RESEARCH ARTICLE

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Trait filtering during exotic plant invasion of tropical rainforest remnants along a disturbance gradient

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Abstract

1. Human-modified tropical landscapes are often invaded by exotic plant species, but relatively few species are able to colonise remnant areas of rainforest embedded within such landscapes. The functional traits of successful invaders of natural versus anthropogenic habitats are poorly known, especially in tropical regions, and identifying such traits provides insight into the mechanisms that drive invasion. Here, we examine the invasion of tropical rainforest remnants along a disturbance gradient, within a human-modified agricultural landscape, and determine whether exotic species that invade these forests are selected according to particular traits.

2. We surveyed the occurrence of 18 exotic species along 100-m transects in four habitats—oil palm road, forest-oil palm edges and disturbed and intact forest within rainforest remnants—at 21 sites across Sabah, Malaysian Borneo. We collated data on four functional traits relevant to the barriers plants encounter when colonising new environments (e.g. dispersal and persistence) and tested whether trait filtering occurs during invasion of rainforest remnants.

3. Exotic species richness declined significantly from oil palm (mean 9.2 species per transect) to forest edge (7.8 species) to inside rainforest remnants (3.1 species in disturbed forest), and only one species, *Clidemia hirta*, invaded intact forest. Exotic communities within rainforest remnants had long-distance (vertebrate) dispersal, were woodier and had taller maximum heights, compared to those found in oil palm. For each trait, the community-weighted mean for the forest edge community was intermediate between oil palm and disturbed forest, suggesting trait filtering during the invasion of rainforest remnants.

4. Our study provides strong evidence that trait filtering occurs during invasion from human-modified agricultural habitats into previously disturbed forests via the forest edge. Successful invasion of rainforest remnants requires relatively

long-distance dispersal, in particular by vertebrates, as well as traits that are more similar to those of native forest species (i.e. tall and woody), making these exotic species more able to compete and persist in that environment. Our results show that disturbed tropical rainforests with open canopies are susceptible to invasion and highlight the traits of exotic species which can invade rainforest habitats, and which may pose a threat to regenerating tropical rainforests.

1 | INTRODUCTION

Understanding the processes driving plant invasion within different ecosystems has been a long-standing goal of ecological science (Elton, 1958; Lodge, 1993). As human population and land-use change increases, it is vital to understand these processes in human-modified landscapes. Successful invasion of any habitat requires species to overcome sequential ecological barriers separating different stages of invasion: introduction, establishment, spread and impact (Levine, Adler, & Yelenik, 2004). Life-history and functional traits of invading species are influential at each stage of invasion and play an important role in key invasion hypotheses (Catford, Jansson, & Nilsson, 2009). As such, identifying the traits of successful invaders provides insight into which mechanisms are driving invasion and can facilitate predictions of whether an invading species will be successful in a particular habitat.

There is no set of traits universal to all invading species and across all invaded habitats, as ecological barriers faced by exotic species vary between ecosystems (Pyšek & Richardson, 2008). However, exotic species will readily spread into new areas if they have traits associated with efficient dispersal (e.g. many seeds produced regularly, small seed mass, long-distance dispersal;Colautti, Grigorovich, & MacIsaac, 2006; Nathan et al., 2008; Pyšek & Richardson, 2006; Rejmánek & Richardson, 1996). Once introduced, invading species will only establish persisting populations if they are adapted to the environmental conditions of the invaded habitat and can compete successfully with the native species community, and those that are not adapted will be filtered out (Procheş, Wilson, Richardson, & Rejmánek, 2008; Weiher & Keddy, 1995). The traits which facilitate invasion in one habitat may not confer the same outcome in another due to differences in environmental conditions (Sher & Hyatt, 1999). In disturbed habitats, the increase in resource availability promotes invasion (Blumenthal, 2006; Davis, Grime, & Thompson, 2000) as the majority of invasive species are light-loving ruderal species (i.e. r-strategists; Pyšek & Richardson, 2008; Rejmánek & Richardson, 1996). Therefore, many exotic species are unlikely to invade undisturbed environments where resource availability (i.e. light and space) is low, including closed-canopy forest

ecosystems. In both temperate and tropical forests, only those exotic species that have some degree of shade tolerance and traits that allow them to compete with the native flora will establish, which could for example include high relative growth rate, large above-ground biomass, high maximum height and high photosynthetic rates (Bufford, Lurie, & Daehler, 2016; Koike, 2001; Pyšek & Richardson, 2008; van Kleunen, Weber, & Fischer, 2010; Weiher et al., 1999). Thus, exotic species that are invasive in highly disturbed anthropogenic habitats may not necessarily be able to colonise adjacent less-disturbed, closed-canopy natural habitats.

The spread of exotic species into natural tropical forest habitats from invaded anthropogenic areas is not frequently considered in the invasion ecology literature as tropical forests have been considered to be robust to plant invasions thus far (Fine, 2002). However, deforestation across the tropics, due to recent expansion of large-scale agricultural practices, has resulted in exotic plant species being frequently introduced by humans via newly created transport networks (Hulme, 2009; Levine & D'Antonio, 2003; Seebens et al., 2015). These heavily invaded agricultural areas may act as sources of exotic propagules that disperse into areas of native forest retained within these landscapes as conservation set-asides (Waddell, Banin, et al., 2020). However, traits that result in successful invasion of open agricultural areas are likely to differ from those that result in successful invasion of natural forest habitats. In this study we investigate, for the first time, the spread of exotic plants along a gradient of disturbance from highly invaded, anthropogenic habitats (oil palm plantations) into native tropical rainforest remnants that are recovering from disturbance, and test whether there is selection for particular traits across the disturbance gradient.

The abiotic conditions and biotic communities of native rainforest remnants are very different to agricultural areas (Laurance et al., 2002), and so the anthropogenic habitat edge is likely to act as a strong ecological barrier to invasion. However, within tropical forest remnants themselves, the forest structure and community can be highly heterogeneous due to a combination of edge effects and intensity of previous disturbance (e.g. logging; Broadbent et al., 2008; Laurance et al., 2011; Lôbo, Leão, Melo, Santos, &

Tabarelli, 2011). These disturbances result in physical gaps in the canopy, which increase light levels and thus facilitate the establishment of introduced exotic propagules (Döbert, Webber, Sugau, Dickinson, & Didham, 2017a; Peters, 2001; Teo, Tan, Corlett, Wong, & Lum, 2003; Waddell, Banin, et al., 2020). Many exotic species are not well adapted to closed canopy, intact forests, however, and habitat filtering may mean that only a few shade-tolerant species present in the landscape can establish and persist in these environments (Dawson, Burslem, & Hulme, 2009; Koike, 2001; Martin & Marks, 2006).

In many parts of South-East Asia, land-use change has resulted in a highly fragmented landscape with disturbed rainforest remnants surrounded by predominately oil palm plantations, particularly in Malaysia and Indonesia (Gaveau et al., 2014). These landscapes provide a useful system to study exotic species that have established populations in the oil palm matrix and examine how they disperse and colonise within remnant forests (i.e. conservation set-asides). The understorey of oil palm plantations are known to be dominated by exotic plant species (Fee, Tui, Bin, & Hoy, 2017; Rembold, Mangopo, Tjitrosoedirdjo, & Kreft, 2017), therefore the threat of invasion into areas of remaining forest is high due to this constant source of propagules. It is important to determine the vulnerability of rainforest remnants to invasion because they have been shown to be crucial for maintaining local and regional biodiversity (Hill et al., 2011), ecosystem services (Koh, 2008; Ricketts, 2004) and carbon storage (Fleiss et al., 2020) within sustainable agricultural tropical landscapes. Therefore, disentangling the mechanisms that drive invasion in disturbed forests will help in the management of human-modified tropical landscapes, as well as advance our knowledge of plant invasion processes within tropical forests.

In order to investigate the processes driving plant invasion of tropical rainforest remnants, we compare species and trait compositions of exotic species found along a gradient of disturbance within a human-modified agricultural landscape in Sabah, Malaysian Borneo. Disturbance and light levels decrease along this gradient from oil palm agricultural areas to closed canopy, intact forest, and so we expect exotic species richness and occurrence to decrease accordingly. We then specifically examine functional traits that address the barriers exotic plants encountered during the colonisation of new environments (i.e. invasion), including dispersal (dispersal syndrome and seed mass) and persistence (potential competitive ability: maximum plant height, longevity: stem density and seed production: seed mass; Weiher et al., 1999). Based on previous studies, we expect the exotic community inside the forest to have traits that indicate efficient dispersal and allow propagules to readily spread from oil palm source populations into rainforest remnants (i.e. long-distance dispersal and small, light seeds), as well as traits that promote the establishment of persisting populations (higher maximum height, woody habit) and populations may either benefit from efficient dispersal of smaller seeds or resource provision of larger seeds.

