation that tropical communities are more stable. However, increases in extreme weather events will have complex and large effects on lowland tropical communities *(12,13)* where plant-insect food webs may be particularly sensitive because of highly-specialized trophic relationships relative to interactions at higher latitudes *(14)*. Here we contribute to understanding species declines and loss of biological interactions in a protected and well-studied tropical wet forest.

Our study area is La Selva Biological Research Station, Heredia Costa Rica (10° 26′ N, 83° 59′ W), a ~1600-ha patch of forest bordered by agriculture (Fig. 1A). We used data from 1997-2018 to examine changes in taxonomic diversity among larval Lepidoptera (“caterpillars”) and associated parasitic Hymenoptera and Diptera ("parasitoids"). Our data reveal that declines in insect richness (Fig.1) and diversity (Fig. S1-S3) are widespread across the two consumer trophic levels. Extrapolation of estimated declines to the 1600 ha of La Selva yielded estimates for the

number of species that have either been lost from the forest since the start of the study or have been reduced to sufficiently low density that they are no longer detected (which likely amounts to effective extirpation from the perspective of ecological interactions). We estimate 1056 fewer herbivore species (with 95% Bayesian credible intervals from 2112 to 352), and 704 fewer parasitoid species (from 1056 to 352). For the herbivores, for which we have the most data, we additionally used the first 5 years of data to estimate a baseline diversity (Chao estimator) from which the losses represent 38.8% reduction (with credible intervals from 77.6% to 12.9%).

In addition to declines in caterpillar diversity, frequencies of encounter for entire genera of caterpillars are decreasing: out of the 64 genera studied, 41% (26 genera) have an 80% probability of being in decline (i.e. at least 80% of the mass of the Bayesian posterior distributions were less than zero for year coefficients in regressions for each of these genera) (Fig. 2, Table S1). These dramatic declines suggest that many caterpillars at La Selva will be losers and few will be winners in response to global change *(15)*, resulting in an overall reduction in their roles as herbivores and food for other animals. Compelling examples of winners and losers include the success of *Eucereon*, which includes outbreak species *(16)* and the failure of formerly common genera such as *Emesis* (Fig.S4). Notably, declines in insectivorous vertebrate predators, including bats and birds within and near La Selva, have already been attributed to reductions in arthropod prey *(17-19)*.

