Classification: Biological Sciences/ Ecology

Loss of dominant caterpillar genera in a protected tropical forest

Authors: Danielle M. Salcido[1*], Matthew Forister[1], Humberto Garcia Lopez[1], Lee A. Dyer[1]

Affiliations:

[1]Department of Biology, Program in Ecology, Evolution and Conservation Biology, University of Nevada, Reno, NV 89557, USA.

*Corresponding author: danisalcido@gmail.com

Keywords: insect declines, tropical, biodiversity, parasitism, extreme precipitation

ABSTRACT

Insects are the most species rich terrestrial taxa and their interactions with plants together comprise the majority of Earth's biodiversity. Recent reports provide evidence for large climate driven declines in the abundance and diversity of insects- some suggest up to 40% of temperate species will go extinct in the next two decades. However, it has been less clear if substantive losses are occurring in intact low-latitude forests, where insect diversity is the highest. Further, the implications of reported declines on ecosystem services provided by these insects are speculated but not quantified. Using 22 years of plant-caterpillar-parasitoid data, we document the loss of entire genera of Lepidoptera and declines in parasitism in a protected tropical forest. Forty-percent of Lepidoptera genera studied are declining in frequency and reductions in parasitism events suggest a 30% drop over the next 100 years. These declines in parasitism represent a reduction in an important ecosystem service: enemy control of primary consumers. Reported reductions in diversity, density and parasitism appear to be partly driven by a changing climate and weather anomalies. Our results demonstrate the ecological costs of climate driven insect declines in intact tropical forests and support predictions that specialized parasitoids are likely to suffer. The consequences of these changes are in many cases irreversible, and declines in parasitism will likely negatively impact surrounding agriculture. The loss of important tropical taxa and erosion of associated ecosystem function underlines the apparent threat to global insect diversity and provides additional impetus for research on tropical diversity.

Significance Statement: Recent reports suggest that there are substantial declines in insect abundance and diversity globally. The extent and severity of declines and their impact on ecosystem function remain to be quantified for low latitudes where the majority of diversity resides. From 22-years of data, we document losses of entire genera of lepidopteran larvae and

declines in parasitoids of those larvae. Parasitism by host-specialists declined the most and is partly driven by increases in extreme precipitation events. These results show the ecological costs of current declines and support predictions that specialized insects are more vulnerable to changes in climate. Reported reductions in parasitism are likely to have economic consequences for tropical countries where conversion of intact forest to agriculture is highest.

INTRODUCTION

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),* relatively few studies have linked climatic variability to interaction diversity, ecosystem stability, and services of parasitoids. Past studies have also been geographically and taxonomically biased towards temperate ecosystems *(5)* and the subset of tropical studies published are focused on vertebrates and focal tree species *(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 insect abundance and diversity in intact tropical forests by examining broad guilds. 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.

RESULTS

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)*.

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, S3). 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). Estimated parasitism decline was 3% per decade which represents a ~6.6% decline during the study period. Further, the probability of negative slope for overall parasitism across time was ~92%. Such declines in parasitism represent an impressive 30% drop in parasitism over

114 the next 100 years and loss of a key ecosystem service that prevents damaging outbreaks of
115 herbivorous insects(4). Losses of species and trophic interactions of this magnitude are
116 particularly relevant in areas with intensified agriculture, where the global economic contribution
117 of biological control is now estimated at $1.56 trillion per year *(27, 28)*. Parasitoids are essential
118 for biological control in banana, and over 10,000 ha of land surrounding La Selva are banana
119 plantations with one of the largest plantations situated <3km from La Selva (Fig. 1A).
120
121 Environmental changes in and around the forest include land use, as well as annual temperature
122 and precipitation which are both increasing at La Selva (Fig. S6-S9, Tables S4, S5). In the last
123 five years, precipitation anomalies have been larger than previous years and the number of
124 positive temperature anomalies are increasing, with the greatest T_{min} and T_{max} anomalies on record
125 occurring during the study period. Structural equation models (SEM) provided support for the
126 hypotheses that precipitation anomalies and their one year time lag are among the most important
127 factors causing lower parasitism frequency, following predictions of Stireman *et al*. 2005 *(29)*
128 (Fig. 3D). Declines in richness appear to be caused by changes in multiple climate variables
129 (Fig.S10-11). With the exception of the effect of minimum temperature on caterpillar richness
130 (Fig. S11A), time had the strongest direct negative association with richness and parasitism
131 frequency compared to other predictors in all SEM models, suggesting that other unmeasured
132 global change variables also contribute to insect declines at La Selva.
133
134 **DISCUSSION**
135 Declines in populations of plants and animals, extinctions, and loss of ecosystem function are
136 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 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.

