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REVIEW

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Lepidoptera research in Puerto Rico: Reconnecting with historical legacies to guide future priorities

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Abstract

The Caribbean archipelago of Puerto Rico supports a diverse flora and fauna and is located in a region characterized by complex socio-economic and environmental change. The diversity of entomofauna across Puerto Rico has received considerable attention in wide-scale research over the last century, with particular emphasis on the order Lepidoptera as the subject of substantial taxonomic and ecological surveys. However, much of this work is incomplete, outdated, or has been obscured in gray literature. Thus, our primary objectives were to contextualize the role of past research in the current understanding of Puerto Rican Lepidoptera and to outline an agenda for future research. Specifically, we provide an overview of taxonomic, ecological, agricultural, and conservation Lepidoptera research in Puerto Rico and highlight key studies and historical datasets. We found that, despite a strong taxonomic legacy, native moth taxonomy remains poorly understood, except for a few major pests. Further, much of the recent Lepidoptera research has focused on short-term evaluations of agricultural pests, necessitated by immediate economic needs. The current ecological status of Lepidoptera on the islands is unknown. Therefore, prioritizing ecological research could provide timely insight for understanding changing Lepidoptera diversity and distribution and for conserving this biologically and economically significant group. Greater emphasis on long-term monitoring and digitization of museum collections would be particularly useful for quantifying past and forecasting future impacts of global change.

Abstract in Spanish is available with online material.

KEYWORDS
butterfly, Caribbean, natural history collection, Puerto Rico

1 | INTRODUCTION

Lepidoptera (butterfly and moth) assemblages in Puerto Rico are in a constant state of flux, due in part to ongoing changes in land use. The natural ecosystems of Puerto Rico were initially disturbed by the introduction of non-native species, predominantly cash crops, by European colonizers during the 16th century. Agriculture dominated the Puerto Rican economy until the 1940s. During this time, deforestation for agriculture led to a reduction of Puerto Rico's original 96% forest cover to only 13% (Weaver & Birdsey, 1990).

Socioeconomic shifts through the later half of the 20th century initiated widespread agricultural abandonment and subsequent forest recovery (Thomlinson et al., 1996). By 2009, forest cover in Puerto Rico had been restored to 55% (Brandeis & Turner, 2013). Future land changes are expected as Puerto Rico undergoes economic depression and concomitant population decline. Coastal privatization and development for tourism may also be on the rise. With these trends come concerns of further deforestation, erosion, and pollution, compounding ongoing threats to Lepidoptera populations.

Climate change and its associated ecological impacts may also affect Lepidoptera biodiversity in the coming years (Hill et al., 2021). Puerto Rico, as a Caribbean archipelago, is highly vulnerable to these ongoing changes (Duvat et al., 2017). A major contributor to its vulnerability is the frequency of tropical storms. Puerto Rico is already experiencing increasingly severe hurricanes (Keellings & Hernández Ayala, 2019), and storm intensity and frequency are predicted to continue increasing with climate change (Seneviratne et al., 2021). Hurricane disturbance and other phenomena associated with climate change will likely result in the reassembly of Lepidopteran fauna across the archipelago, as well as the potential loss of endemic species in favor of generalist and opportunist species. Despite the great diversity of habitats found in Puerto Rico, which vary in altitude, geology, topography, rainfall, soil type, and many other biophysical characteristics, there is little knowledge of the complex distribution patterns of Lepidoptera species within Puerto Rico's relatively small (and relatively accessible) geographic area. This highlights the need for Lepidoptera research across the islands' habitats, especially in the face of increased climatic and land use change (Miller & Lugo, 2009).

Here, we provide an overview of more than a century of Lepidoptera research in Puerto Rico in order to identify priority research questions, taxonomic groups, and geographical locations. We also outline suggestions for improved methodology and emphasize a greater need for ecological (in addition to taxonomic) research. We propose several research approaches for understanding the current and predicted status of Lepidoptera diversity and distributions across Puerto Rico's diverse ecosystems. Finally, we also discuss how this approach can be applied more broadly, throughout the Caribbean.

We acknowledge that much of the fauna of Puerto Rico is shared with the Virgin Islands (Becker & Miller, 2002), and many of the first Lepidoptera species to be described from the region originated from the Danish West Indies, now the U.S. Virgin Islands. However, because of differences in institutional and cultural histories between Puerto Rico, the U.S. Virgin Islands, and the British Virgin Islands, we have restricted the specific examples here to Puerto Rico.

2 | TAXONOMY AND LIFE HISTORY

Taxonomic work on the native Lepidoptera fauna of Puerto Rico has spanned centuries. Early nomenclature established by European entomologists through the 18th and 19th centuries, though not guided by direct observation, provided groundwork for insect taxonomy in the Caribbean. Later, throughout the early- to mid-20th century, U.S. research entities facilitated projects in Puerto Rico that documented native insect fauna, motivated primarily by agricultural interests. Local academic institutions, especially the University of Puerto Rico (UPR), became increasingly prominent in taxonomic research throughout the later half of the 20th century. Many taxonomic insect surveys and checklists were published during this time (e.g., Drewry, 1970; Martorell, 1973; Torres, 1994). These contributions, alongside insect collections and life history records, provided robust knowledge of butterfly assemblages. New taxonomic methods and genetic tools in the 21st century then provided further clarity regarding distinctions between butterfly species and subspecies. However, knowledge of native moth species is far less abundant. Additionally, much of the previously uncovered Lepidoptera knowledge is now outdated or inaccessible. This is due in part to the abandonment of wide-scale surveying and documentation in recent years, leaving gaps in our knowledge of Lepidoptera in these ever-changing ecosystems. Potential sources of Lepidoptera data are also inaccessible to the public and local research efforts because many (perhaps most) museum specimens currently reside in mainland U.S., European, and private collections. In this section, we provide a brief history of Lepidoptera research in Puerto Rico in order to establish the context for advancing future ecological research.

2.1 | History: 18th–19th century

Carl Linnaeus first used the term "Lepidoptera" (meaning "scaly wing") in *Fauna Svecica* (von Linné, 1746). Linnaeus, alongside entomologist Johann Christian Fabricius, named thousands of insect species through the late 18th century. Fabricius focused his attention on Lepidoptera (which he termed "Glossata") in *Systema glossatorum* (Fabricius, 1807), a list of 342 species, including several that were unique to the Caribbean and occurred in Puerto Rico. Using the Linnaean system, the European entomologists Dru Drury, Pieter Cramer, Jacob Hübner, and Jean-Baptiste Godart named numerous Caribbean butterflies between the late 18th century and mid-19th century. Though many species were named during this time, these authors did not visit the islands themselves. Rather, they obtained butterfly specimens from various collectors who traveled on trade routes, limiting knowledge mainly to morphology and muddying distribution information (Smith et al., 1994).

