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60 credits

Effects of Alien Plant Species Removal on Biodiversity and Species Interactions in Two Native Forest Areas on Mauritius.

Effekter av fjerning av fremmede plantearter på biodiversitet og artsinteraksjoner i to innfødte skogområder på Mauritius.

Pauline Johanne Kajl

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With this thesis I would like to express my concern for all animals and the environment.

Ås, August 2015

Pauline Johanne Kajl

Abstract

Mauritius Island is one of the world's most severely ecologically damaged nations, with less than 5% of the original forests remaining as fragments. Yet, it sustains one of the highest tree diversities of all isolated oceanic islands. The most severe threat to Mauritius' remaining threatened flora is exotic species invasions. Weeding of invasive species in native forests have been conducted in Conservation Management Areas on the island over the past decades, to help restore and conserve the remaining native flora and fauna. This study investigates the effects of these restoration measures on biodiversity and species interactions, by comparing weeded and non-weeded forest areas. For this, I used butterfly censuses, as butterflies are known indicators of overall biodiversity, and I used predation of artificial caterpillars and herbivory of native plants under the assumption that this will reflect forest functionality and health. I found that weeding presented a significant positive effect on native butterfly diversity. In addition, predation on artificial caterpillars was higher in weeded areas. At least for birds, this predation appeared to be performed by native species. The herbivory rate and herbivore diversity were not different between weeded and non-weeded forest areas, but this may be explained by higher herbivore predation in weeded forest and a limitation of food resources in non-weeded forest. In conclusion, the results of this study suggest that weeded forests portray a more species rich and functional ecosystems than non-weeded forest areas. Results therefore show that the remaining native forests of Mauritius may, to a large degree, recover and increase in native biodiversity after restoration measures where exotic invasives are removed.

Abstakt

Mauritius er en av verdens økologisk mest påvirkede nasjoner hvor mindre enn 5% av skogens originale omfang er gjenværende i form av fragmenter. Likevel har Mauritius en av de høyeste diversitetene av trær av alle isolerte øyer i havet. Den mest alvorlige trusselen mot Mauritius' gjenværende og truede flora er invaderende, eksotiske arter. Restaurering i form av fjerning av invaderende arter i innfødt skog har blitt utført i små områder satt av til bevaring (Conservation Management Areas) over de siste tiår på øya. Dette med hensikt om å bedre restaurere og bevare gjenværende, innfødte flora og fauna. Denne studien tar for seg og utforsker effektene av den utførte restaureringen ved å se på biodiversitet og artsinteraksjoner. Dette gjøres ved å sammenligne restaurerte områder hvor eksotiske arter har blitt manuelt fjernet, og ikke-restaurerte områder, hvor eksotiske arter er gjenværende. Jeg brukte sommerfugl tellinger, siden sommerfugler regnes som gode indikatorer på generell biodiversitet, samt predasjon av kunstige sommerfugllarver og omfang av herbivori på innfødte planter. Jeg antok at dette ville reflektere skogens generelle tilstand og funksjonalitet som økosystem. Jeg fant ut at fjerning av eksotiske arter viste en signifikant, positiv effekt på innfødt sommerfugl fauna. I tillegg var predasjonen av kunstige sommerfugllarver høyere i områder hvor eksotiske arter har blitt fjernet. I det minste for fugler, ble denne predasjonen utført av innfødte arter. Herbivori og diversitet av herbivorer viste ikke signifikant forskjell mellom de restaurerte og ikke-restaurerte områdene, men dette kan forklares med høyere predasjon av herbivorer i restaurerte områder, og begrensede matressurser i ikke-restaurerte områder. Resultatene fra dette studiet konkluderer med at restaurerte områder fremstiller et mer artsrikt og fullstendig økosystem enn ikke-restaurerte områder. Resultatene viser derfor at gjenværende, innfødt skog på Mauritius kan til en større grad gjenoppbygges og kan gjenopprette sin innfødte biodiversitet etter at restaurering i form av fjerning av eksotiske arter har blitt utført.

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1. Introduction

Tropical forests are thought to support 60% of all known species (Dirzo & Raven 2003; Laurance 2001), yet they are characterized by high rates of habitat degradation and destruction (Lewis 2009). Small island ecosystems where natural habitat is reduced to small, isolated patches and with high rates of endemism are particularly fragile and susceptible to disturbances and deforestation (Denslow 2003; Dulloo et al. 2002; Lorence & Sussman 1986; Vistousek et al. 1987). High extinction rates are often linked to low species diversity, small populations, restricted genetic diversity, reduced competitive ability and narrow ranges (Laurance & Bierregaard Jr. 1997; Lorence & Sussman 1986). Indeed, the vast majority of human-induced plant and animal extinctions have occurred on tropical islands (Clavero & García-Berthou 2005; Sax & Gaines 2008). However, extinctions are not equally distributed across taxonomic groups. For example, birds have lost many species, whereas few plant species have apparently been lost (Blackburn et al. 2004; Sax et al. 2002).

A large number of these extinctions has been attributed to invasive animal species (Sax et al. 2002; Steadman 2006). Nevertheless, the invasion by exotic plant species poses an increasing threat to native tropical island plant communities and their associated biodiversity (Elton 1958; Florens et al. 2010; Heywood 1979; Vistousek et al. 1987). Hundreds of different exotic plant species worldwide currently threaten native island flora and fauna (Denslow 2003; Kueffer 2011; Vistousek et al. 1987). Growing global trade and travel have increasingly permitted more species to overcome natural barriers to dispersal, such as oceans and mountain ranges, and colonize new areas previously inaccessible (Denslow 2003; Dobson & May 1986; Kueffer 2011; Liebhold & Tobin 2010). However, exotic species invasion on tropical islands is not a new phenomenon. Islands have experienced plant invasions from the time of Polynesian voyagers, with pasture grasses, timber trees, food crops, ornaments and sources for fuel and fibre being transported to new areas (Mueller-Dombois & Fosberg 1998). Early human settlers on oceanic islands caused widespread habitat alteration to the extent that native floras are difficult to reconstruct (Denslow 2003; Mueller-Dombois & Fosberg 1998).

Invasion by exotic species is the process by which a species expands its range from a habitat that it naturally occupies to one where it does not (Dobson & May 1986; Liebhold & Tobin 2010). Introduced alien species can become competitively superior and suppress the ability of native species to survive and multiply, and often become regarded as pests (Dulloo et al. 2002; Mandon-Dalger et al. 2004; Reaser et al. 2007; Towns et al. 2006). Biological invasion has phases of arrival, establishment and spread (Dobson & May 1986; Shigesada & Kawasaki 1997), and by each level, the eradication of the alien species becomes more complicated (Liebhold & Tobin 2010; Shigesada & Kawasaki 1997). Invasive plant species, particularly woody plants, can have major impacts on the native ecosystem structure and functioning (Richardson et al. 2004; Versfeld & van Wilgen 1986).

Ecological restoration techniques have been used extensively to tackle invasion by non-native species (Fleishman et al. 2005; Florens & Baider 2013). Restoration ecology is a relatively new branch of ecology, which is growing in importance due to the habitat degradation worldwide, particularly in tropical lower income countries (Florens & Baider 2013; Laurance 2001; Suding 2011). Natural recovery may not be sufficient to restore areas to their pre-disturbance states and there is a growing need to restore tropical forests, improving their environmental functions, productive capacity and biodiversity values (Lamb et al. 2005; Nyafwono et al. 2014). Restoration ecology is likely to be one of the most important fields in the coming century and development of feasible goals for restoration needs to be set by investigating ecosystem health (Hobbs & Harris 2001; Lamb et al. 2005). For tropical areas with their high species richness and endemism, determining the capacity of remaining small forest areas to support biodiversity is important (Daily & Ehrlich 1995). To conserve the remaining biodiversity in the most efficient way, and prevent further extinctions, restoration ecology can help implement specific measures to counteract these (Fleishman et al. 2005). In areas plagued by exotic invasives, this can be accomplished with an understanding of ecosystem functionality and the impact of invasive species on the native biota (Hobbs & Harris 2001; Kueffer 2011).

The island of Mauritius is one of the world's most severely ecologically damaged nations. Mauritius consisted of several forest types, which are now extinct or heavily degraded; open, dry palm-rich woodland, semidry evergreen forest, wet forest and mossy rainforest (Cheke 1987; Florens et al. 2012; Lorence & Sussman

1986; Safford 1997; Vaughan & Wiehe 1941). Human colonization resulted in rapid habitat destruction and reduction of native vegetation cover (Cheke & Hume 2008b; Lorence & Sussman 1986; Safford 1997). Logging of the economically valuable Ebony tree (*Diospyros tessellaria*) and deforestation to make way for sugar cane left only areas less suitable for agriculture (Baider et al. 2010; Baret et al. 2013; Cheke & Hume 2008b). Less than 5% of the original habitats survives as fragments on the island, and only 1,9% of the total area of the country supports native vegetation (Baider et al. 2010; Florens & Baider 2013; Monty et al. 2013; Namah 2010). Several plant and animal species have become extinct, most famously the Dodo (*Raphus cucullatus)* (Baret et al. 2013; Cheke & Hume 2008b; Dulloo et al. 2002; Mauremootoo & Towner-Mauremootoo 2003).

Today, the remaining forest faces threats from human overpopulation, habitat destruction and fragmentation, and invasions by alien species (Florens 2013; Lorence & Sussman 1986). In fact, Mauritius has the world's second most threatened flora worldwide (Florens et al. 2012). Only small areas of wet and dry evergreen forest remain, mainly on mountain slopes in the southwest and east (Florens et al. 2012; Safford 1997). Wet forests of Mauritius retain the highest tree diversity of the Mascarenes, and one of the highest of all isolated oceanic islands (Forens et al. 2012). Mauritius also possesses a rich diversity of endemic plants: of the 691 native flowering plants, 39.5% is endemic to the island. Of these, 81.7% is classed as endangered (Baider et al. 2010; Florens et al. 2012; Monty et al. 2013; Walter & Gillet 1998). The remaining native vegetation is highly degraded due to poor regeneration of native plants and high invasion by exotic plants and animals (Safford 1997).

Strawberry guava (*Psidium cattleianum*), Privet (*Ligustrum robustum*), Rose apple *(Syzygium jambos),* Traveler's Palm (*Ravenala madagascariensis)* and Cinnamon (*Cinnamomum verum)* are among the most invasive plant species (Florens & Baider 2013; Gopal 2003; Kueffer & Vos 2003; Strahm 1999). Vaughan and Wiehe (1941) stated that invasion by exotic plants was already a serious problem by the 1930s, and their spread might have accelerated by introduced birds and mammals of which there are several (Lorence & Sussman 1986). Javese deer *(Cervus timorensis)* and wild pigs *(Sus scrofa)* were introduced for hunting, while dogs *(Canis lupus familiaris),* cats (*Felis catus*) and goats (*Capra aegagrus hircus)* are abundant domestic animals on the island (Cheke & Hume 2008b; Gopal 2003; Strahm 1999; Towns et al. 2006). Species introduced by accident, such as rats (*Rattus rattus* and *R. norvegicus*) and giant African land snails (*Achatina fulica)* are considered major pests (Gopal 2003; Harper & Bunbury 2015; Strahm 1999; Towns et al. 2006). Rats have contributed to the extinction of many endemic birds and reptiles (Dulloo et al. 2002; Harper & Bunbury 2015; Towns et al. 2006), while *A. fulica* has contributed to the extinction of 24 of 106 endemic snail species (Griffiths & Florens 2006; Reaser et al. 2007). Species introduced to eradicate other exotic species are now also posing a threat on their own (V. Florens pers. comm.). This includes mongoose (*Herpestes javanicus*), introduced in Mauritius to control rats (Roy et al. 2002). The common myna (*Acridotheres tristis*) and the red-whiskered bulbul (*Pycnonotus jocosus*) are among the most common exotic birds that compete with native species for food and habitat (Linnebjerg et al. 2010; Namah 2010). These highly mobile birds spread seeds of invasive plants in their droppings (Dulloo et al. 2002; Linnebjerg et al. 2010). Introduced insects such as wasps and honeybees have a negative impact on native flower-visiting insects, and also to some extent on the endemic nectarivorous birds, Grey White-eye (*Zosterops borbonicus mauritianus*) and Olive White-eye (*Z. chloronothos;* Hansen et al. 2002).

