



# Invasive Species in Puerto Rico: The View From El Yunque

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Native flora and fauna of Puerto Rico have a long biogeographic connection to South America. Theory and empirical evidence suggest that islands, particularly those distantly isolated from the mainland, should be more susceptible to naturalizations and invasions of non-native species than continental areas. Anthropogenic disturbances can facilitate accidental and deliberate introductions of non-native species. In this study, we asked: What is the current status of introduced species within El Yunque National Forest (EYNF), the largest and most well-conserved forest area of Puerto Rico? To address this question, we reviewed the literature and surveyed local experts to identify introduced plant and animal taxa that are behaving as invaders within EYNF. We hypothesized that well-conserved forest areas within EYNF would be more resistant to invasions than disturbed areas along roads and ruderal areas with a long history of human activity. We found that there is only partial evidence that supports our hypothesis and this evidence is strongest in vascular plants, but not for the other taxonomic groups analyzed. Our combined results showed that currently the more ubiquitous invasive species in EYNF include some mammals (feral cat, rat, and mongoose) and some invertebrates (earthworms, mosquito, and Africanized honeybee). For many taxa, there is little information to thoroughly test our hypothesis, and thus more detailed surveys of the status of non-native and invasive species in EYNF are needed.

## OPEN ACCESS

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**Keywords:** alien biodiversity, biotic resistance, introduced animals, island biogeography, Luquillo Experimental Forest, non-native plants, tropical montane forest

### Specialty section:

This article was submitted to  
Biogeography and Macroecology,  
a section of the journal  
Frontiers in Ecology and Evolution

**Received:** 10 December 2020

**Accepted:** 25 January 2021

**Published:** 08 March 2021

### Citation:

Zimmerman JK, Rojas-Sandoval J  
and Shiels AB (2021) Invasive Species  
in Puerto Rico: The View From El  
Yunque. *Front. Ecol. Evol.* 9:640121.  
doi: 10.3389/fevo.2021.640121

## INTRODUCTION

Islands are isolated land masses that frequently exhibit simplified ecological systems containing locally adapted and endemic species, often with small population sizes, low reproductive rates, and a lack of predator defenses compared with mainland counterparts (Wilson and MacArthur, 1967; Moser et al., 2018). These attributes make island ecosystems more susceptible than mainland ecosystems to human-related impacts, such as the introduction and establishment of non-native species. The theory of island biogeography (Wilson and MacArthur, 1967) states that isolation and island size are critical factors determining the number of species that can colonize and establish on island ecosystems. Depending on species' vagility, islands near the mainland may have similar native species composition and ecological characteristics and higher species richness than remote islands. Thus, islands with a biogeographic history of lying near continental areas may be more resistant to the establishment of new species than those isolated far from mainland

(Moser et al., 2018). Islands across the Caribbean show strong species affinities with both North and South America because of their shared biogeographic history, which largely results from their proximity to these two continental regions (Roncal et al., 2020). Therefore, we might expect Caribbean islands to be more diverse and therefore more resistant to the establishment of introduced species, including those that are potentially invasive (i.e., species spreading rapidly into new areas; terminology follows Blackburn et al., 2011) than more isolated islands in ocean basins.

Humans are the ultimate ecosystem engineers, altering habitats for shelter, provision, and resource acquisition. Via their activities, they often introduce new species to areas they colonize, either intentionally for provision or ornamentation or unintentionally by bringing along parasites or commensals. Thus, isolation is effectively reduced. Studies have shown that in addition to isolation and island area (typical factors of the island biogeography theory), factors such as levels of anthropogenic disturbance, human activities (e.g., economic development, human population size, trade and transportation rates and pathways), and propagule pressure are key drivers explaining the diversity of introduced species and invasion success on islands (e.g., Gallardo et al., 2015). Human-mediated introductions of non-native species to islands may lead not only to increases in the number and distribution of species that may colonize islands but also to the displacement and/or extinction of native species. In this regard, human-related activities may lead to a breakdown of the “classical” biogeographic theory and may “redefine” species diversity on islands (Capinha et al., 2015; Blackburn et al., 2016; Rojas-Sandoval et al., 2020).