In 1835, C. Moritz published "Notizen zur Fauna der Insel Puertorico" (Moritz, 1836), containing the first thorough report of insects native to Puerto Rico (Wolcott, 1948). "Tagschmetterlinge von Portorico" (Dewitz, 1877) was the first comprehensive report specific to Puerto Rican butterflies (Smith et al., 1994). The report was a collaboration between the German collector Carl Leopold Krug, residing in Puerto Rico, and German entomologist Hermann Dewitz. It contained 84 species, including the culturally significant *Atlantea tulita* and the Puerto Rican harlequin butterfly (referred to as Synchloë Tulita). Leopold Krug's collections were eventually passed to Heinrich B. Möschler, who was among the first to name a wide variety of Puerto Rico's moths, building upon the work of entomologists Achille Guenée and Francis Walker (Möschler, 1890). Entomologists involved in butterfly naming also played an occasional role in moth taxonomy, though the naming of Puerto Rico's moth taxa generally occurred later than butterfly naming, with the majority of moths having been named after 1850. During the late 19th century, the Puerto Rican scientist Agustín Stahl and Cuban naturalist Juan Gundlach cataloged the fauna of Puerto Rico through zoological collections, setting the stage for taxonomic work in the early 1900s (Wolcott, 1948). Gundlach also collaborated with Leopold Krug and German entomologist Gottlieb A. W. Herrich-Schäffer and would eventually publish "Apuntes para la fauna Puerto-Riqueña" (Gundlach, 1891), which included distribution information, known synonymies, and descriptions of host plants for butterflies and moths (Smith et al., 1994).

2.2 | History: 20th century

Colonization by the United States in 1898 heavily influenced the nature of taxonomic work in Puerto Rico. In 1901, the Federal Agricultural Experiment Station at Mayagüez (now the United States Department of Agriculture Tropical Agricultural Research Station; TARS) was founded by the U.S. Congress. This entity's interest in the biological control of pest species motivated further investigation of insect taxonomy. The New York Academy of Sciences also initiated a series of expeditions in 1914 to establish insect collections (Smith et al., 1994). American entomologist George N. Wolcott, among the staff of The Insular Experiment Station in Río Piedras (founded by UPR in 1910), made exceptional taxonomic contributions during this time (Maldonado Capriles, 1996). Wolcott authored two preliminary insect checklists for Puerto Rico, "Insectae Portoricensis" (Wolcott, 1923) and "Insectae Borinquenses" (Wolcott, 1936), ultimately culminating in his 1948 publication "The Insects of Puerto Rico," of which the list for Puerto Rico's butterflies was published separately (Wolcott, 1948). Complete with annotations, descriptions, illustrations, and collection information, this list provides an invaluable guide to Puerto Rico's butterfly fauna. Puerto Rican entomologist Francisco Seín Jr. worked closely with Wolcott and made significant contributions to his work (Martínez, 2017).

The modern foundation of the taxonomy of Puerto Rico Lepidoptera was provided by a series of papers published as part of the "Scientific Survey of Porto Rico and the Virgin Islands," a long-term project organized by the New York Academy of Sciences (Figueroa, 1996). The first volume on Lepidoptera, and a supplement (Forbes, 1930, 1931), covered most of the moth families except Noctuidae (s.l.), Geometridae, and Pyralidae (s.l.), which were treated by Schaus (1940a, 1940b). The butterflies were treated by Comstock (1944). While these volumes provide comprehensive coverage of the then-known fauna, the paucity of illustrations makes them difficult to use.

The late 20th century brought a greater degree of taxonomic work associated with institutions within Puerto Rico. The prominent role of the USDA remained. Jenaro Maldonado Capriles (UPR) and Carmen A. Navarro (UPR) published a list of additions and corrections to Wolcott's work in 1967 (Maldonado Capriles & Navarro, 1967). Numerous taxonomic insect checklists followed. Luis F. Martorell (UPR), having published a thorough survey of Puerto Rico's forest insects in 1945 (Martorell, 1945), also authored and co-authored many notable insect lists throughout the 1970s, including "The Insects of Mona Island, Puerto Rico" (Martorell, 1973), "Preliminary list of the insects of Desecheo Island, Puerto Rico" (Tudurí et al., 1974), "The Insects of Caja de Muerto Island" (Medina-Gaud & Martorell, 1974), and "Annotated Food Plant Catalog of the Insects of Puerto Rico" (Martorell, 1976). The Puerto Rico Nuclear Center (PRNC; now Center for Energy and Environmental Research) also had an interest in documenting local fauna, as this information was relevant to radioecology research following the development of nuclear energy infrastructure in the late 1950s and early 1960s. For example, George E. Drewry (PRNC) published a list of insects specific to El Verde as part of "A Tropical Rain Forest: A Study of Irradiation and Ecology at El Verde, Puerto Rico" (Drewry, 1970), which compiled results of controlled radiation studies taking place at the site between 1963 and 1967.

Location-specific lists became less common in the years that followed, though one notable exception was a list of insects specific to the Luquillo Mountains published by Juan A. Torres (UPR) (Torres, 1994). S. J. Ramos (UPR) published lists of updates to the nomenclature of Puerto Rican butterflies in 1982 and 1996 (Ramos, 1982, 1996), building on the work of Comstock (1944) and Riley (1975). In 1996, Maldonado Capriles (1996) published an up-to-date account of insect taxonomy work in Puerto Rico. Then, Torres and Silverio Medina-Gaud (USDA: TARS) provided an overview of insect families in Puerto Rico, approximating 1045 species of Lepidoptera, in contrast with Wolcott's 939 species in 1948 (Torres & Medina-Gaud, 1998). Of these estimated species, however, only 267 (26%) had been described from Puerto Rico at this time, evidence of the work that still remains to be done. Many of the aforementioned publications provided short summaries of other, more minor expansions and revisions published in the mid- to late-20th century, which are not listed here for the sake of brevity. Despite numerous valuable contributions during the later half of the 20th century, there were none that attempted an updated comprehensive list of Lepidoptera species across the entirety of Puerto Rico.

Following the rise of cladistics, island biogeography, and phylogeography in the late 20th century, research on the biogeography of Puerto Rico and, more broadly, Caribbean Lepidoptera became prominent. The theory of island biogeography (MacArthur & Wilson, 1967) and works like that of Darlington (1957) and Levins and Heatwole (1973) emphasized a dispersalist view, which refers to a model of speciation occurring through dispersal from a center of origin and subsequent crossing of preexisting dispersal barriers. This became the dominant view to explain the biogeography of Caribbean Lepidoptera (e.g., Scott, 1972). Yet, the high degree of endemism and unlikely candidates for long-distance dispersal led Miller and Miller (1989) to propose a model that included both dispersal and vicariance (the development of barriers that fragment a widespread species) to explain the distribution of Caribbean butterflies.

2.3 | Developments and recommendations: 21st century

The turn of the 21st century brought a wave of genetic and genomic tools that have improved methods of taxonomic classification, as well as provided insight into speciation and evolution. In the neotropics, butterflies of the genus *Heliconius* provide a model of adaptive radiation and have thus been prominent subjects of genetic analyses. The Riccardo Papa lab at UPR has participated in three wide-scale studies that sequenced the genomes of *Heliconius* species and revealed the roles of hybridization, selective processes, and modular architecture in the adaptive radiation of the genus (Edelman et al., 2019; The Heliconius Genome Consortium, 2012; Van Belleghem et al., 2017). In addition to genomics, DNA barcoding—which helps identify species based on short segments of DNA—has been prominent for taxonomic decisions regarding tropical Lepidoptera since its development in the early 2000s (DeSalle & Goldstein, 2019; Hajibabaei et al., 2006; Miller, 2007). For example, one study used DNA barcoding to elucidate taxonomic relationships among butterflies in the genus *Calisto*, including the Puerto Rican endemic *C. nubila* (Sourakov & Zakharov, 2011). Similar to *Heliconius*, *Calisto* represents a rich example of adaptive radiation, comparable to a version of "Darwin's finches" endemic to the Caribbean, and was thus of interest for comprehensive analysis. Barcoding has also been used for analysis of the butterfly genus *Dryas*, including *D. iulia iulia* endemic to Puerto Rico, culminating in the reinstatement of a species (*D. alcionea* of Suriname and French Guiana) that had previously been treated as a subspecies (Núñez et al., 2022). Relevant to Puerto Rico, recent analysis of DNA barcodes for butterflies by Núñez et al. (2023) suggests a higher degree of endemism and species richness than previously acknowledged in the Greater Antilles in general, as many current subspecies in the region may be treated more accurately as species.

