



An invasive species spread by threatened diurnal lemurs impacts rainforest structure in Madagascar

Camille M. M. DeSisto · Daniel S. Park · Charles C. Davis ·
Veronarindra Ramananjato · Jadelys L. Tonos · Onja H. Razafindratsima

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Abstract Invasive species are a major threat to biodiversity and ecosystem function. Thus, understanding their spread and ecological impacts is critical for management and control. Strawberry guava (*Psidium cattleianum* Sabine) is an aggressive invader across the tropics and has been rapidly spreading throughout the eastern rainforests of Madagascar. However, both the mechanisms of its spread on the island and the consequences of its invasion on native floral and faunal communities remain largely

unexplored. By surveying multiple sites across Madagascar's eastern rainforests, we demonstrate that the introduction of *P. cattleianum* significantly correlates with changes in forest structure—namely tree/shrub size, taxonomic richness, and taxonomic diversity. Further, at a local scale, the presence of *P. cattleianum* was associated with an increase in frugivore species richness; its primary dispersers during our study period were lemurs. Moreover, we identified species-specific effects of lemur gut-passage on the germination of *P. cattleianum* seeds. Finally, microsatellite analysis of *P. cattleianum* from a variety of locations across Madagascar demonstrated three distinct, highly differentiated, genetic population clusters, each with

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C. M. M. DeSisto · D. S. Park (✉) · C. C. Davis
Department of Organismic and Evolutionary Biology,
Harvard University Herbaria, 22 Divinity Ave,
Cambridge, MA 02138, USA
e-mail: danielpark@fas.harvard.edu

O. H. Razafindratsima (✉)
Department of Natural Resource Management, South
Dakota State University, 1390 College Ave, Brookings,
SD 57007, USA
e-mail: onja.razafindratsima@sdstate.edu

V. Ramananjato
Mention Zoologie et Biodiversité Animale, University of
Antananarivo, Faculté des Sciences, BP 906,
101 Antananarivo, Madagascar

J. L. Tonos
Department of Biosciences, Rice University, 6100 Main
St, Houston, TX 77005, USA

high levels of intra-population diversity, suggesting multiple independent introductions of *P. cattleianum* into Madagascar followed by long-distance dispersal. Collectively, these findings illuminate the complex status of strawberry guava invasion in Madagascar, which poses a growing threat to the island's unique flora and yet provides important forage for threatened and charismatic animal species.

Keywords Tropical forests · Community structure · Conservation · Seed dispersal · *Psidium cattleianum* · Madagascar

Introduction

Biological invasions pose extensive threats to ecosystem function and human livelihoods (Dukes and Mooney 1999; Kull et al. 2015). They can disturb the spatial integrity of native species, alter community structure, and decrease taxonomic and functional diversity (Park et al. 2020b; Gurevitch and Padilla 2004; Vila et al. 2011). In the face of globalization, invasive species are becoming increasingly common worldwide (Seebens et al. 2015), such that identifying solutions for their management is crucial. However, the circumstances and impacts of biological invasions vary greatly, hindering conservationists' ability to draw generalizations from one system to another (Vila et al. 2011; Park et al. 2020). Although tropical forests are often considered to be relatively resistant to biological invasions (Rejmánek 1996), invasive species are not uncommon in the tropics and can have severe impacts on native flora and fauna (Huenneke and Vitousek 1990; Park and Razafindratsima 2019). Islands such as Madagascar are particularly vulnerable to biological invasions (Berglund et al. 2008). Invasive plants are of particular concern, as approximately 10% of the island flora are now non-native (Kull et al. 2015). It is therefore essential to investigate the complex impacts of prominent non-native plant species throughout Madagascar.

Among these non-native species, the strawberry guava (*Psidium cattleianum* Sabine; Myrtaceae) is a particularly aggressive invader. Native to Brazil and Northern Uruguay (Invasive Species Compendium 2018), it has spread to every continent except Antarctica and is primarily found in the tropics (GBIF 2019).

P. cattleianum is thought to have been introduced to Madagascar from Brazil in 1806 for food production, and subsequently escaped cultivation (Turk 1997). It has since become one of the most invasive species in Madagascar, threatening the island's eastern rainforests (Brown and Gurevitch 2004). Their fruits contain small (2.5–5 mm) but numerous (up to 18) seeds, which likely aids in *P. cattleianum*'s ability to invade (Morton 1987; Wagner et al. 1999). The proliferation of *P. cattleianum* may pose a major threat to Madagascar's native forest biodiversity and ecosystem functioning. For example, *P. cattleianum* can alter the soil microbiome (Rajaonarimamy et al. 2017), prevent regeneration of native species (Huenneke and Vitousek 1990), and reduce surface water from aquifers (Patel 2012). However, comprehensive studies exploring the consequences of its invasion on native flora and fauna in Madagascar have been lacking. Evaluating the impacts of *P. cattleianum* on community structure, both in terms of species diversity and functional traits, is a critical step in elucidating invasion dynamics on the island, which harbors one of the most endemic and threatened floras in the world (Enquist et al. 2019; Hannah et al. 2020).

Although the spread of *Psidium cattleianum* is poorly understood in Madagascar, both clonal growth via rhizome and animal-mediated seed dispersal have been reported as reproductive strategies of this species in other tropical ecosystems (Huenneke and Vitousek 1990; Shiels 2011; Shiels and Drake 2011). In Madagascar, several species of lemurs and bats, as well as Malagasy cattle (*Bos indicus*), have been observed to consume the fruits and/or defecate the seeds of *P. cattleianum* (Online Resource 1 Table S1). However, the primary mechanisms of dispersal, as well as the effects of gut-passage on seed germination, remain unexplored. Further, there is no information to date regarding the population genetic structure of *P. cattleianum* across the island, limiting our ability to ascertain the dispersal dynamics of this species. Gaining a nuanced understanding of the spread of this aggressive invader requires an integrative approach that examines its seed dispersal ecology and population genetic diversity.