METHODS

Study sites and sample methods

We collected plant-caterpillar-parasitoid interaction data within La Selva Biological Research Station located in Heredia Province, Costa Rica (10° 26′ N 83° 59′ W). La Selva is a 1600-ha

patch of protected lowland tropical forest on the eastern Caribbean slope of the Cordillera Central connected via a corridor to the Braulio Carllio National Forest. Seasonality is marked by a wet season generally from May to December and a brief dry season beginning January to April. Peak rainfall occurs in June-July and March is the peak dry month. Samples were collected as a larger rearing program cataloguing plant-herbivore-parasitoid associations across the Americas[17,25] from 1995 to present. We limited our results to records starting in 1997 up to 2018, and we excluded 2014 and 2016 because sampling days did not meet our minimum criteria of 20 sampling days/year. We sampled externally feeding immature Lepidoptera (caterpillars) from their host plant (including shelter builders) and reared them to adult moths or parasitoids(5). Caterpillars were located opportunistically by visual inspection along trail transects (distance varies between 50-3000m and select transects are continuously sampled across years), or in 10m diameter plots (149 plots total) by staff scientists, graduate students, parataxonomists and teams of Earthwatch volunteers and students. Due to varied sampling methods across years we weighted observed values by sampling effort. Sampling effort was calculated as the number of volunteer and staff days of sampling multiplied by the average area in square meters covered by each person in a 10-day sampling period (4000 m^2). Hence, observed diversity and frequency is presented and analyzed in models as species equivalents or frequencies per hectare per year. We excluded *Eois* (Geometridae) and *Quadrus* (Hesperiidae) from all analyses because these focal genera present a bias in the rearing dataset due to focused collection for ancillary studies.

Rearing Methods & Processing Data

For our ongoing interaction diversity survey, collected larvae are given a unique voucher code that associate them with their host plant species. Caterpillars are reared individually in plastic

containers or bags with a sample of hostplant. Species identifications are made initially by parataxonomists to lowest taxonomic level or morphospecies and verified by taxonomic experts or by referencing voucher specimens and image libraries. Some morphospecies are confirmed using mtDNA COI sequences, others by examining a mix of morphological characters, and others using genomic data. For the remaining species without morphospecies designations we assign morphotypes based on feeding relationships - consumers from the same family utilizing the same host family are designated a unique morphotype. This method is likely a conservative means to assigning species names, especially for tropical species[31]. Voucher specimens are sent to collaborating institutions including universities and museums (see www. caterpillars.org for a list of participating institutions).

Patterns in Diversity, Parasitism, Climate Variables

Abundance & Diversity

Taxonomic and interaction annual frequencies were obtained to understand patterns in diversity and abundance across time. Species-level and interaction frequencies were used for diversity analyses. Due to the rarity of species level data, we aggregated the data to examine genus-level frequencies of Lepidoptera to evaluate herbivore abundance patterns. Annual frequencies were calculated for each Lepidoptera genera. We limited genus-level abundance data analyses to genera with ≥5 years of data and sample points extending to 2010. Results are reported for the 64 Lepidoptera genera that met criteria. To obtain values of interaction diversity, we modified a community matrix such that rows were comprised of years and columns the unique interactions. Interactions were comprised of bi-trophic (plant-herbivore) and tri-trophic (plant-herbivore-enemy) interactions such that matrix cells represent annual frequencies of those interactions.

Diversity was calculated as Hill numbers, and values were interpreted as interaction or species equivalents(6). Hill numbers vary as a function of the parameter q and indicates the sensitivity of the index to rare species such that q=0, q=1 and q=2 are equivalent to species richness, Shannon's diversity, and Simpsons diversity, respectively. We used functions provided in Chao *et al*. (2015)(7) to calculate Hill numbers. Results for q=0 are reported in text and q=1 & q=2 in the supplemental information. To obtain estimated percent herbivore loss we differenced total diversity (an estimate based on averaged Chao estimates of the first 5 years of data) and the observed species decline extrapolated from beta coefficients of the models predicting diversity across years.

Climate Variables

Climate variables were calculated as annual means of daily precipitation and average, minimum and maximum temperatures. We used meteorological data acquired from weather stations within La Selva from 1983-2018(8). Temperature is reported as degrees Celsius (°C) and precipitation millimeters (mm). To examine effects of extreme weather events and climate variability on patterns of diversity, we calculated anomalies and the coefficients of variation (CV) for each precipitation and temperature variable. Precipitation anomalies were calculated as the sum of daily values exceeding 2.5 standard deviations (sd) of the annual mean. Similarly, for temperature anomalies we used 2sd. The coefficient of variation was calculated as the ratio of standard deviation to the annual mean. We used simple linear regression to evaluate patterns among each climate variable across time and with respect to each season in the supplemental figures.