Established “conservation management areas” (CMAs) on the island have helped restore native forest areas by clearing invasive introduced plant species. About 53% of the Mauritian native flowering plants can be found within the CMAs (Jones 2008). These are therefore areas of native forests where the habitat is generally well preserved (Florens 2008; Jones 2008). These areas are also often protected against large alien mammals via fencing (Baider & Florens 2011; Dulloo et al. 2002; Florens 2013). According to Monty et al. (2013), native tree communities and individual tree health improves after the clearing of invasive plants. For example, an improvement in crown structure has been observed and an increase in fruit production noted (V. Florens pers. comm.). However, little is known about the general health of the entire ecosystem after weeding. In other words, how this recovery of native vegetation affects the associated biodiversity. In the current study, I try to redress this shortfall by investigating differences in butterfly diversity, caterpillar predation and herbivory between weeded and non-weeded forest areas using these as a proxy for ecosystem health and functionality.

Mauritius has a well-developed native insect fauna with a high proportion of endemic species (37%), and the majority of insect orders is represented on the island (Motala et al. 2007). Mauritian butterflies consist of 35 species, of which 25 are common, nine species are endemic and further eight are endemic to the Malagasy sub-region (Madagascar, Comoro islands, Seychelles; Davis & Barnes 1991; Williams 2007). Monitoring butterfly populations is an important means of measuring environmental change, as well as the state of habitats for biodiversity (Pellet et al. 2012; Van Swaay et al. 2012). I use butterflies because they are known to be a good indicator taxon for overall biodiversity and are a relatively well-known group (Caldas & Robbins 2003; Daily & Ehrlich 1995; Florens et al. 2010). Butterfly monitoring in areas with a relatively depauperate butterfly fauna (such as Mauritius) can also be done rapidly through counts along transects, as first proposed by Pollard et al. (1975) and Pollard (1977), and is an effective low-cost method to monitor butterfly community demographics (Caldas & Robbins 2003). I use predation of artificial caterpillars and herbivory of native plants under the assumption that this will reflect forest functionality, and thus health, as the number of interspecific species interactions increase.

More specifically, I tested the predictions that:

1) Butterfly species richness and abundance in weeded areas are higher than in non-weeded areas;
2) Predation on artificial butterfly caterpillars in weeded areas is higher than in non-weeded areas;
3) Herbivory rates and herbivore diversity in weeded areas are higher and more diverse than in non-weeded areas.

2. Materials and methods

2.1. Study area

Mauritius is a 1865 km² volcanic island situated approximately 900 km to the east of the African continent (Cheke & Hume 2008a; Staub 1993). It is part of the Mascarene archipelago in the south-western Indian Ocean, which is recognized as one of the world’s biodiversity hotspots (Baider & Florens 2011; Cheke & Hume 2008a; Myers et al. 2000). The highest point is Black River Peak, 828 meters above sea level

(Safford 1997). Mauritius was first inhabited by the Dutch in 1638 and later went through French and British colonization, before gaining independence in 1968 (Baider et al. 2010; Cheke & Hume 2008b).

Average annual temperature on Mauritius varies between 16°C in the coolest months (July-August), and 26°C in the hottest months (January-February; V. Florens pers. comm.). Mauritius has a series of microclimates, with drier, warmer climate on the west coast, wet temperate climate in the uplands and wind blowing steadily from eastern directions (Cheke & Hume 2008a; Lorence & Sussman 1986). Annual rainfall varies from 3 600 mm on the centre high plateau, 1 400 – 1 800 mm in the coastal south-east, and 800 mm in the driest coastal west part (Cheke & Hume 2008a). During the hotter months, tropical cyclones are formed as a result of the Intertropical Convergence Zone (ITCZ) perturbation, and the annual mean humidity is around 80% (Davis & Barnes 1991).

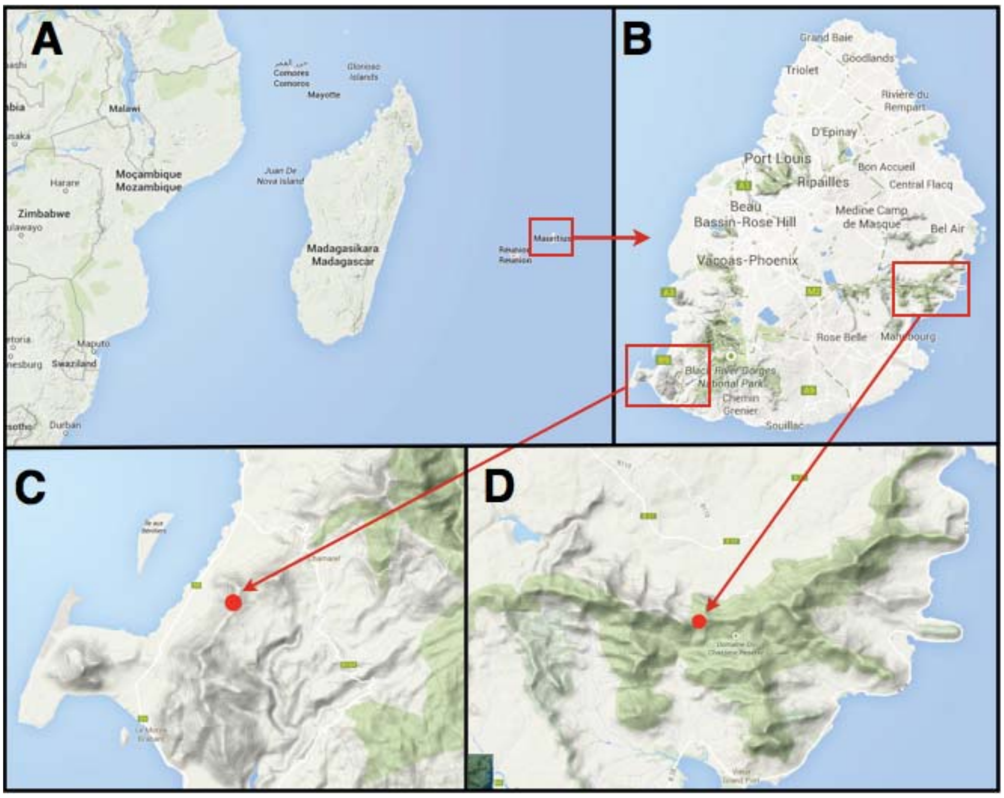


Figure 1: A) Map of Mauritius in the Mascarene Archipelago, in the south-western Indian Ocean. **B)** Mauritius island, with study areas **C)** Chamarel and **D)** Camizard indicated. Source: Google Maps (accessed March 2015).

2.2. Study sites

The current study took place at two study sites, Chamarel and Camizard, between June and August 2014. Chamarel is situated in the southwest of the island (Figure 1), and is located on a steep hill around 250-350 masl. The weeded and non-weeded areas used for the study were immediately adjacent to each other (Figure 2). Camizard is located within the Bamboo Mountains on the windward slope in the southeast of the island (Figures 1 and 3). The site is located on the north part of Mont Camizard, at an altitude of 150-300 masl. At this site, the weeded and non-weeded areas were approximately 1 km apart. Both study sites were situated on privately owned land.

Figure 2: Chamarel study site with non-weeded forest area on the left and weeded forest area on the right. Photo: P. J. Kajl.

Figure 3: Mt Camizard with study sites located approximately 1 km from each other on the windward slope. Photo: P. J. Kajl.

The weeded area at Chamarel was fenced to prevent access of exotic mammals and separate the weeded area from the non-weeded (Figure 2). The weeded area at Camizard was not fenced and frequented by Javanese deer (*C. timorensis*) and wild boar (*S. scofa*) (Figure 3). Weeding of exotic plants has been implemented by manual cutting and stump removal 6-9 years ago (Mauremootoo & Towner-Mauremootoo 2003; pers. obs.; V. Florens pers. comm.). Weeding has been maintained three times per year and gradually reduced to once per year until the seed banks were exhausted (Dulloo et al. 2002). Another implemented method was ring marking; painting the stump of the exotic plants with herbicide with care to minimalize risk of spillage (Dulloo et al. 2002; Florens 2013; pers. obs.). The dead exotic plants were left in the forest to rot and to prevent soil erosion (Florens 2013). After such weeding, the general health of the weeded forest showed improvement, with regeneration of indigenous trees (Dulloo et al. 2002; Monty et al. 2013). Previous research showed that there is a much higher mean species richness of native seedlings in investigated weeded areas compared to non-weeded areas, and species previously thought extinct are also recovering (Baider & Florens 2011; Monty et al.

2013).

Given that weeded and non-weeded areas were located in the same forest at the same location and in close proximity to each other, I assume that weeded and non-weeded areas were similar in all aspects, apart from the control of invasive alien plants. Study sites were chosen based on comparable weeded and non-weeded forest with accessibility.

2.3. Study setup

2.3.1. Measurement of butterfly abundance and species richness

Butterfly censuses consisted of standard Pollard walks (Pollard et al. 1975; Pollard 1977) following the methodology in Florens et al. (2010). Butterfly species were identified using a field guide (Williams 2007). In total, I surveyed 56 randomly selected transects between August 12th and August 21st. This included 30 transects (15 in weeded and 15 in non weeded) in Chamarel and 26 transects (13 in weeded and 13 in non weeded) in Camizard. Each transect was 60 m long, and I surveyed all butterflies within 2,5 m to each side of the transect and 5 m in front and above. The butterfly surveys were carried out from 10 a.m. to 3 p.m., when butterflies are at their most active (V. Florens pers. comm.). During surveys, I walked at a slow pace, stopping every 10 meters for 3 minutes and noting all the observed butterflies within the set range. For each weeded transect a comparable and adjacent non-weeded transect was surveyed, so time of the day would not influence the result.

2.3.2. Predation on artificial caterpillars

To assess predation pressure, artificial caterpillars were placed along transects, following the methodology in Howe et al. (2009), Koh & Menge (2006) and Posa et al. (2007). As predation is hard to quantify and rarely observed, artificial models, such as caterpillars made of plasticine, is a simple way to quantify predation. This methodology has previously been successfully used in several tropical forest areas

(Fáveri et al. 2008; Howe et al. 2009; Koh & Menge 2006; Loiselle & Faraji-Brener 2002; Posa et al. 2007).

Artificial caterpillars were created using plasticine, which is odour and chemical free. All caterpillars were handmade, 3 cm long and 0,5 cm thick, corresponding to native butterfly caterpillars described by Martiré and Rochat (2008). The number of artificial caterpillars was identical in weeded and non-weeded forest areas in both sites. In total, I used 288 caterpillars, 144 of green plasticine and 144 of brown plasticine. These were placed in six plots along two transects of 60 m in each weeded and non-weeded area. Each plot was 10 m apart and contained six caterpillars. Each caterpillar was placed on a different plant, and one of each colour was placed on three different plant parts; leaf, branch and tree trunk. All caterpillars were exposed to potential predators for two weeks, as a pre-study trial showed that one week of exposure was not sufficient to get adequate predation marks. The artificial caterpillars were smooth and free of any marks when glued to the plants, with a minimal amount of superglue (Figure 4). After the 14 days of exposure, they were relocated and carefully collected. To facilitate the relocation process, each plant containing a caterpillar was discretely marked with a flagging tape at the base of the trunk.

Figure 4: Artificial caterpillars of two different colours glued on a **A)** tree trunk, **B)** leaf, and **C)** branch. Photos: P. Kajl.