2 | MATERIALS AND METHODS

2.1 | Study sites and transect surveys

Exotic plant communities were studied over two field seasons (July–October 2017 and February–April 2019) in six large-scale oil palm plantations in Sabah, Malaysian Borneo, which had remaining areas of native forest embedded within them (Figure 1). These forest conservation set-asides (hereafter termed 'rainforest remnants') had usually been left unplanted because they were unsuitable for oil palm cultivation (e.g. too steep or rocky) and had been commercially logged (with varying intensity, e.g. due to differences in topography), prior to plantation development, probably between ~1991 and 2009 (Reynolds, Payne, Sinun, Mosigil, & Walsh, 2011). Most of these rainforest remnants are currently managed retrospectively as sites of 'high conservation value' (HCV; Senior, Brown, Villalpando, & Hill, 2015), and therefore should not have experienced significant ongoing direct human disturbance as indicated by the certification process for sustainability developed in 2005 by the Roundtable on Sustainable Palm Oil (RSPO, 2018). Across the six plantations, exotic species were surveyed at 21 sites, in areas of oil palm abutting rainforest remnants. The majority of these rainforest remnants ($n = 15$ sites) were fully surrounded by oil palm, with six sites connected to a larger area of forest reserve outside the plantation boundary. Even though these sites were connected to other forest patches, these six sites were predominately surrounded by oil palm and had experienced the same disturbance histories as the other sites (see Table S1 for individual site details). Sites were at least 1 km apart to avoid spatial autocorrelation.

At each study site, 100-m transects were surveyed in up to four different habitats (Figure 1c), to capture variation in exotic species occurrences dispersing from oil palm planted areas to forest-oil palm edges and then into disturbed logged forest (hereafter 'disturbed forest') and intact logged forest (hereafter 'intact forest'). The four habitats differed in terms of light levels and past and current disturbance (Table S2 and Figure S1). Oil palm transects ($n = 21$) were located along the roadsides of major unpaved plantation roads. Forest-oil palm edge transects ($n = 21$) were either along small unpaved roads (motorbike traffic only) or along oil palm terraces abutting forest. Disturbed forest transects ($n = 20$) were located on average 53 m from the closest forest-oil palm edge, along old logging skid trails, abandoned oil palm terraces or unpaved roads (no longer in use). They were in highly degraded forest habitat that varied in terms of canopy openness and understorey ground cover. Intact forest transects ($n = 16$) were on average 90 m from the closest edge and were considered to be structurally intact (i.e. closed canopy forest), which was usually on steep slopes with a generally sparse ground cover. Due to previous disturbance (i.e. logging and clearing) and most remnants being small (<100 ha; Table S1) the majority of these forests are likely to have extensive edge effects that extend throughout the rainforest remnant (Lucey et al., 2017). Access inside the forest was not possible at one of the 21 sites because it was too steep, and there was no forest site that was deemed to be 'intact' in five very

FIGURE 1 Study location on Borneo (a), within the Malaysian state of Sabah (b), showing the 21 study site locations (black circles), and areas of primary and logged forest and industrial oil palm plantations (Gaveau, Salim, & Arjasakusuma, 2017). (c) Drone image of site F2, showing transect locations (i.e. four habitats): 1 = oil palm, 2 = forest-oil palm edge, 3 = disturbed forest, and 4 = intact forest. Oil palm = major plantation roadside; Forest-oil palm edge = minor plantation road or terrace where oil palm meets forest; Disturbed forest = skid trail, old road or abandoned terrace; Intact forest = closed canopy forest. (d) Transect sampling. Transects were 100 m × 2 m with presence/absence recorded for each exotic species (n = 18) in each 1-m (2 m^2) section along the transect
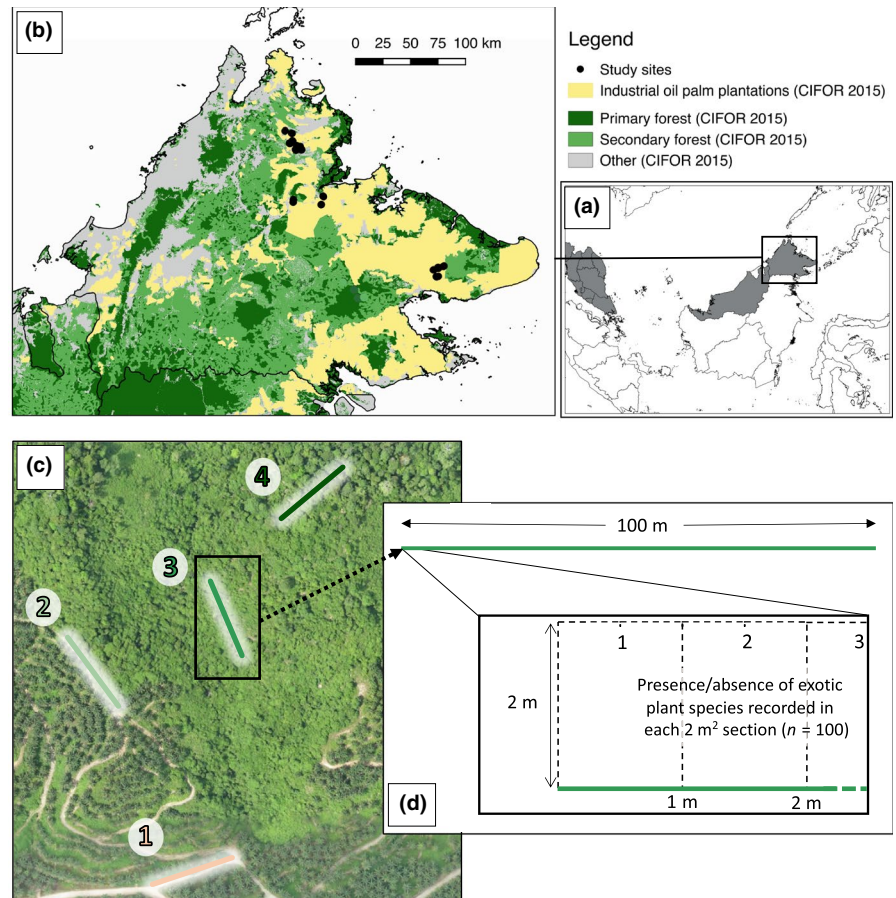
small (<12.5 ha) and highly disturbed rainforest remnants. In oil palm planted areas, active weed management, including herbicide spraying and vegetation cutting, occurred predominantly around the base of oil palm trees. We do not expect these localised management practices to lead to major changes in species composition within the surveyed parts of the oil palm habitat, because our oil palm transects were carried out away from the bases of oil palm trees, in areas which were not sprayed or cleared recently.

Along each 100-m transect, the presence/absence of exotic plant species was recorded within every 1-m section and 1 m either side of the transect (i.e. 2 m^2 sections; Figure 1d). The presence of exotic species in each 1-m section of the transect was our measure of occurrence (i.e. range = 0–100 per species per transect). Pilot transects during the first field season were used to identify exotic species known to be present in Sabah, based on species list produced from literature and online resources (see Bakar, 2004; CABI, 2019; Döbert et al., 2017a; Fee et al., 2017; Pallewatta, Reaser, & Gutierrez, 2003; Peh, 2010), and any additional suspected exotic species encountered in the field (over both field seasons), were identified and their exotic status in Sabah confirmed with the help of local botanists (Danum Valley Research Centre and Sandakan Herbarium). We did not include a leguminous cover crop (*Calopogonium mucunoides*) that was intentionally planted in the oil palm areas, exotic graminoids due to identification challenges, nor any morphospecies that could not be identified to species. This left 18 exotic species, which we believe to be representative of the exotic plant community found within these landscapes.

In order to determine variation in the canopy structure and light levels between and within the four habitats, canopy cover was recorded every 20 m (five points in total per transect, with the mean of four measurements facing each cardinal direction per point) using a concave spherical densiometer (www.forestry-suppliers.com). To examine the complexity of the forest structure, the number of large native trees [>20 cm diameter at breast height (DBH)] along the transect was recorded every 10 m, 5 m either side of the transect and not including oil palm trees. Mean canopy cover (%) and total number of large native trees were used as measures of forest openness and canopy complexity at the transect level.