Evaluating Patterns in Network Structural Properties

We pooled interaction data to the family level for the first (1997-2001) and last (2012-2018) five years of collection to illustrate changes in tri-trophic network structure. For each network illustration we calculated node degrees and relative edge weights and reported link and node richness for each trophic level (Table S2).

Parasitism Frequency

Percent parasitism was calculated as the ratio of parasitism events to the sum of successfully emerged Lepidopteran adults and parasitized individuals for each month from 1997-2018. We examined monthly trends across time to account for intra-annual and seasonal variation in tropical population dynamics. Excluded from analyses were months with zero parasitism, zero eclosed caterpillars and those months without sufficient sample in the denominator (sum of adult eclosion and parasitism events). Sufficient sample was deemed as values exceeding the 1st quantile (Q_1) of the distribution of denominators (IQR=12-103).

<u>Statistical Models</u>

We used Bayesian linear models to estimate coefficients associated with change through time on Lepidoptera, parasitoid and interaction diversity and parasitism frequency. This model was applied to total parasitism and separately for specialized (Hymenoptera) and non-specialized (Diptera) orders. Models were fit in JAGS (version 3.2.0) run with R and the rjags package(9) using (for each analysis) two Markov chains and 1,000,000 steps each; performance was assessed through examination of chain histories (burnin was not required), effective sample sizes

and the Gelman and Rubin convergence diagnostic(10). Response variables were modeled as normal distributions with means dependent on an intercept plus predictor variables (either year alone, or year plus climatic variables), and vague or minimally-influential priors as follows: priors on beta coefficients (for year and climatic variables) were normal distributions with mean of zero and precision of 0.01 (variance = 100); priors on precisions were modeled as gamma distributions with rate = 0.1 and shape = 0.1. All data was z transformed prior to analysis.

An additional hierarchical model (with vague priors as already described) was used to estimate change across years in the frequency at which individual Lepidoptera genera were observed, with the year coefficients (and intercepts) estimated for each genus separately (as the lower level in the hierarchy) and simultaneously across all genera (the response variable for this analysis was log transformed prior to z transformation). For all models (simple and hierarchical) we retained point estimates from posterior distributions for beta coefficients, as well as 95% credible intervals for the diversity models and 80% intervals for the hierarchical model. We used the more liberal calculation of intervals for the latter in the interest of minimizing type II error in a situation involving the decline of entire genera (i.e., we would rather risk the possibility of erroneously inferring decline as opposed to mistakenly concluding that a declining taxon is stable). As a complementary measure of confidence not dependent on an arbitrary cutoff for importance, we calculated (for the beta coefficients estimated for each genus) the fraction of the posterior distribution less than zero, which can be interpreted as the probability that a genus has been observed with decreasing frequency over time.

We used Structural Equation Modeling (SEM) to test causal hypotheses that evaluated the effect of climate and time on taxonomic and interaction richness and parasitism. We used the global estimation method in the lavaan package v.0.6-3(11) in R v 3.5.3 to generate 3 models. Models evaluated casual relationships among caterpillar, parasitoid, interaction richness or parasitism and climate variables. Climate variables included: Tmin and Tmax and their anomalies and precipitation anomalies. A priori predictions facilitated the test of causal hypotheses that parasitism was modeled by precipitation and its one year lag. Models were assessed using the $\chi 2$ and model comparison using Akaike information criterion (AIC). We reported standardized path coefficients and illustrated the SEM results in a path diagram.

ACKOWLEDMENTS:

We thank Earthwatch Institute and volunteers, UNR Plant-Insect Group, G. Gentry, J.O. Stireman, S. Shaw, J. Whitfield, J. Miller, J. Brown, J. Elliot, R. Parry, L. Richards, A. Smilanich, T. Davis, Z. Bousum, B. Carranza, D. Brenes & O. Vargas for substantive contributions to this work. **Funding**: This study was supported by the NSF DGE-1447692, NSF DEB-1442103, Experiment.com. **Author Contributions:** D.M.S., L.A.D., H.G.L. conceived project and supervised field work. D.M.S., L.A.D., M.F. analyzed data and wrote manuscript. Parasitoid illustrations by M.L.F. **Competing interests:** None declared. **Data and materials availability:** All data needed to evaluate the conclusions in the paper are available upon request.

