



# Tracking Caterpillars in Tropical Forests

## EARTHWATCH 2019 FIELD REPORT

Lee Dyer, Angela Smilanich, Chris Jeffery, Lora Richards, Tom Walla, Danielle Salcido, Santiago Villamarin  
Ecology, and Evolution, and Conservation Biology, University of Nevada, Reno Earthwatch Expedition,

Period covered by this report: June 30–December 21, 2019

November 19, 2019


Dear Volunteers,

What another great field season! Thanks to your hard work, we have thousands of new data points that will help us construct and learn from networks of plant-herbivore-enemy interactions. One of the most important networks created this year was the web of volunteers and researchers who can communicate the importance of insects and the threats they face as a result of global change. In 2019, we fielded 7 teams which allowed us to reach diverse audiences. In total, we had 63 volunteers helping us collect across the Americas from three of our research stations including Arizona, Costa Rica and Ecuador. We collected thousands of caterpillars in 2019, and the data from these caterpillars allows us to ask broader questions regarding tri-trophic interactions among plants, caterpillars and associated parasitoids. Further, many of the parasitoids reared from the caterpillars represent new interactions and species! Your help was both timely and important as these networks of interactions are being reshaped rapidly due to the loss of species and interactions. Long term data sets cataloguing insect interactions are rare, yet crucial for understanding the ecological consequences of global change. Our data allow us to quantify abundance, parasitism rates and interaction diversity across time, as well as providing insight into the ecological links between plant chemistry, herbivores and parasitoids. We are appreciative that you joined us to explore fascinating landscapes and the invertebrates that inhabit them.

We made some notable accomplishments in 2019. First, we began participation in a global study with researchers across the world to understand global variation in herbivory- earning its name HerbVar. Earthwatch volunteers were instrumental collecting preliminary data for our pilot studies. Second, we started a project in Costa Rica examining abiotic and biotic factors that explain chemical variation and divergence in *Piper reticulatum*. This study will lend insight into the potential drivers of phytochemical diversification. Lastly, we have focused much of our research efforts in the tropics the past two years to understanding insect declines. This year we submitted this research for peer-reviewed publication to Scientific Reports. Our research and the topic of global insect declines has received a lot of media attention and has enabled us to reach academic and public audiences on this important issue. Mongabay published a 4-part series "The Great Insect Dying" citing our work and we are currently working with National Geographic on a series documenting global insect losses. We hope that our research will help the public understand the ecological consequences of extreme weather events to encourage climate-minded policy and management practices.

The report to follow details results from publications made possible by the hours you spent collecting and photographing caterpillars, cleaning out their frass and feeding them fresh host plant, and the hours estimating herbivory. To put this in perspective, you contributed to over 4,000 person-hours of work in one year. We hope you enjoyed your time on our project and working together toward a common goal. We are fortunate to have worked with so many people of different backgrounds and are continually impressed by the high-quality data that comes from such a collaborative effort. We hope the few weeks or days you spent with us encouraged you to zoom closer to the less explored world of insects, and appreciate all of earth's biodiversity. Those small connections have the potential to make substantive impacts when communicated to citizens who have the power to vote and impact the choices of future generations.

Our best regards,



Danielle Salcido and Lee Dyer

## Summary

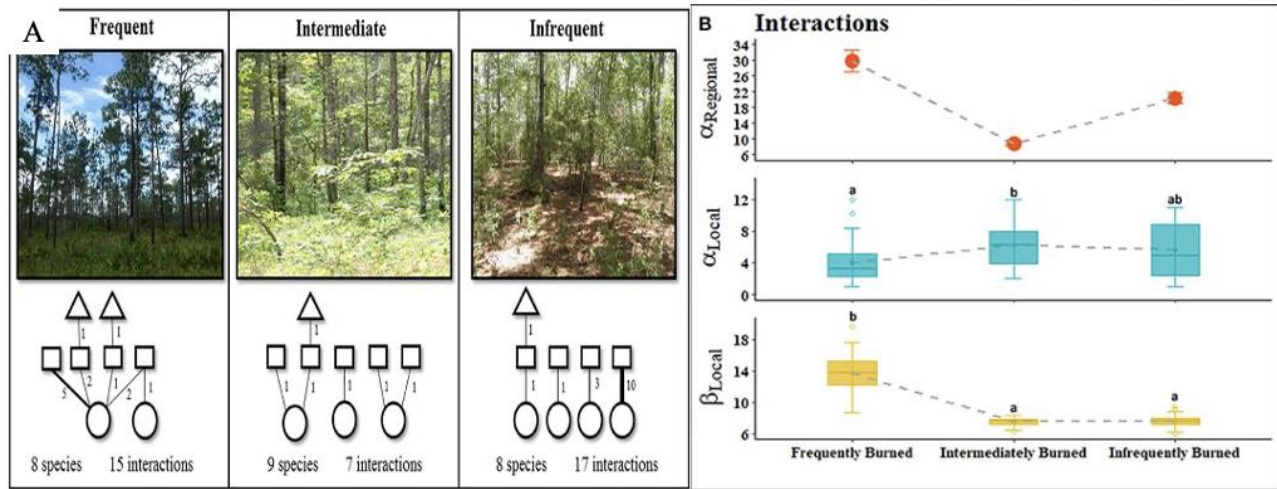
As a collaborative group of 7 Earthwatch teams, we collected over 1795 caterpillars at 4 sites (Arizona, Nevada, Costa Rica, Ecuador), reared out over 275 parasitic flies and wasps, discovered new phytochemicals, discovered dozens of novel interactions, and published over 7 papers in 2019 using years of accumulated Earthwatch data. Earthwatch teams that fielded in 2019 were instrumental in the collection of parasitoid data that will enable us to examine the topic of insect declines across our temperate and tropical sites. Further, we made progress documenting interaction, phytochemical, and species diversity.

