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ORIGINAL ARTICLE

Evidence of biotic resistance to exotic plant invasion in degraded Bornean forests

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Abstract

Intact tropical forests are generally considered to be resistant to invasions by exotic species, although the shrub *Clidemia hirta* (Melastomataceae) is highly invasive in tropical forests outside its native range. Release from natural enemies (e.g., herbivores and pathogens) contributes to *C. hirta* invasion success where native melastomes are absent, and here we examine the role of enemies when *C. hirta* co-occurs with native Melastomataceae species and associated herbivores and pathogens. We study 21 forest sites within agricultural landscapes in Sabah, Malaysian Borneo, recording herbivory rates in *C. hirta* and related native *Melastoma* spp. plants along two 100-m transects per site that varied in canopy cover. Overall, we found evidence of enemy release; *C. hirta* had significantly lower herbivory (median occurrence of herbivory per plant = 79% of leaves per plant; median intensity of herbivory per leaf = 6% of leaf area) than native melastomes (93% and 20%, respectively). Herbivory on *C. hirta* increased when closer to native *Melastoma* plants with high herbivory damage, and in more shaded locations, and was associated with fewer reproductive organs on *C. hirta*. This suggests host-sharing by specialist Melastomataceae herbivores is occurring and may explain why invasion success of *C. hirta* is lower on Borneo than at locations without related native species present. Thus, natural enemy populations may provide a "biological control service" to suppress invasions of exotic species (i.e., biotic resistance). However, lower herbivory pressures in more open canopy locations may make highly degraded forests within these landscapes more susceptible to invasion. Abstract in Malay is available with online material.

KEYWORDS
biological control, *Clidemia hirta*, enemy release, host-sharing, invasive species, Melastomataceae, *Miconia crenata*, phytophagous herbivores, tropical forests

1 | INTRODUCTION

Tropical forests are thought to be less likely to be invaded by exotic plant species than temperate forests due to a combination of low propagule pressure of exotics, low levels of forest disturbance, and high diversity of the native community leading to competitive exclusion and/or reduced establishment from the impact of high herbivore diversity (Chong et al., 2021; Denslow & DeWalt, 2008; Fine, 2002; Rejmánek, 1996). Most recorded incidences of plant invasion in tropical forests occur within highly degraded forests that have altered

forest structures (i.e., low structural complexity and open canopies) and within human-modified landscapes, where propagule pressure is high (Dawson et al., 2015; Döbert et al., 2017a; Mungi et al., 2021; Murphy et al., 2008; Rembold et al., 2017; Teo et al., 2003; Waddell, Banin, et al., 2020; Waddell, Chapman, et al., 2020). However, some exotic plant species do successfully invade tropical forests (e.g., *Chromolaena odorata*, *Lantana camara*, *Miconia calvescens*, *Mikania micrantha*; Fine, 2002; Denslow & DeWalt, 2008; Waddell, Banin, et al., 2020), including closed canopy forest (e.g., *Clidemia hirta*, DeWalt et al., 2004; Waddell, Chapman, et al., 2020), and there is a need to understand why they are successful, to predict future invasions, and their impact within this biome.

Several hypotheses have been proposed to understand invasion processes (see Catford et al., 2009 for an overview) and they are often context specific, differing between taxa and ecosystems (Catford et al., 2021; Jeschke et al., 2012). "Darwin's Naturalization Conundrum" captures two conflicting invasion hypotheses that center around the degree of phylogenetic relatedness between the invading exotic species and the invaded native community (Diez et al., 2008). If an exotic species has close relatives in the native community, then it is likely to be pre-adapted to the local environmental conditions due to shared evolutionary histories and phylogenetic conservatism of functional and life history traits (Flynn et al., 2011). According to this hypothesis, exotic species are unlikely to be filtered out in the early stages of invasion in regions where confamilars occur (i.e., habitat filtering hypothesis; Weiher & Keddy, 1995; Procheş et al., 2008), promoting their invasion success. On the other hand, the occurrence of closely related native species increases the likelihood of strong competition for resources with related natives and pressure from specialist natural enemies, such as herbivores and pathogens, that have evolved to feed on a particular plant family or genus (i.e., biotic resistance hypothesis; Coley & Aide, 1991; Hodkinson & Casson, 1991; Marquis, 1991; Gaston, 1993). These natural enemies can contain the spread of exotic species by limiting their growth and reproduction, as would occur in their native ranges (Levine et al., 2004). These opposing hypotheses highlight the importance of considering closely related species when studying exotic plant invasions, and the strength of each mechanism in a given context will determine whether native relatedness has an overall positive or negative effect for exotic species (Fridley et al., 2007; Tomasetto et al., 2019).

The enemy release hypothesis states that exotic plant species invading new areas may escape natural enemies and have lower herbivore pressure (Colautti & MacIsaac, 2004; Keane & Crawley, 2002). This may enable exotic plants to shift resource allocation from defense to growth and reproduction, giving the invading species a competitive advantage over extant natives (Blossey & Notzold, 1995). The strength of the enemy release effect in invasion is also influenced by the degree of phylogenetic relatedness between invading exotic species and the native community because related species are more likely to share specialist herbivores due to phylogenetic conservatism of insect host choice (Dawson et al., 2009; Lockwood

et al., 2001). In species-rich tropical forests, an invading species will likely have a confamiliar or congener in the native community (Gentry, 1988; Turner, 2001), thereby overcoming the "habitat filtering barrier," but being faced with a potential "biotic resistance barrier" which may limit the invasiveness of the exotic species. However, an invading species may have varied responses in differing contexts, depending on the "receiving" community, including the presence and abundance of native confamiliars.