295 **REFERENCES:**

296 1. P.M. Vitousek, H.A. Mooney, J. Lubchenco, J.M. Melillo, Human domination of Earth's
297 ecosystems. *Science* **277,** 494-499 (1997).
298 2. C. Parmesan, Ecological and evolutionary responses to recent climate change. *Annu.*
299 *Rev. Ecol. Evol. Syst.*, ***37***, 637-669 (2006).
300 3. J.M. Tylianakis, R.K. Didham, J. Bascompte, D.A. Wardle, Global change and species
301 interactions in terrestrial ecosystems. *Ecology letters*, ***11***, 1351-1363 (2008).
302 4. T. Poisot, D.B. Stouffer, D. Gravel, Beyond species: why ecological interaction networks
303 vary through space and time. *Oikos*, ***124***, 243-251 (2015).
304 5. D.A. Clarke, P.H. York, M.A. Rasheed, T.D. Northfield, Does biodiversity–ecosystem
305 function literature neglect tropical ecosystems?. *Trends in ecology & evolution*, ***32***, 320-
306 323 (2017).
307 6. H.M.Pereira, L.M. Navarro, I.S. Martins, Global biodiversity change: the bad, the good,
308 and the unknown. *Annual Review of Environment and Resources*, ***37***, 25-50 (2012).
309 7. R. Dirzo, H.S. Young, M. Galetti, G. Ceballos, N.J. Isaac, B. Collen, Defaunation in the
310 Anthropocene. *Science*, *345*(6195), 401-406 (2014).
311 8. B.C. Lister, A. Garcia, Climate-driven declines in arthropod abundance restructure a
312 rainforest food web. *Proceedings of the National Academy of Sciences*, ***115***, E10397-
313 E10406 (2018).
314 9. T. Hance, J. Van Baaren, P. Vernon, G. Boivin, Impact of extreme temperatures on
315 parasitoids in a climate change perspective. *Annu. Rev. Entomol.*, ***52***, 107-126 (2007).

10. M.A. Jamieson, L.A. Burkle, J.S. Manson, J.B. Runyon, A.M. Trowbridge, J. Zientek, Global change effects on plant–insect interactions: the role of phytochemistry. *Current opinion in insect science*, ***23***, 70-80 (2017).
11. T. Cornelissen, Climate change and its effects on terrestrial insects and herbivory patterns. *Neotropical Entomology*, ***40*****,** 155-163 (2011).
12. T.C. Bonebrake, C.A. Deutsch, Climate heterogeneity modulates impact of warming on tropical insects. *Ecology*, ***93***, 449-455 (2012).
13. R.T. Corlett, Impacts of warming on tropical lowland rainforests. *Trends in ecology & evolution*, ***26***, 606-613 (2011).
14. M.L. Forister, V. Novotny, A.K. Panorska, L. Baje, Y. Basset, P.T. Butterill, L. Cizek, P.D. Coley, F. Dem, I.R. Diniz, P. Drozd, The global distribution of diet breadth in insect herbivores. *Proceedings of the National Academy of Sciences*, ***112***, 442-447(2015).
15. M.L. McKinney, J.L. Lockwood, Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in ecology & evolution*, ***14*****,** 450-453 (1999).
16. S.A. Van Bael, A. Aiello, A. Valderrama, E. Medianero, M. Samaniego, S.J. Wright, General herbivore outbreak following an El Nino-related drought in a lowland Panamanian forest. *Journal of Tropical Ecology*, ***20*****,** 625-633(2004).
17. S.M. Whitfield, K.E. Bell, T. Philippi, M. Sasa, F. Bolaños, G. Chaves, J.M. Savage, M.A. Donnelly, Amphibian and reptile declines over 35 years at La Selva, Costa Rica. *Proceedings of the National Academy of Sciences*, ***104***,8352-8356 (2007).
18. K.A. Cleary, L.P. Waits, B. Finegan, Agricultural intensification alters bat assemblage composition and abundance in a dynamic Neotropical landscape. *Biotropica*, ***48***, 667-676 (2016).

19. B.J. Sigel, T.W. Sherry, B.E. Young, Avian community response to lowland tropical rainforest isolation: 40 years of change at La Selva Biological Station, Costa Rica. *Conservation Biology*, ***20***, 111-121 (2006).

20. L. Dyer, D. Letourneau, Can climate change trigger massive diversity cascades in terrestrial ecosystems?. *Diversity*, ***5***,479-504 (2013).