Here, we seek to determine the overall consequences and mechanisms of the spread of *Psidium cattleianum* in Madagascar's eastern rainforests, by investigating (1) how its invasion impacts the structure of both floral and faunal communities, (2) its potential

seed-dispersal agents and their impacts on seed germination, and (3) the genetic structure of its populations throughout Madagascar. We predict that *P. cattleianum* invasion will negatively impact floral communities, as has been observed elsewhere, but benefit fauna since its consumption by various native animals has been noted in Madagascar. We also expect that its animal seed-dispersers would facilitate seed germination because the passage of seeds through the gut of animals can have beneficial impacts on seed germination, especially for the lemurs and birds in this system (Razafindratsima 2014). Finally, we predict a wide genetic diversity of *P. cattleianum* populations throughout Madagascar because of the high diversity of probable dispersal vectors. Combining an empirical understanding of frugivore-mediated dispersal with analysis of population genetics, we provide a comprehensive picture of biological invasions in one of the most biodiverse regions in the world.

Methods

Study sites This study was mainly conducted in the montane evergreen rainforest of Ranomafana National Park (RNP), focusing on four select field sites, two invaded (Sahamalaotra and Sakaroa) and two uninvaded (Valohoaka and Vatoharanana) (Online Resource 1 Appendix 1 and Fig S1). We also collected data in eight additional sites along Madagascar's eastern rainforest biomes, from North to South: Betampona Special Reserve, Ivoloina Zoological Park, Complex Torotorofotsy-Ihofa, Mantadia National Park, Analamazaotra Special Reserve, Maromizaha Forest Station, Kianjavato Classified Forest, and the Littoral Forest of Sainte Luce (Online Resource 1 Appendix 1 and Fig S1). Data from these additional sites were used to gain a more in-depth understanding of the potential consequences of *Psidium cattleianum* on floral communities and to investigate the genetic patterns of its spread throughout Madagascar.

Plant surveys and traits To assess the impact of invasion in Ranomafana National Park, we conducted botanical surveys in two 1-ha plots in Sahamalaotra and Sakaroa. Each plot was divided evenly into 100 subplots (10 × 10 m), for a total of 200 subplots with varying degrees of *Psidium cattleianum* invasion (hereafter “degree of invasion”). In each plot, we

identified the vernacular names of each tree of > 1 cm in diameter at breast height (DBH, at 1.30 m from the ground) and shrub of > 1 cm in diameter at root collar (DRC) in the plots, with the help of local technicians familiar with the flora (for a total of 16,981 individual trees and shrubs surveyed). We then referred to various literature sources for the scientific names (Razafindratsima et al. 2014, 2017, 2018; Dunham et al. 2018; Razafindratsima and Dunham 2019; Razafindratsima unpublished data). We used the Missouri Botanical Garden's online plant database Tropicos (<https://www.tropicos.org/>) and Plants of the World online (<http://www.plantsoftheworldonline.org/>) to verify taxonomic accuracy and to identify the origin and endemic status of these species. For each plant species, we acquired data on wood density from the literature (Zanne et al. 2009; Chave et al. 2009; Razafindratsima et al. 2017, 2018; Razafindratsima unpublished data). When wood density data was unavailable at the species level, we averaged the available data from other species in the same genus (11.49% of species), or family (5.41% of species) (Lewis et al. 2013; Slik et al. 2013; Razafindratsima et al. 2018). We estimated aboveground biomass using two different allometric equations developed for moist forests by Chave et al. (2009): one considers both diameter and height, and another considers only height.

To gain further insights into the invasion of *Psidium cattleianum* throughout Madagascar, we also conducted similar botanical surveys at eight sites in at least 20 (10 invaded, 10 uninvaded) arbitrarily located plots of 5 m by 5 m, for a total of 174 plots (87 invaded, 87 uninvaded). In each site, the plots were selected along transects in the two habitats (invaded and uninvaded), with each plot located approximately 100 m from the next. We have surveyed a total of 9204 individual trees and shrubs in these sites. Similar to the case of RNP, scientific names corresponding to the vernacular names of the species from these sites were obtained from the literature (Schatz 2001; Phillipson et al. 2010; Schmidt et al. 2010; Razafindratsima unpublished data; Armstrong unpublished data).

We used linear mixed models to examine how *Psidium cattleianum* invasion affects forest diversity and structure. Dependent variables included: taxonomic richness (*i.e.*, number of species, genera, and families present), Shannon diversity index (Shannon

1948; Spellerberg and Fedor 2003), mean DBH, mean height, aboveground biomass, and their standard effect sizes, which were assessed for all taxa in each plot as well as native and non-native taxa separately. Standard effect sizes (SES) represent how much the observed values deviate from random expectations calculated across a null distribution of 1000 random assemblages of individual trees drawn without replacement from the species pool all surveyed taxa at each field site ($M_{obs} - M_{random} / sd(M_{random})$). Random communities comprised the same number of individuals as each plot. A positive SES indicates greater than random values, whereas a negative SES indicates values lower than expected by random chance. The degree of invasion (*i.e.*, the proportion of *P. cattleianum* individuals in each plot) was used as the dependent variable and sampling site as a random effect. We also repeated these analyses using the presence of *P. cattleianum* as the dependent variable (*i.e.*, “invaded” vs. “non-invaded”) and sampling site as a random factor. To account for the spatial autocorrelation between surveyed plots, we incorporated an exponential correlation structure, which was determined to best describe our data. Analyses were conducted in R 3.5.1 (R Core Team 2019) with the package *nlme* (Pinheiro et al. 2017).

