SPECIAL SECTION

Long-term research Area de Conservación Guanacaste

EDITED BY JEFFREY KLEMENS AND JENNIFER POWERS

BIOTROPICA

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Cover photography: *Top:* A white-faced capuchin (*Cebus capucinus*) in Sector Santa Rosa, Areá de Conservación Guanacaste (ACG) (photo credit: A. Melin); *middle:* The historic Santa Rosa Casona, Sector Santa Rosa, ACG (photo credit: F. Pizarro Morales); *bottom:* Specimen collection in the intertidal zone, Sector Marino, ACG (photo credit: Jorge Cortés). *Main image:* A remnant tree in pasture near the rainforest-cloud forest transition, Sector Cacao, ACG (photo credit: A. Smith). See articles on page 1014-1106.

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COMMENTARY

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Insights from five decades of biodevelopment and long-term research at Area de Conservación Guanacaste, Costa Rica

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Area de Conservación Guanacaste (ACG) in northwestern Costa Rica is one of the most remarkable success stories in tropical conservation and ecosystem restoration. The evolution of ACG in many ways mirrors the history and development of tropical ecology as a whole. From its beginnings as a small historic site and nature preserve ACG has expanded to encompass a continuous swath of conserved wildland extending from the Pacific coastal marine zone to the Atlantic slope rainforests of north central Costa Rica. The physical growth of ACG continues today, with a focus that has shifted from large-scale land acquisition to targeted additions of high conservation interest. In the terrestrial realm, parcels of high-quality habitat continue to be acquired in collaboration with the non-profit Guanacaste Dry Forest Conservation Fund. In 2018, the Área Marina de Manejo Bahía Santa Elena was established as an area of sustainable use that complements Sector Marino, ACG's marine protected zone. Conceptually, ACG has grown as much. It began as a classic example of preserve-and-protect conservation. Early research efforts, helmed by mostly extra-national, lone-wolf researchers, were focused on species discovery and natural history in remnant habitats. Eventually, as the dire situation of tropical nature was recognized, new modes of management and avenues of research emerged that were focused on forest restoration, the interconnection of diverse habitats, and biodevelopment to benefit the surrounding society (Allen, 2001).

Approaches developed and fostered in ACG have shaped conservation not just within Costa Rica but throughout the tropics and beyond. Two well-known examples are the invention of the parataxonomist concept (Basset et al., 2004; Janzen, 2004; Pringle, 2017), and the development of the biological education program of ACG (Cruz & Segura, 2010). Both of these programs succeeded by a radical departure from contemporary thinking regarding the relationship between a tropical wildland and its neighbors. Offshoots

include the ongoing marine bio-sensitization project, a hyper-local initiative focused on children in the key neighboring community of Cuajiniquil, and the national bioliteracy project, BioAlfa (Janzen & Hallwachs, 2020). The development and elaboration of these programs have been driven by the efforts of a homegrown community of practical scientists and biodiversity managers who collectively represent a critical component of the ACG project's success.

A unique aspect of ACG is that although it exists today as a large, state-controlled conservation area, it retains some of the character of an academic research station. Scientific research has been central to developing the mission and informing the management of the conserved wildlands that make up the core of ACG. As a result, ACG has generated, managed, and disseminated much knowledge of its biodiversity via in-house efforts, while also consistently attracting researchers from within Costa Rica and around the globe in a virtuous circle of knowledge acquisition. Despite the fact that thousands of scientific papers, theses, and reports have emerged there have been few efforts to publicly collate or synthesize this work. The papers in this special section therefore synthesize results from some long-term ACG research programs that highlight unique aspects of the ACG experiment. The studies represent diverse timescales, disciplines, and levels of biological organization and place those results in the conservation context of northwestern Costa Rica.

As appropriate given their role in envisioning and constructing ACG as it exists today, Janzen and Hallwachs (2020) kick off the special section with a historic overview of the growth of ACG as an exercise in applied biodevelopment. Srivastava et al. (2020) provide a brilliant example of a classic kind of ACG study—showing how a deep understanding of the natural history of a particular site, gained over many years of research (in this case at the Pitilla Biological Station of ACG) can provide insights into underlying ecological principles. Melin et al. (2020) review results from a decades-long investigation into primate biology in ACG initiated by Linda Fedigan in 1983. Their review is focused around the particular aspects of behavior and

ecology that can be revealed by long-term study and provides future researchers at this site or elsewhere with dozens of starting points for future investigation. Hulshof and Powers review plant ecology of ACG, taking as their organizing theme environmental gradients within ACG (this issue). They describe how these studies will play a role in our understanding of tropical communities and response to the environmental changes that face the tropics in the future. Continuing with the theme of gradients, Smith and collaborators (Warne et al., 2020; Smith et al. this issue) provide two examples of the kind of work that takes advantage of not only the elevational gradients within ACG but also the long-history of biodiversity surveys and sample collection in ACG, including DNA barcoding based approaches developed in part using ACG organisms to describe elevational gradients in arthropods distribution and how they may be affected by climate change. Montalvo et al. (2020) present a study that is only possible because of ACG habitat diversity, focusing as it does on the movement of jaguars through a habitat matrix made up of turtle nesting beaches and adjacent tropical dry forest. As evidence that ACG continues to expand its scope of interest and influence, the final paper reports early results of a biodiversity survey of ACG's marine zone, which until recently was a critical knowledge gap (Cortés & Joyce, 2020). This novel collaborative effort between ACG and Costa Rican university researchers has developed from groundwork laid by ACG and its historic commitment to biodiversity inventory, the development of local expertise, and integration or research outputs with ongoing education and outreach efforts.

Although it is difficult to predict the course of research, it is possible to make a few guesses at likely future directions based on the projects that are happening now. As demonstrated by many of the papers in this special section, ACG will continue to be a desirable research site for ecologists conducting work on environmental gradients, natural or anthropogenic, and biological interactions that cross habitat types. ACG will continue to be a flagship site for biodiversity studies due to its well-characterized flora and fauna and its status as the most heavily barcoded site in the world. As a key site in the Tropi-dry network, data from the dry forests of Sector Santa Rosa, including unprecedented data on dry forest physiology and gas exchange, are now linked to other dry forests throughout the hemisphere (Sánchez-Azofeifa et al., 2013). Increased networking of such ecological data will be key to integrating local knowledge into an understanding of global tropical forest dynamics under climate change. Finally, the continued application of biodiversity knowledge to proximate economic and environmental concerns in ways that improve lives in local communities remains an essential area of challenge and promise. Ongoing research at the Horizontes Experimental Forest Research Station of ACG focuses on plantations of native tree species, curation of seed sources, and technologies for forest restoration on degraded lands. This research and associated outreach provide a template for how to conduct and communicate research on scales that are economically meaningful to surrounding communities.

Santa Rosa National Park was declared in 1971, and ACG was born in 1989 (Allen, 2001; Janzen & Hallwachs, 2020). In the nearly five decades that have elapsed since this experiment in tropical conservation began, ACG has already made massive contributions to our knowledge of tropical nature and how we might use and conserve it. It is a given that the future of tropical biology will be defined by the threats posed by habitat destruction and climate change. Both the lessons already learned and the future lessons that ACG surely holds will be critical in rising to meet these challenges.

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ORIGINAL ARTICLE

Área de Conservación Guanacaste, northwestern Costa Rica: Converting a tropical national park to conservation *via* biodevelopment

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Abstract

The ~30,000 hectare classical Costa Rican Parque Nacional Santa Rosa has used about 35 years and $107 million to be converted to the 169,000 ha government-NGO hybrid Área de Conservación Guanacaste (ACG). This semi-decentralized conservation entity has today a staff of ~150 paraprofessional resident Costa Ricans, biodeveloping at least 650,000 multicellular species (Eucaryotes) into perpetuity for ACG survival through being integrated with its local, regional, national, and international society. ACG began in 1985 as an ongoing exercise of landscape-level ecosystem rescue and restoration of a continuous swath from 6 km out in the Pacific ocean, across dry forested lowlands, up and over the volcanic Cordillera Guanacaste, and down into the rain-forested Caribbean lowlands. It is being impacted by climate change, yet its diverse ecosystems hold hope for major biodiversity survival, albeit in new community assemblages. It quickly became simultaneously a biophysical challenge and an administratively novel challenge in decentralized conservation in a democratic tropical country. ACG specializes at being managed by on-the-job stimulated and trained residents with minimal formal education, searching for ways to involve ACG in its society without damaging its wildness, and pioneering ways to render wild biodiversity to being a welcome member at society's negotiating table. It continues to pay its bills through government subsidy, generous donors, payments for services, project grants, and huge in-kind contributions from mutualisms. ACG hopes that the concept will spread south–south to other tropical countries while they still have some of their wild biodiversity with which to integrate.

Abstract in Spanish is available with online material.

KEYWORDS
BioAlfa, biodiversity, bioliteracy, climate change, Parataxonomist, restoration, tropical forest

Winnie and I have been embedded in the planning and actions of the larval Parque Nacional Santa Rosa since its beginning, and then during its molting into today's 6-times larger, still-evolving, Área de Conservación Guanacaste. Biotropica's editors have therefore asked us for a personal account and reflection on what we think we have seen and experienced. True detail for these 169,000 hectares would require many thousands of pages, documents, and photographs. ACG's marine, dry forest, cloud forest, rain forest and a multitude of intergrades are all touched by 400 years of European-style agroscape impact, and restoration. They are an extraordinarily complex array of history, contemporary exploitation, regeneration and now, beset by the brave world of severe climate change created by the

industrialized world's century+ of dumping its gaseous waste into the global atmospheric commons. Please take this story as a once-over lightly viewpoint, to be fleshed out by your own experiences and analogies.

1 | INTRODUCTION

IN 1966, ÁREA DE CONSERVACIÓN GUANACASTE (ACG) BEGAN LIKE MOST TROPICAL NATIONAL PARKS (Janzen,2000). It was, and still is, embedded in a complex mosaic of historical, local, biodiversity, and biopolitical lineages. The initial seed, Hacienda Santa Rosa, was the headquarters of a ranch and farm of Spanish colonial culture established in the 1580s on old-growth forests and indigenous secondary succession dating back thousands of years, and terrain dating back many millions of years above the sea (Janzen, 1983; Janzen & Hallwachs, 2016a). Hacienda Santa Rosa's approximately 30,000 ha of land extended from the Pacific coast to the upper slopes (700–1500 m) of Volcán Orosí and Volcán Cacao in Cordillera Guanacaste and was the third Spanish ranch to be established in Costa Rica, shortly after the neighboring Hacienda Inocentes (buildings extant half way between the Interamerican Highway and Santa Cecilia) and Hacienda Orosí (ruins on the slopes in Sector Orosi, Sector Pocosol, and Sector El Hacha). These three haciendas are now part of Sector Santa Rosa, Sector Santa Elena, Sector Murcielago, Sector Orosí, Sector Pocosol, Sector Cacao, and Sector El Hacha of ACG (Figure 1 in Janzen & Hallwachs, 2016a), and Figure 1 below.

Hacienda Santa Rosa occupied the 300 m Mesa Santa Rosa, its slopes to the coast (Sector Santa Rosa) and up to upper elevation cloud forest (Sector Cacao, Sector Pocosol) and Peninsula Santa Elena (Sector Santa Elena, Sector Murciélago). It is believed that most of the outer boundaries of the property were not defined so much by established limits or stone walls, but rather by how far the herds of livestock (horses, mules, burros, cattle) circulated daily and seasonally spread out from the Casona Santa Rosa, and from food, and fresh water.

To understand the terrain underfoot, it is necessary to imagine Lake Nicaragua extending all the way south to the vicinity of Liberia, with an enormous ~3,000 m volcano on its southeastern margin, centered where lies today's Volcán Rincon de la Vieja complex (Volcán Santa Maria, Volcán Van Seebach, Volcán Rincon de la Vieja, Figure 2).

About 1.5 million years ago, this huge Guanacaste volcano exploded and filled the lake from southern Nicaragua to Liberia with a several hundred-meter layer of its content, obliterating the lake and rain forest. We know it was rain forest because the fossil wood exposed by erosion of the margin of this volcanic deposit (found behind Playa Naranjo in Sector Santa Rosa) comes from species of trees commonplace in today's Costa Rican rain forest to the east (e.g., *Calatola costarricensis* (Metteniusaceae, formerly Icacinaceae) but do not occur in ACG dry forest. We also know the ancient lake bed is below the Santa Rosa mesa because when drilling for a well

in the Area Administrativa of Sector Santa Rosa, rotting vegetation from the lake bed was encountered at about 180 m depth. The crater left by this volcanic explosion was about 25 km wide.

About 50,000 years ago the Rincon de la Vieja complex began to emerge in this crater, then Volcán Cacao to the north about 30,000 years ago, followed by Volcán Orosí yet more to the north about 20,000 years ago. The emerging Cordillera Guanacaste became a barrier and caused uplift of the trade winds from the Caribbean/Atlantic, crowning the volcanoes with cloud forest and generating a dry forest rain shadow in the Pacific lowlands to the southwest. The flatlands at 250–400 m elevation immediately north of Volcán Orosí graded gradually from Caribbean rain forest in the east to the dry margin of the Pacific, an ecotone today obliterated by ranching and farming outside of ACG. Only fragments of this ecosystem intergrade exist today in ACG on the northern slopes of Sector Del Oro. Whatever we call ACG today, as recently as 1.5 millon years ago, post-explosion, it must have looked like the moon; whatever lives there today arrived by immigration from somewhere else. Today, those immigrants for the most part still have major parts of the genomes they evolved "elsewhere." Such a sourcing by immigration and mixing is best termed "ecological fitting" (Janzen, 1985a), rather than being a dry forest community evolved largely in situ out of lowland rain forest stock.

In 1966, what was to become Parque Nacional Santa Rosa as decreed in 1971 was a minimal yield extensive cattle ranch dotted with some frontier settlers, effectively squatters on the land owned by the Somoza family of Nicaragua, and roamed by 2000 + cattle from neighboring ranches (Janzen,2000). Hacienda Santa Rosa had at least 45 different owners from the late 1500s to the 1960s, a reflection of its "bad" soils, dry season water scarcity, far distance from Costa Rican and Nicaraguan centers of social concentration, and ongoing harvesting/destruction of its standing and seasonally regenerating resources. It had been subjected to nearly four centuries of anthropogenic fires, selective logging, deliberate deforestation, feral species introduction, hunting, formal cultivation, small farms, water manipulation, cattle-horse-burro grazing, mining, road building, etc. Its forest and erratically regenerating biodiversity survived in fragments by inaccessibility, excessively bad soils, changing markets, and the whims of European colonization (Janzen & Hallwachs, 2016a). Before that, various portions of ACG's four present-day contiguous major ecosystems (dry forest, rain forest, cloud forest, and marine) were lightly to intensively used by at least three different indigenous cultures—coastal, one from the lake Nicaragua lowlands to the north, and one from the highlands as far away as mid-upper elevation San Jose. One cannot turn around in ACG without walking in the footprints of previous human occupants. Today's neotropical Anthropocene began 9,000 years ago with human extinction of the neotropical megafauna and the consequent obvious food web changes (Hallwachs, 1986; Janzen, 1976a,1976b, 1982a, 1982b, 1982c,1982d,1982e,1982f,1984, 1985b; Janzen & Martin, 1982).

In 1966, Dr. Kenton Miller from the University of Michigan, a Professor of Conservation, was teaching a national park planning
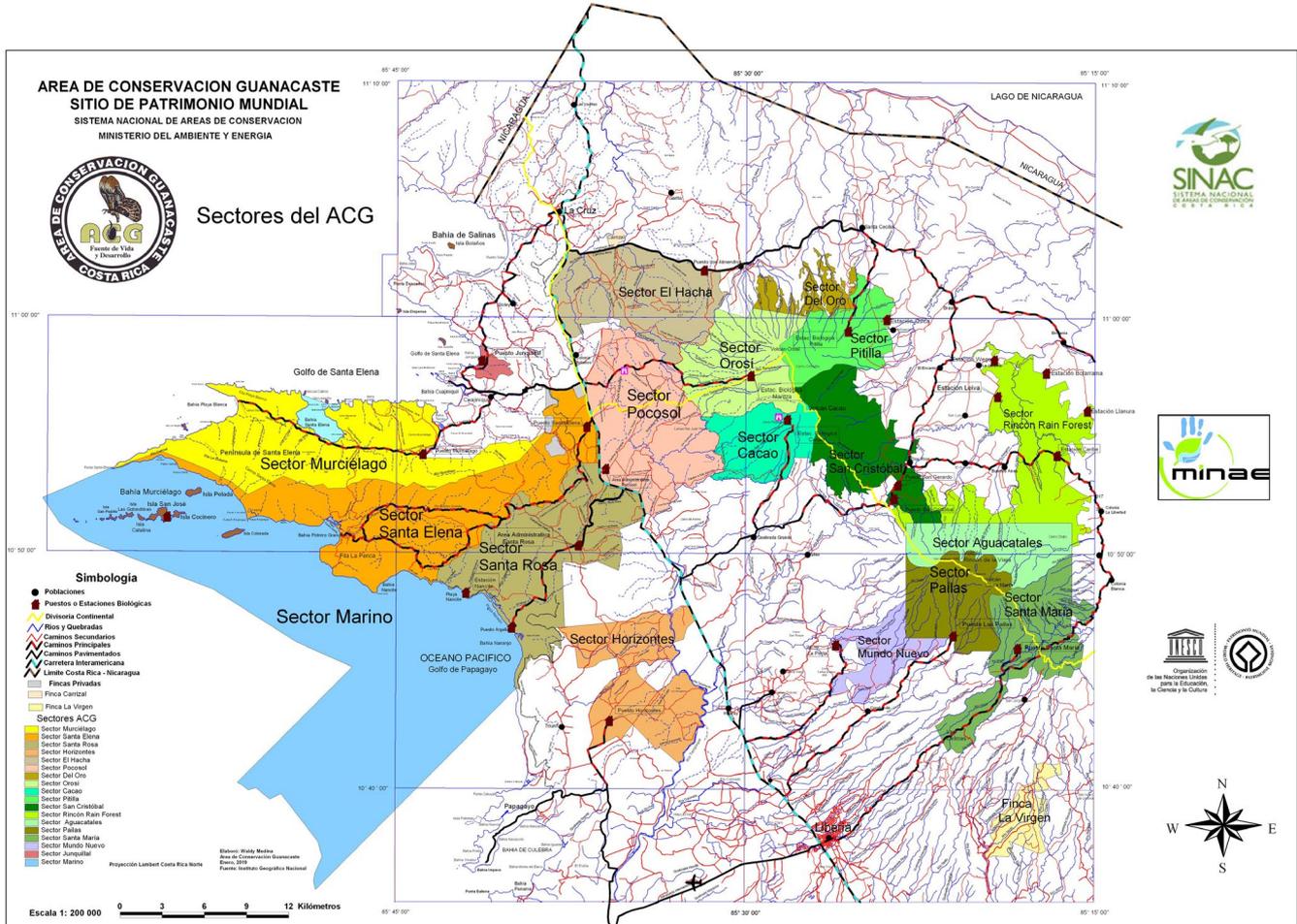
FIGURE 1 Sectors of ACG in northwestern Costa Rica, south of the Nicaraguan border. The faint yellow line NW-SE through ACG is the continental divide and roughly bisects Cordillera Guanacaste (but drops to about 400 m elevation in La Cruz on the Interamerican Highway, and see Figure 1 for a 3D representation of ACG). The green and dark sectors are cloud and rain forest, while those to the east of the Continental Divide are various forms of the dry forest ecosystem (map by W. Medina, 2019)

course at the previous Organization of American States experiment station near Turrialba in eastern Costa Rica. The Costa Rican government had just expropriated Hacienda Santa Rosa from the Nicaraguan Somoza family. The government wished to convert the historic "original" main ranch house (today, the Santa Rosa "Casona") and surrounding 1,000 ha into a recreation center for government employees, making double use of it as a monument to previous military political conflicts (e.g., Jamison, 1906; Wells, 1856). They asked Kenton, a conservation planner by profession (Miller, 1982), to inspect the Casona and its surroundings. He visited with his father, and the "sabaneros" (cowboys) still managing the Hacienda encouraged him to drive down to the beach at Playa Naranjo to see that part of what is today Sector Santa Rosa. He used the dirt road that today we know was the oxen drag trace for harvesting very large mahogany logs (caoba, S*wietenia macrophylla*, Meliaceae) that were hauled through the surf to waiting boats that carried them through the Panama Canal to the mahogany-starved boat-building industry in the Caribbean at the end of WWII. The stumps in the Bosque Humedo of Sector Santa Rosa are still rock-hard, as are the axe-cut chips in the litter. Wearing the hat of a biologist and national

park planner, Kenton went back to the government in San Jose and suggested that instead of a recreation center, they decree the area from the beach to the Interamerican Highway to be Parque Nacional Santa Rosa (PNSR) (Figure 3).

Alvaro Ugalde was the first director of Parque Nacional Santa Rosa, fresh from Kenton's conservation course in Turrialba, a course that toured various US national parks to get an idea of the concept of a national park. He witnessed the outer appearance more than the more difficult aspects of long-term administration and maintenance. Santa Rosa's old pastures were viewed as "savanna" by everyone who wanted a convenient and attractive name. However, they were maintained by anthropogenic fires and cattle eating the introduced African grass "jaragua," pastures dotted and striped with tropical dry forest fragments that had survived for centuries in a cattle and fire face-off (e.g., Figure 4).

The planning of trails, buildings, and other original management aspects was carried out by a US Peace Corps group under Kenton's direction in coordination with Alvaro and the Guardia Rural on loan, plus regular park guards from the central administration as the years passed. One of Alvaro's large and early biopolitical successes was to

FIGURE 2 The active crater of Volcán Rincon de la Vieja, about 1900 m, looking NNW. Downslope to the right is Sector Rincon Rain Forest of ACG; from the peak to the left is Sector Pailas and Sector Santa Maria, and the dim beige mountain in the distance slightly above the center is Cerro El Hacha, a 6-million-year-old volcano core that was an island in the ancient lake Nicaragua. Today, this lake lies below the layer of fire-generated smog in the upper part of the photograph, a lake that stretch south to the town of Liberia, out of sight off the lower left corner (photo, Luciano Capelli, 7 April 2014)

FIGURE 4 Mesa Santa Rosa in Parque Nacional Santa Rosa (today, Sector Santa Rosa of ACG) on 16 March 1987, with ungrazed anthropogenic pastures filled with 1–2 m tall jaragua (*Hyparrhenia rufa*) introduced from East Africa in the 1940s to replace native grasses to achieve higher cattle yield. In 1987, because the cattle had been removed by a court case won by the Costa Rican Servicio de Parques Nacionales, these dense stands of grass generated huge fires that obliterated the woody vegetation and stimulated the urgent necessity of a fire control program (Janzen Janzen, 1988c, 1988e; Janzen, 2002) (photo, D. H. Janzen)

2 | BACKGROUND READING WITH INFORMATIVE TITLES

ALLEN, W. (2001). Green Phoenix: restoring the tropical forests of Guanacaste (310 pp). Costa Rica: Oxford University Press, USA.

FLAGG, J. A. (2018). Carbon neutral by 2021: the past and present of Costa Rica's unusual political tradition. Sustainability 10:296, 16 pp. https://doi.org/10.3390/su10020296

JANZEN, D. H. (1988b). Guanacaste National Park: Tropical ecological and biocultural restoration. In J. J. Cairns (Ed.), Rehabilitating damaged ecosystems, Vol. II (pp. 143–192). Boca Raton, FL: CRC Press.

JANZEN, D. H. AND HALLWACHS, W. (1994). Ethical aspects of the impact of humans on biodiversity. In G. B. Marini-Bettolo (Ed.), Man and his environment. Tropical forests and the conservation of species. Pontificiae Academiae Scientiarum Scripta Varia 84:227–255.

JANZEN, D. H. (1998a). Área de Conservación Guanacaste. Nomination for inclusión in the World Heritage List of natural properties. Submitted by the Government of Costa Rica, 1 July 1998. 32 pages without 10 images and their captions.

JANZEN, D. H. (1998b). Conservation Analysis of the Santa Elena property, Peninsula Santa Elena, northwestern Costa Rica. Submitted to the Government of Costa Rica. 60 pages without images and their captions.

JANZEN, D. H. (1999). La sobrevivencia de las areas silvestres de Costa Rica por medio de su jardinificación. Ciencias Ambientales, 16, 8–18.

JANZEN, D. H. (2000). Costa Rica's Área de Conservación Guanacaste: a long march to survival through non-damaging bio-development. Biodiversity, 1(2), 7–20.

FIGURE 3 Inauguration of Parque Nacional Santa Rosa in March 1971 with the very young Alvaro Ugalde (RIP) in national park uniform, Mario Boza (in glasses and national park uniform), Karen Olson de Figueres, First Lady to President "Pepe" Figueres in black dress, and Fernando Batalla the Minister of Agriculture in pink shirt, two students from the Guanacaste Institute in white, and future Costa Rican president Jose Maria Figueres in light blue shirt to far left (photo, Steve Cornelius, US Peace Corps at that time)

relocate as one unit the settlers and salt harvesters ("saleros") out of the back-beach lowland habitat behind Playa Naranjo, leaving the area to restore its forests. Of these, the assumed "old-growth" forests (e.g., the Ojochal forest) were clearly old secondary succession on ancient indigenous village and farm sites, given the buried pottery fragments and bone and shell middens underlying the forest and that almost all the trees have seeds and fruits edible to humans (e.g., "ojoche," *Brosimum alicastrum*, Moraceae).

Many aspects and details of this brief history have already been published, and we encourage the reader to use the 13 references below to understand the early germination and growth of ACG with respect to details not elaborated here:

JANZEN, D. H. (2002). La sobrevivencia de las áreas silvestres de Costa Rica por medio de su jardinificación. In F. Chapela (Ed.), Manejo comunitario de la biodiversidad biológica en Mesoamérica (pp. 81–105). Mexico: Universidad Iberoamericana Puebla.

JANZEN, D. H. (2008). Restauración del bosque seco tropical: Área de Conservación Guanacaste (ACG), noroeste de Costa Rica. Chapter 10. In M. Gonzalez-Espinosa, J. M. Rey-Benayes, and N. Ramiriez-Marcial (Eds.), Restauración de Bosques en América Latina (pp. 181–210). Mexico: Mundi-Prensa, S.A.

JANZEN, D.H. AND HALLWACHS, W. (2016a). Biodiversity Conservation History and Future in Costa Rica: The Case of Área de Conservación Guanacaste (ACG). Chapter 10. In M. Kappelle (Ed.), Costa Rican Ecosystems (pp. 290–341). Chicago, IL: University of Chicago Press.

JANZEN, D.H. AND HALLWACHS, W. (2016b). DNA barcoding the Lepidoptera inventory of a large complex tropical conserved wildland, Área de Conservación Guanacaste, northwestern Costa Rica. Genome, 59, 641–660. dx.doi.org/10.1139/gen-2016–0005.

JANZEN, D. H., HALLWACHS, W., JIMENEZ, J. AND GÁMEZ, R. (1993). The role of the parataxonomists, inventory managers and taxonomists in Costa Rica's national biodiversity inventory. In W. V. Reid, S. A. Laird, C. A. Meyer, R. Gamez, A. Sittenfeld, D. H. Janzen, M. A. Gollin, and C. Juma (Ed.), Biodiversity Prospecting (pp. 223–254). Washington, DC: World Resources Institute.

GÁMEZ, R. (1999). De biodiversidad, gentes y utopías: Reflexiones en los 10 años del INBio. Santo Domingo de Heredia, Costa Rica. Editorial INBio. 144pp.

PRINGLE, R. M. (2017). Upgrading protected áreas to save wild biodiversity. Nature, 546, 91–99.

3 | JANZEN AND HALLWACHS INVASION, INTERFERENCE AND MEDDLING

In the mid-1970s after spending about ten years setting up study trees and plots from Escazu near San Jose, to La Cruz north of ACG on Costa Rica's drier Pacific side, DHJ had a major part of his esoteric ivory tower research study sites deforested by ICE, the national electric company. Land owners had given permission and assurances to leave the forest in peace. However, that was no barrier to ICE installing the new national electricity grid along most of Costa Rica's roads, and clearing forest to do so. DHJ lost half his "long-term" study sites in one year. Peace Corps group in Santa Rosa invited him to move his research into the park for safety from such unexpected catastrophes (the electric grid was of course very welcome to the rest of Costa Rica, and by 1985, in Santa Rosa's Area Administrativa as well). DHJ did move in, not for conservation (in his mind that was for "other people"), but to do uninterrupted research on seed predators (Janzen, 1970, 1980) and tree phenology (Janzen, 1967, 1986e). It was like going to a secure and safe restaurant to enjoy a calm meal. Indeed, when receiving the Crafoord Prize from the Swedish Royal Academy in 1984 for his coevolutionary studies, a Swedish reporter,

Erika Bjerstrom, asked him "What are you doing for conservation?" DHJ replied "nothing, that is for other people." (This is ironic, since his father had been the Director of the US Fish & Wildlife Service.) But then he added "but if you want to raise funds for conservation, I can get them to other people who do that." Six months later, following Erika's success from simply putting an advert in a Swedish newspaper with a bank account number, she sent $25,000 Swedish donations for forest purchase. Joined with the $100,000 Crafoord Prize, this bought the 395 hectares of Finca Jenny (the northeast-most corner of Parque Nacional Santa Rosa, Figure 1), the first purchase to increase the size of Sector Santa Rosa since the 1970s, and paid for the $46,000 electric line from the same national ICE electricity grid that had driven DHJ into Santa Rosa ten years earlier.

A frame shift gave birth to ACG. In 1985, Alvaro Ugalde, by now the Director of the Servicio de Parques Nacionales (SPN), asked us to carry out an Environmental Impact Assessment (EIA) about the 1,500 placer gold miners that had invaded the rain forest Parque Nacional Corcovado in southwestern Costa Rica, a park that we knew very well as ecologists from years of esoteric field work there and staying at the Sirena and Llorona SPN field stations. A US esoteric tropical field ecologist (DHJ), a former Costa Rican Corcovado goldminer (Gerardo Vega), a Mexican ecologist (Rodolfo Dirzo), a US mammologist (Don Wilson), a Costa Rican-based ornithologist (Gary Stiles), a US-UK conservationist (Gina Green), and the park director (Juan Carlos Romero) arrived to find, as expected, a devastated landscape (Figure 5). WH did not go, though she very much wishes she had, because she was writing up her dissertation on the agoutis who got the fruit and seed handoff when the Anthropocene began with the obliteration of the Neotropical megafauna (Hallwachs, 1986; Janzen, 1986a; Janzen & Martin, 1982).

With a week planned on the ground in the park, from the airplane flight into Puerto Jimenez on Monday to the airplane flight out on Friday, what to spend time on? The environmental impact was immediately obvious and would take no time to write. DHJ decided to spend the week studying the natural history of the gold miners, who we had been told by the government were the worst scum of the earth. He quickly found the opposite. They were quite ordinary Costa Rican citizens ranging from former banana and coffee plantation workers to the chief accountant for one of the largest companies in Costa Rica. We called a general meeting in the Puerto Jimenez dance hall, which was attended by 600–700 people on Thursday evening. We said "all of you know that you are illegal, like being parked on a yellow curb, so you tell us how you will leave. Instead of us calling the tow truck." They argued among themselves all night long. We went back to San Jose and suggested that the park system back off their plans for a military-style eviction, and instead, spend a year getting to know the gold miners and convince them that yes, the park does have an owner and they are doing damage. In one year, anyone there would be arrested and physically removed (Janzen et al., 1985). A year later, there were 272 remaining, almost all of whom were peacefully removed physically, leaving just a very few "old timers." However, the obvious lesson was not adopted by subsequent governments, and today, moderate placer goldmining

FIGURE 5 A major riverbed in Parque Nacional Corcovado subject to months of placer gold mining in 1985, mined by middle to working class Costa Ricans from all walks of life and parts of Costa Rica—frontier farmers to very urban office workers, all ages, each seeking a lump of gold that would support them for years. Approximately 1,500 such miners were working and living inside the park in June 1985 (photo, D. H. Janzen)

and hunting are still killing Parque Nacional Corcovado by a thousand small cuts.

After our Corcovado experience, and a similarly educational one in tropical Australia immediately, a visit that alerted us to the seriousness of long-term fires in tropical dry forest (Janzen, 1988a), we came back to Santa Rosa and found ourselves asking "How can we prevent these kinds of challenges happening to Santa Rosa in the coming years?" Santa Rosa is rich in desirable resources: timber, soil, minerals, town sites, road sites, geothermal deposits, wild animals (including fish and coral), seeds, water, development sites, tourism potential, wind, esoteria, bioprospecting potential, conservation examples, educational potential, etc. In essence, our reply was "evolve Santa Rosa from a protected set-aside with a few park guards, to being, figuratively speaking, a huge hacienda that nondestructively produces goods and services that are welcomed by Santa Rosa's local and national society" (Janzen, 1986b, 1988b; Pringle, 2017). We had no idea how bureaucratically and biopolitically novel and disruptive would be this science-based logical idea and deviation from the tropical conservation song and dance. However, we began to get a whiff when it was presented to the national conservation aficionados at a conservation conference at the US National Zoo in November 1985, arranged by Michael Robinson, the Zoo director. The concept was greeted with dumbfounding and antagonistic silence. However, at that same meeting, a young Costa Rican, Liliana Madrigal, newly working for The Nature Conservancy (TNC) in Washington, D.C., asked "Who is going to be your NGO." DHJ replied "What is an NGO?" We were very naïve members of the ivory tower. Liliana replied "Come over to my office and I will explain." Two hours later, ACG took root as the Guanacaste National Park Project (GNPP) with TNC being our pro bono US tax-deductible accounting system for donations, until 1996 when they decided that they had to charge us 18% overhead and that stimulated the creation of the

Guanacaste Dry Forest Conservation Fund (GDFCF, http://www.gdfcf.org), 100% dedicated to the survival of ACG. Liliana, Randy Curtis, Geoff Barnard, Pete Seligmann, Spencer Beebe, and many others at TNC, thank you all for that starter boost that leads all the way to today's BioAlfa, the beginnings of deep bioliteracy for Costa Rica (Bazilchuk, 2019; Janzen & Hallwachs, 2019b).

We then presented the idea in early 1986 to the newly founded NGO Fundación Neotrópica in San Jose. Professor Rodrigo Gámez, a professor of virology at the Universidad de Costa Rica, was in the front row and said that the new President Oscar Arias should hear this idea. The President's response was "Sounds OK if it does not cost us anything." We replied that we were not asking for funding, but for political permission. In fact, Alvaro Ugalde told us that we could not raise funds in Costa Rica, and that all had to come from the international sector. Gámez then took us to Alvaro Umaña, the new Minister of Energy and Environment (MINAE in today's terminology), and the new home for the Servicio de Parques Nacionales (SPN), formerly in the Department of Agriculture and Livestock (MAG). Alvaro Umaña listened carefully and asked "Can you do it in four years?". The innocent academic scientist in us did a quick mental calculation, as if a grant proposal, and replied "yes." We had no idea why he asked and had no idea how far off we were. However, it is now 33 years later and ACG is not "finished." We have an inkling. Its next major step is the BioAlfa integration of biodiversity with Costa Rica as a whole (Janzen & Hallwachs, 2019b, and Bazilchuk, 2019).

Beginning then in 1986, as scientists are wont to do, we wrote a philosophical and technical booklet about what traits Parque Nacional Santa Rosa should have to initiate to become the Guanacaste National Park Project (GNPP) (Janzen, 1986b, 1988b, 1988f). The name GNPP was later replaced with "Unidad Regional de Conservación," to then later become "Área de Conservación Guanacaste," and then later, that name was extended by the government (not by ACG) to include all of the area from Liberia to the Nicaraguan border. This rendered the original ACG to be the "Área Silvestre Protegida" of the ACG in government vocabulary. The booklet was centered on 4 critical first steps:

1. Regenerating ACG ecosystems to recover from four centuries of European agroscape assault by stopping the anthropogenic fires, hunting, and logging,
2. Growing ACG large and diverse enough to both contain serious populations of its species and tolerate the footprints of users, both on-site and global,
3. Offering direct services and products to the ACG neighbors and its country, and
4. Become self-supporting once past the project startup costs of land purchase and growing an endowment large enough to sustain a career-based management staff and its operations costs. The pursuit and development of these four areas has yielded today's ACG. Throughout this process, we met major to minor resistance from the established bureaucracy of classical national park structures, yet also met strong collaboration from those

working at the level of day-to-day challenges. ACG is a hybrid NGO-government organism that requires constant nursing and is certainly not yet the "perfect product" hoped for, but its current 169,000 ha and 150-member resident Costa Rican staff with an annual budget of ~$5 million is vastly more likely to survive into perpetuity than was the ~ 30,000 ha Santa Rosa in 1986 (10,000 ha terrestrial, 20,000 ha marine) with its $72,000 annual budget and ~17–20-member staff of park guards and administrator. Survival into perpetuity is the only goal that counts. ACG continues to pay its bills in cash and in-kind through the government national budget, generous donors, payments for ACG services, project grants to many different recipients, and huge in-kind contributions from mutualisms. There are many kinds of currency. However, it is headed in the direction of self-sustenance from the combination of endowment yield and payment for its goods and services in many currencies to many users.

4 | ACG ECOSYSTEM RECOVERY FROM FOUR CENTURIES OF EUROPEAN AGROSCAPE ASSAULT

Six major challenges were immediately evident in 1986 (Allen, 2001):

1. On the dry side of ACG, the critical technical need was to stop the annual dry season anthropogenic fires that were burning the habitats and biodiversity of Santa Rosa and adjacent properties off the landscape. The solution was to (i) put cattle back in temporarily as biotic mowing machines until fire control by a fire team SWAT approach was mostly achieved by the ACG fire program (see Figure 4 for the challenge), (ii) hire local residents to be the fire SWAT team, people who had been setting and managing fires all their lives as part of a culture that did not want forest to invade pasture (a process that everyone but the ivory tower science community knew very well), (iii) feel free to use government employees and resources to extinguish fires on private land and with unconventional work schedules, (iv) foster and use an ACG identity commitment that puts out a fire at 2 a.m. on Easter Sunday morning (https://www.acguanacaste.ac.cr/proteccion/programa-de-proteccion-e-incendios), and (v) have the biological understanding to know that a forest with its dispersal agents will move itself to reoccupy pasturelands if allowed to do so (Janzen, 1988a, 1988c, 2002). We quickly came to realize that wind and the vertebrates of lowest interest to the conservation community (deer, coyotes, bats, magpie jays, ctenosaurs, agoutis, horses) were the major reforestation agents, vastly better than human tree planters. On the rain forest side of ACG, we found pastures to be most effectively removed by quasi-commercially planting them with Southeast Asian introduced short-lived trees, *Gmelina arborea* (Verbenaceae), and then walking away. The dense shade that *Gmelina* produces kills rain forest introduced pasture grasses, and later its own seedlings, as thoroughly as if a lethal virus

had been introduced. The animal dispersal agents simultaneously move the rain forest as a whole into the site, since wind dispersal is almost non-existent in ACG rain forest.

2. The expansion of Santa Rosa to be the full-fledged ACG had to be achieved by about 30 years of intense bargaining and purchase of about 350 small-to-very-large farm and ranch properties, a process still ongoing today at a very decreased rate as funds become available and some conservable adjacent forests survive (see Figure 1 in Pringle, 2017). All but one of the purchases were willing seller–buyer transactions. The exception was the 16,000 ha Sector Santa Elena finally expropriated from its US owner after a 23-year court case (Janzen, 1998).

Land purchase was not biologically strategic so much as opportunistically following owners' willingness, a method that is very conservationally strategic and very rarely used by the conservation industry. Many owners had been frontier colonizers. As the decades rolled on, they found their variously isolated lives to be not the best for them and their families. Land purchase was also guided by the certain biological knowledge that heavily damaged landscapes intermingled with somewhat intact forest would, albeit slowly, regain high quality species-rich conservation value. Land purchase on the Caribbean side of ACG was also stimulated and guided by the discovery in the mid-1980s that a large number of ACG dry forest insects seasonally migrate over the volcanos to the more rainy side of ACG to pass the dry season (Janzen, 1987a, 1987c, 1988d), returning with the mid-May beginning of the rainy season. The costs of land purchase were met by international donors (more than 13,500 of them) and by a massive debt-for-nature swap engineered by TNC, the Swedish government (especially the Swedish International Development Coordination Agency), Costa Rica's Fundación de Parques Nacionales, and much Costa Rican sweat equity. The total land and salary costs for ACG, aside from the annual government budget, by 2018 sum to at least $107 million, $16 million of which was a direct payment by the government of Costa Rica for the Santa Elena expropriation case.