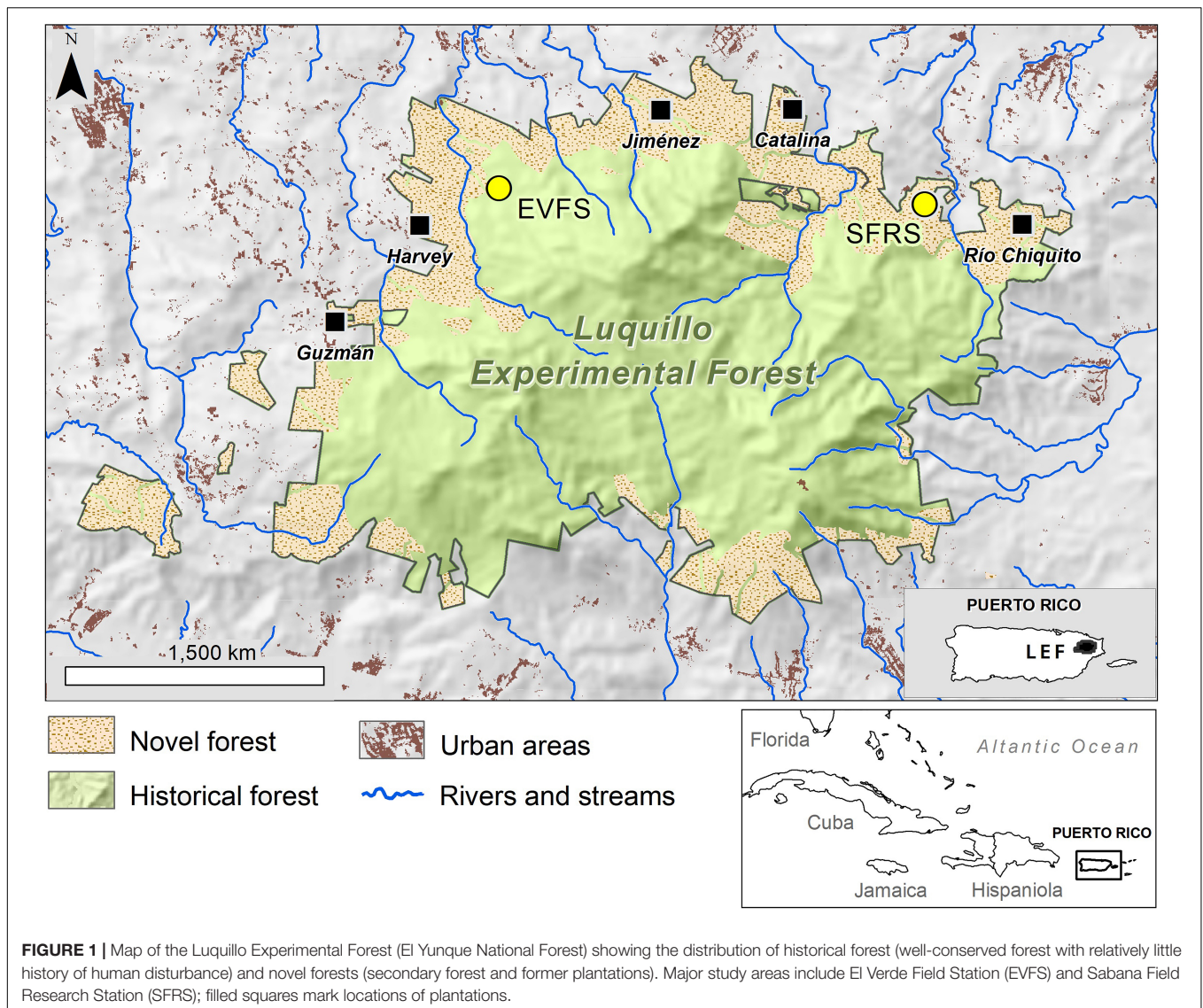
Caribbean islands have a long history of humans intentionally or accidentally introducing non-native species, and a subset of these have become invasive (e.g., Kairo et al., 2003; Reynolds and Niemiller, 2010; Wilson et al., 2011; Borroto-Páez and Mancina, 2017; Rojas-Sandoval et al., 2017; Shiels et al., 2020). Islands within this region have been exposed to pronounced anthropogenic disturbance, which has included ecosystem degradation and natural resource overexploitation, particularly since the beginning of the European colonization (Maunder et al., 2008; Acevedo-Rodríguez and Strong, 2008). These disturbances often facilitated the introduction and establishment of non-native and invasive species (Lugo, 2004; Rojas-Sandoval and Acevedo-Rodríguez, 2015; Rojas-Sandoval et al., 2017, 2020). On the other hand, biodiversity on Caribbean islands is so remarkable that it is considered one of the most important hotspots of diversity in the world (Mittermeier et al., 2004). Elton’s biotic resistance hypothesis proposes that areas of high diversity should be resistant to biological invasions (Elton, 1958). While this may be true at small scales, it is difficult to find evidence for it in larger regional scales (Stohlgren et al., 2003, 2006; Ackerman et al., 2017). Ackerman et al. (2017) evaluated Elton’s theory at different scales using a dataset of plant species in Puerto Rico. They found that there was a strong, positive correlation between invasive and native species richness at large scales (municipality scale), yet the relationship between native and invasive species was weak at local forest scales (forest reserves), suggesting some biotic resistance is present at local forest reserves in Puerto Rico.

The island of Puerto Rico is the smallest of the Greater Antilles, and at the whole-island scale, these dual processes of biotic resistance vs. direct or indirect anthropogenic facilitation of species introductions are present. Occupied first by the indigenous peoples beginning 4,000 years BP, then colonized by the Spanish and eventually annexed by the United States, 95% of the island of Puerto Rico was converted to agriculture, mining, and urban areas (Birdsey and Weaver, 1987). Human activities were absent at the summits of the Luquillo Mountains, and these mountains have remained as the largest forested area on the island (**Figure 1**). Located in the Luquillo Mountains, El Yunque National Forest (EYNF) is currently the largest and the most well-conserved forest area in Puerto Rico. The lower flanks are a mosaic of former human land use, mostly farming and forestry, where forest has recovered naturally or has been partly restored by humans. The summits and higher elevation areas are relatively well-conserved remnants of native forest, away from roads that extend to two of the three dominant peaks.