2.2 | Functional traits of exotic community

Trait data for the 18 study species were obtained from online databases (predominately species datasheets in the Invasive Species Compendium (CABI, 2019) and Kew Seed Database (Royal Botanic Gardens Kew, 2019) but see Table S1 for additional sources) for traits that address potential barriers to colonisation (Table 1). Functional traits were selected for inclusion in the analysis if there were data on at least 75% of the study species (Table 1). This resulted in four species-level traits for analysis: plant maximum height (indication of potential competitive ability), plant woodiness (proxy for stem density), seed dry mass and dispersal syndrome (including both primary and secondary dispersal modes;

TABLE 1 List of plant functional traits linked to invasion success of rainforest remnants. Data were compiled predominately from each species datasheet in the Invasive species compendium by the Centre for Agriculture and Bioscience International (CABI; www.cabi.org/isc/) and Kew Seed Database (data.kew.org/sid/), see Table S1 for additional sources and individual species trait expressions. The number of species for which data are available (out of the 18 species surveyed) are in parentheses. 'Predicted relationship' refers to the expected filtering during invasion from oil palm to forest edge and into disturbed forest and then intact forest, based on previous studies: (Dawson, Burslem, & Hulme, 2011; Pyšek & Richardson, 2008; Rejmánek & Richardson, 1996; van Kleunen et al., 2010; Weiher et al., 1999)

Trait	Data type	Mechanism	Predicted relationship
Plant woodiness/ stem density ($n = 18$)	Binary (woody or non-woody)	Longevity	Increased woodiness
Plant maximum height ($n = 18$)	Continuous	Potential competitive ability (e.g. for light)	Increased height
Seed dry mass ($n = 16$)	Continuous	Reproductive fitness (i.e. seed production and dispersal distance) and establishment success	Smaller seed mass (dispersal), or large (establishment)
Dispersal syndrome ($n = 18$)			
Long-distance	Binary (long-distance or short-distance)	Reproductive fitness	Increase in long distance dispersal
Vertebrate dispersed	Binary (vertebrate dispersed or not)	Reproductive fitness, plant–animal interactions	Increase in vertebrate dispersal
Wind dispersed	Binary (wind dispersed or not)	Reproductive fitness	Decrease in wind dispersal

see Table S3 for species-level trait expressions). Average functional trait values per species were calculated for seed dry mass when multiple data points were available. Dispersal syndromes were classified into a binary code for adaptation to long-distance (i.e. wind, water and vertebrate) or short-distance (e.g. gravity/unspecified, vegetative propagation, ballistic or invertebrate) dispersal. Additionally, binary traits for presence/absence of vertebrate dispersal and wind dispersal were retained for analysis, to determine which long-distance dispersal mode was the most prevalent in the exotic forest community (we excluded the consideration of water dispersal due to lack of rivers in our study sites). Note that these binary dispersal traits are non-exclusive, e.g. *Chromolaena odorata* is dispersed by both wind and vertebrates.

Community weighted mean trait values (CWM; weighted by species occurrence) were calculated per transect using the FD package (Laliberté, Legendre, Shipley, & Laliberté, 2014) in R 3.4.2 (R Core Team, 2019). For binary traits (plant woodiness, long-distance dispersal, vertebrate dispersal, wind dispersal), we calculated the proportion and number of 'occurrences' (presences in 1-m transect sections) with and without the trait. Prior to CWM calculations, plant maximum height and seed dry mass were $\log_{10}$ transformed to improve normality, as well as model convergence (see statistical analyses below). Covariance and phylogenetic relationships amongst traits were tested and it was concluded that these would have little impact on CWM (see Appendix S1).

2.3 | Statistical analyses

2.3.1 | Exotic species community composition

We tested for differences in the occurrences of each study species in the four habitats using Bayesian generalised linear mixed models

(GLMMs; i.e. 18 models), using the BLME R package (Dorie & Dorie, 2015). Unlike traditional GLMMs, Bayesian GLMMs can accommodate complete separation in a logistic regression (i.e. an explanatory variable that completely separates the response variable into all zeros or ones) by allowing priors on the fixed effect terms (Bolker, 2015). This was the case for occurrence data in our study, where some species were never recorded inside rainforest remnants. In our models, we used highly uninformative Gaussian priors for all fixed effects, with means of 0 and variances of 9 and no covariance between them. For each model, the response variable combined the frequencies of presence/absence of the species in each 1-m transect section (ranging 0–100), the fixed effects were habitat (four levels: oil palm, edge, disturbed forest and intact forest) and canopy cover (as both linear and nonlinear quadratic terms to account for nonlinear individual species responses to light). Site and transect-level random effects were included to account for pseudo-replication. Species with very low total occurrence across all transects (<50 occurrences across all 78 transects) were not analysed. For each model, we tested whether geographical distance among transects was influencing our findings using Moran's I autocorrelation tests but found no evidence for geographic structuring in residuals of any of the models (Appendix S1).

To compare compositional similarity of exotic species across the four habitats we conducted an ordination using non-metric multidimensional scaling (NMDS) on a Bray–Curtis dissimilarity matrix (Magurran, 2013). Ordinations were conducted on transect-level data, based upon the total occurrence of species per transect (i.e. total number of 1-m sections where the species was recorded present, range = 0–100/transect) using the VEGAN package (Dorie & Dorie, 2015; Oksanen et al., 2007). We assessed the marginal effect of habitat and structure (canopy cover and number of large trees) on community composition using a permutational multivariate analysis of variance (PERMANOVA), with 999 permutations to calculate significance.

2.3.2 | Functional trait variation across habitats

To test for differences in each of the four functional traits among the four habitats, Bayesian GLMMs were fitted with fixed effects of habitat and canopy cover, and random effects of site and transect. Six separate models were run for the following response variables: CWMs of $\log_{10}$ plant maximum height and seed dry mass (with Gaussian error distributions), and binomial proportion that were woody, long-distance dispersed, vertebrate dispersed and wind dispersed (with binomial errors). Pairwise comparisons between habitats were carried out with a Tukey post hoc test using the EMMEANS package (Lenth & Lenth, 2018). For each model the residuals were tested for geographic structuring and no evidence was found for any trait model (Appendix S1).

Finally, robustness of the results was evaluated by re-fitting the models without the dominant invasive species, *Clidemia hirta*, to determine whether relationships were maintained across the remaining exotic plant community.

3 | RESULTS

3.1 | Exotic species community composition

Oil palm plantations and forest-oil palm edges were highly invaded with similar exotic species richness and occurrence (Figure 2 and Table S4; plantation mean richness = 9.2 species/transect ($SE \pm 0.58$), mean occurrence = 12.94/transect ($SE \pm 3.76$); edge richness = 7.8 species/transect ($SE \pm 0.69$), occurrence = 12.73/

transect ($SE \pm 3.14$) respectively), although the species compositions on each transect differed significantly between the two habitats, as well as between sites within habitat (Figure 3). Species richness and occurrence then decreased markedly in disturbed forests, where a subset of the exotic community present in the oil palm and forest edge habitats was found (Figure 2 and Table S4; mean richness = 3.1/transect ($SE \pm 0.64$); mean occurrence = 3.66/transect ($SE \pm 0.88$)), and only one species (*Clidemia hirta*) was found in intact forest, where it was found at low levels of occurrence (mean = 0.91/transect ($SE \pm 0.21$)).

Whilst 18 exotic species were recorded overall, no single transect contained all 18 species (oil palm: 4–14 species per transect, Forest-oil palm edge: 2–13 species, disturbed forest: 1–10 species; Figure 2). The tropical shrub *Clidemia hirta* made up ~33% of all occurrences (Table S4). Some species had very low occurrence and appeared on only a few transects (e.g. *Lantana camara* and *Crassocephalum crepidioides*; Table S4), whereas some species were very common (i.e. *Asystasia gangetica* and *Ageratum conyzoides*; Table S4 and Figure S2). Of the six most abundant species, some decreased in occurrence from oil palm into disturbed forest (e.g. *A. conyzoides*, *A. gangetica* and *Mimosa pudica*; Table S4 and Figure S2) whereas some species became more common at forest edges than in plantations and decreased again in forest habitats (e.g. *Clidemia hirta*, *Chromolaena odorata* and *Hyptis capitata*; Table S4 and Figure S2).