The empirical support for these hypotheses is mixed (Felker-Quinn et al., 2013; Jeschke et al., 2012; Liu & Stiling, 2006; Meijer et al., 2016), and studies are lacking in tropical regions. There is some support for the enemy release hypothesis in tropical forests (Dawson et al., 2009; DeWalt et al., 2004; Liu et al., 2007), including *C.hirta*, which is highly invasive in Hawai'i where its success is partially due to escape from natural enemies that limit populations to forest edge habitats in its native range (DeWalt et al., 2004). In Tanzanian forests, herbivory rates across multiple exotic species were found to be higher when there were more related species present in the native community (Dawson et al., 2009), implying a role for natural enemies in the invasion process. However, there is little consensus within tropical forests on the role of native communities, with positive, negative, and nonsignificant relationships observed between exotic and native components (Döbert et al., 2017a; Murphy et al., 2008; Teo et al., 2003). This conflicting empirical evidence for these hypotheses is due in part to the lack of studies within tropical forests (Chong et al., 2021) and the context dependency of invasion mechanisms, with the sign and magnitude of any relationship varying with the observed conditions (Catford et al., 2021; Jeschke et al., 2012; Pyšek et al., 2020). In addition, it is unclear how these mechanisms might be affected locally by different abiotic factors, such as the level of disturbance, which is known to alter plant communities (Arellano-Rivas et al., 2016; Laurance et al., 2002, 2011) and in turn their herbivore communities (Basset et al., 2012; Novotny et al., 2006). Therefore, exotic invasions and the hypotheses explaining their success (i.e., biotic resistance or enemy release) need to be studied along environmental and disturbance gradients.

The highly invasive tropical shrub *C.hirta* (L.) D.Don (Melastomataceae) is native to Central and South America (Mexico to Paraguay, and the Caribbean) but is invasive across tropical Africa, Asia, Australia, and Pacific Islands (CABI, 2020), including being the only widespread species invading intact forests in Sabah, Malaysian Borneo (Waddell, Chapman, et al., 2020). The success of *C. hirta* in Hawai'i may be due to escape from natural enemies (DeWalt et al., 2004) because there are no native members of the Melastomataceae there. Host-sharing by herbivores may be more likely in other parts of *C. hirta's* introduced range where it co-occurs with confamiliars, such as Borneo (DeWalt et al., 2004). Due to *C. hirta's* ability to invade and subsequently modify communities of tropical forest interiors (DeWalt et al., 2004; Waddell, Chapman, et al., 2020), it is important to improve understanding of the mechanisms affecting invasion by this species in tropical forests. In this study, we examine evidence for the roles of natural enemy release and biotic resistance in invasion of *C. hirta* within agricultural landscapes of Sabah, Malaysian Borneo, where *C. hirta* co-occurs with

native species of Melastomataceae. First, we look for evidence consistent with enemy release by testing if herbivory in *C. hirta* is lower compared to native Melastomataceae (*Melastoma* spp.) shrubs that occupy a similar ecological niche. Second, we look for context dependency of enemy release by testing whether herbivory rates on *C. hirta* are influenced by proximity to, and herbivory rates of, native *Melastoma* plants (i.e., evidence of biotic resistance), and the influence of local canopy cover. Finally, we test whether herbivory reduces the reproductive output of *C. hirta* plants, and therefore might play an important role in mitigating population growth and spread.

2 | METHODS

2.1 | Related native *Melastoma* plants on Borneo

Related (confamilial) species belonging to the *Melastoma* genus were chosen as the native comparison. There are 41 native *Melastoma* species found in Borneo (Wong, 2016), and identification in the field (as in this study) is difficult due to very similar morphology and hybridization (Wu et al., 2019). However, only three species have distributions within our sampling area (*M. malabathricum*, *M. beccarianum*, and *M. ultramaficum*), with the vast majority of plants encountered being the widespread and very common *Melastoma malabathricum* (Wong, 2016). *M. malabathricum* is a non-forest specialist shrub that occupies similar habitats to *C. hirta* (i.e., roadsides, open-structure forest), and it flowers all year round, as does *C. hirta*. Most *Melastoma* individuals would have been *M. malabathricum*, but because we did not carry out detailed observations of flower morphology or genetic studies, we cannot be certain, and so we refer to *Melastoma* spp. throughout.

2.2 | Study sites

We carried out surveys of herbivory on *C. hirta* and native *Melastoma* spp. plants in 21 forest sites within oil-palm-dominated landscapes in Sabah, Malaysian Borneo (Figure 1a, b) in March and April 2019. Forest sites were conservation set-asides (hereafter "forest sites"), with most specified as being of High Conservation Value (HCVs, Senior et al., 2015), as part of the certification process for sustainability (Roundtable on Sustainable Palm Oil [RSPO], 2018). Forest sites had been commercially logged with varying intensity prior to plantation development, likely between ~1991 and 2009 (Reynolds et al., 2011), and were probably originally retained because they were unsuitable for oil palm cultivation (e.g., too steep or rocky). Forest sites differed in terms of canopy cover and vegetation structure, reflecting these different levels of disturbance prior to plantation development, and varied in size from 3.25 to 1375 ha (forest area surrounded by plantations), with some sites (*n* = 6) adjoining large tracts of forest beyond plantation boundaries (Table S1). Sites were >1 km apart to avoid spatial autocorrelation.

At each site, 100-m transects were established in two forest habitats, one at the forest-plantation edge (hereafter "forest edge"; Waddell, Chapman, et al., 2020) and one in the forest interior (on average 53 m from nearest forest edge; hereafter "forest interior"; Figure 1c). The forest interior transects were located in regenerating forest following clearance, either along logging skid trails, old roads, or abandoned oil palm terraces (Table S1). These two forest habitats were chosen so that our surveys spanned a gradient of canopy cover resulting from previous disturbance that might influence local densities of plants and their herbivore communities. Closed canopy intact forest was not surveyed due to the very low density of *C. hirta* in this habitat (Waddell, Chapman, et al., 2020). The two forest habitats we surveyed differed in terms of light levels and species present, including density of *C. hirta* plants (Waddell, Chapman, et al., 2020).