Each caterpillar was examined for marks on site, before being placed in a plastic tube labelled with an individual caterpillar number. They were re-examined in the Mauritius herbarium for determining marks. The visible marks were assigned to three categories: teeth (rodents), beak (birds) and insects (Figure 5). Small, inconspicuous marks and repeated punctures were assumed to be caused by insects.

Small beak marks were assumed to be from native birds as these are smaller than the exotic birds (V. Florens pers. comm.).

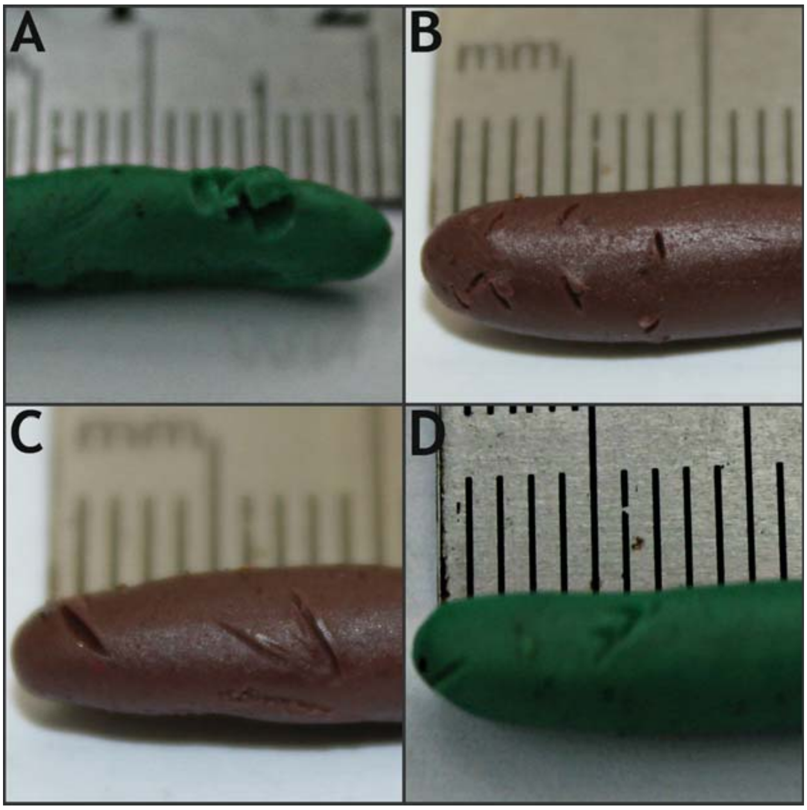


Figure 5: Artificial caterpillars with marks from different predators. **A)** Teeth (exotic rodent), **B)** insect (ant), **C)** big beak and **D)** small beak. Photos: P.Kajl

2.3.3. Herbivory

To measure herbivory, I collected 10 randomly chosen leaves from 15 individuals each of five native species of Mauritian plants; *Calophyllum tacamahaca, Diospyros tessellaria, Erythoxylum macrocarpum, Ixora parviflora* and *Warneckia trinervis* (Figure 6). All of these species are endemic to Mauritius, except for *C. tacamahaca*, which is endemic to the Mascarenes (C. Baider pers. comm.; Florens et al. 2012; V. Florens pers. comm.). More plants were collected in Chamarel due to easier access and location of the plants. *C. tacamahaca* , *I. parviflora* and *E. macrocarpum* and *D. tessellaria* were collected in Chamarel. *W. trinervis* and *D. tessellaria* were collected in Camizard.

Figure 6: Examples of leaves sampled from **A)** *I. parviflora,* **B)** *D. tessellaria*, **C)** *W. trinervis*, **D)** *C. tacamahaca* and **E)** *E. macrocarpum*.

All herbivory sampling, apart from adult trees of *D. tessellaria*, was done with young leaves on young plants so they could be comparable. Younger leaves are often preferred by herbivores with their higher nitrogen content and lower leaf toughness than older leaves (Paul et al. 2011). In tropical forests, where herbivory rates are higher than in temperate regions, most of the damage to leaves occurs when they are young and expanding (Aide 1993; Barone & Coley 1996; Loiselle & Faraji-Brener 2002). Leaves from *D. tessellaria* were all from mature tall trees, and were collected by the help of a telescopic pruner, cutting a randomly selected branch from which 10 leaves were randomly picked.

To measure the extent of herbivory in weeded forest and non-weeded forest I quantified:

1. Proportion of leaves damaged by herbivores for all tree species (incidence).
2. Mean percentage of leaf area damaged per leaf (severity).
3. Herbivore diversity for each leaf and plant species.

Together they provide an estimate of herbivory in the weeded vs. non-weeded forest areas.

I used a methodology described by Lowman (1984) as ‘discrete sampling’, which is a one-time estimation of herbivory. It provides simple means of estimating herbivory intensity for single occasion studies on limited time scale (Lowman 1984). This technique may underestimate the real herbivory losses as it does not account for leaves totally eaten, (Lowman 1984), however, it may provide information on any significant difference in herbivory rates in the restored and non-restored forest areas (i.e. weeded and non-weeded forest).

Further, I used digital image analyses of missing leaf area as described by O'Neal et al. (2002), and Paul et al. (2011). Sampled leaves were scanned and examined for herbivory damage using the computer software Image J Fiji 1.46. Each scanned leaf (Figure 7a) was turned into a black and white picture by adjusting the “threshold tool” in the program (Figure 7b). Contours of missing leaves were then drawn by the help of a “pencil tool” (Figure 7c), and the leaf area to be calculated was chosen using the “wand tool”. The program calculated first the estimated leaf area, and subsequently leaf area present. Herbivory damage was thereby calculated by subtracting the leaf area present from the total estimated leaf area.

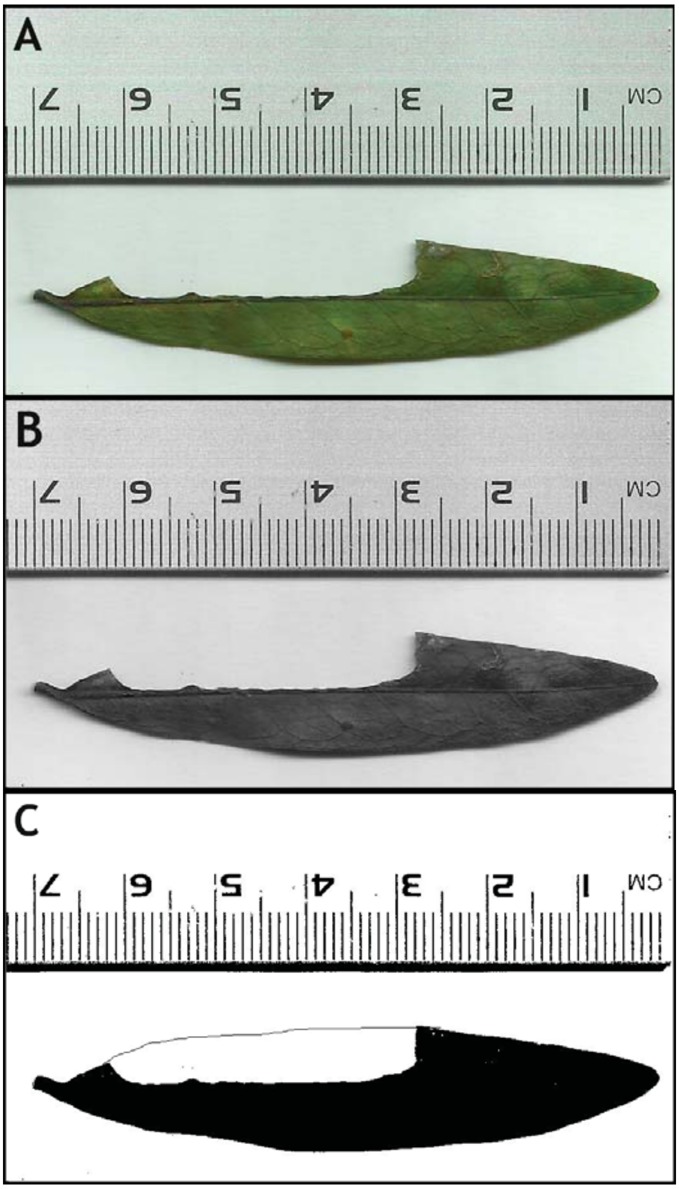
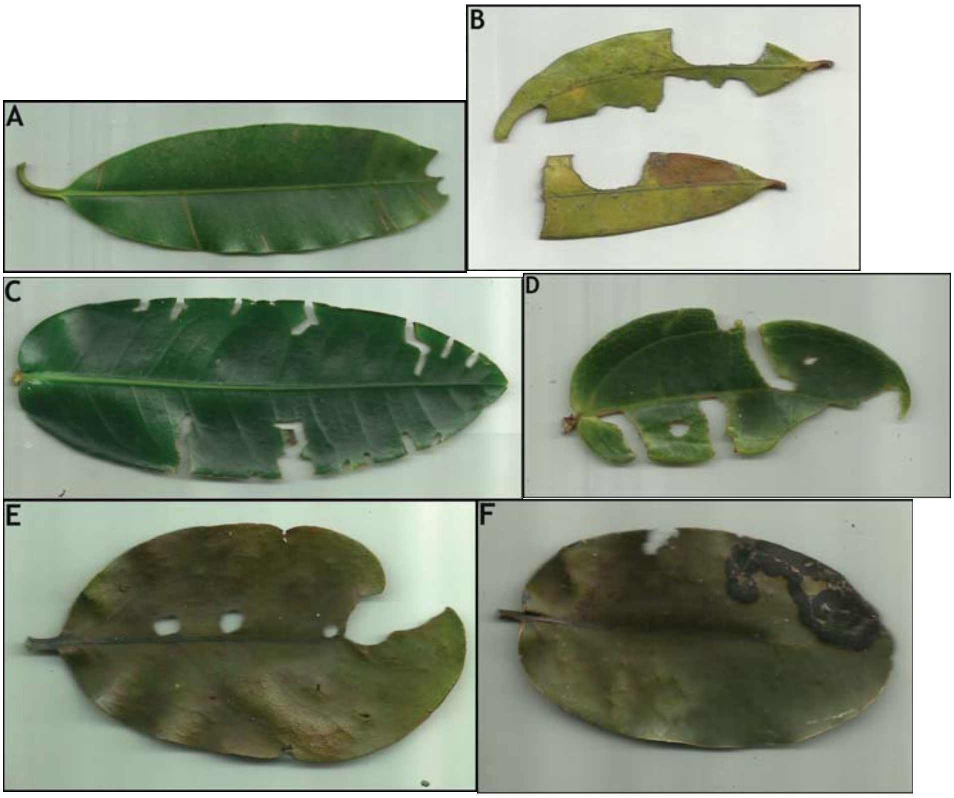


Figure 7: Calculating missing leaf area in Image J computer software. **A)** Scanned leaf of *E. macrocarpum*. **B)** Picture set to 8-bit, black and white. **C)** Picture turned black and white by adjusting threshold level, and drawing missing leaf contour with pencil tool.

A visual estimation of herbivore diversity was done simultaneously. Herbivore diversity was categorized in six groups (Table 1, Figure 8) based on the characteristic of each herbivore attack observed, following Labandeira et al. (2007), Paul et al. (2011) and Dr. V. Florens (pers. comm.). The appearance of each category of herbivore damage is shown in Figure 8.

Table 1: Type of herbivore damage observed and the possible attacker, based on the characteristics of the damage.