As expected, canopy cover and number of large native trees both increased from oil palm to intact forest (Figure 2 and Table S5). Bayesian GLMMs for the 16 species with sufficient occurrence data to analyse, showed that the occurrence of five species (including two
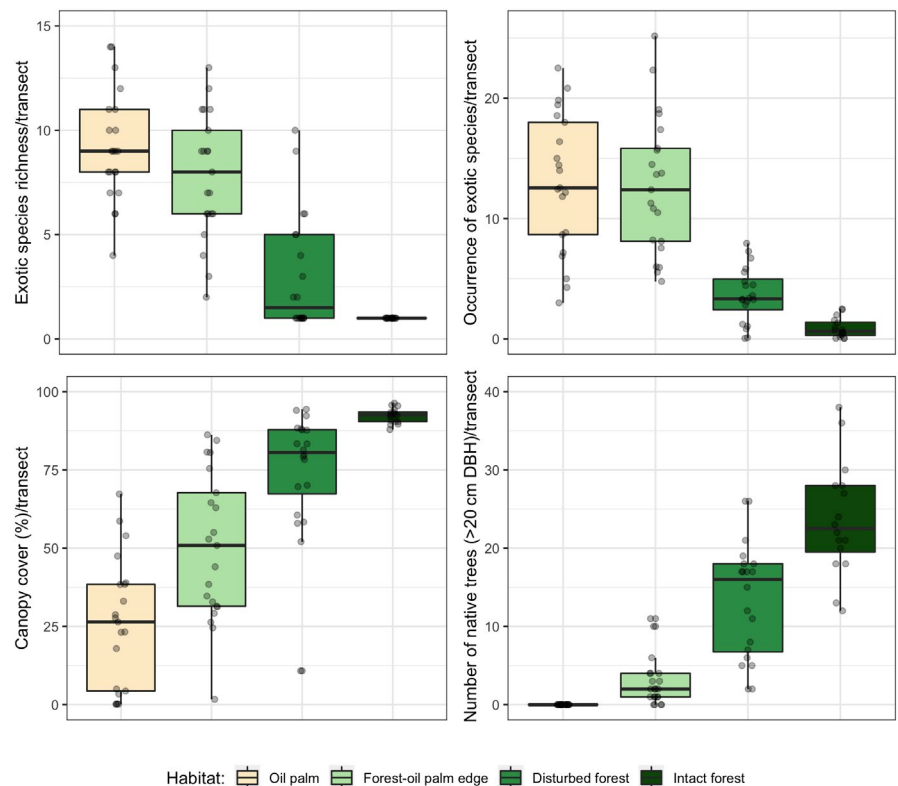

FIGURE 2 Exotic plant species richness and occurrence, and local habitat variables in four habitats in Sabah, Malaysian Borneo. See main text and Table S2 for habitat descriptions
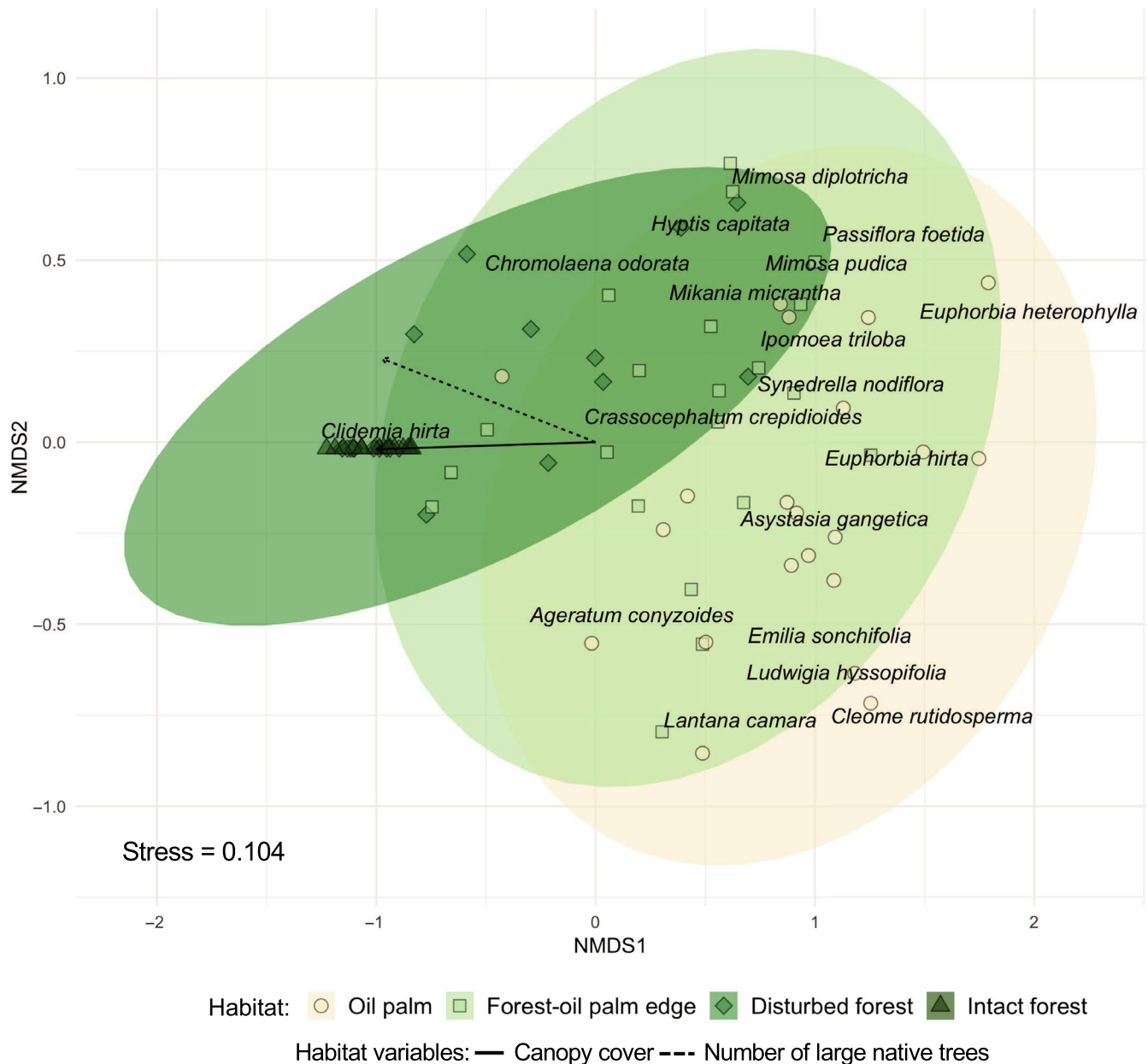
FIGURE 3 Non-metric multidimensional scaling (NMDS) of species composition based on Bray–Curtis index for oil palm, forest edge, disturbed forest and intact forest. Each symbol represents one transect and species names are in italics. Habitat is the same as described in Figure 1. Results of Permutational Multivariate Analysis of Variance, with 999 permutations were: number of large trees, $p = 0.350$; habitat, $p = 0.001$; canopy cover $p = 0.001$. For visualisation, random x-axis jitter has been added to the intact forest points, which were composed of a single species and so had no variation in NMDS scores

of the most abundant; *Clidemia hirta* and *Chromolaena odorata*) was significantly associated with canopy cover, both with linear and quadratic terms (Table S6 and Figure S3). Thus, some species were more common at intermediate light levels (e.g. *A. conyzoides*, *Clidemia hirta* and *Chromolaena odorata*) and others require full light (e.g. *Euphorbia hirta*). Habitat remained significant for most species ($n = 11$) after controlling for the effect of canopy cover (Table S6), suggesting some additional environmental, spatial or biotic factors were also important for affecting the occurrences of these exotic species.

Differences between species composition based on Bray–Curtis distance measures showed that habitat separated on NMDS ordination plots, with oil palm plantation and intact forest the most different, and edge transects intermediate (Figure 3). Both habitat and canopy cover significantly affected species composition and helped to drive the observed separation in community composition (Figure 3; PERMANOVA; habitat, $R^2 = 0.1$, $p < 0.001$; canopy cover, $R^2 = 0.06$, $p < 0.001$). The additional effect of distance to forest edge was tested for forest transects only, as a proxy for propagule pressure, and was found to have no significant effect on the occurrence of any species (Appendix S1). This confirms the role of local environmental conditions in driving observed species compositions.