In this study, we asked the following question: What is the current status of introduced species within El Yunque National Forest (EYNF), the largest and most well-conserved forest area of Puerto Rico? We intended to answer this question by first reviewing the literature on non-native species of vascular plants, invertebrates, and vertebrates that have been deliberately and/or accidentally introduced in EYNF, and then asking local experts to review the species list and identify and provide justification for those species that they considered to be currently behaving as invasive in EYNF. Based on previous studies showing that areas with higher anthropogenic disturbance often provide more opportunities for the introduction and establishment of non-native and invasive species (Lockwood et al., 2009; Blackburn et al., 2016; Dawson et al., 2017; Rojas-Sandoval et al., 2020), we hypothesized that areas within the EYNF with long-standing continuous native forest would have fewer non-native and invasive species than areas subject to high levels of anthropogenic disturbance such as those in the lowlands and areas near roads and other historical land-use sites.

## METHODS

For the purposes of this review, we used the term “introduced” to signify non-native species brought to Puerto Rico intentionally or accidentally via human activities and have already established wild populations. We reserved “invasive” for non-native species that have been shown to spread rapidly and widely and are suspected or shown to have negative ecological or economic effects in the EYNF (Blackburn et al., 2011). Data presented here are based on published literature, museum and herbarium collections, first-hand experience from local and academic experts, and personal field observations. Using all this information, we first compiled a list of all the introduced species occurring within the EYNF including vertebrates, invertebrates, and vascular plants. Then, we identified invasive and potentially invasive species based on the abundance and the risk of causing negative impact on native communities within the EYNF. We found that some groups are better studied (e.g., vascular plants,



earthworms, and vertebrates) than others (e.g., arthropods) and few species have been thoroughly evaluated for their invasiveness (i.e., validated ecological or economic harm). Thus, our conclusions are preliminary in part and, where information is lacking, serve as a guide for future research.

## RESULTS

### Vascular Plants

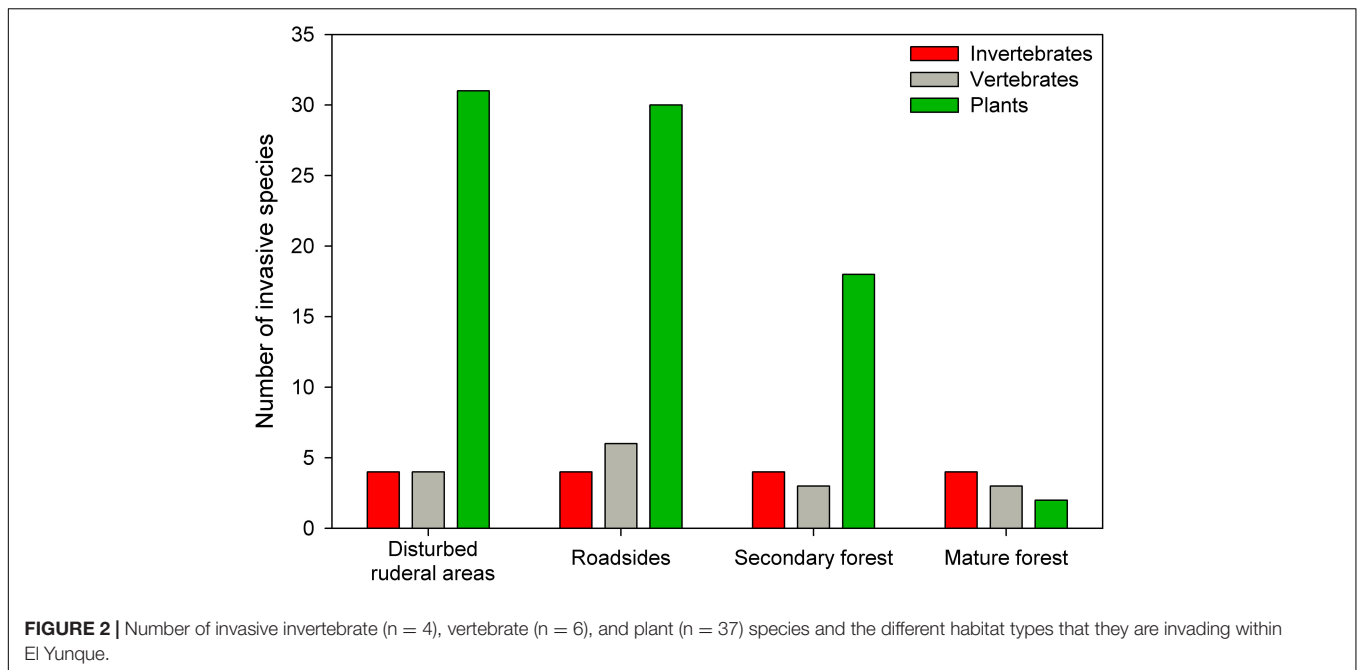
In the EYNF, we identified 168 non-native plant species from 135 genera and 57 families indicating a very heterogeneous group in terms of their taxonomy, life forms, and ecological attributes (**Supplementary Table S1**). About 46% (77 species from the 168 non-native species) are species previously listed as invasive in Puerto Rico (O'Connor et al., 2000; Kairo et al., 2003; Brown et al., 2006; Cohen and Ackerman, 2009; Más and Lugo-Torres, 2013; Ackerman et al., 2014;

