



Perspective

Perspective: Where might be many tropical insects?

Daniel H. Janzen*, Winnie Hallwachs

Department of Biology, University of Pennsylvania, Philadelphia 19104, United States of America



A B S T R A C T

I have been watching the gradual and very visible decline of Mexican and Central American insect density and species richness since 1953 and Winnie since 1978. The loss is very real for essentially all higher taxa, and the reasons are very evident: intense forest and agricultural simplification of very large areas, massive use of pesticides, habitat fragmentation, and at least since the 1980's, ever-increasing climate change in temperature, rainfall, and synchronization of seasonal cues. There is no ecological concept suggesting that this biodiversity and habitat impoverishment is restricted to this portion of the Neotropics, and our 50 years of occasional visits to other parts of the tropics suggest the same. We are losing most of the insect community that is still in the cloud forests due to the drying of the tops of tropical mountains, just as we are losing the huge expanses of insect communities that once occupied the fertile soils, weather, and water of the lowland tropics. Today we have unimaginable access to the world's biodiversity through the internet, roads, dwellings, education, bioliterate societies, DNA barcoding, genome sequencing, and human curiosity. The wild world gains from our understanding that it needs large and diverse terrain, relief from hunting trees and animals, site-specific restoration, profit-sharing with its societies, and tolerance of humans and our extended genomes. But if our terrestrial world remains constructed through constant war with the arthropod world, along with the plants, fungi and nematodes, human society will lose very big time. The house is burning. We do not need a thermometer. We need a fire hose.

In this decade, some of our extra-tropical entomological colleagues have published very real observations that insects are declining in abundance (Stireman et al., 2005; Conrad et al., 2006; Dirzo et al., 2014; Fox et al., 2014; Vogel, 2017; Wagner, 2018, 2019; Hallmann et al., 2017; Leather, 2018; Lister and Garcia, 2018; Wilson et al., 2018; Sanchez-Bayo and Wyckhuys, 2019). We have been telling the same to largely tropical ecology classes in the University of Pennsylvania for at least three decades if not longer. Our observations are based on informal comparison of today with my 1950's youth in Minnesota and Mexico, and with an entomological and conservation research career in Costa Rica since 1963, and Winnie the same since 1978. David Wagner, an entomologist from the University of Connecticut, has asked “what do we think of this decline?” from our vantage in Costa Rica (living for decades in the middle of a once-seething insect community). We offer just a few thoughts, since we have neither the data nor the biopolitical free energy to enter into the detail that belongs with a standard scientific review or documentation.

“Sometimes you're the windshield. Sometimes you're the bug.”
(Mark Knopfler, Dire Straits 1991)

That poetry made as much sense to Mark Knopfler growing up in UK, as to me growing up in Minnesota in the 1940's-1950's. And it made even more sense to me driving through Mexico for eight months (1953–1955) collecting and seeing very abundant insects of thousands of functional kinds and species, not only from windshields, car radiators

and roadsides, but at the lights of every Pemex gas station on the edge of town, every restaurant with a face towards the non-urban, every light where it could be seen by the wild world. And when I arrived in Costa Rica in 1963, despite its four centuries of European assault, I met the same. Half the country was old-growth forest and old secondary succession right up to the edges of the beginning modern urbanization. Well more than half of that standing timber was in rainforest, owing to 400 years of agrocolonization of the seasonally comfortable Pacific dry forested side of Costa Rica. Today, only about 25% of Costa Rica is wild forest with any hope of permanence, and only that if it can make itself welcome to its society. Yes, the huge areas of abandoned pastures and fields are now filling with young woody succession (“forest” in informals), but it is grossly impoverished in its biodiversity, and the moment there are profitable crops to be grown again on those lands, they will be. The heavily deforested mid-elevation mountain slopes, slathered with one of the world's most widely used drug crops, will neither be allowed to return to the wild, nor will the forests and their occupants any more have their original climate.

Today, forget about insects in that gas station illuminated world. On 3 January this year, I reflected on insects at gas station lights to a 64-year-old gas station attendant on the edge of Liberia, just to the south of Area de Conservacion Guanacaste (ACG) in northwestern Costa Rica (www.acguanacaste.ac.cr), where we are writing this. No longer being required to clean bugs off windshields when largely there are none there, he launched into a description of what “used to be” at the Liberia

* Corresponding author.

E-mail addresses: djanzen@sas.upenn.edu (D.H. Janzen), whallwac@sas.upenn.edu (W. Hallwachs).

gas station lights when he was a teen-age attendant – Tettigoniidae, Chironomidae, Ceratopogonidae, Ephemeroptera, Trichoptera, Sphingidae, Saturniidae, Crambidae, Scarabaeidae, Cerambycidae, Vespidae, Meloidae, Passalidae, Erebidae, Noctuidae, Geometridae, Gryllidae, and microlepidoptera (my identifications from his descriptions). In the mornings this was a small feast for the foraging female great-tailed grackles (*Quiscalus mexicanus*) that also enjoyed the mornings collecting big moths and beetles from the car radiators parked in front of the restaurant across the street. No more. There are lots of grackles, but they no longer bother to search the fronts of cars parked in the supermarket nor visit the gas station for the night's moths, beetles or katydids, be it rainy season or dry season. And dramatically gone are the big insects that capture the curiosity of tourists, residents, and students.

I have now spent 60 years, and Winnie 40, watching tropical insect communities and published more than 500 papers about them and their interactions in Malaysia, Australia, Africa, South America, Central America, North America, and UK (we are ecologists, and for us, taxonomy is a tool, not our guild). My most detailed understandings were those of a child and teenager in the intersections of the growing Minneapolis urban and its agroscape, and the ever-shrinking remnants of the wild – hunting, trapping for meat and fur, fishing, and attempting to catch “all” the species of butterflies of that extra-tropical world. Holland's moth and butterfly books were my bibles. The drawers of pinned beetles with their labels in the Smithsonian Institution were my technical guides. Then I discovered tropical butterflies in 9th grade in the Minneapolis Public Library Natural History Museum. In 1953–1954 occurred my family's expeditions to Mexico to “collect” butterflies. I spent the summer of 1955 as a proto-hippie living in the back rooms of the all-night Pemex gas stations so I could collect the hundreds of large insects attracted to them at night.