### OBJECTIVE 1: Determine how climate change and other global change parameters affect biodiversity.

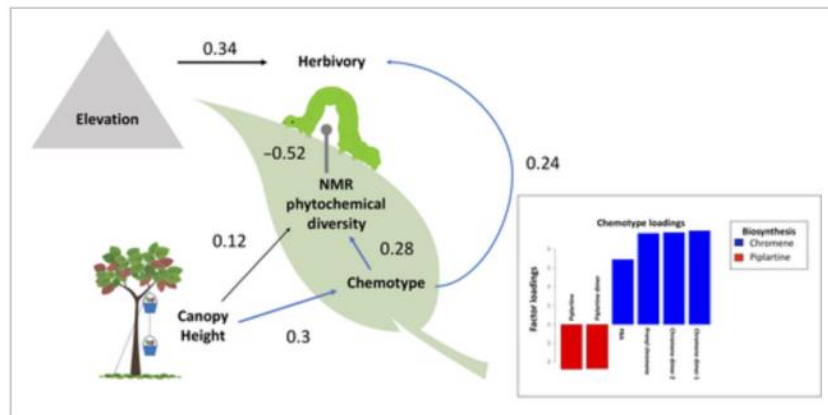
We continue to make progress towards our long-term goals of determining effects of hurricanes, climatic variation, and other large-scale disturbances on interaction diversity through our modeling approach and through empirical data (Scherrer *et al.* 2016). Our models, including analytical, simulation, and statistical approaches are being parameterized using all of the Earthwatch data from all of our sites (e.g., see Dyer & Forister 2016). To enhance these models, it is important we address questions that are seemingly unrelated to the climate-change-biodiversity crisis: *What are the consequences of changes in plant chemistry across climatic (elevation and precipitation) gradients? How do caterpillars and parasitoids respond? How does tri-trophic network structure change? What are the consequences for biodiversity and ecosystem management?* In 2019, we published 7 papers in top journals about these topics (e.g., Dell *et al.* 2018b, Dell *et al.* 2019b, Glassmire *et al.* 2019, Loudermilk *et al.* 2019).

Specifically, in Dell *et al.* (2019) we examined the effects of fire disturbance on interaction diversity in Longleaf Pine forests—fire adapted system (Fig. 1). We found that in frequently burned forests, while species and interaction diversity was low relative to infrequently burned forests, interactions were more variable across space. This indicates that frequently burned forests have a greater fraction of herbivores that are able to consume many different plants—a useful trait when plant colonization post fire is highly variable. Those plants that do establish become locally abundant such that generalists interact with very different subsets of plants in one plot than they do in the next plot. Such redundancy in function across space is an important feature that confers resiliency in fire-adapted systems. For more pervasive global change drivers such as climate change, studies examining the redundancy of interactions will provide insight to their resilience across space. In another study, Glassmire *et al.* 2018 provided important insight into the phytochemical landscape of *Piper kelleyi*. She showed that chemical diversity changes in leaves closer to the canopy compared to those in the understory. This finding indicated that light environment influences the anti-herbivore compounds produced by different parts of plants. Specifically, plants shift their production of certain chemical compounds depending on vertical strata. She found that understory plants tended to produce pipartine whereas those closer to the canopy produced chromenes. As in previous work, leaves with greater phytochemical diversity were associated with lower levels of herbivory. One can imagine that global change drivers such as deforestation or hurricanes that modify the light environment of plants, will cause subsequent changes in patterns of herbivory mediated by changes in plant chemistry. Such findings also have important agricultural applications where methods such as shade versus non-shade cropping can cause a plant to produce a certain class of compounds that may alter its vulnerability to herbivores.

Taken together, these published results are another example demonstrating the complex mechanisms by which climate change can alter biodiversity and provides an impetus to document the vast unknown biodiversity and associated natural history on earth (see also Salcido *et al.* 2019, Pardikes *et al.* 2019). We continue to model the importance of interaction diversity as buffers to climate change and disruptive effects of losing biodiversity and we plan to continue the research over the coming decades.



**Figure 1.** (A) Representative examples of interaction networks among plants (circles), caterpillars (squares) and parasitoids (triangles) for the various burn frequencies of Longleaf pine. (B) Patterns of interaction diversity differ when comparing interaction turnover (yellow boxplot) versus richness (blue boxplot). Variability in interaction diversity across space is highest for frequently burned forests (yellow boxplot), while interaction richness in frequently burned plots is lower (blue boxplots). Such a pattern indicates the importance of observing diversity of species and interactions together to identify more informative processes. Earthwatch volunteers from 2014–2016 help to collect and process these data.



**Figures 2.** A path diagram illustrating the relationships between canopy height, phytochemical diversity, and herbivory in *Piper kelleyi*. Arrows represent positive relationships and blunted lines represent negative relationships. The strength of the relationship is indicated by the value nearest the line. Leaves higher in the canopy had a greater diversity of compounds which was negatively associated with herbivory.