3. Immediate positive rapport with the local, regional, and national social environment was, and is, a major goal from 1986 through today. It began with friendly negotiated property purchase, local purchasing to support the local economy, maximizing employment of neighbors (ACG staff are Costa Ricans and resident), and from the beginning in 1986 establishing the ongoing ACG Programa de Educación Biológica (PEB), that is largely supported by the ACG and GDFCF budget (https://www.acguanacaste.ac.cr/educacion/programa-de-educacion-biologica). PEB is a school program for all 4th, 5th, and 6th grade students in about 50 schools ringing ACG; it asks, in the field, in ACG, why and how does nature carry out what it does? Each student visits/visited ACG field sites 4–6 times per year, exploring the many habitats and ecosystems, as well as visiting neighboring large scale agroscape commercial operations. This is 2,000–2,500 students per year getting to know the forest as their school (Cruz & Segura, 2010). Coupled with this school-level immersion in the forest,

the 35 Costa Rican resident parataxonomists (from 2 in 1984 to 35 at present), drawn from the rural countryside pool of working adults, reinforce the bond between the ACG, its staff, and its social milieu (Janzen, 1991, 2004; Janzen & Hallwachs, 2011; Janzen, Hallwachs, Jimenez, & Gámez, 1993; Schmiedel et al., 2016). While PEB is supported by the government ACG budget combined with GDFCF funds, the 47 parataxonomists and their administration are salaried and operationalized by GDFCF with massive in-kind support from the government.

4. Throughout the small and large management decisions (e.g., fire control, land purchase, neighbor relations, PEB, parataxonomists, and spreading positive ACG interactions to the local, regional and national (and international) communities), detailed and place-specific biodiversity knowledge about the entire growing package of ecosystems, habitats, and various ages of succession was essential. This knowledge is derived, and continues to be derived, from (i) the huge amount of biodiversity inventory conducted by the ACG parataxonomists, (ii) visiting researchers of many kinds, (iii) biodiversity information from other parts of Costa Rica and the tropics, (iv) ecological and evolutionary common sense, and (v) time/dollar budgetary constraints (Janzen, 1983; Janzen & Hallwachs, 2016b).

There are now relatively few bureaucratic constraints to acquiring ACG biodiversity knowledge. As will be elaborated below, DNA barcoding is fully legal and the DNA barcodes (Janzen & Hallwachs, 2016b) are officially public domain, owing to considerable governmental understanding for permits by SINAC (the National System of Conservation Areas), the National Commission for Biodiversity Development (CONAGEBIO), the Minister of Natural Resources and Energy (MINAE), and the ACG government biomanagement staff itself (Bazilchuk, 2019, and http://www.acguanacaste.ac.cr).

5. Integration of the 43,000 ha ACG Sector Marino (Figure 1) into the overall restoration and permanent survival of ACG has been a major challenge. Though initially established with about 20,000 marine hectares from terrestrial Parque Nacional Santa Rosa out to the national limit, it long suffered from the same neglect and market-hunting that plagues generally unprotected marine and terrestrial landscapes. In 1974, three years after PNSR was decreed, the visitor to the Playa Naranjo beach was greeted by a large sign in Spanish that said "No fishing with dynamite." While PNSR was legally expanded out from Sector Murciélago (legally an addendum to PNSR) to include about 6 km out to sea from the coast at a time when the islands were unoccupied, the entire area was both heavily fished by artisanal fishers moved in from further north by the conflicts in Nicaragua, and legally contested by the ongoing expropriation case for Sector Santa Elena from its US owner. Only since about 2005 have serious protection efforts been possible, and these are still hampered by long boat time, high cost for boat maintenance, and the lack of permanent residents on the islands; artisanal fishing pressure is always present as neighboring fishing areas have been exhausted.

6. Given our backgrounds with heavily endowed ivory tower academia, with its contingency support for the ups and downs of income from student tuition and grants, it was an automatic decision to begin building a management endowment to supplement the government annual budget for ACG. The initial endowment was established through a debt-for-nature swap, whereby a $3.5 million cash donation from the Swedish government to "finish" ACG in 1988 was passed to Solomon Brothers to purchase about $28 million of Costa Rican international debt, which in turn was 75% recognized in Costa Rican currency (colones) by the Costa Rican Central Bank (Allen, 2001; Janzen et al., 1993; Klee, 1989). These colones were then used for land purchase, infrastructure, and to pay back the colon loans from Costa Rican banks. These had been secured by dollar collateral donated by thousands of individual international donors for the construction of ACG. The collateral then received by paying off these loans with colones was then used to establish a $11.5 management endowment for ACG, and hiring staff that would devote full interest and enthusiasm to construction of this novel NGO-government hybrid institution (which it still is today). Eventually, this endowment declined in value for many reasons, and the government then provided about 100 positions to ACG through the annual budget. This is today augmented by $1-$2 million input per year from GDFCF while GDFCF simultaneously rebuilds a separate GDFCF endowment for continued ACG operations support (primarily parataxonomists and their administration/guidance), supplemental to the $3.5 million annual support from the government. The parataxonomist cost of about $800,000/year is the largest single GDFCF ACG support. This then provides the base process of "know thy park" by the resident parataxonomists and their facilitators. We are pro bono, supported by DHJ's tenured position at the University of Pennsylvania, as the Paul and Karen DiMaura Professor of Conservation Biology.

5 | AND NOW WHAT HAS HAPPENED?

Just about the time that ACG organismal life as a hybrid NGO-government beast has survived various governments, many small challenges, and the occasional big one, and is about 20 years old and feeling sort of OK, along come two quite different megachallenges and megaopportunities.

5.1 | Climate change

In the mid-1980s, the project to increase the area of PNSR expanded to the eastern wetter and mountainous half of ACG in order to accommodate the seasonal back and forth east–west annual migrations/movements of insects, bats, and birds (Janzen, 1987c, 1988d). In doing so, it unconsciously prepared as best it could for the horizontal rescue of biodiversity as climate change dries and de-synchronizes the ACG dry forest Pacific side. A newspaper graph illustrates; in 1963 when DHJ first arrived, there were

120 days/year at Liberia with 32 C or greater maximum temperatures, while today there are 180 such days (NYT, 2018). In effect, the ACG dry season has become two months longer, to say nothing of the conspicuous unpredictability and asynchrony between the stop/start of the rainy seasons and the other environmental triggers and conditions. Also during the 1980s, while exploring the minimally cloud-forested and swampy-saturated upper slopes of all three volcanos (Orosi, Cacao, Rincon de la Vieja massif), we set the visual baseline for recognizing the drying of this cloud forest, as the heated and drier lowland air mass has moved up the volcanos (Figure 6).

It is an easy prediction that by 2050 there will be essentially no remaining cloud forest on the top of the Cordillera Guanacaste (and consequently, very little water flowing from it). While the large old adult trees of Sector Cacao will perhaps be the "last man standing" (a kind of "living dead," Janzen, 2013), long before 2050, the drying litter, the conspicuous decline in insects, the steadily declining fall of epiphytes from the canopy, and the actual movement of lowland species to the cloud forest previously unoccupied by them has been self-evident right now.

We have not been able to measure this drying in any particularly "scientific" way; when the house is burning, a thermometer is not the thing to call for (Janzen & Hallwachs, 2019a). ACG has done a moderately thorough job of moving all the flanks of the volcanos into national park status, with the exception of one $60 million property (6,000 ha) on the northwestern slope/foothills of Volcan Rincon de la Vieja. The volcano slopes are important because they do give the opportunity for upslope movement, except of course for the biodiversity at the top (Figure 6). At lower elevations, more area of rain-forested lowlands would be good as a partial buffer as well, so that those in the 0–100 m elevation band can move farther laterally, sustain larger populations overall, and have more locally peculiar habitats that allow total or partial survival from changes in both the direction of drying/heating, and surplus of rainfall (as compared to before). However, lowland rain forest expansion for ACG means largely more purchase of agriculturally productive lowland agroscape (therefore costing more per hectare), and additional highly effective *Gmelina* seedling planting ($400/ha) to create the shade conditions that eliminate grass and create a forest understory microecosystem as in the adjacent forest. However, some patches of this habitat are still available for willing seller–buyer negotiations with people for whom the land is simply an income generator.

The interior of ACG has experienced a subtle and generally ignored local climate change. Originally, the rain forest and cloud forest ecosystems were quite distinct from the dry forest on ACG's Pacific side. However, during about two centuries of agroscape (plus logging, ranching, hunting, burning, urbanization) moving from the hospitable dry forest side of ACG to the more continually wet and inhospitable rain and cloud forest sides of ACG, the more continually wet Caribbean ecosystems have become substantially more dry, windy, and sunny. Select sets of "dry forest species" have moved with this agriculturalization into terrain once occupied by
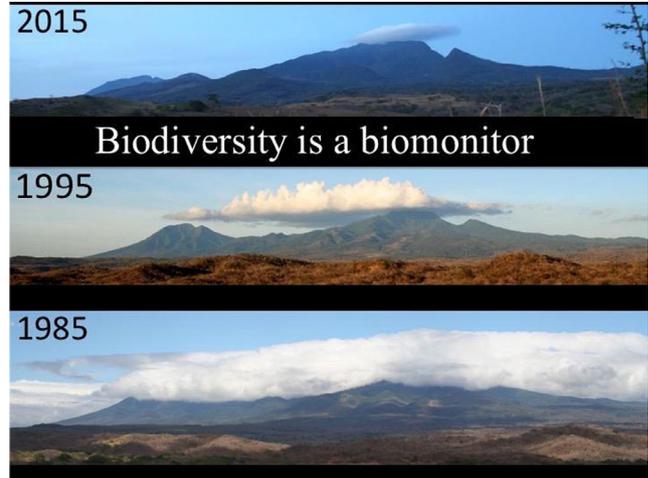
FIGURE 6 In the 1980s, Volcán Orosí (left) and Volcán Cacao (right) of Cordillera Guanacaste were generally swathed in dense clouds created by the uplift of the moist trade winds off the Caribbean blowing southwesterly; the "normal" photograph year-round was as above. By the 1990s, there were many dry season days and some rainy season days like the middle image. Today, it is commonplace to see the former cloud forest cloud free or with broken clouds, or clear at some part of the day. The result is a gradual but intense drying of the cloud forest at 1000–1500 m. Weather station records say the same thing, and the changes to the animal and plant biodiversity as a species-rich biomonitor do as well

year-round evergreen rain forest with its associated biodiversity and have also obliterated the striking original boundaries among ecosystems in the process (Janzen, 1986c, 1986d, 1987b). Much of this biodiversity has remained, albeit at very different densities and microecosystem occupiers, and is interacting with new neighbors. However, much of it has simply disappeared. We have encountered no cases of biodiversity flow in the opposite direction, from former rain forest to dry forest, hectare by hectare. This local microclimate change for ACG is irrespective of industrial countries dumping their carbon waste into the global atmospheric commons. However, it is exacerbated by the general warming, drying, and desynchronization brought by current global climate change resulting from that dumping.

5.2 | National bioliteracy: BioAlfa

The outstanding success of the PEB has made it clear that rural Costa Rican school children quite capably and eagerly absorb natural history and ecology in the field, and all that goes with it. Logic and observation are contagious, as long as the biodiversity information is there to pass on to them. Just as an ecotourist who is not bioliterate sees just a green mass when looking at an ACG forest seething with biodiversity interactions, so does a child forced to memorize a list of names or dissect a pickled frog. Querying the living classroom is another matter. Equally, the adult parataxonomists, drawn from the rural countryside workforce to be biodiversity discoverers,

documentors, and managers, as career-paraprofessionals, irrespective of their high school formal education at best, have proven to be very capable at absorbing, possessing, and repackaging biodiversity information for general bioliteracy (Janzen, 2004; Janzen & Hallwachs, 2011, 2019b; Janzen et al., 1993; Schmiedel et al., 2016; see their Species Pages on the ACG web site) (https://www.acguanacaste.ac.cr/paginas-de-especies).

In 2003, DNA barcoding was added to the ACG inventory process (Janzen & Hallwachs, 2016b, 2019a, 2019b), converting it to an entirely different endeavor from the Victorian era of specimen collecting followed by decades of effort and the expense of getting names put on before biodiversity information could be "used" in its many ways. DNA barcodes are short sequences of mitochondrial COI DNA that differ among species. Through the use of these barcodes as names and identifiers for specimens, inventory via DNA barcoding can be done by anyone with minimal coaching long before the organisms have entered the identification and formal description pipeline connecting them to past centuries of biodiversity discovery. This allows the taxonomists to focus their work on particular species of focal interest at a given time, urgency or cause, while meanwhile literally hundreds of thousands of species can be efficiently worked with and used without having a formal scientific name (Bazilchuk, 2019; Janzen & Hallwachs, 2016b, 2019b; Janzen et al., 2009).

ACG has worked well (with mild friction) as a hybrid NGO-government entity fine-tuned to its peculiar biophysics, bureaucratic place, resources, and available reality. The question has emerged periodically as to why do the other national parks of Costa Rica not abruptly or gradually morph into something conceptually similar, but fine-tuned to their own particular circumstances? The reply bears directly on the stimulus for the emergence of the BioAlfa project (Janzen & Hallwachs, 2019b).

First, bottom-up management, resulting in de facto decentralization, meets with many bureaucratic and social barriers as central political power is weakened and morphed away as decentralization occurs. Second, long-established moderately adequate short-view conservation laws, regulations, traditions, and entitlements resist potential shifts in their bureaucratic structures. Third, there needs to be shift from the conservative older generation to the traditionally more "radical" next generation in search of their own job and intellectual security. For ACG, these hurdles were partly alleviated by:

1. SRNP's long initial distance from the seat of Costa Rica's political and economic power,
2. Tacit approval for its evolution by its original director, Alvaro Ugalde, by then the Director of the National Park Service,
3. A minimalist government employee staff and strong NGO staff,
4. Friendly top-tier politicians,
5. The presence of mission-directed biologists with a strong understanding of the biological nature of the ACG's ecosystem complex to support its restoration and its seasonality, and finally,
6. A hand-made within-bureaucracy "Meddler Section" ("Sección de Metichismo"), invented by SRNP Director Sigifredo Marin to calm

tensions, was occupied by us as biologists with little reverence for established protocols that were not achieving the rescue of the tiny remnants of tropical dry forest remaining, despite having been declared legally protected by its national park status.

The first attempt at spreading the ACG concept of mission-oriented park management to the other Costa Rican national parks led to the original course for parataxonomists in 1989, followed by another in 1990 (Janzen, 2004; Janzen & Hallwachs, 1992a, 2011), and a third female parataxonomist course in 1992 (funded by the Liz Claiborne Foundation; Janzen & Hallwachs, 1992b). The membership of the first two 15–20-member parataxonomist courses was constituted by salaried "guardaparques" (park guards) from different national parks scattered all over Costa Rica, and the third almost entirely female course was drawn from the rural private sector all over Costa Rica, though generally near national parks. The basic activity of the course was hands-on biodiversity inventory. The concept was that after six months of intensely living the ACG protocols, all of these parataxonomists would go back to their home national parks and begin to be a gradual influence toward decentralization. They were not. The established structures absorbed those who stayed in their home parks, while the others moved far afield both nationally and internationally. Their time and training in scientific attitudes and biodiversity inventory were not wasted on them and their neighbors, but did not achieve the intended outreach purpose, despite collecting enormous amounts of data and specimens. From 1989 on, the latter became the starting yeast for INBio (Gámez, 1999), the private National Biodiversity Institute (Janzen, 1991, Gámez, 1999). This 3.5 million-specimen arthropod collection has now moved (on paper but not physically) to the Museo Nacional de Costa Rica where its access and curation is limited, but over time we anticipate that this speed bump will be clarified.

In late 2017, the Luis Guillermo Solís Presidential administration (2014–2018) published decree #40725 officially declaring that Costa Rican DNA barcodes (the diagnostic short sequence of mitochondrial COI DNA) are public domain. This is because, despite being "DNA," barcodes function as scientific information of no more commercial value than is a scientific name. In 2018, the incoming administration of President Carlos Alvarado Quesada and Minister of Environment and Energy Carlos Manuel Rodriguez have expanded this, building on the activities of the ACG and INBio and other Costa Rican entities as pilot projects for a new project, BioAlfa (Janzen & Hallwachs, 2019b). "BioAlfa" is a highly participatory project to prepare the platform for a bioliterate country of 5 million people over about ten years, by Costa Rica for Costa Rica (Bazilchuk, 2019). It will be the first tropical country to have more than an inkling of what biodiversity really does live in it (and especially, in its conserved wildlands), all estimated 1,000,000 + multicellular species (arthropods, fungi, nematodes, and the minor groups – plants, vertebrates, and riff-raff). This will cost $100 million spread over ten years, hoped for from the international sector, coupled with massive sweat equity by the Costa

Rican populace itself, be they amateurs, private employees or government employees. While its initial scope is limited to terrestrial and fresh water, we expect that Costa Rica's marine sector will likely follow along within a few years.

BioAlfa made its debut on 11 June 2019 with Costa Rica's presidential decree #41767, which officialized the National Biodiversity Inventory to be of National Interest (to be published in the government's Gaceta). This decision was announced at the 8th International Barcode of Life biodiversity conference in Trondheim, Norway, on 17–20 June 2019 (Bazilchuk, 2019). The first sets of insect-capturing Malaise traps, equally part of BioScan, the iBOL global biodiversity inventory effort (http://ibol.org), have now been established in nine Costa Rican national parks in addition to ACG, which was the starting point for the pre-BioAlfa in 1978–1985 in Costa Rica. On an international scale, these first Costa Rican BioAlfa traps are also part of the collaborative iBOL (International Barcode of Life) global biodiversity inventory effort named BioScan (http://ibol.org). These first mass sampling and biomonitor traps are being manned and managed by established government payroll park guards as part of their normal activities, and they are also the starting point for the individual parks to find out for themselves what it is that they are conserving. This is how ACG science-based management is beginning to spread to the remainder of the country. The Centre for Biodiversity Genomics (CBG) at the University of Guelph, Guelph, Canada, is fully experienced and prepared for DNA barcoding the anticipated flood of specimens, as they have done for ACG since 2004 (Janzen & Hallwachs, 2016b). The rate and mechanisms of spread of information capture, information processing, and information delivery to the entire user community will depend on international financial resources. However, preliminary discussions with private and government sectors (and especially the Ministry of Education, the Ministry of Environment and Energy and the Ministry of Science and Technology) indicate strongly that the Costa Rican community at large is fully on board to strive for national bioliteracy, assuming that international fund-raising can cover the laboratory costs for sequencing and minimalist administration and equipment/supplies budgets.

6 | CONCLUSION

There are no logical or technical absolute barriers to socially and biologically engineering large conserved tropical wildlands to become sustained and productive members of their surrounding local, regional, national, and international societies. But it is not easy. There are many outstanding traits of human societies that must be self-managed and externally managed for it to actually happen. To convert Parque Nacional Santa Rosa into ACG while embedded in a low-density democratic society, on poor soils, and far from central political forces and desires in 1985, was, and still is, low-hanging fruit. What parts and processes of its experiences can be valuable tools in creating and restoring similar wild areas that are allowed to survive into perpetuity in other parts of the tropics (e.g., Janzen & Hallwachs, 2019b; Pringle,

2017) depends on the specific traits of the other parts. There is no shirt that fits all, but there is the concept of a shirt—sleeves, fabric, pockets, style, buttons, sizes, and colors. And the shirt has to be desired by its wearer(s). Human social desire is the single most needed trait for allowing survival of wild tropical biodiversity.

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PAPER

WILEY **bioTROPICA** ASSOCIATION FOR TROPICAL BIOLOGY AND CONSERVATION

Habitat size thresholds for predators: Why damselflies only occur in large bromeliads

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Abstract

Predators are often more sensitive to habitat size than their prey and frequently occur in only the largest habitats. Four explanations have been proposed for this pattern: (a) Small habitats do not have enough energy to support higher trophic levels; (b) small habitats are less likely to contain particular prey required by specialist predators; (c) small habitats are risky for predators with slow life histories or large body sizes; and (d) small habitats are numerically unlikely to be colonized by regionally rare species, such as predators. We critically examine these four hypotheses in relation to the predatory damselfly larva, *Mecistogaster modesta* Selys. (Pseudostigmatidae), which occurs almost exclusively in bromeliads > 100ml in capacity. We synthesize multiple years of survey data and three manipulative experiments from the Área de Conservación Guanacaste, Costa Rica, to conclude that damselflies do not occur in small bromeliads due to their higher risk of desiccation—not because of energetic limitation, trophic specialization, risk of terrestrial predation, or pure numerical effects. These results suggest that recent and predicted declines in precipitation in northwestern Costa Rica may further restrict bromeliad occupancy by damselflies, with cascading consequences for the rest of the aquatic food web.

Abstract in Spanish is available with online material.

KEYWORDS
Área de Conservación Guanacaste, cannibalism, climate change, Costa Rica, drought risk, energetic limitation, incidence function, *Mecistogaster modesta*, phytotelmata

1 | INTRODUCTION

Predators are often thought to be more sensitive to ecosystem size than their prey. Top trophic levels are typically present in only the largest habitats (McHugh, Thompson, Greig, Warburton, & McIntosh, 2014; Ostman et al., 2007; Roslin, Varkonyi, Koponen, Vikberg, & Nieminen, 2014; Schoener, 1989; Terborgh et al., 2001). Similarly, a number of studies report that reductions in habitat area result in extinctions preferentially at top trophic levels (Davies, Margules, & Lawrence, 2000; Didham, Lawton, Hammond, & Eggleton, 1998; Staddon, Lindo, Crittenden, Gilbert, & Gonzalez, 2010), although

this is not always the case (Martinson & Fagan, 2014; Starzomski & Srivastava, 2007). Patch occupancy by species is also more strongly related to area for carnivores than lower trophic levels (Prugh, Hodges, Sinclair, & Brashares, 2008). A different way to see the same pattern is with species–area relationships: within food webs, top trophic levels often have steeper species–area relationships than lower trophic levels, consistent with greater sensitivity to area (Gravel, Massol, Canard, Mouillot, & Mouquet, 2011; Hoyle, 2004; With & Pavuk, 2011).

At least four explanations have been proposed to explain predators' greater sensitivity to ecosystem size. The *"energetic limitation"*

hypothesis argues that ecosystem size is a proxy for the total amount of energy (Wright, 1983). If the input of resources per unit area is constant, small habitats will have lower absolute amounts of resource inputs than larger habitats. Given the inefficiencies in trophic transfer between trophic levels (Hairston & Hairston, 1993; Lindeman, 1942), in theory there must be a habitat size too small to have enough energy and nutrients to maintain a viable population of a top predator (Hurlbert & Stegen, 2014; Hutchinson, 1959; Schoener, 1989). A variant of this idea is that the diverse prey base of large habitats offers a more productive supply of prey (Holt & Hoopes, 2005). Although some ecological patterns with habitat size are consistent with energy limitation (Schoener, 1989; Terborgh et al., 2001; Vander Zanden, Shuter, Lester, & Rasmussen, 1999), it has so far not been strongly supported (Post, Pace, & Hairston, 2000; Spencer & Warren, 1996).

The *"trophic rank"* hypothesis (Holt, 2009; Holt, Lawton, Polis, & Martinez, 1999) assumes, like classic island biogeography theory, that species encounter large habitats more frequently than small habitats. However, if predators can only consume certain prey species, then predators that colonize small habitats may not be able to establish because their prey has not yet colonized the habitat (Bascompte & Sole, 1998). This compounding of area effects up the food chain can result in the ratio of predators to prey increasing with patch size (Gravel et al., 2011; Holt et al., 1999). Supporting this hypothesis, specialist—but not generalist—parasitoids have steeper species–area curves than their herbivorous prey (Cagnolo, Valladares, Salvo, Cabido, & Zak, 2009).

The *"risky habitat"* hypothesis (Amundrud & Srivastava, 2015) holds that small habitats are inherently riskier for species because they are more likely to experience catastrophic events, such as drought for a rockpool (Vanschoenwinkel et al., 2009) or storm surges for an island (Chui & Terry, 2013), or because their greater edge to area ratio allows disturbances from the matrix to penetrate more of the habitat (as shown for bushmeat hunting in reserves, Brashares, Arcese, & Sam, 2001). Predators have often been reported to be more sensitive to such disturbances than their prey (Menge & Farrell, 1989; Petes, Mouchka, Milston-Clements, Momoda, & Menge, 2008; Voigt et al., 2003). This may occur for several reasons. If predators are larger than their prey, as is typical for engulfing predators, they may not be able to access refuges from disturbance (Nash, Graham, Wilson, & Bellwood, 2013). If predators have low densities or "slow" life histories (long generation times, late age at maturity and low fecundity), their populations may not be able to recover quickly from disturbances (Newbold et al., 2013; Salguero-Gomez et al., 2016). Even if predators and prey individuals are equally susceptible to disturbance, the typically lower density of predators may result in greater likelihood of local extinction following disturbance.

Finally, the *"regional abundance"* hypothesis relates the low incidence of predators in small habitats to their lower regional abundance than prey species. Stochastic models show that species at low regional abundance can appear to be more sensitive to area (e.g., have steeper species–area relationships) than species at higher regional abundances simply through sampling effects, that is, even if individuals are randomly placed in habitat patches irrespective of

trophic requirements (Holt, 2009; Srivastava, Trzcinski, Richardson, & Gilbert, 2008).

In this study, we examine whether these hypotheses can explain the distribution of a key predator in bromeliad food webs. Bromeliads are Neotropical plants that often collect water and detritus between their leaves, providing habitat for detritivorous and predatory macroinvertebrates (Richardson, 1999; Srivastava, 2006). Srivastava et al. (2008) found that predators were more sensitive to bromeliad size than detritivores, but in two field sites (Puerto Rico and Dominica) the regional abundance hypothesis accounted for such differences. The exception was Costa Rican bromeliads with high densities of damselfly larvae (*Mecistogaster modesta* Selys.) whose occurrence increased abruptly when bromeliads exceed 100 ml in capacity. Such damselflies do not occur in Puerto Rican and Dominican bromeliads. In a second analysis, Amundrud and Srivastava (2015) confirmed that *M. modesta* occurs in larger bromeliads than expected simply from its regional abundance. The proximate reason for the occurrence of *M. modesta* in large bromeliads is that adult female damselflies choose to oviposit in bromeliads greater than 100 ml in capacity, and adult males defend territories around such large bromeliads (D. S. and J. N., unpubl. results).

These observations still leave unanswered the question of why adults prefer large bromeliads. If damselflies are optimizing their fitness by choosing large bromeliads, it is likely that damselfly larvae experience lower larval survival in small bromeliads. In this study, we investigate potential reasons for the sensitivity of *M. modesta* larvae to bromeliad size. We have already concluded that the regional abundance hypothesis cannot completely account for this sensitivity, based on previous analyses (Amundrud & Srivastava, 2015; Srivastava et al., 2008). We can also discount the trophic rank hypothesis, as both feeding trials and fecal dissections indicate that *M. modesta* is a generalist predator: It consumes every macroinvertebrate species co-occurring in bromeliads (D.S. and J.W., unpubl. data, see also Srivastava, 2006). We therefore examine in detail the remaining two hypotheses, specifically the energetic limitation hypothesis (insufficient prey availability in small bromeliads) and the risky habitat hypothesis (high risk of terrestrial predation, cannibalism, or desiccation in small bromeliads). Note that although cannibalism by itself could never lead to the absence of a species, it could lead to very low abundances and the likelihood of complete loss through stochastic processes.

In this paper, we use multiple years of survey data as well as three manipulative experiments to test the following predictions. If the energetic limitation hypothesis is important, we would expect that: (a) the amount of resources potentially available to each damselfly larva would diminish as we examined progressively smaller bromeliads until no damselflies were found, and (b) larvae transplanted into bromeliads smaller than 100 ml would fail to grow, and often die of starvation. The risky habitat hypothesis would be supported if small bromeliads had high risk of cannibalism, terrestrial predation, or desiccation. Large hunting spiders may be particularly important terrestrial predators of damselflies. If larval abundance is limited in small bromeliads by cannibalism, we would expect that (c) intraspecific encounter rates are greatest in small bromeliads. If terrestrial predators exclude damselfly larvae from small bromeliads, we would expect that (d) larvae

transplanted into bromeliads with and without terrestrial predators would disappear predominately from small bromeliads with predators. Finally, if drought risk restricts damselfly larvae to large bromeliads, we would expect that (5) the likelihood of desiccation would be greatest in small bromeliads and damselfly larvae would be particularly sensitive to drought as compared to other species.

2 | METHODS

2.1 | Study site and system

We have studied, since 1997, the aquatic macroinvertebrates living in bromeliads in the premontane rain forest surrounding Estación Biológica Pitilla (Área de Conservación Guanacaste, 10°59'N, 85°26'W, 700 m a.s.l.). In this area, bromeliads that trap water between their leaves are either in the *Guzmania* genus (especially *G. scherzeriana* Mez, *G. donnellsmithii* Mez ex Donn.Sm., and *G. desautelsii* Read & L.B.Sm.) or the Vrieseeae tribe (esp *Werauhia gladioliflora* (H. Wendland) J.R. Grant, *W. sanguinolenta* (Linden ex Cogniaux & Marchal) J.R. Grant, *W. kupperiana* (Suessenguth) J.R. Grant). Water-filled bromeliads passively collect detritus through leaves and other organic matter that fall in their tanks. This detritus is an important basal energy source for the aquatic food web in the bromeliads, supplemented by algal production in open areas (Farjalla et al., 2016). The detritus is conditioned by bacteria and fungi and then consumed by a diverse suite of shredding, scraping and collecting detritivores. The microbes also fuel a community of protists (ciliates, flagellates, rotifers, amoeba), which in turn are prey to filter-feeding mosquito larvae. The detritivore and filter-feeding invertebrates are preyed upon by small-bodied predators (Ceratopogonidae, Tanypodinae, Hirudinae), and large-bodied piercing (Tabanidae) and engulfing predators (Dytiscidae, and the damselfly *Mecistogaster modesta* (Pseudostigmatidae)). Over the last 22 years, we have found > 70 species of aquatic invertebrates in bromeliads at Pitilla.

2.2 | Observational surveys: Damselflies and prey communities

We determined abundances of *M. modesta* larvae in bromeliads from the secondary forest between September and November in 1997, 2000, and 2002 (*n* = 20, 20 and 18 bromeliads, respectively). Prey communities in these bromeliads were also recorded in 1997 and 2002, but not 2000. Bromeliads were selected to represent a wide range of water capacity: 0.4–1530 ml in 1997, 35–4,690 ml in 2000, and 18–7,132 ml in 2002. In 1997 and 2000, both *W. sanguinolenta* and *Guzmania* spp bromeliads were included. In 2002, only *W. sanguinolenta* bromeliads were examined.

Bromeliad insect communities were censused as follows. Bromeliads were harvested from the forest and transported upright in buckets to the field station, where they were each inverted over a funnel (80 cm diameter) to collect the contained water. The

water-holding capacity of the bromeliad was determined by pouring a known volume of water into all leaves of the empty bromeliad until it overflowed, and subtracting the overflow amount. Bromeliad capacity is arguably the most relevant measure of habitat size for aquatic insects and correlates better with species richness and abundance than other measures such as diameter, amount of detritus, number of leaves, or water volume on the sampling date (Srivastava et al., 2008). Each bromeliad was carefully dismantled over the funnel, leaf by leaf, and all leaf surfaces were washed into the funnel.

All collected debris and water were searched by eye for living larvae by mixing small amounts of debris with water in white trays. Individual larvae were counted and identified to species or morphospecies, and body length (excluding caudal lamellae for *M. modesta*) was measured and converted to fresh mass using empirically determined relationships (r^2 = 0.96, N = 46 for *M. modesta* and r^2 = 0.75–0.94 for prey taxa). This allowed us to estimate the total predator and prey biomass in each bromeliad. Although cannibalism occurs (based on fecal dissections and gut analyses), *M. modesta* larvae were not themselves included as prey items to avoid confounding the response and explanatory variables. Cannibalism cannot be directly measured in field surveys, but for sit-and-wait predators we might expect cannibalism to lead to a pattern of no more than one damselfly per leaf tank.

Large spiders (Trechaleidae: *Cupiennius coccineus* F.O. Pickard-Cambridge) occur in the terrestrial portion of bromeliad leaves. We visually searched for *C. coccineus* spiders in 48 bromeliads in the pastures and secondary forests surrounding the station from 29 to 31 October, 2005. We measured the maximum distance between leaf tips as an estimate of bromeliad size.

2.3 | Hydrology monitoring: Desiccation risk

To examine the effect of bromeliad size on desiccation risk, we measured water depth (± 1 mm) in three leaves (central and two peripheral) of 30 bromeliads every two days from October 2012 to October 2013. Bromeliads representing a range in capacity (12–33 ml; 6 bromeliads, 34–67 ml: 6 bromeliads, 68–100 ml: 10 bromeliads, 100 ml–580 ml: 8 bromeliads) were selected from the vicinity and transplanted to a homogeneous 1 ha of mature secondary forest. Each bromeliad was attached to the side of a vertical tree trunk using broad strips of plastic screen mesh. For each bromeliad, we calculated the sum of all drought days over the survey period, where drought was defined as all three leaf wells being completely dry (i.e., 0 mm water depth) simultaneously. We used linear regression to quantify the effect of bromeliad capacity (log-transformed) on desiccation risk (total drought days) and quantile–quantile and residual plots to check for model assumptions of linearity and homogeneous variance.

2.4 | Experiment 1: Effect of bromeliad size on damselfly survival and growth

In October 2002, we collected 29 *M. modesta* larvae (10–12 mm long, excluding caudal lamellae) and marked these insects by amputating

the right middle leg, removing the last two segments (tarsus, tibia) just below the femur. Each larva was placed in a leaf axil (one larva per bromeliad), near the center of a bromeliad in the secondary forest (14 *Guzmania* spp., 15 *Werauhia* spp., 8–2,636 ml in volume). Twenty days later, we searched for marked larvae by dismantling each bromeliad leaf by leaf to search and measured bromeliad capacity. The amputated legs had only partially regrown, and the experimental damselflies could be easily recognized. To measure larval growth, we weighed larvae to the nearest 0.002 g before the experiment (but after amputation) and at the end of the experiment and calculated specific growth rate as the change in mass as a proportion of the initial mass. Recovery of larvae as a function of bromeliad capacity (log-transformed) was analyzed in a logistic generalized linear model with a logit link and binomial errors. This model was a good approximation of the data as the dispersion coefficient was approximately one.

2.5 | Experiment 2: Effect of bromeliad size on spider predation

The spider *C. coccineus* frequently lives in the terrestrial portion of bromeliads and may be an important terrestrial predator of *M. modesta* larvae. We had previously observed *C. coccineus* spiders diving underwater to capture *M. modesta* larvae in water-filled plastic cups. Twenty *Werauhia* bromeliads ranging from 68 to 700 ml in maximum capacity were collected in the vicinity of Pitilla and divided into two groups (control, experimental) with similar size ranges. Bromeliads were hung in a common garden and enclosed with netting to prevent spider and insect dispersal. Any resident spiders were removed prior to the experiment.

Twenty damselfly larvae ranging from 0.034 to 0.110 g were collected from the vicinity of the field station during surveys of bromeliad insect communities. We marked damselflies by amputating the last two segments of one leg (tarsus and tibia) as before. Each damselfly was added to a bromeliad and left to acclimate for a day before one spider was added each of the ten experimental bromeliads.

Ten *C. coccineus* spiders were collected from bromeliads near the field station, and one spider was added to each of the experimental bromeliads. After 24 hr, all bromeliads were dismantled leaf by leaf to collect the experimental spiders and damselflies, and damselfly survivorship was recorded. Survivorship was analyzed in a logistic generalized linear model with a logit link and binomial errors, and with spider presence, bromeliad capacity (log-transformed) and their interaction as explanatory factors. The dispersion coefficient was approximately one, indicating that the model error structure was a good approximation of the data.

2.6 | Experiment 3: Effect of drought on damselfly survival and growth rate

To examine the effects of drought on damselfly survival and growth, we manipulated drought length (defined as 0 mm water depth) in

artificial microcosms, imposing droughts of 10, 15, 20, 25, and 30 days in length. We also had an equal number of controls, which were treated identically, except that they were not subjected to drought. Each microcosm housed a single damselfly larva. Each drought length treatment or matching control was represented by two microcosms, except for the 30-day drought treatment with six microcosms. Damselflies were fed small larvae of chironomids, tipulids, or mosquitos every two days to ensure starvation did not contribute to mortality.

The microcosms were constructed to approximate the size of a single *Werauhia* bromeliad well, but to allow water levels to be manipulated without handling or disturbing the damselflies (Amundrud & Srivastava, 2015). Each microcosm consisted of a 50-ml centrifuge tube sitting in a 207-ml plastic cup. To allow water, but not damselflies, to move between the tube and cup, we first cut off horizontally the tapered bottoms of the tubes and covered the now open bottom end of the tube with Nitex screen (80 μm mesh size). To increase the flow of water even further, we also drilled three holes into the side (d = 7 mm), covering these holes with the same type of Nitex screen. In natural bromeliads, overlapping bromeliad leaves form crevices that may act as refugia from drought, similar to the crevices in tree holes (Srivastava, 2005). We created artificial crevices by aligning two pieces (2 cm × 6 cm) of green polyethylene, gluing these together along one edge and bending back one the unglued edge. We placed one artificial crevice in each microcosm.

On 6 November 2012, we filled 28 microcosm cups with filtered stream water to a volume of 15 ml inside the tubes (an approximate water depth of 2.1 cm), a typical volume per bromeliad leaf well (Amundrud & Srivastava, 2016). We added one damselfly to each microcosm and placed microcosms on an outdoor veranda with ambient conditions similar to those of the adjacent rain forest.

On 8 November 2012, we removed all water from half of the microcosms by emptying the cups to initiate drought. After completion of each drought length treatment, we added water to the cups to return to a volume of 15 ml inside the tube. In the controls (which were never subjected to drought), 50% of water was replaced every two days to prevent hypoxia. Two days after the completion of the drought, we emptied the mesocosms of that drought treatment, as well as their corresponding controls and checked for damselfly survival. We employed a logistic generalized linear model with quasibinomial errors (due to overdispersion) to determine the drought length at which damselfly mortality equaled 50%.

3 | RESULTS

3.1 | Damselfly abundances and bromeliad size (Observational surveys, Experiment 1)

In all three years of surveys, *M. modesta* abundances were strongly correlated with bromeliad capacity (Figure 1a, Poisson GLMM with year as random effect: z = 15.4, n = 58, p < .0001): Small bromeliads rarely contained *M. modesta* larvae whereas the largest bromeliads

contained up to 36 larvae. This resulted in a steep incidence function (binomial GLMM: z = 3.12, n = 58, p = .0018) centered on 194 ml (50% likelihood of occurrence) in which damselflies switched from only a 10% likelihood of occurrence at 100 ml to a 90% likelihood of occurrence at 365 ml (Figure 1c). The two bromeliad genera occupy different size ranges, with *Guzmania* spp. at most holding 400 ml of water, and *Werauhia* spp. holding up to 6 L of water. As genus was collinear with bromeliad size, we did not attempt to separate their effects.

In order to determine whether the observed incidence function is due to larvae experiencing different conditions in small and large bromeliads, we transplanted damselflies into bromeliads of differing size. Approximately a third (10/28) of the marked *M. modesta* larvae transplanted into bromeliads were still present when the bromeliads were dismantled 20 days later (Figure 2a). Recovery of damselflies increased with bromeliad capacity (χ^2 = 11.8, df = 1, p = .001), with 50% likelihood of recovery predicted from bromeliads of 118 ml (10% likelihood at 23 ml, 90% likelihood at 623 ml). We generally did not recover cadavers of the marked damselflies, suggesting that larvae were either consumed or voluntarily left the bromeliad.

3.2 | Energetic limitation (Observational surveys, Experiment 1)

Bromeliads exhibited large variation in the availability of prey per *M. modesta* larva in both 1997 and 2002, ranging from 0.02 g prey/

larvae to 0.35 g prey/larvae (Figure 1b; analysis restricted to bromeliads with damselflies). Although per capita prey availability tended to be highest in small bromeliads, there was no significant association between per capita prey availability and bromeliad capacity (LMM with year as random effect: $F_{1,18}$ = 3.51, p = .077). This contradicts Prediction 1 of the energetic hypothesis, which anticipated that predators would depress prey biomass most in small bromeliads.

If damselflies starved to death in small bromeliads (i.e., negative growth rates indicating mass loss), we would expect to find that surviving damselflies would have near-zero growth rates in just slightly larger bromeliads and positive growth rates in much larger bromeliads (Prediction 2). However, in the transplant experiment (Experiment 1), the specific growth rate of the ten surviving larvae was uncorrelated with bromeliad size. (Figure 2b, r = −.03, p = .92, n = 10).