21. A. Valiente-Banuet, M.A. Aizen, J.M. Alcántara, J. Arroyo, A. Cocucci, M. Galetti, M.B. García, D. García, J.M. Gómez, P. Jordano, R. Medel, Beyond species loss: the extinction of ecological interactions in a changing world. *Functional Ecology*, ***29***, 299-307 (2015).

22. J.M. Tylianakis, T. Tscharntke, O.T. Lewis, Habitat modification alters the structure of tropical host–parasitoid food webs. *Nature*, ***445***, 202 (2007).

23. T. Poisot, C. Guéveneux-Julien, M.J. Fortin, D. Gravel, P. Legendre, Hosts, parasites and their interactions respond to different climatic variables. *Global ecology and biogeography*, ***26***, 942-951(2017).

24. D.L. Finke, W.E. Snyder, Niche partitioning increases resource exploitation by diverse communities. *Science*, ***321***, 1488-1490 (2008).

25. T. Poisot, N. Mouquet, D. Gravel, Trophic complementarity drives the biodiversity–ecosystem functioning relationship in food webs. *Ecology letters*, ***16***, 853-861(2013).

26. R. Costanza, R. d'Arge, R. De Groot, S. Farber, M. Grasso, B. Hannon, K. Limburg, S. Naeem, R.V. O'neill, J. Paruelo, R.G. Raskin, The value of the world's ecosystem services and natural capital. *Nature*, ***387***, 253 (1997).

27. R. Costanza, R. de Groot, P. Sutton, S. Van der Ploeg, S.J. Anderson, I. Kubiszewski, S. Farber, R.K. Turner, Changes in the global value of ecosystem services. *Global environmental change*, ***26*,**152-158 (2014).

28. J. Stireman *et al*., Climatic unpredictability and parasitism of caterpillars: implications of global warming. *Proc. Natl. Acad. Sci. U. S. A.* **102**, 17384-17387 (2005).

29. C. Howson, P. Urbach, *Scientific reasoning: the Bayesian approach*. (Open Court Publishing), 2006.

30. F. Sánchez-Bayo, K.A. Wyckhuys, Worldwide decline of the entomofauna: A review of its drivers. *Biological Conservation*, ***232***, 8-27 (2019).

31. C.D. Thomas, T.H. Jones, S.E. Hartley, "Insectageddon": a call for more robust data and rigorous analyses. *Global change biology*, (2019).

32. G.L. Gentry, L.A. Dyer, On the conditional nature of neotropical caterpillar defenses against their natural enemies. *Ecology*, ***83***, 3108-3119 (2002).

33. L.A. Dyer, M.S. Singer, J.T. Lill, J.O. Stireman, G.L. Gentry, R.J. Marquis, R.E. Ricklefs, H.F. Greeney, D.L. Wagner, H.C. Morais, I.R. Diniz, Host specificity of Lepidoptera in tropical and temperate forests. *Nature*, ***448*,** 696, (2007).

34. L. Jost, Partitioning diversity into independent alpha and beta components. *Ecology*, ***88*,** 2427-2439 (2007).

35. A. Chao, L. Jost, Estimating diversity and entropy profiles via discovery rates of new species. *Methods in Ecology and Evolution*, ***6***, 873-882 (2015).

36. D.A. Clark, NPP Tropical Forest: La Selva, Costa Rica, 1975-1994, R1. Data set. Available on-line [http://daac.ornl.gov] from Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, USA. doi:10.3334/ORNLDAAC/218

37. M. Plummer, JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. In *Proceedings of the 3rd international workshop on distributed statistical computing*. **124** (2003).

38. S.P. Brooks, A. Gelman, General methods for monitoring convergence of iterative simulations. *Journal of computational and graphical statistics*, ***7*****,** .434-455(1998).

39. Y. Rosseel, Lavaan: An R package for structural equation modeling and more. Version 0.5–12 (BETA). *Journal of statistical software*, ***48***, 1-36(2012).

406 **FIGURE CAPTIONS:**

407 **Figure 1. Insect declines across 22-years of sampling at La Selva Biological Research**
408 **Station.** Braulio Carillo National Forest (A.l) and surrounding areas, including La Selva (A.2),
409 which has experienced declines in caterpillar diversity (β=-0.03, 95% credible intervals (CI)
410 [-0.06,-0.01]) (B), associated parasitoid diversity (β =-0.02, [-0.03,-0.01]) (C) and interaction
411 diversity (β =-0.07, [-0.13,-0.02]) (D) over the past 22 years (1997-2018). A large adjacent
412 banana plantation is indicated by dashed white lines (A.3). Dotted lines on graphs are best fit
413 lines from Bayesian regression, with 95% credible intervals in gray.