Rojas-Sandoval and Acevedo-Rodríguez, 2015; Burman et al., 2017). When considering their invasive status within the EYNF, we identified a total of 37 species (**Table 1**). Most invaders in the EYNF are vines (14 species), herbs (9 species), and grasses (8 species) that are colonizing primarily disturbed areas (e.g., landslides), wastelands, river edges, and roadsides (**Figure 2** and **Table 1**). Only three species of non-native trees (*Schefflera actinophylla*, *Spathodea campanulate*, and *Syzygium jambos*) are regarded as invasive within the EYNF. There are just two plant species regarded as invasive in mature forest, and these included the tree *S. actinophylla* and the orchid *Oeceoclades maculata* (**Figure 2** and **Table 1**). We also found that many of the documented invaders in EYNF are species that were originally intentionally introduced into Puerto Rico as ornamentals (Valdés Pizzini et al., 2011; Areces-Berazain and Rojas-Sandoval, 2017) that have escaped cultivation (e.g., *Calathea lutea*, *Hedychium coronarium*, and *Spathoglottis plicata*). One example of this pathway of introduction is *Selaginella willdenowii*, a



**TABLE 1** | Invasive plant species in El Yunque National Forest, Puerto Rico.

Species	Habitats invaded	Impacts/notes	References
<i>Ardisia elliptica</i>	Roadsides, disturbed areas along trails. Common by El Toro trail, from sea level to 600 + m. Rapidly spreading along Rd-186	Aggressive invader displacing and smothering native vegetation	J.D. Ackerman pers. comm.
<i>Bambusa</i> spp. ( <i>B. vulgaris</i> , <i>B. longispiculata</i> , <i>B. tulda</i> , and <i>B. tuldooides</i> )	Disturbed areas, roadsides, riparian areas	Native vegetation, native stream macro-invertebrate communities	O'Connor et al., 2000; Blundell et al., 2003
<i>Calathea lutea</i>	Roadsides, disturbed areas. Rapidly spreading along Rd-191 and Portal-Sabana Rd	Native vegetation	Rojas-Sandoval, pers. obs.
<i>Cenchrus purpureus</i>	Roadsides, abandoned agricultural fields, lowlands, forest margins, disturbed areas	Native vegetation. Forming dense stands	Olander et al., 1998; Areces-Berazain et al., 2014
<i>Coix lacryma-jobi</i>	Riparian areas	Native riparian vegetation	Areces-Berazain and Rojas-Sandoval, 2017
<i>Dendrocalamus strictus</i>	Disturbed areas, roadsides, riparian areas	Native vegetation, native stream macro-invertebrate communities	O'Connor et al., 2000; Blundell et al., 2003
<i>Dioscorea alata</i>	Disturbed areas, forest margins, secondary forests at lower and middle elevations	Native vegetation	Acevedo-Rodríguez, 2005; EYNF, 2008
<i>Epipremnum pinnatum</i>	Disturbed areas, roadsides, secondary forests climbing on the trunks of trees and getting into the canopy	Native vegetation. Smothering native epiphytes	Acevedo-Rodríguez, 2005; Rojas-Sandoval and Acevedo-Rodríguez, 2015
<i>Hedychium coronarium</i>	Edges of shaded secondary forests, and disturbed areas along trails	Native vegetation. Forming dense stands	EYNF, 2008
<i>Impatiens walleriana</i>	Shaded secondary forest, roadsides	Native vegetation	Torres, 1992
<i>Ipomoea</i> spp. ( <i>I. batatas</i> , <i>I. carnea</i> , <i>I. nil</i> , <i>I. ochracea</i> , <i>I. purpurea</i> , <i>I. quamoclit</i> , and <i>I. tricolor</i> )	Roadsides, waste places, thickets in secondary forests, forest margins, riparian areas	Locally abundant especially after hurricanes. Spreading and smothering native vegetation	Acevedo-Rodríguez, 2005; Ackerman, pers. comm.
<i>Megathyrsus maximus</i>	Roadsides, abandoned agricultural fields, lowlands, forest margins, disturbed areas	Native vegetation. Forming dense stands	Rojas-Sandoval and Acevedo-Rodríguez, 2015
<i>Melinis minutiflora</i>	Roadsides	Native vegetation	Olander et al., 1998
<i>Nephrolepis brownii</i>	Disturbed areas, roadsides, landslides	Native vegetation	Sharpe and Shiels, 2014; Shiels, pers. obs.
<i>Oeceoclades maculata</i>	Penetrates mature forest but is most abundant in areas with moderate levels of past disturbance	Native vegetation	Cohen and Ackerman, 2009
<i>Paspalum fasciculatum</i>	Roadsides, abandoned agricultural fields, lowlands, forest margins, disturbed areas	Native vegetation. Forming dense stands	Areces-Berazain et al., 2014
<i>Pueraria phaseoloides</i>	Disturbed areas, roadsides, forest margins, secondary forests	Spreading rapidly, forming dense colonies that engulf native vegetation	Acevedo-Rodríguez, 2005; EYNF, 2008
<i>Schefflera actinophylla</i>	Disturbed areas, secondary forests, and lowlands. Also invading primary forests	Native vegetation	Rojas-Sandoval and Acevedo-Rodríguez, 2015
<i>Selaginella willdenowii</i>	Roadsides. Very abundant along Rd-186	Spreading and smothering native vegetation	EYNF, 2008; Zimmerman, pers. obs.
<i>Spathoglottis plicata</i>	Roadsides, landslides, disturbed areas	Native vegetation, fungi	Ackerman et al., 2014
<i>Spathodea campanulata</i>	Lowlands, secondary forest	Native vegetation	Thompson et al., 2007
<i>Sphagneticola trilobata</i>	Roadsides, waste areas, landslides	Native vegetation	Shiels, pers. obs.
<i>Syngonium podophyllum</i>	Disturbed areas, roadsides, secondary forests	Form dense colonies that engulf native vegetation	Acevedo-Rodríguez, 2005; Rojas-Sandoval and Acevedo-Rodríguez, 2015
<i>Syzygium jambos</i>	Riparian areas, secondary forests, lowlands	Native vegetation	Brown et al., 2006; Burman et al., 2017
<i>Thunbergia alata</i> and <i>T. fragrans</i>	Roadsides, waste places, secondary forests, forest margins, riparian areas	Spreading rapidly, forming dense colonies that engulf native vegetation and shade-out native vegetation in the understory	Acevedo-Rodríguez, 2005; Rojas-Sandoval and Acevedo-Rodríguez, 2015
<i>Talipariti tillaceum</i>	Roadsides, disturbed areas along trails. Dense thickets near El Toro trail	Native vegetation. Forming dense stands	EYNF, 2008
<i>Tradescantia spathacea</i>	Disturbed areas and roads along the wilderness boundary	Native vegetation	EYNF, 2008