3.3 | Cannibalism (observational surveys)

We typically found a maximum of one damselfly larva per leaf compartment, suggesting that either cannibalism had reduced abundances within leaf compartments to one survivor, or that larva dispersed between compartments to reduce intraspecific encounters or resource competition. Given this distribution of larvae, cannibalism rates will depend in part on the occupation
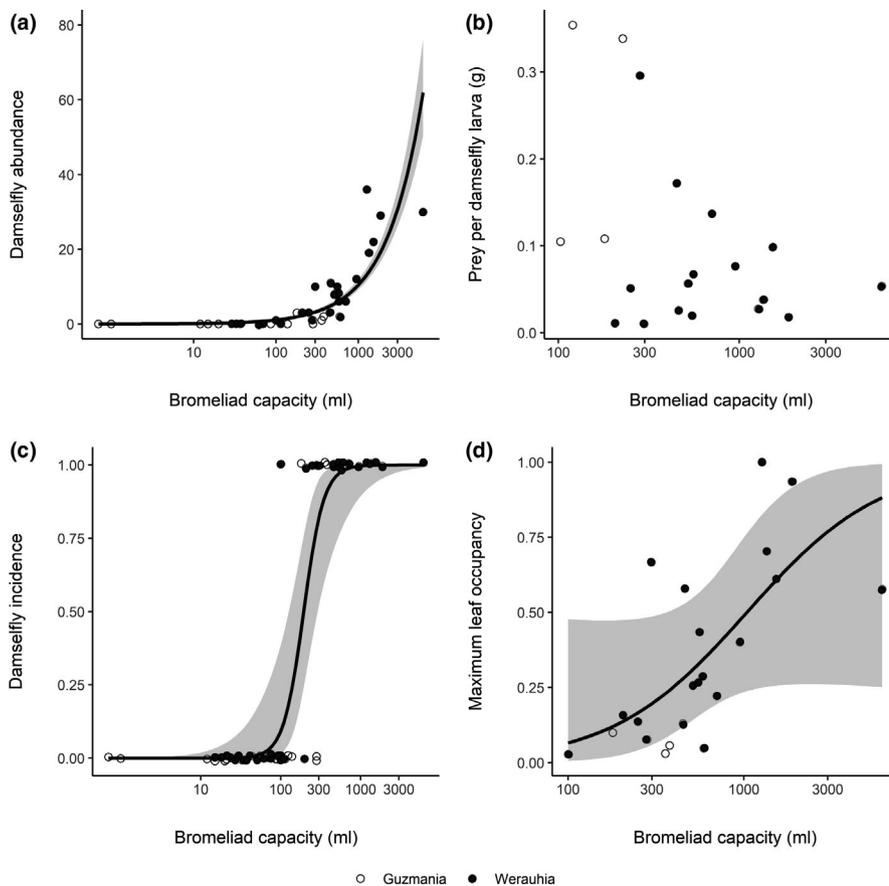
FIGURE 1 *Mecistogaster modesta* larvae were quantified in bromeliads of differing capacity (log scale in this and all figures). The (a) abundance and (c) incidence of larvae increased rapidly with bromeliad capacity. The (d) maximum occupancy of leaf compartments also increased with bromeliad capacity, assuming one damselfly per leaf. However, (b) prey availability per damselfly was unrelated to bromeliad capacity. Bromeliads were surveyed over three years at Estación Biológica Pitilla, in the Área de Conservación Guanacaste, and represented two genera, *Guzmania* and *Werauhia*. Fitted models (solid lines, with the 95% confidence band indicated by shading) are shown only when significant
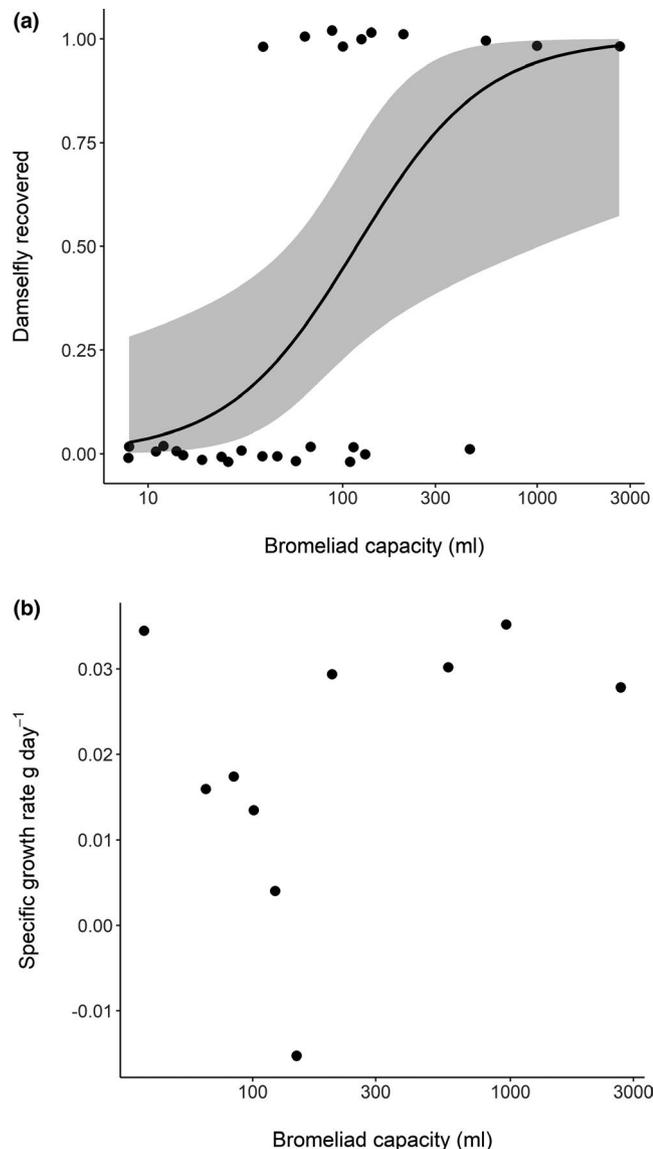
FIGURE 2 *Mecistogaster modesta* larvae that were transplanted into bromeliads of varying sizes were (a) recovered preferentially in bromeliads of > 118 ml capacity, but (b) the growth of the recovered larvae was unrelated to bromeliad capacity. Fitted models (solid lines, with the 95% confidence band indicated by shading) are shown only when significant

of leaf compartments by damselflies, as dispersing larvae will be most likely to encounter a conspecific when all leaf compartments are occupied. We calculated the proportional occupancy of compartments based on a maximum of one larva per compartment, restricting our analysis only to bromeliads with damselflies (as bromeliads without damselflies necessarily have zero occupancy). Smaller bromeliads had lower proportional occupancy of leaf compartments than larger bromeliads, where occupancy approached 100% (Figure 1d, binomial GLMM with year as a random effect: $z = 2.20$, $n = 25$, $p = .027$). If cannibalism limited damselflies in small bromeliads, the opposite pattern (Prediction 3) would have been expected.

3.4 | Terrestrial predation (Experiment 2, Observational survey)

In a second experiment, we transplanted *M. modesta* into bromeliads with and without the bromeliad-associated spider, *Cupiennius coccineus*. Damselfly larvae survived in only 30% of bromeliads with spiders. By contrast, damselflies survived in 80% of bromeliads without spiders—a significant difference in damselfly survival (spider effect: $\chi^2 = 5.30$, $df = 1$, $p = .02$; Figure 3a). However, spider consumption of damselflies did not depend on bromeliad capacity (spider x log-capacity: $\chi^2 = 0.18$, $df = 1$, $p = .67$, Figure 3b), contrary to Prediction 4 (risky habitat hypothesis: terrestrial predation), nor was there an overall effect of bromeliad capacity on damselfly survival (log-capacity: $\chi^2 = 0.0001$, $df = 1$, $p = .99$). Even in the absence of an effect of bromeliad size on per capita rates of spider predation, *C. coccineus* spiders could still limit *M. modesta* to large bromeliads if these spiders primarily occurred in small bromeliads. Our survey shows this not to be the case, if anything, spiders are slightly more frequent in large bromeliads ($r = 0.4$, $p = .005$, $n = 48$).

3.5 | Desiccation risk (Hydrology monitoring, Experiment 3)

Desiccation risk, measured over an entire year, was greatest in small bromeliads (Figure 4). As bromeliad capacity increases, the risk of whole-plant desiccation (i.e., the number of days when all three leaf wells simultaneously had a water depth of 0 mm) decreased exponentially ($R^2 = .42$, $F_{1,28} = 20.477$, $p < .001$). We also examined, for each bromeliad, the longest number of consecutive days the plant was without water. On average, bromeliads were dry for 20.4 ± 6.83 (mean ± SE) consecutive days at least once during the year.

In microcosms, drought significantly decreased damselfly survival and tended to decrease damselfly growth rate. All damselflies subjected to control treatments survived the experiment, but no damselfly survived past the 15-day drought treatment (Figure 5). Logistic regression predicted 50% damselfly mortality at a drought length of 17.51 days (± 0.03 SE, $\chi^2 = 16.75$, $p < .001$).

4 | DISCUSSION

This study documents a non-linear increase in damselfly larval abundance with bromeliad size, crossing an apparent threshold for damselfly presence at approximately 100 ml capacity, with abundances approaching 40 larvae per bromeliad once bromeliads contain several liters of water. There are two potential explanations for the threshold for damselfly presence: (1) There are insufficient resources in small bromeliads to support even a single damselfly larva; or (2) small bromeliads are risky habitats for damselfly larva, either in terms of cannibalism, terrestrial predation, or desiccation (other explanations were discounted in the Introduction). We now examine the evidence for each of these two types of explanation.

Three lines of evidence suggest that damselflies are not limited to large bromeliads because of insufficient resources. First, the amount of prey biomass available per damselfly decreases as bromeliads increase in size, suggesting that resource competition among damselflies intensifies as bromeliads become larger. If resources limited damselfly occurrence in small bromeliads, we would expect the opposite pattern: for resource availability to increase with bromeliad size (Prediction 1). Second, larval growth rate did not differ with bromeliad size, contrary to Prediction 2. This contrasts with tree hole-dwelling odonates where larger adults emerge from larger tree holes (Fincke, 1992). However, in that case, tadpoles (restricted to the larger tree holes) probably provided substantial amounts of prey biomass to the odonates (Fincke, 1992). There were no tadpoles in the bromeliads in this study (e.g., the mid-elevation study site is outside of the range of *Oophaga* spp.), and no similar large-bodied prey item occurs exclusively in large bromeliads.

A second suite of explanations for damselfly incidence patterns involves risk associated with small habitats, whether risk of cannibalism, terrestrial predation, or desiccation. As bromeliad size increases, damselfly larvae occupy an increasing proportion of leaf compartments. If cannibalism was reducing damselfly abundances in small bromeliads, we would expect instead (Prediction 3) greatest leaf occupancy in the smallest bromeliads. Instead, cannibalism is more likely to limit abundances in large bromeliads (> 1 liter of water) where leaf occupancy approaches 80%–100%.

Small bromeliads could have a high risk of predation for damselfly larvae. Although there are other aquatic predators in Costa Rican bromeliads (e.g., tabanid larvae, ceratopogonid larvae), we have not found any aquatic predator able to kill a damselfly larvae in feeding trials; conversely, damselfly larvae are able to kill virtually every other species in the bromeliad as long as the damselfly is larger (D.S.S., unpubl. obs.). However, terrestrial spiders are able to prey upon damselfly larvae, as we demonstrate in Experiment 2, where 70% of damselflies disappeared in the presence of spiders. Similarly, in Brazil, the hunting spider *Corrina* gr. *rubripes* has been observed preying on damselfly larvae within bromeliads (pers. comm. GQ Romero, GC Piccoli, PM de Omena). Since spiders often capture damselfly larvae by entering the water impounded in "tanks" formed by bromeliad leaves, it is possible that small bromeliads have higher predation risk because they have shallower water in their tanks. However, this hypothesis (prediction 4) is not supported by Experiment 2, where loss of damselflies in the presence of *C. coccineus* spiders is unrelated to bromeliad size; nor do these spiders occur more often in small bromeliads. Although we only examined predation by one spider species, *Cupiennius coccineus*, it is the most common large spider associated with bromeliads at the study site. *C. coccineus* naturally occurs in large *Werauhia* spp. bromeliads and dives underwater when under threat, so this species may readily prey on damselfly larvae regardless of bromeliad size.

The final hypothesis is that small bromeliads present a high desiccation risk for larvae because their leaves contain a lower volume and depth of water (Zotz & Thomas, 1999). At the study site, there is typically a long dry season (<20 cm precipitation/month) from February to

April and a shorter dry spell in September, as well as periods without rain throughout the wet season (meteorological data courtesy of Área de Conservación Guanacaste). An analysis of collection records for adult *M. modesta* suggests that, in this part of Costa Rica, their larvae may spend at least 9 months developing in the bromeliad before metamorphosis (Figure 5 in Hedstrom & Sahlen, 2001). Tree hole-dwelling odonates in the same family, Pseudostigmatidae, are estimated to require at least 5.5 to 7 months or more in the larval stage (Fincke, 1992; Fincke, Yanoviak, & Hanschu, 1997). This contrasts with the larval period of damselfly prey, typically on the order of weeks (Srivastava, 2006; Starzomski, Suen, & Srivastava, 2010). Damselflies are therefore at higher risk than other macroinvertebrates of experiencing a dry or near-dry bromeliad during their larval stage, and this difference in cumulative risk between damselflies and their prey is particularly acute in smaller bromeliads (Figure 3 in Guzman et al., 2019).

Drought could lead to damselfly mortality by exceeding physiological limits to desiccation. Our data show *M. modesta* is unable to survive with more than 17 consecutive days of drought, a threshold that was exceeded by 60% of bromeliads in our yearlong monitoring. *M. modesta* larvae may anticipate the risk of drought and leave their natal bromeliad in search of a better bromeliad; in other experiments, we have occasionally recorded larvae dispersing from the bromeliads in which they have been placed (Atwood, Hammill, Srivastava, & Richardson, 2014). However, dispersal must be a fairly risky behavior, as the nearest large bromeliad may be far away with many terrestrial predators along the route. All of the above factors are probably responsible for the loss of damselfly larvae from small bromeliads in Experiment 1.

The importance of drought in determining a bromeliad size threshold for *M. modesta* is consistent with other observations. In a study of ten species of bromeliad insects, we found that the species' physiological sensitivity to drought was a strong predictor of its preference for large bromeliads (Amundrud & Srivastava, 2015). In water-filled tree holes, which contain similar macroinvertebrate communities to bromeliads, drought has also often been reported as the main driver of community composition (Bradshaw & Holzapfel, 1988; Paradise, 2004; Srivastava, 2005). In Panama, larger tree holes contain water for a month longer than small tree holes and produce more and larger odonate larvae (Fincke, 1992). The dominant odonate species in these tree holes, *Megaloprepus coerulatus*, preferentially chooses large tree holes to oviposit (females) and defend (males), reminiscent of adult *Mecistogaster modesta* preferences for large bromeliads. Similarly, in vernal ponds, large dragonflies and fish are often at low abundance or absent in ponds that dry out periodically because of the duration of their aquatic stage or lifespan exceeds the permanence of the habitat (Schneider & Frost, 1996; Stoks & McPeek, 2003). Temporary lentic habitats, in general, are associated with macroorganisms with rapid development, such that a terrestrial or resistant stage is reached before the end of the hydroperiod. Only when these hydroperiods become so long as to be essentially permanent do such lentic habitats have large engulfing predators like odonates (Wellborn, Skelly, & Werner, 1996). The patterns we see along the bromeliad size gradient echo those seen along a lentic hydroperiod gradient, as the size of a bromeliad determines its hydroperiod.

FIGURE 3 Recovery of *M. modesta* larvae transplanted into bromeliads with and without *C. coccineus* spiders was (a) almost three times greater in the absence of spiders, but (b) unrelated to bromeliad capacity
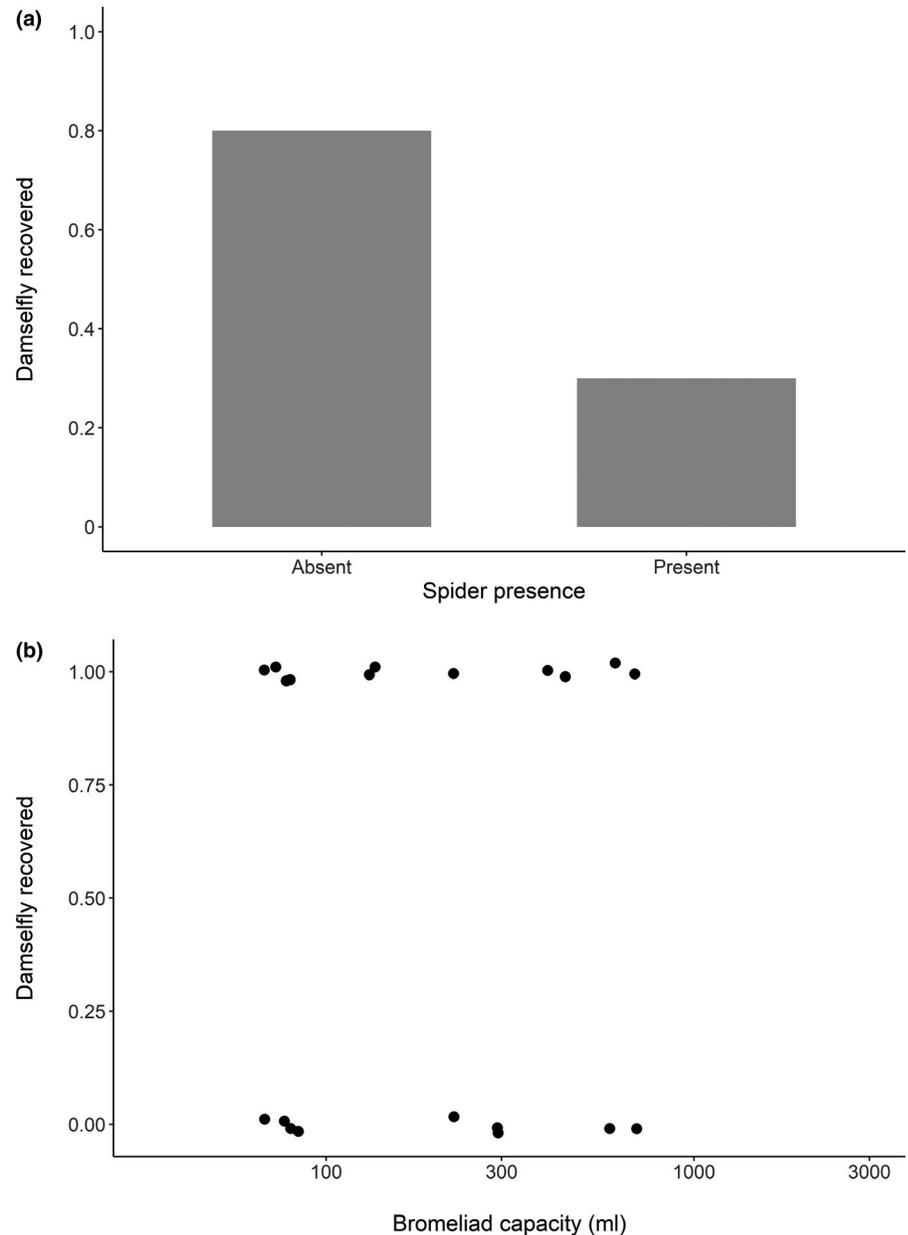
More broadly, we expect disturbance to explain greater predator (than prey) sensitivity to habitat size under the following two conditions: (a) Disturbance is more frequent in small than large patches; and (b) predators require longer disturbance-free intervals for individual or population growth. These conditions may be met in a number of other systems, such as islands susceptible to storm surges and lakes susceptible to anoxia. For example, storm surges following hurricanes can submerge small islands in the Bahamas, causing extinction of all lizards and spiders. The longer generation time and lower dispersal ability of lizards relative to spiders (spiders are both prey and competitors of lizards: Schoener, 1989) results in slower recolonization of islands by lizards (Spiller, Schoener, & Piovia-Scott, 2018). Consequently, lizards only occur on large islands, whereas spiders can also occur on small islands (Schoener, 1989; Spiller et al., 2018). As in our transplant experiment with *M. modesta*, lizards transplanted to small islands may voluntarily abandon these islands (Schoener & Schoener, 1983). Temperate and boreal lakes may also satisfy the dual conditions of small habitats being disturbance-prone and predators being disturbance-sensitive. Shallow lakes are more prone to low oxygen levels in the winter, after the lake freezes over, and as the top predators (Northern pike, largemouth bass) are more sensitive to these conditions than their prey, these predators are restricted to the deepest lakes (Tonn & Magnuson, 1982). While the above systems are particularly well-documented examples of how disturbance restricts predators to the largest habitats, we would expect a wide range of systems to also show similar patterns. Disturbances are often more frequent or intense in small habitats due to their larger edge effects, lower thermal buffering, and fewer physical refuges. Predators may be particularly susceptible to disturbances when their longer life-cycle or larger body size prevents them from accessing refuges or dispersing.
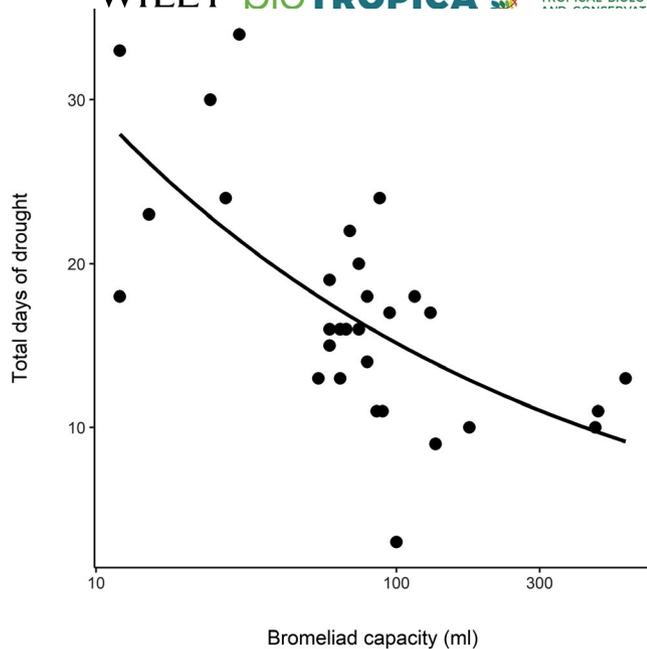
FIGURE 4 Bromeliad desiccation risk decreases with bromeliad size. Total days of drought (defined as the three tracked leaf wells being dry simultaneously) experienced by 30 bromeliads from October 2012 to October 2013 decreased rapidly with bromeliad capacity

4.1 | Implications

Mecistogaster modesta occurs primarily in tropical moist or tropical wet forest at low to mid-elevations, from Mexico to northern Venezuela (Amundrud, Videla, & Srivastava, 2018). In such forests, the largest bromeliads are found at low elevations, in well-lit environments provided by forest gaps, stream edges, and the canopy. Our results indicate that any change in either the size distribution or hydrology of bromeliads will directly impact *M. modesta* populations. Unfortunately, climate change models predict that Central America will lead the world in terms of reduced and more variable precipitation (Giorgi, 2006; Rauscher, Giorgi, Diffenbaugh, & Seth, 2008), with premontane areas of Costa Rica estimated to lose up to 40% of their annual precipitation (Karmalkar, Bradley, & Diaz, 2008). In Guanacaste, variation in precipitation has more than doubled since the year 2000, as compared to the preceding half-century, including the most severe drought on record in 2015 (Cooley et al., 2019). During the 2015 drought, the most affected area of Guanacaste was the northeast (Cooley et al., 2019), coinciding with the distribution of *M. modesta* in this province (Amundrud et al., 2018; Hedstrom & Sahlen, 2001). The global distribution of *M. modesta* is limited by low annual precipitation and high annual mean temperature (Amundrud et al., 2018), suggesting that increased drought in Guanacaste will result in a contraction of its range toward the wetter areas of the province and expansion up mountain slopes.

Any reduction in the incidence of *M. modesta* is likely to have important repercussions for the function and structure of bromeliad food webs. *M. modesta* is the only bromeliad-dwelling damselfly in its range (Mexico to northern Venezuela), and in NW Costa Rica represents up

to 85% of predator biomass when it occurs. Larvae of *M. modesta* are voracious predators on detritivore larvae (Srivastava, 2006) and influence detritivore emergence more than interactions among detritivores themselves (Starzomski et al., 2010). As a result, *M. modesta* has strong top-down effects on decomposition (Srivastava, 2006), microbial communities (Srivastava & Bell, 2009), and consequently CO_2 emissions (Atwood et al., 2013). Predation of larval detritivores by *M. modesta* prevents emerging adults from exporting nutrients and thus can increase nitrogen uptake by bromeliads by an order of magnitude (Ngai & Srivastava, 2006). The sensitivity of damselflies to drought thus has the potential to transmit the effects of drought throughout the bromeliad food web (Amundrud & Srivastava, 2016). By uncovering the mechanisms behind the preference of *M. modesta* for large bromeliads, we have opened a window on understanding the sensitivity of an important freshwater ecosystem to climate change.

FIGURE 5 Damselfly survival decreases with drought length. Solid dots/solid line represent drought treatment, and empty dots/ dashed line represent control. The continuous-water control had 100% damselfly survival, whereas 0% of damselflies survived more than 15 consecutive days of drought

Association (Worldwide Dragonfly Fund 1997), and the University of British Columbia (Martha Piper Fund 2011).

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Primate life history, social dynamics, ecology, and conservation: Contributions from long-term research in Área de Conservación Guanacaste, Costa Rica

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Abstract

Research on non-human primates in the endangered tropical dry forest of Sector Santa Rosa (SSR), Área de Conservación Guanacaste (ACG), was launched in 1983 and is now one of the longest running studies of primates globally. Such continuous study provides a rare opportunity to ask questions that are only answerable through decades-long monitoring of these long-lived monkeys. In turn, the mounting data generated by long-term study, including knowledge of lifetime reproductive success, familial relatedness, comprehensive behavioral and dietary repertoires, and patterns of inter- and intra-annual variation in forest productivity, provide diverse opportunities to researchers, and facilitate studies that are of shorter duration. Here, we review some of the contributions of our longitudinal research on white-faced capuchins and Geoffroy's spider monkeys, together with newer studies on mantled howler monkeys. We begin by synthesizing findings from our research on demography, dispersal, social relationships, and reproduction. These life history and social traits interact with their

foraging and sensory ecology, which we review next. We end by highlighting how the longitudinal study of primates in Sector Santa Rosa has made direct and indirect contributions to the conservation of the critically endangered dry forest biome and its inhabitants, as well as to education, community, and forest restoration initiatives. In particular, we focus our review on how long-term research is uniquely positioned to make key contributions spanning different topical areas.

Abstract in Spanish is available with online material.

KEYWORDS

life histories, longitudinal research, plant–animal interactions, reproductive strategies, sensory ecology, social relationships

1 | INTRODUCTION

Primates and other long-lived mammals exhibit slow life histories and low population densities. Accordingly, field biologists studying these species are typically plagued with small sample sizes that limit power for addressing questions related to fitness, variation, and adaptation. Additionally, primate habitats often show seasonal and inter-annual variation, making it difficult to use short-term studies to understand their ecology and adaptive complexes (Chapman et al., 2017). Only through longitudinal study of tens to hundreds of animals are we able to begin to answer key questions about animal social systems and relationships, ecological niches, and behavioral plasticity, and to measure the fitness consequences of individual variation (Schradin & Hayes, 2017). Field primatology in Sector Santa Rosa (SSR), Área de Conservación Guanacaste (ACG), has been ongoing since its inception in 1983 by Linda Fedigan, making this project one of the longest running continuous studies of primates globally (Kappeler et al., 2012). Over the past 37 years of study in this tropical dry forest, much has been learned about its three resident species of primates: white-faced capuchins (*Cebus imitator*), Geoffroy's spider monkeys (*Ateles geoffroyi*), and mantled howler monkeys (*Alouatta paliatta*; Figure 1). Here, we review key advances in our understanding of

the demography, life history, dispersal patterns, social relationships, reproduction, diet, sensory ecology, and conservation of the SSR primates that have been directly enabled by longitudinal research. Our review focuses primarily on the capuchin and spider monkeys, which we have intensively studied for decades. Only one group of spider monkeys has been studied at SSR given their large home range. To combine data from multiple groups and make our review more comprehensive, we include findings on spider monkeys from Punta Laguna, our team's other field site in the Yucatan peninsula, Mexico, which is the longest running project on spider monkeys (Ramos-Fernández et al., 2018). Further, we include details of howler monkey foraging ecology and demography, which have also been investigated, although not continuously, in SSR. We end by highlighting how our research has contributed to current conservation and education initiatives, and how the knowledge gained will promote the future protection of these iconic mammals.

2 | DEMOGRAPHY AND LIFE HISTORIES

Evolutionary biologists seek to quantify life-history variables in order to model population dynamics and to understand
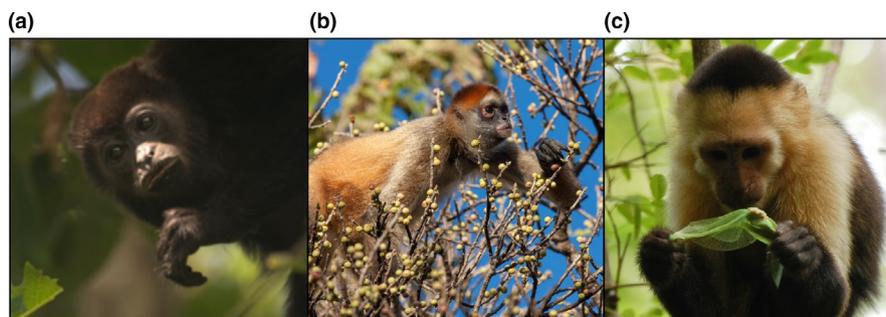
FIGURE 1 Three primate species live sympatrically in the tropical dry forests of Sector Santa Rosa, Área de Conservación Guanacaste: (a) folivorous–frugivorous mantled howler monkey (*Alouatta paliatta*), (b) frugivorous Geoffroy's spider monkey (*Ateles geoffroyi*), and (c) omnivorous white-faced capuchin (*Cebus imitator*). Howler and capuchin monkeys live in cohesive social groups, whereas spider monkey groups are fluid with the formation of subgroups highly variable in size and composition. These species overlap in the fruits they consume, but also show considerable divergence, with capuchins eating the widest range of plant species. Photo credit: Amanda Melin (a, c), Fernando Campos (b)

TABLE 1 Basic biological and life history variables for ACG primates

	Ateles geoffroyi	*Alouatta palliata*	*Cebus imitator*	References/notes
Adult weight (♂/♀)	♂: 8.375 kg ♀: 6.624 kg	♂: 6.528 kg ♀: 4.02 kg	♂: 3.333 kg ♀: 2.283 kg	Glander et al. (1991)[a]
Adult length (♂/♀)	♂: 1,227 mm (body 466 + tail 761) ♀: 1,148 mm (body 425 + tail 723)	♂: 1,111 mm (body 479 + tail 632) ♀: 1,070 mm (body 455 + tail 615)	♂: 843 mm (body 372 + tail 471) ♀: 809 mm (body 365 + tail 444)	Glander et al. (1991)[a]
Brain volume (endocranial volume)	♂: 101 cc ♀: 110 cc	♂: 52 cc ♀: 48 cc	♂: 74 cc ♀: 72 cc	Isler et al. (2008)[a]
Dietary category[b]	Frugivore	Folivore–frugivore	Omnivore	Terborgh (1983)[a]
♀ age at first birth	7.1 years	3.5 years	median 6.70 years, $SD = 0.7$, $N = 42$;	Di Fiore et al. (2010)[a], Glander (1980)[a], Fedigan unpublished data
Interbirth interval	34.7 months	19.9–22.5 months	26.4 months	Di Fiore et al. (2010)[a], Glander (1980)[a], Fedigan and Rose (1995), Fedigan et al. (2008)
Gestation	~7.5–7.7 months	~6.2 months	5.5 months	Di Fiore et al. (2010)[a], Carnegie et al. (2011)
Weaning age	19–31 months	~12 months	14–23 months	Di Fiore et al. (2010)[a], Sargeant et al. (2015)
♀ max life span (wild/captive)	47 years (captive) conservatively estimated at 35 years (wild)	20 years (captive) 15 years (wild)	unknown (captive) 37 years (wild)	Hakeem et al. (1996), Fragaszy et al. (2004), Fedigan et al. (2008), Di Fiore et al. (2010) https://genomics.senescence.info/species/entry.php?species=Ateles_geoffroyi https://genomics.senescence.info/species/entry.php?species=Alouatta_palliata Aureli & Schaffner, unpublished data
♂ puberty	4–5 years (earliest behavioral correlates of maturity)	Pubertal growth spurt at 3–5 years; sexual maturity at 3.5 years	6 years	Glander (1980)[a], Froehlich et al. (1981)[a], Di Fiore et al. (2010)[a], Jack et al. (2014), Aureli & Schaffner unpublished data
♂ age at adult size/Maturity	Adult body size at 8 years	3.5–5 years	10 years, but does not attain full suite of secondary sex traits unless alpha status is attained	Fedigan and Jack (2004), Di Fiore et al. (2010)[a], Aureli & Schaffner unpublished data
♂ max life span (wild/captive)	40+ years (captive) 20 years (wild)	Unknown (captive) 16.6 years (wild)	54 years (captive) >25 years (wild)	Di Fiore et al. (2010)[a], Crilly (2017)[a] Weigl (2005)[a] Aureli & Schaffner unpublished data, Jack & Fedigan unpublished data
Age at dispersal	♀: mean 5.5 years, range 4.9–6.3 (based on age of disappearance from natal group)	♂: mean 2.5 years; range 1.5–5.5 years ♀: mean 2.6 years; range 1.5–6.5 years	♂: 4.5 years (5.5. for confirmed dispersers only); range 20 months to 11 years	Jack and Fedigan (2004a), Clarke and Glander (2008)[a], Vick (2008)[a], Jack et al., 2012
Secondary dispersal (yes/no)	♀: Typically, no	♂♀: Yes; at a mean age of 10 years	♂: Yes; males change groups approximately every 4 years	Shimooka et al. (2008)[a], Clarke and Glander (2010)[a], Jack and Fedigan (2004b)

[a]Indicates a source that is not based on the SSR primate populations. In these cases, we have selected sources that come from populations as close to SSR as possible.

[b]See Table 2 for a detailed breakdown of plant species consumed.

life-history evolution (Oli & Dobson, 2003). Overall, primates are characterized by their long life spans and slow life histories (Kappeler & Pereira, 2003), yet there is wide variation in the order. For example, gray mouse lemurs (*Microcebus murinus*) typically live 8–12 years (Languille et al., 2012). While this is triple the life span of a mouse (3–4 years; (Strong et al., 2008), it is comparatively short for a primate. Free-ranging but provisioned macaques (*Macaca fuscata*, *Macaca mulatta*) can live into their early 30s, and great apes in the wild may live more than 40–50 years (*Pan troglodytes* 63 years, *Pongo abelii* 53 years, *Gorilla gorilla beringei* 44 years, (Fedigan & Pavelka, 2011)). Given their body sizes (weight range for capuchins is 3–4 kg and for spider monkeys is 6–9 kg, Table 1), these monkeys are remarkably long-lived. Capuchins and spider monkeys have both been documented to live to >45 years in captivity and estimated to live into their late 30s in the wild (Crilly, 2017; Di Fiore et al., 2010; Perry, 2012). However, to understand the evolution of life history traits such as life span, data from wild populations are essential. However, most data on primate life spans are derived from captive populations, as many primates simply live longer than the duration of most research programs (but see Bronikowski et al., 2002, 2011; Colchero et al., 2016; Wood et al., 2017). Here is a clear area where long-term field research in which known individuals are tracked from birth to death is well-positioned to contribute valuable data on important life-history traits, including life expectancy and life span under natural conditions.

The capuchins at SSR represent one of very few wild primate populations for which enough individual-based long-term demographic data have been collected to study natural processes of senescence and aging in the wild (Strier et al., 2010). Life tables constructed from demographic data based on capuchins in Santa Rosa have enabled us to characterize age- and sex-specific trajectories of mortality in capuchins. By placing them in comparative context with other primates for which longitudinal data are available, we have been able to illuminate the evolutionary landscape of primate aging (Bronikowski et al., 2016). These efforts have revealed ways in which human aging lies on a continuum with that of other primates (Bronikowski et al., 2011; Colchero et al., 2016), as well as ways in which humans are distinct. For example, mid-life female reproductive senescence—a universal phenomenon across human populations—does not occur in capuchins or in other wild non-human primates (Alberts et al., 2013). Such insights are only made possible by cross-species comparisons of long-term life history data from multiple primate populations. In SSR, the presence of three closely related, sympatric, and continuously monitored primate species with different paces of life invites a future research program on comparative biological processes and behavioral dynamics during aging.

Thirty-four years of data on reproductive and mortality rates of individuals tracked longitudinally have allowed us to quantify their life-history parameters in this habitat and to begin assessing the adaptive significance of different phenotypes. Among the three species of primates in SSR, we find that spider monkeys have the oldest median age at first birth (7.1 years; Di Fiore et al., 2010), followed by capuchins (6.7 years; Fedigan unpublished data) and howlers (3.5 years, Glander, 1980). Gestation length, age at weaning, and interbirth intervals follow this same pattern, with spider monkeys showing the longest periods for each of these variables, and howlers the shortest (Table 1).

Intriguingly, male life histories do not follow the same general pattern across the three sympatric species in SSR. For example, capuchin males take much longer to attain full adult body size (10 years) in comparison to the larger spider (8 years) and howler monkeys (5 years). Though male capuchins are capable of reproduction around age 7, most do not reproduce prior to attaining full adult body size (Jack et al., 2014; Perry, 2012). We hypothesize that the prolonged subadult phase experienced by capuchin males is adaptive, for example, if delaying physical maturity enables males to move more easily between social groups during dispersal events (Jack, 2003a, see also Perry et al., 2017). A remarkable discovery, revealed only after many years of study, was the existence of male dimorphism in capuchins (Jack & Fedigan, 2018; Jack et al., 2014). While we observed from the beginning of our studies that alpha male capuchins were consistently the largest males in a social group, we initially predicted that they achieved alpha status due to their large size and increased competitive ability. However, only after collecting years of long-term behavioral data on males through multiple dispersal events, and combining these data with multi-year non-invasive fecal hormone sampling, did it become clear that alpha males exhibit a distinct phenotype in both appearance and behavior, which emerged once they (or as they) became the most dominant male. Though both *types* of males are reproductively viable (i.e., able to sire offspring), alphas maintain significantly higher androgen levels than subordinate adult males (Jack et al., 2014; Schoof et al., 2011). This phenomenon is similar to (though far more subtle than) the pattern of alternative male morphologies observed in mandrills (Setchell & Dixson, 2001) and orangutans (Dunkel et al., 2013). There is some indication that spider monkeys also delay the full expression of some secondary sex traits, such as the orange coloration around a sternal gland, which appears only on some males and females (Aureli & Schaffner, unpublished data). Further study, including the collection of additional behavioral, morphological, and endocrinological data on both spider and howler monkeys, will aid in our ability to compare and contrast patterns of interspecific differences in male life-history traits and their evolution.