Animal surveys To analyze the impacts of *Psidium cattleianum* on the vertebrate faunal community in RNP, we compared animal communities in invaded and uninvaded sites. We conducted surveys along line transects of ~ 383 m within four 1-ha plots in the invaded sites of Sahamalaotra (13 days) and Sakaroa (24 days) as well as in the uninvaded sites of Valohoaka (14 days) and Vatoharanana (11 days). These surveys took place four times per day for 62 non-continuous days (~ 380 km walked over the study period). During the dry season (May–July; 32 survey days), we conducted these surveys at 07:00, 10:00, 14:30, and 19:00, whereas in the wet season (February–April; 30 survey days), we delayed the surveys for about 30 min, except the first (7:00), to accommodate variable peaks in animal activity during different seasons. We did not conduct transect surveys in heavy rain conditions due to severely decreased visibility and animal activity. During each survey, we walked along a transect for approximately 1 h (depending on the number of animals observed) and recorded the presence, identity, and behavior of all visually detected animals. Each day, we switched

between two different directions of the transect so that each part of the transect is observed at different times of the day. For each identified species, we assigned its trophic category as frugivorous or not, based on the literature (Razafindratsima et al. 2018). Using these data, we fit linear mixed-effects models with the R-package *lme4* (Bates et al. 2015) to assess how *P. cattleianum* invasion affects the species richness of the animal community. We applied this analysis on the mean species richness per day and treated the habitat type (“invaded” vs. “non-invaded”) as a fixed effect and site as a random effect.

Examination of reproductive structure To descriptively assess the reproductive strategy of *Psidium cattleianum*, we randomly selected 42 guava trees in RNP and dug up the roots of all saplings within a 1 m radius of each tree (n = 427 saplings). True saplings were distinguished by their branched root systems, whereas clones were attached to horizontal roots or rhizomes by unbranched connections (Huenneke and Vitousek 1990).

Identification of seed dispersers To identify the potential vertebrate seed dispersal vectors of *Psidium cattleianum* in RNP, we conducted direct observations of clusters of fruiting trees and animal tracking in Sahamalaotra (June–July 2017) and Sakaroa (March–April 2018 and Jun 2018), from 07:00 to 16:00 and from 19:00–22:00. We also deployed two camera traps (Abask Trail Surveillance Waterproof Digital Camera) in both sites in front of *P. cattleianum* clusters for 58 days (24 h per day) to record any animal visitors. During each observation, we recorded all frugivore-guava interactions, defined as the consumption of *P. cattleianum* fruit(s) by any frugivore at one individual tree for continuous time (455 interactions observed in total). We then recorded the time and duration of the feeding event, as well as the animal species. We followed diurnal lemur visitors until they defecated and collected fecal samples in small paper envelopes. When multiple individuals were consuming fruits simultaneously, we randomly chose one focal animal to follow. We did not follow nocturnal species, birds, or rodents because of logistical constraints in tracking them. All diurnal lemur species in this area are well-habituated to the presence of researchers because of long-term behavioral research in the area (Wright et al. 2012), making the follows possible.

Seed germination experiments We extracted *Psidium cattleianum* seeds from the collected feces

for germination experiments (491 seeds in total). We also extracted seeds from both ripe and unripe fresh fruits of *P. cattleianum* to use as control (139 seeds in total). We placed the seeds on filter paper (SEOH, Texas USA) wet with 2 mL distilled water, in Petri dishes with no more than 10 seeds per dish (Online Resource 1 Fig S2). We stored the Petri dishes together in opaque boxes in field conditions. We monitored the experiment every week for three months; during each monitoring, we added 2 mL of distilled water to maintain humidity and recorded the germination of each seed.

We used linear mixed-effects models to determine the effects of lemur gut-passage on seed germination rate using the R-package *lme4* (Bates et al. 2015). We considered seed treatment (defecated vs. control) as the dependent variable and treated lemur species and site as random effects. We then conducted simple linear regressions to assess the effect of gut-passage on seed germination rate for each of the three diurnal lemur species observed dispersing *Psidium cattleianum* (*Eulemur rubriventer*, *Eulemur rufifrons*, and *Varecia variegata editorum*). These lemur species are categorized, respectively, as Vulnerable, Near Threatened, and Critically Endangered, according to IUCN (Andriaholinirina et al. 2014a, b, c), and play an important role as seed dispersers of the diverse plant community in RNP (Razafindratsima and Dunham 2015, 2016).

Population genetic analysis We collected leaf samples from *Psidium cattleianum* plants across 11 sites throughout Madagascar's eastern rainforests (Online Resource 1 Fig S1) for population genetic assessment. In each site, we collected five leaves per tree from 10 individual trees, which were at least 100 m away from each other. The leaves were stored in paper envelopes, which were dried in silica gel. We exported these samples to Harvard University Herbaria (Cambridge, MA, USA) where we conducted all genetic analyses. We also sampled *P. cattleianum* leaves from six herbarium specimens from Harvard University Herbarium collections (non-native New World population) and 13 samples of *P. cattleianum* from the New York Botanical Garden (NYBG; native, Brazilian population) for comparison (Online Resource 1 Table S2).

We extracted DNA from these samples following a modified protocol using custom Promega Maxwell Purification kits. To identify population structure, we

investigated variation in microsatellite loci among different populations (Abdelkrim et al. 2005; Barkman et al. 2017). We tested 22 non-fluorescent primer pairs for microsatellite loci, previously developed for *Psidium guajava*, some of which had been tested on *P. cattleianum* (Risterucci et al. 2005; Kherwar et al. 2018). Successful primer pairs were used to amplify and sequence five microsatellite loci. See Online Resource 1 Appendix 2 for detailed methods.