**TABLE 2 |** Top invasive animal species in El Yunque National Forest (EYNF), Puerto Rico.

Species	Common name	Habitats invaded	Impact	References
<b>Terrestrial vertebrates</b>				
<i>Felis catus</i>	House cat	All	Birds, reptiles, invertebrates	Engeman et al., 2006
<i>Herpestes auropunctatus</i>	Mongoose	All	Birds, reptiles, invertebrates	Engeman et al., 2006
<i>Rattus</i>	Black rat	All	Native vegetation birds, reptiles, invertebrates	Shiels et al., 2018, 2019
<i>Mus musculus</i>	House mouse	Roadsides, grassy areas	Native vegetation invertebrates	Shiels et al., 2018
<i>Rhinella marina</i>	Cane toad	Roadsides	Reptiles, invertebrates	Stewart, 1995
<i>Iguana</i>	Green iguana	Roadsides	Native vegetation	Lugo, 2005
<b>Terrestrial invertebrates</b>				
<i>Pontoscolex corethrurus</i>	Amazonian earthworm	All	Invertebrate soil communities, soil dynamics, native vegetation	González et al., 2007
<i>Ocnoderilus occidentalis</i>	Earthworm	All except Palo Colorado forest type	Invertebrate soil communities, soil dynamics, native vegetation	González et al., 2007
<i>Apis mellifera hybrid</i>	Africanized honeybee	All	Native parrots and other cavity nesting birds, humans	Blundell et al., 2003
<i>Aedes aegypti</i>	Yellow fever mosquito	All	Humans	Weinbren and Weinbren, 1970

popular ornamental spikemoss that escaped cultivation and has become one of the most aggressive plant invaders in EYNF (EYNF, 2008), and it can be found forming dense patches along forest margins near El Verde Field Station and elsewhere (Figure 3).

Our survey also revealed a prevalence of invasive vines (14 species) in the EYNF. Seven of the 14 species are morning-glory (*Ipomoea* spp.) that quickly respond to disturbances and have become a serious problem especially after hurricanes (Table 1). They display rapid growth and an ability to outcompete and smother native vegetation (J.D. Ackerman, personal communication). Moreover, vines such as *Epipremnum pinnatum*, *Pueraria phaseoloides*, *Dioscorea alata*, *Thunbergia alata*, and *Thunbergia fragrans* are also locally abundant

across the EYNF and often can be found along roadsides colonizing forest margins.

In the case of grasses, three species were identified as the dominant invaders in the EYNF: *Cenchrus purpureus*, *Megathyrus maximus*, and *Paspalum fasciculatum*. These three invaders are robust perennial C<sub>4</sub> grasses that grow rapidly, colonizing new areas and forming dense monospecific stands that displace native plants and wildlife. Across the EYNF, these grasses are locally abundant in disturbed areas and along roadsides mainly at low and middle elevation, but *C. purpureus* has also been reported invading disturbed areas at upper elevations (Olander et al., 1998).

Comprehensive studies of the distribution of native vs. non-native plants for the EYNF are missing. Rather, perspectives



**FIGURE 3** | *Selaginella willdenowii*: one of the dominant invasive plant species that is rapidly spreading across El Yunque National Forest. This picture corresponds to a heavily invaded area along the PR-Highway 186. Photo: J. Zimmerman.

come from individual studies that focus on research areas or conspicuous species. For example, Thompson et al. (2007) found that 12 agricultural, mostly woody species (e.g., coffee, mango, and breadfruit) occurred within mature forest but exclusively in the northern two-thirds of the 16-ha Luquillo Forest Dynamics Plot. This area was traced to a history of logging and agriculture dating to the 1920s (Thompson et al., 2002). The remaining one-third of the plot located in the southern end had species representative of the native forest and no non-native species. Thus, the distribution of native and non-native plant species appears to be demarcated by the “anthropogenic ecotone.” None of these 12 introduced species were regarded as invasive by Thompson et al. (2007) since none of them were increasing strongly in abundance during the course of the 10-year study. One exception could be *Simarouba amara*, a tree species planted for timber across the Luquillo mountains, which has increased in numbers in areas of less intense land use since hurricane Georges passed through in 1998 (Thompson et al., 2007) and extensively since 2017 after hurricane Maria (Zimmerman, personal observation).