3 | DISPERSAL PATTERNS

Among group-living mammals, one or both sexes typically disperse from their natal groups, which is favoured by natural and kin selection as it decreases inbreeding and the deleterious consequences of mating with close kin, and can facilitate kin cooperation or reduce kin competition (Lukas & Clutton-Brock, 2011; Pusey & Packer, 1987; West et al., 2002). Importantly, dispersal patterns have far-reaching consequences for the quality and quantity of social relationships of individuals within and between groups, as well as the nature of

mate choice and inter- and intrasexual competition (ibid). Patterns of male and female dispersal patterns are hypothesized to be influenced by the distribution and defensibility of food resources, as well as by phylogenetic inertia (i.e., a species evolving from a species with male-biased dispersal tends to retain this pattern unless the new environment favors a different pattern). This topic has received

TABLE 2 Plant species and parts observed to be consumed by capuchin, howler, and spider monkeys Sector Santa Rosa, Área de Conservación Guanacaste, Costa Rica

Family	Species	FRUIT Capuchin	FRUIT Howler	FRUIT Spider	LEAVES Capuchin	LEAVES Howler	LEAVES Spider	FLOWERS Capuchin	FLOWERS Howler	FLOWERS Spider
Anacardiaceae	*Astronium graveolens*					■	■		■	
	Spondias mombin	■		■		■			■	■
	Spondias purpurea	■	■	■		■				
	Spondias radlkoferi	■		■		■				
Annonaceae	*Annona holosericea*	■								
	Annona purpurea	■		■				■		
	Annona reticulata	■		■			■	■		■
	Desmopsis bibracteata	■								
	Sapranthus palanga	■						■		■
Apocynaceae	*Forsteronia spicata*	■				■	■			
	Gonolobus barbatus	■								
	Prestonia riverae	■								
	Stemmadenia pubescens	■		■						
Araceae	*Syngonium angustatum*						■			
Araliaceae	*Aralia excelsa*	■	■	■		■				
Arecaceae	*Acrocomia aculeata*	■								
	Bactris guineensis	■								
Asclepiadaceae	*Blepharodon mucronatum*	■								
	Matelea quirosii	■								
	Marsdenia engleriana			■			■			
Bignoniaceae	*Amphilophium crucigerum*	■								
	Amphilophium paniculatum	■								
	Callichlamys latifolia	■								
	Ceratophytum tetragonolobum	■								
	Handroanthus ochracea	■				■			■	■
	Pseudobombax septenatum		■	■						■
	Tabebuia rosea		■			■			■	
Boraginaceae	*Cordia alliodora*					■			■	
	Cordia guanacastensis	■						■		
	Cordia panamensis	■		■		■	■			
Bromeliaceae	*Bromelia karatas*	■								

References: Aureli, Schaffner and Murillo-Chacon (unpublished data), Melin, Webb, and Cheves Hernandez (unpublished data), Zandona (unpublished data), Hogan et al. (2016), Melin et al. (2012), Melin, et al. (2014)), Welker (2004), Larose (1996), Morera-Avila (1996).

Note that howler monkeys have been studied least intensively in ACG and their dietary repertoire might not be fully represented relative to the other two species.

Family	Species
	Bromelia pinguin
Burseraceae	*Bursera simaruba*
	Bursera tormentosa
Cactaceae	*Hylocereus costaricensis*
Capparidaceae	*Capparis indica*
Celastraceae	*Maytenus segoviarum*
	Semialarium mexicanum
Chrysobalanaceae	*Hirtella racemosa*
	Licania arborea
Clusiacea	*Garcinia intermedia*
Cochlospermaceae	*Cochlospermum vitifolium*
Combretaceae	*Combretum farinosum*
	Terminalia spp.
Cyperaceae	*Cyperus luzulae*
Dilleniaceae	*Curatella americana*
	Davilla kunthii
	Doliocarpus dentatus
Ebenaceae	*Diospyros salicifolia*
Elaeocarpaceae	*Sloanea terniflora*
Erythroxylaceae	*Erythroxylum havanense*
Euphorbiaceae	*Manihot aesculifolia*
	Mabea occidentalis
	Margaritaria nobilis
	Sapium glandulosum
	Sapium macrocarpum
	Sebastiania pavoniana
Fabaceae	*Albizia adinocephala*
	Albizia saman
	Andira inermis
	Bauhinia ungulata
	Cassia grandis
	Centrosema macrocarpum
	Dalbergia retusa
	Diphysa americana
	Enterolobium cyclocarpum
	Gliricidia sepium
	Hymenaea courbaril
	Inga vera
	Lonchocarpus costaricensis
	Lonchocarpus minimiforus

(Continued)

Family	Species	1	2	3	4	5	6	7	8
	Lysiloma divaricatum				■				■
	Machaerium biovulatum				■				
	Quercus oleoides	■		■					
	Swartzia cubensis	■	■	■					
	Vachellia collinsii	■		■			■		
	Vachellia cornigera	■							
Lauraceae	*Ocotea veraguensis*	■		■		■			
Malpighiaceae	*Bunchosia polystachia*	■		■					
	Byrsonima crassifolia	■		■					
	Malpighia glabra	■							
Malvaceae	*Apeiba tibourbou*	■		■	■	■			
	Guazuma ulmifolia	■	■	■	■				
	Luehea candida	■		■	■		■	■	■
	Luehea speciosa	■		■	■		■	■	■
	Malvaviscus arboreus	■					■		
	Pochota fendleri			■	■			■	■
	Sida latifolia	■							
	Sterculia apetala	■		■	■				
Melastomataceae	*Miconia argentea*	■							
	Mouriri myrtilloides	■		■					
Meliaceae	*Cedrela odorata*	■							
	Swietenia macrophylla	■							
	Trichilia americana	■		■					
	Trichilia glabra	■							
	Trichilia havenensis	■							
	Trichilia martiana	■		■	■				
	Trichilia trifolia	■			■				
Mimosaceae	*Lysiloma auritum*				■			■	
Moraceae	*Brosimum alicastrum*	■		■	■	■		■	
	Castilla elastica	■		■	■				
	Ficus bullenei	■		■					
	Ficus citrifolia	■		■					
	Ficus cotinifolia	■	■	■	■	■			
	Ficus goldmanii	■	■	■	■	■			
	Ficus hondurensis	■	■	■	■	■			
	Ficus morazaniana	■		■					
	Ficus obtusifolia	■		■					
	Ficus ovalis	■	■	■	■				
	Maclura tinctoria	■	■	■	■			■	
	Trophis racemosa	■							
Muntingiaceae	*Muntingia calabura*	■		■	■			■	

(Continued)

Family	Species
Musaceae	*Musa acuminata*
Myrtaceae	*Eugenia acapulcensis*
	Eugenia salamensis
	Psidium guajava
Nyctaginaceae	*Pisonia macrantocarpa*
Olacaceae	*Ximenia americana*
Orchidaceae	*Brassavola nodosa*
Papilionaceae	*Acosium panamense*
Passifloraceae	*Passiflora platyloba*
	Passiflora vitifolia
Poaceae	*Lasiacis nigra*
	Lasiacis sorgnoidea
	Streptochaeta spicata
Polygonaceae	*Coccoloba guanacastensis*
Primulaceae	*Ardisia revoluta*
Rhamnaceae	*Karwinskia calderonii*
	Krugiodendron ferreum
Rubiaceae	*Alibertia edulis*
	Calycophyllum candidissimum
	Chomelia spinosa
	Exostema mexicanum
	Genipa americana
	Guettarda macrosperma
	Hamelia patens
	Ixora floribuna
	Randia monantha
	Randia thurberi
Rutaceae	*Citrus aurantifolia*
	Zanthoxylum setulosum
Salicaceae	*Casearia arguta*
	Casearia nitida
	Casearia sylvestris
	Prockia crucis
	Xylosma flexuosa
	Zuelania guidonia
Santhalaceae	*Phoradendron quadrangulare*
	Phoradendron racemosum
Sapindaceae	*Allophylus racemosus*
	Cupania guatemalensis
	Dilodendron costaricense
	Thouinidium decandrum

Sapotaceae — *Chrysophyllum brenesii*
Chrysophyllum cainito
Manilkara chicle
Sideroxylon capiri

Simaroubaceae — *Simarouba glauca*

Solanaceae — *Solanum candidum*
Solanum hazenii

Styracaceae — *Styrax argenteus*

Theophrastaceae — *Bonellia nervosa*

Urticaceae — *Cecropia peltata*

Verbenaceae — *Lantana camara*

Vitaceae — *Cissus fuliginea*
Cissus rhombifolia
Cissus verticillata

extensive attention in primatology (Clutton-Brock & Janson, 2012; Kappeler & Pereira, 2003; Pusey & Packer, 1987). An thorough review of these topics is beyond the scope of this manuscript, but long-term studies make important contributions of data that inform evolutionary theory about group residency patterns, competition landscapes, and mechanisms of sexual selection. This includes data on: (a) *dispersal patterns* and the extent to which these are flexible; (b) *nature of social relationships* among and between group members, and sources of variation; (c) the *fitness landscapes*, that is, patterns of reproductive success and skew, including patterns of mortality, not only as a snapshot in time (e.g., offspring sired in a group during a small window in time), but also across the reproductive lifetimes of individuals. Below, we highlight examples of these contributions from our research at Santa Rosa.

While short-term studies of a few years may be sufficient to document which sex(es) typically disperse, we have learned from longer studies that dispersal patterns can be far more variable than initially believed. Each of the three primates in SSR displays a different "typical" dispersal pattern: howler monkeys show male dispersal and at least some female dispersal, spider monkeys tend toward female dispersal and male philopatry, and capuchins are male-dispersed and female philopatric. These divergent dispersal patterns, accompanied by the differing diets of the three species, provide an exceptional natural experiment for investigating the selective pressures driving these differences, and their consequences, within the same habitat.

The male-biased dispersal pattern found in capuchins is shared with Cercopithecinae, a prominent radiation of African and Asian monkeys, including the baboons (*Papio* spp.) and macaques (*Macaca* spp.), although not without exception (e.g., Guinea baboons, Kopp et al., 2015). Male white-faced capuchins typically disperse from their natal group prior to attaining sexual maturity and continue to disperse throughout their lives (Jack & Fedigan, 2004a; Jack et al., 2012). Our analysis of residency patterns for 61 immigrant males in five study groups over a total of 38 observation years

found that males disperse on average every 3.4 years, and group residency lengths ranged 4–67 months (Jack & Fedigan, 2004b). By analyzing relatedness through genotyping fecal DNA, combined with all-occurrences' records of group movement over 20 years, we have shown that many males emigrate in parallel with other males, often continue to reside with close male kin in their breeding group, and have opportunities to form long social relationships with these related males (Wikberg et al., 2014, 2018). Males dispersing from their natal group often do so with similar-aged paternal half-siblings (Wikberg et al., 2018), and capuchin males join groups containing familiar males more often than expected by chance (Jack, 2003b, Jack & Fedigan, 2004b, see similar findings from the nearby study site of Lomas Barbudal in Perry, 2012). While this pattern of parallel dispersal from the natal group is common in many male dispersed primates, the practice usually wanes during secondary dispersal events when males move between breeding groups (Jack, 2003a). Similar to dispersal patterns reported for male lions, male capuchins continue to disperse in parallel throughout their lives thereby enabling the maintenance of coalitionary partners that are crucial for gaining access to a social group (Jack & Fedigan, 2004b; Packer & Pusey, 1997).

The female-biased dispersal pattern observed in spider monkeys closely parallels chimpanzee dispersal and thus represents an interesting case of socioecological convergence among two distantly related taxa. Studies of spider monkeys at multiple sites have now documented that some females do not emigrate and instead reproduce in their natal group, indicating that, similar to chimpanzees, this pattern of female-biased dispersal can be flexible under some conditions (Shimooka et al., 2008; Walker & Pusey, 2020). Genetic data indicate that some breeding female spider monkeys are immigrants while others are natal (Wikberg, unpublished data), which corresponds to observations of the SSR study group. All but one of the natal females that reached sexual maturity (N = 14) disappeared when they reached emigration age (Table 1). The female that

remained reproduced in the natal group when she was 8 years old. A few similar cases have occurred among spider monkeys at Punta Laguna, Mexico (Vick, 2008). We have not witnessed parallel dispersal, and it is unclear whether secondary dispersal occurs among spider monkey females as we have not observed any cases of adult female immigration (i.e., females with offspring) at SSR, though some cases have been observed at Punta Laguna (Vick, 2008). In study sites where monkeys of multiple groups were individually recognized, females did not immigrate from neighboring groups (Shimooka et al., 2008), indicating they travel considerable distances to find a new group.

In addition to the insights gained by characterizing the most common dispersal pattern within each study species, cases of dispersal by the more philopatric sex have important implications for the costs and benefits of dispersal as well as each species' capacity for behavioral flexibility (Clutton-Brock & Lukas, 2012; Lukas & Clutton-Brock, 2011; Walker & Pusey, 2020). Understanding the conditions under which these cases occur, as well as their frequency, can also help us interpret data on patterns of genetic diversity in these species. Between 1986 and 2007, we documented five cases of female capuchins immigrating into our study groups, often in association with alpha male replacements (Jack & Fedigan, 2009). Only one of these immigrant females remained in her new group for several years (6.7 years, Jack & Fedigan, 2009), and genetic analysis demonstrated that she had the same mtDNA haplotype as the natal females, possibly indicating that she dispersed between relatively recent fission products (Wikberg, unpublished data). Evidence from the study of group fissions among capuchins, which have occurred twice in our study history, suggests such a scenario is possible. In both occurrences, the split occurred along matrilines and at group sizes over 30 monkeys. Genetic analyses also revealed an additional case of female immigration, and this female remained in the group until old age (Wikberg unpublished data).

Among the SSR spider monkeys, when the number of adult males in the group is high relative to the number of adult females, maturing males can be ostracized and the potential for lethal aggression, or the peripheralization of younger males, can result in male dispersal and immigration to other groups (Aureli et al., 2013). We have also witnessed two cases of immigration by multiple males and the subsequent disappearance of resident males during our 17 years of study (Aureli et al., 2013). Contrary to what would be expected if males were invariably philopatric, analysis of nuclear DNA of all group members indicates that the males were no more closely related to one another than were group females (Aureli et al., 2013), nor does our analysis of mitochondrial DNA find any evidence of sex-biased dispersal (Wikberg unpublished data). These data establish that it is possible for the typically resident sex to disperse and successfully establish themselves as long-term residents in their new group, highlighting the plasticity of dispersal patterns that can only be revealed through long-term study. Evidence of male dispersal has also been found among white-bellied spider monkeys (*Ateles belzebuth*, Di Fiore et al., 2009), as well as in chimpanzees

(Sugiyama, 2004), which converge on numerous aspects of spider monkey sociality, including male philopatry and a high degree of fission–fusion dynamics (Sugiyama, 1999). Overall, there seems to be greater flexibility in dispersal patterns among spider monkeys than capuchins, and our long-term research has provided important data about the demographic circumstances leading to these rare events, but much work remains to be done.

4 | SOCIAL RELATIONSHIPS

Group-living primates form enduring relationships with others throughout the course of their long lives. Due to the considerable variation in the form, strength, and nature of social relationships, comparative studies among primates can be used to ask questions about the costs and benefits, and, ultimately, the evolution of social bonds (Isbell, 2004; Shultz et al., 2011; Sterck et al., 1997; Wrangham, 1980). By combining the intensive and repeated observations needed to study the social patterns of primates with detailed demographic data and non-invasive sampling to estimate body condition, physiological state, and exposure to pathogens, biologists can examine how social relationships affect fecundity, health, and survival. Such studies provide key insights into the costs and benefits of sociality and allow us to study its evolution (Ostner & Schülke, 2018; Snyder-Mackler et al., 2020; Thompson, 2019).

Patterns of dispersal are predicted to be tightly linked to strength of social bonds (West et al., 2002; Wrangham, 1980; Sterck et al., 1997, p. 19), and empirical studies often (but not always) document a kin bias in affiliation (Archie et al., 2006; Carter et al., 2013; Di Fiore & Fleischer, 2005; Gompper et al., 1997; Griffin & West, 2003; Guilhem et al., 2000; Hirsch et al., 2012; Kapsalis, 2004; Möller, 2012; Wahaj et al., 2004; Wikberg et al., 2012, 2014; Wilkinson, 1986) with relatively weak bonds among dispersed individuals (Di Fiore & Fleischer, 2005; Möller, 2012; Wikberg et al., 2012). The primates at Santa Rosa appear to fit this general pattern relatively well. In capuchins, females form stronger bonds than males as expected, showing a significant maternal kin bias in grooming during one study period (Bergstrom & Fedigan, 2013), and our long-term data show that mother–daughters and full-siblings form stronger relationships than other kin categories (Kalbitzer et al., 2017). Similar to previous findings from the Lomas Barbudal capuchins, females do not bias friendly behaviors to paternal siblings (Kalbitzer et al., 2017; Perry et al., 2008), and the more costly alloparenting behaviors, including nursing and carrying others' infants, were biased to maternal but not paternal kin (Sargeant et al., 2015, 2016). Female capuchins are categorized as displaying relaxed despotic dominance relationships with moderate kin bias (Bergstrom & Fedigan, 2013). Their dominance hierarchies are linear, with females entering the dominance hierarchy at approximately 6.5 years of age and assuming the rank immediately below their mother and, when applicable, their older sisters (Bergstrom & Fedigan, 2010). Female rank is relatively stable across an individual's lifetime, although rank reversals have been observed

during our years of study following deaths or other disruptive events (Fedigan unpublished data, see also Manson et al., 1999).

Despite the frequency with which male capuchins change groups throughout their lifetimes (see above), they nonetheless form relatively tolerant and often affiliative relationships with one another (Jack, 2003b; Perry, 1998; Schoof & Jack, 2014). Such tolerant relationships, which are generally reserved for the philopatric sex (van Hooff & van Schaik, 1994; Patzelt et al., 2014), can partly be explained by the high rate of parallel dispersal discussed above (Wikberg et al., 2018). However, parallel dispersal is not necessarily sufficient to maintain tolerant relationships in other species (e.g., black-and-white colobus: Teichroeb et al., 2014; Wikberg et al., 2012, 2014), and these relationships likely evolved due to the costs and benefits associated with forming cooperative, neutral, or aggressive relationships that we discuss further in the section on reproductive success.

Spider monkeys at SSR also generally follow the expected pattern of strong male bonds and weak female bonds in species with female dispersal (Silk & Kappeler, 2017, but see Furuichi, Yamagiwa, & Aureli, 2015). Male philopatry leads to a high degree of familiarity among males from a young age facilitating the formation of strong relationships among them (Aureli & Schaffner, 2008). Indeed, proximity, grooming, and other friendly interactions are more common in male–male dyads than in female–female dyads (Fedigan & Baxter, 1984; Slater et al., 2009). Males also cooperate to defend the group territory, traveling more often than females at the territory boundaries (Chapman, 1990), possibly to patrol them (Di Fiore et al., 2010), and perform raids into neighboring territories (Aureli et al., 2006). Interestingly, and in stark contrast to male chimpanzees where dominance relationships are prominent with frequent aggressive interactions (e.g., Preis et al., 2019), male spider monkeys rarely exchange aggressive interactions with other males, a factor that, accompanied by the complete lack of submissive signals, makes it difficult to discern any dominance relationships among adult males (Aureli & Schaffner, 2008). Nonetheless, more subtle forms of male–male competition may exist in this species. In a principal component analysis using social interactions, embraces and aggression had a high load in the same component, which was categorized as "risk" (Rebecchini et al., 2011). Male–male dyads had higher scores than female–female dyads and female–male dyads not only in the component reflecting affiliation, as traditionally expected, but also in the risk component, contributing to the emerging view of a more ambiguous nature of male–male relationships in spider monkeys than previously thought (Rebecchini et al., 2011).

Despite the infrequent social interactions among female spider monkeys, our long-term research has uncovered many nuances about their relationships (Aureli & Schaffner, 2008). First, although females receive substantial aggression from other resident females during the first months after immigration (Asensio et al., 2008), especially from other recent immigrants (Riveros et al., 2017), there is little aggression among females with long tenure in the group (Riveros et al., 2017). Aggression by resident females against immigrating females is consistent with predictions that intra-group competition for food or other resources is costly

to females (Schülke & Ostner, 2012; Snaith & Chapman, 2007; Sterck et al., 1997). While this pattern of aggression might suggest dominance effects, our long-term project has clearly shown this is driven by an initial, temporary hostile phase, and not due to wider dominance patterns (Asensio et al., 2008). The difference in group tenure appears to have another important consequence that is usually mediated by dominance in other species, access to high-quality food (Thompson et al., 2007). In SSR, the longer a female's tenure in her group, the better the quality of her core range in terms of food availability (Asensio et al., 2015). The second factor that modulates female–female relationships in spider monkeys is the presence of young infants. Several studies, including ours, have found an increase of embraces received by females with young infants (Eisenberg & Kuehn, 1966; Fedigan & Baxter, 1984; Schaffner & Aureli, 2005; Slater et al., 2007). We see similar effects in capuchin monkeys, where females with young infants receive a temporary spike in group centrality and tolerance from higher-ranking females (Kalbitzer et al., 2017).

5 | REPRODUCTIVE SUCCESS

Because of their relatively larger investment in offspring, female mammals are predicted to show little interindividual variance in lifetime reproductive success relative to males (Bateman, 1948; Clutton-Brock, 1988; Emlen & Oring, 1977; Trivers, 1972). Among long-lived animals, it takes decades of data collection to achieve the sample sizes needed to generate reliable estimates of lifetime reproductive success. Our capuchin data indicate that female reproductive success is impacted by a host of social, biological, and ecological factors including: age at death, the strength of her social relationships, the number of kin that reside in her group, the number/ratio of adult males that reside in the group, the frequency of alpha male replacements (and resultant infanticide events), and food resources available to her and her offspring over time (Campos et al., 2020; Fedigan et al., 2008; Fedigan & Jack, 2011; Kalbitzer et al., 2017). For example, the length of a female's interbirth interval decreases as the number of matrilineal kin present in the group increases (Fedigan et al., 2008). This may be due to the high rates of maternal infant handling and allonursing in this species, which are more common among maternally related kin (Sargeant et al., 2015, 2016).

In several species of primates, dominance rank (Majolo et al., 2012) and strength and/or number of social relationships (e.g., Ostner & Schülke, 2018) are positively related to offspring survival. In capuchins, however, this link is more complicated because of the frequent occurrence of infanticide committed by new alpha males (Brasington et al., 2017; Kalbitzer et al., 2017). Risk of infanticide by adult males varies extensively among primates, and numerous research efforts to understand the variation and evolution of this behavior have been undertaken (Henzi & Barrett, 2003; Lukas & Huchard, 2014; Palombit, 2012). Infanticide appears to be more common in species characterized by non-seasonal breeding, high reproductive skew and paternity

certainty, and prolonged infant dependency, and numerous lines of evidence suggest that infanticide is an adaptive strategy for males (reviewed by Palombit, 2012). Female capuchins have an extensive range of strategies that are hypothesized to reduce infanticide, including unpredictable and concealed ovulation, situational receptivity, polyandrous and postconceptive mating, reproductive synchrony, mate choice, and alliances with resident males (Fedigan & Jack, 2013). Despite these strategies, infanticide is the leading source of infant mortality among capuchins in SSR and we have directly witnessed numerous cases (Brasington et al., 2017; Kalbitzer et al., 2017).

Our analyses of these events have found that offspring of higher-ranking and socially well-integrated females are more likely to survive during stable periods with no change in the alpha male (Kalbitzer et al., 2017), a finding that is similar to the relationship between rank/social integration and offspring survival generally observed in some other primate species (Majolo et al., 2012; Ostner & Schülke, 2018). However, during periods associated with changes in a group's alpha male, these more social and dominant females are at greater risk of having their infants killed by immigrant males (Kalbitzer et al., 2017). We attribute this to the increased proximity of high-ranking and highly social females to new males due to the central position in the group that these females maintain.

Infanticide by males has been reported for a number of spider monkey species, though it is still considered rare in the genus and has not been associated with changes in male dominance structure as is typical of other primates (Alvarez et al., 2015; Gibson et al., 2008; Teichroeb & Jack, 2017). Cases from outside of SSR described to date involved instances of males killing infants residing in neighboring groups ($N = 2$; Gibson et al., 2008) or adult males killing male infants residing in their own group ($N = 8$; Alvarez et al., 2015). While instances of infanticide have not been directly observed in the SSR spider monkey study group, preliminary analysis suggests that infant survivorship was negatively affected by the two cases of male immigration described above (Aureli, unpublished data). Collectively, these observations of infanticide and male dispersal between groups, accompanied by several reports of adult males killing subadult males residing in their own group ($N = 3$; Campbell, 2006a; Valero et al., 2006), indicate that male reproductive competition also negatively affects spider monkey female reproductive success, though the extent of this impact remains unknown.

Male reproductive success in mammals can vary widely and is dependent on multiple factors such as male condition (e.g., age, physiology, and health: Bercovitch et al., 2003), female strategies (Stumpf et al., 2011), a variety of social circumstances (e.g., maternal presence: Surbeck et al., 2019; social bonds and coalition partners: Schülke et al., 2010), and behavior and personality can play a role (e.g., Perry et al., 2017; Rosenbaum et al., 2018). Following capuchin males across their lives, we have been able to document extended periods of no reproductive output by males while they are subordinates interrupted by periods where these same males sire offspring during relatively short tenures in an alpha position. The reproductive success of males is largely dependent upon their ability

to become an alpha male, and in our dataset consisting of 20 years of genetic and observational data, the most successful male sired over 24 infants (Fedigan & Jack, 2004; Wikberg et al., 2017, 2018). Because most alpha male capuchins monopolize reproduction, only about a third of the subordinate males sire any offspring (Wikberg et al., 2017, 2018). However, some subordinate males reside with, and provide coalitionary support to, their alpha male kin and thereby gain inclusive fitness benefits through the alpha male's reproductive success (Jack & Fedigan, 2004b; Wikberg et al., 2014, 2017).

When subordinate males do reproduce, it is often with the alpha male's adult daughters, which likely results from aversion to mating with close kin (Wikberg et al., 2017), similar to the pattern reported from the Lomas Barbudal capuchins (Godoy et al., 2016; Muniz et al., 2006). Cooperating with the alpha male, or at least forming a tolerant relationship with him, may allow these subordinate males to remain in the group and access these mating opportunities (Wikberg et al., 2017, 2018). A subordinate male that resides with a long-term alpha male and is able to produce offspring with the alpha male's mature daughters experiences reproductive success at levels similar to that of alpha males (Wikberg et al., 2018). This unexpected finding of high reproductive success for some subordinate males was revealed only after many years of study at our site and at Lomas Barbudal (Godoy et al., 2016; Muniz et al., 2006; Wikberg et al., 2017), a consideration for others when evaluating estimates of reproductive skew based on snapshots of short windows of time. Like other male-dispersed primate species (Silk et al., 2019), male capuchins likely switch among strategies, depending on age, group membership, and dominance rank. Being able to collect data from the same males as they age, disperse, and change dominance ranks is therefore necessary to assess their lifetime reproductive success. Long-term studies thus make an impactful contribution to our understanding of the nature of male reproductive strategies and lifetime reproductive success, and can also help us interpret patterns of genetic diversity in populations.

Reproductive skew among male spider monkeys is less steep than we observe in capuchins likely because reproduction is not mediated by dominance relationships and female choice plays a major role (Campbell, 2006b; Campbell & Gibson, 2008). The high degree of fission–fusion dynamics allows males to avoid overt competition for mating, as a single male and female can fission from the group to mate in secret (Campbell, 2006b; Gibson, 2010; Slater et al., 2008), possibly reducing the need to have well-established dominance relationships.

6 | LIVING AND REPRODUCING IN A SEASONAL ENVIRONMENT

The dry forests of ACG are among the most seasonal habitats in the tropics (Campos, 2018; Feng et al., 2013). Large oscillations in rainfall and temperature, concomitant with leaf shedding of trees and drying of water sources, lead to large shifts in the abundance of foods and the types of foods available, the availability of drinking water, and the thermoregulatory challenges facing the primates (Campos & Fedigan, 2009). We have been tracking the temperature

and rainfall daily since the inception of our primate observations in the early 1980s. Additionally, since 2003, we have been monitoring the phenology of trees whose parts are consumed by the resident primates, and we have additionally conducted a transect study of old growth and regenerating forest around the administration area of SSR, recording 48,799 trees and saplings at least 1-m tall (Campos et al., 2014; Orkin, et al., 2019). By combining the phenology and transect data, we are able to estimate monthly fruit abundance in the home ranges of our study groups of capuchins and spider monkeys (Bergstrom et al., 2020). Taken together, this rich ecological dataset allows us to examine how intra- and inter-annual fluctuations in rainfall and linked productivity of the forest affect the resident primate populations.

Although inter-annual variation in overall fruit production can be large (Hogan & Melin, 2018), the mid-to-late dry season (March–April) is typically a period of high ripe fruit productivity, while the beginning of the dry season (November–December) and the early rainy season (June–July) are typically periods of low fruit productivity (Bergstrom et al., 2017). However, we join other researchers (e.g., Hanya & Aiba, 2010; Mitani et al., 2005) in cautioning against using rainfall as a proxy for fruit abundance, a practice that has been used in the past to model resource abundance in the SSR region before comprehensive data on food plant abundance and phenology were available (Chapman & Balcomb, 1998). Most tree species in SSR show marked seasonality in fruit production (Hogan & Melin, 2018) although *Ficus* trees are notable exceptions. Through their production of figs at irregular intervals, *Ficus* trees provide an important resource to primates and hundreds of other animal species, especially when other fruits are scarce (Hogan & Melin, 2018; Parr et al., 2011).

The primates inhabiting the dry forest of SSR show different responses to the seasonality of the forest. Spider monkeys, the most frugivorous of the three, exhibit fission–fusion dynamics (Aureli et al., 2008) in which they split into subgroups of variable size and composition for effective foraging (Aureli & Schaffner, 2008). In SSR, subgroup size is positively correlated with food availability (Asensio et al., 2009; Chapman et al., 1995). Spider monkeys also range in markedly different areas of the forest during different seasons (Asensio et al., 2012). Whereas there is high consistency in the location of the group's home range across years, core areas (i.e., areas of intense use) vary in size and location across seasons and years. This means that the yearly home range includes all the core areas from different seasons (Asensio et al., 2012). The pattern of variable core areas across time within a relatively stable home range could result from preferred usage of the areas currently most productive and at the same time the defense of future resources from other groups.

Capuchins in SSR remain in cohesive groups year-round and do not undergo fission during periods of low fruit abundance. Like spider monkeys, capuchins also shift their areas of use to track the availability of water and fruit patches (Campos et al., 2014), but switch their diet to rely more on insect and other invertebrate prey when fruit is less abundant (Melin et al., 2014; Mosdossy et al., 2015). In addition, capuchins also use floral resources seasonally, and for at least one common tree species, *Luehea speciosa*, their behavior (licking but not

destroying flowers, presence of pollen on faces, moving from tree to tree in rapid succession, i.e., "traplining" behavior), together with morphology and nectar composition, suggests the capuchins may contribute to pollination of *L. speciosa* flowers (Hogan et al., 2016). Importantly, access to water is an important driver of home range use by capuchins (Campos et al., 2014; Campos & Fedigan, 2009), as they are the only primate in SSR that routinely drinks daily during the dry season rather than water from their foods (Chapman, 1988).

Despite these behavioral strategies, capuchin monkeys show evidence of energetic distress during periods of low fruit abundance. Research on female capuchins in SSR has demonstrated that periods of low fruit production correlate with indicators of metabolic stress, C-peptide, and urinary ketones, especially for pregnant and low-ranking females (Bergstrom et al., 2017, 2020). In addition, capuchins of both sexes exhibit elevated glucocorticoid secretion during periods of reduced access to food and water (Carnegie et al., 2011; Schoof et al., 2016). Our research on the gut microbiota of capuchins across seasons indicates that rainfall and diet have substantial effects on the diversity, composition, and function of the capuchin gut microbiome. The social group membership also impacts gut microbiome structure, although this effect may be weaker than seen among other wild primates (Orkin, et al., 2019; Orkin et al., 2019).

Given the seasonal fluctuations in food and water resources, it is perhaps unsurprising to see evidence of reproductive seasonality in the births of primates in the dry forest (Fedigan & Rose, 1995). Births peak at the beginning of the dry season (December–January) among spider monkeys (Aureli and Schaffner, unpublished data) and at the end of the dry season and early wet season (April–July) among capuchins (Campos et al., 2017; Carnegie et al., 2011). Unlike the extreme seasonality in births seen in ring-tailed lemurs and Verreaux's sifaka (Pereira, 1991; Richard et al., 2000), these peaks are not steep, indicating that births occur asynchronously and throughout the year in both capuchins and spider monkeys (Carnegie et al., 2011; Schaffner et al., 2012). Reasons for this might include high inter-annual variation in fruit production and rainfall (Hogan & Melin, 2018; Melin, et al., 2014) and, as discussed in detail above, the impact of infanticide by immigrating males.

By comparing data on fruit productivity to birth seasonality over many years, we observe that capuchin reproductive seasonality fits the predictions of the "maternal survival" model (Carnegie et al., 2011; Janson & Verdolin, 2005). According to this model, the mean peak in energy abundance will be aligned with the maximum energetic demands of lactation to increase maternal health and survival during this costly period. This strategy appears to be employed by some primate and other mammalian females. In other mammals, females appear to store nutrients during the months of high food abundance and then give birth after the mean peak in food abundance (Bronson, 2009). We have yet to examine whether spider monkey birth peaks coincide with periods of high fruit production but spider monkey mothers nurse their offspring well into the second year of the infant's life, and we have witnessed females nursing infants until their next offspring is born, spanning a three-year

period (Schaffner, unpublished data). Whether spider monkeys show any reproductive seasonality or follow a more stable investment strategy over a long period of time, such as has been suggested for Bornean orangutans (van Noordwijk et al., 2013), will be an interesting question to examine in the future.

Over the past few decades, our data have spanned extreme climate events, such as drought, offering a rare opportunity to examine primate ecological, behavioral, and demographic responses. At SSR, as in many other tropical regions, inter-annual climate variability is strongly driven by the El Niño–Southern Oscillation (ENSO). By combining long-term life-history data with climate data, we have documented that ENSO-associated severe rainfall deficits are associated with declines in capuchin female fertility rates, high capuchin infant mortality, and disruptions in spider monkey female reproductive function (Campos et al., 2015, 2020). When considered in a comparative context with other primate species and populations around the world, such data provide invaluable information for modeling the impact of climate change and extreme weather events in tropical environments (Campos et al., 2017; Carvalho et al., 2019; Graham et al., 2016; Zhang et al., 2019).

7 | FORAGING ECOLOGY

Studies of dietary range and plasticity, food preferences, and feeding patterns strongly benefit from inter-annual research, as short-term studies under-represent dietary breadth (e.g., see Chapman et al., 2018), and indices of food selectivity are influenced by the availability of different foods, which varies within and across years. Our studies of the dietary ecology of sympatric primates in a well-characterized ecosystem have provided insights into how three sympatric primate species partition their dry forest habitats intra- and inter-specifically.

Howler, spider and capuchin monkeys occupy distinct but partially overlapping feeding niches. White-faced capuchins, the smallest of the three species, are highly omnivorous and have remarkable dietary breath (Bergstrom et al., 2018; Chapman & Fedigan, 1990; Fragaszy et al., 2004; Hogan & Melin, 2018). In SSR, we have observed them to eat primarily fruits (and some flowers and pith, but almost never leaves) from 144 species of plants and a wide range of invertebrates (Table 2; Melin et al., 2008). Searching for insects makes up about 70% of capuchin foraging time and 50% of ingestion events (Bergstrom et al., 2018; Melin et al., 2007). The spider monkey population at SSR has been observed to consume food items from 89 different plant species and is more frugivorous than capuchins, devoting approximately 71% of their feeding time to fruits, while supplementing their diet mostly with young leaves and flowers (Table 2). The only animals eaten regularly by spider monkeys are caterpillars (Chapman, 1988). The most folivorous of the three primates, the howler monkeys, have been observed to eat the leaves, fruits, and flowers of at least 71 plant species, which is almost certainly an underestimate, as it is based on by far the least amount

of observational data (Table 2). A large component of our research program on primate feeding ecology involves asking how primates find and select their foods using their sensory systems.

8 | ADVANCES IN PRIMATE SENSORY ECOLOGY: COLOR VISION AS A CASE STUDY

Sensory ecology has long been involved in hypotheses of primate origins and adaptive radiation. Evolutionary anthropologists have used morphology of sensory structures to infer ancestral activity patterns and other aspects of behavior (Cartmill, 1992; Ross et al., 2007; Smith et al., 2007; Sussman, 1991). These hypotheses are strengthened by data on sensory behaviors, diets, and activity patterns of extant species. The important role that sensory systems play in the lives of wild primates is increasingly understood through studies uniting behavior, genetics, and models of sensory system function. Over the last 15 years, considerable advances have been made in understanding the surprising color vision variation among primates. Much of this progress has come from studying the capuchin, spider, and howler monkeys living in SSR (Kawamura, 2018). Unlike many other tropical forests, the observational conditions at SSR are remarkably good due to the relatively low, deciduous forest. Due to careful and complementary ecological studies, described in the previous section, we also have the necessary ability to control for food–tree phenology when comparing feeding rates among monkeys and to examine not only the impacts of receiver sensory variation on this short-term feeding, but also the effects on reproductive success. Through application and refinement of non-invasive methods for the isolation of primate DNA from feces, our research additionally unites examination of sensory gene sequences relative to other genomic areas to scan for evidence of natural selection (e.g., Hiwatashi et al., 2010; Orkin et al., 2020).

One of the derived characteristics of primates that has captivated biologists for decades is their trichromatic color vision—that is, a visual system based on three different cone types. With the emergence of a third cone type, primates have evolved a red-green color channel not present in other mammals (Jacobs, 2008; Lucas et al., 2003; Martin & Ross, 2005). Perhaps even more intriguingly, there is considerable variation within and among species in their capacity to distinguish different hues. With the exception of the completely colorblind owl monkeys (genus *Aotus*) and the routinely trichromatic howler monkeys (genus *Alouatta*), all primates living in Mexico, Central, and South America, have X-linked color vision variation (Dulai et al., 1999; Melin, et al., 2017). In this system, all males and typically a third to a half of females have dichromatic vision (red-green colorblindness). The link between opsin genotype and color vision phenotype is well established for primates, lending itself to natural experiments to test for impacts of color vision type on foraging, perception of social signals, or predator detection among individuals living in the same social groups (Changizi et al., 2006; Melin et al., 2012; Pessoa et al., 2014).

Like most monkeys in the Americas, capuchin and spider monkeys possess different alleles of the cone opsin gene (underlying primate color vision variation) and correspondingly different cone pigment tuning mechanisms resulting in different sensitivities to different wavelengths of light. In SSR, capuchins have 3 alleles, whereas two alleles are found among the spider monkeys (Hiramatsu et al., 2005). We have also discovered that spider monkeys at SSR differ from those in the Yucatan peninsula of Mexico in their opsin genes (Aureli & Matsushita, unpublished data). In howler monkeys, all males and females are trichromatic due to an opsin gene duplication; however, minor variations in the sensitivities of opsins are present among howler monkeys (Matsushita et al., 2014). Additionally, we found strong genetic evidence of balancing selection maintaining the opsin variation in capuchin monkeys and spider monkeys: the nucleotide sequences of the exons containing sites important for color vision tuning are more variable than the intron regions distantly located from theses exons and the "neutral reference" regions in the same genome in both species (Hiwatashi et al., 2010). This indicates that natural selection maintains the functional variation over the amount of opsin variation that would be present if the sites were evolving neutrally or under purifying selection (Hiwatashi et al., 2010).

Turning to behavior, there are noticeable effects of color vision type on foraging behavior. The strongest evidence for this is found among capuchin monkeys where multiple thousands of sequences of food investigation behaviors for a relatively large number of individuals (>80) across dozens of plant species have been examined. Trichromatic monkeys had higher feeding rates on reddish ripe fruits. Interestingly, the effect of trichromacy on feeding efficiency seems to be greatest among juvenile monkeys, whereas adults may learn to more efficiently use non-visual senses to forage; more research is needed in this area (Melin, et al., 2017; Melin et al., 2019). Color space models of food conspicuity using cone sensitivities for each species, and illumination profiles taken in SSR forest, suggest trichromacy should confer a detection advantage for important foods types including a majority of dietary fruits, flowers, and young leaves consumed by the three primates in SSR (Hiramatsu et al., 2008; Melin, et al., 2014; Melin, et al., 2017; Valenta & Melin, 2012). We also presented the first behavioral evidence that trichromats find small, ephemeral food patches, and likely experience a high finders' reward by depleting them before they are joined or displaced by conspecifics (Hogan et al., 2018; Melin, et al., 2017). Trichromacy may also be useful in narrowing down which fruits are ripe and desirable, although over short distances other sensory systems come into play (Hiramatsu et al., 2008, 2009; Melin et al., 2019).

Despite the predicted and demonstrated foraging advantages to monkeys with red-green color vision, analysis of fitness measures over the duration of the project for adult female capuchins indicates that trichromatic females do not have more offspring, more surviving offspring, or reproduce sooner than dichromatic females. This suggests that the color vision variation is not maintained in the population due to fitness advantages to trichromats (Fedigan et al., 2014). Importantly, this is *not* evidence that this variation is neutral. Rather, we have strong evidence from patterns of opsin

gene diversity in SSR (Hiwatashi et al., 2010), not to mention the persistence of polymorphisms across millions of years in dozens of species, that color vision variation is maintained by balancing selection (Carvalho et al., 2017; Frentiu et al., 2007; Melin et al., 2012). Mechanisms of balancing selection, aside from heterozygous advantage, include niche divergence, frequency dependence, and mutual benefit of association. These hypotheses have not yet been extensively evaluated but seem promising, especially given that foraging benefits to trichromats are not ubiquitous (Caine et al., 2010; Melin et al., 2008; Melin, et al., 2014; Smith et al., 2012).