## OBJECTIVE 2: Determine how hurricanes and variation in climate affect levels of parasitism and caterpillar densities.

Models of climate change have predicted greater frequency and duration of droughts and floods and a widespread increase in the frequency of extreme weather events (e.g., Rahmstorf and Coumou 2011). Such increased unpredictability and variability in regional climates will likely impact all aspects of biodiversity, including interactions between plants, caterpillars, and their natural enemies. In 2017 we began exploring long-term trends in parasitism rates at our tropical site in Costa Rica and found evidence declines in parasitism. In 2019 with the help of Earthwatch volunteers, we continued focused collection of parasitoids at the Ecuador and Arizona sites and wrote our manuscript detailing results in Costa Rica (Salcido et al. 2019). Costa Rica continues to experience an increased frequency of flooding events and prior investigations exploring the relationship between precipitation variability and parasitism (Stireman et al. 2005) indicate that greater precipitation variability is strongly correlated with parasitism frequency and has disproportionate effects on specialized parasitoids. Over 33 years of local precipitation data at La Selva corroborate observations of the increased frequency of extreme precipitation events and for lowland tropical forests like La Selva which is surrounded by two large rivers, the Rio Sarapiquí and Rio Puerto Viejo, flooding events impact population sizes and cycles of caterpillars and associated parasitoids through its direct and indirect effects on survival rates, development time and the availability and quality of host plants. Flooding likely has disproportionate effects on understory species, particularly those that pupate in the soil or feed externally on understory shrubs as larvae. In addition to declines in caterpillar and parasitoid diversity, we found evidence for the loss of entire caterpillar genera across the 22-years (Fig. 3A,B). These declines are associated with loss of ecosystem function in the form of biocontrol by parasitoids-particularly specialized parasitoids (Fig. 3C). Declines in parasitism are linked to precipitation anomalies and their time lags (Fig. 3D). We have continued to pursue causal effects of these declines including changes in climate parameters and other global change drivers such as land-use changes. Meanwhile, our results of these studies are currently in review at Science Reports and have captured the attention of the National Geographic so that this message reaches a broader public audience.

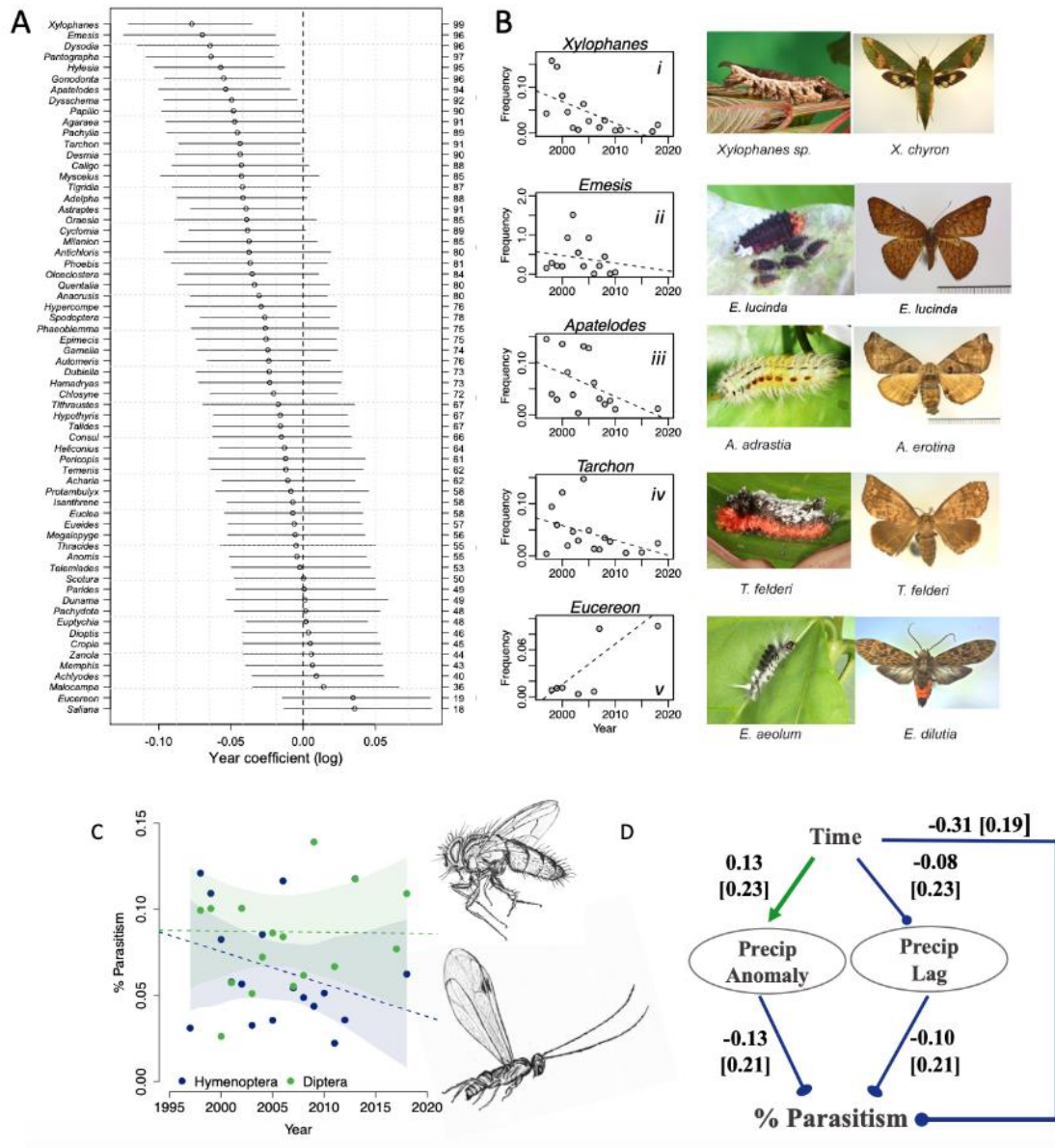
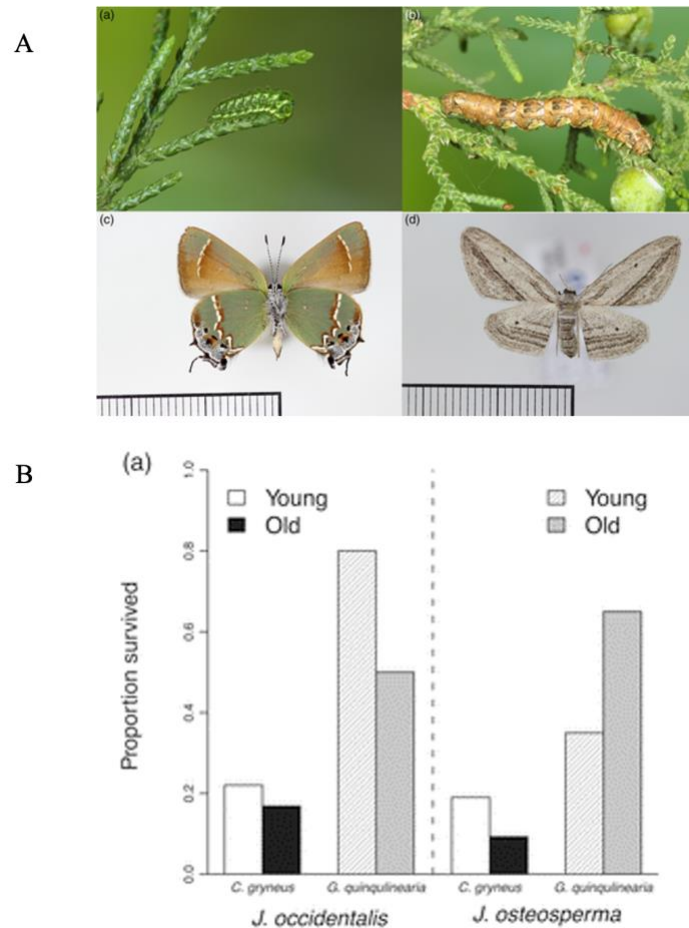