Today's Mexico no longer has them at those lights. While it is tempting to fully blame agriculturalization, it needs to be remembered that the tropical lowland Mexico that I met in the 1950–1960's had been under intense agriculturalization for centuries before Europeans arrived. Both agricultural industrialization (where I did my dissertation research in Veracruz is today thousands of km² of sugar cane) and pesticides have taken their heavy toll, but it would be dumbfounding to find that climate change is not hitting those Mexican ecosystems just as hard as it is hitting its Costa Rican analogues.

I arrived in Costa Rica in 1963 to be part of Jay Savage's tropical biology course taught by the incipient Organization for Tropical Studies (<https://tropicalstudies.org>). I met a small tropical country the size of West Virginia that was half covered with old-growth forest and literally crawling, walking, flying away with unbelievable numbers of species and individual insects. I recognized it, from its species composition, as a robust reflection of what once covered the lowlands of Veracruz, Mexico before it became indigenous + European agroscape (though already damaged by centuries of agroscape fragmentation and pesticides). That is where I spent 1962–64 peering intently at *Pseudomyrmex* ants and their *Acacia* (now *Vachellia*) treelets, and all that swirled around them, as my dissertation research at UC Berkeley (Janzen, 1966), while also collecting for the California Insect Survey. CIS efforts in Mexico are now largely extinct for reasons of both tropical biopolitics and the obvious insect declines in Mexico.

The 1963 Costa Rica I met still had the entomological face described in its 1800's literature by European visitors, a face generally findable with a 30-min bus ride from old urban San Jose. I stayed, while also sampling the rest of the world's tropics for two decades. Winnie arrived in 1978. As we waited for food in Costa Rican roadside restaurants, we studied the ceilings, floors, and bathrooms to collect the moths and beetles that had arrived the night before. Those exact same restaurants, still standing, and many others like them, are today as clean of nocturnal insects as are the Costa Rican hospital rooms where I now took my broken arm.

The initial cause of the decline was and is obvious – conversion of a

400-year-old intense checkerboard of forest, brushy extensive pastures, low-income cultivation, logging and hunting, to today's highly polished “industrial” agroscape, tree plantations, and pastures, rich in monocultures and pesticides. By about 1990, Costa Rica was 49% cattle pasture (I constructed the map for Costa Rica's Ministry of Agriculture and Ranching, MAG) and the remaining original forest was melting like a snowdrift in March in Minnesota - logged for charcoal, for timber, and to just plain get rid of it to make room for the cattle, horse, and crop extensions of the human genome (Janzen, 1973c, 1988a; Janzen and Hallwachs, 1994). But climate change was already warming/drying ACG cloud forests on the volcanos from their 1985 cold wet soupy facies and rushing water output, but we were too busy purchasing and seeking funding for ACG rain forest as a moist lifeboat for the denizens of the heating/drying dry forest, to have had the luxury to be studying minutely the consequential conservation and population dynamics and details (Janzen, 2000, <http://janzen.sas.upenn.edu/saveit.html>).

In the early rainy season (June) 1978, I slipped in an ACG ravine and broke three ribs, after 15 years of intense examination of whole Costa Rican insect communities (and comparing them with other parts of the tropical world) with sweep nets, malaise traps, yellow-pan traps, and light traps, while doing very detailed studies of seed predator insects and rodents (e.g., Janzen, 1973a, 1973b, 1975). I walked/crawled myself 3 km back to a shack in the then Parque Nacional Santa Rosa (today Sector Santa Rosa of ACG), where I and Winnie are squatters today. I strapped myself into a rocking chair at the front door and waited a month (frontier medicine). Each night the park generator was on for 2 h, so I got 2 h of a 25-watt bulb over the front door. Each night the wall was plastered with moths and beetles and insect riff-raff, the open room behind me an insect zoo in the morning. During the 1980's we set up a large tent in the living room to be able to work at night among the hoards of beetles and moths. And then by the early 1990's the need faded away, despite that we were in the center of 1200 km² of tropical dry forest, cloud forest and rain forest busily restoring itself (Janzen, 1988b). Now, 39 years later, deep inside the same forest and same house, and with much brighter lights all night, we have never seen this spectacle again.

Beginning about 1580, this crumbly ex-agroscape has been carved out of dry forest with its six-month rainy season (Janzen and Hallwachs, 2016a). Santa Rosa's dry forest and the rest of ACG (all three ecosystems) have lived through 400+ years of European farming, logging, burning, ranching, hunting, and surface water manipulation. However, since the 1970–80s, we have felt and seen the decline and vaporization of many of the species of rain forest insects (and lizards, frogs, birds, and trees) that in 1980 still occupied the small patches of old growth dry forest, and the more extensive 100-year-old secondary dry forest. As these patches in ACG dried through the increased heating and seasonal asynchronies, they gave us our first glimpses of climate change in the 1980's, along with watching the cloud forest clouds retreat up the sides of the volcanos.

When I could walk again freely in 1978, it occurred to me that there must have been a caterpillar behind each of those moths arriving at the light bulb for 2 h. I walked into the forest to see. I was dumbfounded to meet a 150-species dry forest tree canopy that looked like a hurricane had ripped off easily half the annual leaf crop, from both evergreen and deciduous species. It was due to voracious herbivory by gazillions of caterpillars. The ground was a sheet of caterpillar turds. That scene, familiar to me since my introduction to tropical lowland Mexico in 1953, instantly seduced me away from seed-predator beetles (Janzen, 1980) and onto leaf-parasite-caterpillars (Janzen and Hallwachs, 2016b). This is now the ACG on-going caterpillar inventory of them and their food species, and their parasitoids. It is carried out by ~20–28 full-time parataxonomists spread over ACG's 1200 km² of dry forest, rain forest, and cloud forest from the Pacific coast to the Caribbean lowlands (Janzen and Hallwachs, 2011, 2016b). 750,000 wild-caught and (attempted) reared caterpillars later, drawn from a Lepidoptera fauna of at least 15,000 species, tell us that I would never have given a

second thought to caterpillars had I not broken those ribs in ACG after about 1990. In no year since the early 1990's have caterpillars ever been sufficiently abundant to attract the attention of someone intent on an ivory tower study of all species of foods eaten by each species of these plant parasites. That reduction means severely reduced food for practically every kind of predator that eats caterpillars, pupae and adults, from scorpions to armadillos, from minute parasitoid wasps to tarantulas, from 100's of bird species to *Liomys*-eating spotted cats and snakes (http://janzen.sas.upenn.edu/TSHP/English/Heteromyidae/Liomys_salvini_Home_Page/English_Text/Liomys_salvini_Eng.html).