3.2 | Functional trait filtering

The exotic community showed clear trends in mean functional trait values along the disturbance gradient, despite there being different exotic source communities in the oil palm across sites (Figure 4; Tables S4 and S5). Plant height and woodiness increased, and seed dry mass decreased from oil palm into intact forest. Additionally, exotic species adapted for long-distance dispersal (i.e. vertebrate or

FIGURE 4 Trends in six functional traits of exotic species ($n = 18$) across three habitats from oil palm plantation into rainforest remnants with all species included (block outline) and dominant invasive *Clidemia hirta* excluded (dotted outline). *p*-values are from ANOVA, after controlling for canopy cover, on Bayesian generalized linear mixed models (***$p < 0.001$; **$p < 0.01$; *$p < 0.05$; NS = non-significant). Pairwise comparisons between habitats detailed in Table S8
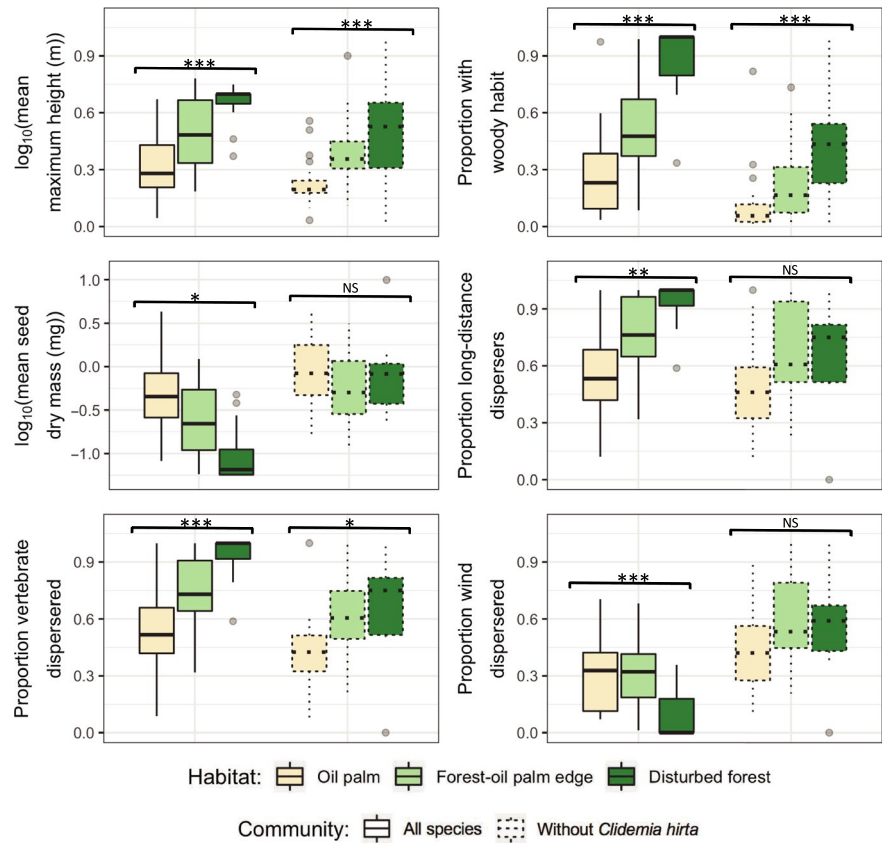

FIGURE 5 Trends in six functional traits of exotic species ($n = 18$) in relation to canopy cover, with all exotic species included (orange) and with dominant invasive *Clidemia hirta* excluded (grey). Regression lines are on the raw data of those significant relationships from the results of Bayesian generalized linear mixed models, after controlling for habitat. *p*-values are the significant results of ANOVA tests
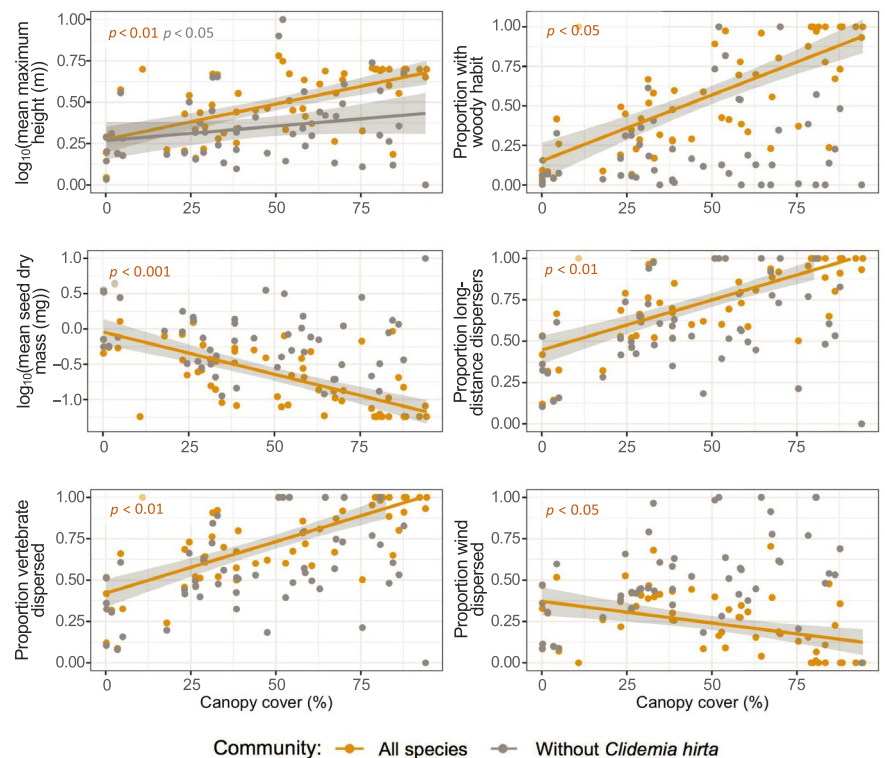
wind dispersed) were more common inside rainforest remnants. All traits were significantly related to habitat as well as to canopy cover (Figures 4 and 5; Table S7).

To test the robustness of the trait results, we removed the dominant exotic species, *Clidemia hirta*, from the analyses, but found this did not substantively change the main findings. The remaining exotic community (n = 17 species) exhibited increased height, woodiness and vertebrate dispersal from plantation to disturbed forest (Figure 4; Tables S7). Whilst the direction of effect was the same, the effect of canopy cover became non-significant when *C. hirta* was removed (Figure 5), apart from woodiness which remained significant. As with the species composition analyses, distance to forest edge had no significant effect on the mean functional trait value of forest communities for any trait (Appendix S1).

4 | DISCUSSION

Our results revealed for the first time that exotic plant communities inside rainforest remnants, retained for conservation, were not random subsets of the species established in the oil palm. Although most species were found in low numbers inside rainforest remnants, with the exception of *C. hirta*, clear trends in traits that are important in colonisation processes were seen along the disturbance gradient from oil palm to inside rainforest remnants. Species with traits which are advantageous for persistence within oil palm planted areas (i.e. herbaceous species with local dispersal, e.g. *A. gangetica*) start to decrease in abundance at the forest edge, and exotic communities are rather more dominated by vertebrate dispersed shrubs inside the disturbed areas of rainforest remnants. This shift suggests locally dispersed herbaceous species that dominate outside rainforest remnants, cannot disperse readily into the forest and/or are not sufficiently well adapted to forest environmental conditions to compete with the native community.

Our study also supported previous findings that closed canopy rainforest have low levels of invasion (Dawson, Burslem, & Hulme, 2015; Döbert et al., 2017a; Teo et al., 2003), and provided the first evidence of this result in conservation set-asides embedded within oil palm plantations. Despite most remnants being small in size (<100 ha; no. sites = 15) and the intact forests being on average <100 m from a heavily invaded anthropogenic matrix (Appendix S1) only one exotic species was found. However, we found that the most disturbed areas of these rainforest remnants are much more susceptible to invasion predominantly due to disturbance history and a more open canopy, and not because they were on average closer to the forest edge and therefore sources of propagules. The number of exotic species and their occurrence decreased along the disturbance gradient (from oil palm to intact forest), which is likely partly attributed to the reduction in resource availability (e.g. light), as well as other factors that vary between habitat.

The most common species we recorded, *Clidemia hirta*, is known to be found only in open areas in its native range but can invade closed canopy forest throughout its introduced range (DeWalt,

Denslow, & Ickes, 2004), and was the only species found in closed canopy forest in this study. Indeed, we noted that *C. hirta* was smaller in the very shaded parts of these forests, which may indicate growth restriction in shaded, closed canopy areas. However, we report for the first time that this species is significantly more abundant in a forest edge habitat, which we believe is due to *C. hirta* favouring intermediate light levels as supported by the relationship with canopy cover.

4.1 | Dispersal into rainforest remnants

We found that rainforest remnants are more likely to be invaded by exotic species with longer-range dispersal syndromes, presumably because they are better able to disperse seed inside rainforest remnants without the requirement of human assistance. Other studies have shown that landscape-scale habitat heterogeneity reduces the spread of short-distance dispersed invasive species but has little impact on species that disperse long-distances (Marco, Montemurro, & Cannas, 2011). This may explain our finding that long-distance dispersal (i.e. vertebrate, wind and water) promotes invasion in our highly heterogeneous anthropogenic landscape.