According to the Barcode of Life Data Systems (BOLD), the global DNA barcode data base, 987 public barcode records exist for Lepidoptera in Puerto Rico (http://www.boldsystems.org/; accessed July 12, 2023). Three hundred sixteen BIN clusters are represented in these records, with only 89 identified species (528 BINs are represented when private records are also considered; Table 1). Considering that the estimated number of Lepidoptera species in Puerto Rico sat at 1045 in 1999 (Torres & Medina-Gaud, 1998), including 106 butterfly species (Ramos, 1996), these numbers indicate that the Lepidoptera population is undersampled. This is especially true for moths, as they represent the vast majority of Puerto Rican Lepidoptera species (compare ~400 BINs for ~940 moth species to 83 BINs for ~100 butterfly species). The number of public BINs represented in the BOLD data base for Puerto Rico seems to be generally comparable to other islands in the Caribbean (e.g., 212 in Cuba; 302 in Jamaica), but pales in comparison with certain nearby mainland regions in Central America (e.g., 1826 in Panama; 14,577 in Costa Rica). However, this disparity can likely be attributed in part to the gap in biodiversity between islands and mainland regions in the tropics (Zimmerman et al., 2021). Puerto Rico is considered species poor relative to other Caribbean regions (Crews & Esposito, 2020), perhaps due to its position at the ends of the Greater and Lesser Antilles, which create barriers to dispersal from mainland regions.

TABLE 1 Numbers of species from Puerto Rico represented by DNA sequences in the Barcode of Life Data Systems data base (http://www.boldsystems.org/) as of July 2023, as estimated by BIN clusters.

Higher taxon	Number of BINs
Butterflies	83
Noctuoidea	142
Geometridae	47
Other "Macrolepidoptera"	13
Pyraloidea	119
Gelechioidea	51
Other "Microlepidoptera"	54
Unidentified Lepidoptera	19
Total	528

Among the 542 barcoded specimens in Puerto Rico that were identified at the family level, 396 (or roughly 73%) belong to eight moth families, reflecting an ongoing moth barcoding initiative by Alonso-Rodríguez (unpublished). DNA barcoding of moths native to the Luquillo Experimental Forest (LEF) will be used by Alonso-Rodríguez (unpublished) to evaluate changes in phylogenetic and functional diversity from before to after Hurricane María in 2017, a use that serves as an illustration of the importance of barcoding in ecological research. Ongoing barcoding efforts by Alonso-Rodríguez, alongside those of the Smithsonian National Museum of Natural History, will continue to increase the availability of barcode data for Puerto Rican Lepidoptera in the coming years.

Accessibility of information related to Lepidoptera in Puerto Rico has vastly improved in the 21st century through digitized museum collections (e.g., by the Smithsonian National Museum of Natural History [https://naturalhistory.si.edu/research/entomology]), biodiversity data bases (e.g., LepNet [https://scan-all-bugs.org/?page_id=2712], iDigBio [https://www.idigbio.org/], and the Global Biodiversity Information Facility [https://www.gbif.org/]), DNA barcode data bases (e.g., BOLD [https://www.boldsystems.org/]), online photograph sets (e.g., the Moth Photographers Group [https://mothphotographersgroup.msstate.edu/AC-PR/ACindex.shtml], Butterflies and Moths of North America [https://www.butterfliesandmoths.org/photo-checklist/45166]), and online archives of early research publications that would otherwise be obscure (e.g., the Biodiversity Heritage Library [https://www.biodiversitylibrary.org/]). Butterflies of America (https://www.butterfliesofamerica.

com/) provides images and species lists for the Americas, including a detailed bibliography of neotropical butterflies (Lamas, 2023). Genomic data bases through the National Center for Biotechnology Information (https://www.ncbi.nlm.nih.gov/), alongside taxon-specific resources such as Lepbase (http://lepbase.org/) and LepidoDB (https://bipaa.genouest.org/is/lepidodb/) have also made genetic information for Puerto Rico's Lepidoptera available online. The quality and availability of online Lepidoptera resources will likely continue to improve in the coming years with the development of efficient, standardized digitization practices (Echevarría Ramos & Hulshof, 2019; Hebert et al., 2013; Nelson et al., 2012).

A taxonomic bibliography compiled by Martínez (2017) suggested that Lepidoptera was the fourth most taxonomically studied order of true insects in Puerto Rico after Hemiptera, Coleoptera, and Diptera. The majority of studies included in the bibliography were published before the year 2000. Outside of one preliminary survey in Patillas (LoCascio & Kudryashova, 2013), surveying of Lepidoptera in Puerto Rico has been uncommon in the last two decades. Rather, recent publications consist mainly of genetic work for individual butterfly genera and additions to the existing taxonomy (e.g., Brown & Brown, 2004; McCabe, 2003; Pinheiro, 2016; Pogue, 2013; Razowski & Becker, 2007). Future research should seek to provide genetic data for a wider range of lepidopteran species and strategically employ surveys as a means to interpret changes in Lepidoptera assemblages over time. It is imperative that these changes come to be understood as they relate to ecological disturbances, ongoing climatic events, and shifts in land use. Considering that a comprehensive list of Lepidoptera in Puerto Rico has not been attempted since the Scientific Survey (Comstock, 1944; Forbes, 1930, 1931; Schaus, 1940a, 1940b), an updated taxonomic list that is representative of today's Lepidoptera assemblages, incorporating new taxonomic findings and life history records, is also of interest.

2.4 | Life history research

Taxonomic publications on Lepidoptera in Puerto Rico have sometimes included information on morphology, host plants, and developmental stages, as these factors have the potential to influence classification. While the life histories of some species have been investigated individually, life history data overall is largely lacking, especially for moths. Rare and/or charismatic species have been subject to more detailed life history studies, as this knowledge is imperative for their conservation (e.g., Homziak & Homziak, 2010; Matthews & Pérez, 2014; Torres-Bauzá, 1991). Agricultural pests have also been of interest due to their economic significance (e.g., Inglés Casanova & Medina-Gaud, 1975; Segarra-Carmona et al., 2010). In addition to life history studies, brief records documenting new findings about host plants and natural enemies for lepidopteran agricultural pests are also published periodically (e.g., Cabrera-Asencio et al., 2013; Gregory et al., 1991; LaSalle & Peña, 1997; Santiago-Blay, 1983). Life history data is not only important for Lepidoptera identification and habitat management efforts for vulnerable and/or pest species, but also for advancing research in functional ecology. Knowledge of feeding habits, larval behavior, and other functional traits can shape our understanding of the ecological roles fulfilled by lepidopterans across developmental stages, which are likely essential for conserving ecosystem function amid climatic and land use change. Given the growing scientific evidence that assessing changes in biodiversity is better achieved through a lens of functional diversity rather than taxonomic diversity (Córdova-Tapia & Zambrano, 2015), gathering life history and functional trait data for a greater number of Puerto Rican Lepidoptera species is crucial.