Dichromatic capuchin monkeys have an advantage in foraging for cryptic foods as evidenced by higher capture rates of surface-dwelling, camouflaged insects (Caine et al., 2010; Melin et al., 2010; Smith et al., 2012). Given that insects represent a considerable proportion of their diet, this advantage is non-negligible. Intriguingly, dichromats seem to rely more on non-visual senses during foraging, such as olfaction (Melin et al., 2009, 2019). This is a remarkable example of behavioral plasticity revealed through the "natural experiment" of having multiple sensory phenotypes living and feeding in cohesive groups of the same species. We are presently testing for niche divergence among monkeys in the same groups based on their color vision type to evaluate this possible mechanism of decreasing intra-group competition, which might favor the persistence of sensory variation over evolutionary timescales (Kawamura, 2018; Melin et al., 2008; Mollon et al., 1984).

The advantages (if any) of dichromacy to spider monkeys remain to be elucidated but may lie in search for cryptic fruits or predators among these specialized frugivores. As with capuchins and spider monkeys, studies of howler monkeys in SSR reveal that trichromats should have advantages for preferred foods types (ripe fruits). Unlike capuchins, however, howler monkeys eat leaves, not insects, to supplement their diets. Many key plant species have reddish young leaves, which are preferred by howler monkeys because they are softer, more proteinaceous, and easier to digest than mature leaves (Lucas et al., 2003; Melin, et al., 2017). It has been suggested that a ripe fruit diet, combined with fallback on reddish leaves, has favored the emergence of routine trichromacy in both howler monkeys and the ancestor of African and Asian primates. Field study of howler monkeys in SSR has provided independent support for this hypothesis. Importantly, given that the selective pressure(s) leading to polymorphic versus routine trichromacy likely vary, seeking a unifying explanation for the emergence of any form of primate trichromacy—a practice present in much of the historical literature—may be missing key distinctions between these systems. Study of sympatric primates with different color vision systems as found in SSR, together with comparative study of allopatric primates with the same color vision system (e.g., howler monkeys and catarrhines), may present a promising way forward (Melin, et al., 2017).

Promising areas of inquiry that remain to be addressed in primate sensory ecology include understanding plant–animal interactions more directly and their evolution. Opportunities offered by naturally occurring variation in sensory systems and behaviors of primate receivers, and signal variation via different food colors, odors, mechanical properties, tastes, and sounds are well-suited for examining how, when, and

why different senses are used and the impacts of variation in signal structure. To date, we have shown differences in the taste receptors among our study species in SSR and elsewhere (Tsutsui et al., 2016), and among the behaviors, genes, and morphology associated with the olfactory sense (Veilleux et al., 2019). Our work examining the interplay among sensory systems is also in its infancy (Melin et al., 2019), and future work will explore these topics within and between species.

9 | CONSERVATION AND EDUCATION INITIATIVES

Around the world, primate populations are increasingly at risk: 75% of primate populations are declining, and over 60% of species are considered to be threatened with extinction (Estrada et al., 2017). While the specific threats differ by region, they are all anthropogenic in origin: habitat loss and degradation, climate change, hunting, and capture for the pet trade are chief among them (Almeida-Rocha et al., 2017; Estrada et al., 2017; Kalbitzer & Chapman, 2018). Yet, hope remains, and researcher presence can deter active threats (e.g., poaching, habitat loss) and serve as "umbrella" protection to the ecosystem at large (see Wrangham & Ross, 2008 for detailed analysis of the conservation benefits of long-term research). Perhaps most importantly, it is near-impossible to successfully run a long-term research program without establishing strong and meaningful relationships with local stakeholders. These relationships can benefit the local communities (e.g., employment and education opportunities, the prestige of local projects and protected areas) as well as the researchers (e.g., access to traditional knowledge and improved logistic outlooks; Durant et al., 2007; Kasenene & Ross, 2008; Pusey et al., 2007). Friendly relationships with government officials can also result in the establishment of protected areas and legislation (Wrangham, 2008), and evidence suggests that long-term research contributes disproportionately to environmental policy (Hughes et al., 2017).

In this regard, ACG is a success story (Janzen, 2000) and one that is at least partly due to the myriad of long-term research projects ongoing within its boundaries (data from many of which are summarized in this issue). Ecological research in the remnant fragments of tropical dry forest surrounding the historic "Casona" in Santa Rosa National Park led to advocacy for improved conservation measures, political action, and ultimately the protection of large swaths of cultivated land, which were allowed to regenerate. The effect of forest protection and regeneration on the local primate populations in SSR has been unmistakably positive: Capuchin and howler populations grew quickly, eventually stabilizing at approximately twice their original numbers (Fedigan & Jack, 2001, 2012). Since primates provide critical seed dispersal and pollination services in the dry forest and other tropical ecosystems (Chapman, 1995; Hogan et al., 2016; Valenta & Fedigan, 2008), the growing populations of these species may, in turn, contribute to the regeneration of the forest in ACG (Chapman et al., 2020). We do not have similar data for spider monkeys, as their high degree

of fission–fusion dynamics makes it more difficult to assess population size with traditional techniques, but we continue to test different methods for collecting and analyzing spider monkey survey data, including drones with thermal cameras (Spaan et al., 2017; Spaan, Burke, et al. 2019; Spaan, Ramos-Fernández, et al. 2019).

The conservation benefits of our research extend beyond direct protection of the primates and their habitat living in SSR. Our study groups range in the tourist areas, providing us opportunities to engage with numerous local and foreign tourists and student groups. In recent years, increasing tourism in ACG has seen a rise in capuchins accessing human-sourced foods from garbage cans (https://www.acguanacaste.ac.cr/biodesarrollo/huella-verde). High tourism in other regions of Costa Rica has led to high rates of primate-sourced food theft and direct contact, increasing the health risk to humans and monkeys alike (McKinney, 2014; Russon et al., 2014). Primatologists are working with ACG administration and SSR ecotourism experts to contribute recommendations about "best practices" that are passed on to visitors, such as the development of the "Quiero Dejar Una Huella Verde" ("I Want to Leave a Green Footprint") project in 2016 by SSR staff and primatologists. This project's goal was to more effectively manage the garbage and recycling accumulating in SSR and other ACG sectors, which was quickly leading to problematic foraging behaviors by capuchins and other wildlife. In addition to a successful public outreach campaign designed to raise awareness of proper waste disposal, this project led to the installation of new waste receptacles throughout ACG, preventing animal access to food scraps and diverting recyclable materials out of the landfill.

Yet, there is still much more to do, and many areas to improve in the realms of training programs, education, and collaboration. Given the importance of this site on many levels—its role in knowledge generation, the intrinsic value of the forest and animals, its status as a World Heritage Site, and the rare and critically endangered forest biome—it is imperative that we continuously build upon past and current efforts to protect this irreplaceable forest and its inhabitants.

10 | CONCLUSIONS

In today's age of widespread deforestation and anthropogenic disturbance globally, ACG has been an outlier and a positive, forceful example of ways that reforestation and conservation can succeed through collaboration via local, regional, national, and international communities spanning academia, government, and paraprofessional resident Costa Ricans (Janzen and Hallwachs, this issue). Over the past 37 years, primatologists in ACG have integrated study of plant community ecology, drought, population biology, and genetics, with fine-grained behavioral observations to ask and answer questions about the demography, social relationships, foraging ecology, conservation, community ecology, and more. This integrative approach has improved our ability to understand the adaptation and evolution of our study species specifically as well as primates and their

habitat more generally. The progress we have made in studying the life history, social dynamics, foraging ecology, and impacts of climate on primate health, behavior, and population trends would not have been possible without detailed, continuous study of these long-lived species. Through comprehensive and multifaceted study at a single location, we can integrate vastly different kinds of data touching on multiple levels of biological organization within a species, interactions among species, and interactions between the community and ecosystem, into a more comprehensive whole. Importantly, this work has practical and primate conservation contributions as well. For example, information on diet and food preferences will inform potential reforestation initiatives to emphasize species important for feeding. Finally, by our membership in the broader ACG community, other researchers can benefit from data originally collected to study primates. For example, our historical data on tree abundance in monkey home ranges enabled a study on bird community recovery with forest succession (Owen et al., 2020). Likewise, primatologists have strongly benefited from data collected by others, such as comprehensive climate data. Moving forward, we strive to expand and integrate data sharing across projects and to increase direct collaborations among the researchers studying vertebrate and invertebrate communities, vegetative ecosystems, and community ecology to fuel new discoveries and to optimize and reinforce conservation and education initiatives.

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REVIEW

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Tropical forest composition and function across space and time: Insights from diverse gradients in Área de Conservación Guanacaste

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Abstract

Environmental gradients have played a pivotal role in the history and development of plant ecology and are useful for testing ecological and evolutionary theory. Área de Conservación Guanacaste is a spatio-temporal mosaic of forests that have evolved continuously across elevation, topography, soil types, succession, and annual and inter-annual climatic change. Studies of plant ecology across diverse gradients of ACG have shaped functional ecology, successional theory, community assembly, plant–herbivore interactions, among many other fields. In this review, we synthesize the, perhaps overlooked, role plant ecological studies of ACG have had on our understanding of tropical forest dynamics. We outline present-day processes that will have major impacts on forest dynamics of ACG in the future and highlight how ACG will continue to shape future research priorities in plant ecology.

Abstract in Spanish is available with online material.

KEYWORDS
climate change, conservation, Costa Rica, ecological theory, environmental gradient, forest dynamics, tropical forest restoration

1 | A BRIEF HISTORY OF PLANT ECOLOGY AND THE DEVELOPMENT OF ÁREA DE CONSERVACIÓN GUANACASTE AS A RESEARCH HUB

The study of species distributions across spatial and temporal gradients has been central to the development of plant ecology. The latitudinal gradient in species diversity, for example, is a cornerstone of many ecological and evolutionary theories (Pianka, 1966). Elevational gradients have also played a central role in the development of plant ecology. Alexander von Humboldt was not the first to note the global relationship between diversity, elevation, and latitude—but he did set an important precedent for understanding mechanistic relationships between species distributions and climate (von Humboldt, 1807). More than a century later, plant

ecologists were still grappling with the development of techniques for quantitative analyses of vegetation patterns, as can be seen in Whittaker's treatment of gradient analyses of montane plant distributions (e.g., Whittaker, 1956, 1960). The emphasis on elevational and latitudinal gradients early in the history of plant ecology also gave rise to the climatic variability hypothesis (Janzen, 1967), which has received renewed interest at macroecological scales in the context of global climate change (Sheldon, Huey, Kaspari & Sanders, 2018). Finally, temporal gradients like chronosequences were integral to the development of successional theory (Pickett, 1989), which led to an emphasis (and much debate) on the statistical properties of plant communities. The heated debates that typified the early history of plant ecology were fueled by the study of plant distributions across latitude, mountains, and through succession.

The history of plant ecology in Área de Conservación Guanacaste (ACG) has followed a nearly identical trajectory. Foundational ideas in plant ecology, such as the climatic variability hypothesis (Janzen, 1967), the Janzen-Connell hypothesis (Janzen, 1970), neutral theory (Hubbell, 1979) and optimal foraging theory (e.g., Rockwood & Hubbell, 1987) were rooted or tested within ACG. This is in part due to the spatio-temporal landscape mosaic that characterizes ACG, making it a model system for plant ecological studies (Figure 1). In the rest of this review, we argue that understanding the past, present, and future of plant ecology research in ACG can motivate and inspire all ecologists, regardless of where any particular study site is located, or which particular taxa are in question. Specifically, we argue that plant ecology research within ACG is a case study for marrying conservation, forest management, and research. We highlight key studies that have informed major conservation issues within ACG and other studies that have benefited from the research infrastructure of ACG. Finally, we demonstrate how future plant ecology research in ACG can serve as a model for other regions (and field stations) around the world.

2 | SETTING THE STAGE FOR BECOMING A CENTER OF TROPICAL PLANT ECOLOGY RESEARCH

ACG's creation during the nexus of Costa Rica's scientific reform and the growth of the Organization for Tropical Studies in the 1970s positioned it to become an important stage for the development of plant ecology research. The landscape mosaic that characterizes

ACG (Figure 1) results from four centuries of European ranching, logging, road building, hunting, and anthropogenic fires. Historical records provide evidence that wood extracted from ACG was used for buildings in Lima, Peru in the 1600s (Janzen, 1998). A second major wave of deforestation occurred during a boom and bust cycle of the cattle industry between 1920 and 1980, which converted 65% of the Costa Rican landscape into a predominantly agricultural one (Savitsky & Lacher, 1998). The collapse of the cattle industry coupled with the adoption of sustainable development and the expansion of the ecotourism industry promoted the preservation and regeneration of large forest tracts (Calvo-Alvarado, McLennan, Sánchez-Azofeifa & Garvin, 2009). Within this context, ACG was born. Prior to its creation, plant research in ACG was largely taxonomic in nature. Because ACG was initially designed to regrow tropical dry forest habitat, plant ecology research in ACG emphasized two of its most prominent features: the seasonality and regeneration of tropical dry forests.

Arguably, a taxonomic focus on insects led by husband and wife team, biologists and conservationists Dan Janzen and Winnie Hallwachs (see Hebert, Penton, Burns, Janzen & Hallwachs, 2004; Janzen, 1970), inspired an emphasis on plant seasonality as it related to insects and other taxa. The deciduousness of dry forests was shown to influence foraging behaviors of leaf-cutter ants (Rockwood, 1975) and frugivorous bats (Fleming & Heithaus, 1986), and to result in seasonal changes in plant secondary compounds affecting insect herbivores (Hubbell, Howard & Wiemer, 1984; Janzen & Waterman, 1984). The study of plant secondary compounds in ACG occurred during the 1980s resurgence of interest in surveying plant species for drug development and the
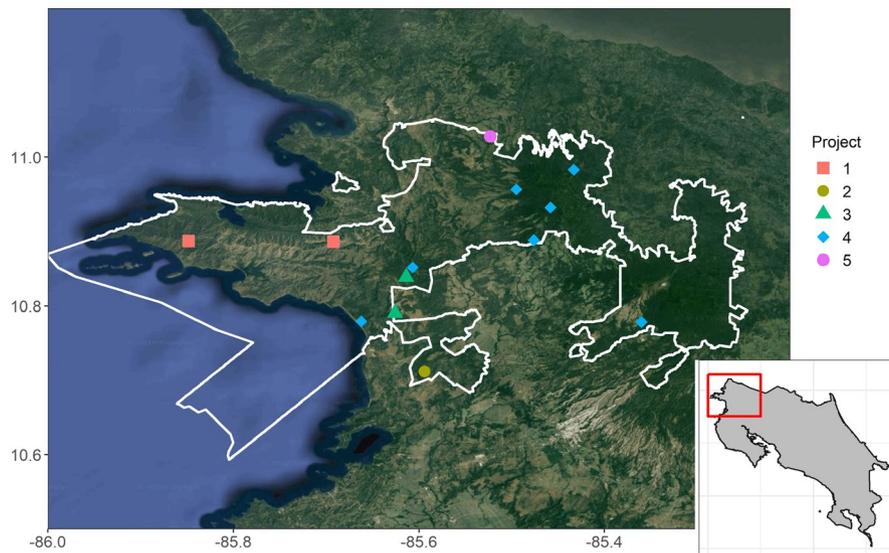
FIGURE 1 The spatially and temporally complex landscape of Área de Conservación Guanacaste (boundaries shown in white) provides a backdrop for testing ecological theory, habitat restoration, and environmental monitoring. Key research projects are highlighted. (1) Ultramafic plant communities of Peninsula de Santa Elena (Reeves et al., 2007; Hulshof *unpublished*); (2) Estación Experimental Forestal Horizontes, the location of a tropical dry forest fertilization and throughfall exclusion experiment (Waring et al., 2019); (3) the San Emilio Long-Term Forest Dynamics Plot (Enquist & Enquist, 2011; Swenson & Enquist, 2009) and the Environmental Monitoring Super Site (Castro et al., 2018) both located within Sector Santa Rosa; (4) studies including tropical rain and cloud forest communities at high elevations (Gotsch et al., 2010; Hulshof et al., 2013; Ramírez-Valiente & Cavender-Bares, 2017; Smith et al., 2014; Srivastava, 2006); (5) orange biodegradation and forest regeneration experiment (Treuer et al., 2018)

development of evolutionary models of plant defense allocation (e.g., Coley, Bryant & Chapin, 1985) (Theis & Lerdau, 2003). During this time, the popular film Medicine Man (1992) was, of course, modeled after Dan Janzen and Winnie Hallwachs (Janzen *pers. comm.*) who played (and continue to play) a pivotal role in the creation (and expansion) of ACG, its forest restoration and environmental education programs.

Later studies highlighted the interaction between plant phenology and seasonality, though these were generally narrow in focus and treated a single species at a time (e.g., Fleming, Williams, Bonaccorso & Herbst, 1985; Howe & Vande Kerckhove, 1979). In nearby dry forests 90 km south of ACG, the study of phenology was much more comprehensive including work relating the underlying drivers of dry forest phenology (Daubenmire, 1972; Opler, Frankie & Baker, 1980), detailed physiological measurements such as stomatal function and tree water status, the influence of topography on phenological patterns (Reich & Borchert, 1984, 1988), and phenological comparisons between dry and wet forests and among plant growth forms (Borchert, 1983; Frankie, Baker & Opler, 1974; Opler, Frankie & Baker, 1976). Collectively, these studies and others point to the major influence of individual researchers on themes and trajectories of place-based research.

During the 1980s, heightened public awareness of rain forest deforestation (see Myers, 1981) ignited a new wave of research relating forest fragments and succession (e.g., Lovejoy & Oren, 1981). Janzen wrote at length about the regeneration of dry forests (Janzen, 1983, 1988) including the use of orange peels and biodegradation to aid in forest restoration (Janzen, 2000). Other research related to forest succession primarily emphasized dry forests and the relationship between forest succession and food availability for other taxa like primates (e.g., Chapman & Chapman, 1990). As the first IPCC Assessment Report of 1990 underlined, the importance of climate change, and as ACG became a UNESCO World Heritage Site in 1999, more long-term research programs were established within ACG. One of the longest-running tropical forest dynamics plot was established in 1976 with a 25 hectare stand of late second growth dry forest in the San Emilio forest of ACG's Sector Santa Rosa. The mapped area included spatial positions of 50,000 juvenile and adult woody individuals (Hubbell, 1980) and was subsequently remeasured in 1996 and 2006 (Enquist & Enquist, 2011; Swenson & Enquist, 2009). Forest dynamics of this plot, in part, led to the neutral theory of biodiversity (Hubbell, 2001) and has revealed important interactions with large-scale climatic processes like the Pacific Decadal Oscillation, the El Niño Southern Oscillation, and precipitation trends in dry forests of ACG.

Early plant ecology studies in ACG created an important precedent and established ACG as a center for plant ecology research. These early studies emphasized the rainfall seasonality of tropical dry forests and the effects of rainfall seasonality on dry forest flora and fauna. However, more recent work (see Table 1 for a few key examples) has highlighted finer-scale spatial gradients like the role of topography and soils on forest structure and biomass (Becknell & Powers, 2014; Leiva, Mata, Rocha & Gutiérrez Soto, 2009; Powers, Becknell,

Irving & Peréz-Aviles, 2009). Edaphic variation plays a dominant role in forest structure as can be seen across major edaphic formations such as the volcanic tuffs, limestone outcrops and the ultramafic formations of Peninsula de Santa Elena, which host plant communities distinct from dry forests on volcanic soils (Reeves, Baker & Romero, 2007; Hulshof *unpublished*). Beginning in the 1970s and continuing today, the political boundaries of ACG have expanded to include tropical rain and cloud forests with the purchase of neighboring land. As a result, more research has taken advantage of ACG's unique elevational gradient, one of the few uninterrupted dry to cloud forest gradients in the world. Both temperature and rainfall gradients vary predictably across elevation (Figure 2), making this an ideal location for work on shifting ranges of plants, animals, and other taxa.

3 | CURRENT PLANT ECOLOGY RESEARCH THEMES EMPHASIZE TROPICAL DRY FORESTS

New technologies and a growing and diverse network of ACG researchers have enabled larger scale approaches to field research, mirroring shifting research priorities in other parts of the world. Ongoing plant ecology research in ACG is continuing the tradition of developing and testing ecological and evolutionary theories, and advancing insights relating the re-assembly and maintenance of plant communities across time and space and its applications to forest management and conservation (Table 1). Disturbance (e.g., extreme events, climate change, succession, invasive species) is a unifying theme among current plant ecology studies in ACG, with succession playing a prominent role. These studies recognize that the modern study of tropical forests is the study of secondary forest succession. Tropical dry forests, in particular, received renewed global interest with the realization that, despite worldwide public awareness campaigns to save the rain forest, rain forests were, in fact, not the most endangered tropical ecosystem (Janzen, 1988). Successional studies in Neotropical dry forests, including within ACG, highlighted the dominance of legumes early during succession (Leiva et al., 2009), the decrease in conservative traits related to drought tolerance and drought avoidance during succession (opposite to the acquisitive to conservative trend observed in wet forests) (Becknell & Powers, 2014; Buzzard, Hulshof, Birt, Violle & Enquist, 2016; Lohbeck et al., 2013) and that regenerating tropical dry forests tend to converge on functional, structural and diversity metrics characteristic of mature forests in about 60–90 years (Buzzard et al., 2016; Powers et al., 2009). The application of remote sensing in dry forests of ACG also emphasized differences in forest structure due to succession and the importance of satellite imagery for monitoring forest structure over time (Kalacska et al., 2007) at much broader spatial scales that can be studied using a plot-based approach. Remote sensing studies have noted the technical challenges imposed by dramatic changes in leaf phenology during the dry season and the challenges imposed by cloudy conditions during the rainy season. Finer-scale successional processes have been studied in detail.

TABLE 1 Environmental and ecological gradients in Área de Conservación Guanacaste, Costa Rica including key results from selected studies and a few suggested priorities for future research

Gradient	Description	Key findings	Some suggested research priorities
Elevation	ACG encompasses mangroves at sea level to elfin cloud forests above 1100 m on Volcán Orosí, Cacao, Rincon de la Vieja, and Volcán Santa Maria.	Volcanoes provide large elevational gradients across ACG. Community weighted mean of specific leaf area decreased across a ~1,000 m gradient (Hulshof et al., 2013). Another study documented variation in leaf traits and water status in the wet and dry seasons for 12 evergreen species that occur in both dry (285 m elevation) and wet forest (500 m elevation) (Gotsch et al., 2010).	Drivers of plant species distribution across elevation and potential limits to dispersal and migration with future climate change Forest dynamics and functioning of transition zones between dry and wet forests Gene flow of plant populations across elevation
Rainfall seasonality and intra-annual variation	Rainfall in lowland dry forests is strongly seasonal; 87–100% of annual rainfalls from May to November, based on 38 years of rainfall from Santa Rosa.	Studies investigating how plant processes vary within wet or dry seasons, or across the year, have found that the timing of acorn production during the wet season influences subsequent fitness (Center et al., 2016); fine-root mass and nodule mass in legume tree species are higher in wet compared to dry seasons (Gei & Powers, 2015); dry seasons impose a strong bottleneck for seedling survival (Gerhardt, 1993); leaf and flower phenology and sap flux of *Enterolobium cyclocarpum* vary seasonally (Rojas-Jiménez, Holbrook, & Gutiérrez-Soto, 2007).	Climatic variability of higher elevations and down-scaled climate models for the region Documentation and modeling of cloud line and fog interception of cloud forested volcanoes
Inter-annual variation in climate and ENSO events	Inter-annual variation in rainfall is high, with dry years corresponding to El Niño years; mean annual rainfall at Santa Rosa is 1,693 mm, ranging from 627 to 3341 mm.	Inter-annual variation in rainfall, and ENSO-linked droughts in particular, have been linked to decreases in forest productivity (Castro et al., 2018) and seed production (O'Brien et al., 2018), and result in long-term, directional shifts in forest composition from mesic to more xeric species (Enquist & Enquist, 2011).	The role of fluctuating primate populations and inter-annual rainfall variability for seed production, dispersal and forest regeneration
Geology and soil parent materials	The great soil diversity at ACG results from diverse parent materials and weathering times including volcanic tuff, basalt, and serpentine soils derived from ultramafic rocks (Hartshorn, 1983; Reeves et al., 2007; Vargas-Ulate, 2001).	Soil orders include Entisols, Inceptisols, Alfisols, Mollisols, Ultisols, and Vertisols (Leiva et al., 2009). Tree species composition varies across soil gradients (Becknell & Powers, 2014; Powers et al., 2009; Vargas-Ulate, 2001). Soil nutrient availability, fine-root production, and decomposition vary in response to edaphic gradients (Waring et al., 2016; Powers & Peréz-Aviles, 2013; Schilling, Waring, Schilling, & Powers, 2016, Werden, Becknell & Powers, 2018b).	Interactions between soil nutrient availability, precipitation variability, and forest dynamics (including tree growth and leaf function) The role of edaphic variation for plant community composition and functional traits and the resulting effects on the insect herbivore community
Succession and forest regeneration	The history of deforestation, grazing, and agriculture, and the subsequent abandonment of these land uses has resulted in a mosaic of secondary forests in different stages of recovery (Calvo-Alvarado et al., 2009).	There are two dominant modes of secondary forest regeneration, via wind-dispersed seeds into large patches, or via animal-dispersed seeds into smaller fragments, which differ in deciduousness and habitat suitability for animals (Castillo-Nunez et al., 2011; Janzen, 1988). Community weighted mean values of functional traits vary over succession from conservative to acquisitive values (Becknell & Powers, 2014; Buzzard et al., 2016), which is due to both species replacement and intra-specific variation (Derroire, Powers, Hulshof, Varela & Healy, 2018). Edaphic variation modulates successional processes (Leiva et al., 2009; Powers et al., 2009).	Successional trajectories of wetter forests especially mid-elevational forests adjacent to pastures Restoration of regions between lowland dry forests and higher elevation rain forests

A rare example of the direct application of agricultural waste for forest regeneration occurred within ACG (Daily & Ellison, 2012). The waste from a nearby orange juice company—1,000 truckloads in total—was directly applied to 3 hectares of degraded lands,

accelerating forest regeneration. Aboveground woody biomass increased by nearly 200% over 16 years relative to an adjacent control plot (Treuer, Choi & Janzen, 2018). This experiment is a case study of partnerships between private businesses and protected areas, as

well as the politics that can limit the broad adoption of biodegradation practices. Active restoration techniques are, however, often required on extremely degraded soils. Species have pronounced effects on soil properties in unmanaged forests and plantations (Gei & Powers, 2013), and the use of soil amendments and screening native plant species based on water-use and photosynthetic traits shows promise for dry forest restoration on extremely degraded soils (Werden, Alvarado & Zarges, 2018). The influence of edaphic variation and soil fertility on forest structure (Powers et al., 2009; Vargas-Ulate, 2001), fine-root biomass (Powers & Peréz-Aviles, 2013), tree seedling development (Gerhardt, 1993), soil bacteria (Becklund, Kinkel & Powers, 2014), nitrogen cycling, and soil fungal communities (Waring, Adams, Branco & Powers, 2016) cannot be ignored when considering successional processes (Leiva et al., 2009).

Legumes play a unique role in the succession of tropical forests and are a dominant feature of Neotropical dry forests (Gentry, 1995), especially during early stages of succession (Gei et al., 2018). New findings from ACG show that the success of legumes may be attributed to their rapid germination rates coupled with higher seedling growth rates (Smith-Martin et al., 2017; Vargas, Werden & Powers, 2015), or their distinct functional traits such as high leaf carbon and nitrogen (Powers & Tiffin, 2010) and their ability to fix nitrogen. Another example of plant species that have been extensively studied in ACG is *Quercus oleoides* Cham. and Schlecht., the lowland tropical live oak. *Quercus oleoides* once formed vast mono-dominant stands (Boucher, 1981; Janzen, 1987). Its inability to recolonize abandoned pastures was thought to be due to positive density dependent acorn survivorship (Boucher, 1981). It is more likely, however, that seed dispersal is the primary limitation to recolonization (Klemens, Deacon & Cavender-Bares, 2011). Its primary seed disperser, the Central American agouti, rarely crosses open pastures necessitating an active restoration strategy to avoid local extinction of small populations (Klemens et al., 2011). Despite its inability to recolonize abandoned pastures within its former range, disjunct populations have a complex genetic structure (Deacon & Cavender-Bares, 2015) and notable intra-specific variation in traits related to growth and drought resistance (Ramírez-Valiente & Cavender-Bares, 2017), emphasizing the conservation value of this unique keystone species. The increasingly fragmented populations of *Q. oleoides* and its declining regeneration potential are echoed by the decline of oak tree populations across eastern deciduous forests of the United States. By comparison, in the eastern United States, oak regeneration is strongly limited by deer overpopulation and the eventual loss of dominant oak forests will have long-lasting effects on wildlife and forest dynamics (McShea et al., 2007). In both cases, active restoration strategies may be required to perpetuate remnant oak forest stands.

Other advances in functional ecology have been made by focusing on one of the most conspicuous features of seasonally dry forests—the wide range of leafing phenologies and leaf habits on display (Figure 3). Dry forest species are renowned for their remarkable adaptations to drought, with species often grouped into deciduous and evergreen categories (Eamus, 1999). However, a surprising degree of variation of hydraulic strategies occurs within deciduous species

from high xylem conductivity and dry season water retention to highly vulnerable xylem, large embolism, and low wood conductivity during dry periods (Brodribb, Holbrook & Gutierrez, 2002; Werden, Waring, Smith-Martin & Powers, 2018). Further, leaf physiology was a poor predictor of leaf habit in comparisons of evergreen and deciduous dry forest species of ACG (Brodribb, Holbrook, Zwieniecki, & Palma, 2005). Other plant traits also failed to distinguish between leaf habits in dry forests (Powers & Tiffin, 2010), underlining the variation of dry forest plant strategies and the limitations of using plant functional type classifications for vegetation models in dry forests. Indeed, modeling approaches incorporating plant hydraulic traits outperformed models using plant functional types and better predicted the seasonality of growth, phenology and other vegetation dynamics in dry forests across the Neotropics (Xu, Medvigy, Powers, Becknell & Guan, 2016).

Climate change is another prominent theme among ongoing plant ecology research in ACG. A general trend of decreasing precipitation, ENSO-induced drought, the rise of cloud line, the increased number of cloudless days at high elevations (Ugalde-Gómez et al., 2009; Alvarado, Contreras, Jimenez, Alfaro & Solano, 2012; Durán *In Review*), and more frequent extreme events like hurricanes have and will continue to impact plant communities and forest structure and function of ACG. The long-term datasets in ACG have already begun to reveal consequences of strong ENSO events on forest processes. The 63% reduction in rainfall during the 2015 ENSO event was accompanied by a decrease in forest productivity (Castro, Sanchez-Azofeifa & Sato, 2018) and an increase in tree mortality (Powers *pers. obs.*).

The ability to conduct experiments at the ecosystem scale in ACG's Estación Experimental Forestal Horizontes (Horizontes Experimental Forestry Station) is also transforming our understanding of nutrient limitation. In the first large-scale forest fertilization experiment in tropical dry forests, 25 × 25 m patches of forest were fertilized with nitrogen, phosphorus, or their combination, or remained unfertilized (Waring, Perez-Aviles, Murray & Powers, 2019). These results show clear evidence of phosphorus limitation, but it is manifested differently compared to tropical rain forests. In the first three years of fertilization, P-addition strongly stimulated fine-root production (Waring et al., 2019). The explanation for this effect is that once P-limitation is overcome, plants invest in fine-root biomass to overcome water limitation. Thus, nutrients and water appear to interact in dry forests, which underscores that forest responses to inter-annual variation in rainfall and increasing climate variability may depend on underlying edaphic conditions.

Beyond the ecosystem-level consequences of drought or nutrient availability on forest scale processes described above, the physiological responses of individual plants to climate variation can result in whole-tree variation in growth, reproduction, and survival. Applications of resource allocation theory in the context of climate change could improve predictions related to changes in plant biomass and carbon storage under future climates. Annual changes in precipitation, for example, were shown to influence the allometric relationship between plant growth and fruit production in an
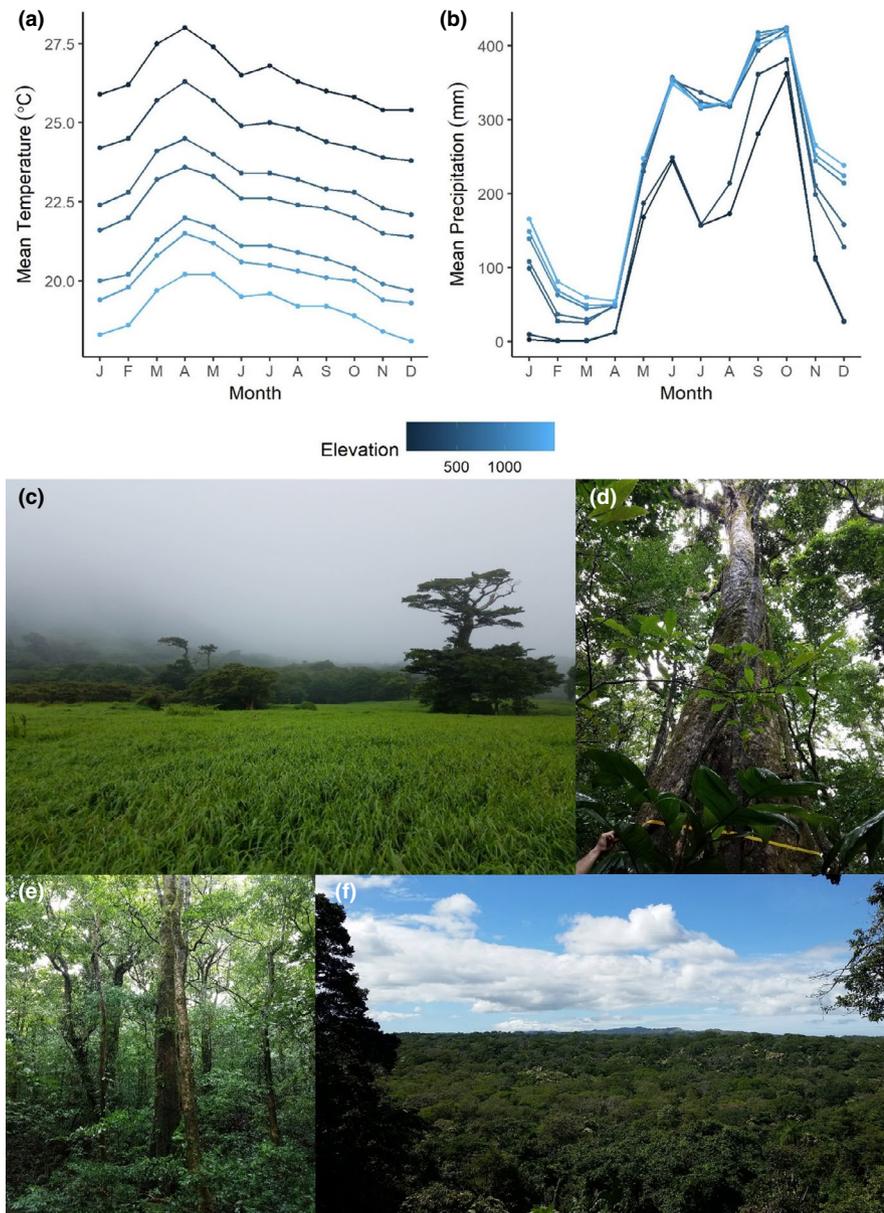
FIGURE 2 Average monthly temperatures (a), and rainfall (b) as a function of elevation in Área de Conservación Guanacaste, Costa Rica. Climate data are from WorldClim (https ://www.worldclim.org/; Hijmans et al., 2005). ACG encompasses coastal mangroves, lowland tropical dry forests, mid-elevational wet and rain forests, and cloud forested volcanoes. This landscape also includes intermittent streams, estuaries, riparian zones, and headwaters of major rivers, the primary water source for agriculture and human consumption in the northwestern region of Costa Rica. Tropical rain and cloud forests (c-d) are cooler, wetter, and have greater canopy height and aboveground biomass compared to lowland tropical dry forests (e-f)

iconic dry forest species (*Bursera simaruba* L. Sarg; Hulshof, Stegen, Swenson, Enquist & Enquist, 2012) as well as tree ring growth for two dry forest species with contrasting rooting depths (Enquist & Leffler, 2001). At coarser spatial scales, the extreme drought caused by the ENSO event of 2015 promoted seed production for early successional species such as lianas and wind-dispersed species and reduced seed production for deciduous species and species dispersed by vertebrates and gravity (O'Brien, Peréz-Aviles & Powers, 2018), with major implications for long-term shifts in forest composition and structure. Indeed, across two decades, a typical late successional dry forest shifted from a mesic forest dominated by evergreen species to a more xeric forest dominated by deciduous, compound-leaved species (Enquist & Enquist, 2011).

Together, these studies all point to the wide species-level variation in responses and differential sensitivities to climate change (Allen

et al., 2017). As plant ecology embraced a trait-based approach, in part, to predict assembly processes and how these may be altered under future climate scenarios, the number of trait-based studies in ACG also increased. The spatial and temporal gradients of ACG make a trait-based approach especially compelling considering the dramatic variation in functional diversity found in dry forests both between (Hulshof et al., 2013) and within species (Figure 3; Hulshof & Swenson, 2010). These and other studies highlighted that dry forests are as functionally diverse, if not more, compared to nearby rain forests and calls into question the use of traditional taxonomic-based diversity metrics for setting conservation priorities. Plant functional diversity of mid- and high elevation sites in ACG remain poorly studied though cloud forest species have highly conservative strategies (Gotsch, Powers & Lerdau, 2010) including low values of specific leaf area (Hulshof et al., 2013). Conservative strategies (including long-lived leaves and slow
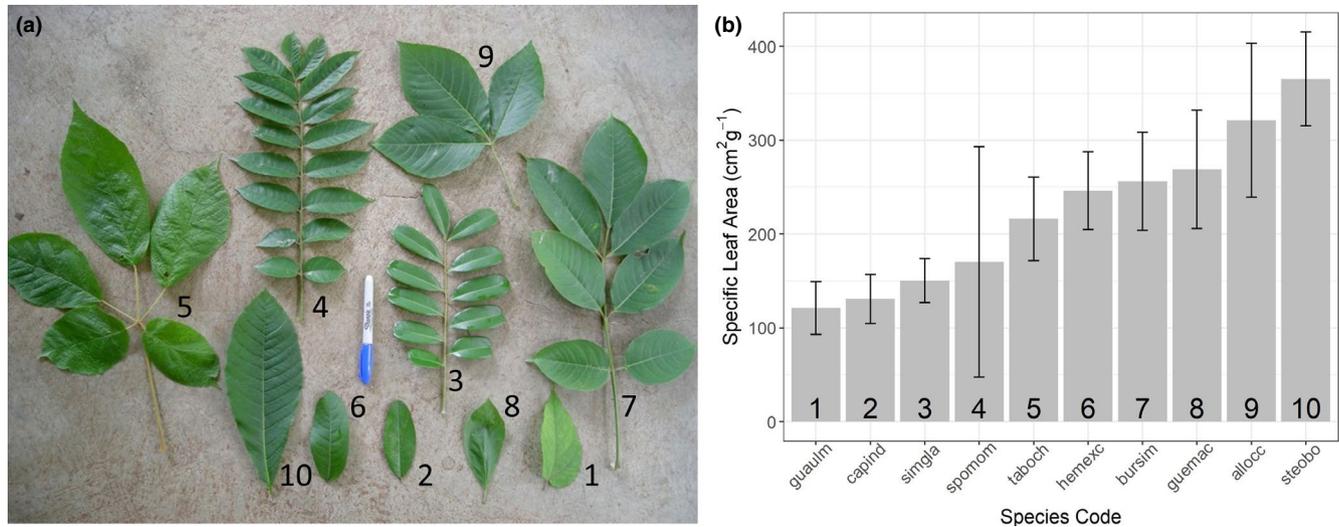
FIGURE 3 Variation in (a) leaf shapes and sizes in tropical dry forests of Área de Conservación Guanacaste, Costa Rica and (b) the mean and standard deviation of their specific leaf area (cm²/g). Trait data can be found in the Supporting Information section of Hulshof and Swenson (2010). Species codes are as follows: 1 = Sterculiaceae *Guazuma ulmifola* (Lam.); 2 = Capparaceae *Capparis indica* (L.) Fawc. and Rendle; 3 = Simaroubaceae *Simarouba glauca* DC.; 4 = Anacardiaceae *Spondias mombin* L.; 5 = Bignoniaceae *Tabebuia ochracea* Standl.; 6 = Celastraceae *Hemiangium excelsum* (H.B.K.) A.C. Smith; 7 = Burseraceae *Bursera simaruba* (L.) Sarg.; 8 = Rubiaceae *Guettarda macrosperma* Donn. Sm.; 9 = Sapindaceae *Allophylus occidentalis* (Sw.) Radlk.; 10 = Apocynaceae *Stemmadenia obovata* (Hook & Arm.) Schum.. Taxonomic nomenclature follows Janzen and Liesner (1980). Note: compound-leaved legume species with small leaflets were not included in this study (and thus not shown here) even though they are characteristic of Neotropical dry forests

growth rates) of cloud forest tree species may make it difficult to observe plant community responses to climate change using a standard trait-based approach. Physiological measurements like photosynthesis or hydraulic traits, however, are likely to reveal the immediate impacts of climate change at higher elevations. The trait-based approach to plant community assembly has been applied extensively in ACG dry forests where the use of plant functional traits helped explain patterns of species distributions across soil types (Figure 4; Powers et al., 2009; Werden, Waring et al., 2018) and succession (Becknell & Powers, 2014; Buzzard et al., 2016; Werden, Waring et al., 2018). The same dry forest plot that played a role in Hubbell's neutral theory, also played an important role in linking phylogenetic and functional approaches in community ecology (e.g., Swenson & Enquist, 2009). From these studies, it becomes clear that most of the plant ecology in ACG has primarily occurred in dry forests. The emphasis of dry forest ecology in ACG is, in part, due to the accessibility and infrastructure of Sector Santa Rosa (the heart and administrative center of ACG), the historical importance of Santa Rosa as a model Neotropical dry forest, and a well-documented flora that is relatively easy to identify (e.g., Enquist & Sullivan, 2001; Janzen & Liesner, 1980).