We found species that are vertebrate-dispersed (internally and externally, and both primary or secondary dispersal modes) are more likely to invade forests than those dispersed solely by wind or without long-distance dispersal adaptations. In these landscapes it is likely that small birds and bats are effective dispersers of species with fleshy fruit (e.g. *C. hirta*), having been identified as the main dispersers of exotic woody species in tropical rainforests (Rejmánek, 1996), as well as preferentially foraging in and adjacent to areas of recovering tropical rainforest canopy gaps (Schupp, Howe, Augspurger, & Levey, 1989). Secondary dispersal by terrestrial mammals is also likely to occur for those species with different primary dispersal mechanisms (e.g. the wind dispersed *Chromolaena odorata*). It is likely that bearded pigs *Sus barbatus*, observed residing inside most rainforest remnants and foraging in the oil palm matrix, are picking up propagules in their fur and dispersing them inside the forest (CABI, 2019; Fujinuma & Harrison, 2012; Peters, 2001). Although, there is significantly reduced mammal (Bernard, Baking, Giordano, Wearn, & Ahmad, 2014), and bird (S.A. Scriven, A.J. Suggitt, R.S. Madrid, J.M. Lucey, S. Fleiss, E. Waddell, S. Benedick, L.F. Banin, K.C. Hamer, H. King, C.J. McClean, G. Reynolds, J. Tangah, E. Warren-Thomas, & J.K. Hill, unpublished data) richness inside these rainforest remnants, and within surrounding oil palm planted areas (Edwards et al., 2014), our results suggest that there are sufficient vertebrates present in these landscapes to disperse exotic plant seeds into rainforest remnants. Our most dominant exotic plant species, *C. hirta*, is most likely dispersed by generalist bird species, which make up a larger percentage of the bird community in these conservation set-asides compared with primary forests (41% cf. 29%; S.A. Scriven, A.J. Suggitt, R.S. Madrid, J.M. Lucey, S. Fleiss, E. Waddell, S. Benedick, L.F. Banin, K.C. Hamer, H. King, C.J. McClean, G. Reynolds, J. Tangah, E. Warren-Thomas, & J.K. Hill, unpublished data).

In this study, we considered only natural dispersal agents as there should be no significant ongoing disturbances in these rainforest remnants. However, previous disturbance may have facilitated early propagule arrival into these forests on the machinery used during timber extraction; this has been observed as a mechanism in the introduction of invasive grasses in tropical dry forests (Veldman & Putz, 2010), as well as the role of domestic vehicles across a range of habitats (Ansong & Pickering, 2013). In addition, forest set-asides may experience low levels of human disturbance, and so propagules may be dispersed by people moving through the forest, by transporting seeds attached to clothing (Mount & Pickering, 2009).

4.2 | Persistence within forest environments

The shift to exotic species with greater maximum heights inside rainforest remnants indicates that the ability to compete for light is an important marker of success in the forest environment (Weiher et al., 1999). Other invasive exotic species have been found to be taller when compared with non-invasive exotic species (Gallagher, Randall, & Leishman, 2015). In addition, the increased woodiness (i.e. stem density) of the exotic forest community is indicative of increased longevity and so species that survive longer (i.e. perennial shrubs) are more likely to persist within the disturbed areas of these rainforest remnants than herbaceous annuals. The ability to survive and successfully compete with native forest species is necessary for persistence within new environments (Weiher et al., 1999) and there is likely greater niche overlap and therefore competition between young native trees and exotic shrubs, than small herbaceous exotic species.

The positive relationship between canopy cover and woodiness in our results (and same trend with maximum height) suggests that light is driving some of the observed patterns of trait filtering. In the more shaded forest, shrubby exotic species may be more likely to successfully compete for light with native species. Dominant herbaceous species found in the oil palm, and at the forest-oil palm edge, with the capacity for long-distance dispersal (e.g. *Ageratum conyzoides*) by contrast are unable to establish and persist in large numbers inside the forest. The inclusion of data on leaf functional traits could provide additional insight on the trait filtering mechanisms occurring during colonisation, especially the relationship with light, because they provide information on another dimension of resource acquisition and allocation. Specific leaf area (SLA) is also well-correlated with growth rates (Lambers & Poorter, 1992) and high SLA is often attributed to invasive species (Grotkopp & Rejmánek, 2007; Hamilton et al., 2005). Although foliar data were lacking for our species, this would be a useful focus of future work to help ascertain whole-plant trade-offs.

4.3 | Habitat and other influential factors

Our finding that trait patterns and differences in species occurrences are significantly explained by habitat may derive from differences in land-use history that impact environmental conditions other than light. For example, along the disturbance gradient there is likely to be a change in the soil conditions, with high compaction in the most disturbed areas (those outside forest and on skid trails or roads inside rainforest remnants), which is known to promote exotic plant establishment in logged tropical rainforests (Döbert et al., 2017a). In addition, increased soil compaction can have a negative impact on native species regeneration (Hattori et al., 2013) and thus reduce competition between exotic and native species. Soil pH and nutrients are known to influence exotic plant richness in tropical rainforests (Teo et al., 2003), however, a previous study in these rainforest remnants found characteristics of the soil (specifically pH and available P) to be less important for invasion than other drivers (Waddell, Banin, et al., 2020). Outside the rainforest remnants, soil characteristics are likely to be more influential on the exotic plant community due to the addition of fertilisers (that add N, P and K to the soil) and presence of leguminous cover crops which increase N availability (Huenneke, Hamburg, Koide, Mooney, & Vitousek, 1990).

The role of exotic species traits is likely to be one of several processes driving invasion within this landscape, and it is probable that other factors are also at play. Species-specific biotic interactions that vary among habitats may also be influential, as exotic species are known to both lose and gain biotic interactions when invading new areas [e.g. presence of available pollinators (Sargent & Ackerly, 2008), soil microbes (Reinhart & Callaway, 2006), damage from herbivory and pathogens (DeWalt et al., 2004)]. Therefore, specific interactions with abiotic and biotic factors not recorded in this study may contribute to individual species invasion success alongside the variables we analysed.

In addition, invasion is a dynamic process and therefore species persisting in oil palm plantations may still be expanding their populations into rainforest remnants (resulting in a time lag on colonisation) as has been recorded in temperate rainforest remnants (Essl, Mang, & Moser, 2012). Invasion time lags are thought to be shorter in tropical regions than in temperate regions, and shorter for exotic herbaceous species than woody species (Daehler, 2009). However, invasions within tropical rainforests are poorly understood and therefore lag times may still be occurring in these forests, especially in the newer plantations. For example, *Lantana camara* is a prolific invader across the tropics (Lowe, Browne, Boudjelas, & De Poorter, 2000) but it was present only in very low numbers in this study, and only outside the forest, despite being frequently grown as an ornamental in settlements, suggesting invasion lag effects. Additional studies which track compositional changes over time would help to elucidate the relative influence of these different factors.

4.4 | Conservation implications and management suggestions

Our results suggest that exotic plant invasion might not be an imminent threat to native rainforest remnants if they have low levels of previous disturbance and high canopy cover. However, rainforest

remnants within agricultural areas are often small and highly degraded due to disturbance from logging and extensive edge effects (Haddad et al., 2015; Lucey et al., 2017; Reynolds et al., 2011), as well as being isolated from larger tracts of primary forest. These disturbances are known to alter the native plant community to include a higher proportion of pioneer and non-forest specialists (Laurance et al., 2006; Pütz, Groeneveld, Alves, Metzger, & Huth, 2011) and isolation can reduce pollination and dispersal of native trees (Ghazoul & McLeish, 2001), both of which negatively impact the natural regeneration of forest species (Haddad et al., 2015) and may result in the intact parts of these forests becoming degraded over time. In these circumstances, exotic species may be able to spread through the forest into new gaps, using the disturbed areas of these forests (i.e. old skid trails and roads) as 'stepping stones' to invade deeper into the forest core.

Although we believe the 18 species we recorded in this study to be a good representation of the exotic plant community in these landscapes, we recognise that other species may be present in other parts of these landscapes, especially in the oil palm. In addition, native non-forest generalists that proliferate with disturbance and increased light availability (e.g. *Callicarpa*, *Melastoma*, *Uncaria*) were also observed in the rainforest remnants but were not recorded during this study. This native 'weedy' community may follow the same trait patterns observed in the exotic community, because native understorey tropical plants are known to become less functionally diverse inside primary rainforest when compared with repeatedly logged rainforest (Döbert, Webber, Sugau, Dickinson, & Didham, 2017b). Our results provide useful information about which exotic plant species and their associated traits, are invading these forests, including species that are known to suppress the regeneration of native species through competition and allelopathic effects (e.g. *Clidemia hirta* and *Chromolaena odorata*; Ambika, 1980; Ishmaini & Lesstari, 2015; Nakamura & Nemoto, 1993).