2.5 | Insect collections

Insect collections in Puerto Rico are vital resources for Lepidoptera research, providing knowledge for classification and identification, as well as providing insight into patterns related to biodiversity and occurrences of invasive species. The Museo de Entomología y Biodiversidad Tropical at the Agricultural Experiment Station of UPR is home to the largest insect collection in Puerto Rico, with over 200,000 insect specimens (Franqui et al., 1997), followed by the collection held by the University of Puerto Rico at Mayagüez (UPRM), which includes over 130,000 (Franz & Yusseff Vanegas, 2009). The abundance of specimens in both collections follows the general trend for abundance of taxonomic publications, that is, Hemiptera and Coleoptera are most abundant, followed by Lepidoptera. There are over 10,000 Lepidoptera specimens in each collection. Nymphalidae, Pieridae, and Noctuidae are the most abundant lepidopteran families in the UPRM collection. The frequency of specimens in insect collections may reflect actual abundance to some degree, though collection bias (i.e., collector/institutional research interests, insect activity, site selection, ease of capture, etc.) should also be considered. Given economic cutbacks and understaffing across the UPR system in recent years, support for improving and maintaining the collections within these museums should be made a priority in order to preserve their historical, economic, and ecological value. Some opportunities for improvement include building maintenance and upgrades, taxonomic revisions (including updated nomenclature), the addition of new specimens, and digitization.

3 | ECOLOGY

In tandem with the shift from agriculture to industrialization beginning in the mid-20th century, much of Puerto Rico is undergoing successional forest recovery, particularly in abandoned agricultural lands and areas disturbed by hurricanes, floods, and landslides (Miller & Lugo, 2009). Understanding the responses of lepidopterans to these successional changes, especially in the context of hurricane disturbance, has been of particular research interest. Relationships between lepidopterans and other ecologically significant species (e.g., their host plants, parasitoids, and vertebrate predators) have also been of interest, as described below.

3.1 | Community-level interactions

Butterflies and moths interact with organisms of other trophic levels as herbivores, pollinators, hosts for a variety of parasitic insects, and prey for secondary consumers. Associations between lepidopterans and host plants were well documented in mid-20th century Puerto Rico, especially in detailed surveys composed by Martorell (1945, 1976) and Wolcott (1948). Parasitism, particularly by insects of the orders Diptera and Hymenoptera, has also been a topic of interest, given its potential use in bioremediation. Wasps in the family Braconidae are especially abundant parasitoids in Puerto Rico and are frequently investigated as biological control species for agricultural applications (e.g., Borkhataria et al., 2012; Gallardo-Covas, 1988, 2005; Inglés Casanova & Medina-Gaud, 1975).

A variety of vertebrate fauna native to Puerto Rico also feeds on lepidopterans, including birds, amphibians, reptiles, bats, and other small mammals. One study in Puerto Rico found that lepidopterans were a staple in the diet of mormoopid bats. Dietary differentiation between bats that consume soft-bodied lepidopterans and those that consume hard-bodied insects was found to be a mechanism for the coexistence of multiple mormoopid bat species (Rolfe & Kurta, 2012). Another study found that the removal of an invasive rat (*Rattus rattus*) from Desecheo Island was immediately followed by an outbreak of the uncommon dingy purplewing butterfly (Nymphalidae: *Eunica monima*), with population release from rat predation as one possible explanation (Shiels et al., 2017). The relationship between anole lizards and lepidopteran agricultural pests has also been investigated, as predation by lizards is a viable form of biological control for some Lepidoptera species (Borkhataria et al., 2006; Perfecto et al., 2021; Segarra-Carmona & Barbosa, 1988).

Several vertebrate species that consume lepidopterans in Puerto Rico are considered to be of conservation priority by the Puerto Rico Departamento de Recursos Naturales y Ambientales (Puerto Rico Department of Natural and Environmental Resources [DRNA], 2015; Table 2). It is thus of interest to explore how these at-risk species are affected by fluctuations in Lepidoptera abundance and, more broadly, insect abundance.

3.2 | Research localities

Though many areas of Puerto Rico are rich with insect life, the two most popular sites for ecological insect research in Puerto Rico are the Sierra de Luquillo and the municipality of Guánica. Both are home to UNESCO biosphere reserves (Luquillo Experimental Forest Biosphere Reserve and Guanica Biosphere Reserve). The Luquillo range contains the Luquillo Experimental Forest (LEF), a densely forested reserve site that is frequently the subject of successional forest change research involving Lepidoptera (e.g., Aparicio-Jiménez, 2020; Barberena-Arias & Aide, 2002; Schowalter & Ganio, 1999; Torres, 1992). The LEF is also a Long-Term Ecological Research (LTER) site, a project supported by the National Science Foundation in collaboration with the University of Puerto Rico and the USDA Forest Service (Zimmerman et al., 2021). The program has facilitated a range of entomological research with an emphasis on long-term monitoring, though Lepidoptera has not been a common research subject at the LEF site. Rather, emphasis has been placed on canopy arthropods (e.g., Richardson et al., 2018; Schowalter, 2017, 2018; Schowalter et al., 2014, 2017, 2021) and walking sticks (e.g., Prather et al., 2018; Willig et al., 2011). The Guánica reserve is a subtropical dry forest along the coast, a “mosaic of ecological systems” (UNESCO, 2019), and thus a critical habitat for a diverse array of Puerto Rico's insect fauna (Allan et al., 1973). The site is often used for short-term monitoring of lepidopterans, especially pests (e.g., Hight & Carpenter, 2009; Homziak & Homziak, 2006, 2010; Trujillo, 2018). A compilation of biogeographical data from the online data base iDigBio (https://www.idigbio.org/) revealed Guánica to be the municipality with the highest frequency of digitized Lepidoptera specimen occurrences in Puerto Rico. Areas surrounding the UPR campuses in Río Piedras and Mayagüez also displayed significant frequencies (Figure 1).

Outside these sites, data regarding Lepidoptera populations is scarce. Disparities in frequency between localities can likely be attributed in part to collection bias rather than to differences in actual Lepidoptera abundance. Mountainous areas such as the Cordillera Central and the Sierra de Cayey displayed a moderate frequency

TABLE 2 Endangered vertebrate species in Puerto Rico that consume lepidopterans.