Figure 3. (A) Encounter frequencies across the 33 years of the study for 64 caterpillar genera. Genera in decline have point estimates on the left side of the dashed line and are ranked by the size of the negative effect (B) Frequencies across time for select genera. (C) Trends in percent parasitism across time for specialized parasitoids (blue) and generalized parasitoids (green). (D) Path diagram showing relationships among percent parasitism and extreme precipitation. Negative effects are represented in blue and positive effects in green. Earthwatch volunteers have contributed to data collection for this site since 1997. This long-term study would not have been possible without the continued effort of Earthwatch volunteers.

### OBJECTIVE 3: Specialization, trophic interactions, and biodiversity

The diet breadth or host range of insects has been a focal point for understanding current levels of biodiversity, which are increasingly threatened by global change. Estimates of species richness (counts of the numbers of species in an area) that are published for the most diverse forests on earth are only crude approximations, and the methods for estimating biodiversity rely on poor natural history data and untested assumptions about herbivore specialization (Basset et al. 2012). For years our Earthwatch data have facilitated investigation of specialization and co-diversification across multiple trophic levels (Forister et al. 2015), a long-standing challenge in biodiversity research and evolutionary theory. In 2019 we published a paper detailing the effect of juniper tree age on preference and performance of its specialized herbivores, the Juniper hairstreak *Callophrys gryneus* and *Glena quinquelinearia* (Pardikes et al. 2019). In these papers we report strong relationships between tree age, plant chemistry, and specialization (Fig. 4). Caterpillars that fed on young trees were healthier but adults preferred older trees for oviposition. This suggests that intraspecific variation among these specialized herbivores is partly explained by differences in chemistry across tree age.

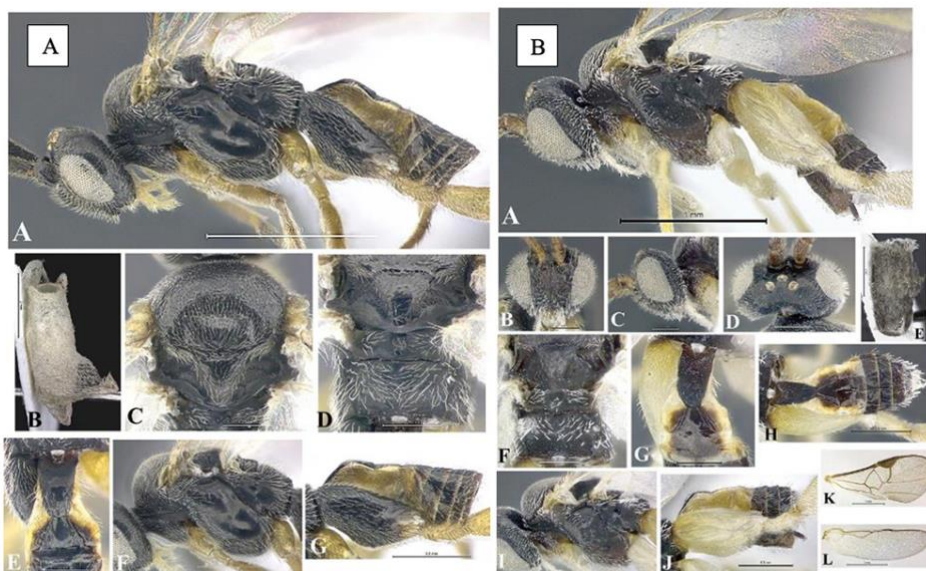


**Figure 4.** (A) Adult and larval images of two specialist herbivores of Juniper: Juniper hairstreak *Callophrys gryneus* and *Glena quinquelinearia*. (B) Performance measured as survival for the two specialists on two species of Juniper (*Juniperus occidentalis* and *J. osteosperma*) fed a diet of old or young leaves.