Type of damage	Characteristics	Possible attacker
"Bites"	Round bites from edge of the leaf of varying size.	Caterpillars, larvae, beetles
"Corridor"	Corridors from edge into center of leaf.	Weevils: *Cratopus*
"Extensive"	More than 60% of leaf tissue missing.	Several possible attackers
"Gall"	Tight bulbs, often with circular points.	Gall wasps, larvae
"Hole"	Various size of holes inside the leaf.	Beetles, snails, slugs
"Miner"	Serpentine tunnels within leaf, dark or beige colour.	Leaf miner, larvae



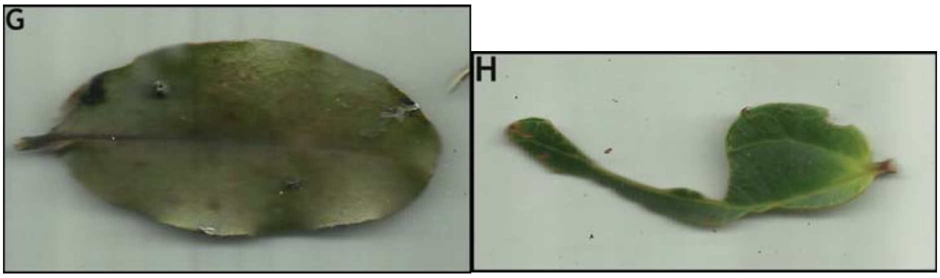


Figure 7: Herbivore damage found on native plants (according to table 1); **A)** Bites from the edge, *C. tacamahaca*. **B)** Bites from the edge, *E. macrocarpum*. **C)** Bites from the edge, and corridors, *I. parviflora*. **D)** Corridors, bites from the edge, holes, *W. trinervis*. **E)** Bites from the edge and holes, *D. tessellaria*. **F)** Bites from the edge and leaf miner, *D. tessellaria*. **G)** Gall on upper left part of leaf, *D. tessellaria*. **H)** More than 60% of leaf area missing, several possible herbivore categories, *W. trinervis*.

2.4. Statistical analyses

Statistical analyses were performed with the software R, version 3.10.0 To investigate any significant difference between the weeded and non-weeded forest areas, generalized linear mixed-effects models in the ‘lme4’ package (R Development Core Team 2014) were used. The analysis was based on mixed-effects logistic regression models (GLMM) (Pinheiro & Bates 2000), in which the response variable had two outcomes (binomial distribution). These models consisted of a response variable, fixed explanatory variables and random effects; see Table 2 for model specifications. GLMM is an extension of generalized linear models to include both fixed and random effects (Zuur et al. 2009). In this study, the predation and herbivory damage was specified as response variable while the variables forest area (weeded or non-weeded), colour, plant part or plant species were included as fixed explanatory variables (Table 2). Random effects were included as control for the repeated measurements within each site, transect and plot (Pinheiro & Bates 2000; Table 2). The setup of the dataset is summarized in Figure 9 for the three parts of this study, while the models for the five different statistical tests were specified as shown in Table 2.

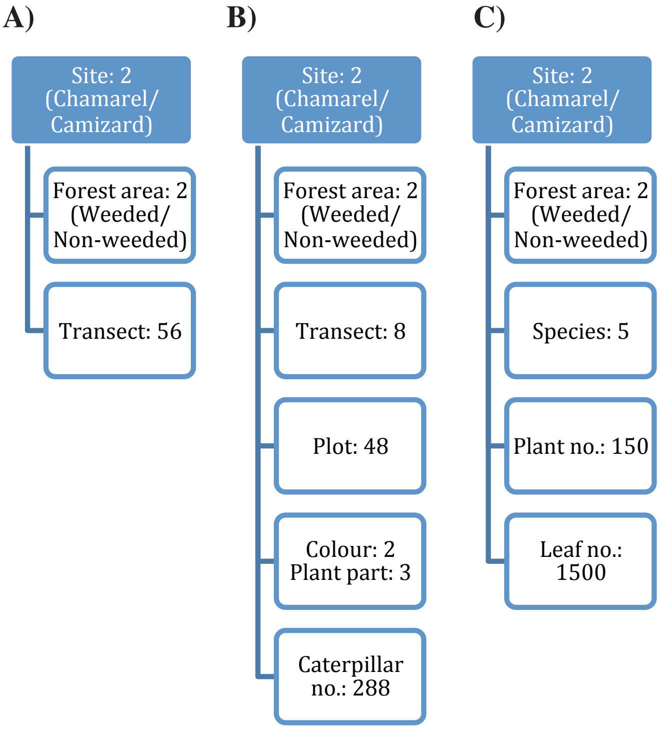


Figure 9: The study setup for **A)** measurement of butterfly abundance and species richness **B)** predation on artificial caterpillars and **C)** extent of herbivory and herbivore diversity. Each of the two sites consisted of two forest areas and further transects for **A)** and **B)**, plots, colours, plant parts and caterpillars for **B)**, and plant species, individual plants and leaves for **C)**.

Each model fit (full model vs. reduced model) was evaluated by assessing AIC values compared with the model that included only the random term. The Akaike Information Criterion (AIC) is a method for finding the model with the best trade-off between model complexity and goodness of fit (Akaike 1974). It gives a value of this trade-off relative to other models with different combinations and variables (Akaike 1974). The model fits were ranked according to their AIC values, the model with the lowest AIC value being considered the 'best'. Models in which the difference in AIC relative to AIC_{min} is < 2 can be considered also to have substantial support (Burnham & Anderson 1998; Burnham & Anderson 2002). The model selection with the best fitted models, including the AIC value are included in Table 2. Predictions from the best fitted models, were created from the parameter estimates (mixed-effects logistic regression models) with the probability function (odds ratio) $(f(x) = \exp(a+bx)/(1+\exp(a+bx))$. These were results were expressed as bar plots (±SE).

For predation on artificial caterpillars, three tests were performed (Table 2):

One for the overall predation, one for insects as predators and one for birds as predators. Rodents as predators were not included due to too small frequency of predation, though analysis is included in Appendix I.

For the herbivory part, two tests for overall herbivory were performed (Table 2). The first test was for the amount of damaged leaves vs. intact leaves in the weeded and non-weeded forest areas, and the second for proportion of damage on the leaves in both forest areas.

3. Results

In this study, the models were chosen from the GLMM analysis according to their AIC value. The model selection is presented in Table 2.

Table 2. Overview of the model selection of the best fitted models for the five statistical tests of this study. The response variable, fixed explanatory variables and random factors are described for each model. Each model is also presented with its degrees of freedom and AIC value. The chosen model for each test is presented in bold.

Test	Response variable	Fixed explanatory variables	random factors	df	AIC
1.1 Predation, overall	Damaged ~	W/NW + colour + plant part +	(1 | site / transect / plot)	272	365.6
1.2 Predation, overall	**Damaged ~**	**W/NW + colour +**	**(1 | site / transect / plot)**	**275**	**361.7**
1.3 Predation, overall	Damaged ~	W/NW +	(1 | site / transect / plot)	276	363.8
2.1 Predation, insect as predator	Insect ~	W/NW + colour + plant part +	(1 | site / transect / plot)	275	361.7
2.2 Predation, insect as predator	**Insect ~**	**W/NW + colour +**	**(1 | site / transect / plot)**	**275**	**323.7**
2.3 Predation, insect as predator	Insect ~	W/NW +	(1 | site / transect / plot)	276	324.2
3.1 Predation, bird as predator	Beak ~	W/NW + colour + plant part +	(1 | site / transect / plot)	275	151.5
3.2 Predation, bird as predator	**Beak ~**	**W/NW + colour +**	**(1 | site / transect / plot)**	**275**	**148.9**
3.3 Predation, bird as predator	Beak ~	W/NW +	(1 | site / transect / plot)	276	154.0
4.1 Herbivory, intact leaves	**Intact ~**	**W/NW + species +**	**(1 | site / sp_plantnr)**	**1508**	**1330.5**
4.2 Herbivory, intact leaves	Intact ~	W/NW + species + W/NW : species +	(1 | site / sp_plantnr)	1504	1331.5
5.1 Herbivory, proportion	**Prop_eaten ~**	**W/NW + species +**	**(1 | site / sp_plantnr)**	**1178**	**274.7**
5.2 Herbivory, proportion	Prop_eaten ~	W/NW + species + W/NW : species +	(1 | site / sp_plantnr)	1174	278.4

3.1. Measurement of butterfly abundance and species richness

A total of 51 butterflies of 5 different species were observed during transect censuses (Table 3). All butterflies were observed in weeded forest. Not a single butterfly was detected in non-weeded forest (Table 3). The most commonly observed forest butterfly was *Henotesia narcissus* (Table 3; Figure 10a), followed by *Neptis frobenia* (Table 3; Figure 10b).

Table 3: Total number of butterfly observations from weeded and non-weeded forest areas at both study sites (Chamarel and Camizard).

Species	Weeded	Non-weeded
H. narcissus	42	-
N. frobenia	5	-
Phalanta phalanta	2	-
Danaus chrysippus	1	-
Zizula hylax	1	-

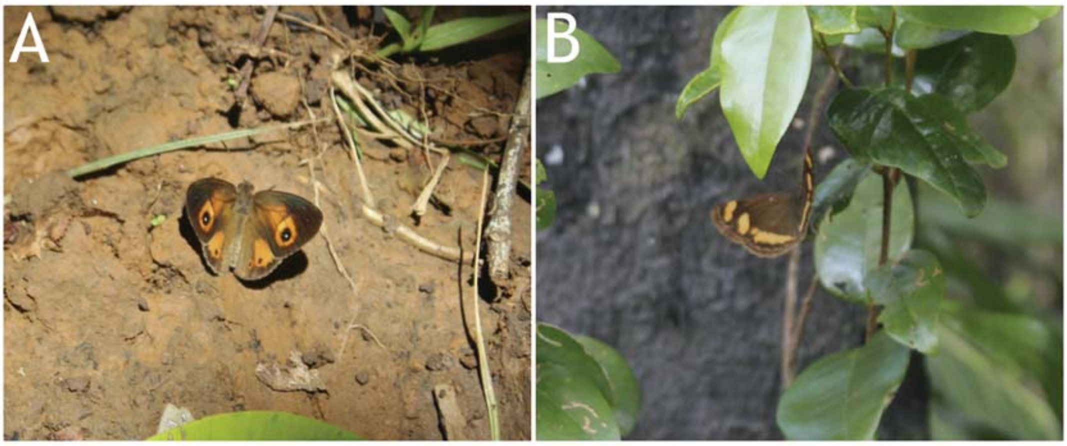


Figure 10: A) *H. narcissus* and **B)** *N. frobenia* in weeded part forest at Camizard and Chamarel, respectively. Photos: P.J. Kajl.

3.2. Predation on artificial caterpillars

Of the 288 artificial caterpillars deployed in weeded and non-weeded forest, 281 were relocated and collected. Seven caterpillars were lost and therefore excluded from the analysis. In total, 100 artificial caterpillars were attacked by predators.

GLMM analysis showed that the probability of attacks was significantly higher in weeded (n=63) than non-weeded areas (n=37; Table 4; Figure 11 and 12). Insects accounted for the highest number of attacks (n=39), followed by birds (n=11) and rodents (n=7). Brown caterpillars (n=57) were attacked more frequently than green caterpillars (n=43; Table 4; Figure 11 and 12).

Table 4: Output table from GLMM analysis including p-values and stars for the significant variables. Intercept presents a reference variable as the mean level of the response variable.