414

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

421

422 **Figure 3. Patterns in plant-caterpillar-parasitoid interactions, climate, and parasitism**
423 **across time.** Tri-trophic networks illustrate host plants (green), caterpillars (blue), and associated
424 parasitoids (yellow) for the first (A) and last 5 years (B). Nodes represent families within each
425 trophic level and are grouped by suborder (Heterocera: light blue and Rhopalocera: dark blue)
426 and order (Hymenoptera: light yellow and Diptera: mustard yellow) then ranked by node degree.
427 Edge thickness represents relative link weights. Parasitism levels declined over time (C)
428 (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-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.

FIGURES

Figure 1

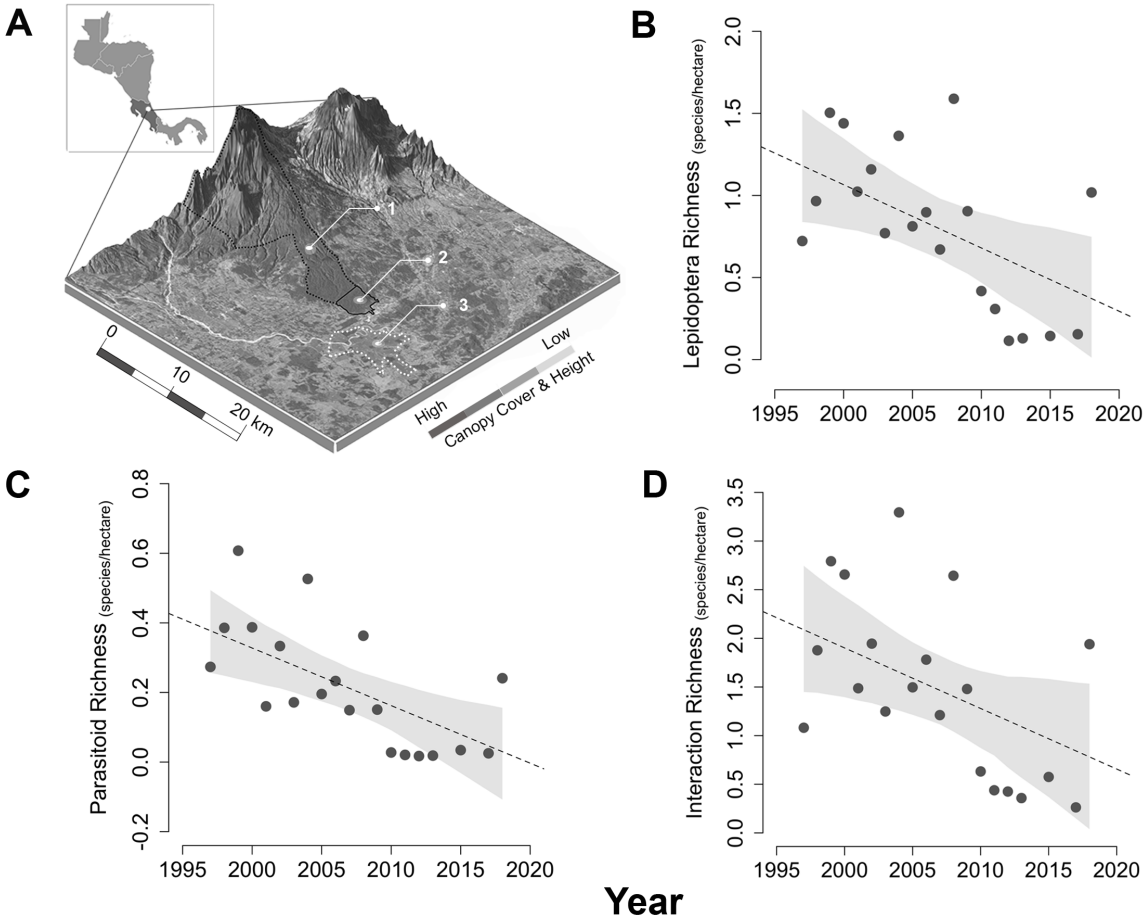


Figure 2

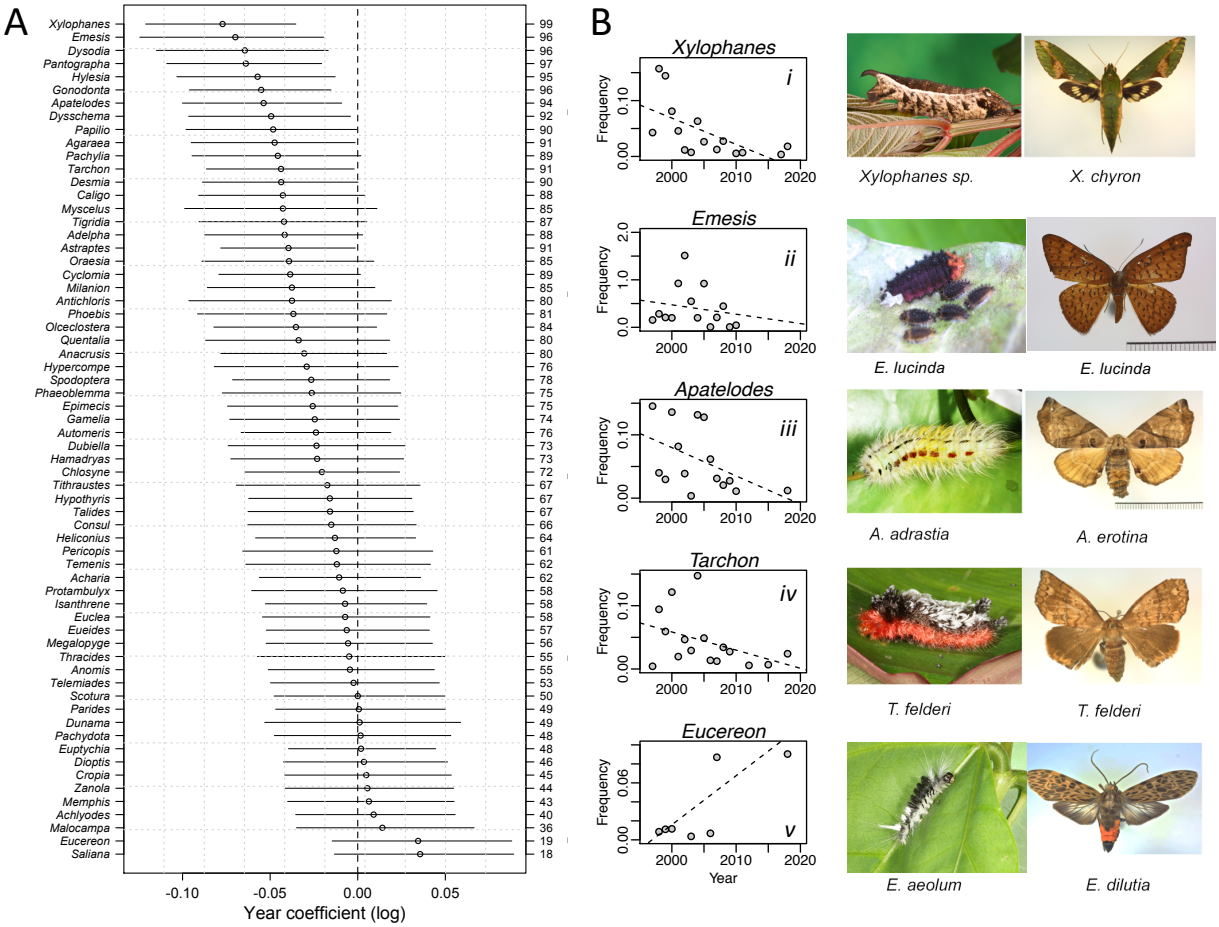
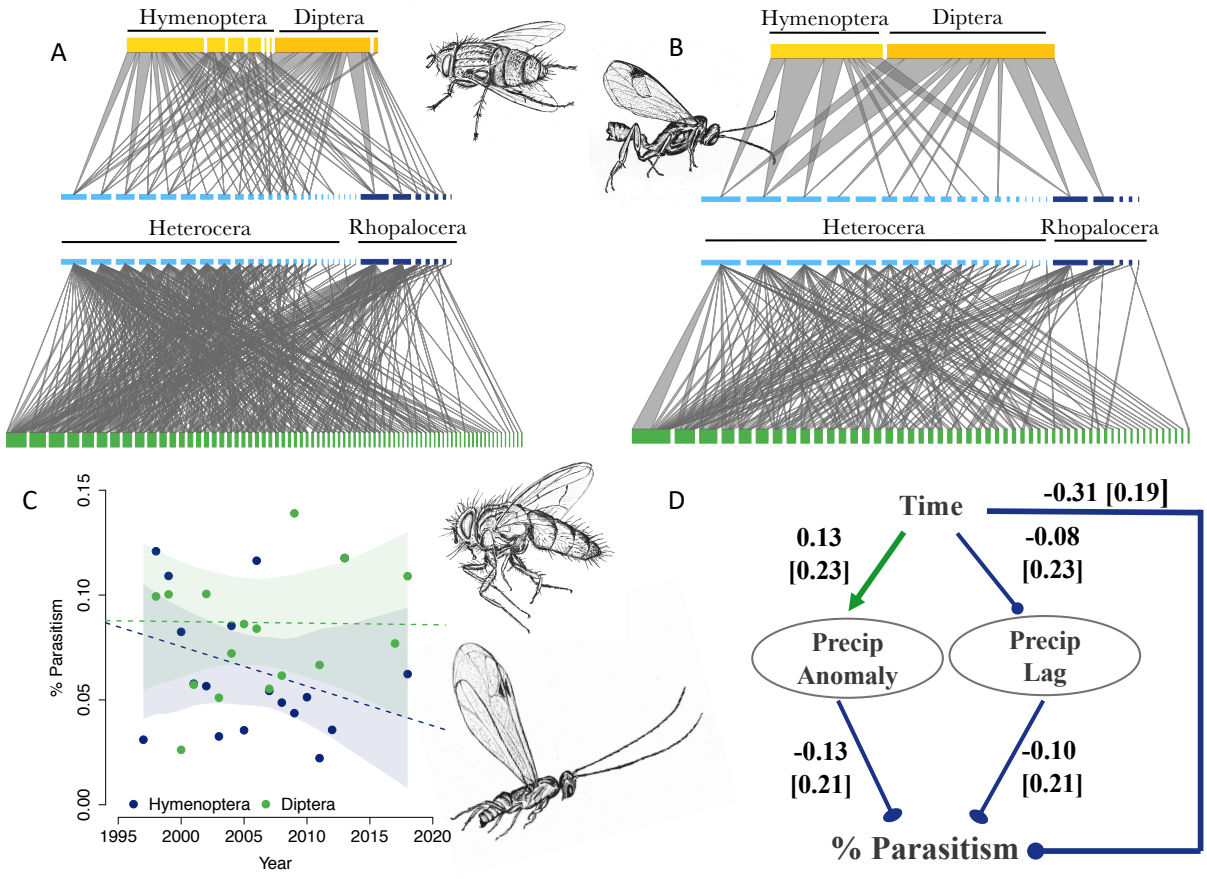