In total, we obtained data for 39 transects (one forest interior transect was too steep to survey and two other forest interior transects had no suitable *C. hirta* to survey). Within each transect, up to 10 *C. hirta* plants were surveyed for measures of herbivory (selected as the nearest individual to each 10 m mark along the 100-m transect; Figure 1d). For each *C. hirta* plant surveyed, the nearest native *Melastoma* individual (<10 m), if present, was also surveyed for herbivory. Only plants >30 cm height were selected, as these plants typically had at least four fully developed leaves for examining herbivory rates (median = 22 and 19 leaves per *C. hirta* and *Melastoma* plant, respectively; Table S2), in line with our leaf sampling strategy (see below).

2.3 | Herbivory measurements

In this paper, we use the term "herbivory" to refer to any type of leaf damage including by invertebrates (e.g., galls, tissue removal by chewing and leaf scarring), mammals, and pathogens, reflecting the difficulty in distinguishing causes of leaf damage (Coley & Barone, 1996). For each individual plant, both *C. hirta* and *Melastoma* sp., we recorded two measures of herbivory to capture different sources of variation that may occur because of herbivore feeding behavior: herbivory occurrence and intensity (Figure 1d). Herbivory occurrence was recorded by counting the total number of leaves and the number that had sustained herbivore damage to derive a proportion of damaged leaves per plant. To measure herbivory intensity, the first four fully expanded leaves closest to the shoot apical meristems were sampled. New leaves were chosen to minimize effects of leaf age on accumulated herbivory over time. Both sides of the leaves were scanned into high-resolution color images within 6 hours (to avoid leaf degradation) using an Epson Perfection V39 Scanner. Herbivory intensity for each leaf was graded by eye from scanned images to the nearest 10%, with the lowest category of <10% further divided into 0%, 0–2%, 2–5%, and 5–10%, due to the relatively high proportion of leaves within this category of herbivory. The middle value for each category was used as the herbivory intensity score in analyses (e.g., 0, 1, 3.5, 7.5, 15%) and treated as a continuous variable for analysis (see "Statistical analyses" section). We used "by eye" measurements carried out by the same person

(EHW) to reduce any observer biases. This robust measure is a cost-effective approach for measuring large datasets in comparative studies and has been shown to yield similar results to digital image processing methods (Kozlov & Zvereva, 2018 and references within). We used it to integrate damage from multiple different sources (e.g., pathogen attack as well as removal of tissue by herbivorous insects) and it has the benefit that it does not require the original leaf margin to be manually "re-created" as would be necessary for imagining software (e.g., ImageJ; Johnson et al., 2016).

To test whether leaf herbivory reduced reproductive fitness of *C. hirta*, the numbers of reproductive organs (buds, flowers, immature fruits, and ripe fruits) per plant were recorded. These were also recorded for native *Melastoma* spp. plants to draw comparisons between the species groups.

2.4 | Variables influencing herbivory

To examine their influence on herbivory damage in *C. hirta*, we recorded the distance to the closest native *Melastoma* plant and the herbivory rate on this plant. In addition, we recorded habitat type (forest edge vs. forest interior) and local canopy cover, as light levels influence herbivory rates in some species (Eichhorn et al., 2006; Folgarait et al., 1995; Whitham, 1991). We also accounted for *C. hirta* plant size and the density of surrounding *C. hirta* plants, given that adult plants can act as reservoirs for enemies to attack nearby conspecific saplings and seedlings (the Janzen–Connell hypothesis of negative density dependence (Connell, 1971; Janzen, 1970).

To test whether there is spillover of herbivores and pathogens from native *Melastoma* plant onto *C. hirta* plants, we calculated a
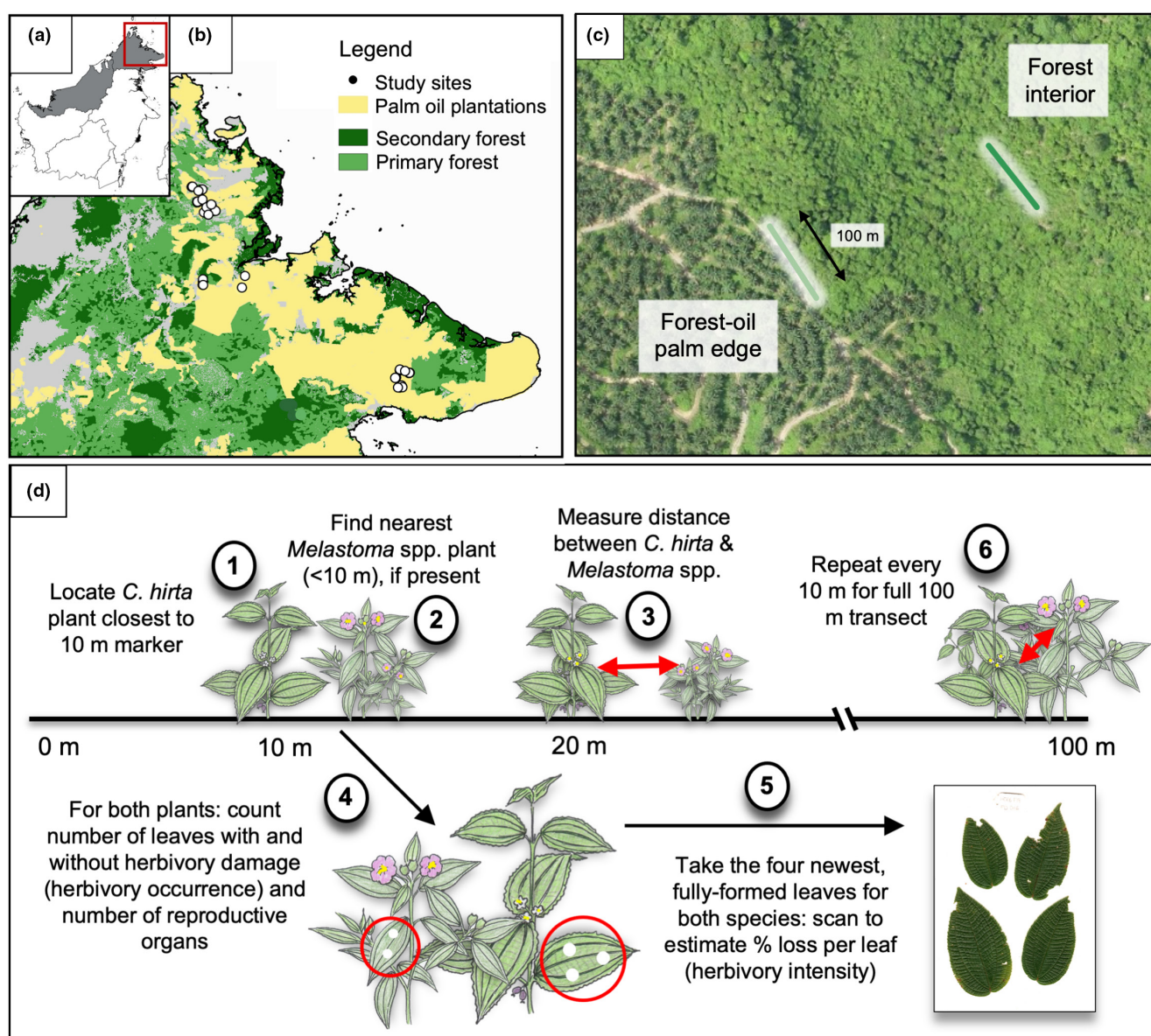