1. Causes of decline

In contrast to some recently published extra-tropical studies, we do not have detailed numbers on the rates of decline of ACG insects since we first explicitly noticed climate change in the early 1980's, or since I started interacting with tropical insects in 1953. First, when a house is burning down, I need the fire department to keep it from spreading, not a thermometer to measure the obvious heat and flames. Second, the caterpillar inventory was designed and conducted to know who eats what, when, and where, rather than how many individuals of a species are doing what. Third, it has been evident, since the ACG forests began drying and changing in about 1985, that there was nothing that we or ACG could do to halt, deflect, and avoid the global impacts of climate change on centuries of agriculturization, fragmentation, and insularization of Costa Rican forests, and the tropics as a whole. All we could do is frantically increase ACG's size and ecosystem diversity, and work towards the acceptance of this very large lump of landscape by Costa Rican society. This is society-based amelioration and mitigation. And we also hope that some other tropical countries will use the example. This is now beginning to happen (Pringle, 2017).

Equally, the increased heating and drying of all ACG forests from climate change shows its signals as many single events, rather than one huge red light. Measuring and reporting each of the changes likely caused or exacerbated by ACG climate changes had, and would have, no impact on the world as a whole. Our strategy was to focus on amelioration and mitigation for ACG itself as a very large and very species-rich biophysically diverse unit, as part of the practical rescue of a neotropical dry forest ecosystem (Janzen, 1988b) and long-term survival through integration with its society (Janzen, 1999, 2000; Janzen and Hallwachs, 1994, 2016a, 2016b). This meant integrating it with its owner societies as an acceptable producer of goods and services. Would ranting globally about the conspicuous declines of insects, changes in weather/climate, shifts in plant communities, have done any "good"? No. The forces that create the agriculturization and insularization of ACG as a whole, and then layer climate change on that, receive no perceived fitness gain at that moment by acting on social alarm calls from a "small" tropical "national park," and would not respond or change. All three problems need to be left to others focused at a global scale, and in the last decades are driven by economic and political forces that do not currently value the survival of 1,000,000 species of tropical eukaryotes in tiny Costa Rica.

Our focus in this Perspective is on insect decline in the Costa Rican tropics, and it is best to highlight a few concrete examples among many over the years. However, any "decline" (or increase) is clearly the product of multiple interwoven processes. Dissecting them in an attempt to find THE single cause, a behavior so beloved by humans and especially scientists, helps to grasp the ecology of the situation for any particular person, place or species, but at best leads to very local ameliorations or mitigations (sometimes possible). Our experience is that it does not lead to big-picture, global cessations of impacts. We can say overall that multiple factors – the grand scale removal of old-growth and old secondary forests (the refuges and sources of potential recolonization), the modern widespread use of pesticides and herbicides, the land use changes and impacts on weedy patches, and the climate changes – all contribute. But one cause followed by one solution

emphatically does not fit all situations, in terms of area and time-series protocols for wildland survival and acceptance by its owner society.

It is reasonable to ask "What actually happens to the enormously species-rich array of insects presently occupying a tropical ecosystem when there is a major shift, gradual or abrupt, in the climate or other assaults such as fragmentation, insularization or a veritable snow storm of pesticides?" The simple reply is that some species disappear from that ecosystem and place, some go extinct, some become more abundant (we think of the many liters of *Phyllophaga* beetles (Scarabaeidae) now arriving at an ACG dry forest light trap with the first rains), some become rare but are still present, some move to another ecosystem or simply persist there with a narrower ecological distribution than before, some are quickly selected to adjust to their new partners or weather (just as insect populations also quickly develop resistance to massive assaults from pesticides), some invade "new" ecosystems (Hingston et al., 2002), and indeed, there are just about all possible other imaginable outcomes. In short, when the cloud forest is burned off the top of ACG (and other) tropical mountain tops by the rising heat and dryness of climate change, some species will disappear from there but "persist" on other mountain tops, some will persist at other densities and relationships, some will evolve compatibility with the new site traits, and some will go extinct as a population and/or species. What proportion of species will experience any given fate is quite unknown at this stage of biological illiteracy.

The algebra of many multiple-multiple-to-one interactions in the specific ACG tropics are multifactorial and require dedicated study to even begin to puzzle out. We list here a few, which could be multiplied by hundreds of thousands, given ACG's currently estimated 750,000 species of eukaryotes.