## OBJECTIVE 4: Discovery and descriptions of new species and new life histories

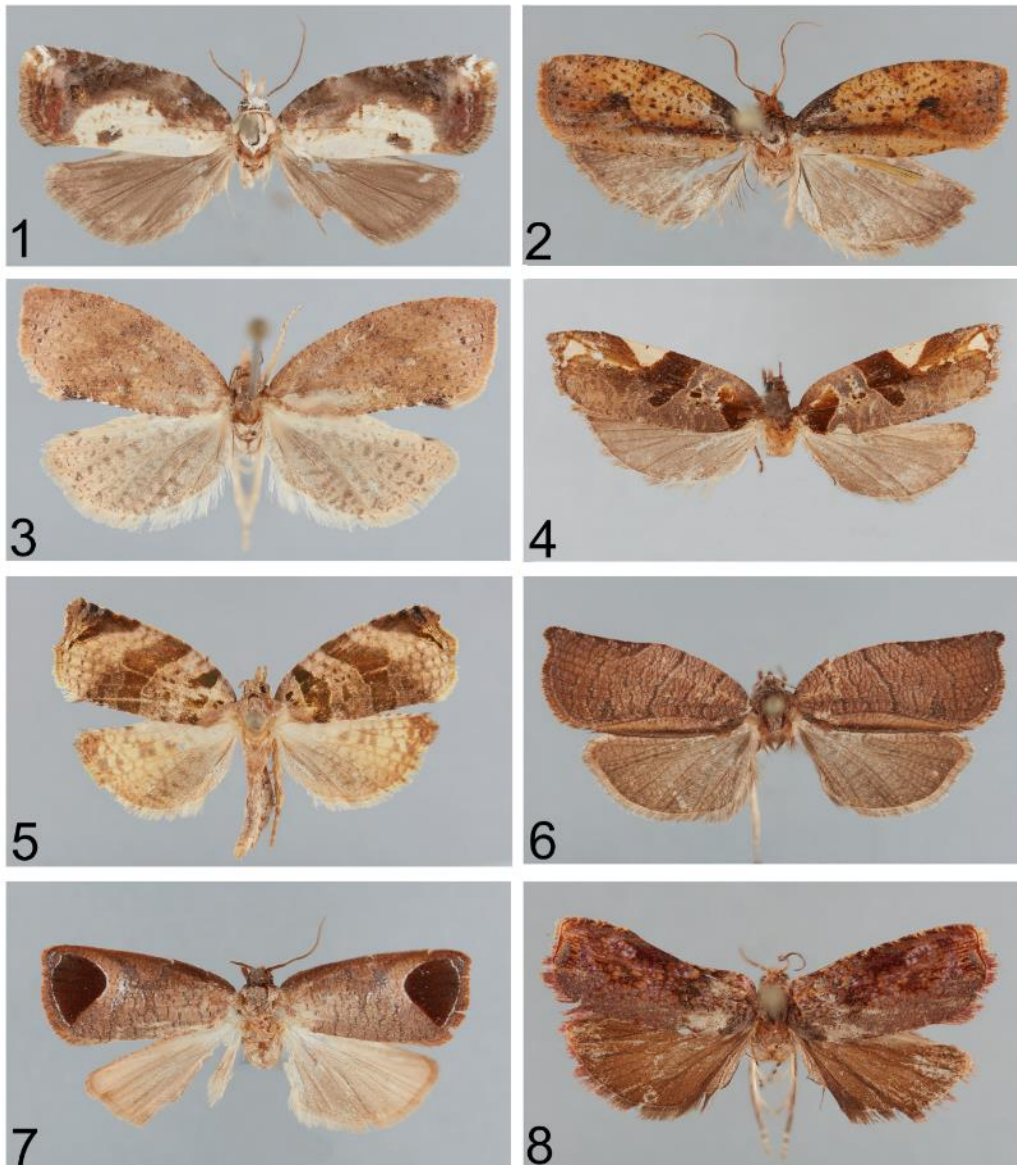
As we have reported in past years, another significant accomplishment for 2019 came in the form of new species and new chemistry discoveries. Notably, Earthwatch collected and reared specimens of caterpillars and parasitic wasps have led to two important publications in 2019 (Arias-Penna et al. 2019, Brown et al. 2019). In Arias-Penna et al. (2019), 136 new species of *Glyptapanteles* (Braconidae), a genera of specialized parasitic wasps, were described in over 600 pages of work. Over 30 of these were collected and reared from our Earthwatch projects with a few inspired by people and places related to our project. For example, *Glyptapanteles betogarciai* is named after our parataxonomist in Costa Rica- Beto Garcia (Fig.5A) and *Glyptapanteles yanayacuensis* is named after the Yanayacu Biological Research Station in Ecuador (Fig. 5B). In Brown et al. (2019), new host records for tropical moths in the family Tortricidae. Forty-two caterpillar species were described identifying over 46 unique host plant records (Brown et al. 2019). We continue to make progress developing pioneering methods to describe and analyze phytochemical compounds. These methods have helped us to further characterize the temperate and tropical model genus, *Juniperus* and *Piper*, respectively. We have reported in many other papers that plant chemistry changes with increases in temperature and CO<sub>2</sub> (Dyer et al. 2013). Chemical compounds produced by plants are not only responsible for the plants' unique flavors, aromas, and colors, but also possible deterrent or toxic properties and resistance to herbivores (e.g., Hansen et al. 2016).