FIGURE 1 Map of the island of Borneo (a) showing the study locations, forest cover, and industrial oil palm plantations within Sabah (b). Drone image of forest site embedded within oil palm plantation showing the locations of the two transects (c). Schematic diagram of sampling design (d). The forest cover dataset (CIFOR) displayed in (B) is available at Gaveau et al. (2017).

composite variable, termed "spillover index," to capture simultaneously the proximity to the nearest native *Melastoma* spp. plant, and the level of herbivory on that *Melastoma* plant. We hypothesized that these would jointly drive spillover. This composite variable uses an exponential distance decay function (Moilanen & Nieminen, 2002), which is commonly used in landscape ecology (Chandler & Hepinstall-Cymerman, 2016; Lowe et al., 2022) and assumes a constant decline in spillover rate with increasing distance. This distance decay is multiplied by herbivory damage on that *Melastoma* plant, such that a *Melastoma* plant at the same distance will have a higher spillover index value if it is more damaged. The equation we formulated was $S = h*exp(-d/x)$, where h is herbivory damage on the nearest native *Melastoma* plant, d is the distance between *C. hirta* and that nearest *Melastoma* plant, and x is the distance decay parameter. We investigated different values of x and found the exact choice of x in our spillover index is not crucial for our conclusions. Nevertheless, we choose the value of x based on model AIC, which was $x = 2$ for *C. hirta* herbivory occurrence and $x = 5$ for *C. hirta* herbivory intensity (see Appendix S1 and Table S3 in the Supporting Information for details of spillover index calculations and parameter optimization).

The degree of forest disturbance was captured by surveying the two habitats, either highly disturbed forest edges or previously disturbed forest interiors. Percentage canopy cover was recorded every 20 m along transects (five points per transect, with the mean of four measurements facing each cardinal direction per point; recorded by the same observer each time) using a concave spherical densiometer (www.forestry-suppliers.com). As an indicator of the light levels experienced by each surveyed plant, we used the nearest canopy cover measurement or the average of the two closest if the plant was equally spaced between two densiometer measurements.

We recorded the total number of leaves as a measure of *C. hirta* plant size. We recorded the presence/absence of *C. hirta* in each 1 m section (and 1 m either side of the transect line; 2 m²), along the length of the 100-m transect (total sample area 200 m²) and defined the "local density of *C. hirta*" as the number of plants within 5 m either side of each focal *C. hirta* plant (presence out of ten 2 m² sections; 1–10).

2.5 | Statistical analyses

We modeled herbivory occurrence and herbivory intensity separately, as we found these two herbivory measurements to be only weakly positively correlated (Spearman rank correlation coefficient=0.28, $p < .001$; SI Figure S1), and they measure different components of variation in herbivory. We used generalized linear mixed models (GLMMs) using the "lme4" R package (Bates et al., 2015). For "herbivory occurrence," all models had a binomial error distribution with the frequencies of damaged and undamaged leaves as the response variable. "Herbivory intensity" was natural log +1 transformed and modeled with a Gaussian error distribution. While the fixed effects of models varied according to the question being addressed (detailed below), the random effect structure stayed the same for all models (individual plant nested within transect nested within site). To improve model

convergence across all models, continuous fixed effects were scaled to unit variance and centered on zero. For each model, all possible combinations of terms in the maximal model were compared using the "*dredge*" function in the "MuMIn" R package (Bartoń, 2013) and the best model selected based on minimizing the Akaike information criterion (AIC$_c$). The variance explained by the best model (conditional R^2) and each of the fixed effect terms (marginal R^2) were estimated for each model using the "rsquared.GLMM" function in "MuMIn" (Nakagawa et al., 2017). The variance explained by each fixed effect included in the top model was estimated separately by removing effects one by one and calculating the difference in the marginal R^2 value.

To test whether herbivory damage was lower in exotic *C. hirta* than in related native plants, herbivory was compared between species (Table 1: Models 1a and 1b). GLMMs were fitted for herbivory occurrence and herbivory intensity separately, with fixed effects of species type (exotic or native), and an interaction with habitat (forest edge or forest interior) to test whether interspecific differences in herbivory varied with forest disturbance.