1.1. Changes in heat duration and synchrony

When I arrived in Costa Rica in 1963, the Liberia weather station, a 45-min drive southeast of ACG and originally part of the same ACG dry forest ecosystem, registered about four months a year of days with greater than about 32 °C (90° F) temperatures (NYT, 2018). That was essentially the core of the five-month-long dry season from late-December to mid-May. Today, the same temperatures are recorded 6.5 months of the year – effectively making the dry season 2.5 months longer (thank you, climate change). And in the ACG cloud forest and rain forest, what used to be a brief "drier season" is now being displayed as 1–3 months of a conspicuous dry season, with crunchy leaf litter under foot and dried out ravines. It is very biologically disruptive to add those extra days to the weather cycle and sprinkle some of them among the "rainy season" months throughout ACG ecosystems. This change wreaks havoc with the many thousands of species that cue (or otherwise depend) on the almost exact timing and amounts of both wet (cool) and dry (hot) days during the year to construct the pre-climate change arrays and abundances (Sheldon et al., 2018). These cues initiate and end multiple different stages in their lives. For example, during the 1980–1990s, in mid-May, in the first week of the rainy season, hundreds of the resident univoltine non-migratory moth *Manduca dilucida* (Sphingidae) appeared at Santa Rosa light traps. They were newly eclosed from their 11-month old underground pupae. Then in the mid-1990's some adults started appearing at lights in September, in the middle of the rainy season, cued by the abrupt temperature decline when the elongating hot, short dry season (veranillo) of August gave way to the cool September resumption of the rainy season. Today, one is lucky to find a half dozen adults at lights at either time of year. Their Bignonaceae food plants are still common, but the caterpillars have become rare, and their host-specific tachinid fly and ichneumonid wasp parasitoids along with them. We are certain that the two common species of ACG dry forest *Trogon*, birds that are specialists at raising their nestlings on whole sphingid larvae, have very much noticed the sphingid caterpillar declines in the last half of May and first half of June. The many species of flowers that provide food for adult

Sphingidae are still somewhat present, but unpredictably erratic in amounts and timing, and sphingid visitors to these flowers have declined drastically as well as have their captures in light traps.

1.2. Synchrony of the beginning and end of the rainy season

In the 1960–1980's, I could win a case of beer betting that the first Santa Rosa rains of the long rainy season would fall on 15 May. Today, the rains can begin anywhere between late April and late May (and are often followed by 1–3 weeks more of dry season weather and drought-stressed leaves, lethal for first instar caterpillars). The result is that we no longer see the highly synchronized emergence of so many flashing Lampyridae as to make the forest visible in deepest night. The bud-breaking of *Randia aculeata* and *R. monantha* (Rubiaceae) were perfectly timed for the ovipositing *Aellopos titan* (Sphingidae), annually returning from their dry season refuge in the wetter cloud and rain forests to the east. The *Randia* now flush their new leaves erratically and asynchronously, and also scattered across the rainy season calendar. The days of masses of *Randia*-defoliating *A. titan* caterpillars are gone, and their once-common Ichneumonidae, Eulophidae and Tachinidae parasitoids with them. The same applies to the various species of much smaller *Eulepidotis* (Erebidae) caterpillars and the new leaves they eat, each on their own species of tree. We must emphasize that these species are not necessarily extinct in Costa Rica or even ACG, but certainly have modified distributions and abundances where they still persist; these distributions are already as fragmented as can be any ecosystem by 400 years of logging and agriculture, leaving invisible insect islands that are highly sensitive to the impact of insularization exacerbated by climate change.

Some of the caterpillars' hosts seem to be cued to the calendar (daylength?), some to the new rains, some to the abrupt decline of temperature with the new rains, some to the wind, and some to nothing that is outstanding to us. But what is noticeable is the lack of synchrony now. Imagine attempting to run a machine with tens of thousands of moving parts, each one adjusted by both its traits and its interactants to perform its particular action at a particular speed at a particular point in a time series, for an “expected” output. And then you drop in a quart of oil, a pound of sugar, and three tablespoons of salt – haphazardly sprinkled. The output changes to some degree. That is what we are seeing with climate change added on top of the centuries of agriculturalization followed by industrial agrosapes. Some parts survive, some jam, some corrode, some burn out, some move, and some spin aimlessly until worn to nothing. And then we add the living dead (Janzen, 2013) – the adults or stunted/starved juveniles or dormant seeds that can survive, each species a different number of hours, days or decades before dying. Humans only superficially and incompetently notice the few species that *they* happen to care about. A mine canary may drop dead rather suddenly, but a tropical forest made up of hundreds of thousands of interacting species dies a slow and very variable death of a million cuts, repairs, shifts, stitches, and bruises. But the ecosystem that was before, does die. The clean windshields, the gas station lights with no moths, the foliage with no bites and nibbles, the forest with no biting and stinging insects, the mountain passes (Sheldon et al., 2018) with empty light traps, the declining insectivorous birds, bats, lizards, and the things that eat them, all say the same thing. And it is repeated loud and clear by the ants now common in the ACG upper-elevation cloud forest dry litter, where once shimmered billions of isopods over perpetually wet and cool litter with essentially no ants in this perpetual terrestrial wet refrigerator; today, there are *Eciton burchelli* army ant swarms on the dry litter for ecotourists to enjoy in what is for the tourists is wonderful weather. A US visitor declared, looking in the late 1990's at the fallen branchlets festooned with epiphytic orchid plants in the cloud forest litter, “you have millions of dollars sitting in your litter”; those days of high orchid litter fall are long gone and the cloud forest canopies that once gardened them drying everywhere (Beaumont, 2018).

1.3. Caterpillar harvest by parataxonomists

A time-honored method to search for caterpillars in all the ACG different forest types was visual inspection of leaves for consumer damage. This methodology, undoubtedly used for millions of years by many vertebrates, and at times, parasitoids, was highly productive when caterpillars were abundant in the 1960–1980s. Today's stroll through ACG rain forest, dry forest and cloud forest is like walking through a well-fumigated forest between cotton or rice fields, or a botanical garden/greenhouse. Gone are the spiderwebs that decades back entangled those leaves. Gone is the nighttime sparkle in the leaves reflected from thousands of lycosid spider eyes. Yes, there is leaf damage, yes there are caterpillars, yes there are spiders. And, yes, there is now and then an insect sitting on the foliage. But from about 1992 to 2014, 10–30 professionally searching parataxonomists (who also reared and processed the caterpillars, Janzen and Hallwachs, 2011, 2016b) found ~1500 to ~2000 caterpillars/year/person, whereas from 2014 to 2018 it is 800–1100 per year and in 2019 still declining. And they are professional caterpillar hunters for whom the scarcer the prey, the harder they search, night and day. 2015 was also the severe El Niño drought year, and to date there is no sign of insect recovery to pre-2015 levels. In the early years, rearing levels were set when the number of wild-caught caterpillars being reared approached saturation of the rearing barns. Today, the declining numbers of caterpillars being reared are set by the simple absence of caterpillars. And all of this is occurring in a landscape progressively agriculturalized until reversed through massive forest restoration that started in 1971 and became intensive in 1985. In other words, today's ACG insect and other declines are occurring in a restoring world with no pesticides, no agricultural monocultures, and fully free forest restoration processes in motion over 120,000 ha from 0 to 1500 m elevation and three major ecosystems. The direct impact of agriculturalization was before the start of ACG conservation in 1971. Now we are dealing with climate change and ACG large scale insularization impacting the restoration process.