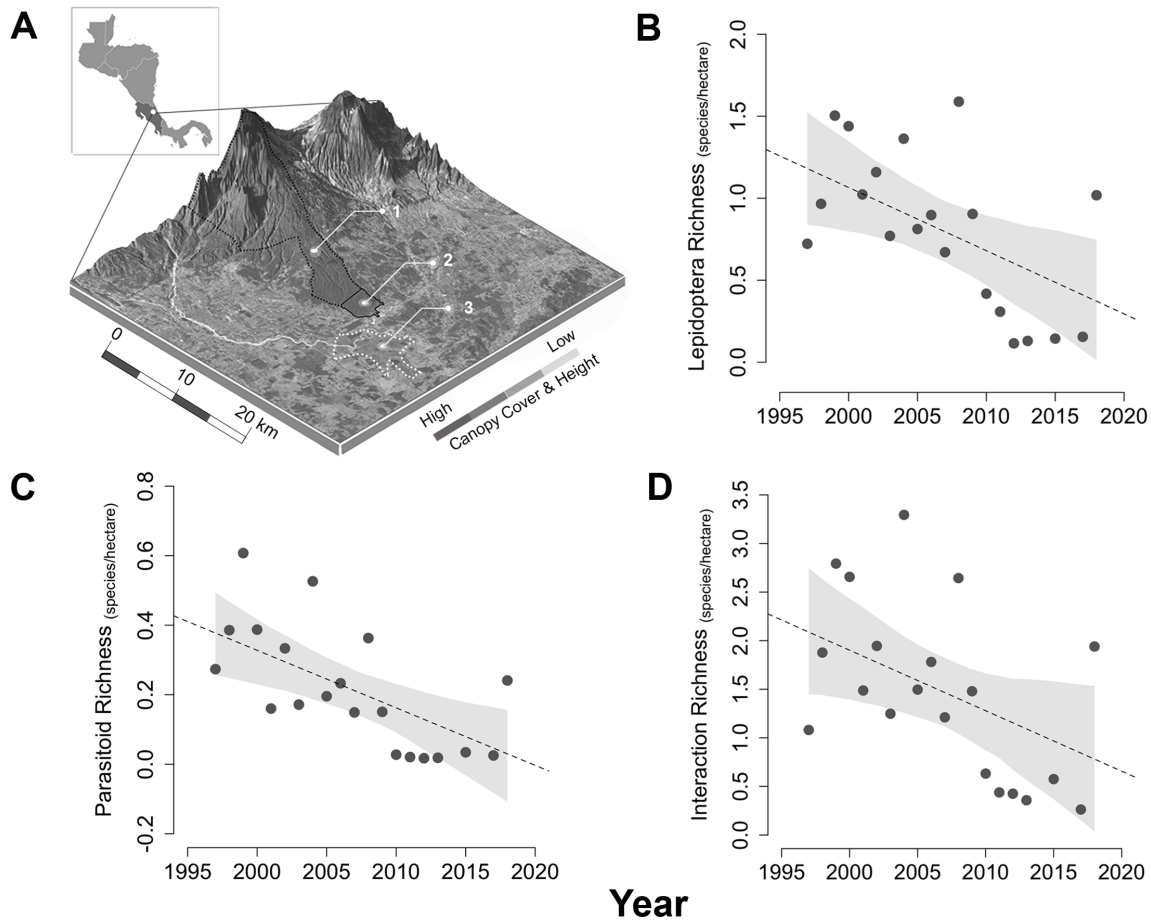

Figure 1. Braulio Carillo National Forest (A.l) and surrounding areas, including La Selva (A.2), which has experienced declines in caterpillar diversity (β=-0.03, 95% credible intervals (CI) [-0.06,-0.01]) (B), associated parasitoid diversity (β =-0.02, [-0.03,-0.01]) (C) and interaction diversity (β =-0.07, [-0.13,-0.02]) (D) over the past 22 years (1997-2018). A large adjacent banana plantation is indicated by dashed white lines (A.3). Dotted lines on graphs are best fit

lines from Bayesian regression, with 95% credible intervals in gray.