To test the drivers of herbivory levels in *C. hirta*, we fitted models which include the fixed effects of proximity to herbivory in native species (i.e., our spillover index), habitat (edge vs. interior), and local canopy cover (%), while controlling for plant size (total number of leaves per plant) and local density of *C. hirta* (number (from 0 to 10) of 2 m² transect sections with *C. hirta* present surrounding focal *C. hirta*). These two models (Table 1: Models 2a and 2b) included those *C. hirta* plants that were co-occurring with a *Melastoma* individual only (i.e., within 10 m; n=196 individuals). To test whether these variables influence herbivory differently under different levels of disturbance (i.e., forest edge vs forest interior), an interaction with habitat type was included for all fixed effects. We re-fit these two models (2a and 2b) using our full dataset (all *C. hirta* plants recorded, n=366, not just those co-occurring with native *Melastoma*), to test the effect of habitat, local canopy cover, plant size, and *C. hirta* density on herbivory in *C. hirta*, but without testing for the spillover index (Table 1: Models 3a and 3b).

To examine the effect of herbivory on the reproductive output of *C. hirta*, a GLMM was fitted with the total number of reproductive organs per plant (buds, flowers, immature fruit, and ripe fruit) as the response variable with a Poisson error distribution and fixed effects of herbivory occurrence, herbivory intensity, habitat type, local canopy cover, plant size, and local density of *C. hirta* (Table 1: Model 4). We also tested for interacting effects between all fixed effect terms and habitat to examine whether these variables influence reproductive output differently under different disturbance levels.

3 | RESULTS

3.1 | Comparison of herbivory in *C. hirta* and related natives

Herbivory was significantly lower in exotic *C. hirta* than in native *Melastoma* plants for both herbivory occurrence (15.0% fewer leaves damaged in *C. hirta* plants compared with *Melastoma* plants; Table 1

and Figure 2a; $p < .001$) and herbivory intensity (15.9% lower per leaf for *C. hirta* compared with *Melastoma*; Table 1 and Figure 2b; $p < .001$). For both measures of herbivory (occurrence and intensity), we found higher damage on *C. hirta* plants closer to related native plants with high levels of herbivory (i.e., higher spillover index; Figure 3a and Table 1; $p < .001$). Disentangling the two components of the spillover index showed that the rate of herbivory damage in native *Melastoma* was more associated with herbivory in *C. hirta* than the distance between the plants (Appendix S1; Table S4). For example, there was no difference in expected herbivory occurrence in *C. hirta* plants that were 0–10 m from a native *Melastoma* plant with low (1%) herbivory intensity but expected herbivory occurrence increased to 13% in *C. hirta* that were between 0 and 10 m from a native plant with the highest (92.5%) recorded native herbivory damage (Appendix S1; Table S4).

3.2 | Influence of canopy cover and habitat on exotic herbivory

Canopy cover was nearly twice as high inside the forest than at the forest edge (median cover on edge transect = 49%, range = <1–94%, interior = 83%, range = 8–96%; Figure S2; $p < .01$). We found that herbivory occurrence in *C. hirta* was significantly higher at locations with higher canopy cover (Figure 3b and Table 1; $p < .05$), although there was no effect of habitat type on herbivory (occurrence and intensity) for either exotic or native species, despite differences in canopy cover between forest edge and forest interiors (Figure 2c). This suggests that light levels are influential in determining rates of herbivory in *C. hirta*, although canopy cover explained less variation than proximity to native plants in our models (Table 1). On average, there was little difference in plant size between habitats (Table S2; $p = .38$) or between species (Table S2; $p = .22$). While we found no direct influence of habitat type on herbivory, there was a significant interaction between plant size and habitat (Table 1; $p < .05$) which revealed that the occurrence of herbivory was lower on larger *C. hirta* plants, but only within the forest interior. There was little difference in the local density of *C. hirta* at forest edges (median 8 plants surrounding focal *C. hirta* plant) compared with interior transects (6 plants; Table S2; $p = .49$), and we found no evidence of density-dependent herbivory occurring on *C. hirta* across models (i.e., there was no significant effect of local *C. hirta* density on either herbivory measurement; Table 1).

We found evidence that canopy cover, plant size, and proximity to native *Melastoma* affect herbivory in *C. hirta* but overall, we found considerable unexplained variation around the significant relationships between herbivory in *C. hirta* and our tested drivers. The data

TABLE 1 Summary of best generalized linear mixed models for herbivory in exotic shrub *Clidemia hirta*, in Sabah, Malaysian Borneo. Model numbers correspond to our three hypotheses (see aims) and full model descriptions are outlined in "Statistical analyses" in the methods, including all fixed effects tested. "Herbivory occurrence" = percentage of leaves per plant that are damaged by herbivory and "Herbivory intensity" = percentage of leaf area that is damaged by herbivory. R^2_m = Marginal R^2, which indicates the R^2 for all fixed effects included in the model, R^2_c = Conditional R^2, which indicates the R^2 of the full model (Fixed effects + random effects). Interactions between fixed effects are denoted by an "x."