Vertebrate group	Lepidoptera consumption by at-risk species
Insectivorous birds	The elfin woods warbler (*Setophaga angelae*), Puerto Rican nightjar (*Caprimulgus noctitherus*), and yellow-shouldered blackbird (*Agelaius xanthomus*) all use lepidopterans as a key food source (Arroyo-Vazquez, 1992; Cruz-Burgos, 2000; Vilella, 1995)
Insectivorous bats	The Brazilian free-tailed bat (*Tadarida brasiliensis*) and the brown flower bat (*Erophylla bombifrons*) feed on lepidopterans (Soto-Centeno & Kurta, 2006; Whitaker & Rodriguez-Durán, 1999)
Coquí frogs (genus: *Eleutherodactylus*)	Eight species of this genus are of conservation priority (e.g., *E. eneidae*, *E. jasperi*, and *E. juanriveroi*), and individuals belonging to this taxon are known to feed on lepidopterans in Puerto Rico (Lavigne & Drewry, 1970)
Anole lizards (genus: *Anolis*)	Feeding data is not available for many at-risk reptile species, but several belong to this genus (i.e., *A. roosevelti*, *A. cooki, and A. poncensis*), a taxon that contains a variety of lepidopteran-feeding species in the West Indies (Lister, 1976)

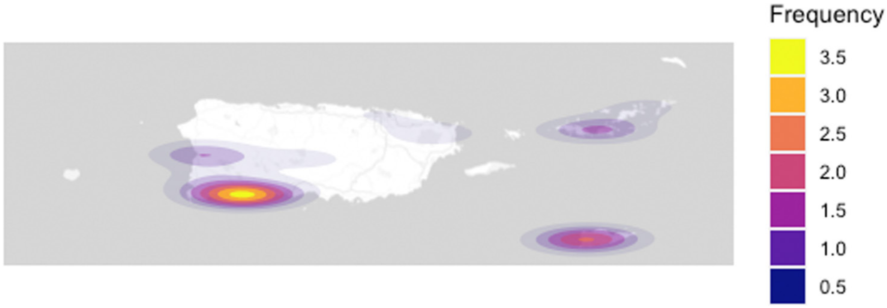

FIGURE 1 iDigBio records of "Lepidoptera" in Puerto Rico. Latitudinal and longitudinal data for species occurrences with the order Lepidoptera in Puerto Rico and the U.S./British Virgin Islands were downloaded from the online data base iDigBio (https://www.idigbio.org/). The data were then converted into a spatial heat map using the *ggplot2*, *ggmap*, and *viridis* packages in R (R Core Team, 2023). A 2D kernel density estimation using the stat_density2d function in *ggplot2* was performed to determine frequency levels. Map tiles by Stamen Design, under CC BY 3.0. Data by OpenStreetMap, under ODbL.

of species occurrences (Figure 1), though considering plant density and predicted Lepidoptera abundance in these areas, documentation of species occurrences leaves room for vast improvement. Mountainous areas in Puerto Rico provide habitats to a wide variety of lepidopterans, as illustrated by work in the LEF (Torres, 1994). Montane Lepidoptera populations may also be particularly sensitive to climate change, as suggested by the global literature (Chen et al., 2009, 2010; Hill et al., 2021; Rödder et al., 2021). Therefore, greater research emphasis on understudied mountainous areas is needed in order to elucidate long-term ecological patterns for the conservation of montane butterflies and moths.

3.3 | Methods and challenges

Long-term monitoring of Lepidoptera populations is complicated by sampling and analysis biases, which are inherent to traditional methods commonly used in Puerto Rico (e.g., insect nets, passive methods such as malaise, light, and bait traps). Targeted sampling of organic matter, including leaf litter and foliage-bearing tree branches, is also common (e.g., Barberena-Arias & Aide, 2002; Schowalter & Ganio, 1999). In instances where physical capture of butterflies or moths is not possible due to rapid or out-of-reach flight patterns, some studies have relied on inferences based on observation of associated plants (e.g., Ackerman & Moya, 1996) or, simply, qualitative observation of lepidopteran activity (e.g., Torres, 1992). All of these methods have the potential to be skewed by varying levels of insect activity, site selection bias, and faulty baseline identification, altering their ability to accurately reflect species abundance. Similar challenges exist for non-insect animal communities, though frequent fluctuation, ecological sensitivity, and diverse mechanisms of dispersal amplify these concerns for entomological research.

Seasonality of Lepidoptera populations may also present a sampling challenge for entomologists who primarily collect during major seasonal holidays in the Northern Hemisphere (December and Summer). The seasonality of many species is not well known, though work by Aparicio-Jiménez (2020) indicated seasonal peaks (January) and valleys (October) in species abundances in two forests in the municipality of Adjuntas during the year following Hurricane María. In contrast, Davila and Asencio (1992) reported the opposite for Lepidoptera in nearby Maricao in 1984, more than a decade past any major hurricane disturbance (the 1970 Caribbean–Azores hurricane).

Because of these challenges associated with Lepidoptera and, more broadly, insect monitoring, great care must be taken to understand fluctuations in abundance and diversity within the historical context of Puerto Rico. Specifically, emphasis should be placed on improved baseline estimation, trend estimation, and population inference (Didham et al., 2020). In general, future research should be transparent in scope, long term, wide scale, and consistent in location and methods between sampling occurrences (Schowalter et al., 2021). The use of a variety of sampling methods across different parts of the island will also be necessary to determine population dynamics and identify possible declines among a diverse Lepidoptera assemblage (Schowalter et al., 2019). Otherwise, the status of many Lepidoptera species in Puerto Rico will remain unknown.

3.4 | Hurricanes

As an archipelago in the hurricane belt, Puerto Rico is particularly vulnerable to habitat disturbance caused by tropical storms. Hurricanes are not thought to result in overall arthropod decline, but can impact insect populations directly (through increased mortality and redistribution events) and indirectly (through environmental changes (Schowalter et al., 2014) and the loss of host plant resources (Boose et al., 2004; Lugo, 2000)). Herbivorous insect populations like Lepidoptera are sensitive to shifts in host plant availability and forest cover and are therefore susceptible to significant changes in species composition following hurricane-induced changes in plant assemblages (Schowalter et al., 2021). Therefore, in light of the ongoing and predicted increases in storm frequency and intensity, the Lepidoptera population may be especially impacted (Seneviratne et al., 2021). Natural history collections are also vulnerable to hurricane damage, threatening our ability to use historical records for ecological research like DNA barcoding. Damage caused by

Hurricane María (September 2017) impacted zoological and botanical collections at the University of Puerto Rico by causing electricity outages and, subsequently, heat and humidity levels unsuitable for specimen preservation (Schizas, 2018).

Due in part to frequent hurricane activity, the islands of Puerto Rico are in a constant state of secondary succession. Early successional stages are typically associated with low insect diversity caused by a decrease in the availability of habitats and host plant species (Southwood et al., 1979). Herbivorous insects may be more severely harmed by these disturbances when compared to insects of other feeding guilds (Willig & Camilo, 1991). Indeed, a study conducted in the LEF considered Lepidoptera as part of a wider "defoliator" functional group and reported a decline in abundance following Hurricane Hugo over a 6-year period (Schowalter & Ganio, 1999). Another LEF study found that, in three sites of varying successional stages (early, mid-, and late), insect richness, abundance, and trophic composition rapidly returned to pre-hurricane conditions in the year following Hurricane Georges. However, species composition varied significantly between prehurricane and posthurricane evaluations. Taxonomic diversity of Lepidoptera declined for all sites during this period due to a prolonged recovery period for leaves and flowers (Barberena-Arias & Aide, 2002).

Although Lepidoptera populations in general seem to be negatively impacted by hurricane-induced defoliation events, some species thrive in early successional conditions. Torres (1992) documented outbreaks of 15 lepidopteran species in Puerto Rico immediately following the passage of Hurricane Hugo (September 1989), attributing these outbreaks to the appearance of new foliage in the LEF. Certain lepidopteran larvae benefited from the presence of younger leaves and from a newfound abundance of pioneer plant species in disturbed areas. A similar phenomenon was reported by Schowalter et al. (2017) when two moth species exhibited elevated abundances after Hurricane Georges, resulting in accelerated herbivory of some early successional plant species.