During 1989, 1990, and 1992, six-month parataxonomist courses were taught throughout ACG. It was highly profitable in species and specimens to turn 10–15 apprentice rural parataxonomists loose in a forest for a few hours of general collecting from foliage and tree trunks. In both dry seasons and rainy seasons, they returned with so many specimens of thousands of species as to be occupied for 1–2 days just processing their collections. Today this kind of general collecting would be a major waste of time, because so few insects would be found. Today the focus would be instead on various mass trapping methods (light traps, litter sorting, sweep samples, Malaise traps, yellow pan traps) to generate enough specimens of enough variety to keep the entomology portion of a parataxonomist course occupied full time.

1.4. Seasonal migrations

Six months of the year during the 1960–1990's, we have lived our lives in an open house in ACG dry forest, with many excursions into the adjacent and contiguous cloud forest and rain forest, as well as the 7–365 searching by the parataxonomists in all three ecosystems. In those decades, we were often witness, in August and at the end of the rainy season in December–January, to millions of dragonflies (Odonata, Anisoptera), migrating from the dry forest to the rain forest uplands to the east. On 30 December 2018 a mere wisp of a few thousand passed overhead in the mountain pass from the Pacific drying forest to the wetter Caribbean rain forest. In May–June 2018, did not enough returnees arrive from the formerly rain-forested Caribbean lowlands? Did the returning predaceous adults not find enough of their tiny insect meals? Did the dry forest seasonal pools not have enough insect prey for the naiads to reach adulthood? There is no way to know but the decline in adults is obvious, and any and all causes may be operating.

The once-annoyingly-common *Polistes instabilis* wasps, professional dry forest caterpillar predators in the rainy season, nest in waist-high

tangles of secondary vegetation and aggressively announce themselves by attacking people. At the end of the rainy season, presumably due to the normal seasonal decline in prey caterpillars, they migrate up to ACG cloud forest heights (1000–1500 m) to aggregate and become dormant, with many liters of females in hollow trees and human outbuildings. That was the phenomenon in the late 1980's when discovered (Hunt et al., 1999). Today, with luck, a half a liter of them might be encountered huddled under the roof of an old building, with most such sites empty. Their conspicuous decline in the formerly refrigerated cloud forest is mirrored by the conspicuous near absence of rainy season nests in the lowlands below the volcanoes.

Is it that the conspicuous gradual rise of warmer air up the volcanoes with climate change has rendered their dormancy less physiologically favorable (i.e., like extra-tropical dormant animals burning out their reserves during a warm winter)? Is it that the conspicuous decline in caterpillars has made their lowland nesting less productive, leading to fewer elevational migrants? Is it that lowered survivorship in the clouds leads to fewer lowland nests, which in turn leads to fewer arrivals to the clouds? Is it that as the cloud forest rises it shrinks in area occupying the conical form of a mountain, so that the wasps have fewer choices of prime dormancy sites? Is it that the *Eciton* army ants, now foraging 500 m higher than in the *Eciton*-free 1980's, are now killing too many of them in their dormant state? Is it that when the wasps leave their hibernacula to fly aimlessly on a hot day, they burn up so much energy that they starve by the end of the dry season?

Whatever, the cause, the decline is real and its basic form applies to tens of thousands of species that seasonally move between different ACG habitats in which they pass different stages of their lives (Janzen, 1987). In the 1960–1990's, the cool and shady understory of old growth forest and moist creek beds/rivers were a seething with non-reproducing dry forest insects refuging through the dry season, while the adjacent open pastures, fields and highly deciduous secondary forest were nearly an insect desert; when the rains hit, the situation was reversed, with insulated habitats quickly becoming hyper-rich in reproducing populations and the primary forest understory appearing to have been fumigated (Janzen, 1973a, 1973b, 1983). Today, this dynamic is almost invisible, whether measured by eye, Malaise trap, sweep net, or light trap. There are not enough insects to be able to record it with a single malaise trap or by eye. Today, a one-km walk of the same dry forest dry creek bed in the dry season is likely to encounter just a single *Urbanus* butterfly, presumably in sexual diapause (its caterpillars eat rainy season fabaceous herbs), sheltering in the shade of the bank overhang, whereas in the 1980–2000's there would be an *Urbanus* adult every few meters.

1.5. Malaise trap records

From 1988 to 1990 we ran multiple ACG Malaise traps in dry forest old growth and secondary forest, cloud forest, and rain forest to assist the beginning effort by Ian Gauld, RIP (Hanson et al., 2009) to understand the ACG parasitic wasp fauna through traditional trapping and morphological methods. In parallel we were rearing parasitoid wasps from caterpillars in the same forest. We now know that those traps caught only 5–10% of the species present, and worse, their morphological species descriptions exposed only a fraction of their species richness (Janzen et al., 2009, Janzen and Hallwachs, 2016b and papers in prep). But of direct relevance to these comments, those 300 ml alcohol bottles collected weekly from the Malaise traps were half full of Diptera, Hemiptera, micromoths, Orthoptera and Coleoptera, all of which we discarded to get at the masses of Hymenoptera in the bottom. With today's Malaise trapping in the same dry forest with the same Townes-type Malaise traps, the annual yield from one trap during 2012–2013 was just 5666 species of insects (all Orders) among the 95% of 63,514 specimens that were successfully DNA barcoded by the Centre for Biodiversity Genomics (<http://ibol.org/site/>). The average of ~1200 specimens/week/trap was so low that we were budget-wise able to

DNA barcode everything. The same result was obtained with seven other Malaise traps during 2013–2014 in nearby forest.