| Relationship tested	Model no.	Response variable	R^2_m	R^2_c	Fixed effects in top model	Estimate	p
Comparison of herbivory between *C. hirta* and *Melastoma* spp.	*1a*	*Herbivory occurrence*	0.056	0.085	Species (*C. hirta*)	1.036	**<.001**
	1b	*Herbivory intensity*	0.158	0.554	Species (*C. hirta*)	0.988	**<.001**
Influence of proximity to native plants (spillover index), habitat, and canopy cover on herbivory in *C. hirta*	*2a*	*Herbivory occurrence*	0.013	0.026	Canopy cover	0.126	.082
					Spillover index	0.173	**.011**
	2b	*Herbivory intensity*	0.025	0.384	Spillover index	0.165	**.002**
Influence of habitat and canopy cover on herbivory in *C. hirta* (full dataset)	*3a*	*Herbivory occurrence*	0.009	0.031	Habitat (*Forest interior*)	0.022	.870
					Plant size	0.011	.837
					Canopy cover	0.127	**.031**
					Habitat × plant size	−0.199	**.016**
	3b	*Herbivory intensity*	0	0.414	–	–	–
Effect of herbivory on reproductive output in *C. hirta*	*4*	*Number of reproductive organs*	0.282	0.284	Plant size	1.659	**<.001**
					C. hirta density	0.827	**.003**
					Herbivory intensity	−0.769	**.018**
					Habitat (*Forest interior*)	0.483	.192
					Habitat × density	−0.498	.186
					Habitat × herb. intensity	0.819	.056
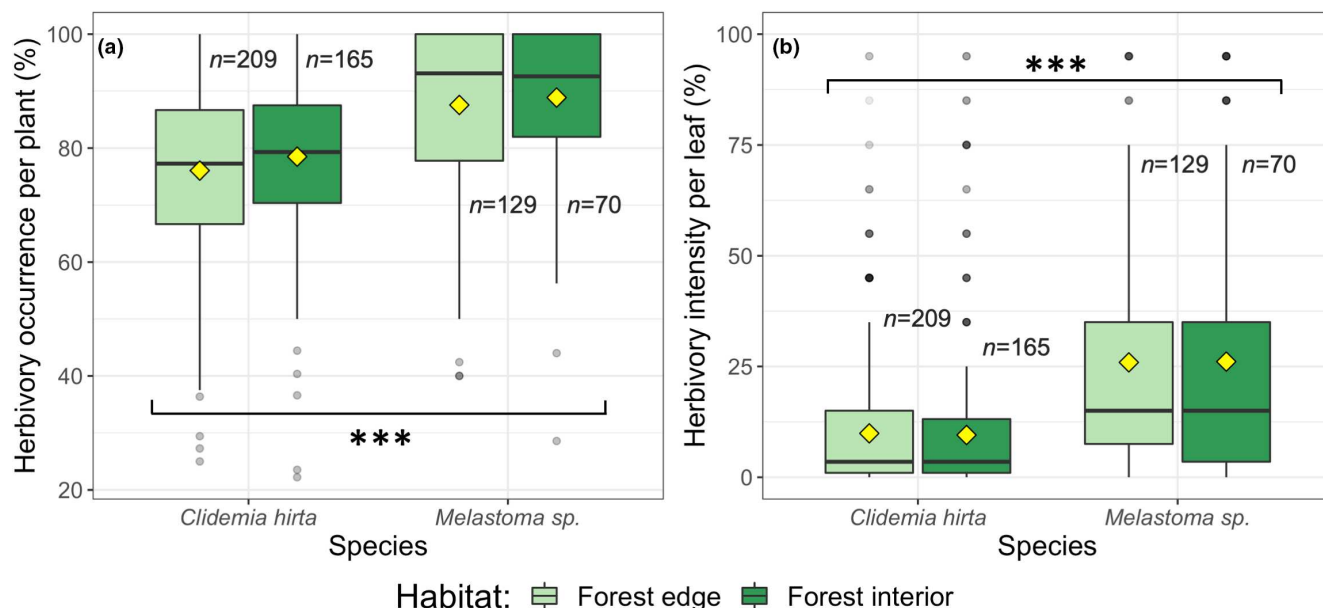
FIGURE 2 Herbivory rates in exotic *Clidemia hirta* and native *Melastoma* spp. plants at forest-oil palm edge (light green shading) and within disturbed forest set asides (dark green shading), in Sabah, Malaysian Borneo. (a) Difference in herbivory occurrence between species and habitat ("herbivory occurrence"=percentage of leaves per plant that are damaged by herbivory). (b) Difference in herbivory intensity between species and habitat ("Herbivory intensity"=percentage of leaf area that is damaged by herbivory). Boxplots show the median (central line) and mean (yellow diamond) values. Significant *p*-values displayed are from ANOVA on generalized linear mixed models (***$p < 0.001$). Details of tests in Table 1 (Models 1a and 1b).

shown in the scatterplots (Figures 3a, b), and the low R^2 terms for fixed effects in our models (R^2 ranging 0.004–0.231; Table 1) suggest there are other factors influencing herbivory in *C. hirta* that we did not record.

3.3 | Effect of herbivory on reproduction

We found a significant negative relationship between herbivory intensity and the number of reproductive organs produced by *C. hirta* (Table 1; $p < .05$). In addition, there was greater reproductive output on larger plants (Table 1; $p < .001$) and where there was a higher local density of *C. hirta* ($p < .01$). Overall, reproductive output was significantly higher for exotic *C. hirta* with 44.5% of *C. hirta* individuals being reproductively active compared to only 6.0% of native *Melastoma* individuals (Table S2; $p < .001$). Additionally, of those reproductively active plants, *C. hirta* had significantly more organs per plant (median of 15) compared to *Melastoma* plants (3.5 organs; Table S2; $p < .001$). Across *C. hirta* and *Melastoma* spp. plants, reproductively active plants were significantly more likely to be larger (Table S2; $p < .001$) and more organs were found on large plants (Table S2; $p < .001$).

4 | DISCUSSION

We found evidence that herbivory damage in invasive *C. hirta* is affected by proximity to native *Melastoma* plants with high rates of herbivory. This suggests that spillover of specialist herbivores and

disease is occurring, and potentially impacting the performance of *C. hirta* within its introduced range in Sabah, Malaysian Borneo. We found that herbivory was greater in areas with higher canopy cover, showing that *C. hirta* plants in more intact forests experience increased herbivory damage, offering a potential means to suppressing *C. hirta* populations in structurally intact forests. Higher rates of herbivory were associated with lower reproductive output of *C. hirta* plants, as measured by the number of reproductive organs present, suggesting that damage by herbivores may be having a negative impact on the fitness of *C. hirta*. Overall, we found *C. hirta* plants experienced lower herbivory and were more likely to be reproductively active compared with native *Melastoma* plants (Figure S3), which is likely to place *C. hirta* at a competitive advantage over confamiliar native species. However, despite being ecologically very similar (i.e., shrubs, similar maximum heights, flowering year-round), there may be temporal differences in the reproductive output of *C. hirta* and *Melastoma* spp.; therefore, year-round monitoring would be needed to confirm our observations.