Results

Impacts of *Psidium cattleianum* invasion on plant community structure

Out of the 151 tree species surveyed in the RNP plots, there were 126 native species (104 of which are endemic to Madagascar). Among all taxa and when only considering native species, we found that increasing invasion had a significantly negative effect on plant diameter (Fig. 1, Online Resource 1 Table S4) and a positive effect on plant height (Fig. 1, Online Resource 1 Table S4). Trees and shrubs within invaded subplots were associated with a significant increase in the diameter of all plants, but not among just native plants, compared to uninvaded sections (Fig. 2; Online Resource 1 Table S4). The mere presence of *Psidium cattleianum* did not have a significant effect on height (Fig. 2; Online Resource 1 Table S4).

Overall, the degree of invasion had a negative effect on taxonomic richness (Fig. 3, Online Resource 1 Table S4). The degree of invasion tended to have a significantly negative effect on the entire plant community (Fig. 3, Online Resource 1 Table S4). On the other hand, both the degree of invasion and the presence of invasion had a negative effect on the native plants (Fig. 3, Online Resource 1 Table S4).

Among the total plant community in RNP and when just considering native plants, the degree of invasion had on average a negative effect on species and genus diversity (H) (Fig. 4, Online Resource 1 Table S4). However, the Shannon diversity index (H) between invaded and uninvaded plots did not differ from random expectations (Online Resource 1 Table S4). When non-native plants were excluded from the analyses, only the presence of *Psidium cattleianum*

Fig. 1 Mean standard effect sizes (SES) of plant trait values mean height, per section/plot compared to the degree of invasion in RNP— **a** mean DBH, **b** DBH standard deviation, **c** mean height, **d** height standard deviation. Orange triangles represent all plants and blue circles represent only native plants

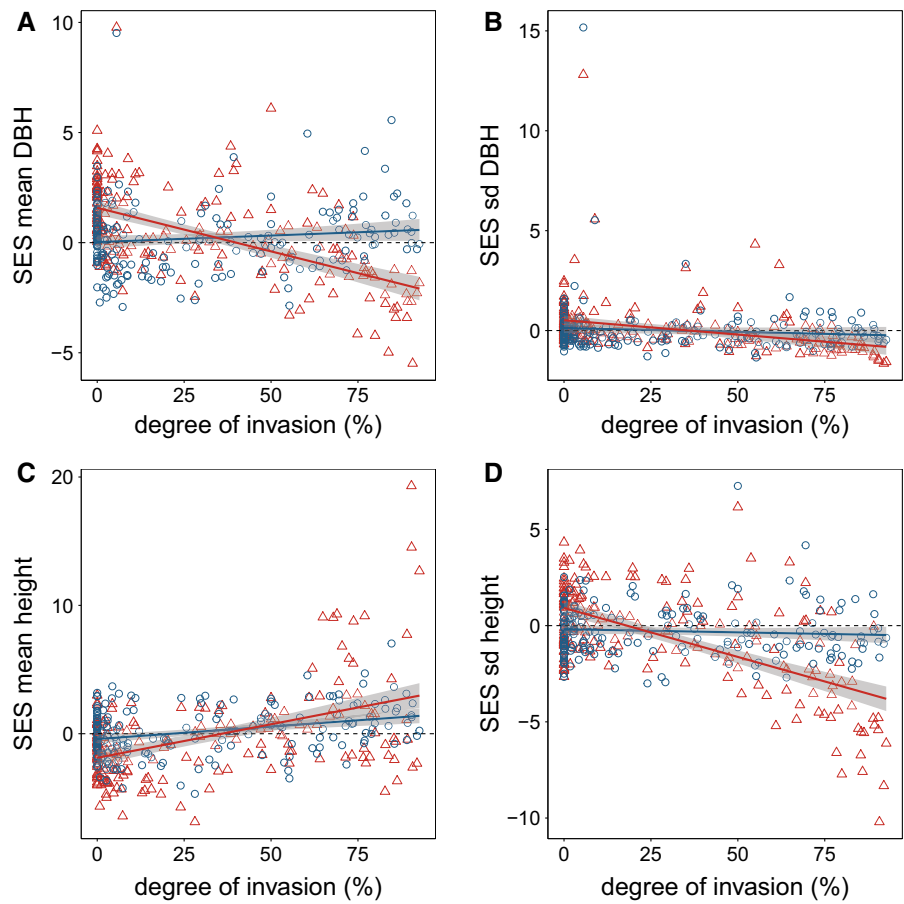
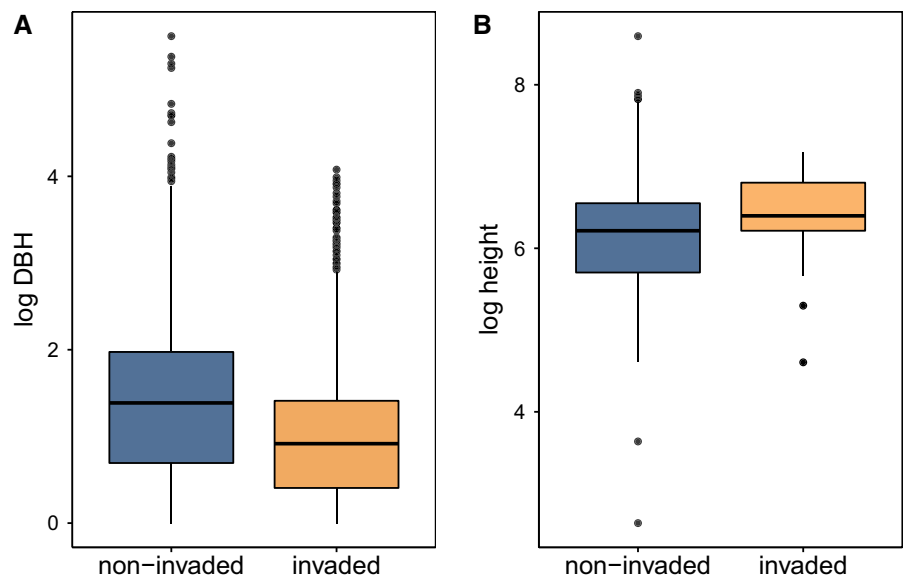