Additionally, despite overall pollinator decline and plant defoliation immediately following hurricanes, plant–pollinator relationships involving Lepidoptera display adaptability and resilience (Ackerman & Moya, 1996; Cabrera-Asencio & Meléndez-Ackerman, 2021). More work is needed to understand the long-term effects of hurricane damage on Lepidoptera populations. Research on moths is especially lacking, though work by Alonso-Rodríguez (unpublished) suggests forest type in the LEF plays an important role in determining the recovery of moth species richness and diversity following major hurricane disturbance.

In addition to the impact of hurricanes on existing Lepidoptera populations, winds associated with hurricanes can also facilitate insect dispersal, which Torres (1988) deemed "an adaptive feature of the phylum" that can influence both colonization and the abundance of insect species. Little has been reported on the role of this dispersal method for Lepidoptera. However, wasps, aphids, and locusts have appeared after hurricanes in Puerto Rico (Torres, 1988), and in 1933 and 1967, hurricanes reportedly led to the appearance of tropical butterflies in Texas (Doyle, 1970; Heitzman & Heitzman, 1972; Kendall, 1970; Neck, 1934). Additionally, an unusual flight of monarch butterflies was reported in San Juan a month after the passing of San Felipe (Williams et al., 1942). Further, hurricane-mediated dispersal events appeared to drive invasion routes of the cactus moth (Pyralidae: *Cactoblastis cactorum*) from the Caribbean (Andraca-Gómez et al., 2015). Together, these results suggest hurricane-mediated transport may be a common, albeit understudied, phenomenon.

3.5 | Forest conditions

The effects of forest type, elevation, and cover on invertebrate communities have been investigated in Puerto Rico. A study on the effects of forest type and elevation on leaf litter invertebrates, including lepidopteran larvae and adults at an estimated 1–12% biomass, found that species richness generally declined with elevation in non-palm leaf litter. In contrast with non-palm litter, palm litter was richer in nutrients, had a greater abundance of Lepidoptera, and, instead of a gradient, exhibited similar species richness across elevations. Differences in species richness between elevations in non-palm forests were suggested to be primarily influenced by forest composition rather than by rainfall or temperature (Richardson et al., 2005). Generally, decreasing species richness with elevation is accepted as a pattern worldwide (Rahbek, 1995). With regard to forest cover, Aparicio-Jiménez (2020) found no correlation between canopy openness and lepidopteran abundance in two different-aged forests following Hurricane María; however, wing size and color were correlated with changes in canopy cover, suggesting that environmental conditions likely select for certain functional traits.

In addition, lepidopterans can influence tropical forest productivity through herbivory. Schowalter et al. (2011) investigated these influences through experimental additions of herbivore inputs to the LEF. Lepidopteran frass was found to increase soil N and P fluxes, indicating that herbivore outbreaks may help ameliorate the effects of defoliation, increasing plant productivity through its effects on soil nutrients.

3.6 | Climate change

The present and potential effects of climate change on Lepidoptera populations are starting to be well studied in temperate and some tropical countries. In Puerto Rico, this is a pressing topic that merits more research, especially because tropical ectotherms, including Lepidoptera, are thought to be particularly vulnerable to warming temperatures (Laurance et al., 2011). Lepidoptera are excellent for understanding climate change responses, owing to their diversity, ecological sensitivity as ectotherms, ease of capture, rapid generational turnover, and widespread research interest. Tropical lepidopterans are particularly diverse, as the tropics are home to roughly 90% of identified butterfly species (Bonebrake et al., 2010). Additionally, a rich taxonomic legacy in the region means that location-specific surveys, alongside publicly accessible biodiversity data bases, have the potential to provide convenient baseline data for understanding changing Lepidoptera diversity and distributions in Puerto Rico. For these reasons, Caribbean Lepidoptera are an ideal model for global change research. As charismatic fauna with widespread interest from both hobbyists and researchers, demonstrating the ecological effects of climate change on Lepidoptera can be a meaningful tool for connecting public interest, public policy, and scientific research.

Based on two global reviews, possible responses of lepidopterans to climate change include up-regulation of thermoregulation genes, early emergence from diapause, shifts in reproductive strategy, geographical expansion, and changes in interactions between lepidopterans and their parasitoids (Hill et al., 2021; Kocsis & Hufnagel, 2011). Thus, in Puerto Rico, Lepidoptera diversity and distribution patterns are likely to shift in response to shifting temperature and precipitation regimes (Hulshof et al., *Under Review*). Upslope migration of lowland plant and animal populations has been reported in other tropical regions (e.g., Feeley et al., 2010; Freeman & Class Freeman, 2014; Shah et al., 2020) and may lead to biotic homogenization (e.g., Ogan et al., 2022) of the Lepidoptera fauna where rare, narrowly distributed species are replaced by common, wide-ranging species. In other tropical regions, climate change has resulted in decreased nutritional quality of vegetation, decreased herbivore performance, and shifts in the range boundaries of tropical butterflies and moths (Au & Bonebrake, 2019; Chen et al., 2010; Coley, 1998). Similar to hurricane disturbance, responses to climate change appear to be highly variable among Lepidoptera populations, depending on differences in diet, habitat, and life history. As a result, comprehensive studies comparing entire assemblages (community-level) of Lepidoptera in Puerto Rico are urgently needed.

No studies evaluating lepidopteran responses to climate change exist that are specific to Puerto Rico or the Caribbean at large, outside those connected to hurricanes as a climate change outcome. This is a significant knowledge gap. Caribbean islands are vulnerable to climate change not only because of intensified tropical storms, but also because of the ongoing outcomes of intensified floods, droughts, and wildfires, rising temperatures, rising sea levels, longer dry seasons, shorter wet seasons, decreased air quality, and effects on forest health and species composition (Beckford & Rhiney, 2016). Specific to the LEF, climate change has been predicted to intensify the expansion of invasive species and facilitate outbreaks of certain insects and pathogens (Jennings et al., 2014). Future studies in Puerto Rico and surrounding areas should seek to connect these climate change outcomes to their long-term effects on butterfly and moth populations.

4 | AGRICULTURE

4.1 | Pests

Sugarcane, coffee, tobacco, cotton, and corn crops have all historically had economic significance in Puerto Rico, and all have been threatened to some extent by Lepidopteran pests (Dietz, 1986; Martorell, 1976). Research involving the agricultural pests of Puerto Rico is vast, with much work on insecticide responses, feeding preferences, and natural enemies (Table 3). Although insecticide use remains a prominent form of control, there has been a shift in strategy toward integrated pest management (IPM) for some insect pests (e.g., Aristizábal et al., 2017; Hall & Gottwald, 2011). The shift to IPM has been aided by the identification of natural enemies, as reflected in the recent literature. Though the majority of documented natural enemies in Puerto Rico are invertebrate parasitoids and predators, vertebrate predators such as birds and lizards have also been found to provide additive effects for pest control (Borkhataria et al., 2006).