4.1 | Evidence for enemy release in *C. hirta* invasion in Sabah

Across our sites, we found *C. hirta* to have much lower herbivory damage than native *Melastoma* spp. (6.1% cf 20% herbivory intensity per leaf), providing potential evidence for enemy release occurring in Sabah. However, the overall levels of herbivory intensity (i.e., percentage leaf area removed) we recorded in *C. hirta* were higher
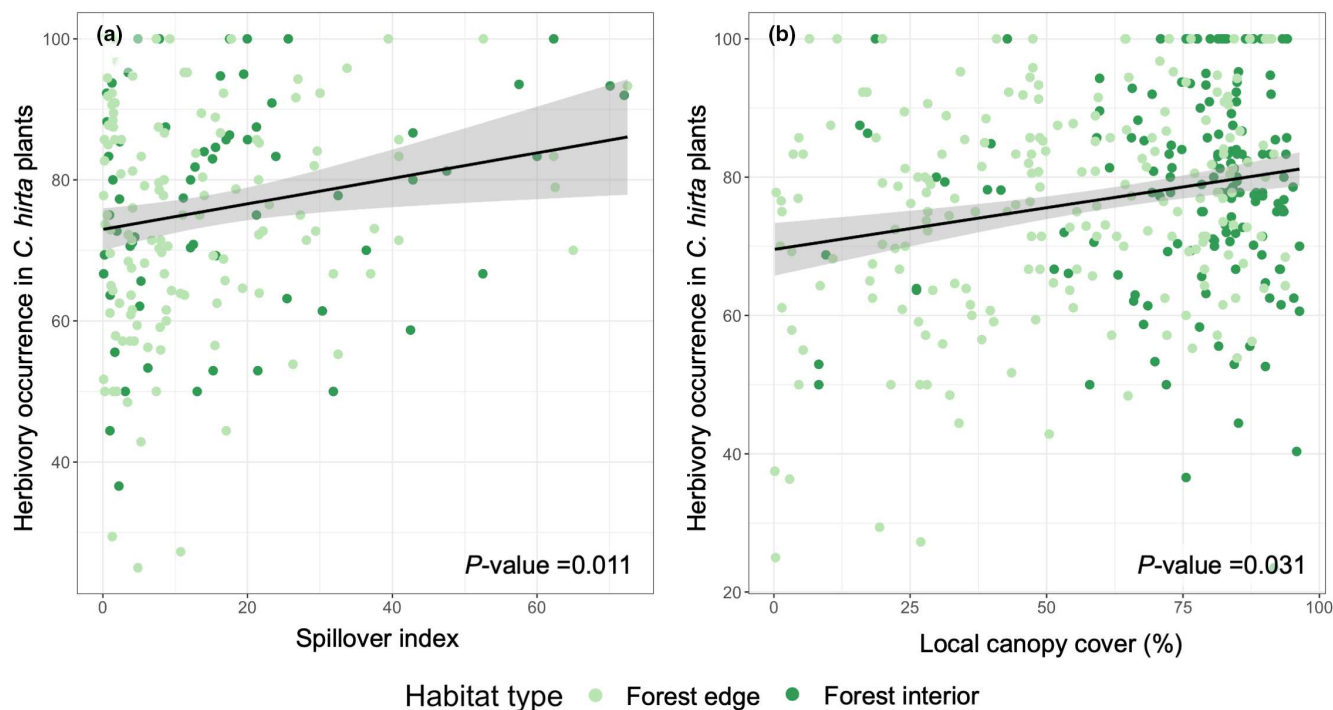
FIGURE 3 Relationship between herbivory occurrence in exotic *Clidemia hirta* plants and (a) index of spillover from native *Melastoma* spp. ($n=196$) and (b) local canopy cover ($n=366$). "Spillover index"=composite variable based on distance decay, combining distance to nearest native plant and herbivory intensity recorded on that plant (Appendix S3 for full details). Regression lines with a 95% confidence interval (gray shading) are on the raw data and does not control for other variables included in the GLMM. Significant *p*-values displayed are from ANOVA on generalized linear mixed models. Details of tests in Table 1.

than those recorded in Hawai'i where no native Melastomataceae are present (median 6.1% of leaf area removed in Sabah cf 0.9% in Hawai'i; DeWalt et al., 2004). The levels of herbivory damage we recorded were comparable to the native range of Costa Rica (4.4%; DeWalt et al., 2004) and another part of the introduced range where native confamiliar species are also present (Tanzania, 4.7%; Dawson et al., 2009), suggesting that herbivory is generally higher where confamiliars are present within the native flora. This gives strength to the argument that host-sharing is occurring in our sites, and hence some evidence of biotic resistance.

4.2 | Evidence for biotic resistance to *C. hirta* invasion by herbivores and pathogens

Our finding of a positive association between herbivory damage in *C. hirta* and proximity to native related species may mean there are shared diseases and herbivores that are adapted to feeding on Melastomataceae plants, including *C. hirta*, despite not being native to Sabah. This finding agrees with other studies that found evidence of phylogenetic conservatism of herbivores in tropical plant species (Ødegaard et al., 2005; Weiblen et al., 2006), including in exotic species (Dawson et al., 2009). In our study, herbivores and pathogens were not explicitly observed but evidence of the same family of moth (tussock moths, Lymantriidae; Georg Hantke *pers. comm.*) was observed on leaves of both exotic and native species (Figure S4a-b)

as well as similar patterns of disease (Figure S4c-e). The significance of the spillover index indicates that melastome herbivores and pathogens are driving patterns in herbivory that we observe, but further investigation to identify the role of specific herbivores and pathogens would confirm whether they belong to specialist or generalist groups.