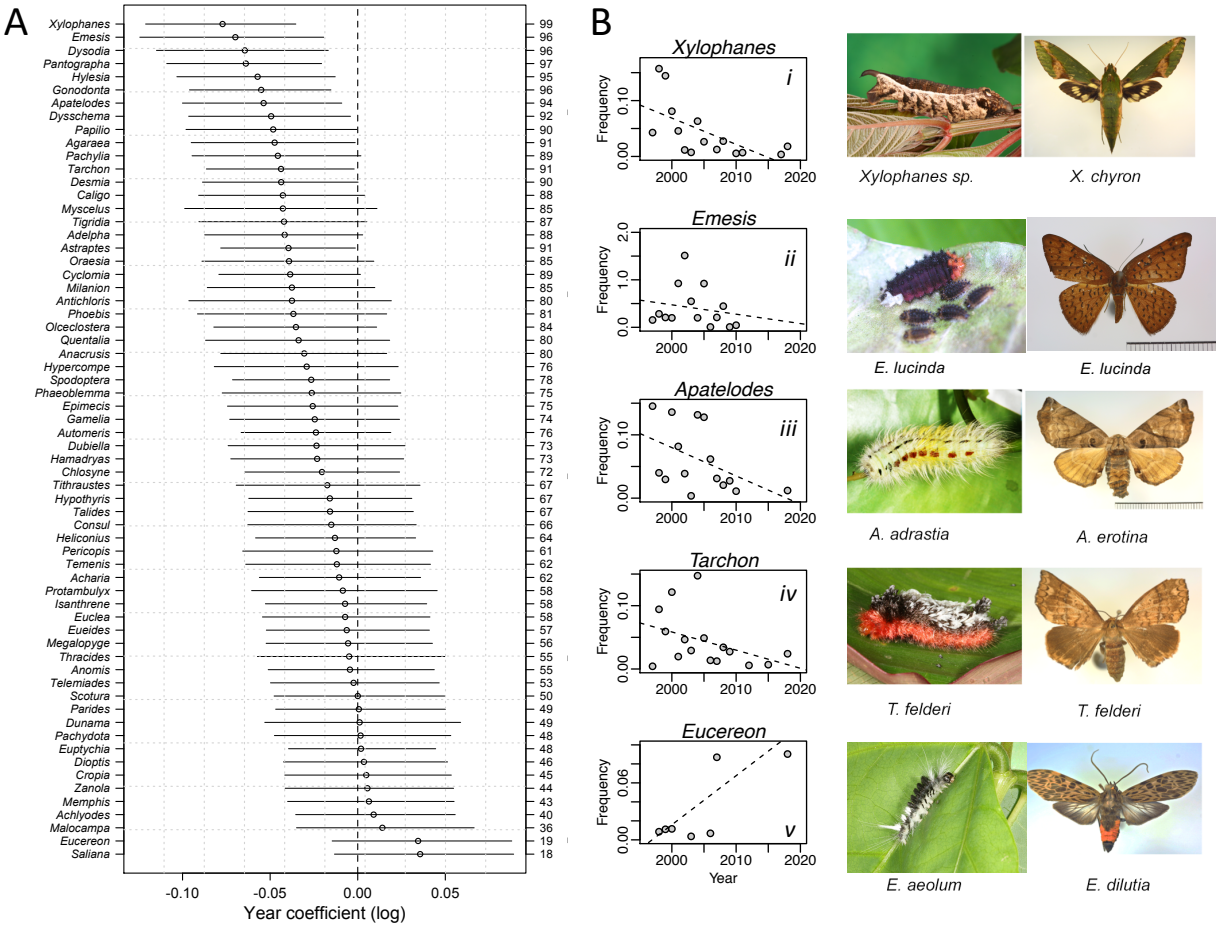

Figure 2. Genus-level patterns in caterpillar encounter frequencies across years. A) Point estimates for beta coefficients and associated 80% credible intervals (CI) for 64 genera that comprise a subset of all genera collected that met criteria for this analysis. Genus names are listed on the left margin and probabilities of a negative effect are on the right margin. Units of the year coefficient are the natural log of frequency per year. B) Frequency (untransformed) across years for select genera and representative larval and adult images.

One of the consequences of extirpation is the loss of interspecific interactions, which underlie ecosystem stability and ecosystem services *(20)*, but questions about loss of interaction diversity are largely absent from global change literature, due to a dearth of quantitative empirical data

(21-24). Along with taxonomic declines, interaction diversity at La Selva is decreasing: assemblages today have approximately 2,464 fewer unique interactions (30.9% reduction) than networks of interactions 22-year ago (Fig. 3A-B, Table S2). Herbivore-enemy interactions were disproportionately affected, with over 77% of connections disappearing between herbivores and parasitoids when comparing networks of interactions in the first and last five years of the study. Reduction in species *(25)* and interaction diversity *(26)* can cause reduced ecosystem function via loss of functional redundancy, with likely cascading effects on natural biological control, pollination, plant diversity, primary productivity, and nutrient cycling. In fact, parasitism frequency, an important measure of natural biological control, also decreased over time (Fig.S5). The overall rate of parasitism decline was -0.003 fewer instances of parasitism per year (with 95% credible intervals from -0.007 to 0.001) and that change seems largely driven by reduced attack from Hymenoptera (Fig. 3C). Losses of species and trophic interactions of this magnitude are particularly relevant in areas with intensified agriculture, where the global economic contribution of biological control is now estimated at $1.56 trillion per year *(27, 28)*. Parasitoids are essential for biological control in banana, and over *10,000 ha of land surrounding La Selva are banana plantations with one of the largest plantations situated <3km from La Selva (Fig. 1A)*.