The emphasis on tropical dry forest research in ACG is in contrast to the majority of tropical ecology research, which historically neglected dry forests in favor of tropical rain and wet forests (Meli, 2003; Myers, Mittermeier, Mittermeier, Da Fonseca & Kent, 2000). It is possible that our understanding of tropical ecology is severely limited by not considering interactions between forest types. Across evolutionary time scales, for example, dry forest species evolved from genera characteristic of other vegetation types and, vice versa, recent rain forest radiations have occurred in primarily dry forest

genera (Pennington et al., 2004). This type of ecotonal speciation may be especially important in Neotropical flora and suggests that conservation planning must allow for migration across ecotones (Bush, 2002). Thus, the successful conservation of tropical forests requires the conservation of large swaths of adjacent, intact biomes, as occurs throughout ACG.

Work in other taxa at higher elevations highlights the importance of considering ACG as a whole to understand plant ecology. For example, the seasonal migration of moths (Janzen, 1986, Janzen, 1987) and wasps (Hunt, Brodie, Carithers & Goldstein, 1999) from dry to wet forests demonstrate the strong linkages between forest types. The narrow elevational ranges and phylogenetic clustering of ants in cloud forests of ACG and the upward migration of lowland ant species points to major changes in ant diversity and composition with climate change (Smith, Hallwachs & Janzen, 2014). Similarly, the drought sensitivity of bromeliad insects played a dominant role in predicting community and trophic composition (Amundrud & Srivastava, 2015; Srivastava, 2006), again pointing to potential climate change effects on these taxa. ACG's iconic elevational gradient is vastly understudied and merits research that untangles the dynamics that have occurred for thousands of years between lowland dry forests, rain forests and higher elevation cloud forests. The interfaces between forest types are regions of intense species mixing, likely providing a preview to the future effects of climate change at larger spatio-temporal scales. A recent initiative aims to extend dry forest plant ecology into higher elevations (Hulshof *unpublished*) and leverage the vast network of ACG researchers to develop and sustain long-term monitoring across taxa, across this rare elevational gradient. ACG's elevational gradient from tropical dry forests

through rain and cloud forests would provide valuable comparisons with similar gradients across the Pacific watershed such as those occurring across the Sierra de Manantlán Biosphere Reserve in central Mexico (Vázquez & Givnish, 1998) and the southern slope of the Sierra Madre del Sur in Oaxaca (Salas-Morales & Meave, 2012).

4 | THE IMPORTANCE OF LOCAL AND GLOBAL COLLABORATIONS FOR THE FUTURE OF PLANT ECOLOGY RESEARCH IN ACG

The future of plant ecology research in ACG will increasingly emphasize local and global collaborations, technological advances, and experimental and modeling approaches. Here, we outline major research trends and priorities, as well as the infrastructure and human resources of ACG that enable significant advances in ecological research and conservation. Previous work established the ubiquity of drought tolerance and drought avoidance strategies of tropical dry forest plant species. Despite the large influence of drought for dry forest species, long-term monitoring suggests that tropical dry forests may be as vulnerable to decreasing precipitation trends as nearby wetter forests. Experimental approaches have begun to disentangle drought responses from germination to adult stages in the first tropical dry forest large-scale throughfall exclusion experiment (Figure 5; Vargas, Perez-Aviles, Waring, Medvigy & Powers, 2018). Other experiments are testing for local adaptation to water availability using reciprocal transplant and germination experiments in *Quercus oleoides* (Center, Etterson, Deacon & Cavender-Bares, 2016; Ramírez-Valiente & Cavender-Bares, 2017) as well as other common dry forest species (Smith-Martin et al., 2017; Vargas et al., 2015). In addition, high-resolution down-scaled climate models are becoming increasingly available
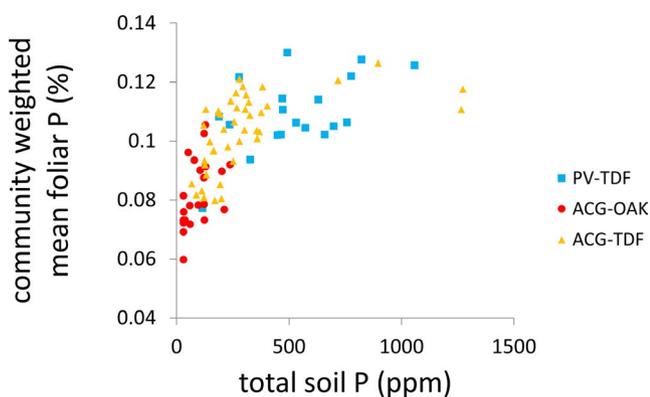
FIGURE 4 Community weighted mean values of foliar phosphorus (%) weighted by basal area of tree species from 84 0.1 ha forest inventory plots in relation to total soil phosphorus (ppm) in the top 10 cm of mineral soil. Forest plots are located in Palo Verde National Park (PV-TDF), lowland dry forest in ACG (ACG-TDF) and lowland *Quercus oleoides* forest (ACG-OAK) in ACG. Redrawn with forest inventory and soil data from Werden, Becknell, et al. (2018a) and foliar P in the Supporting Information section of Powers and Tiffin (2010)

for ACG (Ugalde-Gómez et al., 2009; Alvarado et al., 2012; Durán *In Review*) and will aid predictive models of forest dynamics (Xu et al., 2016).

Modeling approaches are further enabled by long-term forest monitoring and observational datasets such as that within San Emilio forest (Enquist & Enquist, 2011; Hubbell, 1979; Swenson & Enquist, 2009), an eddy covariance flux tower and environmental monitoring site within dry forests of ACG (see Castro et al., 2018), and longitudinal studies of chronosequence plots (O'Brien et al., 2018; Powers pers. obs.). Continued long-term monitoring is and will continue to be a major research priority, particularly across biomes. Again, we emphasize that the majority of plant ecology research in ACG remains dry forest-focused and extending outward will require a collaborative network of researchers (both established and new) as well as the integration of multiple taxa. As an example, the recent drought of 2015 provided plant ecologists and primate behavior researchers to pool observations of forest mortality and collaborate to achieve a deeper understanding of the patterns and mechanisms of tree response to extreme drought (Powers *pers. obs.*). Advances in technology, such as the increasing availability of high-throughput DNA sequencing to examine community-level patterns of soil microbes or fine roots (Waring et al., 2016), or drones to image forest canopy processes with high spatial and temporal resolution (Treuer et al., 2018), promise to expand our understanding of plant ecology and may help integrate across forest types. Another research priority for plant ecology in ACG (and around the world more generally) will be a tighter integration between ecological research and conservation goals, such as detailed studies on the conditions that facilitate forest restoration (see Werden, Alvarado, et al., 2018).

Achieving these research goals and sustaining research into the future in ACG is highly dependent on a few key characteristics that facilitate new research projects and collaborations among established researchers. Early on, ACG adopted online portals for serving as the interface between researchers and park management. This includes the process for submitting research and collection permits as well as Geographic Information System resources. As in other tropical protected areas (e.g., Pitman, Azáldegui, Salas, Vigo
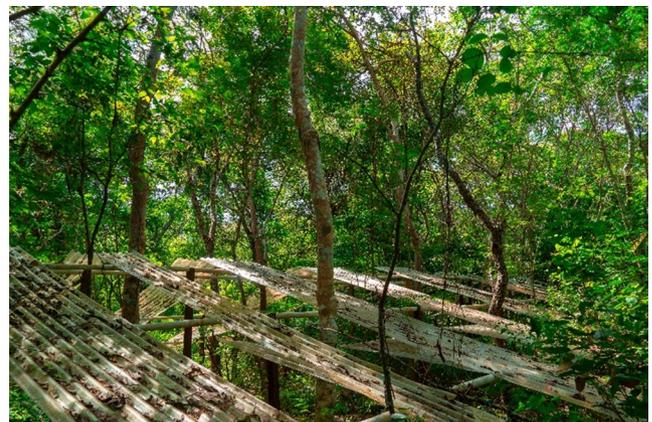
FIGURE 5 A large-scale throughfall exclusion experiment in tropical dry forests of Estación Experimental Forestal Horizontes (photo credit: Dan Du)

& Lutz, 2007), a gap exists between Spanish publications that are inaccessible outside of the country and English publications inaccessible within the country. To remedy this within ACG, an online repository of data types like publications, gray literature, and aerial photography is currently under construction (Repositorio COPA Ciencia, Organismos y Programas ACG). Further, to facilitate the interaction between researchers and ACG directors, managers, and staff a non-profit organization, investigadoresACG (iACG, http://investigadoresacg.org/blog/) was created in 2007 and has contributed to the organization and digitization of online data and other resources. iACG also serves as an important node between researchers and between researchers and ACG staff by hosting activities that encourage interactions and knowledge transfer. This has provided an important platform for researchers to translate their results and make specific management recommendations as well as for ACG directors and managers to convey their priorities to the research community. The restoration of degraded soils described in Werden, Alvarado, et al. (2018) exemplifies the relationship between managers and researchers, and research that addresses specific conservation and restoration needs of ACG.

In summary, ACG provides the ecologist with a diversity of gradients over which to study the form and function of plant communities. The spatial mosaic of forest types, land uses, successional stages, and soil interact with temporal variation in rainfall at a variety of scales—from daily to seasonal to decadal. This endlessly fascinating variability provides fodder for both testing ecological theories (e.g., Hubbell, 1979) and at the same time addressing applied concerns such as the selection of native species for restoration under changing climate regimes (Werden, Alvarado, et al., 2018). The future of plant ecological research in ACG will increasingly depend on collaborative networks and cross-site comparisons with other well-studied tropical forests like the forest dynamics plots of ForestGEO (Anderson-Teixeira et al., 2015), La Selva Research Station (Costa Rica), Guánica State Forest and Biosphere Reserve (Puerto Rico) and Chamela-Cuixmala Biosphere Reserve (Mexico), to name a few. Plant ecology research in ACG should also increasingly consider the movement and exchange of species between habitat types and land uses, and consider the influence of the larger agro-landscape in which ACG is embedded. ACG will continue to be a hotspot for basic research as wide ranging as eco-physiology to ecosystem and atmospheric science and for applied research to aid in the conservation and management of tropical forests worldwide.

ACKNOWLEDGMENTS

DATA AVAILABILITY

Climate data used to create Figure 2 are available at https://www.worldclim.org/ Hijmans, Cameron, Parra, Jones & Jarvis, 2005). Specific leaf area for ten dry forest species included in Figure 3 can be found in the Supporting Information section of Hulshof and Swenson (2010). Forest inventory and soil data used to create Figure 4 are available at Dryad (Werden, Becknell & Powers, 2018b; https://doi.org/10.5061/dryad.kv2002g) and foliar P in the Supporting Information of Powers and Tiffin (2010).

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ORIGINAL ARTICLE

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Influence of sea turtle nesting on hunting behavior and movements of jaguars in the dry forest of northwest Costa Rica

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Abstract

Jaguars (*Panthera onca*) are opportunistic predators that prey on large profitable prey items, such as sea turtles at nesting beaches. Here, we use jaguar and sea turtle track-count surveys, combined with satellite telemetry of one jaguar, to evaluate whether jaguar hunting behavior and movements are influenced by seasonal sea turtle nesting in the Sector Santa Rosa of Área de Conservación Guanacaste in northwest Costa Rica. We used generalized linear models to evaluate the effect of moon phase and sea surface temperature on olive ridley (*Lepidochelis olivacea*) and green turtle (*Chelonia mydas*) nesting abundance, as well as the combination of these predictors on the frequency of jaguar predation activity (proximity to nesting beaches) and movements. For home-range size and location analyses, we calculated kernel density estimates for each season at three different temporal scales. Sea turtle nesting season influenced jaguar activity patterns, as well as sea turtle abundance was related to jaguar locations and predation events, but jaguar home-range size (88.8 km[2] overall) did not differ between nesting seasons or among temporal scales. Environmental conditions influenced sea turtle nesting and, as a consequence, also influenced jaguar movements and foraging activity. Our study defined the home range of a female jaguar in the tropical dry forest and its relationship to seasonally abundant turtles. Additional information related to the effect of tourism on jaguar–sea turtle interactions would improve conservation of these species at unique nesting beaches in the area.

KEYWORDS

Chelonia, Guanacaste, home range, *Lepidochelis*, moon phase, *Panthera*, seasonal ecosystem, telemetry

1 | INTRODUCTION

Highly seasonal ecosystems present a combination of challenges for wildlife that lead to physiological and behavioral adaptations (Astete et al., 2017; Blaum, Rossmanith, Schwager, & Jeltsch, 2007;

Stoner & Timm, 2011). For example, jaguars (*Panthera onca*), which are widely distributed from northern Mexico to northern Argentina (UICN, 2019), exhibit seasonal movement patterns related to peaks of prey availability and abiotic factors (Carrillo, Fuller, & Saenz, 2009; Cavalcanti, 2008; Guilder, Barca, Arroyo-Arce,

Gramajo, & Salom-Pérez, 2015). In the Pantanal of Brazil during the dry season, jaguars spend more time foraging near caiman (*Caiman crocodilus*) habitats (Cavalcanti, 2008), whereas in Corcovado, Costa Rica jaguars switch activity patterns related to spatiotemporal distribution of white-lipped peccaries (*Tayassu pecari*) and sea turtles (*Lepidochelys olivacea*, *Chelonia mydas*) (Carrillo, 2000).

Jaguars, however, are opportunistic predators preying on as many as 85 species, including most available animals weighing > 1kg (Carrillo, 2000; Rabinowitz & Nottingham, 1986); thus, efforts to understand the relationship of abiotic factors (seasonality and moon phases) and prey on jaguar spatial dynamics are area-specific. By using Global Positioning Satellite (GPS) telemetry, researchers can determine correlations between animals and their habitats, and thus record patterns of space use that likely influence their persistence (Gonzales- Borrajo, Lopez-Bao, & Palomares, 2017; Morellett et al., 2013). Not surprisingly, previous research emphasizing on jaguar spatial dynamics (e.g., Carrillo, 2000; Cavalcanti, 2008; De la Torre, Núñez, & Medellín, 2017; Gese, Terletzky, Cavalcanti, & Neale, 2018; Morato et al., 2018; Rabinowitz & Nottingham, 1986) has shown that seasonality influences area-specific movements of jaguars.

Sector Santa Rosa (SSR) in the dry forests of northwestern Costa Rica is likely home to one of the largest recovering jaguar populations in Costa Rica (Montalvo, Saenz, Ramirez, & Carrillo, 2015). It also contains two important sea turtle (olive ridley [*L. olivacea*] and green turtles [*C. mydas*]) nesting beaches, one characterized by a rare, seasonal sea turtle nesting aggregation (*arribada*; Playa Nancite), and the other (Playa Naranjo) characterized by year-round but seasonal solitary nesting (Behm, Hagerty, Drake, & Spotila, 2000; Cornelius, 1976; Cornelius & Robinson, 1982; Hughes & Richard, 1974; Valverde, Cornelius, & Claudettte, 1998). Here in particular, we hypothesize that during sea turtle nesting peaks, seasonal prey availability directly influences jaguar hunting behavior by increasing foraging activity near beaches and predation rates on sea turtles. In this study, we sought to identify the effect of seasonality and moon phases on jaguar foraging distances to sea turtle nesting beaches; seasonal spatiotemporal patterns on jaguar home-range size, and frequency of jaguar's sea turtle predation events related to season, sea turtle abundance, and moon phases.

2 | Methods

2.1 | Study area

This study was conducted in SSR, within one of the three national parks of Área de Conservación Guanacaste (ACG) located in northwest Costa Rica (10°53′01″N 85°46′30″W; Boza, 1992). SSR encompasses 387 km^2 and is dominated by the few remaining tropical dry forests in Central America (Gillespie, Grijalva, & Farris, 2000; Janzen, 1988), with average annual rainfall of 1,600 mm that is highly seasonal (monthly averages from 0 mm to 1,040 mm); the wet season (months with ≥ 40mm of rain) is May to November, and the dry season (with almost no rain and temperatures over 37°C) is December

to April. Due to the rarity of dry forest ecosystems, a large-scale restoration effort was initiated in the 1980s involving protected area status, the recovery of abandoned pastures by active fire suppression (Klemens, Deacon, & Cavender-Bares, 2011), and protection from many human activities of the Park's two important sea turtle nesting beaches. At Playa Nancite (length = 1.05 km), where thousands of turtles come ashore during the wet months (Fonseca, Murillo, Guadamuz, Spínola, & Valverde, 2009; Valverde et al., 1998), only researchers are allowed visit during the arribada. At Playa Naranjo (length = 5.64 km), there is a staffed ranger station and campground where up to 40 tourists may stay and use the beach year-round, even though there is an increasing pattern of seasonal turtle nesting (Drake et al., 2003). There is a significant ridge that separates the beaches, and an estuary that cuts through the northern part of Playa Naranjo, but neither of these is likely a barrier to jaguar movements.

2.2 | Data collection

We gathered previous sea turtle nesting data surveys from peer-reviewed and technical papers for both Playa Nancite (1980–2011) and Playa Naranjo (2013–2015). When the raw data from turtle nesting surveys was not available, we used the R package "digitalize" to retrieve data from old figures (Poisot, 2011). Opportunistic sea turtle track-count surveys also were conducted at Playa Naranjo during 2013–2015. Each morning, we walked along Playa Naranjo at 2 km/hour and registered activity from the previous night; sea turtle track-counts by species, jaguar presence (i.e., jaguar tracks on the beach), and jaguar predation events (i.e., jaguar-killed turtles). Additional information such moon phase (Lazaridis, 2014) was gathered for analysis.

We also monitored the movements of a single three-year-old jaguar female fitted with a GPS collar (Lotek Engineering; http://www.lotek.com) programmed to record the jaguar's position every 2 hr, and activity every 5 min, during 577 days (12/1/2014–6/30/2016). The jaguar was captured using a foot snare (Frank, Simpson, & Woodroffe, 2003), and chemically immobilized using a dart projectile (Dan-inject; https://www.dan-inject.com) with a combination of 5 mg/kg of ketamine (10% ketamine; Bremer Pharma GmbH) mixed with 2mg/kg xylazine (Procin Equus 10%, Pisa Agropecuaria) (Deem, & Keresh, 2001). Handling and capture protocols followed guidelines of the American Society of Mammalogists (Silkes & Gannon, 2011) and also were approved by the Environmental Minister of Costa Rica (ACG-PI-034–2014), following the ethics and research procedure guidelines of the National University.

2.3 | Statistical analysis

To fulfill the model assumptions, we followed the data exploration protocol designed by Zuur, Ieno, and Elphick (2010), by using the statistical software R version 3.1.3 (R Core Team, 2015) to perform data analysis. For the turtle count data (Tur) and the distance data from

FIGURE 1 Monthly mean-normalized counts of sea turtles (olive ridley *Lepidochelis olivacea*, and green turtle *Chelonia mydas*) at Naranjo Beach (2013–2015) and Nancite Beach (1980–2011) in Sector Santa Rosa of Area de Conservación Guanacaste in northwestern Costa Rica. Actual average peak counts were 212 nesting turtles at Naranjo in September versus 2,197 at Nancite in October
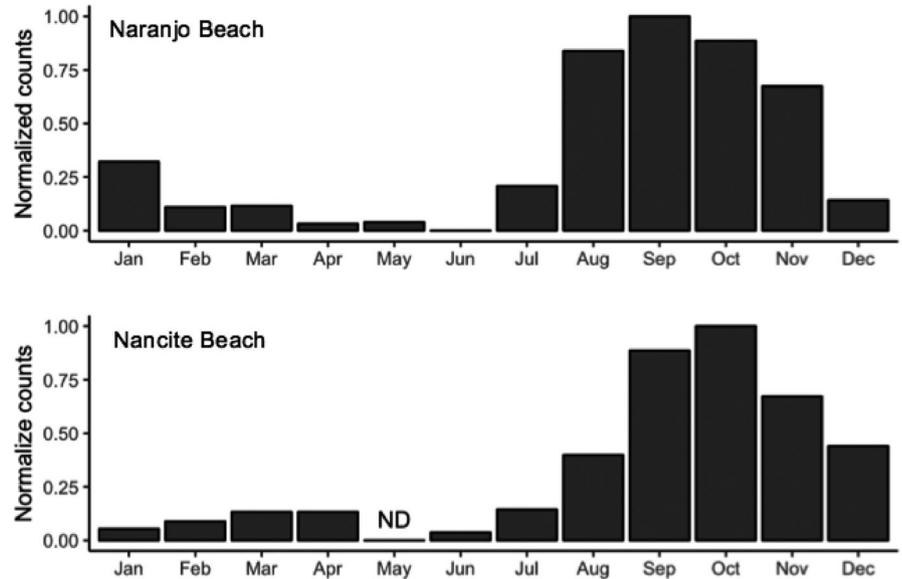
each jaguar location to the nesting beaches (Dist. beach), we used generalized lineal models (GLM—) with a log link function (Venables & Ripley, 2002), assuming negative binomial error distribution due to overdispersion issues, and a binomial distribution for the jaguar predation data (Pred. events) (Forte, 2015). In order to assess the effect of turtle nesting abundance season (seas) and moon phases (moon) on the jaguar's distances from nesting beaches and the frequency of jaguar predation events, our models include these variables as predictors (moon, seas).

Daily activity patterns were estimated from the collar's motion sensor, and aggregated seasonally by hour, using a Welch *t* test to compare seasonal differences. For home-range analysis, we calculate the KDE (kernel density estimate) using both 50% and 95% isopleth contours with the R package "rhr" (Signer & Balkenhol, 2015), using season (peak versus. off season) at three different temporal scales (month, week, and season) as covariates. Additionally, side fidelity tests also were used to determine whether the animal showed patterns associated with specific areas within SSR by contrasting the mean squared distance (MSD) and a linearity index (LI) from the center of activity with a permuted distribution (i.e., if the mean observed

value for the MSD and LI are below the permuted threshold one can conclude there is site fidelity) following Signer and Balkenhol (2015) method..

3 | RESULTS

Mean-normalized peak counts of sea turtles (species combined) at both beaches depicted the same seasonal nesting trend (peak from July to January; Figure 1) throughout the year, with maximum mean sea turtle counts at Playa Naranjo of ~ 212 in September versus

TABLE 1 Models describing the effect of turtle nesting season (seas) and moon phases (moon) on distances of a GPS-collared jaguar to the closest nesting beach (Dist. beach) in Sector Santa Rosa of Area de Conservación Guanacaste in northwestern Costa Rica

Model	df	AIC	Δ AIC	ω
Dist. beach = seas ×moon	9	106,419	0	1
Dist. beach = seas +moon	6	106,435	16	<0.001
Dist. beach = seas	3	106,450	31	<0.001
Dist. beach = Moon	5	106,789	369	<0.001
Dist. beach = intercept	2	106,809	389	<0.001
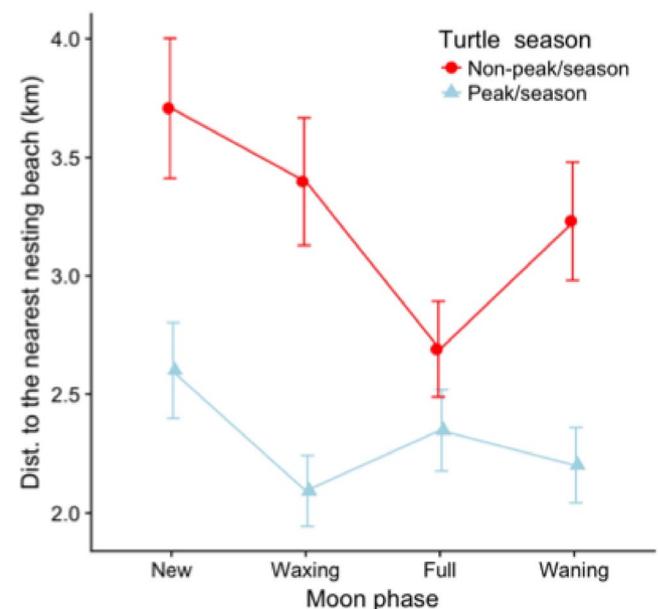
FIGURE 2 Mean GPS-collared jaguar distances (km) to the nearest turtle nesting beach [mean ± 95% confidence interval] as influenced by moon phase and turtle nesting abundance season in Sector Santa Rosa of Area de Conservación Guanacaste in northwestern Costa Rica

(a)

(b)
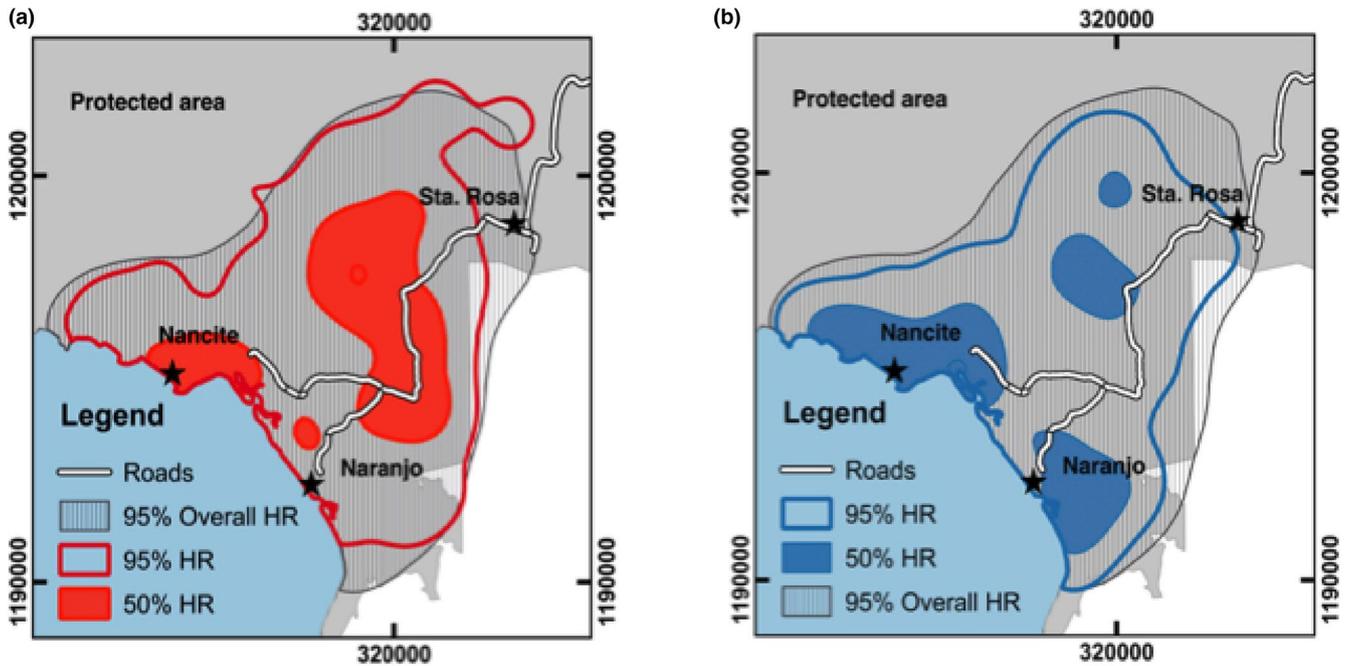
FIGURE 3 Seasonal home-range sizes (km) of a GPS-collared female jaguar during the non-peak (A) and peak season of sea turtle nesting (B) at Sector Santa Rosa of Area de Conservación Guanacaste in northwestern Costa Rica

~2,197 at Playa Nancite in October, and strong evidence of sea turtle nesting seasonality.

We also collected 5,924 GPS locations of the collared jaguar during December 2014–June 2016. GLM modeling testing for seas and moon effects on jaguar distances to the closest nesting beach produced a top model with the interaction of moon and seas (Table 1; AIC ω = 1) markedly influencing jaguar location distances to nesting beaches. As expected, the collared jaguar was farther (~1.06 km) from nesting beaches during non-peak nesting season (Figure 2). With regard to moon phase, during peak nesting season, the collared jaguar stayed closer to nesting beaches on waxing and waning moon phases, whereas during the non-peak season the closest mean distances registered for this jaguar were on full and waning moon phases (Figure 2).

The overall home range (95% HR) size of the collared jaguar was 88.8 km^2, and the HR estimates for the non-peak (50% HR: 17.6 km^2, 95% HR: 72.3 km^2) and peak nesting seasons (50% HR: 18.1 km^2, 95% HR: 68.2 km^2) were similar, though the spatial distribution of the 50% HRs varied (Figure 3). We observe more spatial aggregation at Naranjo and Nancite Beaches during the nesting peak season (Figure 3), whereas during the non-peak nesting season 50% HR was concentrated in the middle of SRNP and a small section of Nancite Beach (Figure 3). Further analysis of site fidelity indicated that the mean square distance from the center of activity (6.8 km; CI 95%: 4.01–9.08), as well as the linearity index (0.050; CI 95%: 0.015–1.55), did not show statistical evidence of site fidelity. With regard to spatiotemporal variation of the GPS-collared jaguar's HR sizes, we did not find statistical evidence of variation between monthly ($t = 0.20$, $df = 14.83$, $p = .84$) and weekly ($t = 0.8$, $df = 50$, $p = .4$) HR sizes (Figure 4), but during the
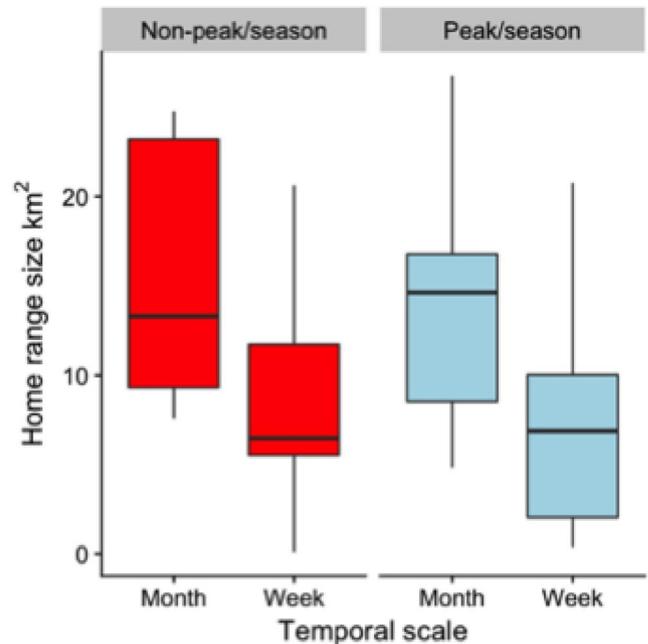
FIGURE 4 Spatiotemporal variation of a GPS-collared jaguar's monthly and weekly home-range sizes (km^2) between seasons of differing turtle nesting abundance at Sector Santa Rosa of Area de Conservación Guanacaste in northwestern Costa Rica

non-peak nesting season the HRs were larger (Figure 4). The jaguar activity patterns for both non-peak and peak nesting seasons followed similar trends, being more active from 0:00 to 11:00–12:00 and gradually start decreasing until the lowest activity peak at 18:00, followed by a gradual increase until 0:00 (Figure 5). The

FIGURE 5 Activity patterns of a GPS monitored female during the non-peak and peak season of sea turtle nesting in Sector Santa Rosa of Area de Conservación Guanacaste in northwestern Costa Rica (The number of automatic activity records per hour was 12)
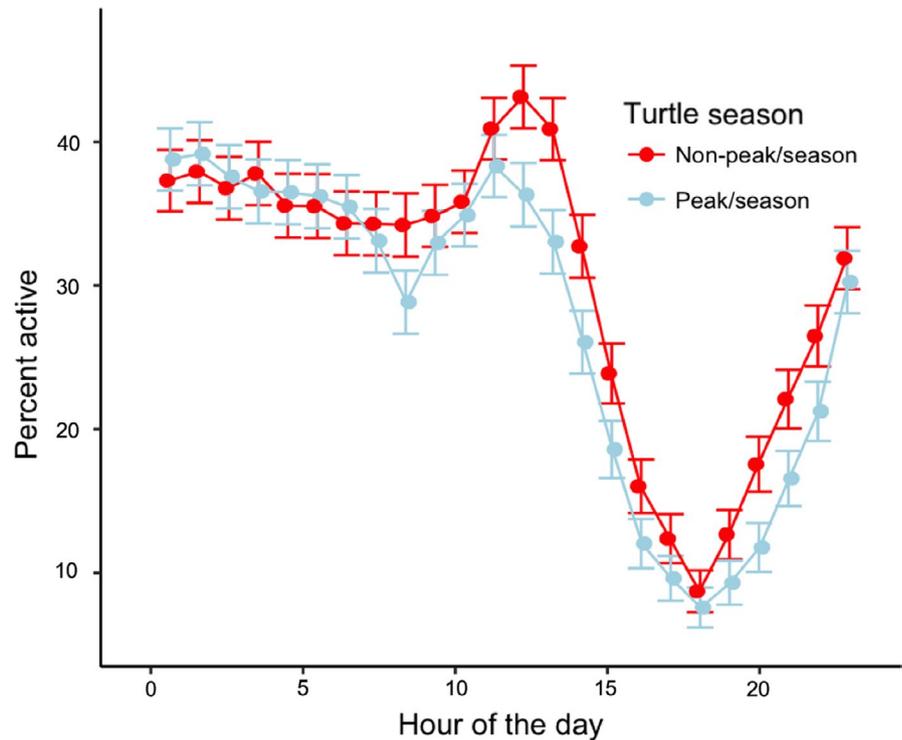
overall pattern showed this jaguar was active the most at night, decreasing its activity during the day. Activity patterns comparison showed statistical differences between non-peak and peak nesting seasons (t = 3.6582, df = 18,942, p = .0002), suggesting this jaguar slightly increased activity during day hours on non-peak nesting season (Figure 5).

The GLM modeling of the occurrence of predation events at Playa Naranjo showed turtle abundance as the top model (Table 2; AIC ω = 0.6), as well as the interaction of peak nesting season (Table 2; AIC ω = 0.39). Jaguar predation hot spots at both beaches showed a specific pattern of aggregation at Playa Naranjo with most of the sea turtle carcasses at the southern section (Figure 6), whereas predation hot spots at Playa Nancite were evenly distributed, with the highest carcass concentrations at both north and southern sections (Figure 6). GPS locations of the collared jaguar matched the pattern of predation hot spots determined from carcasses (Figure 6),

TABLE 2 Models describing the effect of sea turtle abundance (tur), turtle nesting season (seas) and moon phase (moon) on jaguar predation events (Pred. Events; i.e., jaguar-killed turtles) at Playa Naranjo in Sector Santa Rosa of Area de Conservación Guanacaste in northwestern Costa Rica

Model	df	AIC	Δ AIC	ω
Pred. events = tur	2	228	0	0.60
Pred. events = tur × Seas	4	229	1	0.39
Pred. events = tur × moon	1	237	9	0.007
Pred. events = tur × moon + seas	8	239	11	0.002
Pred. events = intercept	1	137	16	0.001

suggesting high concentration of jaguar locations near the estuary at Playa Naranjo where, due to difficult accessibility on this beach section, we could not sample turtle carcasses; nevertheless we speculate the same pattern previously observed across both beaches.

4 | DISCUSSION

We used track-count surveys of sea turtles and GPS telemetry of a female jaguar to evaluate the influence of turtle nesting season on jaguar hunting behavior assessing home-range size, activity patterns, and predation patterns on sea turtles. Our results indicated a seasonal increase in sea turtle availability (Behm et al., 2000; Cornelius & Robinson, 1982; Fonseca et al., 2009; Valverde et al., 1998) that shaped ecological interactions. Moon phase, sea surface temperature, and the time of the year influence the number of sea turtles that come ashore, perhaps due to sea surface temperature affecting the internal physiology of sea turtle, as well as constraining sea grass nutrition quality in need to prepare clutches to laying (Hamann, Limus, & Owens, 2003; Houtan, Halley, & Marks, 2015). Additionally, observations by us and others (Carrillo et al., 2009; Herrera, 2016; Houtan et al., 2015) indicate sea turtles likely choose specific moon phases to nest, perhaps due to the amount of energy intake and time spent to come ashore and nest, as well as because the moon brightness might make sea turtles more vulnerable to predators.

Jaguar location distances from nesting beaches were frequently closer on the peak nesting season, interacting with moon phases, similar to the finding of previous studies (e.g., Carrillo, 2000; Carrillo et al., 2009); this suggests a seasonal foraging strategy by jaguars to maximize their energy budget. Jaguars may also synchronize births
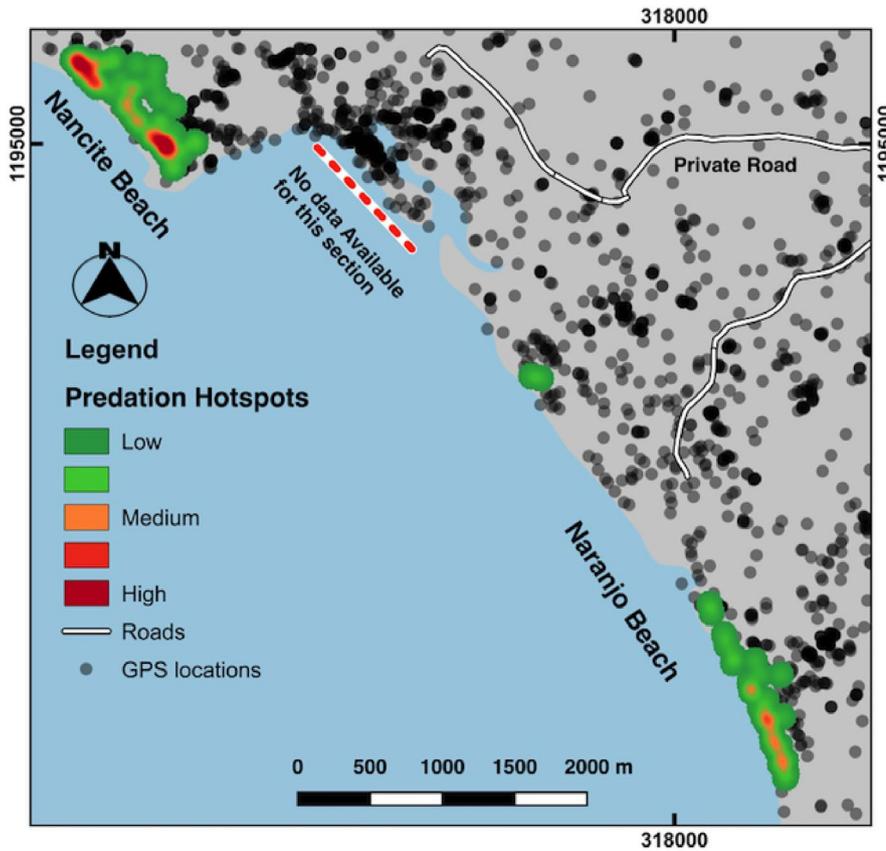
FIGURE 6 Locations of jaguar-predated turtle carcasses ("Predation hot spots"; cf. Escobar-Lasso et al., 2017) and a GPS-collared jaguar at Nancite and Naranjo beaches in Sector Santa Rosa of Area de Conservación Guanacaste in northwestern Costa Rica

with peaks of sea turtle abundance as a strategy to increase offspring survival and recover body mass after birthing (Bergstrom, Thompson, Melin, & Fedigan, 2017; Campos et al., 2017); we have recorded frequent field sightings of females with offspring at nesting beaches during peak nesting (unpublished information).