The negative association we found between herbivory intensity and number of reproductive organs suggests that damage by herbivores and pathogens may reduce *C. hirta* fitness within Sabah. However, despite our significant finding, our effect sizes are small, which tells us other factors are much more influential in driving reproduction in *C. hirta* in Sabah (e.g., plant age, nutrients, pollination, that were not measured in the study). Nevertheless, herbivory can reduce fitness as plants move resources away from reproduction to defense (Eichhorn et al., 2010; Marquis, 1984), and the patterns we observed could potentially affect local population growth and dispersal, reducing spread rates and local dominance of *C. hirta* in Sabah. However, *C. hirta* is widespread in these landscapes, despite increased herbivory pressure in sites with higher canopy cover and reduced reproductive output, including in continuous "old-growth" rainforests (with ~92% mean canopy cover; Waddell, Banin, et al., 2020). Although herbivory intensity is apparently not high enough to exclude *C. hirta* from these forests, it may be enough to regulate populations, preventing *C. hirta* from gaining the competitive advantage it has in Hawai'i to become a dominant species in sites with intact forest understory.

This effect of herbivory would be a form of biotic resistance called biotic containment (Levine et al., 2004), in which natural enemies contribute to limiting populations by lowering growth, reproduction and spread. However, a thorough investigation into the impact of herbivory on growth rates and reproductive output over time using natural enemy exclusion experiments such as in DeWalt et al. (2004) is required to draw robust conclusions on the contribution of herbivory on *C. hirta* fitness, population dynamics and persistence in Sabah.

4.3 | Role of canopy cover in herbivory pressure

We found the occurrence of herbivory on *C. hirta* and native *Melastoma* plants was greater in locations with higher canopy cover (Appendix S3), contrasting with DeWalt et al. (2004) who found no difference in herbivory levels in *C. hirta* between fully open and partially closed canopy in introduced ranges (Hawai'i). The increase in herbivory in more closed canopy locations in our sites may be due to adaptations by the plant to low light and/or responses of the invertebrate community to these abiotic conditions.

Specific leaf area (SLA) increases with declining light levels, indicating thinner leaves in the understorey of tropical forests where light is a limiting factor (Poorter, 1999; Steinger et al., 2003). This adaptation may explain the relationship we found between canopy cover and *C. hirta* herbivory, if thinner leaves are less protected from herbivory, and/or have higher nutritional value. Indeed, SLA data collected for *C. hirta* plants ($n = 294$) in the same forest study sites showed strong increasing trends for thinner leaves over a gradient from oil palm plantation to intact forest, with increasing canopy cover (Figure S3). This trend (i.e., higher SLA in low light conditions) has also been observed in *C. hirta* in a common garden experiment comparing native Costa Rica and introduction Hawai'ian populations (DeWalt et al., 2004). Support for a positive relationship between herbivory and SLA in tropical forests is mixed, with support for (Coley, 1983; Coley, 1988) and against (Poorter et al., 2004), and so evidence in our study for relationships between SLA and canopy cover requires further investigation to explore influences on herbivory patterns. Also, greater herbivory in areas with high canopy cover may be explained by differences in the invertebrate and microbial communities driven by abiotic conditions (e.g., temperature and humidity; Boyle et al., 2021) or biotic factors (e.g., understory pant community; Novotny et al., 2006; Basset et al., 2012), and warrants further investigation.

4.4 | Other potential drivers

This study tested a small part of the overall system in which interactions between exotic *C. hirta* and native *Melastoma* spp. are occurring, and although significant, our fixed effects of spillover and canopy cover in our models explain low variation (R^2 values in Table 1), revealing that other unaccounted factors are driving variation in herbivory in *C. hirta*. Sampling more individual *Melastoma* plants could add strength to our finding that our spillover index drives herbivory in *C. hirta* and is a worthwhile line of enquiry for future studies, to explore the distances and densities at which these biotic relationships are occurring. The distribution of microbial and invertebrate communities (e.g., local species richness and abundance) within these heterogeneous degraded landscapes, which are likely to be locally patchily distributed according to abiotic conditions (e.g., microclimate) and biotic factors (Boyle et al., 2021), would likely be highly influential in driving herbivory patterns in both *C. hirta* and *Melastoma* spp. The presence of trichomes (i.e., hairs) or leaf toughness are unlikely to be influential as both *C. hirta* and *Melastoma* have hairs and similar leaf toughness (Shiels et al., 2014; Turner & Tan, 1991), but other plant defenses (e.g., chemicals) may be important in driving difference between species. Future studies could test the influence of additional drivers (e.g., *Melastoma* density, SLA, microbial and invertebrate communities, plant defenses) as well as experimentally test our spillover finding, using insecticides and fungicides on native *Melastoma* spp. similar to DeWalt et al. (2004), and develop a better understanding of the specific taxa involved in the herbivory, their behavior, and spatiotemporal distributions.

4.5 | Conclusion

C. hirta is one of the most prevalent exotic invaders of tropical forests, including forest patches embedded in oil palm landscapes in South-East Asia, which are crucial for maintaining biodiversity within human-modified tropical landscapes. Our findings that there is reduced herbivory and potentially higher reproductive output in more open habitats, may result in the spread and colonization of *C. hirta* in the most degraded of these forest patches. Overall, our results suggest that herbivory pressure for exotic species is higher when native confamiliars are present in the native flora, and shared herbivores may act as a "biological control," limiting their reproduction and thus the long-term spread. These results highlight that other exotic species that have no native confamiliars may pose the highest risk to these human-modified habitats, especially those species with the traits known to increase colonization within tropical forests (Dawson et al., 2009; Waddell, Chapman, et al., 2020). By restoring these forests to have intact canopy cover, the number of exotic species will decrease (Waddell, Chapman, et al., 2020) and this high canopy cover may also limit the spread of *C. hirta* due to reservoirs of herbivores inside intact forest that provide a natural control, lowering reproductive outputs and therefore fitness within Sabah.

AUTHOR CONTRIBUTIONS
EHW, LFB, MH, JKH, and DSC conceived the ideas. EHW, LFB, MH, JT, JKH, ABS, and DSC designed the methodology; EHW and ABS collected the data; EHW and DSC analyzed the data; EHW led the writing of the manuscript.

CONFLICT OF INTEREST STATEMENT

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available at NERC EDS Environmental Information Data Centre. https://doi.org/10.5285/2e2e2970-eb78-4005-b271-7101e615186a (Waddell et al., 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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