Fig. 2 Mean SES of plant **a** log DBH and **b** log height per section/plot in RNP. Tan boxes represent *P. cattleanum* plants whereas blue boxes represent non-*P. cattleanum* native plants



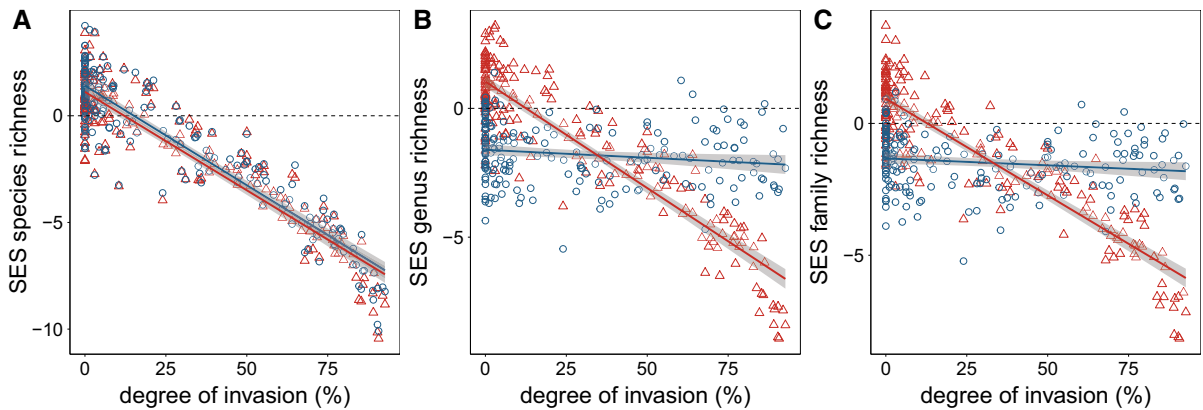


Fig. 3 Mean SES of plant taxonomic richness per section/plot compared to the degree of invasion in RNP—**a** species richness, **b** genus richness, **c** family richness. Orange triangles represent all plants and blue circles represent only native plants

invasion also had negative effects on H at the genus level (Fig. 4, Online Resource 3 Table S4).

The degree of invasion had a negative effect on aboveground biomass, whereas the mere presence of *Psidium cattleianum* did not have a significant effect (Online Resource 1 Table S4). When non-native plants were excluded from the analysis, there was no significant effect (Online Resource 1 Table S4).

Similar patterns are also observed for the impacts of *Psidium cattleianum* invasion on plant community structure throughout eastern Madagascar, except the impacts on aboveground biomass, which we did not investigate at a larger scale (Online Resource 1 Appendix 3 and Online Resource 1 Table S4).

Impacts of *Psidium cattleianum* invasion on animal species richness

We recorded 52 vertebrate species in the four selected field sites in RNP (Online Resource 1 Table S5). We did not find a significant difference in total animal species richness between the invaded and uninvaded habitats ($t = 0.395$, $p = 0.694$, Online Resource 1 Fig S7A). There were more lemur species but fewer bird species in invaded areas (Online Resource 1 Fig S7A); however, these patterns were not statistically significant ($t = 3.207$, $p = 0.081$; and $t = -0.915$, $p = 0.452$ respectively). We also did not find a significant difference in the species richness of the other animal types between invaded and uninvaded sites (Online Resource 1 Table S6), and these species made up only a small proportion of the total species richness (Online Resource 1 Fig S7B). However, we

found significantly higher frugivore species richness in invaded compared to uninvaded habitats ($t = 2.730$, $p < 0.001$, Online Resource 1 Fig S7B).

Reproductive strategy and seed dispersal of *Psidium cattleianum*

Psidium cattleianum reproduced both clonally and by seed set in RNP. Of the 472 saplings examined, 427 were clones whereas 45 were true saplings. Based on our direct observations and camera traps, three diurnal lemur species (*Eulemur rubriventer*, *E. rufifrons*, and *Varecia variegata editorum*) were observed regularly feeding on both ripe and unripe fruits of *P. cattleianum*, swallowing the small seeds within the fruit, and therefore potentially dispersing them. There were observations of two forest rats (*Nesomys* spp.) feeding off *P. cattleianum* fruits from the forest floor. Additionally, we observed one nocturnal lemur (*Microcebus rufus*), and four species of birds (*Zosterops maderaspatanus*, *Philepitta castanea*, *Phyllastrephus cinereiceps*, *Hypsipetes madagascariensis*) consuming *P. cattleianum* fruits during our study. However, contrary to our expectations, the birds were only observed to feed on the pulp of the fruit but not the seeds. The diurnal lemurs fed on *P. cattleianum* fruits for an average of 95.58 ± 0.048 s (*E. rubriventer*: 107.46 ± 0.058 s; *E. rufifrons*: 91.13 ± 0.042 s; *V. v. editorum*: 78.27 ± 0.032 s) before moving onto another tree, either to continue feeding or to engage in other activities (grooming, sleeping, etc.).