2. The future of biomonitoring the Costa Rican insect community

Today, ACG and all of Costa Rica are embarking on a massive nation-wide program of Malaise trapping, along with all other methods – termed BioAlfa, derived from “BioAlfabetizado” (biologically literate or bioliterate) – to comprehensively document the current multicellular biodiversity of Costa Rica. BioAlfa will set a contemporary baseline against which multiple years of future biomonitoring and census of both species and individuals will be compared at national and local levels. At present, for the insect subproject, there are five continuous trap-years (2013–2018) from nine Malaise traps, weekly collected and frozen, waiting for adequate funding for their analysis and discrimination through DNA barcoding. However, like the biodiversity crisis overall, hand-wringing seems to be the only operational international response.

We could continue mushily describing case by case in detail for days of reading and writing. We feel our time is best spent on actions of amelioration and mitigation rather than the ceaseless and immense task of describing and documenting each species of all of what we see all around us. DNA barcoding, databases and aggregating analyses (Janzen et al., 2009; Janzen and Hallwachs, 2011) will offer a more wholistic view, supplemented by case-by-case studies that fit particular agendas, especially to integrate the information into Costa Rican society itself. Again, the house is on fire and we need the fire department more than a thermometer.

We do not see groups of insects that are immune to the general reduction of ACG insect numbers and species richness among which we live. And the destruction of ecological networks through both direct impact and decline in numbers (Janzen, 1974) is even harder to see when the participants are tiny animals. We caution that while reduction of insect individuals (biomass if you will) is quite evident in the past 10–20 years, the reduction of species richness is also real. There is an inseparable tangle of local to general extinction/migration/evolution that can be variously coupled with a decline or dip in population numbers so severe that our crude census methods do not encounter individuals. A species of insect may persist at densities excruciatingly low from our census standpoint, yet they are detectable to each other by mating pheromones. Numerous times we have seen this among the many thousands of species of ACG insects that we have studied for decades. The only way that I was able to confirm the presence of a large well-known saturniid moth, *Rothschildia lebeau*, in the rainforests of Corcovado National Park (CNP) in southwestern Costa Rica, a place where it was firmly believed to not occur, was to airmail a virgin female from ACG to CNP and put her out as bait. The question was resolved by 9 pm.

Can the beginning of the obvious decline in insects overall in ACG be pinned to specific years? No. Different species and groups of species have become “scarce” gradually and erratically since we started paying attention more closely in the 1980's. It is only after years that one gradually comes to realize that “wow, I have not seen one of those in years or decades.” This is usually prompted by encountering a single individual of what was once a common species. And any index of presence/absence of a species is confounded yet more by the normal population behavior of fluctuating abundance, from being extraordinarily abundant for 1–2 years to just ordinarily low-density present for many years to decades. While that is the “normal” population behavior throughout ACG ecosystems, it is the year of extraordinary abundance that catches the notice and research of the visiting biologist. The year of abundance is viewed by biologists as a whole as “normal,” and the low-density years viewed as catastrophic. What we are now seeing is that the low-density years are VERY low, so low that a given species is viewed as locally or even regionally extinct by those who care. Living dead (Janzen, 2013) species may well be actually extinct as

a viable population, and often is locally, but tropical field science is not incentivated to ask that question.

It is tempting to want to know if the declines are accelerating. That is a level of detail/analysis not possible to tease out when we have only our general observation of the decline overall. Equally complicating is that when normal densities for normal species are already low, a changing rate of decline among them becomes yet more inconspicuous. And the worst weather events – the extreme heat and drought of the 2015 El Niño, and the three-day intense rain of near-hurricane Nate in 2017, which were tree- and branch-killing, forest-altering events, are very recent. During the 2015 drought, the always-present insect-eating warbler *Basileuterus rufifrons*, was driven to desperation, hawking at *Trigona* nests, and was then locally absent until this year. An entire year's young of the heavily insect-dependent white-faced monkeys died in 2015 (Monica Myers, pers. comm.).

3. What to do about it?

What might be done about all of this? Conserve and restore very large and habitat-diverse and ecosystem-diverse wild areas; at least give the beasts the chance to search out more habitable habitats and ecosystems, when they will or can. Strongly protect old-growth forests and those that are becoming so. They slow climate change impacts and hold a wide genomic range for the possible survivors. Establish baselines against which to measure future changes, their sites and their biological traits, and continue the monitoring for decades. Facilitate the emergence of bioliterate tropical societies that will favor individual actions, actions for which wild biodiversity survival raises the cultural and genomic fitness of tropical individuals and institutions. ACG has been trying this for 38 years. It is a rough road but it does function (<http://www.acguanacaste.ac.cr>; <http://www.gdfcf.org>) (Pringle, 2017; Janzen, 2000). It has been rife with surprises and discovery.

While we have been watching neotropical insects since 1953 (Dan) and 1978 (Winnie), since 1985 we have been deeply embedded in the dance of amelioration and mitigation. This was initially through ecological restoration and expansion beginning in 1985 (Janzen and Hallwachs, 1994; Janzen, 2000) to reverse the conspicuous trashing of ACG wild biodiversity by European culture and agriculturization since about 1580; restoration has continued through today for all ACG ecosystems. Second, as climate change (warming and drying of all ACG ecosystems) became evident by the mid-1980's, the climate change layer of concern emerged. Third, as the northwestern Costa Rican frontier has tightened down socioeconomically, the local, regional, and national communities in which ACG is embedded have become the challenge to biodiversity survival and restoration. Pragmatically, this has meant that the solution to tropical insect declines is to focus on conserving a few very large topographically diverse ecosystems, documenting what truly is in them as a base line and starting point for conservation through biodevelopment and integration with their neighbors near and far, rather than through police protection. Simultaneously, there has to be facilitation of the emergence of a bioliterate society, local to national to international, that accepts the existence of large conserved wildlands as part of the socioeconomic fabric of human society, through its own bioliteracy, rather than forced on it by decrees, guns, and gold badges.