To help reduce invasion and thus minimise any potential negative impacts on native rainforest regeneration, as well as improve overall habitat quality for forest biodiversity, we recommend active forest restoration within canopy gaps in conservation set-asides, which may combine enrichment planting and weed removal. This would be especially beneficial in highly disturbed sites which lack closed canopy forest, in order to decrease light levels in the understorey and reduce colonisation by most exotic species. In addition, we suggest targeted removal of exotic species with the traits highlighted in this study from the source population in oil palm areas to stop or slow the spread into rainforest remnants, especially in new plantings where exotic populations may not yet have established. Likewise, we caution against planting of exotic species for ornamental reasons, for example, the ornamental species, *Lantana camara*, which has the traits that would, according to our results, make it a successful invader of remnant forests (i.e. it is a vertebrate dispersed shrub). Furthermore, as the anthropogenic forest-oil palm edge is the avenue for invasion in these forests, as seen in other tropical rainforests (Dawson et al., 2015), decreasing the edge to area ratio in rainforest remnants is likely to help minimise invasion, as well as reduce edge effects on native forest species richness and structure, which are known to be greater in irregular shaped fragments (Bennett & Saunders, 2010; Didham & Lawton, 1999). These suggested measures could be incorporated into certification procedures and documentation (e.g. RSPO) to help ensure that exotic species do not become a threat to the conservation status and long-term sustainability of these important remnants.

5 | CONCLUSIONS

Our study is the first to show strong evidence for trait filtering of exotic species as the environment changes from anthropogenic habitats into remnant areas of recovering native tropical rainforests along a disturbance gradient. Successful invasion of rainforest remnants requires species to have both adaptation for long-distance dispersal, in particular vertebrate dispersal, and traits that facilitate competition with native forest species (i.e. tall and woody), but there must also be a level of disturbance (i.e. canopy openness). Our results highlight both the type of forest susceptible to invasion (i.e. previously disturbed with an open canopy) and the type of exotic species that can invade remnant areas of native forest within increasingly anthropogenic tropical landscapes (Potapov et al., 2017). These rainforest remnants maintain biodiversity within agricultural tropical landscapes, and our findings provide a first view of which exotic species invade the understorey of these conservation set-asides. Although, it is not yet clear whether these exotics affect long-term regeneration of native forest communities, a precautionary approach is to introduce management practices that facilitate native seedling regeneration and increase canopy cover, to decrease the occurrence of most exotic species and reduce potential impact.

AUTHORS' CONTRIBUTIONS

E.H.W., D.S.C., J.K.H., M.H. and L.F.B. conceived the ideas; E.H.W., D.S.C., J.K.H., M.H., J.T., A.B.S. and L.F.B. designed the methodology; E.H.W. and A.B.S. collected the data; E.H.W. and D.S.C. analysed the data; E.H.W. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

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REFERENCES

Ambika, S. R. (1980). Suppression of plantation crops by Eupatorium weed. *Current Science*, *49*(22), 874–875.

Ansong, M., & Pickering, C. (2013). Are weeds hitchhiking a ride on your car? A systematic review of seed dispersal on cars. *PLoS ONE*, *8*(11), e80275. https://doi.org/10.1371/journal.pone.0080275

Bakar, B. H. (2004). Invasive weed species in Malaysian agro-ecosystems: Species, impacts and management. *Malaysian Journal of Science*, *23*, 1–42.

Bennett, A. F., & Saunders, D. A. (2010). Habitat fragmentation and landscape change. *Conservation Biology for All*, *93*, 1544–1550.

Bernard, H., Baking, E. L., Giordano, A. J., Wearn, O. R., & Ahmad, A. H. (2014). Terrestrial mammal species richness and composition in three small forest patches within an oil palm landscape in Sabah. *Malaysian Borneo. Mammal Study*, *39*(3), 141–154. https://doi.org/10.3106/041.039.0303

Blumenthal, D. M. (2006). Interactions between resource availability and enemy release in plant invasion. *Ecology Letters*, *9*(7), 887–895. https://doi.org/10.1111/j.1461-0248.2006.00934.x

Bolker, B. (2015). *GLMM worked examples*. Retrieved from https://ms.mcmaster.ca/~bolker/R/misc/foxchapter/bolker_chap.html

Broadbent, E. N., Asner, G. P., Keller, M., Knapp, D. E., Oliveira, P. J. C., & Silva, J. N. (2008). Forest fragmentation and edge effects from deforestation and selective logging in the Brazilian Amazon. *Biological Conservation*, *141*(7), 1745–1757. https://doi.org/10.1016/j.biocon.2008.04.024

Bufford, J. L., Lurie, M. H., & Daehler, C. C. (2016). Biotic resistance to tropical ornamental invasion. *Journal of Ecology*, *104*(2), 518–530. https://doi.org/10.1111/1365-2745.12534

CABI. (2019). *Invasive species compendium*. Retrieved from https://www.cabi.org/isc/

Catford, J. A., Jansson, R., & Nilsson, C. (2009). Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Diversity and Distributions*, *15*(1), 22–40. https://doi.org/10.1111/j.1472-4642.2008.00521.x

Colautti, R. I., Grigorovich, I. A., & MacIsaac, H. J. (2006). Propagule pressure: A null model for biological invasions. *Biological Invasions*, *8*(5), 1023–1037. https://doi.org/10.1007/s10530-005-3735-y

Daehler, C. C. (2009). Short lag times for invasive tropical plants: Evidence from experimental plantings in Hawai'i. *PLoS ONE*, *4*(2), e4462. https://doi.org/10.1371/journal.pone.0004462

Davis, M. A., Grime, J. P., & Thompson, K. (2000). Fluctuating resources in plant communities: A general theory of invasibility. *Journal of Ecology*, *88*(3), 528–534. https://doi.org/10.1046/j.1365-2745.2000.00473.x

Dawson, W., Burslem, D. F. R. P., & Hulme, P. E. (2009). Factors explaining alien plant invasion success in a tropical ecosystem differ at each stage of invasion. *Journal of Ecology*, *97*(4), 657–665. https://doi.org/10.1111/j.1365-2745.2009.01519.x

Dawson, W., Burslem, D. F. R. P., & Hulme, P. E. (2011). The comparative importance of species traits and introduction characteristics in tropical plant invasions. *Diversity and Distributions*, *17*(6), 1111–1121. https://doi.org/10.1111/j.1472-4642.2011.00796.x

Dawson, W., Burslem, D. F. R. P., & Hulme, P. E. (2015). Consistent effects of disturbance and forest edges on the invasion of a continental rain forest by alien plants. *Biotropica*, *47*(1), 27–37. https://doi.org/10.1111/btp.12183

DeWalt, S. J., Denslow, J. S., & Ickes, K. (2004). Natural-enemy release facilitates habitat expansion of the invasive tropical shrub clidemia hirta. *Ecology*, *85*(2), 471–483. https://doi.org/10.1890/02-0728

Didham, R. K., & Lawton, J. H. (1999). Edge structure determines the magnitude of changes in microclimate and vegetation structure in tropical forest fragments. *Biotropica*, *31*(1), 17–30. https://doi.org/10.2307/2663956

Döbert, T. F., Webber, B. L., Sugau, J. B., Dickinson, K. J. M., & Didham, R. K. (2017a). Logging, exotic plant invasions, and native plant reassembly in a lowland tropical rain forest. *Biotropica*, *50*(2), 254–265. https://doi.org/10.1111/btp.12521

Döbert, T. F., Webber, B. L., Sugau, J. B., Dickinson, K. J. M., & Didham, R. K. (2017b). Logging increases the functional and phylogenetic dispersion of understorey plant communities in tropical lowland rain forest. *Journal of Ecology*, *105*(5), 1235–1245. https://doi.org/10.1111/1365-2745.12794

Dorie, V., & Dorie, M. V. (2015). *Package 'blme'. Bayesian Linear Mixed-Effects Models*. Retrieved from https://CRAN.R-project.org/package=blme

Edwards, D. P., Magrach, A., Woodcock, P., Ji, Y., Lim, N. T. L., Edwards, F. A., … Yu, D. W. (2014). Selective-logging and oil palm: Multitaxon impacts, biodiversity indicators, and trade-offs for conservation planning. *Ecological Applications*, *24*(8), 2029–2049. https://doi.org/10.1038/nature11318

Elton, C. S. (1958). *The ecology of invasions by animals and plants*. London, UK: Methuen & Co Ltd.

Essl, F., Mang, T., & Moser, D. (2012). Ancient and recent alien species in temperate forests: Steady state and time lags. *Biological Invasions*, *14*(7), 1331–1342. https://doi.org/10.1007/s10530-011-0156-y

Fee, C. G., Tui, L. C., Bin, C. S., & Hoy, C. K. (2017). *Pictorial guide to common weeds of plantations and their control*. Selangor, Malaysia: Agricultural Crop Trust, ACT.