Martorell's (1976) "Annotated Food Plant Catalog of the Insects of Puerto Rico" is the most thorough record of pests in Puerto Rico and includes detailed host plant records for both pests and non-pests, which we have digitized (available on Dryad, https://datadryad.org/stash/share/tR6-8ISAEVOtzXIOmm-6l_TZM6l29hzCad0sPx43-80), and which could be used for preliminary insect–host plant network analyses. Here, we highlight research on a few species with major agricultural impacts. Where the taxonomy has undergone revision, we use the most recent nomenclature (e.g., Martorell's *Heliothis zea* is now *Helicoverpa zea*).

4.2 | Pollination

Pollination of tropical crops is predominately facilitated by insect visitors in the order Hymenoptera, though adult butterflies and moths also play a documented role (Roubik, 1995). For example, a recent study in Puerto Rico found that Lepidopterans were among 50 mango crop pollinator species (*Mangifera indica*; Cabrera-Asencio & Meléndez-Ackerman, 2021). While it is challenging to elucidate general patterns regarding pollination efficiency across tropical crops, a worldwide literature search concluded that the families Nymphalidae and Pieridae may be the most significant crop pollinators within Lepidoptera (Rader et al., 2020). These families are especially abundant and species-rich in Puerto Rico (Ramos, 1996).

Despite the paucity of research on the overall role of lepidopterans in crop pollination, a few beneficial relationships between lepidopteran pollinators and non-crop plants have been highlighted in Puerto Rico. For example, the frangipani hornworm (Sphingidae: *Pseudosphinx tetrio*) is known to pollinate the fringed star orchid (*Epidendrum ciliare*) in Puerto Rico as an adult (Ackerman & Montalvo, 1990; Ackerman & Moya, 1996). Lepidopterans have also been documented as pollinating visitors of *Gesneria viridiflora* (Martén-Rodríguez & Fenster, 2008), *Strophanthus intermedius* (Spencer & Winters, 1957), *Palicourea crocea*, and *Psychotria berteroana* (González et al., 2009) in Puerto Rico. Based on the limited available data from temperate regions, lepidopteran visitors may generally be more essential to the pollination of non-crop species than they are to the pollination of crop species (Hahn & Brühl, 2016). Further research is needed to quantify the value of Lepidoptera for pollinating crop and non-crop species in Puerto Rico and tropical regions at large.

TABLE 3 Summary of major agricultural pests, impacted crops, and focus of research to date.

Pest	Crops	Research summary
Noctuid fall armyworm (*Spodoptera frugiperda*)	Corn, rice, sugarcane, cotton	Heavy insecticide use has led to declining effectiveness (Belay et al., 2012; Gutiérrez-Moreno et al., 2019; Viteri et al., 2019). Transgenic Bt corn provides some resistance, though cross resistance has developed in Puerto Rico (Niu et al., 2013; Storer et al., 2012; Zhu et al., 2015). High genetic diversity but little genetic differentiation among populations in Puerto Rico, the United States, Argentina, and Panama (Belay et al., 2012) points to the high gene flow and potentially high adaptability of this species
Noctuid corn earworm (*Helicoverpa zea*) and cotton bollworm (*Helicoverpa armigera*)	Corn, sorghum, tomato, cotton	*H. zea* is native to Puerto Rico, while *H. armigera* is considered an invasive species (Smith, 2014). *H. armigera* has only appeared in small numbers (Gilligan et al., 2019). Morphological differences between the two species are slight, and hybridization is possible (Trujillo, 2018) Studies on *Helicoverpa* spp. in Puerto Rico have evaluated insecticide resistance, flight phenology, hybridization, morphology, and efficacy of pheromone trapping (da Silva et al., 2020, Flores-Rivera et al., 2022 preprint)
Noctuid soybean looper (*Chrysodeixis includens*)	Tomato, tobacco, sweet potato, soybean	Hymenopteran and dipteran parasitoids have been identified for this species, suggesting the potential for a viable biological control alternative (Gallardo-Covas, 2005)
Pyralid melonworm (*Diaphania hyalinata*)	Pumpkin, squash	Predators and parasitoids of the pest occur in the orders Hemiptera, Hymenoptera, and Diptera (Medina-Gaud et al., 1989) Accessions of *Cucurbita moschata* (pumpkin) from the Americas were most resistant to the melonworm in screenings (Pérez-Arocho, 2011) Phenotypic recurrent selection of pumpkin crops has been attempted as a method of control in Puerto Rico but did not appear effective (Linares-Ramírez & Wessel-Beaver, 2014)
Pyralid lima bean pod borer (*Etiella zinckenella*)	Legumes	Listed by Martorell (1976) as a lima bean, pigeon pea, kidney bean, and cowpea pest A variety of parasitic wasps and anole lizards were identified as natural enemies of this species (Segarra-Carmona & Barbosa, 1988). Rates of parasitism by larval parasitoids were found to be influenced by host herbivore density but not by plant density for soybean plants. (Segarra-Carmona & Barbosa, 1990)
Pyralid sugar beet webworm (*Spoladea recurvalis*)	Beet, pumpkin, tomato	Listed by Martorell (1976) as a threat to beet, pumpkin, and tomato crops. However, horse purslane (Aizoaceae) was found to be the pest's preferred host plant, and beet was the only cultivar eaten by larvae in feeding trials (Figueroa et al., 2005)
Lyonetid coffee leaf miner (*Leucoptera coffeella*)	Coffee	Parasitic wasps are popular biological control species for this pest, especially the braconid *Mirax insularis* (Daza Montoya, 2008; Gallardo-Covas, 1988, 1992) Moths and butterflies in general were found to be more abundant in shaded coffee plantations, though this species showed no difference in abundance between shade and sun (Borkhataria et al., 2012). Birds and lizards have additive effects on the control of this species (Borkhataria et al., 2006). Certain ant species have negative effects on anole lizards and therefore deter predation by *L. coffeella* (Perfecto et al., 2021)
Papilionid Asian lime swallowtail (*Papilio demoleus*)	Citrus	First recorded in Puerto Rico in 2006 (Homziak & Homziak, 2006) Life cycle stages and insecticide resistance were investigated in Puerto Rico (Segarra-Carmona et al., 2010) A species of biting midge (Diptera: Ceratopogonidae) was identified as an ectoparasite (Abreu-Rodríguez et al., 2011)
Sphingid tobacco hornworm (*Manduca sexta*)	Tobacco	Life cycle stages, estimated leaf consumption, and natural enemies were investigated in Puerto Rico (Inglés Casanova & Medina-Gaud, 1975) Listed by Martorell (1976) as "one of the most important pests of tobacco since very early times"

5 | CONSERVATION

The Caribbean is among the top five biodiversity hotspots worldwide, with an exceptionally high number of total endemic species relative to land area (Myers et al., 2000). It is therefore an area of high conservation priority. Insects are considered to be of especially high concern due to their ecological sensitivity and species richness. In fact, it is estimated that 5373 of Puerto Rico's 5847 native wildlife species (or 92%) are insects (DRNA, 2015; Torres & Medina-Gaud, 1998). However, while there is significant data on threatened and endangered vertebrate animal species, very few invertebrate species in Puerto Rico have been identified as at risk. A possible explanation for this is the complicated and costly nature of invertebrate population monitoring. Lack of long-term data means it is difficult to recognize declining insect populations and identify specific areas of concern. In general, entomofauna seem to be declining on a global scale (van der Sluijs, 2020), though reports of this phenomenon in Puerto Rico are mixed, with hurricane-induced species turnover more likely occurring than an overall decline (Schowalter et al., 2021).