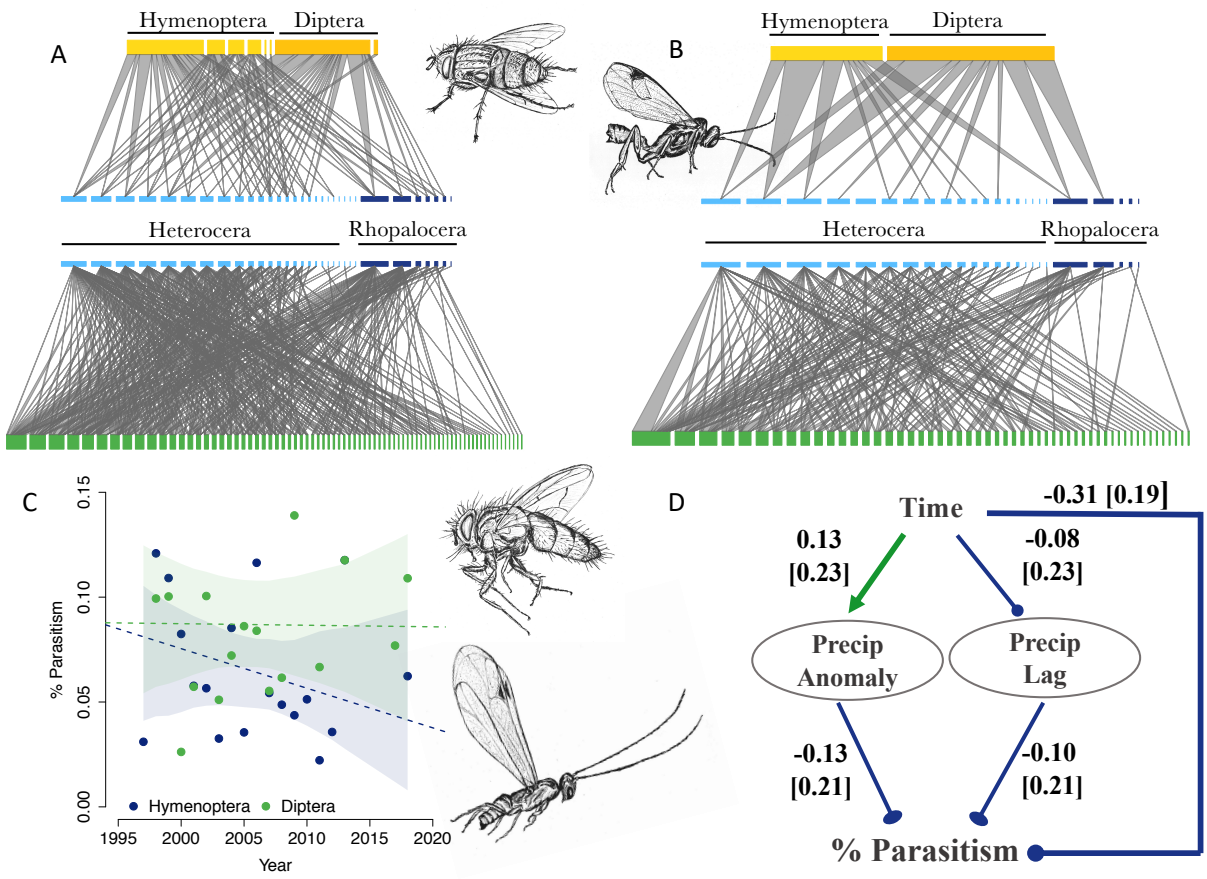

Figure 3. Patterns in plant-caterpillar-parasitoid interactions, climate, and parasitism across time. Tri-trophic networks illustrate host plants (green), caterpillars (blue), and associated parasitoids (yellow) for the first (A) and last 5 years (B). Nodes represent families within each trophic level and are grouped by suborder (Heterocera: light blue and Rhopalocera: dark blue) and order (Hymenoptera: light yellow and Diptera: mustard yellow) then ranked by node degree. Edge thickness represents relative link weights. Parasitism levels declined over time (C) (Hymenoptera: -0.001 [-0.004,0.002] and Diptera: -0.00007 [-0.003, 0.003] and these declines were associated with climatic changes (D). The structural equation model (good fit to the data: (χ^2=0.887, p=0.346, df=1) illustrating these associations estimates effects of time on climate and time and climate on percent parasitism. Models for species richness and interaction diversity yielded similar coefficients as did models for parasitism with more climate variables (Fig. S10-

110 S11). Path coefficients are standardized and width of arrows are scaled based on magnitude of path coefficients. Standard errors are reported in brackets. Arrows represent positive associations and lines with circles represent negative associations. Parasitoid illustrations by M.L.F.

Environmental changes in and around the forest include land use, as well as annual temperature
115 and precipitation which are both increasing at La Selva (Fig. S6-S9, Tables S3, S4). In the last five years, precipitation anomalies have been larger than previous years and the number of positive temperature anomalies are increasing, with the greatest T_{min} and T_{max} anomalies on record occurring during the study period. Structural equation models (SEM) provided support for the hypotheses that precipitation anomalies and their one year time lag are among the most important
120 factors causing lower parasitism frequency, following predictions of Stireman *et al*. 2005 *(29)* (Fig. 3D). Declines in richness appear to be caused by changes in multiple climate variables (Fig.S10-11). With the exception of the effect of minimum temperature on caterpillar richness (Fig. S11A), time had the strongest direct negative association with richness and parasitism frequency compared to other predictors in all SEM models, suggesting that other unmeasured
125 global change variables also contribute to insect declines at La Selva.

Declines in populations of plants and animals, extinctions, and loss of ecosystem function are defining features of the Anthropocene *(7)*. From a general Bayesian perspective in which new results are used to update prior knowledge *(30),* additional corroborations of these
130 Anthropocene-associated losses are useful in that they provide more precise estimates of decline probability for specific taxa, regions and ecosystems. Although insect declines have been the subject of recent high profile studies *(8,31),* the taxonomic and geographic breadth of the

phenomenon is not without controversy *(32)* and reports have been rare from the planet's most species-rich ecosystems. Thus we suggest that the results reported here strengthen the growing probability that insects are facing what indeed may be a global crisis. The hard work that still faces ecologists is to try to figure out which traits and habitats most expose species to risk, while the challenges for taxonomists and natural historians are to discover and describe new species and interactions before they disappear. All scientists should be considering how to use existing data to focus on the most imperiled taxa, ecosystems, and biogeographic regions. Tropical wet forests are clearly one biome requiring more precise estimates of species declines and a better understanding of determinants of these declines. For La Selva, we found that climate change is causing declines in species and entire genera of herbivores as well specialized parasitoids. Although such multi-trophic connections are not frequently studied in the context of global change, if results such as ours are widespread, then cascading results to other guilds and trophic levels can be expected (*20*) and warrant immediate concern and management effort.

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