We found a positive but not statistically significant effect of lemur gut-passage on the germination success

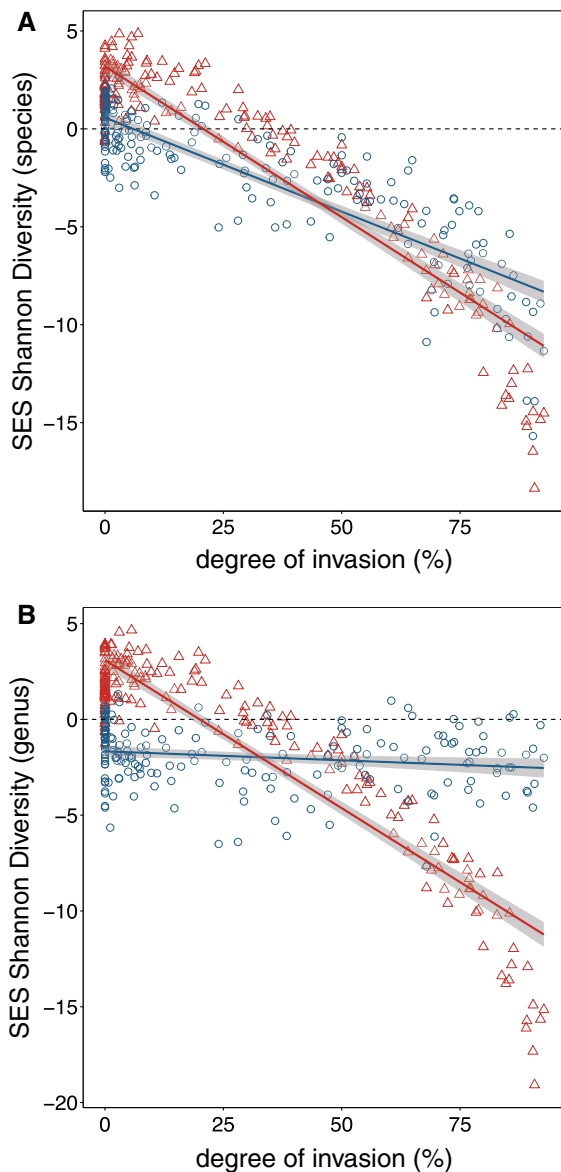


Fig. 4 Mean SES of plant diversity (H , according to Shannon's Diversity Index) per section/plot compared to the degree of invasion in RNP—**a** species diversity, **b** genus diversity. Orange triangles represent all plants and blue circles represent only native plants

of the *Psidium cattleianum* seeds compared to that of control seeds ($t = -0.091$, $p = 0.937$, Fig. 5). However, the seeds dispersed by *E. rubriventer* had a significantly lower germination success rate than control seeds ($t = -2.199$, $p = 0.0332$; Fig. 5). Germination rates of seeds dispersed by *E. rufifrons* ($t = 1.007$, $p = 0.327$, Fig. 5) and *V. v. editorum*

($t = 1.229$, $p = 0.238$, Fig. 5) were higher, but not significantly so.

Population genetic structure

Four distinct, inferred population clusters represented the pool of all sampled *Psidium cattleianum* individuals, and the 13 populations were statistically represented by three of these clusters (determined by which clusters best represented the highest percentage of individuals within a given population; Fig. 6, Online Resource 1 Table S7). Heterozygosity was high between individuals in the same cluster for all four of the inferred clusters ($H_{EA} = 0.8482$, $H_{EB} = 0.8650$, $H_{EC} = 0.9055$, $H_{ED} = 0.7233$). Additionally, there was low allele frequency divergence within all population clusters (Online Resource 1 Table S8).

Discussion

Our study documents three important findings about the spread of the invasive species *Psidium cattleianum* in Madagascar's eastern rainforests. First, we demonstrate that this invasion was associated with significant changes in both floral and faunal community structure. Second, *P. cattleianum* spreads both via vegetative reproduction and animal-mediated seed dispersal. In the case of the latter, endemic, frugivorous lemurs likely play a role. Third, microsatellite analysis of this species shows three distinct, highly differentiated, genetic population clusters, each with high levels of intra-population diversity. This raises the distinct possibility that *P. cattleianum* in Madagascar arose via multiple invasions. Collectively, these findings highlight the threat *P. cattleianum* represents to Madagascar's forest ecosystems, as well as the complexity of its introduction and spread.

Psidium cattleianum alters floral and faunal community structure

The invasion of *Psidium cattleianum* affected various aspects of plant community structure in the rainforests of Madagascar. However, these effects varied across the surveyed plots. *P. cattleianum* had a negative effect on the taxonomic richness and diversity (H) of the flora. As in other invaded areas in the tropics

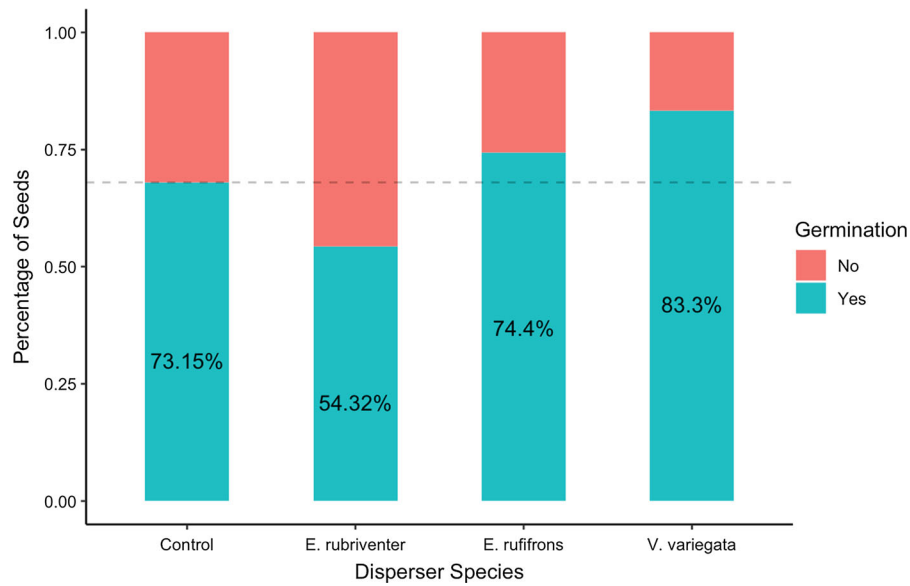


Fig. 5 Germination success rate of *P. cattleianum* seeds that have traveled through the gut of distinct lemur species compared to control seeds. The dashed line represents the germination success rate of the control seeds