Early telemetry studies described seasonal responses on jaguar home-range sizes owing to prey abundance peaks on time (Astete et al., 2017; Carrillo, 2000; Cavalcanti, 2008; Gese et al., 2018). Though we found no statistical evidence of seasonal changes in home-range sizes, seasonal core areas changed location from one season to another, concentrating mostly on nesting beaches during sea turtle peak season and matching with locations of predated sea turtle carcasses (Alfaro et al., 2016; Escobar-Lasso et al., 2017). Changes in prey distribution over time and though space has consequences for predators, because if prey respond to environmental changes, predators follow the same trend (Sunquist & Sunquist, 2002). For example, in the Kalahari Desert when large prey are dispersed, the home-range size of a lion (*Panthera leo*) pride increases 5 times the regular home-range size (Sunquist & Sunquist, 1989). The home-range size estimated in this study for a female jaguar was larger (88.8 km^2) than that reported by Carrillo (2000; 20.5 km^2), the only other one in Costa Rica. Even though multiple studies have elsewhere estimated varying female jaguar home-range sizes (15.3–722.5 5 km^2), there is still little knowledge concerning the relationship of home-range size with prey availability (McBride & Thompson, 2017; Morato et al., 2018). Thus, the enormous seasonal turtle availability and the number of solitary nesting beaches across the Área de Conservación

Guanacaste make this area unique, and likely allow for the long-term persistence of jaguars and other potential predators that opportunistically use this marine resource. Elsewhere, analysis of jaguar predation events upon sea turtles showed a strong positive relationship between turtle abundance and the frequency predation events (Guilder et al., 2015). Jaguar activity patterns also showed how this individual was less active during peak nesting season, suggesting synchronic prey availability patterns may lead predator aggregation and coordinated movements as behavioral response in places where prey are seasonally abundant (Penteriani, Fortuna, Melián, Otalora, & Ferrer, 2006). Therefore, jaguars may save energy by aggregating themselves in places such Playa Naranjo and Playa Nancite where easy-to-capture sea turtles also are concentrated in high densities.

In addition to jaguar behavioral responses due to seasonal marine prey availability in this study, is worthwhile to mention the important role of jaguars as a top predator (Estes et al., 2011), linking marine biomass with terrestrial ecosystems. Jaguar are known for their biting strength (Moral-Sachetti, Lameda-Camacaro, Vázquez, & Zenteno Cárdenas, 2011), thus enabling the use of a variety of potential prey not available to other carnivores (Weckel, Giuliano, & Silver, 2006). Therefore, sea turtle predation by jaguars, by moving marine biomass to terrestrial ecosystems, may benefit multiple scavenger organisms that could take the advantage of sea turtle remains acting as a top-down cascade effect in this unique place.

In summary, our results provide strong evidence of jaguar behavioral responses linked to peaks of seasonal availability of sea turtles in the dry forest ecosystem. Climate and environment

conditions directly influenced biology of sea turtle nesting and, as a consequence, also constrains jaguar movements and foraging activity. Optimal foraging theory predicts that predators seek out prey in terms of energy (MacArthur & Pianka, 1966), and our study partially fulfilled this prediction. Even though our study only used GPS telemetry data from one individual, our results were consistent with the sea turtle track and carcass count surveys and previous data. Finally, knowledge of jaguar home-range sizes and their variation with prey in seasonal ecosystems might contribute to improved conservation, especially in places such Playa Naranjo with the dual values of conservation of endangered species and tourism; our study defines a baseline home-range size for jaguars in the tropical dry forest, and focuses the importance of seasonal sea turtle availability in influencing the terrestrial dynamics of large predators and making this resource accessible for other organisms.

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DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.2bvq83bmr (Montalvo et al., 2020).

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ORIGINAL ARTICLE

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Functional and genetic diversity changes through time in a cloud forest ant assemblage

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Abstract

Climate change in the Neotropics is causing upslope range shifts. We used arrays of ant species collected in a cloud forest at 1,500 m in Área de Conservación Guanacaste (ACG), northwestern Costa Rica, collected in two time periods (1998–2000 and 2008–2011) to measure changes in species richness and diversity over a decade. Using metrics of community structure, we found that the species assemblage in the collections from the 1990s was significantly phylogenetically clustered and functionally less diverse as compared to collections from the early 2000s. At both time points, the assemblages were significantly phylogenetically clustered and while the difference in functional diversity between the time points was not significant, the ant assemblage has become lighter in color (on average) over time. When individual species are considered, the overall pattern of replacement is consistent with the cloud forest ant assemblage being colonized by arrivals from lower elevation forests. The invertebrate communities on cloud forested mountain tops are especially vulnerable to a changing climate as there are two factors working together; no higher terrain to which they can move and the invasion of more and more taxa from lower downslope. This vulnerability is already measurable.

KEYWORDS
Área de Conservación Guanacaste, Costa Rica, DNA barcode, Formicidae, Malaise

1 | INTRODUCTION

Tropical montane cloud forests typically contain less biodiversity, and their ecosystems occupy smaller areas than do lower elevation forests (Anderson & Ashe, 2000; Bruijnzeel et al., 2011; Stadtmuller, 1987). Cloud forests are characterized by consistently low temperatures and high precipitation/humidity and tend to be inhabited by species that exhibit multiple adaptations related to abiotic conditions that are stressful for the generally thermophilic ants (Bruijnzeel & Proctor, 1995; Gentry, 1992; Still et al., 1999). Climate change is expected to cause dramatic biotic transformations in cloud forest (Hulshof & Powers, 2020; Nadkarni & Solano, 2002; Pounds et al., 1999) and surveys of cloud forest species over time aid our understanding of these changes.

We sampled ant communities from a cloud forest at the top of 1,500 m tall Volcán Cacao within Área de Conservación Guanacaste (ACG) in northwestern Costa Rica (10.9329, −85.4530). This single location is part of an ongoing inventory project examining elevational and temporal structure of ants and other leaf-litter arthropods (Dolson et al., 2020; Smith et al., 2014, 2015). Ants were sampled between 2008 and 2011 using multiple methods, including Malaise traps (Malaise, 1937; Townes, 1972) and were compared to samples from collections made at the same site a decade earlier (1998 to

2000) using Malaise traps only. This unplanned comparison was possible because the samples from the initial dates were continuously maintained in ethanol in a freezer for the intervening time period. We used these specimens to compare the array of ant species in this cloud forest, using both phylogenetic and trait-based measures. Our objective was to document any change in the species richness, community structure, and species demography in this cloud forest over a decade.

Using morphological measurements, estimates of lightness, and DNA barcodes, we showed that the ant community in an ACG cloud forest has become less species rich, less phylogenetically clustered, more functionally dispersed and generally lighter in color. The cloud forest array is becoming more similar to species arrays living at lower elevations, as is expected when the traditionally lower elevation ant arrays move up the volcano with global warming.

2 | MATERIALS & METHODS

2.1 | Study site and specimen collection

Ants were collected (Smith et al., 2014) from Área de Conservación Guanacaste (ACG) in Costa Rica (Figure 1), a 163,000 hectare UNESCO World Heritage site containing at least an estimated 500,000 species of arthropods (Janzen, 2000a). ACG contains

dry forest and rain forest, and disappearing cloud forest on upper volcanic slopes, along with every imaginable intergrade. The Malaise traps (Malaise, 1937; Townes, 1972) were placed along a trail running along the rim of the old crater near the top of Volcán Cacao (1480–1500 m). The Holdridge lifezone classification (Holdridge, 1967) for the forest at the top of Cacao is "Low Montane Rain Forest" and is dominated by tree species of *Podocarpus*, *Clusia*, and *Quercus* and other species of Ericaceae, Lauraceae, Sapotaceae, Fabaceae, Hypericaceae Malvaceae and numerous smaller woody plant species from Melastomataceae, Sabiaceae, Primulaceae, Ericaceae, Clusiaceae, Cunoniaceae, Fabaceae, Cyclanthaceae, Chloranthaceae, Schlegeliaceae, Juglandaceae, Rutaceae, Rubiaceae, Pentaphylacaceae, Monimiaceae. In the 1990s, two Malaise traps were placed approximately 20 m apart along the crater rim. Collecting in the 2000s was conducted with only one trap maintained at the same location as the earlier collections (see Smith et al. (2014) supplemental information for a photograph of the loca, and for a high-resolution panoramic photographs of the collection area forest visit: http://www.gigapan.com/galleries/13759/).

Ants were collected in two distinct periods of sampling. The first sample was a set of collections made between August 1998 and June 2000 using Malaise traps emptied weekly and frozen ("the 1990s"). The second set was collected from the same kinds of traps at the same location between June 2008 and February

1998-2001

(a)

PD = 18.7
NTI = 4.02, p=0.001

2008-2011

(b)

PD = 17.33
NTI = 2.19, p=0.016

1998-2000

Subfamilies: 1
Genera: 7
Species: 42

Shared

Subfamilies: 7
Genera: 20
Species: 37

2008-2011

Subfamilies: 0
Genera: 3
Species: 32

(c)
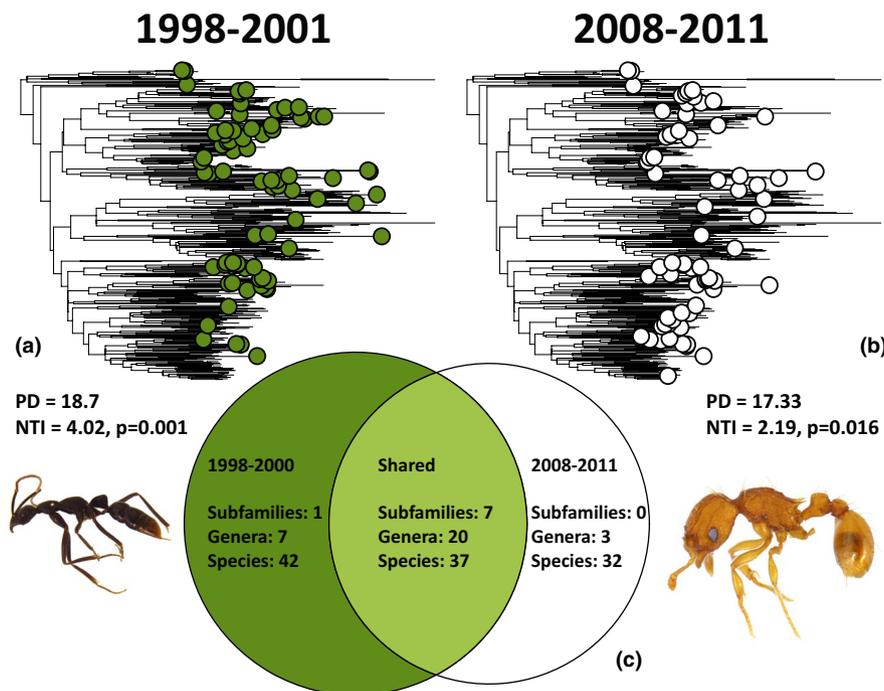
FIGURE 1 Representing a changing ant assemblage on a cloud forest between two time periods. (a) Maximum Likelihood (ML) tree for the local ant community at Volcán Cacao between 1998 and 2000 (green). (b) ML tree for the ant assemblage in the cloud forest on Volcán Cacao between 2008 and 2011 (white). The remainder of the phylogeny without circles represents the local array of ant species at Volcán Cacao not seen in the cloud forest. This ML phylogeny was used in subsequent phylogenetic metrics tests (PD and NTI) applied to the cloud forest ant arrays. (c) A Venn diagram outlining the taxonomic diversity sampled only in the 1990s, only in the 2000s and those that are shared between both periods. Also represented are images of two species in the genera (*Leptogenys* and *Wasmannia* respectively) discussed in the text as case studies for the loss (L) and gain (W) of taxa in the cloud forest

2011 ("the 2000s"). Collection protocols in the 2000s also contained multiple standardized collection methodologies including pitfall and mini-Winkler traps, baits, and Davis sifters (see Smith et al., 2014 for more details). During each time period, the traps were placed in the exact the same location. Collections in the cloud forest at Volcán Cacao between 1998–2000 (59 collection events) and 2008–2011 (11 collection events) captured 652 and 342 ant specimens, respectively. Within the earlier time period, the majority of these ants were winged males or queens (27/652 in the earlier and 63 of 342 in more recent time periods). We deliberately maintained this reduced, worker-only, sample size in each time period for the morphological analysis to minimize variance caused by multiple collection methods and castes. All ants collected in each time period were preserved in 95% ethanol and frozen at –20°C until used for morphometric and cytochrome *c* oxidase I (COI) DNA sequence analyses.

Specimens were sorted to genus and morphospecies using Dino-Lite AD413 digital microscopes (Dino Canada) and Wild M4A and Leica S8AP0 stereomicroscopes (Wild Switzerland; Leica Microsystems Switzerland). After sorting to morphospecies, a single ant leg was removed as a tissue source for DNA extraction, amplification, and sequencing. DNA extracts were prepared for amplification and sequencing following standard protocols (Ivanova et al., 2006) and as in Smith et al. (2014).

To assess the species richness, phylogenetic diversity, and community structure between the two periods of sampling, we assigned sequences to molecular operational taxonomic units (MOTU) using the BOLD implemented Barcode Index Number (or BIN Ratnasingham & Hebert, 2013). While no single difference threshold will be congruent with all species, thresholds of between 2% and 3% have been used successfully in the past as provisional species hypotheses (Smith et al., 2005, 2009) and we use these BIN codes as provisional species designations.

For each time period, we calculated species accumulation curves with 95% confidence intervals in EstimateS (Colwell, & Johanna, 2014) based on 100 randomizations. Accumulation curves (or sample-based rarefaction curves (Colwell et al., 2004)) were created using the expected species richness functions (Mao Tau) and Sobs (Colwell & Johanna, 2014).

We also calculated two non-parametric estimates of total species richness in EstimateS, the bias-corrected second order Chao, and second order jackknife estimators (Colwell & Johanna, 2014). These two estimators have both been shown to be reliable in estimating total species richness from incidence data, when sample grain size is small and is kept constant (Hortal et al., 2006). They are also less sensitive to certain sampling issues such as the patchiness of species distributions, sample coverage, and variation in the probability of sampling (Hortal et al., 2006). Our metrics are based on species counts using BINs.

We calculated the Jaccard classic index of similarity between the two sampling time periods using EstimateS (Colwell & Johanna, 2014) based on the presence/absence of species in paired arrays (Chao et al., 2005).

To compute phylogeny-based metrics (phylogenetic diversity (PD) and the Nearest Taxon Index (NTI)) for each of the two sampling periods, we used both a Neighbor-Joining (NJ) and a Maximum Likelihood (ML) tree created using high-quality sequences (658 bp with no ambiguities, when available) of the COI gene for one representative sequence from the 355 ant species sampled. This species total includes local array of ant species of the volcano peak sampling site (from Smith et al., 2014) as well as the species sampled at both sampling times. Neighbor-Joining (Saitou & Nei, 1987) is a distance-based method of tree construction, and while not an explicitly evolutionary model, it has been shown with ants that estimates of phylogenetic diversity and community structure were similar when calculated using an NJ tree as with a likelihood or Bayesian analysis (Smith et al., 2014). The patterns observed here between NJ and ML were similar, so for simplicity, we only present and discuss the ML tree data here. The ML tree was created using MEGA 6.0 (Tamura et al., 2013) after selecting the best substitution method from the ML fit of 24 different substitution models based on the lowest BIC scores (Bayesian Information Criterion) (GTR + G+I: General Time Reversible).

2.2 | Phylogenetic diversity metrics

We calculated phylogenetic diversity (PD) and the nearest taxon index (NTI) for both of the two time periods. For each, the same presence/absence matrix for the local ant community at Volcán Cacao was used (local species pool). We used the picante package (Kembel et al., 2010) in R 2.12 (R Development Core Team, 2008) to calculate PD and NTI using 1,000 randomizations and 1,000 iterations using the independent swap algorithm (Gotelli, 2000).

2.3 | Morphological measurements

We used morphological measurements of the ant species to estimate functional diversity for each sampling time frame. Nine morphological characters and measurements compared to their inferred functional role—as in Silva and Brandao (2010) and Macedo et al. (2011) and references contained within. Briefly, morphological measures were taken from each species at each sampling site (the measurements used, and the functional significance inferred from these measurements, Table S1). Ants were measured using two stereomicroscope systems; Wild M4A and Leica S8AP0 (Wild Switzerland; Leica Microsystems Switzerland). Up to 5 specimens per ant species were selected (worker caste only) for morphological measurements. When multiple worker castes were present (e.g., as in the genus *Pheidole*), only the smaller minor workers were selected for measurement. An ocular micrometer (12 units in 0.1 graticule intervals) was fitted to both stereomicroscopes and measurements were taken in graticule intervals to the nearest 0.01 interval. Measurements in graticule intervals were then converted to millimeter units using a multiplication (1X – 12.5X) using
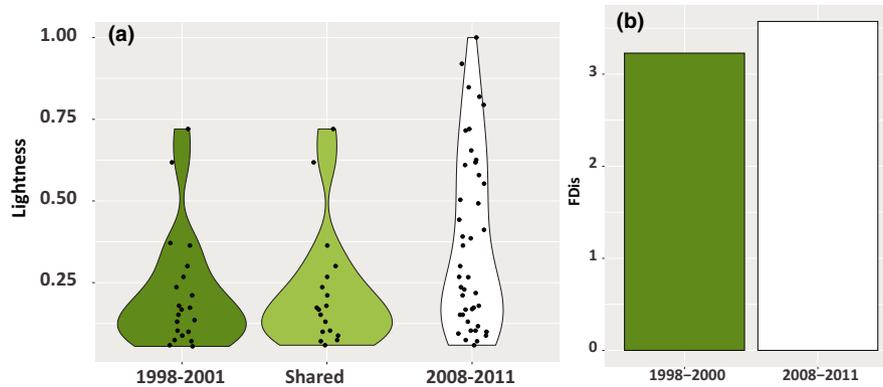
FIGURE 2 A changing ant assemblage on a cloud forest between two time periods. (a) Lightness through time. Violin plots representing the lightness values of the assemblages of ants from the two time periods (and those shared between those time periods). (b) Functional diversity through time. While functional diversity did increase slightly between timeframes in the cloud forest (functional dispersion values increase from 3.23 to 3.57), this increase fell within the 90% and 95% confidence intervals and was not significant

a stage micrometer (2 mm in 0.01 mm intervals). The mean of each measurement for each species was used in subsequent analyses after being log_{10} transformed.

2.4 | Lightness

To estimate the lightness of ant cuticle, we followed Bishop et al. (2016) by comparing the insect cuticle (on head, thorax and abdomen) to a standardized color wheel. Focus-stacked images of each species were taken using a Leica Z16 APO. The categorical color of each body section from each species was then converted to RGB (red, green, and blue) values which were then converted to HSV (hue, saturation and value) using R (rgb2hsv). In HSV, the higher the value, the greater the lightness. We averaged these values across body segments for each species. Values closer to one are lighter and values closer to zero are darker. We then compared the mean lightness values for arrays of ants from the 1990s and the early 2000s and those that were shared between the two time periods.

2.5 | Functional diversity

We quantified levels of functional diversity (FD) of each time period using the functional dispersion (FDis) index (Laliberté & Legendre, 2010) computed using the FD package (Laliberté & Legendre, 2010) in R (R Core Team, 2018) using 1,000 randomizations in which species identities were shuffled and species abundances (presence/absence here) were maintained as constants.

2.6 | Community composition

To visualize how these the recent and older cloud forest communities arrayed compared to each other and to the other forest

locations on Volcán Cacao, we summarized the community composition of assemblages from the larger dataset of Smith et al. (2014) and then used non-metric multidimensional scaling ordination (NMDS) based on the Bray–Curtis coefficient of community dissimilarity using the package vegan (Oksanen et al., 2018) in R (R Core Team, 2018).

Throughout, we cautiously interpret our trends as the chance of making Type I or Type II errors regarding community change is increased because we are sampling from only two time periods with an unequal number of samples between them. However, from our perspective, it is important that we do report these changes and include such data as has been collected.

3 | RESULTS

While sampling since 2008 is part of a larger study that is replicated across ACG mountains (including Volcan Cacao and also nearby Volcan Orosi and Volcan Rincon de la Vieja), sampling in the earlier time period was restricted to a single location on one volcano. To make an unplanned, site-specific comparison to historical data as we have is desirable, but precludes replication given the nature of the initial data collection.

3.1 | Phylogenetic metrics

Community phylogenetic diversity and the nearest taxon index were calculated from ML regional ant phylogeny (i.e., all species on Volcán Cacao; Figure 1a,b) for each period. Phylogenetic diversity decreased between periods ($PD_{1998-2000} = 18.7$ and $PD_{2008-2011} = 17.33$). NTI values decreased ($NTI_{1998-2000} = 4.02$, $p = .001$ and $NTI_{2008-2011} = 2.19$, $p = .016$). These changes suggest that while the ant community remains phylogenetically clustered, it has become less so through time.

3.2 | Species richness/Similarity

Ant species richness was higher in the 1990s (Chao2 = 97.61 (95% CI = 78.13, 151.21)) compared to the 2000s (Chao2 = 79.32 (95% CI = 65.02, 122.73)). Species overlap between timeframes was low (Jaccard = 0.333), with 37 species shared between the two sampling periods. (Figure 1c).

3.3 | Lightness

The average lightness of the assemblage of cloud forest ant species became lighter through time ($F = 4.515$, $df = 2$, $p = .014$ Figure 2a).

3.4 | Functional diversity

Functional diversity was quantified for each time period using the functional dispersion index (FDis). Functional diversity (Figure 2b) increased between timeframes, and functional dispersion values increased from 3.23 to 3.57; however, this increase was not significant ($p > .05$).

3.5 | Community composition

We used a non-metric multidimensional sampling (NMDS) approach plot to visualize the betadiversity of the arrays encountered in two time periods in the cloud forest on Volcán Cacao (and also included other elevations from Smith et al. (2014)). An NMDS is a useful simplification of data from multiple communities to two dimensions if a

measure of stress is generally less than 10%. Using NMDS, we found that the more recent cloud forest array has become more similar to lower elevation communities (stress = 6.6%, Figure 3).

4 | DISCUSSION

Like most Central American mountains, Volcán Cacao lacks long-term historic climate data and so we are unable to directly compare the temperature and precipitation that we expect to have changed between the two time periods. However, what is known by the people who have worked on and around the mountain before during and since these collections is that the number of days the mountaintop is embedded in the clouds is reduced and the frequency of days with precipitation is unambiguously decreasing (Janzen & Hallwachs, 2020). The climate change in this part of Costa Rica is heating and drying the formerly perpetually wet and cold cloud forests. We have shown here that as the forest has become hotter and drier, the cloud forest ant community have become more similar to lower elevation arrays, both by the loss of species and by species arriving from lower elevations. By comparing two measures of community structure (nearest taxon index and NMDS), we found that the cloud forest assemblage of ant species between 1998 and 2000 was both significantly phylogenetically more clustered and some evidence of being less functionally diverse than today. The recent cloud forest community of ants has become less diverse, less phylogenetically clustered, and more functionally dispersed (suggesting that a greater functional diversity was present). In short, the cloud forest now more closely resembles lower elevation species arrays. The patterns we have shown here with ants mirror the kind of changes that are
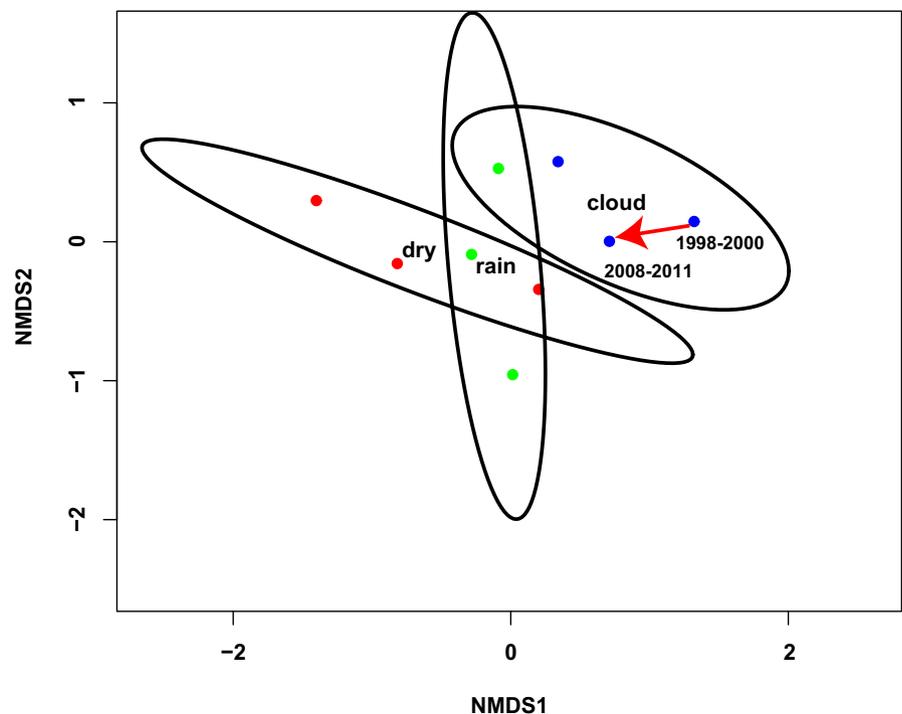
FIGURE 3 The cloud forest community is drifting toward lower elevation assemblages (red arrow). A non-metric multidimensional scaling (NMDS) ordination for communities of ant assemblages known from across Volcán Cacao (data for the figure (forest types and communities) are from Smith et al. (Smith et al., 2014) (stress = 6.6%). Red = dry forest (0-~600m), green = rain forest (>600-~1200m), and blue = cloud forest (1,300 (sampled only in one time period) and 1,500 m) and 95% confidence ellipsoids for each of the three forest types are shown

being seen with many insect groups throughout ACG (Janzen & Hallwachs, 2020). To explore these patterns, we present a brief examination of which ant genera and species may have been lost, or have appeared, in the cloud forest between our two sampling periods.

4.1 | Gains and losses of particular species

Each of five genera appears to have disappeared over time (*Acropyga*, *Belonopelta*, *Leptanilloides*, *Leptogenys*, and *Myrmelachista*). These genera all have relatively widespread distributions along Volcán Cacao's entire elevational gradient (Smith et al., 2014), but the particular species living in the cloud forest earlier could easily be species specifically adapted to cloud forest life, and the lower elevation members of their genera have not yet moved up. One possible exception is the genus *Leptanilloides* which has only been sampled in the 1990's collections (reproductives from Malaise traps) and not at any other elevations. *Leptanilloides mckennae* is the only species currently known from Costa Rica (Longino, 2012b). This species has been collected in a leaf-litter sample at 1,300 m in the Bajo del Tigre Reserve (Monteverde, Costa Rica) in an area of abrupt habitat change, from highly seasonal conditions a few kilometers downslope to cold, wet cloud forest conditions a few kilometers upslope (Longino, 2012b). The collection of *Leptanilloides mckennae* from similar conditions suggests that this Costa Rican *Leptanilloides* species could be a cloud forest adapted ant, and its disappearance from samples over a 10-year period suggests that it could have been lost due to a mountaintop extinction event caused by increased temperatures and decreased precipitation. However, *Leptanilloides* is also known as a rare tropical genus (Borowiec & Longino, 2011). *Leptanilloides* is completely subterranean (Brandão et al., 1999) and notoriously difficult to collect, so they are severely under-sampled compared to other ants. Many species of *Leptanilloides* are known from one collection event (singletons), and there are many more species to be found (Longino, 2012b). Therefore, the apparent loss of this genus may only be due to its general rarity and not indicative that it was lost due to climate warming and lower elevation species range shifts.

The ponerine genus *Anochetus* appeared in collections from both the 1990s and the 2000s. This genus has also been collected in the 2000s from multiple lower elevation sites (*Atta* at 324 m, 690 m, 740 m and 1,200 m; *Anochetus* at 1,080 m and 1,200 m) indicating that their current presence in the cloud forest could have been a result of upslope range shifts in these genera, probably due to the drying and warming climate at Volcán Cacao. However, the *Anochetus* was only sampled as reproductives (no worker specimens) in the 2000s from the cloud forest, suggesting that their appearance might have been due to the dispersal of reproductive flying ants to this high elevation site from their obvious nests at 1,200 m. Establishment is dependent on arrival, and if conditions continue to change (as with the significant warming and drying observed in the 2015/16 El Nino event), it is easy to envision that these "areal plankton" could become established. Indeed, we offer the anecdote that during these El Niño years (~2015–2016), the number and size of leaf-cutter (*Atta*) colonies up to and above the forest edges surrounding the rearing station at Cacao (1,100 m elevation) have increased markedly.

"Invasive" ants are known for their ability to displace local ant species in an introduced range for many species and habitats (Holway et al., 2002). *Wasmannia auropunctata*, for example, can have dramatic harmful effects on local ant fauna (Clark et al., 1982; Le Breton et al., 2003) and an addition such as this to the cloud forest ant fauna would be of great concern for the long-term viability of that community. Recording *Wasmannia* worker ants in the cloud forest (collected via multiple collection methods) reinforce our conclusion that the "seeds" of low-elevation ants do arrive in the cloud forest on Volcán Cacao—and that their impending establishment is imminent pending an increase in temperature and/or decrease in precipitation.

4.2 | Diversity

Species richness estimators (Sobs and Chao2) and phylogenetic diversity (PD) and community (NTI) estimates indicated that ant species diversity has decreased over time in the cloud forest, apparently due to loss of upper elevation species and those numbers not fully replaced by others moving uphill. Considering these diversity metrics, and that species similarity over the decade was also low (Jaccard = 0.333), the ant community at this site has changed drastically in that time. Taken in isolation, these results do not provide information on the possible causes of this change.

4.3 | Community structure

We found that phylogenetic (nearest taxon index (NTI)) and functional (lower estimates of functional dispersion) measures indicated a clustered cloud forest ant community in the 1990s. These results suggest that the species present were most likely strongly influenced by abiotic (or environmental) filtering of which species can survive in the cloud forest (Donoso, 2014; Smith et al., 2014; Webb et al., 2002; Wilson, 1989, 1999). Overall, these results suggest the invasion and establishment of lower elevation genera (e.g., *Wasmannia*), and the displacement of ant genera sampled in the 1990s due to global climate change and invasive species will shift ranges upslope.

Malaise traps preferentially capture flying insects, and so the ant specimens sampled are usually reproductives. This poses a problem for any study concerning the morphology of ant specimens, as male reproductives are often drastically different in appearance to workers and queens of the same species and obviously cannot be compared. Male morphological characters are not well incorporated into ant taxonomy (Yoshimura & Fisher, 2012), nor is it understood how these characters might (if at all) relate to resource utilization. While the preponderance of males was an impediment to the worker-based morphological sample size of this work, it enhanced the genetic comparison by indicating the presence of species for which there were no workers encountered.

4.4 | Lightness

Ectotherms in cool environments are expected to be dark in color to match their backgrounds and so as to maximize heat gain. Indeed, montane ants are darker than ants from lower elevations (Bishop et al., 2016). We found that the ants in the cloud forest assemblage from the 1990s were darker than those of the 2000s. Along with the changes in functional dispersion and phylogenetic change, this also suggests that the cloud forest ant community is now becoming more similar to the lower elevation communities. If the forest is drying and the number of cloud-immersed days is decreasing, the selective advantage of thermal melanism may be declining, though also the background colors are becoming lighter, making dark-colored diurnal ants more susceptible to predation by visually orienting predators.

5 | CONCLUSIONS

We used morphology and COI barcodes to document ant diversity and community changes over a decade in a Costa Rican cloud forest, one of the most threatened forest types in the Neotropics. Recent global climate changes are affecting species ranges. Long-term monitoring using standardized and transparent methods is necessary to inform conservation efforts for cloud forests, if indeed they can be saved at all. However, when such a priori sampling plans are not possible museum or herbarium collections (Graham et al., 2004; Nudds & Petitt, 1996) or earlier collections made by others in the same locations can be proxies. "Happy accidents" of collection location or preservation are an important tool in our capacity to monitor changes such as the one we have shown here, where cloud forest ant communities are becoming more similar to communities from lower elevation forests. There has been a continuity of research activities in the ACG, as well as people, facilities, and resources for preserving specimens over time, and it is these factors that help make this type of research possible. Indeed, it is the very continuity of the ACG has allowed us to make this observation that cloud forest invertebrate communities are vulnerable to a changing climate—this vulnerability is already measurable—and these changes will continue.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

ORIGINAL ARTICLE

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Spider diversity across an elevation gradient in Área de Conservación Guanacaste (ACG), Costa Rica

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Abstract

Throughout the Neotropics, temperature and precipitation change with elevation and these changes affect the assemblage of species at any particular elevation. We documented the diversity of litter-inhabiting spiders, (Arachnida: Araneae) along a Costa Rican elevational gradient as it relates to covarying abiotic factors such as temperature and precipitation. The spiders we collected were principally unidentifiable juveniles, and so we used Barcode Index Numbers (BINs) derived from DNA barcodes as proxies for species-level interim names. We contrasted these taxon-based estimates with phylogenetic measures of alpha- and beta-diversity derived from both the mitochondrial DNA barcode region and a multi-gene phylogeny of spiders and found that neither the abundance nor the species richness of spiders was significantly correlated with elevation, temperature, or precipitation. However, we did find that spider assemblages in the upper elevation cloud forests were phylogenetically clustered, (and this pattern was unrelated to whether the phylogenetic patterns were derived mitochondrially or from a multi-gene analysis). One standard explanation for such a pattern is that harsh abiotic conditions in higher elevation forests have selected for particular spider lineages; however, this remains to be tested fully. The diversity of leaf-litter spider species we uncovered was high and further sampling of spider abundance and diversity across the ACG is likely to yield many new species.

KEYWORDS
neotropical, barcode, community structure, phylogeny, Araneae

1 | INTRODUCTION

Tropical species are less tolerant of large changes in temperature or precipitation than temperate SPECIES (Janzen, 2016). Therefore, in the tropics the impact of elevational diversity gradients is exaggerated with more unique communities across smaller areas than is the case in extra-tropical mountains with greater seasonality and daily fluctuations in abiotic conditions (Janzen, 2016; Ghalambor et al., 2006; Smith et al., 2014; Polato et al., 2018; Sheldon et al., 2018; Smith, 2018). We are broadly interested in

how such environmental stress (defined as the negative impact that the abiotic environment has on an organism causing reductions in performance and fitness (Schulte, 2014)) shapes species assemblages. Species successfully colonizing stressful environments tend to possess traits for tolerance to such conditions—potentially a different set of adaptations than those selected for in less stressful environments. If the traits which permit tolerance to stressful conditions are phylogenetically conserved, then one might expect that species in these assemblages to be more phylogenetically clustered, or more closely related than by chance

(Webb et al., 2002; Cadotte & Tucker, 2017). While analyses of phylogenetic clustering of species assemblages can provide inference regarding the factors that drive patterns of community assembly (Tucker et al., 2018), they should not be understood to be the end all and be all (Losos, 2011). One important benefit of approaching diversity from a phylogenetic perspective is how it allows us to understand the biology of taxa for which we know little—arthropods (Smith, 2015). Hypothesizing that genetic and functional diversity is coupled (i.e., that ecological differences can be estimated from phylogenetic relationships) is a reasonable initial hypothesis and thus, examining these diversity trends from a phylogenetic perspective is a useful perspective into the distribution of understudied neotropical arthropod alpha- and beta-diversity.

Spiders (Arachnida: Araneae) are abundant and diverse predators in almost all terrestrial ecosystems (Symondson et al., 2001). Many species-level identification keys for spiders are restricted to adult males (Blagoev et al., 2016; Platnick, 2018; Foelix, 2011); however, most ecological collections are dominated by juveniles (Davey et al., 2013; Freitas et al., 2013). In the tropics, such an impediment is exacerbated by the paucity of identification resources for most tropical taxa, even for adults (Robinson et al., 2009; Cardoso et al., 2011). One way to avoid such impediments is by using DNA barcodes and barcode index numbers (BINs) as proxies for species-level identification (Ratnasingham & Hebert, 2007).

Assemblages of spider species respond directly to abiotic changes and fluctuations, and indirectly via trophic dependence on prey species that are themselves susceptible to changing conditions (Voigt et al., 2007; Staunton et al., 2011). Where the association between spider diversity and elevation has been tested, it appears to vary idiosyncratically. The literature contains cases where diversity monotonically increases with elevation (Uetz, 1976), declines with elevation (Greenstone, 1984; Yanoviak et al., 2003; Binkenstein et al., 2017; González-Reyes et al., 2017), exhibits a mid-elevation peak (McCoy, 1990; Chatzaki et al., 2005; Jimenez-Valverde & Lobo, 2007; Peters et al., 2016), or contains multiple responses (Bowden & Buddle, 2010). Despite this variation, there is one common element: warm and hot conditions often have greater species richness than cool and cold conditions (Yanoviak et al., 2003; Finch et al., 2008). While much of the work that has been done on spiders in Costa Rica was completed in Guanacaste, it was predominately focused on larger more colorful web weavers (Brescovit et al., 2017) and much of the diversity of the smaller and less ornate leaf-litter fauna remains undescribed. Thus, in order better understand if and how environmental stress shapes species assemblages of leaf-litter spiders we first need to know what species are present in the leaf litter of forests of ACG.

Área de Conservación Guanacaste (ACG) is a protected area in northwestern Costa Rica that contains three stratovolcanoes (Janzen & Hallwachs, 2020). Temperature and precipitation change dramatically across the elevation of these volcanoes

resulting in three distinct forest types (low elevation dry forest, mid-elevation rain forests, and high elevation cloud forests) (Janzen & Hallwachs, 2016; Hulshof & Powers, 2019). In the dry forest, temperature can spike to greater than 40°C with months between rainfalls in the dry season, while in the rainy season, temperatures can be reliably 20°C cooler with torrential rains. Thus, we asked how spider diversity and assemblage structure changes in correlation with the abiotic variables that covary with elevation as we progress from the lowlands to the top of these volcanos. We examined these patterns using BINs as species proxies and the DNA barcodes as substrate for our phylogenetic analysis. In addition, we used these mitochondrial barcodes in order to create a phylogeny from which we calculated estimates of diversity and community structure. We then contrasted these mitochondrial phylogenetic estimates using a multi-gene genus-level spider phylogeny of Wheeler et al. (2017). In our collections of leaf-litter spiders, we found a surprisingly large number of species within this small (and historically well sampled) area. Neither the abundance nor the species richness of spiders was significantly correlated with elevation, temperature, or precipitation. However, cloud forest spider assemblages were phylogenetically clustered, and this pattern was not related to whether the phylogenetic patterns were derived from a multi-gene analysis or from mitochondrial DNA barcodes. One critical tool for diversity inventory and testing in a hyperdiverse environment such as the ACG is the existence of an infrastructure for doing barcode-based biodiversity assessments. Work such as what we describe here is an example of the essential groundwork necessary for the success of the nation-wide BioAlfa initiative to gather and share DNA barcodes for every species in the country (Bazilchuk, 2019; Janzen & Hallwachs, 2019, 2020).

2 | MATERIALS AND METHODS

2.1 | Study site and specimen collection

Collections were made within the Área de Conservación Guanacaste (ACG) (a 169,000 hectare national conservation area in northwestern Costa Rica, 10.93285 –85.45748) between 2008 and 2014 using transects established from sea level to the summit of Volcano Cacao (See Smith et al. (2014) Appendix S1). Sampling was conducted at eight sites including tropical dry forest (10 m ~ 300m +), mid-elevation rain forest (600 ~ 1,200 m), and tropical montane cloud forest (~ 1,300 – 1,500 m). High-resolution GigaPan panoramic photographs of each of these sites are publically accessible at: <http://gigap an.com/galleries/10092>. For the purpose of our study, we defined a community as the assemblage of species found at a given elevational sampling site. At each site, terrestrial arthropods were sampled using standardized collection methods (active searching, bait (cookies and tuna), pitfall traps, Malaise traps, leaf-litter sifting, and mini-Winkler sifting. Each site was visited the same number of times, and each visit was for the same amount of time (For further detail

see Smith et al. (2014). Upon collection, specimens were preserved in 95% ethanol and later preserved at −20°C. We extracted mean annual temperature and mean annual precipitation data for each of the eight sites from Worldclim (http://www.worldclim.org; Hijmans et al., 2005).

2.2 | DNA extraction, amplification, and sequencing

Many more specimens were collected than we were able to analyze molecularly and so we randomly selected specimens for barcoding from the total number of spiders collected (278 specimens across the eight collection sites). High-resolution focus-stacked photographs were taken of each specimen in ethanol under a Leica Z16 APO microscope using Leica Application Software V4.3.