Brown et al. (2006) studied the ecology of *S. jambos* in the Luquillo Mountains with the goal of identifying whether this introduced ornamental was an invasive species. They concluded that where it occurs in areas of secondary forest within 30 m of stream beds, it is invasive and appears to outcompete other species due to its extreme shade tolerance. In their words: “After nearly 185 years since its introduction to the island, *S. jambos* is well-established” and “its presence does not appear limited,” suggesting “a new vegetation assemblage in the regenerating secondary forests in the Luquillo Mountains.” This case deserves further study as *S. jambos* is now the subject of an introduced

pest, the guava rust, which appears to be negatively affecting its naturalized populations in Puerto Rico (Burman et al., 2017).

Another plant group that has been studied within the EYNF are bamboos. The planting of bamboo in this area started in the 1930s and has led to present-day bamboo monocultures in many riparian and roadside areas. Bamboos were originally introduced to stabilize recently constructed roadbeds (O’Connor et al., 2000; Blundell et al., 2003) and now there are about five species recognized as invasive in the EYNF (four species of *Bambusa*, and *Dendrocalamus strictus*; Table 1). Invasive bamboos are spreading along rivers and colonizing areas along roadsides, and they currently occupy about 2% of the forest area (O’Connor et al., 2000).

## Terrestrial Invertebrates

In the EYNF, our survey for introduced arthropods was not as exhaustive as for plants, partly because of the bias of fewer studies and infrequent reporting of non-native arthropods. However, four species are regarded as invasive in this area: the Africanized honeybee (*Apis mellifera* of European origin hybridized with *A. mellifera scutella* of African origin; Rivera-Marchand et al., 2008), the mosquito, *Aedes aegypti*, and two species of introduced earthworms, *Pontoscolex corethrurus* and *Ocnerodrilus occidentalis* (González et al., 2007). We also found that these four invasive species are occurring ubiquitously across all habitat types in EYNF: from well-conserved mature forests to highly disturbed ruderal areas (Figure 2 and Table 2).

In Puerto Rico, Africanized honeybee hybrids were first reported in 1994 (Cox, 1994), which was also the first report of these bee hybrids on an oceanic island. In the EYNF, Africanized honeybee hybrids have occupied 80% of tree cavities and threatened the endangered Puerto Rican Parrot (*Amazona vittata*) and other cavity nesting bird species (Blundell et al., 2003). Although it was several years ago, attacks to field researchers have been reported (Zimmerman, personal observation). As documented elsewhere on the island, the Africanized honeybees eventually evolved gentle behavioral characteristics and have ceased to be a great threat. The one persistent introduced insect in EYNF is the mosquito, *A. aegypti* (Weinbren and Weinbren, 1970). This mosquito, which originated in Africa and can be easily recognized by its white markings on the legs, is known as a vector of dengue fever, chikungunya, and Zika fever, and other human-disease agents. It is likely that *A. aegypti* is not reproducing in the elevations encompassed by EYNF, but instead the adult mosquitos observed within the EYNF could be transported by cars from San Juan and other low-elevation urban areas (Yee, pers. comm.).

González et al. (2007) studied the earthworm communities along the elevational gradient in the Luquillo Mountains, identifying eight different forest types from elfin forest at the summits to mangroves at the coast. Along this gradient, they found three introduced species of earthworms, *P. corethrurus*, *O. occidentalis*, and *Drawida barwelli*, and all of them are regarded as invasive species; however, *D. barwelli* was only found in lower-elevation forest areas located outside EYNF. *P. corethrurus*, a species introduced from Europe, was found in four forest types (i.e., elfin, palm, Colorado, and tabonuco)

in the EYNF, and in one low-elevation forest type outside the EYNF. *O. occidentalis*, which is native to Central and South America (Shen et al., 2015), was found in all but one forest type (Colorado forest) in EYNF and in two additional lower-elevation forest types outside EYNF. These earthworm species are considered invasive because they alter biogeochemical cycling in the soil, which may further influence plant community dynamics (González et al., 2007). Additional invertebrates that may be of concern in the future, especially due to their ephemeral expansion after hurricanes, are non-native slugs and snails (e.g., *Allopeas gracile*; Bloch, unpubl. data). However, such invaders do not appear to be spreading rapidly or causing plant damage like they do on other islands such as Hawaii (e.g., Shiels et al., 2014).

## Vertebrates

Our survey for introduced vertebrates identified a total of six species in the EYNF (Table 2), and all of them are regarded as invasive despite only some species occurring across all habitat types and others are confined to disturbed areas along roadsides and ruderal areas (Figure 2 and Table 2). Out of the six, there are three dominant invasive mammals: black rats (*Rattus rattus*), mongoose (*Herpestes auropunctatus*), and feral cats (*Felis catus*). These three mammal species are widespread through disturbed and undisturbed mature forest (Engeman et al., 2006; Shiels et al., 2018), and each represents a threat to many native species, including the endangered Puerto Rican Parrot (*A. vittata*) (Engeman et al., 2006). In fact, some lethal trapping is regularly performed during the parrot nesting season to reduce local populations of these invasive mammals to mitigate their impact on the population of the endangered parrot (Engeman et al., 2006). Whereas rats and cats are acclaimed climbers, mongooses are not, but apparently, they consume birds that fall from the nest upon first flights (Engeman et al., 2006). Beyond parrots, diet studies of these three invasive mammals reveal their omnivorous behavior, as many species of native birds, reptiles, and invertebrates are susceptible to their consumption. Furthermore, a recent study of the black rat diet demonstrated that several native tree species (e.g., *Guarea guidonia*, *Buchenavia capitata*, and *Tetragastris balsamifera*) are at risk from seed removal and predation by rats in the EYNF (Shiels et al., 2019).