(Huenneke and Vitousek 1990) and elsewhere (Elton 1958), *P. cattleianum* forms dense stands in the rainforests of Madagascar, which appear to be strongly associated with declines in the percentage and abundance of native and endemic trees. It is important to note that many of these stands were previously logged (Brown and Gurevitch 2004) and that this disturbance additionally played a role in shaping the tree community. In addition, the positive correlation between the degree of invasion and the height of the trees that were not *P. cattleianum*, in RNP suggest that the typically small *P. cattleianum* trees (mean height = 5.87 m and mean DBH/DRC = 3.6 cm in our plots) are possibly displacing other small understory trees via competitive exclusion (Hardin 1960). Plants tended to be taller in invaded areas at a local scale, while shorter trees and shrubs prevail at a larger scale. This suggests that *P. cattleianum* invasion reduces species richness by outcompeting, and replacing, other plant species of similar size locally, similar to what has been observed in other systems (Olden and Poff 2003; Asner et al. 2008). Increased percentage of *P. cattleianum* invasion had a significant negative effect on taxonomic diversity at the local scale, but non-significant negative effects at larger scales (Online Resource Appendix 3). This is especially alarming since the loss of endemic plant species is a major conservation concern in Madagascar (Goodman and Benstead 2005; Allnutt

et al. 2008). Although the degree of invasion had a negative effect on aboveground biomass, it is important to note that our study did not consider understory vegetation or belowground biomass, despite their potentially significant role as carbon sinks in forests (Asner et al. 2008; Martin et al. 2017).

The presence of *Psidium cattleianum* did not seem to be associated with changes in overall vertebrate species richness; however, there were significantly more frugivore species in invaded areas, which may facilitate its seed dispersal. Further comparative studies across more sites, throughout the entire year, and with similar faunal communities, however, are required to clarify the impacts of *P. cattleianum* on faunal communities. Our results demonstrate that *P. cattleianum* plays an important role in providing forage for lemurs in this altered landscape, a result that is consistent with patterns reported in other systems (Date et al. 1996; Graves and Shapiro 2003). The fruits of *P. cattleianum* contain various chemicals, including aliphatic esters and terpenic compounds (Pino et al. 2001), which create a distinct flavor profile that may increase their attractiveness to frugivores compared to other native fruit options. Lemurs may also favor foraging on this species because of the comparatively low nitrogen and protein availability in Malagasy fruits (Donati et al. 2017). In addition to providing lemurs with food sources, exotic and invasive plant

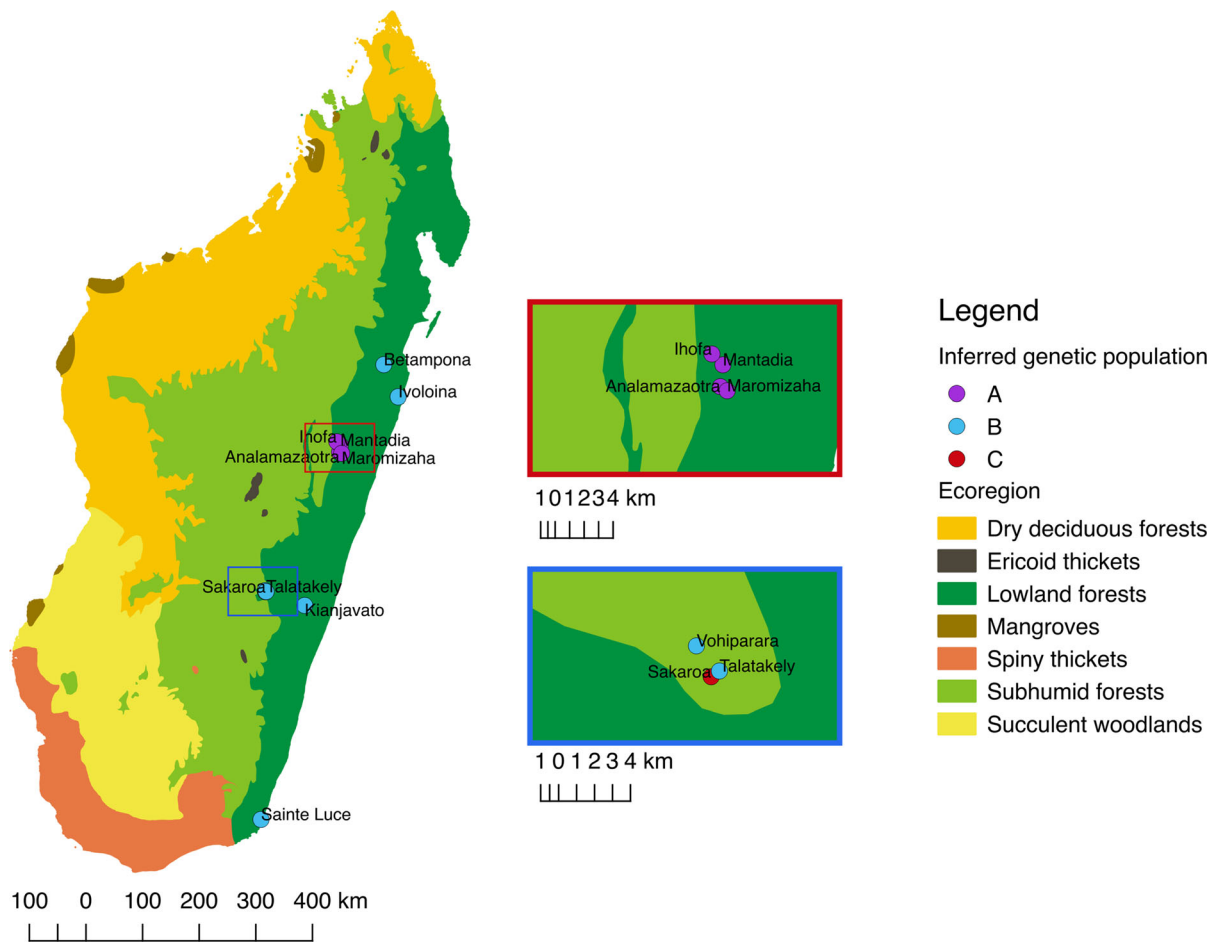


Fig. 6 Inferred genetic clusters of the given *P. cattleianum* populations in Madagascar. Purple dots represent cluster A, blue dots represent cluster B, and red dots represent cluster C. The map is colored according to the WWF ecoregion of the country (Olson et al. 2001)