Also similar to previous years, in 2019, continued to improve our sister sites to caterpillars.org – most notably the site created in collaboration with the Encyclopedia of Life (EOL). The URL for the site is: <http://caterpillars.lifedesks.org/>. Both of these websites are in serious need of updates, and we plan to completely revamp them in the next two years, with the help of volunteers. One success toward this goal was recruiting the help of former Earthwatch volunteer, Julie Elliot. Julie has fielded 5 Caterpillar and Climate Change expeditions and has continued work with our team to curate and update caterpillars.org. In addition to updates to the life history data and images newly available on the web, we published several new life history descriptions for our focal taxa, many of which are the first biological information known for particular genera. We continue to rear out new species from the project at a rapid rate and we continue to publish species descriptions for as many of these as possible. At the Arizona site, volunteers contributed to the Western North America caterpillar guide, the sequel to Dave Wagner's Eastern Caterpillars book. Finally, we were awarded a grant from the National Science Foundation (NSF) to integrate images of all our adult specimens with all other museums in North America—this effort is called "LepNet" and is summarized in Seltmann et al. (2017).



**Figure 5.** Images from Arias-Penna (2019) of two specialized parasitic wasps within the genera *Glyptapanteles* (Braconidae) reared from caterpillars collected by Earthwatch volunteers participating in the Costa Rica and Ecuador teams (A) *Glyptapanteles betogarciai* (B) *Glyptapanteles yanayacuensis*.





**Figure 6.** Sample of Tortricids collected in Ecuador for which host records were described in Brown et al. (2019). These images are adults of larvae collected and reared by Earthwatch volunteers and include: 1) *Lypothora roseochraon*, 2) *Inape* nr. *Cinnamobrunnea*, 3) *Inape* sp. 4, 4) *Paraptila* nr. *Argocosma*, 5) *Sisurcana fasciana*, 6) *Sisurcana* sp. 1, 7) *Anacrusis yanayacana* 8) *Episimus* sp.

## Project Impacts

### Increasing Scientific Knowledge

#### TOTAL CITIZEN SCIENCE RESEARCH HOURS

Eight hours per day, across 62 volunteer days, amounts to 864 hours for the 7 teams (63 volunteers). Approximately half the time was spent collecting data and the other half processing data. This is over 4,000 person-hours of volunteer time.

#### PEER-REVIEWED PUBLICATIONS

- Carolina Arias-Penna D, Whitfield JB, Janzen DH, Hallwachs W, Dyer LA, Smith MA, Hebert PD.N, Fernández-Triana JL (2019) A species-level taxonomic review and host associations of *Glyptapanteles* (Hymenoptera, Braconidae, Microgastrinae) with an emphasis on 136 new reared species from Costa Rica and Ecuador. *ZooKeys* 890: 1-685.
- Brown, J. W., Dyer, L. A., Villamarín-Cortez, S., & Salcido, D. (2019). New larval host records for Tortricidae (Lepidoptera) from an Ecuadorian Andean cloud forest.
- Dell, J., Salcido, D., Lumpkin, W., Richards, L. A., Pokswinski, S., Loudermilk, E. L., ... & Dyer, L. (2019). Interaction diversity maintains resiliency in a frequently disturbed ecosystem. *Frontiers in Ecology and Evolution*, 7, 145.
- Dell, J. E., Pokswinski, S. M., Richards, L. A., Hiers, J. K., Williams, B., O'Brien, J. J., ... & Dyer, L. A. (2019). Maximizing the monitoring of diversity for management activities: Additive partitioning of plant species diversity across a frequently burned ecosystem. *Forest ecology and management*, 432, 409–414.
- Glassmire, A. E., Philbin, C., Richards, L. A., Jeffrey, C. S., Snook, J. S., & Dyer, L. A. (2019). Proximity to canopy mediates changes in the defensive chemistry and herbivore loads of an understory tropical shrub, *Piper kelleyi*. *Ecology letters*, 22(2), 332–341.
- Loudermilk, E. L., Dyer, L., Pokswinski, S., Hudak, A. T., Hornsby, B., Richards, L., ... & O'Brien, J. J. (2019). Simulating groundcover community assembly in a frequently burned ecosystem using a simple neutral model. *BioRxiv*, 635169.
- Pardikes, N. A., Forister, M. L., & Dyer, L. A. (2019). Preference and performance of Lepidoptera varies with tree age in juniper woodlands. *Ecological entomology*, 44(1), 140–150.
- Salcido, D. M., Forister, M. L., Lopez, H. G., & Dyer, L. A. (2019). Loss of dominant caterpillar genera in a protected tropical forest. *Scientific Reports (in review)*

#### Presentations:

##### Panel Member

Win-Win Partnerships: How collaboration between citizen science and corporations leads to meaningful impacts, Citizen Science Association Conference 2019, March 16<sup>th</sup>, 2019.

##### Poster Presentation

Muchoney ND, Bowers MD, Mason PA, Carper AL, Teglas MB, Smilanich AM. June 2019. Disease dynamics of wild butterfly populations utilizing native and novel host-plant species. Poster presentation: 17th Annual Ecology and Evolution of Infectious Diseases (EEID) Meeting. Princeton, NJ.

## Outreach and Mentoring

### GRADUATE STUDENTS

Student Name	Graduate Degree	Project Title	Anticipated Year of Completion
Danielle Salcido	PhD	Global change, citizen science, and effective outreach for all ages	2021
Heather Slinn	PhD	Tritrophic interactions mediated by chemistry and fungal endophytes.	2019
Santiago Villamarin	PhD	The value of scientific collections: Examining patterns of change in diversity and structure of Lepidoptera	2022
Chanchanok Sudta	PhD	Relationship between diet breadth and distribution of Lepidoptera	2024

### COMMUNITY OUTREACH

Name of school, organization, or group	Education level	Participants local or non-local	Estimated number of participants	Details on contributions/ activities
Nevada Bugs and Butterflies	All levels	local	50	Worked with Earthwatch volunteers and uses Earthwatch data as part of general outreach.
Daugherty Summer Science Exploration	K-9	local	10	Worked with Earthwatch volunteers in the field.
UNR Museum	All levels	local	50	Earthwatch volunteers assisted with National Pollinator Week activities.
NevadaTeach	Undergraduate	local	2	Prospective high school science teachers volunteer in our lab to diversify laboratory experience and expose prospective local Washoe County teachers to UNR research.