A
Xylophanes 99
Emesis 96
Dysodia 96
Pantographa 97
Hylesia 95
Gonodonta 96
Apatelodes 94
Dysschema 92
Papilio 90
Agaraea 91
Pachylia 89
Tarchon 91
Desmia 90
Caligo 88
Myscelus 85
Tigridia 87
Adelpha 88
Astraptes 91
Oraesia 85
Cyclomia 89
Milanion 85
Antichloris 80
Phoebis 81
Olceclostera 84
Quentalia 80
Anacrusis 80
Hypercompe 76
Spodoptera 78
Phaeoblemma 75
Epimecis 75
Gamelia 74
Automeris 76
Dubiella 73
Hamadryas 73
Chlosyne 72
Tithraustes 67
Hypothyris 67
Talides 67
Consul 66
Heliconius 64
Pericopis 61
Temenis 62
Acharia 62
Protambulyx 58
Isanthrene 58
Euclea 58
Eueides 57
Megalopyge 56
Thracides 55
Anomis 55
Telemiades 53
Scotura 50
Parides 49
Dunama 49
Pachydota 48
Euptychia 48
Dioptis 46
Cropia 45
Zanola 44
Memphis 43
Achlyodes 40
Malocampa 36
Eucereon 19
Saliana 18
-0.10
-0.05
0.00
0.05
Year coefficient (log)
B
Xylophanes
i
Frequency
0.00
0.10
2000
2010
2020
Xylophanes sp.
X. chyron
Emesis
ii
0.0
1.0
2.0
E. lucinda
E. lucinda
Apatelodes
iii
A. adrastia
A. erotina
Tarchon
iv
T. felderi
T. felderi
Eucereon
v
0.06
Year
E. aeolum
E. dilutia

Figure 3


A
Hymenoptera
Diptera
Heterocera
Rhopalocera
B
Hymenoptera
Diptera
Heterocera
Rhopalocera
C
% Parasitism
0.00
0.05
0.10
0.15
1995
2000
2005
2010
2015
2020
Year
Hymenoptera
Diptera
D
Time
-0.31 [0.19]
0.13
[0.23]
-0.08
[0.23]
Precip
Anomaly
Precip
Lag
-0.13
[0.21]
-0.10
[0.21]
% Parasitism