	Estimate	Std. Error	z value	Pr(>lzl)	Significance
(Intercept)	0.803	0.231	3.471	<0.001	***
Forest area (weeded/non-weeded)	-0.882	0.266	3.319	<0.001	***
Colour (green/brown)	0.520	0.259	2.009	0.044	*

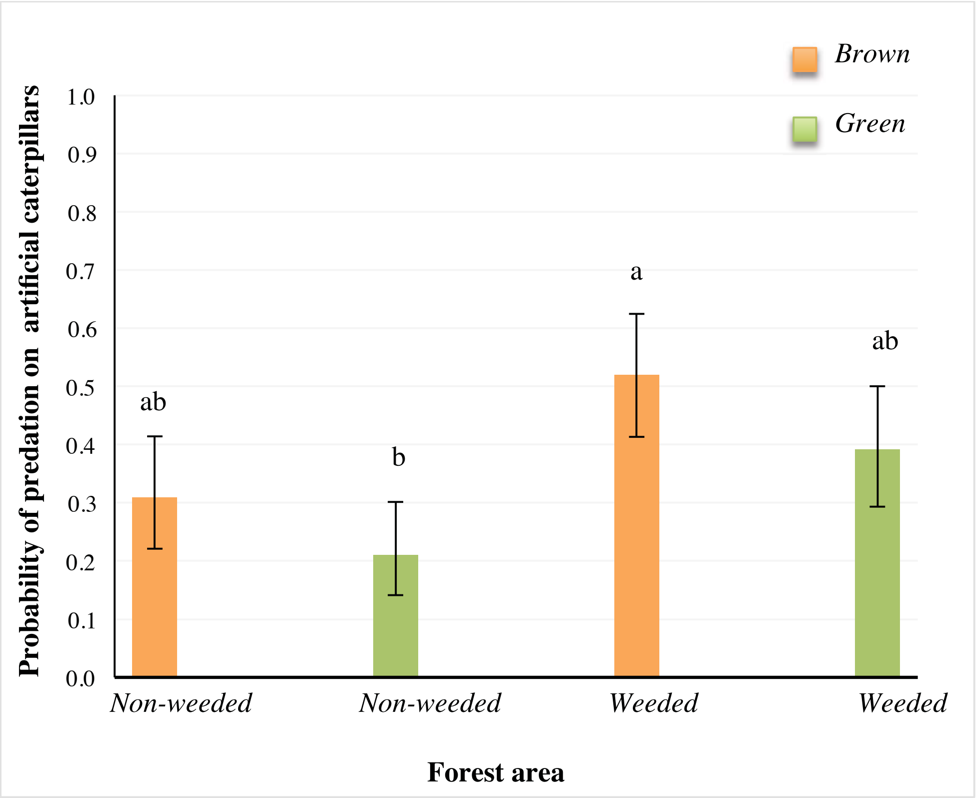


Figure 11: Probability of predation on brown and green artificial caterpillars in weeded and non-weeded forest areas (probability from 0 to 1 (0-100%)). Bars show mean ± standard error. Means having the same letter are not significantly different at p=0.05, according to GLMM test.

Insect predation was significantly different between forest types, with a higher probability of predation in the weeded forest areas, whereas colour was not (Table 5, Figure 12a) For predation by birds, forest area had only a trend of more probability for predation in weeded areas, while colour was significant with more probability of predation on brown caterpillars (Table 6, Figure 12b).

Table 5: Output table from GLMM analysis for insects as predators. Significance level is marked by stars where (***) is highly significant and no star is not significant.

	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**	**Significance**
(Intercept)	-0.985	0.237	-4.155	<0.001	***
Forest area (weeded/non-weeded)	-0.649	0.280	-2.316	0.020	*
Colour (green/brown)	0.435	0.278	1.565	0.118	

Table 6: Output table from GLMM analysis for birds as predators. Trend is marked by a (.) and significance by number of stars (*).

	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**	**Significance**
(Intercept)	-3.182	0.611	-5.205	<0.001	***
Forest area (weeded/non-weeded)	-1.063	0.576	-1.846	0.065	.
Colour (green/brown)	1.342	0.542	2.474	0.013	*

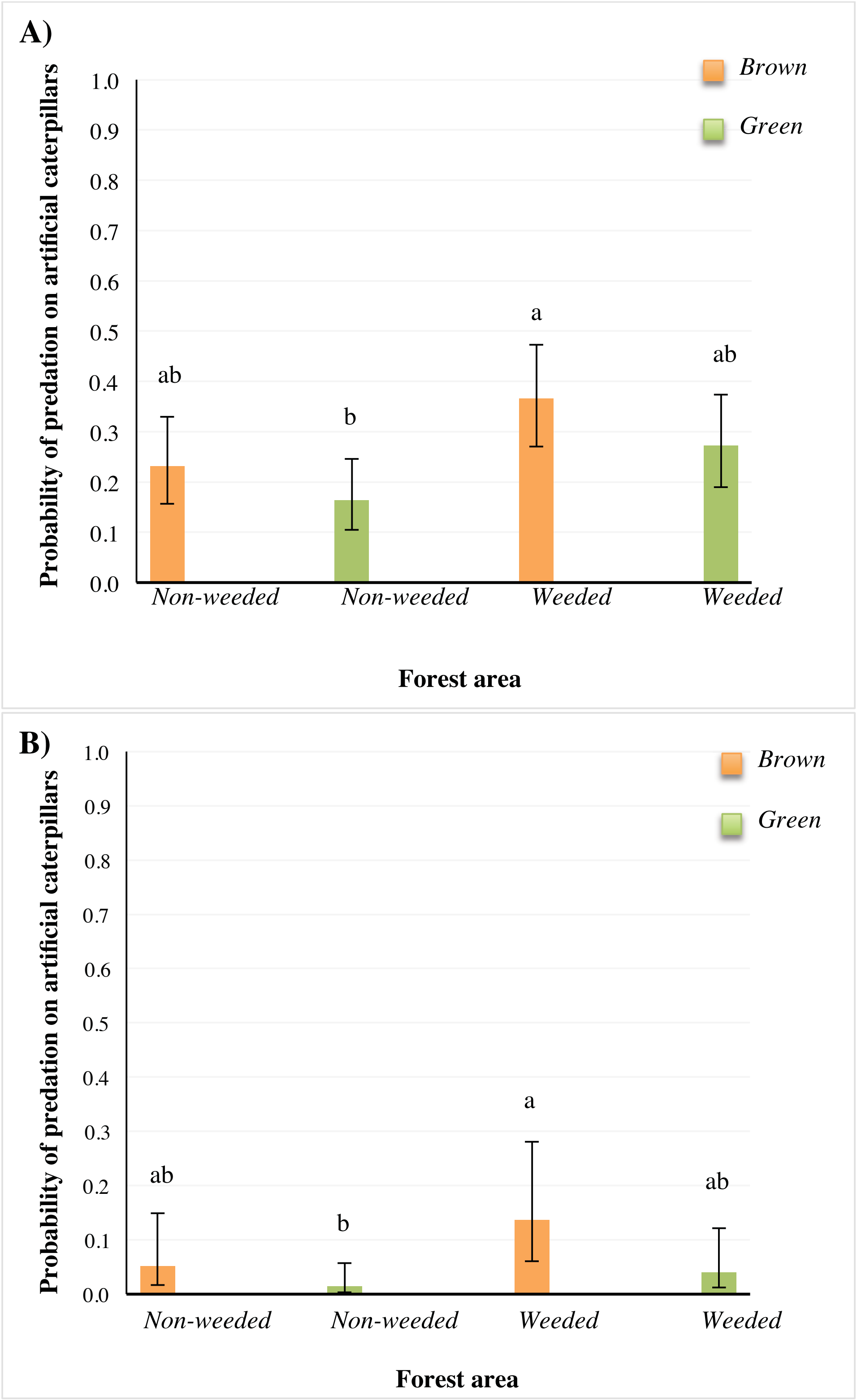


Figure 12: Probability of predation on brown and green artificial caterpillars in weeded and non-weeded forest areas for **A)** insects and **B)** birds. Bars show mean ± standard error. Means having the same letter are not significantly different at p=0.05, according to GLMM test.

3.3. Herbivory

Overall herbivory did not show any significance between weeded and non-weeded forest areas (Tables 7 and 8; Figure 13a,b). However, there were species-specific differences in herbivory between the five native plants (Figure 13a,b,; Appendix II). *W. trinervis* had significantly higher probability of herbivore damage than the other four species (Figure 13a,b). The largest number of intact leaves was found on *C. tacamahaca*, while *W. trinervis* and *D. tessellaria* had the least probability of intact leaves (Table 8; Figure 13a; Appendix II).

The species that experienced the highest proportion of herbivory damage was *W. trinervis*, followed by *C. tacamahaca* (Figure 13b). There was no significance between weeded and non-weeded forest areas for the proportion of herbivory damage on damaged leaves for all five species (Table 8, Figure 13 b; Appendix II).

Table 7: One of the output tables from GLMM analysis for intact leaves in weeded and non-weeded forest areas for five native plant species. The intercept here is presented by *C. tacamahca* as reference species to which the other species are compared. All species show significantly more damaged leaves than C. tacamahaca (***), while forest area is not significant, with only a trend of more intact leaves in weeded areas (.).

	Estimate	Std. Error	z value	Pr(>lzl)	Significance
(Intercept - *C. tacamahaca*)	0.309	0.205	1.509	0.131	
Forest area (weeded/non-weeded)	-0.332	0.194	-1.709	0.087	.
D. tessellaria	-3.134	0.349	-8.977	<0.001	***
E. macrocarpum	-1.933	0.286	-6.757	<0.001	***
I. parviflora	-1.270	0.264	-4.801	<0.001	***
W. trinervis	-2.928	0.329	-8.902	<0.001	***

Table 8: One of the output tables from GLMM analysis for proportion of leaves eaten by herbivores in weeded and non-weeded forest areas for the five native plant species. All had lower proportion of damaged leaves than the intercept, the reference species *W. trinervis* (***), while forest area was insignificant as variable (no star).

	Estimate	**Std. Error**	**z value**	**Pr(>lzl)**	**Significance**
(Intercept - *W. trinervis*)	-2.302	0.269	-9.167	<0.001	***
Forest area (weeded/non-weeded)	0.006	0.357	-1.709	0.987	
D. tessellaria	-2.429	0.739	5.082	0.001	**
E. macrocarpum	-3.215	1.022	2.958	0.002	**
I. parviflora	-3.325	1.022	-0.543	0.001	**
C. tacamahaca	-1.485	0.618	8.905	0.016	*