### PARTNERSHIPS

Partner	Support Type(s) <sup>1</sup>	Years of Association (e.g., 2006–present)
Serra Bonita Reserve, Bahia, Brazil	partners in research, access to specimens, accepts voucher specimens in museum, contributes to conservation goals	2014–present
Fundo Genova, Chanchamayo, Peru	partners in research, access to specimens, contributes to conservation goals	2013–present
Organization for Tropical Studies	partners in research, access to specimens, contributes to conservation goals	1991–present
Smithsonian National Museum of Natural History (UNMSM)	partners in research, provides space and access to specimens, accepts voucher specimens in museum	2004–present
American Museum of Natural History	partners in research, provides space and access to specimens, accepts voucher specimens in museum	2004–present

Museo de Historia Natural, Lima, Peru	partners in research, provides space and access to specimens, accepts voucher specimens in museum	2012–present
Instituto Nacional de Biodiversidad–Ecuador (INABIO)	partners in research, provides space and access to specimens, accepts voucher specimens in museum	2002–present
University of Nevada Natural History Museum	partners in research, provides space and access to specimens, accepts voucher specimens in museum	2015–present
University of Brasilia	partners in research, access to specimens	2008–present
FAPESP Sao Paulo Research Foundation	provides additional funding and contributes to outreach goals	2014–present
Conselho Nacional de Desenvolvimento Científico e Tecnológico	provides additional funding and contributes to outreach and training goals (Science without Borders)	2013–present
Yanayacu Biological Station	partners in research, contributes to conservation and outreach goals	2001–present
Southern Research Station, USFS	provide funding for the Florida site, collaborate, contribute to management plans for Eglin	2012–present

<sup>1</sup>. Support type options: funding, data, logistics, permits, technical support, collaboration, academic support, cultural support, other (define)

## Conserving natural and sociocultural capital

### CONSERVATION OF ECOSYSTEMS

Habitat type	Habitat significance <sup>7</sup>	Description of contribution	Resulting effect <sup>8</sup>
Cloud forest	Extremely high levels of diversity and endemism.	Providing an economic incentive for managing lands for biodiversity by supporting the only research station in the area and providing long-term employment to local citizens.	Yanayacu Biological Station and surrounding lands are still protected from logging, grazing, and development.

<sup>7</sup>. Habitat significance options: nursery, breeding ground, feeding site, corridor, migration path, refuge, winter range, summer range, spring range, fall range or other (define)

<sup>8</sup>. Resulting effect options: extent maintained, condition achieved, restored, expanded, improved connectivity or resilience

## ECOSYSTEM SERVICES

Provisioning Services	Regulating & Support Services
<input checked="" type="checkbox"/> Fisheries (Fresh & Marine)	<input checked="" type="checkbox"/> Carbon sequestration/storage
<input type="checkbox"/> Energy (fuelwood/hydropower)	<input type="checkbox"/> Coastal protection
<input type="checkbox"/> Livestock grazing	<input type="checkbox"/> Erosion control
<input type="checkbox"/> Material extraction (e.g., resin, grass)	<input type="checkbox"/> Flood regulation/protection
<input type="checkbox"/> Timber	<input checked="" type="checkbox"/> Pest and disease control
<input type="checkbox"/> Water supply	<input type="checkbox"/> Pollination
<input type="checkbox"/> Other food (crops, wild foods, spices)	<input type="checkbox"/> Seed dispersal
<input checked="" type="checkbox"/> Preserving/maintaining Biodiversity	<input type="checkbox"/> Water purification/quality
	<input type="checkbox"/> Nutrient cycling
Cultural Services	Other Services
<input type="checkbox"/> Cultural/historical values	<input type="checkbox"/> Employment/Livelihoods
<input type="checkbox"/> Health (mental & physical)	
<input type="checkbox"/> Research & knowledge	
<input type="checkbox"/> Recreational	
<input type="checkbox"/> Spiritual/aesthetic values	
<input type="checkbox"/> Pharmaceuticals	

## DETAILS:

We continued to utilize a methodology that combined data using completely standardized methods in Costa Rica, Ecuador, Brazil, Argentina, Peru, and the United States to create plant-caterpillar-parasitoid diversity databases that can be used by land managers to search for natural enemies of agricultural pests and to examine relationships between enemy diversity and outbreak potential. Parasitoids provide an important, yet mostly unquantified ecosystem service that needs to be documented globally before it is enhanced, restored, or maintained. This is especially true for the tropics where pesticide inputs are not regulated and used in large quantities relative to temperate agricultural systems.