species in Madagascar, including agricultural crops and plantations, are known to provide them with key structural habitats (Ganzhorn 1987; Ganzhorn et al. 1997; Eppley et al. 2015; Hending et al. 2018; Webber et al. 2019). On the other hand, the lower species richness of birds in invaded areas, though non-significant, could be explained by the fact that birds in these invaded areas did not appear to be attracted to *P. cattleianum* fruit; they were seldom observed consuming guavas (DeSisto, personal observation). This was unexpected since birds are known to feed on *P. cattleianum* in Hawaii and Mauritius (LaRosa et al. 1985, Linnebjerg et al. 2010).

Psidium cattleianum spreads vegetatively and by lemur-mediated dispersal

Various traits likely facilitate the successful invasion of *Psidium cattleianum* in Madagascar's dense rainforests. For example, *P. cattleianum* is shade-tolerant and can reproduce both vegetatively and by seed (Huenneke and Vitousek 1990; Pattison et al. 1998). Clonal growth can facilitate the rapid spread of invasive plants (Dong et al. 2006). Despite the low percentage (9.5%) of true saplings we observed, non-vegetative reproduction is critical for preventing density or distance-dependent seedling mortality, hereby encouraging the establishment of new populations in favorable microhabitats (Wenny 2001), and maintaining genetic diversity (Dong et al. 2006). *P.*

cattleianum also has a high growth rate along with high initial germinability and short dormancy, which likely contribute to its invasion success (Rejmánek and Richardson 1996; Pattison et al. 1998). Overall, we observed no significant negative effects of lemur gut passage on *P. cattleianum* seed germination. This establishes that the lemur species we examined can indeed serve as dispersal vectors and facilitate the spread of this species. However, variation in germination success between seeds defecated by different lemur species suggests that they may influence the species' spread to different degrees. Since the seeds dispersed by *E. rubriventer* had a lower germination success than the control seeds, this lemur species could restrict the spread of *P. cattleianum*, whereas the higher germination success of those dispersed by *E. rufifrons* and *Varecia variegata* suggest that these species may be facilitating the survival, and possible spread, of *P. cattleianum*. A nocturnal lemur species, *Microcebus rufus*, has also been found to have similar impacts as *E. rubriventer* on the germination of *P. cattleianum* (Ramananjato et al. 2020). More studies are needed to conclusively determine the mechanisms and role of native animals in the invasion process. Other primate dispersers, including bats, birds, and secondary dispersers, such as rodents, could also be contributing to the spread and genetic diversity of strawberry guava throughout Madagascar (Online Resource 1 Table S1).

Along these lines, we observed high genetic isolation between populations of *Psidium cattleianum*, evidenced by high levels of intrapopulation diversity, genetic differentiation between *P. cattleianum* genetic clusters, and low allele frequency divergence. This suggests strong divergence patterns and/or high migration rates of *P. cattleianum* in Madagascar (Allendorf and Phelps 1981), potentially mediated by animal dispersal. The three distinct genetic populations of *P. cattleianum* throughout eastern Madagascar we observed displayed high intrapopulation variation. However, such high heterozygosity within the clusters is unexpected given the clonal nature of *P. cattleianum*. Multiple distinct introductions of *P. cattleianum* into Madagascar are most likely to explain these findings given the consistently low allele frequency divergence observed between populations. In general, populations within close geographical proximity were within the same inferred genetic clusters. The large genetic differences between

Sahamalaotra/Talatakely and Sakaroa (within RNP) suggest that there may have been multiple introductions of *P. cattleianum* in RNP, specifically. Moreover, in some cases, populations in widely separated geographic locations are also within the same inferred population clusters, suggesting the presence of long-distance dispersal. Though animal-mediated long-distance dispersal may have contributed to the spread of *P. cattleianum*, we cannot rule out the role of human activity in the establishment of genetically similar populations in different geographic areas throughout the country (Sakai et al. 2001), especially since Malagasy people occasionally use this plant for food and construction materials (Novy 1997; Carrière et al. 2008; Razafimanantsoa et al. 2012; Riondato et al. 2019). A broader sampling of both the native and invaded ranges, and the examination of additional microsatellite loci, may further elucidate the origin and spread of *P. cattleianum* in Madagascar.

Conclusions and applications

Our findings highlight the ecological complexity of biological invasions and the importance of planning adaptive management approaches to preserve biodiversity. Despite the negative consequences that *Psidium cattleianum* likely poses to Madagascar's unique biodiversity, its management is complex owing to the potential benefits it provides to humans and other animal species (Novy 1997; Gérard et al. 2015; Riondato et al. 2019). As we demonstrate, *P. cattleianum* provides a food resource for threatened lemurs suggesting that there may be unforeseen consequences associated with the removal of this invasive species on native animal communities (Bergstrom et al. 2009), especially where invasive species have supplanted the functional role of native species (Zavaleta et al. 2001). Additionally, exotic and invasive species can also provide structural habitats that allow animals to disperse between native forests, in addition to providing food resources (Eppley et al. 2015; Webber et al. 2019). Thus, *P. cattleianum* management must consider both its removal and the replacement of its functional role in these communities. Further research examining the predicted spread and impacts of invasion (including both costs and benefits) is required for effective management and control of the species.

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