Total genomic DNA was extracted from tissue samples of 1 – 3 legs using NucleoSpin® 96 Tissue Kit (Macherey-Nagel Duren, Germany). We amplified the barcode region of cytochrome c oxidase I (CO1) following standard protocols (Ivanova et al., 2006; Smith & Fisher, 2009; Smith et al., 2014). After amplification, amplicons were visualized on a 2% agarose E-Gel® 96-well system (Invitrogen) and samples containing clean single bands were directly sequenced using BigDye v3.1 on an ABI 3730xl DNA Analyzer (Applied Biosystems). Samples with failed amplification for the full 658 bp region were re-amplified and sequenced using internal primers that amplify a shorter (~400 bp) fragment.

2.3 | Sequence analysis

Sequences were reviewed and edited in Sequencher 5.4.1 (Sequencher, 2015) and aligned using MUSCLE (Edgar, 2004) in MEGA6 (Tamura et al., 2013), and BioEdit (Hall, 1999). Alignments were checked by eye, and then sequences were uploaded to the Barcode of Life Data System (Ratnasingham & Hebert, 2007).

We quantified diversity using a specific kind of molecular operational taxonomic unit (MOTU - Blaxter et al., 2005) used for DNA barcodes, the Barcode Index Number (or BIN) (Ratnasingham & Hebert, 2007). BINs have been shown to be useful species proxies, and especially as pragmatic work-arounds due to the lack of taxonomists and identification resources associated with species-level identification of neotropical spiders (Robinson et al., 2009). For simplicity we refer to these as species from this point on. All specimen information, DNA sequences, and corresponding metadata are available on BOLD (dx.doi.org/10.5883/DS-ASSPIDER).

We constructed a maximum likelihood tree in MEGA6 using one high-quality sequence (greatest length and fewest ambiguities) for each species. This tree was created using a general time reversible model with discrete gamma distribution (Nei & Kumar, 2000; Tamura et al., 2013). Calculations of the best substitution pattern were made in MEGA6 using the "find best DNA model" function.

2.4 | Multi-gene phylogenetic estimate of phylogenetic diversity

A recent comprehensive spider phylogeny was published comprising more than 700 genera based on six genes (3 nuclear and 3 mitochondrial, including COI) (Wheeler et al., 2017). We used Wheeler *et al.*'s COI dataset to compare our sequences to make interim generic assignments based on sequence similarity. Using these generic assignments, we then calculated genera richness, phylogenetic diversity, and community structure as inferred from comparison with the larger multi-gene Wheeler et al. (2017) phylogeny.

2.5 | Statistical analysis

We created an incidence matrix of species and sites and then randomized the matrix maintaining species richness and frequency using both the "taxa.labels" and "independentswap" null models as suggested by (Gotelli & Graves, 1996). We then calculated species richness and nearest taxon index (NTI) in each site using picante package (Kembel et al., 2010). For the Wheeler et al. (2017) multi-gene phylogeny, we followed the same strategy to calculate PD and NTI and also calculated Net Relatedness Index (NRI). To determine whether PD changes across the gradient were different than what would be predicted by species richness alone, we analyzed the residuals of phylogenetic diversity and species richness.

We analyzed species diversity using EstimateS 9 (Colwell et al., 2012). As is common with many examinations of neotropical arthropods (Coddington et al., 2009), we anticipated that many of the specimens collected would be unique—because of the way they are collected and the duration of the collection (< a decade)—so we used CHAO1 (Chao, 1987) models to estimate species richness and to create an accumulation curve to determine if we had thoroughly sampled the total diversity present in the community. We extrapolated this accumulation curve to a hypothetical sampling of all collected individuals (780) using the iNEXT package in R (Hsieh et al., 2018).

To calculate beta-diversity, we used a pairwise Jaccard Index (Jaccard, 1901; Jost et al., 2011) to determine the number of shared species between each elevation site and analyzed this using a Mantel test (Mantel, 1967). We tested whether the beta-diversity between sites was a result of nestedness (species from one community are nested within other communities) or turnover (distinct communities across the gradient with limited species shared between sites) using the package betapart (Baselga, 2010; Baselga & Orme, 2012)in R Studio.

We tested the relationship between dependent variables of spider species richness, and phylogenetic diversity against independent variables of elevation, precipitation, and temperature. A monotonic relationship (via linear regression) or a mid-elevation peak (via the quadratic term) in a polynomial was teste as in Smith (2015) in R (R Core Team 2019).

3 | RESULTS

3.1 | Spider abundance

Across the gradient, we collected 780 spiders in total across multiple trap types, and found that abundance was not significantly related to elevation ($F = 0.212$, $df = 7$, $p = .661$; Figure S1). From these collections, we randomly subsampled a third of them (278) for DNA extraction and amplification (10 m: $n = 30$, 300 m: $n = 32$, 600 m: $n = 39$, 700 m: $n = 34$, 1,000 m: $n = 33$, 1,200 m: $n = 45$, 1,300 m: $n = 28$, 1,500 m: $n = 37$). Of these, only 57 were identifiably male, leaving 80% of the samples unable to be identified using standard taxonomic keys.

3.2 | Spider alpha diversity

CHAO estimates of species richness accumulation (measured per sample) demonstrated that the diversity was approaching an asymptote (Figure S2). Spider species richness was related to elevation neither monotonically ($F = 0.575$, $df = 7$, $p = .477$; Figure 1), nor with a mid-elevation peak ($F = 0.755$, $df = 5$, $p = .517$; Figure 1). Furthermore, species richness was not related to mean annual temperature ($F = 0.733$, $df = 7$, $p = .425$; Figure 2) or precipitation ($F = 0.619$, $df = 7$, $p = .461$; Figure 2).

Assemblages across the gradient followed the distinct elevational bands and showed high species turnover among sites, as opposed to the diversity at lower diversity sites being nested within that found at other sites (Simpson dissimilarity = 0.905, Sorenson dissimilarity = 0.012, Figure S3, Figure S4, Figure 3). Distance between elevation site was not related to Jaccard Classic values (Mantel $r = .177$, $p = .207$).

3.3 | Phylogenetic community structure (DNA barcode mtDNA phylogeny)

The patterns we observed using null models of "taxa.labels" and "independentswap" were similar, and so for simplicity, we present the findings from "taxa.labels." When we calculated phylogenetic estimates from the mtDNA tree, phylogenetic clustering was evident at 1,000 m (NTI = 1.95, $p = .023$) and 1,500 m (NTI = 2.22, $p = .009$). When sites across the entire gradient were compared, NTI was positively related to elevation ($F = 7.62$, $df = 7$, $p = .032$; Figure 4a). This strong trend was evident when evaluating phylogenetic community structure (NTI) against mean annual temperature (a negative relationship; $F = 14.3$, $df = 7$, $p = .009$; Figure 4), and with mean annual precipitation ($F = 11.8$, $df = 7$, $p = .014$). When phylogenetic diversity was measured between forest types, we found that cloud forest spider assemblages were phylogenetically clustered, as expected (NTI = 2.60, $p = .005$). Phylogenetic diversity was positively, but not significantly, related to species richness at a $p < .05$ level ($F = 5.29$, $df = 7$, $p = .061$; Figure 5).

3.4 | Phylogenetic community structure (wheeler multi-gene phylogeny)

Patterns of NRI and elevation were similar to NTI, and so for simplicity, we present only NTI. When we estimated phylogenetic diversity based on the Wheeler et al. (2017) multi-gene phylogeny, a subtle mid-elevation peak in PD was not statistically significant ($F = 2.53$, $df = 6$, $p = .163$; Figure 5). Phylogenetic clustering was positively related to elevation ($F = 15.5$, $df = 6$, $p = .008$). Individual sites that were significantly clustered included the sites at 1,000 (NTI = 1.83, $p = .020$) and 1,500 m (NTI = 1.75, $p = .030$), while the site at 600 m was significantly dispersed (NTI = −1.9, $p = .966$).

4 | DISCUSSION

High-elevation forests across the neotropics are becoming drier and hotter and shrinking in area. Compounding this problem is our lack of a detailed understanding of the natural history or diversity of the "little things that run the world" living within these forests (Wilson 1987). We worked toward improving our understanding of the cast of characters within these neotropical forests and the structure of these characters. By using DNA barcodes as a diversity proxy, we were able to improve our understanding of the phylogenetic structure of spider communities within these sites. We found that species assemblages in high elevation forests tended to be more phylogenetically clustered than the drier low elevation forests which were more phylogenetically dispersed. Spider species richness had high turnover across the whole elevation gradient. Spider richness was not strongly related to elevation in our sample size (or abiotic variables like temperature and precipitation that covary with elevation). While phylogenetic- or richness-based indices appeared to decline with elevation after reaching a moderate mid-elevation peak, this trend will require further testing to elucidate.

Elevational diversity gradients are likely to differ between regions, topographies, and taxa. Other studies of spider diversity across elevation have displayed monotonic declines(Greenstone, 1984; Yanoviak et al., 2003; Binkenstein et al., 2017; González-Reyes et al., 2017), mid-elevation peaks (McCoy, 1990; Chatzaki et al., 2005; Jimenez-Valverde & Lobo, 2007; Peters et al., 2016), monotonic inclines (Uetz, 1976), and multiple responses (Bowden & Buddle, 2010), just as is the case with elevational transects of other arthropods and plants. Along the same elevation gradient studied here, other arthropod groups have shown variable relationships with elevation. For example, ants display a mid-elevation peak in diversity (Smith et al., 2014), while isopods, microgastrine wasps, and their host caterpillar species diversity decline (Crozier et al. 2008, Smith et al., 2015). If elevational patterns of diversity differ among taxa, how useful is an analysis of any one taxon (Peters et al., 2016)? Multiple taxa and systematic scales are required to answer questions of diversity and elevation. For example, while assemblages of various arthropod taxa from cold and wet high elevations are often phylogenetically clustered

FIGURE 1 The relationships between phylogenetic calculations of alpha diversity and elevation and taxonomic richness. In each plot, the red line is a LOESS line of best fit (Cleveland & Loader, 1996). (a) The relationship between phylogenetic Diversity calculated using the Wheeler multi-gene phylogeny and elevation. (b) The relationship between phylogenetic diversity calculated using a DNA barcode mtDNA phylogeny and elevation. (c) The relationship between phylogenetic diversity when calculated using the Wheeler et al. (2017) multi-gene phylogeny compared to PD derived only from the DNA barcode region. (d) Taxonomic richness (species:genus)
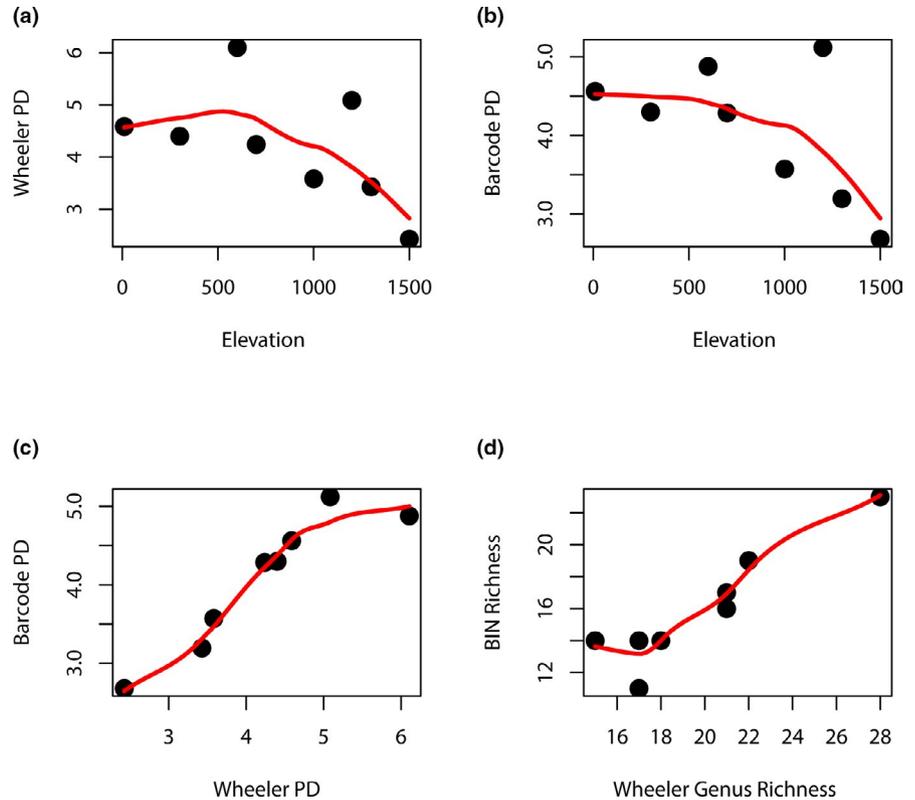
FIGURE 2 Spider alpha diversity (species richness and phylogenetic diversity (PD)) with the climatic factors that covary with elevation. (a & c for SR and PD, respectively) mean annual temperature and (b & d for SR and PD, respectively) mean annual precipitation. Note that the x-axis of a & c is plotted in reverse order to mirror the rise in elevation associated with each point
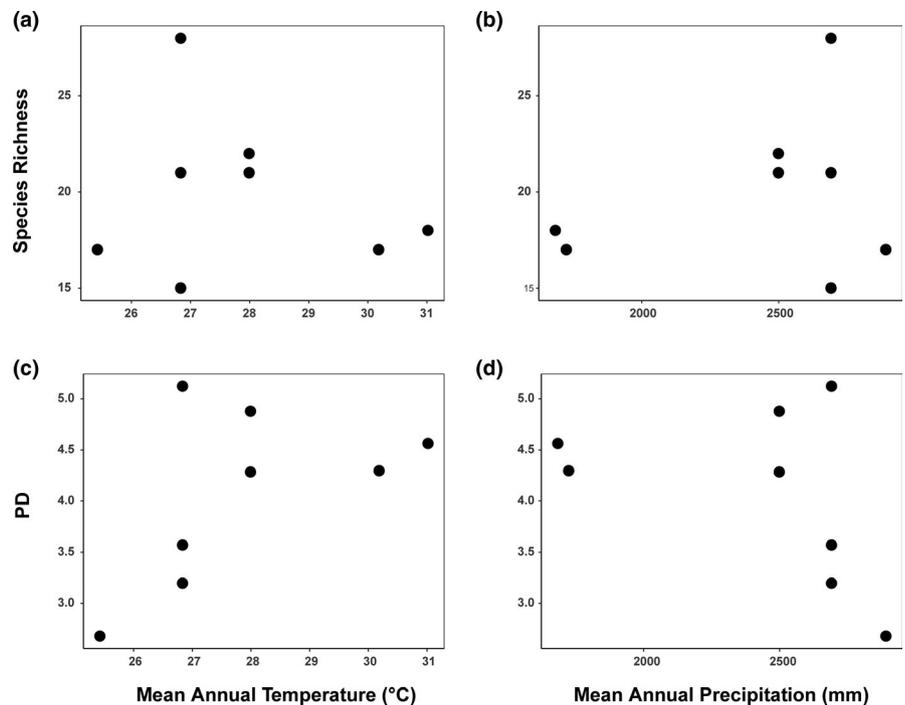
(Webb et al., 2002; Tucker et al., 2018), this is not always the case—even within specific taxa (Smith, 2015).

The phylogenetic structure of these litter-inhabiting spider assemblages changed unambiguously with increasing elevation. Some higher elevations (1,000 m and 1,500 m) were phylogenetically clustered, while the hotter and drier forests lower on the volcano tended to be more dispersed. This pattern is consistent with an environmental filter (such as temperature) that restricts which

species can live in certain environments. Indeed, temperature and NTI were strongly negatively related (Figure 5), and spider richness and community composition are strongly affected by temperature (Jimenez-Valverde & Lobo, 2007; Finch et al., 2008; Smith, 2015; Peters et al., 2016; Privet et al., 2018). While subtle, the relationship between diversity, community structure, and elevation were made more evident by examining the residuals of these relationships (Figure 5). Comparisons of the residuals of the relationship

(a)

(b)

FIGURE 3 Boxplot of pairwise distances of phylobetadiversity and elevation (m) between sites. When sites are more than 500 m apart, they are more isolated. (a) Calculated with the Wheeler et al. (2017) multi-gene phylogeny. (b) Calculated with DNA barcodes
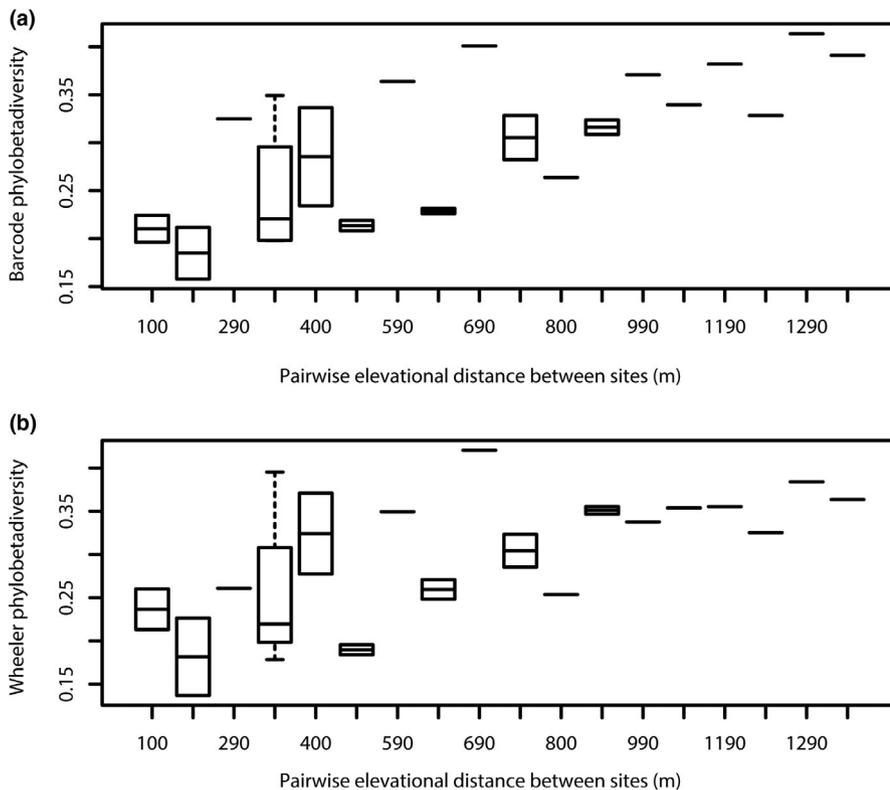
between phylogenetic diversity and species richness show that low elevation environments have higher phylogenetic diversity than expected, and high elevations have lower phylogenetic diversity than expected by a linear relationship (whether PD was derived from either the Wheeler et al. (2017) or the barcode tree). Clearly, using a multi-gene tree to calculate estimates of PD would be preferable; however, for most taxa, the data to make such trees do not yet exist. In this case, as in Smith et al. (2014), the similarity between our results derived from the barcode only tree and the Wheeler et al. (2017) tree supports the pragmatic decision to use available DNA barcode libraries to produce single gene mtDNA phylogenies for preliminary studies of phylogenetic community structure in understudied taxa and areas.

Janzen's Mountain Passes paper (1967) predicted that assemblages of species in tropical mountains should be characterized by narrow physiological tolerances, large costs of dispersal across climatic gradients, low gene flow among populations, and high rates of allopatric speciation (Smith, 2018). Here, we found high species turnover across all elevation sites. This finding may suggest that there are high or low elevation specialists due to ecological fitting or evolution (or both). While our among-site estimates of beta-diversity were low between all elevation sites, we note that beta-diversity estimates at lower elevations (in the dry forest) were particularly small—smaller even than those between high elevations (within rain and cloud forest). Tropical species are adapted to a small range of abiotic conditions—and thus the larger variation in temperature and precipitation between dry forest sites and other locations likely presents a more impermeable barrier to dispersal and successful colonization (Janzen, 2016). In the rain and cloud forests,

the annual variation in temperature and rainfall is much lower thus creating both an even smaller climate envelope for the arthropods living there, but more similar envelopes than between dry forest and rain or cloud forests(Ghalambor et al., 2006). Similarly, Staunton et al. (2011) found clear distinctions between spider assemblages from lower elevation sites (300 – 700 m) and higher elevation sites (900 – 1,100 m). Our findings of more phylogenetically clustered assemblages at higher elevations in the ACG could indicate a shared trait or ecological strategy among the members of high elevation communities, which leads to a higher rate of co-occurrence here and exclusion of species that do not have it (Swenson 2013). However, it is important to note that even when niche conservatism holds, phylogenetic structure does not always match trait variation (Mayfield & Levine, 2010; Cadotte & Tucker, 2017).

Spider diversity and abundance were not significantly related to elevation or the climatic factors of temperature and precipitation that covary with elevation monotonically or with a mid-elevation peak. This trend is likely due to many separate variables at play in this system affecting richness within spider communities at each site. For example, Jimenez-Valverde and Lobo (2007) found that in addition to temperature, habitat complexity influenced spider richness. In spiders, habitat vegetation (Jimenez-Valverde & Lobo, 2007; Finch et al., 2008), predation pressure (Kozlov et al., 2015), and habitat area (Finch et al., 2008) have been shown to drive community changes in spiders. While our study investigated the specific environmental factors of temperature and precipitation in relation to species richness and community structure, it is likely that a combination of factors influence structure. Future work would ideally investigate these links.

FIGURE 4 Positive relationship between phylogenetic clustering (Nearest Taxon Index—NTI) and elevation. There is a negative relationship of phylogenetic clustering and mean annual temperature. The high elevation and low temperature sites are clustered (significant sites marked by red) and the low elevation and high temperature sites are phylogenetically dispersed. (a&b) NTI calculated using DNA barcode only phylogeny. (C&D) NTI calculated using the Wheeler et al. (2017) phylogeny
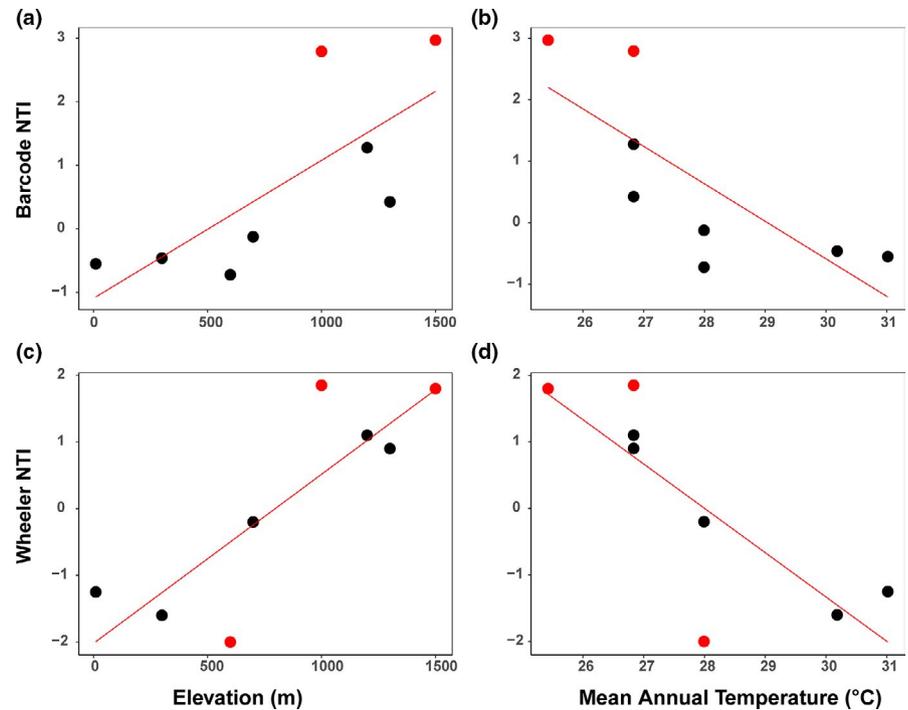
FIGURE 5 Low elevation species assemblages have more phylogenetic diversity than predicted by taxon richness (genus or species). We controlled for the expected relationship between taxon diversity and phylogenetic diversity by comparing the residuals of this relationship to elevation. (a) Wheeler et al. (2017) phylogeny and genus richness. (b) Barcode phylogeny and species richness by comparing the residuals of this relationships to elevation. (c) Wheeler et al. (2017) residuals to elevation. (d) Barcode residuals to elevation
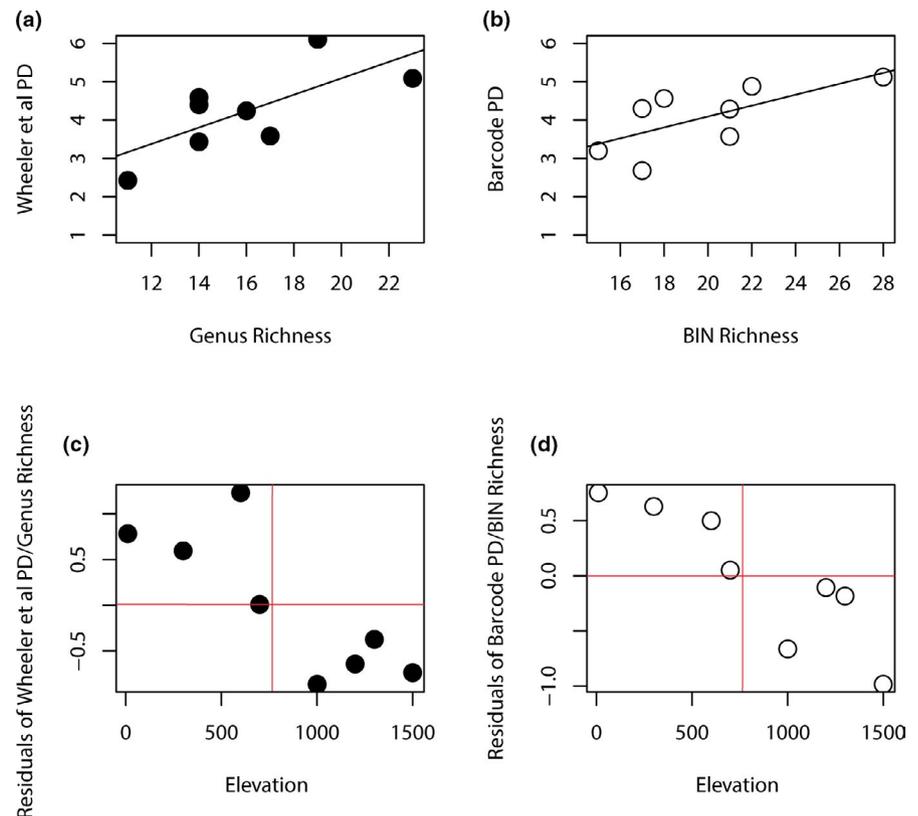
Surveys of tropical arthropod diversity are characterized by singletons and doubletons (species observed only once or twice) (Coddington et al., 2009). While this rarity can be due to under-sampling, it can also be a feature of the biology of the tropical species. Coddington et al.'s, 2009 review reported that 32% of the species found in 71 publications of tropical arthropods were

singletons. In our case, 61 of the 127 species we documented were singletons (48%). While this proportion is high, it is not out of the ordinary for tropical surveys (nor for the Araneae in Coddington *et al.* where the average proportion of singletons was ~ 37%). We adopted CHAO indices in our calculations because we agree with Coddington *et al.* that the principal explanation for the prevalence

of singletons is likely undersampling. When we analyzed the accumulation of diversity with sampling (of individuals or sites), we found that while our search for diversity is not complete—the accumulation curve was beginning to reach an asymptote. We concluded that while continued sampling would clearly be advantageous, we have sufficient data in hand to complete this preliminary analysis of diversity across elevation. Indeed, publications of preliminary analyses of species occurrence and distribution are critical steps in reducing both the Linnean (of names) and Wallacean (of space) shortfalls which dramatically plagues our understanding of neotropical spider diversity (Santos et al., 2017). For example, the 130 species we report here already exceed the 104 species from Guanacaste province databased in the collections of Costa Rica's National Museum; Guanacaste is already one of the more intensively sampled provinces in Costa Rica (Brescovit et al., 2017). Santos et al. (2017) used Zúñiga-Vega's (1980) estimate of just over 500 species of spider in Costa Rica to calculate a density of 0.01 spider species/km^2. According to this, admittedly "back of the napkin" calculus, our finding of ~ 130 spider species in one part of a 169,000 hectare national conservation area is dramatically greater than the density of 500 species within Costa Rica would predict. Our results suggest that there are many more species to be discovered and named in both Costa Rica in general and within the ACG specifically.

Many of the species we document here are small, drab leaf-litter specimens while much of the named neotropical spider diversity is larger, colorful, and ubiquitous spiders that build orb-webs (Santos et al., 2017). Based on this observation, it is likely that many of these samples represent new species. Within these assemblages, we found that spider diversity and phylogenetic community structure changed dramatically across a 1,500 m elevation gradient in Área de Conservación Guanacaste in Costa Rica. We found low phylogenetic diversity at high elevations, and high phylogenetic diversity at low elevations. High elevation spider communities are more phylogenetically clustered than lower elevations. While one potential explanation for this pattern is through shared traits that enable persistence in cold wet high elevations, other alternative hypotheses would suggest that such clustering might be due to competition (Mayfield & Levine, 2010). While the challenge (for an invertebrate) of low temperatures and high moisture is frequently thought to be a harsh environmental filter (Machac et al., 2011; Hoiss et al., 2012; Smith et al., 2014), one can easily imagine an argument that the strong seasonality of rainfall in the dry forest may actually be a more harsh environmental filter. Our data to date do not support this later hypothesis. While the trait data to ultimately differentiate between these two hypotheses do not yet exist—one of the necessary first steps toward collecting such data is to understand what species lives where—as we have done here. The spiders collected in most ecological datasets are juveniles that cannot be identified morphologically. By initiating this database of DNA barcodes for ACG spiders, it is our hope that the problem of alpha diversity estimation can begin to be resolved, even without the desired scientific name as collateral. We used this library of

images and DNA sequences as our window into neotropical spider communities, and uncovered little overlap between elevational assemblages, little support for any monotonic relationship of diversity with elevation, and suspect that the high-elevation assemblages are shaped by stressful abiotic factors. As this elevational gradient warms, whatever factors that structure the high elevation assemblages will change, and a species assemblage structured by cold and low temperature variation will be dramatically altered in a warmer and drier world.

While much of the diversity we have revealed is likely new (especially considering the sampling focus on the leaf litter and on the small specimens), to properly compare these immature spiders—we need to get COI barcodes on that which is known and housed in the National Museum of Costa Rica and derived from the Instituto Nacional de Biodiversidad (INBio). This is what will reduce the inherently parallel nature of spider taxonomy (from one based on adult males) to one that can include via comparisons with DNA all samples regardless of sex or age. This is part of what the BioAlfa initiative will do (Janzen & Hallwachs, 2019, 2020). BioAlfa is an effort to make Costa Rica the first tropical country to know what biodiversity lives within its borders (Bazilchuk, 2019). It will help to both uncover that diversity which is currently unknown as well as align our capacity to delineate that diversity with that which we already know from years of extensive collections housed in the National Museum. The ACG, with varied and diverse habitats (marine, tropical dry forest, rain forest, cloud forest on both Pacific and Caribbean and slopes and multiple stratovolcanoes providing thousands of meters of elevational change), a decades-long tradition in research, in-country biodiversity bio-management and on the ground integration of DNA barcoding will be both source of the raw data for the Bioalfa initiative as well as a pilot for how BioAlfa is beginning to be laid out across the country.

DATA AVAILABILITY STATEMENT

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

INSIGHTS

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BioMar-ACG: A successful partnership to inventory and promulgate marine biodiversity

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Abstract

Initiated in 2015, the marine inventory of Área de Conservación Guanacaste (BioMar-ACG) is rapidly advancing knowledge of biodiversity. Key aspects include synergizing with parataxonomists, barcoding specimens and making information available. After 85 years, 594 species were reported. Now, after four years, BioMar-ACG documented 1,123 species, for a total of 1,479.

Abstract in Spanish is available with online material.

KEYWORDS

barcode, collaboration, Costa Rica, parataxonomists, partnerships

1 | INTRODUCTION

Taxonomic inventories of marine biodiversity are necessary to develop and enhance protection and conservation programs and to ensure sustainable harvesting of the country's natural resources. They also serve as a baseline to document changes over time. In Costa Rica, marine biodiversity has been studied since the late 19th century and in Área de Conservación Guanacaste (ACG) since the mid 20th century (Cortés 2009). The biodiversity of marine protected areas is less well-known than terrestrial ecosystems, but the combination of technology and new field research techniques are changing this situation. Here, we explain how a synergistic mutualism between four entities is meeting the daunting challenge of knowing and documenting the organisms in a wild, marine area.

ACG has been a leader throughout the tropics in the study of terrestrial biodiversity through a bioinventory program that started in the 1980s. But until, recently, the marine area of ACG was not part

of this work. ACG's marine sanctuary of 43,000 ha (*Sector Marino*), comprises 150 km of coastal zones, rocky intertidal zones, beaches, mangroves, coral reefs, soft and rocky bottoms, deep water and a complex archipelago of seven islands (Islas Murciélago) extending from 6 to 19.2 km offshore. *Sector Marino* is in the northern Pacific region of Costa Rica, part of the Golfo de Santa Elena that is exposed to seasonal upwelling resulting in significant temperature drops, increased nutrients and lower pH (Cortés 2016). ACG is a UNESCO World Heritage site, a designation that requires ongoing research, inventories of biodiversity and monitoring of organisms and ecosystems.

In 2015, the inventory of marine species of ACG (BioMar-ACG project) started as a focused project carried out by a government agency (ACG), an academic institution, University of Costa Rica, specifically the Centro de Investigación en Ciencias del Mar y Limnología (CIMAR), the Museo de Zoología (UCRMZ) and the Herbario de Biología (USJ), and a private NGO (Guanacaste Dry

TABLE 1 Total number of marine species in ACG

Taxonomic group	# species (BioMar-ACG)	# species (Cortés 2017)	Spp. in common[a]	Total number species
Bacteria	0	15	0	15
Cyanophyta	5	4	1	8
Chlorophyta	19	4	4	19
Ochrophyta	23	6	4	25
Rhodophyta	62	15	3	74
Mangroves	0	7	0	7
Foraminifera	0	24	0	24
Porifera	18	0	0	18
Cnidaria	47	46	40	53
Platyhelminthes	0	7	0	7
Acanthocephala	0	1	0	1
Mollusca	166	187	29	324
Annelida	70	27	24	73
Nemertea	5	1	0	6
Kinorhyncha	4	0	0	4
Gastrotrichia	9	0	0	9
Brachiopoda	1	0	0	1
Phoronida	1	0	0	1
Crustacea	209	193	110	292
Bryozoa	0	9	0	9
Echinodermata	57	15	12	60
Chordata	427	33	11	449
Totals	1,123	594	238	1,479

[a]Species reported in Cortés (2017) and found with the BioMar-ACG project.

Forest Conservation Fund). Expanding on ACG's success in training and deploying parataxonomists in terrestrial biodiversity surveys (Janzen & Hallwachs 2011), the project also includes two marine parataxonomists who are from the local community and who have been trained in specialized tasks such as collecting specimens, preparing them, and assembling a detailed database. These parataxonomists allow specialized taxonomists to greatly enhance their efficiency in documenting and naming collected material, and in some cases, discovering and describing new species.

2 | MATERIALS AND METHODS

The BioMar-ACG project is an inventory of marine organisms in all coastal and marine sites of ACG. Localities include sandy beaches, rocky outcrops, mangrove forests, coral reefs, rocky reefs, and soft sediment bottoms, and range from the upper intertidal to the deepest areas within ACG, 150 m depth. Sampling has been as deep as 45 m, but there are plans to go deeper using dredges, drags and underwater vehicles. The particular methodology of collecting, fixing and curating is dictated by the group of organisms being collected. The objectives of the project are to: collect (Figure S1a); photograph in situ and in the laboratory (Figure S1b); initially identify in

the field and corroborate at the museum (Figure S1c); excise tissue samples for barcoding analysis (Figure S1d); catalogue and archive at the Museo de Zoología, Universidad de Costa Rica (Figure S1e);

FIGURE 1 Comparison of different sites in the Eastern Tropical Pacific and the change for ACG with the BioMar-ACG project (data in Table S3). BC, Bahía Culebra; CLI, Clipperton; CRP, Costa Rica Pacific; ELS, El Salvador; GAL, Galápagos; GC, Gulf of California; GD, Golfo Dulce; IC, Isla del Coco; OAX, Oaxaca

publish, and share information of the marine biodiversity of ACG. We are in the process of building a barcode reference library (Hebert et al. 2003) that will form the foundation of the inventory and the bases for many different types of ecological studies. Samples from all vouchered specimens are sent to the Center for Biodiversity Genomics, University of Guelph for DNA barcoding. The information generated will be used by ACG to define management and conservation strategies and for their bio-literacy programs (Janzen 2010). Additionally, this project aims to advance and share knowledge about the marine biodiversity of Costa Rica using a novel model of organization: the synergistic merger of government (ACG), university (UCR), private funding (GDFCF) and local community (parataxonomists).

3 | RESULTS

Cortés (2017) generated the base line on marine biodiversity knowledge of ACG compiling published accounts of marine organisms collected within ACG. This list included 594 marine species. Since the project started in late 2015 and including a pre-project fish survey (Lowenstein et al. in prep.), over 7,300 samples of algae, invertebrates and fishes have been collected, consisting of 1,123 species in 16 phyla, of which 69 are likely new species, 885 are new records (species that have been previously described but were not known from the region) to ACG and 119 new records to Costa Rica (Table S1). With these results, the number of species of ACG comes to 1,479, an almost 2.5-fold increase (Table 1).

4 | DISCUSSION

The results of this project and the rate of progress indicate the success of the partnership between government, academia, a private NGO and the local community. In the previous 85 years, 594 marine species were reported for ACG. After 4 years of BioMar-ACG (and one year of pre BioMar-ACG fish collecting and barcoding), new records for 885 species for ACG and Costa Rica have been added. Of these 885 species, 69 may be new species, based on specimens that we have that do not match any known species and on barcode divergences. This number will increase as new areas and ecosystems are explored and as new groups are added to the project. Although we are in the early stages of analyzing results from barcoding, it is clear that this is an extraordinarily powerful addition to existing taxonomic inventories. Even though the success of extraction of some species is relatively low, barcoding has revealed numerous sequences that do not correspond to sequences of known species. In other cases, the barcode sequences of previously described species are placing those species in different locations in *cox1* trees. These results flag potential cryptic diversity, deserving additional scrutiny, as has been shown with butterflies from ACG (Hebert et al., 2004). Since we are dealing

with a large number of phyla, we plan to increase the number of genes analyzed because for some groups, COI is not adequate to separate species.

Compared to other regions in the eastern tropical Pacific, ACG is among the most species rich areas (TABLE S2). All of the areas with more species are also much larger than ACG, with the exception of Isla del Coco, which is the most diverse region of Costa Rica (Figure 1). The change in species number in the ACG marine zone has caused a major shift in our perception of this area, what appeared to be a relatively species-poor site now looks more typical compared to the rest of the region. It is quite possible that with continued sampling ACG may be found to possess higher diversity than some of the other sites, due to the diversity of habitats and the effect of the seasonal upwelling and its associated productivity (Cortés et al. 2014).

Students are being trained with this project in the field and working in the laboratory (Figure S2a,b). But also, an effort has been made to present the project and the initial results to the local communities. During most field trips, the taxonomist in charge presents a public talk explaining their part of the project, detailing the groups they study, and preliminary results, with photographs of the organisms collected in ACG. The public talks in Cuajiniquil have been well attended by diverse groups of people including fishermen, tourism operators, school children, homemakers, general public, business people and teachers (Figure S2c). We perceive that the impact has been positive from the feedback received, and observe that these talks are creating awareness in the local communities about their marine surrounding.

Additionally, all the information is passed on to the authorities of ACG to be used for their bio-literacy program, management, protection and implementation of more strict conservation of their marine resources. Having more research and outreach on the marine environments of ACG will result in less illegal fishing in the protected area.

The partnership of a regional government unit for conservation and sustainable development, ACG, research units of the University of Costa Rica, and a private non-profit charitable organization, GDFCF, has resulted in a successful project to inventory and promulgate marine biodiversity. Additionally, BioMar-ACG includes three novel aspects to enhance the inventory and sharing of information: (a) synergism with parataxonomists; (b) barcoding of all species; and (c) explicitly putting the information online so that anyone can access this information. We have demonstrated that we can advance the knowledge of marine biodiversity at a relatively fast rate with this project. For these reasons, the BioMar-ACG project is an example for the rest of Costa Rica and other countries as a model to rapidly advance the knowledge of marine biodiversity.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.76hdr7stn (Cortés & Joyce 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.