Another very common invasive species in EYNF is the house mouse (*Mus musculus*), which is a frequent invasive rodent of island ecosystems and it often coexists with invasive rats. While mice are typically less problematic for insular biodiversity than rats, their diet suggests that some native herbs and invertebrates are frequently consumed (Shiels et al., 2018). During a survey of small mammals along the elevation gradient of the PR-Highway 191 through EYNF, Shiels et al. (2018) found the presence of invasive black rats (*R. rattus*) at all elevations and habitat types, whereas house mice were also present at most elevations but were restricted to roadside habitats. Therefore, based on distribution and the range of dietary impact, it has been suggested that the black rat is a more damaging rodent in EYNF than the house mouse.

Two species of invasive herpetofauna have been reported in EYNF (Table 2), particularly near roadsides, and these include the cane toad (*Rhinella marina*) and green iguana (*Iguana*

*iguana*). Whereas green iguanas are a relatively recent addition to the invasive fauna of EYNF (Lugo, 2005) and have been rarely observed in EYNF, cane toads have been established much longer and they are frequently seen nocturnally after heavy rains (Stewart, 1995).

For birds, Wunderle and Arendt (2011) provide a list of 99 bird species found in EYNF, including 23 species that breed there. Twelve breeding species are endemic. No introduced bird species are found in the EYNF, even in areas with a history of anthropogenic disturbance. Naturalized species of finches and psittacines are otherwise common on the forest's periphery, mostly in anthropogenic-disturbed habitats (Vázquez Plass and Wunderle, 2013). Similarly, no introduced species of fish are found in streams of the EYNF except anecdotal findings of aquarium species in recreation areas. These non-native species apparently do not survive frequent flood events (Ramírez, pers. comm.). Non-native fish species are found in urban streams in areas nearby the EYNF and increases in their abundances are facilitated by drought events (Ramírez et al., 2018). Domestic dogs (*Canis familiaris*) are occasionally abandoned along lowland roads of EYNF, but they rarely establish and are not spreading to our knowledge.

## DISCUSSION

As the theory of island biogeography predicts, the island of Puerto Rico is relatively poor in species richness compared to mainland tropical areas, with concomitantly reduced biological complexity. For example, among comparable-sized areas (16–25 ha), in a forest dynamics plot (FDP) in Puerto Rico (in wet forest), there are as many as 150 freestanding woody species, while one plot in central Panama has ~300 species and one in Ecuador has > 1,000 species (Condit et al., 2005; Ostertag et al., 2014). Similarly, the food web at El Verde, a field station located within the EYNF, shows a complete absence of large herbivores and predators, low faunal richness compared to the tropical mainland, and an abundance of frogs and lizards (Reagan and Waide, 1996).

Nevertheless, Puerto Rico is much more diverse than other more isolated islands from other regions. For example, the 4-ha FDP in Palamanui, Hawaii has only 15 tree species (Ostertag et al., 2014). Does this roughly 10-fold difference in plant species richness between EYNF and Palamanui impart any resistance to species introductions for EYNF? A widely recognized pattern in island biogeography is the species–isolation relationship (SIR), in which a decrease in the number of native species on oceanic islands will occur with increasing island isolation, linked to lower rates of natural dispersion and colonization on the remotest islands (Wilson and MacArthur, 1967). While the negative SIR has been well-documented for native species, the response of non-native species to geographic isolation is less clear and remains an open question. In this regard, Moser et al. (2018) tested the SIR for a large dataset of native and non-native species on islands worldwide and they found that the number of introduced species increased with island isolation for all taxa studied except for birds, which is a pattern that is opposite to the widely recognized negative SIR for native species.



Moser et al. (2018) argue that this pattern is due to reduced native diversity and greater ecological naiveté of native biota on more remote islands. Furthermore, their analyses removed the influence of factors such as island size, climatic and topographic heterogeneity, and socioeconomic development [using per capita gross domestic product (GDP) as a proxy]. Thus, the expectation is that, all else being equal, the close biogeographic history of Puerto Rico and nearby mainland areas should provide a relative degree of biotic resistance to invasions of new species into the island's biotic communities.