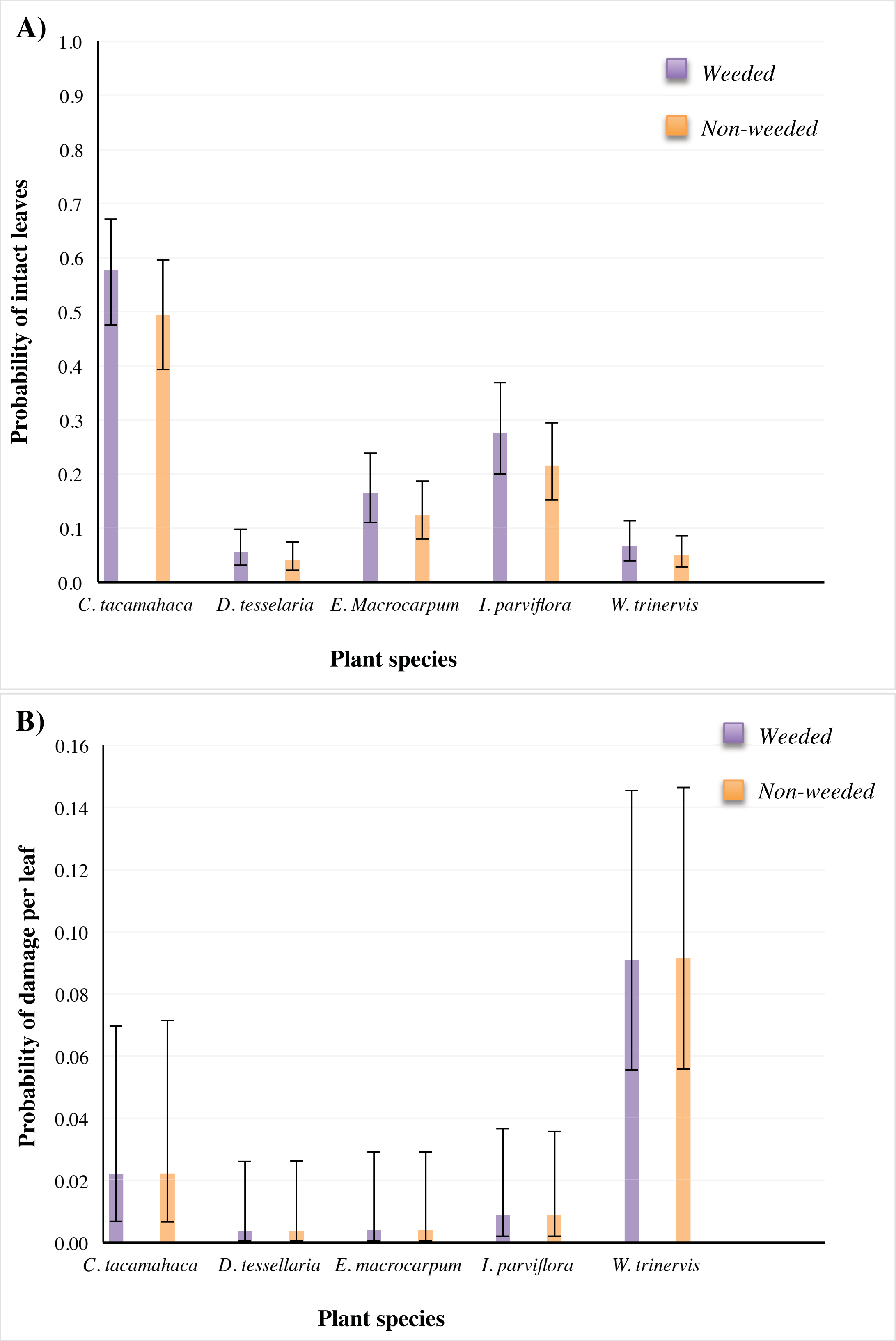
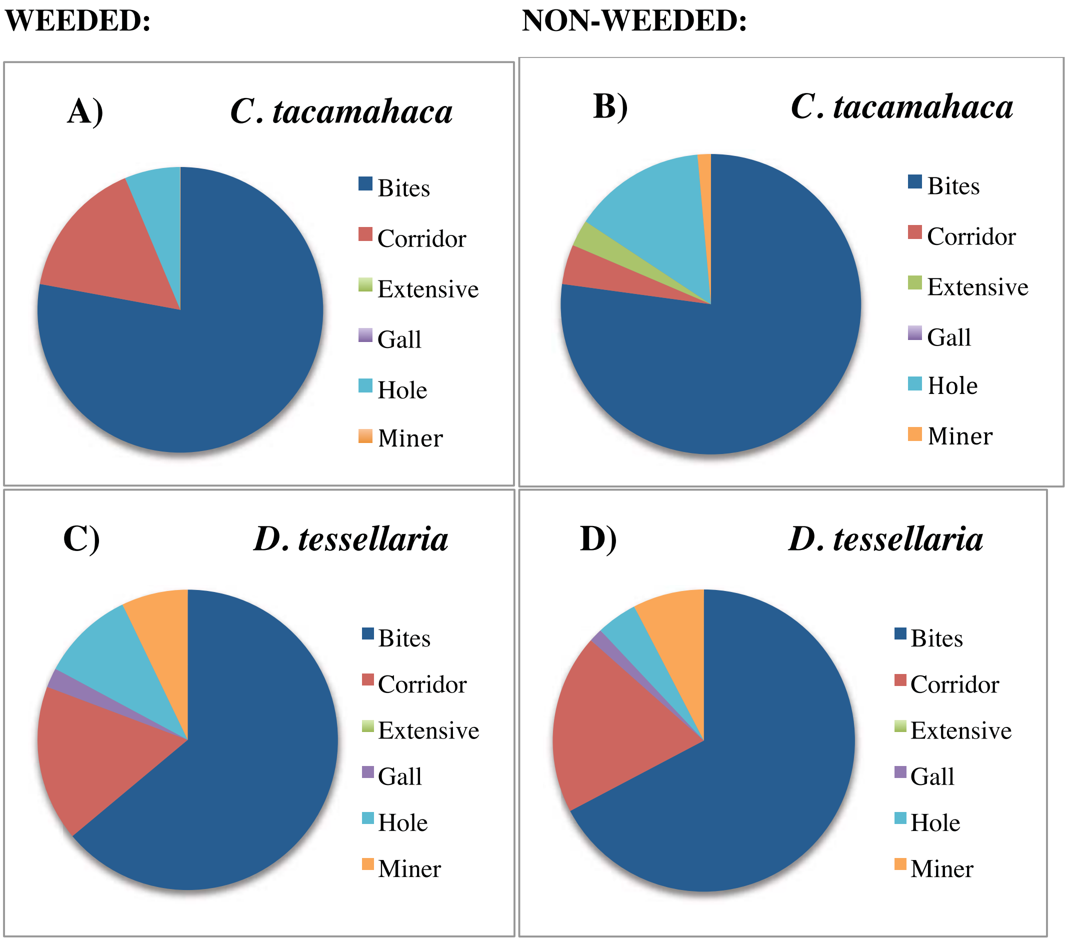


Figure 13 A): Probability of intact leaves (± SE) and **B)** probability of average herbivore damage per leaf (± SE), in weeded and non-weeded forest areas for five native plant species.

The herbivore damage categories as specified in Table 1, are presented in Figure 14, in form of pie charts. According to pie charts, there are similar patterns of herbivory categories in weeded and non-weeded forest areas. Bites from the edge were by far the most present herbivore category on all species. There are also species-specific differences (Figure 14; Appendix III). *C. tacamahaca* had more diversity of herbivore attacks in non-weeded area, while *W. trinervis* experienced more herbivore diversity in weeded forest area (Figure 14; Appendix III). *D. tessellaria*, *E. macrocarpum* and *I. parviflora* experienced more herbivore damage in form of corridors in non-weeded areas than in weeded areas (Figure 14; Appendix III).



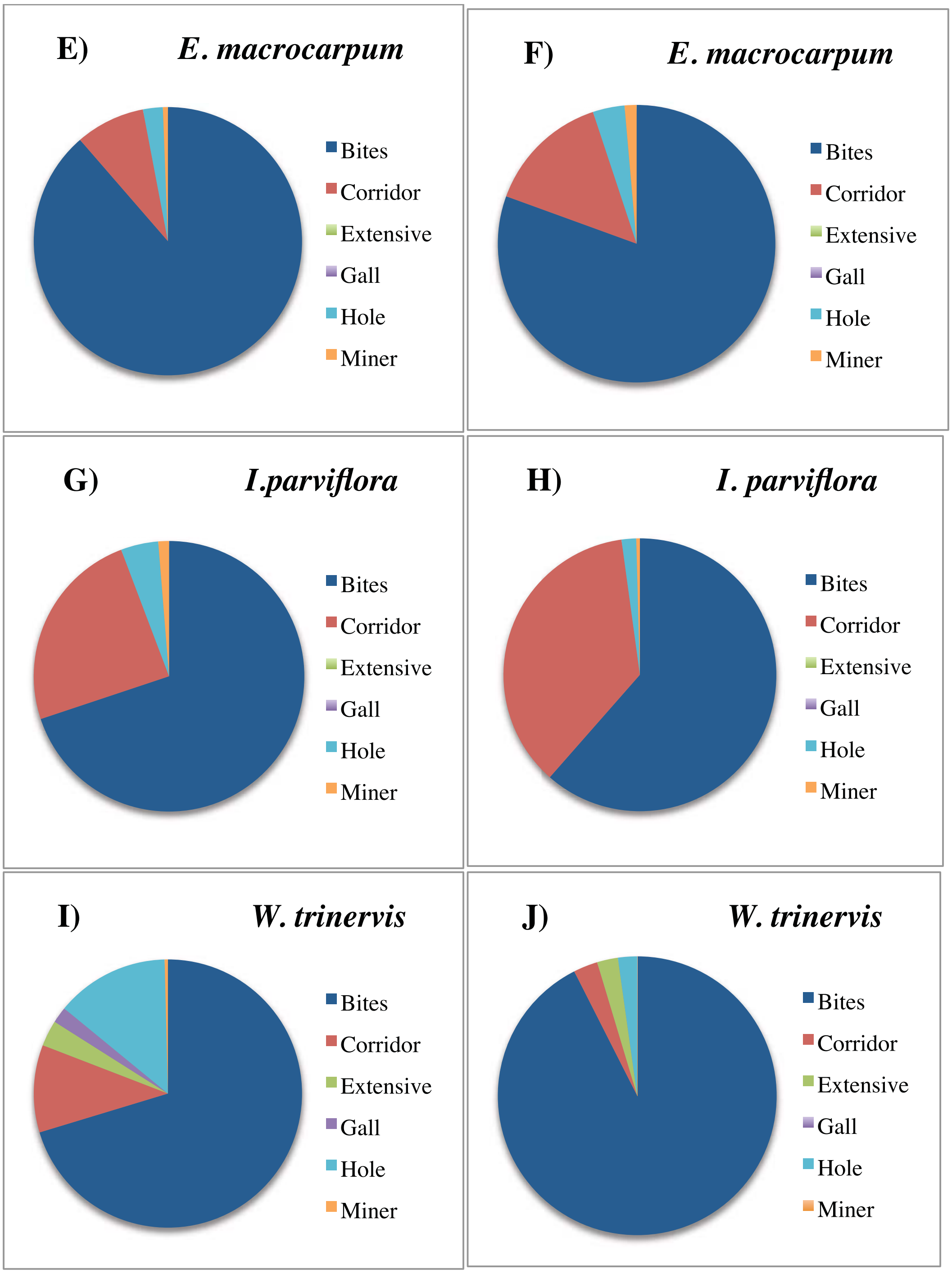


Figure 14: Herbivore diversity found on **A)** *C. tacamahaca* in weeded and **B)** non-weeded forest, **C)** *D. tessellaria* in weeded and **D)** non-weeded forest, **E)** *E. macrocarpum* in weeded and **F)** non-weeded forest, **G)** *I. parviflora* in weeded and **H)** non-weeded forest, **I)** *W. trinervis* in weeded and **J)** non-weeded forest.

4. Discussion

4.1. Measurement of butterfly abundance and species richness

I found that weeded areas contained a higher number of butterflies than non-weeded areas (Table 3), which supports my first prediction. This result is consistent with Florens et al. (2010), indicating that alien plant invasion has a strong negative impact on butterfly assemblages. It is also in line with recent results from Uganda and Brazil, where butterfly abundance increased with time after forest restoration (Nyafwono et al. 2014; Sant'Anna et al. 2014). The result shows that weeded areas, although small patches surrounded by invaded forest, provided better habitats for butterflies than the non-weeded forest areas that remained beset with non-native invasive species.

The dense vegetation in non-weeded forest areas had low light penetration and high density of alien plant stems, which can disrupt butterfly activity, and thereby abundance (Florens et al. 2010). Most butterflies are dependent on direct sunlight to fly, feed, court and oviposit (Clench 1966). A similar study conducted in a temperate region by Bergman (2001) found same trends for the butterfly species *Lopinga achine*, were the population density decreased dramatically with a canopy cover of more than 90% and changes in the woodland habitat. Forest density was not quantified in my study, but there are major differences in plant stem density between weeded and non-weeded forest areas (Figure 15a,b; Monty et al. 2013; V. Florens pers. comm.).