## IMPACTING LOCAL LIVELIHOODS

Local livelihood impact(s)	Description of contribution	Number of people impacted
Provide opportunities for work	Our projects support the employment of the kitchen, maintenance and lodging staff and local parataxonomists. Our sizable projects are critical to the overall annual income earned by these rural families. In particular our projects provide opportunities for the employment of women. At the Costa Rica site we can support a local parataxonomist.	8 (2 parataxonomists, 3 Yanayacu kitchen staff, 3 lodging staff)

## Acknowledgements

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## Literature Cited

- Carolina Arias-Penna D, Whitfield JB, Janzen DH, Hallwachs W, Dyer LA, Smith MA, Hebert PD.N, Fernández-Triana JL (2019) A species-level taxonomic review and host associations of *Glyptapanteles* (Hymenoptera, Braconidae, Microgastrinae) with an emphasis on 136 new reared species from Costa Rica and Ecuador. *ZooKeys* 890: 1–685.
- Basset, Y., Cizek, L., Cuénoud, P., Didham, R. K., Guilhaumon, F., Missa, O., ... & Tishechkin, A. K. (2012). Arthropod diversity in a tropical forest. *Science*, 338(6113), 1481–1484.
- Brown, J. W., Dyer, L. A., Villamarín-Cortez, S., & Salcido, D. (2019). New larval host records for Tortricidae (Lepidoptera) from an Ecuadorian Andean cloud forest.
- Dell, J., Salcido, D., Lumpkin, W., Richards, L. A., Pokswinski, S., Loudermilk, E. L., ... & Dyer, L. (2019). Interaction diversity maintains resiliency in a frequently disturbed ecosystem. *Frontiers in Ecology and Evolution*, 7, 145.
- Dell, J. E., Pokswinski, S. M., Richards, L. A., Hiers, J. K., Williams, B., O'Brien, J. J., ... & Dyer, L. A. (2019). Maximizing the monitoring of diversity for management activities: Additive partitioning of plant species diversity across a frequently burned ecosystem. *Forest ecology and management*, 432, 409–414.
- Dyer, L.A. and M.L. Forister. 2016. Wherefore and whither the modeler: understanding the population dynamics of monarchs will require integrative and quantitative techniques. *Annals of the Entomological Society of America* 109:172–175.
- Dyer, L.A., Richards, L.A., Short, S. A., Dodson, C.D. 2013. Effects of CO2 and temperature on tritrophic interactions. *PLOS ONE* 8(4): e62528.
- Dyer, L.A., T.J. Massad, and M.L. Forister. 2015. The question of scale in trophic ecology. Pages 288–317 in: Hanley, T. and K. La Pierre (eds.). *Trophic Ecology: Bottom-Up and Top-Down Interactions across Aquatic and Terrestrial Systems*. Cambridge University Press, Cambridge, MA.
- Forister, M. L., Novotny, V., Panorska, A. K., Bajé, L., Basset, Y., Butterill, P. T., Cizek, L., Coley, P. D., Dem, F., Diniz, I. R., Drozd, P., Fox, M., Glassmire, A., Hazen, R., Hrccek, J., Jahner, J. P., Kama, O., Kozubowski, T. J., Kursar, T. A., Lewis, O. T., Lill, J., Marquis, R. J., Miller, S. E., Morais, H. C., Murakami, M., Nickel, H., Pardikes, N., Ricklefs, R. E., Singer, M. S., Smilanich, A. M., Stireman, J. O., Villamarín-Cortez, S., Vodka, S., Volf, M., Wagner, D. L., Walla, T., Weiblen, G. D., and L. A. Dyer. 2015. Global distribution of diet breadth in insect herbivores. *Proceedings of the National Academy of Sciences* 112:442–447.

- Glassmire, A. E., Philbin, C., Richards, L. A., Jeffrey, C. S., Snook, J. S., & Dyer, L. A. (2019). Proximity to canopy mediates changes in the defensive chemistry and herbivore loads of an understory tropical shrub, *Piper kelleyi*. *Ecology letters*, 22(2), 332–341.
- Hansen, A.C., A.E. Glassmire, L.A. Dyer, and A.M. Smilanich. 2016. Cascading effects of diet induced variation in the immune response of two specialist herbivores. *Ecography*.
- Loudermilk, E. L., Dyer, L., Pokswinski, S., Hudak, A. T., Hornsby, B., Richards, L., ... & O'Brien, J. J. (2019). Simulating groundcover community assembly in a frequently burned ecosystem using a simple neutral model. *BioRxiv*, 635169.
- Pardikes, N. A., Forister, M. L., & Dyer, L. A. (2019). Preference and performance of Lepidoptera varies with tree age in juniper woodlands. *Ecological entomology*, 44(1), 140–150.
- Rahmstorf, S. and Coumou, D., 2011. Increase of extreme events in a warming world. *Proceedings of the National Academy of Sciences*, 108(44), pp.17905–17909.
- Salcido, D. M., Forister, M. L., Lopez, H. G., & Dyer, L. A. (2019). Loss of dominant caterpillar genera in a protected tropical forest. *Scientific Reports (in review)*
- Scherrer, S., C. Lepesqueur, M.C. Vieira, M. Almeida-Neto, L.A. Dyer, M.L. Forister, I. Rezende Diniz. 2016. Seasonal variation in host plant specialization by folivorous lepidopterans: contrasting patterns at the species and community levels. *Biotropica*.
- Seltmann, K.C., Cobb, N.S., Gall, L.F., Bartlett, C.R., Basham, M.A., Betancourt, I., Bills, C., Brandt, B., Brown, R.L., Bundy, C., Dyer, L.A., Pardikes, N., et al., 2017. LepNet: The Lepidoptera of North America Network. *Zootaxa* 4247:73–77.
- Stireman III, J.O., L.A. Dyer, D.H. Janzen, M.S. Singer, J.T. Lill, R.J. Marquis, R.E. Ricklefs, G.L. Gentry, W. Hallwachs, P.D. Coley, J.A. Barone, H.F. Greeney, H. Connahs, P. Barbosa, H.C. Morais, and I.R. Diniz. 2005. Climatic unpredictability and caterpillar parasitism: implications of global warming. *Proceedings of the National Academy of Sciences* 102:17384-17387.