Among the important elements set aside by Moser et al. (2018) was anthropogenic disturbance, which has factored considerably in Puerto Rico, and the Caribbean in general (Kueffer et al., 2010; Rojas-Sandoval et al., 2017, 2020). Puerto Rico currently has one of the highest GDPs in the Caribbean and a high population density (Kueffer et al., 2010; Rojas-Sandoval et al., 2017) relative to many other islands, and its original forest cover was reduced to ~5% (Birdsey and Weaver, 1987), all indicating a high degree of human disturbance. All of this has led to a high rate of introduction and naturalization of non-native and invasive species. For example, Rojas-Sandoval and Acevedo-Rodríguez (2015) found that about 32% of the total flora in Puerto Rico is introduced, a percentage relatively high when compared to other islands in the Greater Antilles such as Cuba (12%), Dominican Republic (18%), and Jamaica (21%). For Puerto Rico and other Caribbean islands, previous studies have shown that successful establishment of non-native plant species is more likely to occur in human-modified habitats than in pristine habitats. On these islands, disturbance and human-related activities seem to be major drivers influencing and facilitating the introduction and establishment of non-native plant species (Kueffer et al., 2010; Rojas-Sandoval and Acevedo-Rodríguez, 2015; Ackerman et al., 2017; Rojas-Sandoval et al., 2017, 2020).

To understand the diversity and richness of invasive species in EYNF, it is necessary to take into account the socioeconomic history of human-modified areas where farmland and logging occurred until the 1930s (e.g., Thompson et al., 2002). Our initial hypothesis was that undisturbed natural areas within EYNF would harbor fewer non-native species and be more resistant to invasion than disturbed areas away from protected areas. The information we garnered in our literature reviews and surveys of experts lends only partial support of this hypothesis. In general, vascular plants seem to hold to the pattern quite well, and a large number of the non-native plant species were more common in disturbed areas with a history of agriculture or other human land use. We found no evidence from managers suggesting that those species are rapidly spreading into better-conserved forest areas (Thompson et al., 2007; EYNF, 2008). On the other hand, the non-native vertebrates and invertebrates currently invading EYNF were not restricted in their distributions, for the most part. For example, introduced earthworms were found in both disturbed and undisturbed forests and at elevations covering all forest types described for EYNF. Similarly, invasive mammals such as black rats, cats, and mongoose roam freely throughout EYNF, and at least, the rats do not appear to be more active or abundant in disturbed habitats such as roads, landslides, riparian areas, or treefall and hurricane gaps relative to the interior mature

forest (Shiels et al., 2018, 2019). Birds and fish were exceptions, with introduced species not found even in areas with long histories of human disturbance. One outcome that is clear from our review is the lack of detailed information on the distribution and abundance of non-native species within EYNF, as well as the concomitant lack of information on ecological or economic impacts of non-native species and their classification as invasive species. One of the caveats of this work is that the information that we were able to obtain was for the most part too coarse in both space and time to fully evaluate our hypothesis.

Few species have been fully studied in EYNF for their invasiveness as we have defined it. Six plant species, *S. jambos* and five bamboos (four *Bambusa* spp. and *D. strictus*), appear to ecologically dominate riparian areas where they were initially planted and are slowly spreading across the area (O'Connor et al., 2000; Brown et al., 2006). Additional plant species such as *S. wildenowii*, *Ipomoea* vines, and the grasses *C. purpureus*, *M. maximus*, and *P. fasciculatum* are behaving as invaders and forming dense patches that outcompete and smother native vegetation, and thus, they have been on the radar of managers (EYNF, 2008). Introduced earthworms are altering soil processes (González et al., 2007) and could potentially influence other ecological processes. Africanized honeybees and *A. aegypti* mosquitos threaten human visitors to EYNF. Introduced black rats are a nuisance and may cause significant harm to native vegetation (Shiels et al., 2019) and birds, while mongooses, rats, and feral cats may prey on critically endangered wildlife (Engeman et al., 2006). In sum, we find some worrisome trends in the effects of invasive species but no strong evidence that the EYNF ecosystem as a whole is challenged by these invaders such that a novel ecosystem will take over.

Our combined results showed that many non-native and invasive species in the EYNF are yet confined to the lowlands and to areas with high levels of anthropogenic disturbance. However, accurate data on their distribution, abundance, and impacts are very limited. Therefore, systematic surveys and detailed studies monitoring non-native and invasive species are needed to draw conclusions on the invasive potential and social, economic, and/or ecological impacts caused by non-native invasive species within this protected area. Considering that EYNF is one of the few (and the most important) remnants of original native forest in Puerto Rico, the potential of significant impacts by invasive species on its unique native biodiversity is high. The control and management of the current and potentially invasive species within EYNF should remain a high priority.

## DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

## AUTHOR CONTRIBUTIONS

JZ initiated the study, provided guidance, wrote much of an initial draft, and finalized the text. JR-S analyzed plant



distribution data and contributed to synthesis and writing. AS synthesized information on animals and contributed to the writing. All authors contributed to the article and approved the submitted version.

## FUNDING

Support provided by the National Science Foundation (DEB-1831952) to the Luquillo Long-term Ecological Research Program, the University of Puerto Rico, and the International Institute of Tropical Forestry, USDA Forest Service.

## ACKNOWLEDGMENTS

We are grateful to the organizers of the conference “Puerto Rico Honey Bee and Evolution of Invasive Species on Islands”

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for their efforts. We thank J. D. Ackerman, M. Caraballo-Ortiz, and A. Lugo for contributing their expert knowledge and unpublished data on the presence, abundance, and impact of invasive plant species in EYNF. Financial support was provided by National Science Foundation grant DEB-1831952 to the University of Puerto Rico. Additional support was provided by the International Institute of Tropical Forestry, USDA Forest Service, USDA National Wildlife Research Center, and the University of Puerto Rico.

## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2021.640121/full#supplementary-material>

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**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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