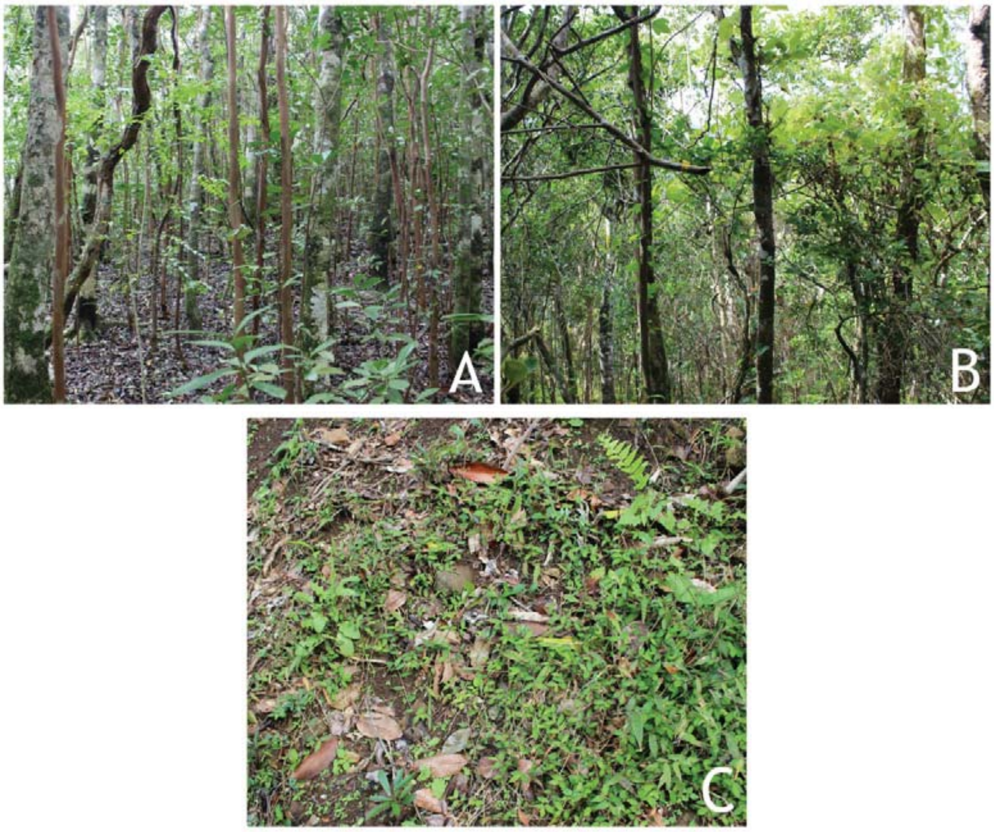


Figure 15 A) Non-weeded forest area, **B)** weeded forest area and **C)** common larval food plants in weeded area of Chamarel. Photos: P.J. Kajl.

The abundance of larval food plants is also important for the distribution of butterflies, and may be one of the reasons why butterfly abundance was higher in weeded areas (Tallamy & Shropshire 2009; V. Florens, pers. comm.). Larval food plants were not quantified, but were clearly more abundant in weeded forest. For example, weeded forests often sustained more larval food plants of the family Gramineae (Figure 15c). Indeed, the two most frequently observed butterfly species, *H. narcissus* and *N. frobenia* are species that prefer shady wooded areas and depend on Graminae, among other plants, as larval food plants (Davis & Barnes 1991). In non-weeded areas, dense vegetation and less light penetration may have decreased the amount of larval food plants.

However, in general I detected very few butterflies. This may have several explanations. Few flowers and fruits were observed at this time of the year, which may have affected the abundance of fruit and nectar feeding butterflies. A study should be conducted in the warmer and wetter season to account for these butterflies. Butterfly counts in this study were conducted during a short time period in August, which is in the dry, cool season in Mauritius. Clouded and windy weather may have affected butterfly activity and possibly underestimated their abundance. Seasonal fluctuations in the tropics may also influence observed butterfly abundance, as butterflies may use different habitats at different times of the year (Bonebrake et al. 2010; Clench 1966). Some species of Mauritian butterflies may therefore have occupied other habitats at the time of my study. Seasonal polymorphism is also common among Mauritian butterflies, where some species form a well-developed sub-marginal ring of eyespots on the brown ventral surface of the wing in the wet, warmer season (Brakefield 1987). In the dry, cooler season, these are greatly reduced or absent, which make the butterflies more cryptic and less active (Brakefield 1987). This may have affected the detection rates of some species.

In any case, the complete absence of butterflies in non-weeded forest may have significant consequences for the native plant species. Butterflies are important pollinators for native plants, reflecting their mutualistic adaption to native plants in their habitat (Fleishman et al. 2005). For example, Tallamy and Shropshire (2009) showed that butterfly species richness and abundance was higher on native than exotic plants in America. In Mauritius, the higher abundance of butterflies in weeded areas supports these findings. These results also suggest that the alien plant invasion may significantly reduce butterfly pollination success in the tropical forests of Mauritius (Florens et al. 2010; Ghazoul 2004). In areas with a lack of such pollinators, native plant regeneration may thus be significantly reduced. Any reduction in butterfly abundance and diversity due to loss of host plants can also be reflected higher up in the food chain, for example on predators of butterflies and their larva (Tallamy & Shropshire 2009).

4.2. Predation on artificial caterpillars

Probability of overall predation on artificial caterpillars was significantly higher in weeded than non-weeded areas, which supports my second prediction. According to the GLMM analyses and corresponding AIC values, the probability of predation depended on forest area (weeded and non-weeded), and to some extent the colour of the caterpillar (Table 4 and 5; Figure 11 and 12 a, b). There are several possibilities to why there was more overall predation in the weeded areas. For example, the weeded areas may have a higher food availability and therefore higher predator abundance than non-weeded forest areas. The physical conditions of the weeded areas may also be more accommodating for predators, whereby birds can more easily manoeuvre through the more open forest. For example, study by Tvardikova and Novotny (2012) show that artificial caterpillars are predated upon at a higher rate in more open forest.

However, the dominant predator group in this study was insects (n=72), which correspond to similar studies quantifying predation marks on artificial caterpillars (Fáveri et al. 2008; Howe et al. 2009; Koh & Menge 2006; Loiselle & Faraji-Brener 2002). In tropical forests, invertebrate attacks on artificial caterpillars mostly come from ants, predatory wasps, beetles and stinkbugs (Fáveri et al. 2008; Howe et al. 2009; Loiselle & Faraji-Brener 2002; Stamp & Bowers 1991). Arthropod predation on artificial caterpillar has previously been shown to be higher in pristine forests than in disturbed forest areas (Posa et al. 2007), which is similar to the results found in the current study where forest type was the main predictor of insect predation (Figure 12a). This may be due to arthropods being sensitive to habitat modification (Kremen et al. 1993) as they tend to be influenced by plant species richness and surrounding vegetation complexity (Gaston 1992; Haysom & Coulson 1998).

One unexpected result in this study was that brown caterpillars were preferred over green by predators especially by birds, which are visually oriented predators (Posa et al. 2007). Given that brown caterpillars were more conspicuous on green plant leaves, green caterpillars more conspicuous on brown tree trunks and branches, and plant part did not show any effect in the statistical analysis, it appears that brown caterpillars simply were preferred over green by birds in both weeded and non-weeded areas. The marks from birds were mainly from small beaks (n=21), rather than big beaks (n=2). This is consistent with a higher degree of attack from smaller billed native birds, such as Grey White-Eye (*Zosterops borbonicus mauritianus*) and Mascarene paradise flycatcher (*Terpsiphone bourbonnensis*), rather than the larger exotic birds (red-whiskered bulbul, *Pycnonotus jocosus* and common myna, *Acridotheres tristis*). Since the weeded forest area had a trend of higher predicted predation by birds than non-weeded forest (Figure 12b), this suggests that native birds prefer restored forest areas to areas invaded by exotics and this is clearly of conservation significance.

The teeth marks on artificial caterpillars portray attempted predation by rodents, such as rats (*Rattus rattus*, *R. norvegicus*), mice (*Mus musculus*) and shrews (*Suncus murinus*). These are all common in Mauritian forest, but are all invasive exotics (Checke & Hume 2008b; Motala et al. 2007). The fact that neither forest type (weeded or non-weeded), colour nor plant part influenced the likelihood of depredation, these rodents appear to be generalists in the forest settings studied. Although accounting for the smallest number of attacks (n=17), their presence is clearly negative as shown by their contribution to extinctions of several endemic birds and reptiles (Dulloo et al. 2002; Harper & Bunbury 2015; Strahm 1999; Towns et al. 2006). In assessing ecosystem health and functionality through a higher number of species interactions, these rodents should clearly not be included. Nevertheless, overall results indicate that predation does not negatively influence butterfly abundance, but rather indicate a more complete food web in the weeded forest areas.

Although the use of artificial caterpillars is a frequent, cost-effective and easy way to quantify predation, there are some caveats that should be recognized. For example, a lack of chemical or plant derived cues may prevent predators from locating the artificial caterpillars, as they do not impact plants as real herbivores (Howe et al. 2009). The artificial caterpillars do not react when they are attacked, which can make them suspicious to potential predators and therefore underestimate real predation rate of the forest area (Brodie 1993; Howe et al. 2009). However, the high predation rates seen in this study suggests that these issues were likely of little influence to the overall result.

4.3. Herbivory

Predicted overall herbivory did not differ significantly between weeded and non-weeded forest, disagreeing with the third prediction. An explanation may lie in the fact that herbivore populations are influenced by both bottom-up (food availability, host plants) and top-down (predation and parasites) control (Barone & Coley 1996; Hairston et al. 1960; Power 1992; Richards & Coley 2007). I have already established that predation on herbivores (artificial caterpillars) are higher in weeded forest compared to non-weeded, and this may limit herbivory in these forests. In non-weeded forest on the other hand, the examined native plants existed in a sea of exotic species. This may have limited herbivore populations and herbivory, leading to the similar herbivory rates observed between weeded and non-weeded areas in this study. This interpretation is consistent with studies that show that the composition, diversity and density of surrounding plants may increase or decrease herbivory on particular species and thereby influence the overall herbivory rate (Brown & Ewel 1987).

However, the results show that herbivory rates are species-specific (Figure 13a,b). This may be due to species-level differences in physical and chemical features of each plant, such as their toughness, defensive compounds and nutrient composition (Paul et al. 2011). It may also reflect a disruption of interactions between certain native plants and their specialist herbivores due to invasion of either exotic plants, exotic insects or both (Motala et al. 2007). It was not possible in the current study to determine whether the herbivores were exotic or not, but native insect arthropods generally only inhabit weeded forests (Hugel 2014; Kitson et al. 2013; Motala et al. 2007). For example, the genus *Cratopus* in Mauritian forest remnants reflects its coevolution with native host plants in dietary analyses (Kitson et al. 2013), while endemic grasshoppers are more frequent in weeded forests compared to forests invaded by exotic species on both Mauritius and Rodrigues island (Hugel 2012; Hugel 2014).

Leaves in tropical forests are damaged by a diverse set of herbivores and pathogens, although the most important plant consumers are insects in the understory (Barone & Coley 1996). In fact, leaf consumption by herbivores has a significant impact on plants and plant communities and about 10% of plant production in tropical forests is consumed annually by herbivores at the community level (Poorter et al. 2004). Since forest arthropods are sensitive to disturbance (Kremen et al. 1993; Motala et al. 2007), and trophic interactions between native plants and specialist herbivores may be sensitive to disturbance such as species invasions (Kitson et al. 2013), lower herbivore diversity was expected in the non-weeded forests. Species-specific differences were observed (Figure 14; Appendix III), with little difference between weeded and non-weeded forest areas. It would be appropriate to link herbivore categories to specific insects in these forest areas and to establish which herbivore categories are native or not, in order to provide a better picture of the ecosystem as a whole.

The most frequent categories of herbivory were bites of varying size from the edge, followed by corridors into the leaf. These were present on all plant species. Small to large bites are probably from larvae and caterpillars of different species as well as beetles (Labandeira et al. 2007; Paul et al. 2011; V. Florens pers. comm.; Table 1). Corridors most likely correspond to the genus *Cratopus*, which consists of 80 species found on the Mascarene islands (Réunion, Mauritius and Rodrigues; V. Florens pers. comm.; Kitson et al. 2013). These feed on broad range of Mauritian plant species (Kitson et al. 2013). Holes with even edges were less frequent, but also present on all native plants. These probably correspond to beetles of family Crysomelidae, which are common leaf consumers (F. Midtgaard pers. comm.; Labandeira et al. 2007), whereas uneven holes of varying sizes probably are a result of snails and slugs (Labandeira et al. 2007; V. Florens pers. comm.). For example, large snail *Achatina fulica* is a frequent exotic species in Mauritian forest remnants, and a major consumer of leaves (Gopal 2003; Reaser et al. 2007). Less common were minors and galls, which were found mainly on *D. tessellaria*. This may be due to samples being taken from the canopy of mature trees rather than the understory as was the case for the other species.