To us as card-carrying entomologists, and as biopolitical meddlers with technical backgrounds, “what to do about it” has meant serious deviations from what we enjoy doing as field scientists. It is not enjoyable to attempt to fund-raise to purchase, for the conservation crop, large expanses of tropical biodiversity-rich terrain. It has meant intense deviations to engage in local to international biopolitics to encourage social governance and commercial systems that facilitate the presence and survival of a few large conserved areas per country or in amalgamations of countries. It is not wise to put all the conservation eggs in the baskets of the few conservation-friendly tropical countries, but human societies dictate that as one strategy. And it means applying our

nitty-gritty knowledge of insects and all the other biodiversity stuff to baseline monitoring and trying to understand what actually is going on with the millions of ACG and Costa Rican species – who they are, where they are, what are they doing, how to find or census them, and put all of that into the public domain through the internet. The mission throughout has to be to awaken the public to this ultradiverse and only superficially explored tangle of tropical ecosystems, their macrobiomes, and their microbiomes.

The world of insects is being strongly impacted by climate change and human shuffling of biodiversity's nests and factories, be they doing it with concrete, AI, or agriculture's biodiverse extensions of our genome. Give the bugs at least the terrain and space needed to reorganize, evolve, restore, and become what they may with what we allow them, and they can buy, plunder, or kidnap from us. There will be and are many new normals, new set points. The goal posts wander and retreat from our playing fields; today we hate them, tomorrow we love them. If we watch the melee forming, coevolve with it as best we can, a multitude of win-win-win actions will emerge, even though there will also be a plethora of lose-lose and win-lose events among them. We will lose much of the insect community that today is still in the cloud forests being burned off the tops of tropical mountains, just as we lose the deep valley ecosystems drowned out by the hydroelectric impoundments or plowed under by industrial farming. We have long ago already lost huge expanses of the insect communities that once occupied the fertile soils, weather, and water of the lowland tropics. Today we do gain unimaginable access to the world's biodiversity through the internet, roads, dwellings, education, bioliterate societies, DNA barcoding, genome sequencing, and human curiosity. Somewhat equally the wild world will gain from our understanding that it needs large terrain, relief from hunting of trees and animals, site-specific conservation/restoration, profit-sharing with its societies, and tolerance of humans and their extended genomes. If our terrestrial world remains one that is constructed through constant war with the arthropod world, along with the plants, fungi and nematodes, together being 95%+ of the species of Eukaryota, human society will lose very big time.

Acknowledgments

We thank David Wagner for asking for this perspective, and Richard Primack and Vincent Devictor for encouraging it. We thank Area de Conservacion Guanacaste for conserving the biodiversity on which the perspective is based, and we thank thousands of individual donors and hundreds of institutions for supporting ACG as a process evolving towards achieving tropical wildland conservation through non-damaging biodevelopment and integration with its society. We thank six rapid reviewers whose comments we have done our best to address.

References

- Beaumont, P., 2018. Head in the clouds: the woman scaling fresh climate change heights. *The Guardian*. (16 December). <https://www.theguardian.com/global-development/2018/dec/16/head-in-the-clouds-climate-change-nalini-nadkarni-costa-rica-monteverde>.
- Conrad, K.F., Warren, M.S., Fox, R., Parsons, M.S., Woiwod, I.P., 2006. Rapid declines of common, widespread British moths provide evidence of an insect biodiversity crisis. *Biol. Conserv.* 132, 279–291.
- Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B., Collen, B., 2014. Defaunation in the Anthropocene. *Science* 345, 401–406.
- Fox, R., Oliver, T.H., Harrower, C., Parsons, M.S., Thomas, C.D., Roy, D.B., 2014. Long-term changes to the frequency of occurrence of British moths are consistent with opposing and synergistic effects of climate and land-use changes. *J. Appl. Ecol.* 51, 949–957.
- Hallmann, C.A., Sorg, M., Jongejans, Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Muller, A., Surnser, H., Horren, T., Goulson, D., de Kroon, H., 2017. More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS One* 12 (10), e0185809. <https://doi.org/10.1371/journal.pone.0185809>.
- Hanson, P., Janzen, D., Knapp, S., Scoble, M., Wahl, D., West-Eberhard, M.J., 2009. Obituary. Ian Gauld FLS (1947–2009). *Master taxonomist and morphologist. The Linnean* 25, 46–47.
- Hingston, A.B., et al., 2002. Extent of invasión of Tasmanian native vegetation by the exotic bumblebee *Bombus terrestris* (Apoidea: Apidae). *Austral Ecology* 27,