5.1 | Known species of conservation priority

The only insect listed as "threatened" in Puerto Rico by the U.S. Fish and Wildlife Service (FWS) is the Puerto Rico "quebradillana" or harlequin butterfly, *Atlantea tulita* (Nymphalidae). This is a recent listing, which granted it a level of protection under the Endangered Species Act of 1973 (U.S. Fish and Wildlife Service, 2022). Prior to the listing, Carrión-Cabrera (2003) noted the decline of *A. tulita* caused by habitat destruction, described its life history and geographical limitations, and recommended that it be granted this protection. A petition was put forward by Biaggi-Caballero (2009), which cited Carrión-Cabrera, and following a series of deliberations, the rule ultimately went into effect in January 2023 (though the original request for "endangered" status was substituted with "threatened"). The species has been referred to by the DRNA as "critically endangered" since its release of the Comprehensive Wildlife Conservation Strategy (now the Puerto Rico State Wildlife Action Plan) in 2005 (DRNA, 2015). In a recent study, Ramirez-Reyes et al. (2023) used an ensemble modeling approach to map suitable conditions for *A. tulita* in Puerto Rico and proposed critical habitat in both mountainous and coastal regions. Because much of its habitat occurs near or along the coast, its protection encourages the preservation of these regions, which may otherwise be threatened by coastal development.

There is also a body of work on monarch butterflies (Nymphalidae: *Danaus plexippus*) in Puerto Rico due to global interest in the species as a pollinator and a flagship conservation species. Outside of Puerto Rico, the migratory monarch (*Danaus plexippus*) is considered a candidate for "threatened" or "endangered" status by FWS but has not been officially listed. The decision regarding the status of this species is due in part to a lack of information surrounding distinctions between subspecies (U.S. Fish and Wildlife Service, 2022). A non-migratory Puerto Rican subspecies (*Danaus plexippus portorricensis*) was described in 1941 (Clark, 1941), but it is currently considered a color form, not a valid endemic subspecies (Smith et al., 1994, 2005). The widespread protozoan monarch parasite *Ophryocystis elektroscirrha* was not reported in Puerto Rican monarchs until 2020, though it was likely present much earlier (Rosario-Rodríguez & Acevedo-Suárez, 2020). In the recent literature, the Puerto Rican monarch population is most often considered in the context of larger research related to monarch morphology, coloration, migration patterns, range expansion, and toxin sequestration across islands and countries (see Altizer & Davis, 2010; Freedman et al., 2020, 2021; Li et al., 2016; Pierce et al., 2014; Zhan et al., 2014). One study specific to Puerto Rican monarchs documented protein profiles for its three developmental stages and found that those of the larvae and adult stages were nearly identical (Rosario-Rodríguez, 2015). Another used digitized museum collections to identify trends in monarch wing coloration and reported that darker coloration was prevalent in coastal habitats, contrary to expectations based on thermal biology (Echevarría Ramos & Hulshof, 2019) and perhaps an immune response to increased parasitoids or pathogens in coastal habitats.

5.2 | Conservation efforts

The USDA, especially through the USDA Forest Service and the International Institute of Tropical Forestry (IITF), regularly releases information relevant to the conservation of butterflies and moths. Local to Puerto Rico, organizations such as the DRNA, the University of Puerto Rico, and the Conservation Trust of Puerto Rico (in collaboration with Para la Naturaleza) are invested in the conservation of native fauna. Efforts by these organizations are complemented by smaller institutional efforts such as local *mariposarios* and targeted conservation projects (e.g., the butterfly farm at Casa Pueblo, a nonprofit organization in Adjuntas; the Feria de Polinizadores event held by Jardín Botánico UPR; the Liga Ecológica Quebradillana, a nonprofit group that is leading conservation efforts for the harlequin butterfly and its habitat). Future entomological research in Puerto Rico should seek to collaborate with these organizational efforts by identifying lepidopteran species of concern and providing concrete, evidence-based recommendations for their preservation.

6 | CONCLUSION

The order Lepidoptera is among the most well-studied insect taxa on Earth due to its diversity, economic significance, public interest, and rearing potential (Rocha-Ortega et al., 2021). The body of taxonomic work for the order in Puerto Rico is significant, dating back to the 1700s and given heavy emphasis throughout the 20th century in comprehensive surveys. Agricultural research on lepidopteran pests became prominent during the mid-20th century, in contrast with the economic decline of agriculture in Puerto Rico during the same period. Lepidoptera research for purely ecological purposes was not prominent in Puerto Rico until the late 20th century, but has continued to be relevant and, as we have described, is currently a pressing priority. Recent years have also brought conservation efforts for the order as ongoing ecological changes put native species at risk of extinction. However, these risks are poorly understood, especially in the Caribbean tropics.

Overall, Lepidoptera work in Puerto Rico has historically been focused on taxonomic surveys, short-term evaluations of hurricane response, and agricultural studies, while long-term monitoring for ecological and conservation purposes is comparatively less studied. We therefore recommend future work occupy a wider temporal scale and suggest some priority areas for Lepidoptera ecological research in Puerto Rico (Table 4). The Puerto Rican archipelago presents a unique opportunity to observe the effects of human activities and climate change on tropical biodiversity due to

TABLE 4 Priority research areas for understanding Lepidoptera ecology in Puerto Rico.

Priority area	Examples
Long-term monitoring	Monitoring of Lepidoptera populations to determine impacts of tropical storm damage, climate change, and seasonality Species distribution modeling using biodiversity collections to determine current and predicted trends in diversity and distributions (Hulshof *Under Review*) Thermal biology of species and their possible vulnerabilities to warming temperatures Changes in parasitism/pathogen load over time
Understudied regions	Lepidoptera diversity and dynamics in: Topographically complex regions (Cordillera Central, northern coastal *mogotes* or limestone haystacks, Sierra de Cayey) and across elevational gradients Artificial ecosystems (agroecosystems, urban environments) to determine the effects of various land use activities as they relate to deforestation, light pollution, induced changes in species composition, etc.
Digitization	Compilation of specimens and data across disparate collections and museums iDigBio (https://www.idigbio.org/) specimens (of the 2076 Puerto Rico specimens listed in iDigBio, 159, or <1%, have images as of July 2023) Development of functional and phylogenetic data bases
Native moths	Expansion of taxonomic and ecological knowledge of moths in Puerto Rico, as much of the research to date has focused on butterflies Moth disturbance dynamics in forest ecosystems (Alonso-Rodríguez, unpublished) Addressing disparities in taxonomic and life history knowledge Evaluating the effectiveness of different conservation efforts in reducing local extinctions and biodiversity loss

its vulnerability, accessibility, and ecological diversity across ecosystems. Additionally, this work has the potential to make significant contributions to the unresolved question of global insect decline and its relation to global change.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Barcode of Life Data Systems at http://www.boldsystems.org/index.php/Public_BINSearch?searchtype=records using the search terms "Lepidoptera" and "Puerto Rico" and in iDigBio at https://www.idigbio.org/portal/search when filtered to the order "Lepidoptera" within the geographical bounds of Puerto Rico and the U.S./British Virgin Islands. The digitized insect host plant catalog based on Martorell (1976) is available on Dryad (https://datadryad.org/stash/share/tR6-8ISAEVOtzXIOmm-6I_TZM6l29hzCad0sPx43-80).

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