Comparing herbivory in weeded and non-weeded native forest plots has not previously been done in Mauritius. Here, herbivory measurements could help understand plant fitness, regeneration and turnover in areas weeded of alien invasive species and in non-weeded forest areas. However, measuring herbivory is complex and several factors can influence herbivory rates, such as physical features of each plant, its defences, age of the leaves, their toughness and nutrient composition (Paul et al. 2011). Therefore, my methodology clearly has its limitations. For example, it does not account for totally defoliated leaves and long-term observations of labelled leaves and shoots would be preferable (Lowman 1984). This would also account for any potential seasonal differences in herbivory prevalence (Barone 2000). Since herbivores were not identified, it is also unknown whether herbivory on the chosen native plant species was carried out by native or exotic herbivores. Further studies on herbivory and herbivore diversity in Mauritius are therefore clearly desirable to understand: 1) herbivory rates on native versus exotic species and test the results that invasive exotics tend to sustain less herbivore damage (Jogesh et al. 2008); 2) the role of native versus exotic species in herbivory on native plants in weeded and non-weeded areas; and 3) the role of specialists and generalists in herbivory on native plants in weeded and non-weeded areas. This will be important since invasions by exotic forest insects are growing worldwide (Liebhold & Tobin 2010; Wetterer et al. 2012), and exotic herbivores may have a negative influence on native plant recovery. Understanding native insect diversity in Mauritian forest remnants is also important for conservation purposes, as there is currently lack of information on the insect fauna and how to best preserve it (Motala et al. 2007).

4.4. Conclusion

The aim of this study was to assess the overall health of the restored versus non-restored forest at a community scale, using an indicator taxon (butterflies) and species interactions as a proxy. I found that weeding presented a significant positive effect on native butterfly diversity. In addition, predicted predation on artificial caterpillars was higher in weeded areas and, at least for birds, appeared to be performed by native species. Herbivory rates and diversity of herbivore attacks did not differ significantly between weeded and non-weeded forests, but this may be explained via top-down and bottom-up control of herbivores where herbivore predation is higher in weeded forest and a limitation of food resources in non-weeded forest. In conclusion, the results of this study suggest that weeded forests portray a more species rich and functional ecosystem than non-weeded forest areas. Results therefore show that with the right restoration measures, the remaining native forests of Mauritius may, to a large degree, recover and increase in native biodiversity. This underlines previous studies showing that removal of invasive plants and exclusion of invasive animals from CMAs can have rapid and significant positive effects on the recovery of native biodiversity (Baider & Florens 2011; Florens et al. 2010; Kueffer, 2011; Monty et al. 2013).

This study therefore clearly suggests that the conservation of native biota can be applied at the habitat level with success. Much of the restoration work carried out in Mauritius has focused on particular endangered species, such as the Pink Pigeon (*Columba mayeri*) and Mauritius kestrel (Florens 2008; Jones & Swinnerton 1997; Jones 2008). Although individual species may be more vulnerable to extinction, it is difficult to preserve a species unless the habitat on which it depends is considered simultaneously. In addition, a better health of the entire ecosystem preserves more species interactions and species that have the same ecological roles and niches (Hooper et al. 2005; Palmer et al. 1997). Conservation and management of the native Mauritian biota should therefore perhaps gradually move away from the species-centred approach currently practiced, towards a more habitat-centred approach for native biodiversity recovery as previously argued (Donlan et al. 2002; Zavaleta et al. 2001).

The weeded areas in Chamarel and Camizard are examples of areas where such habitat-centred restoration measures have been practiced. Although weeding of highly invaded forests is challenging, expensive and time consuming (Jogesh et al. 2008), and potentially even impossible to completely reverse (Hooper et al. 2005), these forests can go through a restoration process and allow more native species to recover. Yet, the CMAs in Mauritius are very small patches of weeded forests surrounded by increasingly degraded and invaded forest (Florens 2008; Namah 2010). In addition, the effects of habitat alteration through exotic species invasion are still poorly understood (Koh & Menge 2006; V. Florens pers. comm.). The conservation and management of native forests in Mauritius are therefore still in need of development, and more and larger managed areas are necessary in order to safeguard the region’s endemic and threatened species.

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Appendix I

Statistical analysis on rodents as predators of artificial caterpillars, excluded from the main results.

Table 1: Model selection for rodents as predator group. The best model included explanatory variables forest area, colour and plant part and is indicated in bold.

Model	df	AIC
Teeth ~ W/NW + Colour + Plant Part + (1|Site/Transect/Plot)	**273**	**133.7**
Teeth ~ W/NW + Colour + (1|Site/Transect/Plot)	275	137
Teeth ~ W/NW + (1|Site/Transect/Plot)	276	135.1

Table 2: Output table from GLMM analysis. None of the explanatory variables were significant (p<0.005).

	Estimate	Std. Error	z value	Pr(>|z|)	Significance
(Intercept)	-3.307	0.799	-4.141	<0.001	***
Forest area (weeded/non-weeded)	-0.793	0.661	-1.199	0.230	
Colour (green/brown)	-0.108	0.532	-0.203	0.839	
Plant part (leaf)	-0.540	0.898	-0.602	0.547	
Plant part (stem)	1.1876	0.629	1.888	0.059	.

Appendix II

Species specific differences between five native plant species. Remaining plant species are presented as reference species (intercept), forest area is not significant for any of the species.

Table 1: Output table from GLMM analysis showing prediction for intact leaves. Species-specific differences between plants for all species presented as reference species (intercept). Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' are presented.

A)

	Estimate	Std. Error	z value	Pr(>lzl)	Significance
(Intercept - *D. tessellaria*)	-2.824	0.306	-9.216	<0.001	***
Forest area (weeded/non-weeded)	-0.332	0.194	-1.710	0.087	.
C. tacamahaca	3.134	0.349	8.977	<0.001	***
E. macrocarpum	1.201	0.358	3.358	<0.001	***
I. parviflora	1.863	0.348	5.360	<0.001	***
W. trinervis	0.206	0.387	0.534	0.593	

B)

	Estimate	Std. Error	z value	Pr(>lzl)	Significance
(Intercept - *E. macrocarpum*)	-1.623	0.235	-6.907	<0.001	***
Forest area (weeded/non-weeded)	-0.332	0.194	-1.709	0.087	.
D. tessellaria	-1.201	0.358	-3.358	<0.001	***
C. tacamahaca	1.932	0.286	6.757	<0.001	***
I. parviflora	0.662	0.286	2.312	0.020	*
W. trinervis	-0.995	0.336	-2.957	0.003	**

C)

	Estimate	Std. Error	z value	Pr(>lzl)	Significance
(Intercept - *I. parviflora*)	-0.961	0.215	-4.470	<0.001	***
Forest area (weeded/non-weeded)	-0.332	0.194	-1.709	0.087	.
E. macrocarpum	-0.662	0.286	-2.311	0.020	*
D. tessellaria	-1.863	0.348	-5.360	<0.001	***
C. tacamahaca	1.270	0.265	4.801	<0.001	***
W. trinervis	-1.657	0.326	-5.081	<0.001	***

D)

	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**	**Significance**
(Intercept - *W. trinervis*)	-2.618	0.286	-9.167	<0.001	***
Forest area (weeded/non-weeded)	-0.332	0.194	-1.709	0.087	.
I. parviflora	1.657	0.326	5.082	<0.001	***
E. macrocarpum	0.995	0.336	2.958	0.003	**
D. tessellaria	-0.206	0.386	-0.543	0.594	
C. tacamahaca	2.928	0.329	8.905	<0.001	***

Table 2: Output table from GLMM analysis showing prediction for proportion of herbivory damage. Species-specific differences between plants for all species presented as reference species (intercept). Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' are presented.

A)

	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**	**Significance**
(Intercept - *C. tacamahaca*)	-3.787	0.605	-6.257	<0.001	***
Forest area (weeded/non-weeded)	0.006	0.357	0.016	0.987	
D. tessellaria	-1.840	1.160	-1.587	0.113	
E. macrocarpum	-1.730	1.160	-1.491	0.136	
I. parviflora	-0.944	0.921	-1.025	0.305	
W. trinervis	1.285	0.618	2.403	0.016	*

B)

	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**	**Significance**
(Intercept - *D. tessellaria*)	-5.627	1.018	-5.527	<0.001	***
Forest area (weeded/non-weeded)	0.006	0.357	0.016	0.987	
W. trinervis	3.325	1.022	3.254	0.001	**
I. parviflora	0.896	1.228	0.730	0.465	
E. macrocarpum	0.110	1.417	0.078	0.938	
C. tacamahaca	1.840	1.156	1.587	0.116	

C)

	Estimate	Std. Error	z value	Pr(>|z|)	Significance
(Intercept - *E. macrocarpum*)	-5.516	1.020	-5.408	<0.001	***
Forest area (weeded/non-weeded)	0.006	0.357	0.016	0.987	
D. tessellaria	-0.110	1.417	-0.078	0.938	
W. trinervis	3.215	1.022	3.145	0.002	**
I. parviflora	0.786	1.228	0.640	0.522	
C. tacamahaca	1.730	1.160	1.491	0.136	

D)

	Estimate	Std. Error	z value	Pr(>|z|)	Significance
(Intercept - *I. parviflora*)	-4.730	0.740	-6.386	<0.001	***
Forest area (weeded/non-weeded)	0.006	0.357	0.016	0.988	
E. macrocarpum	-0.785	1.228	-0.639	0.522	
D. tessellaria	-0.897	1.229	-0.730	0.465	
W. trinervis	2.429	0.739	3.286	0.001	**
C. tacamahaca	0.944	0.920	1.025	0.305	

Appendix III

Table 1: Herbivore diversity on damaged leaves per plant species. Raw data presenting frequency of each herbivore category.

Category	Species	Presence in Weeded areas	Presence in Non-Weeded areas	Total
Bites	*C. tacamahaca*	74	54	128
Corridor	*C. tacamahaca*	15	3	18
Extensive	*C. tacamahaca*	0	2	2
Gall	*C. tacamahaca*	0	0	0
Hole	*C. tacamahaca*	6	10	16
Miner	*C. tacamahaca*	0	1	1
Bites	*D. tessellaria*	152	185	337
Corridor	*D. tessellaria*	40	53	93
Extensive	*D. tessellaria*	0	0	0
Gall	*D. tessellaria*	5	4	9
Hole	*D. tessellaria*	24	12	36
Miner	*D. tessellaria*	17	21	38
Bites	*E. macrocarpum*	148	174	322
Corridor	*E. macrocarpum*	14	31	45
Extensive	*E. macrocarpum*	0	0	0
Gall	*E. macrocarpum*	0	0	0
Hole	*E. macrocarpum*	4	8	12
Miner	*E. macrocarpum*	1	3	4
Bites	*I. parviflora*	109	142	251
Corridor	*I. parviflora*	38	84	122
Extensive	*I. parviflora*	0	0	0
Gall	*I. parviflora*	0	0	0
Hole	*I. parviflora*	7	4	11
Miner	*I. parviflora*	2	1	3
Bites	*W. trinervis*	181	229	410
Corridor	*W. trinervis*	27	7	34
Extensive	*W. trinervis*	8	6	14
Gall	*W. trinervis*	5	0	5
Hole	*W. trinervis*	35	33	68
Miner	*W. trinervis*	1	0	1

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