- 162–172.
- Hunt, J.H., Brodie, R.J., Carithers, T.P., Goldstein, P.Z., Janzen, D.H., 1999. Dry season migration by Costa Rican lowland paper wasps to high elevation cold dormancy sites. *Biotropica* 31 (1), 192–196.
- Janzen, D.H., 1966. Coevolution of mutualism between ants and acacias in Central America. *Evolution* 20, 249–275.
- Janzen, D.H., 1973a. Sweep samples of tropical foliage insects: description of study sites, with data on species abundances and size distributions. *Ecology* 54, 659–686.
- Janzen, D.H., 1973b. Sweep samples of tropical foliage insects: effects of seasons, vegetation types, elevation, time of day, and insularity. *Ecology* 54, 687–708.
- Janzen, D.H., 1973c. Tropical agroecosystems. These habitats are misunderstood by the temperate zones, mismanaged by the tropics. *Science* 182, 1212–1219.
- Janzen, D.H., 1974. The deflowering of Central America. *Nat. Hist.* 83, 48–53.
- Janzen, D.H., 1975. Interactions of seeds and their insect predators/parasitoids in a tropical deciduous forest. In: Price, P.W. (Ed.), *Evolutionary Strategies of Parasitic Insects and Mites*. Plenum Press, New York, pp. 154–186.
- Janzen, D.H., 1980. Specificity of seed-attacking beetles in a Costa Rican deciduous forest. *J. Ecol.* 68, 929–952.
- Janzen, D.H., 1983. *Costa Rican Natural History*. University of Chicago Press, Chicago (816 pp. (Strongly Seasonal Habitats, pp. 624–627)).
- Janzen, D.H., 1987. When, and when not to leave. *Oikos* 49, 241–243.
- Janzen, D.H., 1988a. Buy Costa Rican beef. *Oikos* 51, 257–258.
- Janzen, D.H., 1988b. Guanacaste National Park: Tropical ecological and biocultural restoration. In: Cairns, J.J. (Ed.), *Rehabilitating damaged ecosystems. II*. CRC Press, Boca Raton, Florida, pp. 143–192.
- Janzen, D.H., 1999. La sobrevivencia de las areas silvestres de Costa Rica por medio de su jardinificación. *Ciencias Ambientales No. 16*, 8–18.
- Janzen, D.H., 2000. Costa Rica's area de conservación guanacaste: a long march to survival through non-damaging biodevelopment. *Biodiversity* 1 (2), 7–20.
- Janzen, D.H., 2013. Latent extinction - the living dead. *Encyclopedia of Biodiversity*, Elsevier, vol. 4, 590–598. <https://doi.org/10.1016/B978-0-12-384719-5.00085-X>.
- Janzen, D.H., Hallwachs, W., 1994. Ethical aspects of the impact of humans on biodiversity. In: *Man and his environment. Tropical forests and the conservation of species*, ed. G. B. Marini-Bettolo. Pontificiae Academiae Scientiarum Scripta Varia 84, 227–255.
- Janzen, D.H., Hallwachs, W., 2011. Joining inventory by parataxonomists with DNA barcoding of a large complex tropical conserved wildland in northwestern Costa Rica. *PLoS One* 6 (8), e18123. <https://doi.org/10.1371/journal.pone.0018123>.
- Janzen, D.H., Hallwachs, W., 2016a. Biodiversity conservation history and future in Costa Rica: the case of area de conservación guanacaste (ACG). Chapter 10. In: Kappelle, M. (Ed.), *Costa Rican Ecosystems*. University of Chicago Press, Chicago, pp. 290–341.
- Janzen, D.H., Hallwachs, W., 2016b. DNA barcoding the Lepidoptera inventory of a large complex tropical conserved wildland, Area de Conservación Guanacaste, northwestern Costa Rica. *Genome* 59, 641–660. <https://doi.org/10.1139/gen-2016-0005>.
- Janzen, D.H., Hallwachs, W., Blandin, P., Burns, J.M., Cadiou, J., Chacon, I., Dapkey, T., Deans, A.R., Epstein, M.E., Espinoza, B., Franclemont, J.G., Haber, W.A., Hajibabaei, M., Hall, J.P.W., Hebert, P.D.N., Gauld, I.D., Harvey, D.J., Hausmann, A., Kitching, I., Lafontaine, D., Landry, J., Lemaire, C., Miller, J.Y., Miller, J.S., Miller, L., Miller, S.E., Montero, Munroe, J., Rab, E., Green, S., Ratnasingham, S., Rawlins, J.E., Robbins, R.K., Rodriguez, J.J., Rougerie, R., Sharkey, M.J., Smith, M.A., Solis, M.A., Sullivan, J.B., Thiaucourt, P., Wahl, D.B., Weller, S.J., Whitfield, J.B., Willmott, K.R., Wood, D.M., Woodley, N.E., Wilson, J.J., 2009. Integration of DNA barcoding into an ongoing inventory of complex tropical biodiversity. *Mol. Ecol. Resour.* 9 (Supplement 1), 1–26. <https://doi.org/10.1111/j.1755-0998.2009.02628.x>.
- Leather, S.R., 2018. “Ecological Armageddon” – more evidence for the drastic decline in insect numbers. *Ann. Appl. Biol.* 172, 1–3.
- Lister, B.C., Garcia, A., 2018. Climate-driven declines in arthropod abundance restructure a rainforest food web. *PNAS* 115 (44), E10397–E10406. <https://doi.org/10.1073/pnas.1722477115>.
- NYT 2018. <https://www.nytimes.com/interactive/2018/08/30/climate/how-much-hotter-is-your-hometown.html> (use 1963 to present for Liberia, Costa Rica; last visit 3 February 2019).
- Pringle, R.M., 2017. Upgrading protected areas to conserve wild biodiversity. *Nature* 546, 91–99.
- Sanchez-Bayo, F., Wyckhuys, K.A.G., 2019. Worldwide decline of the entomofauna: a review of its drivers. *Biol. Conserv.* 232, 8–27.
- Sheldon, K.S., Huey, R.B., Kaspari, M., Sanders, N.J., 2018. Fifty years of mountain passes: a perspective on Dan Janzen's classic article. *Am. Nat.* 191 (5), 553–565.
- Stireman, J.O., Dyer, L.A., Janzen, D.H., Singer, M.S., Lill, J.T., Marquis, R.J., Ricklefs, R.E., Gentry, G.L., Hallwachs, W., Coley, P.D., Barone, J.A., Greeney, H.F., Connahs, H., Barbosa, P., Morais, H.C., Diniz, I.R., 2005. Climatic unpredictability and parasitism of caterpillars: implications of global warming. *Proc. Natl. Acad. Sci.* 102, 17384–17387.
- Vogel, G., 2017. Where have all the insects gone? *Science* 356, 576–579.
- Wagner, D.L., 2018. Trends in biodiversity: insects. In: DellaSala, Dominick A., Goldstein, Michael I. (Eds.), *The Encyclopedia of the Anthropocene*, Vol. 3. Oxford, Elsevier, pp. 131–143.
- Wagner, D.L., 2019. Insect decline in the Anthropocene. *Annu. Rev. Entomol.* (in press).
- Wilson, J.F., et al., 2018. A role for artificial night-time lighting in long-term changes in populations of 100 widespread macro-moths in UK and Ireland: a citizen-science study. *J. Insect Conserv.* 22, 189–196.