Fine, P. V. A. (2002). The invasibility of tropical forests by exotic plants. *Cambridge University Press Stable*, *18*(5), 687–705. https://doi.org/10.1017/S0266467402002456

Fleiss, S., Waddell, E., Ola, B. B., Banin, L. F., Benedick, S., Sailim, A. B., … Hill, J. K. (2020). Conservation set-asides improve carbon storage and support associated plant diversity in certified sustainable oil palm plantations. *Biological Conservation*, *248*, 108631. https://doi.org/10.1016/j.biocon.2020.108631

Fujinuma, J., & Harrison, R. D. (2012). Wild pigs (*Sus scrofa*) mediate large-scale edge effects in a lowland tropical rainforest in Peninsular Malaysia. *PLoS ONE*, *7*(5), 1–7. https://doi.org/10.1371/journal.pone.0037321

Gallagher, R. V., Randall, R. P., & Leishman, M. R. (2015). Trait differences between naturalized and invasive plant species independent of residence time and phylogeny. *Conservation Biology*, *29*(2), 360–369. https://doi.org/10.1111/cobi.12399

Gaveau, D. L. A., Salim, M., & Arjasakusuma, S. (2017). *Deforestation and industrial plantations development in Borneo*. Center for International Forestry Research (CIFOR). https://doi.org/10.17528/CIFOR/DATA.00049

Gaveau, D. L., Sloan, S., Molidena, E., Yaen, H., Sheil, D., Abram, N. K., … Meijaard, E. (2014). Four decades of forest persistence, clearance and logging on Borneo. *PLoS ONE*, *9*(7), 1–11. https://doi.org/10.1371/journal.pone.0101654

Ghazoul, J., & McLeish, M. (2001). Reproductive ecology of tropical forest trees in logged and fragmented habitats in Thailand and Costa Rica. *Plant Ecology*, *153*(1), 335–345. https://doi.org/10.1023/A:1017542124699

Grotkopp, E., & Rejmánek, M. (2007). High seedling relative growth rate and specific leaf area are traits of invasive species: Phylogenetically independent contrasts of woody angiosperms. *American Journal of Botany*, *94*(4), 526–532. https://doi.org/10.3732/ajb.94.4.526

Haddad, N. M., Brudvig, L. A., Clobert, J., Davies, K. F., Gonzalez, A., Holt, R. D., … Townshend, J. R. (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances*, *1*(2), 1–9. https://doi.org/10.1126/sciadv.1500052

Hamilton, M. A., Murray, B. R., Cadotte, M. W., Hose, G. C., Baker, A. C., Harris, C. J., & Licari, D. (2005). Life-history correlates of plant invasiveness at regional and continental scales. *Ecology Letters*, *8*(10), 1066–1074. https://doi.org/10.1111/j.1461-0248.2005.00809.x

Hattori, D., Kenzo, T., Irino, K. O., Kendawang, J. J., Ninomiya, I., & Sakurai, K. (2013). Effects of soil compaction on the growth and mortality of planted dipterocarp seedlings in a logged-over tropical rainforest in Sarawak, Malaysia. *Forest Ecology and Management*, *310*, 770–776. https://doi.org/10.1016/j.foreco.2013.09.023

Hill, J. K., Gray, M. A., Khen, C. V., Benedick, S., Tawatao, N., & Hamer, K. C. (2011). Ecological impacts of tropical forest fragmentation: How consistent are patterns in species richness and nestedness? *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*, 3265–3276. https://doi.org/10.1098/rstb.2011.0050

Huenneke, L. F., Hamburg, S. P., Koide, R., Mooney, H. A., & Vitousek, P. M. (1990). Effects of soil resources on plant invasion and community structure in Californian serpentine grassland. *Ecology*, *71*(2), 478–491. https://doi.org/10.2307/1940302

Hulme, P. E. (2009). Trade, transport and trouble: Managing invasive species pathways in an era of globalization. *Journal of Applied Ecology*, *46*(1), 10–18. https://doi.org/10.1111/j.1365-2664.2008.01600.x

Ishmaini, L., & Lesstari, A. (2015). Allelopathic potential of *Clidemia hirta* for bioherbicide usage. *Prosiding Seminar Nasional Masyarakat Biodiversitas Indonesia*, *1*(6), 1467–1471.

Koh, L. P. (2008). Birds defend oil palms from herbivorous insects. *Ecological Applications*, *18*(4), 821–825. https://doi.org/10.1890/07-1650.1

Koike, F. (2001). Plant traits as predictors of woody species dominance in climax forest communities. *Journal of Vegetation Science*, *12*(3), 327–336. https://doi.org/10.2307/3236846

Laliberté, A. E., Legendre, P., Shipley, B., & Laliberté, M. E. (2014). *Package 'FD' Measuring functional diversity from multiple traits, and other tools for functional ecology*. Retrieved from https://cran.r-project.org/web/packages/FD/index.html

Lambers, H., & Poorter, H. (1992). Inherent variation in growth rate between higher plants: A search for physiological causes and ecological consequences. *Advances in Ecological Research*, *23*, 187–261.

Laurance, W. F., Camargo, J. L. C., Luizão, R. C. C., Laurance, S. G., Pimm, S. L., Bruna, E. M., … Lovejoy, T. E. (2011). The fate of Amazonian forest fragments: A 32-year investigation. *Biological Conservation*, *144*(1), 56–67. https://doi.org/10.1016/j.biocon.2010.09.021

Laurance, W. F., Lovejoy, T. E., Vasconcelos, H. L., Bruna, E. M., Didham, R. K., Stouffer, P. C., … Sampaio, E. (2002). Ecosystem decay of Amazonian forest fragments: A 22-year investigation. *Conservation Biology*, *16*(3), 605–618. https://doi.org/10.1046/j.1523-1739.2002.01025.x

Laurance, W. F., Nascimento, H. E. M., Laurance, S. G., Andrade, A. C., Fearnside, P. M., Ribeiro, J. E. L., & Capretz, R. L. (2006). Rain forest fragmentation and the proliferation of successional trees. *Ecology*, *87*(2), 469–482. https://doi.org/10.1890/05-0064

Lenth, R., & Lenth, M. R. (2018). Package 'lsmeans'. *The American Statistician*, *34*(4), 216–221.

Levine, J. M., Adler, P. B., & Yelenik, S. G. (2004). A meta-analysis of biotic resistance to exotic plant invasions. *Ecology Letters*, *7*(10), 975–989. https://doi.org/10.1111/j.1461-0248.2004.00657.x

Levine, J. M., & D'Antonio, C. M. (2003). Forecasting biological invasions with increasing international trade. *Conservation Biology*, *17*(1), 322–326. https://doi.org/10.1046/j.1523-1739.2003.02038.x

Lôbo, D., Leão, T., Melo, F. P. L., Santos, A. M. M., & Tabarelli, M. (2011). Forest fragmentation drives Atlantic forest of northeastern Brazil to biotic homogenization. *Diversity and Distributions*, *17*(2), 287–296. https://doi.org/10.1111/j.1472-4642.2010.00739.x

Lodge, D. M. (1993). Biological invasions: Lessons for ecology. *Trends in Ecology & Evolution*, *8*(4), 133–137. https://doi.org/10.1016/0169-5347(93)90025-K

Lowe, S., Browne, M., Boudjelas, S., & De Poorter, M. (2000). *100 of the world's worst invasive alien species: A selection from the global invasive species database* (Vol. 12). Auckland, New Zealand: Invasive Species Specialist Group.

Lucey, J. M., Palmer, G., Yeong, K. L., Edwards, D. P., Senior, M. J., Scriven, S. A., … Hill, J. K. (2017). Reframing the evidence base for policy-relevance to increase impact: A case study on forest fragmentation in the oil palm sector. *Journal of Applied Ecology*, *54*(3), 731–736. https://doi.org/10.1111/1365-2664.12845

Magurran, A. E. (2013). *Measuring biological diversity*. Oxford, UK: John Wiley & Sons.

Marco, D. E., Montemurro, M. A., & Cannas, S. A. (2011). Comparing short and long-distance dispersal: Modelling and field case studies. *Ecography*, *34*(4), 671–682. https://doi.org/10.1111/j.1600-0587.2010.06477.x

Martin, P. H., & Marks, P. L. (2006). Intact forests provide only weak resistance to a shade-tolerant invasive Norway maple (*Acer platanoides* L.). *Journal of Ecology*, *94*(6), 1070–1079. https://doi.org/10.1111/j.1365-2745.2006.01159.x

Mount, A., & Pickering, C. M. (2009). Testing the capacity of clothing to act as a vector for non-native seed in protected areas. *Journal of Environmental Management*, *91*(1), 168–179. https://doi.org/10.1016/j.jenvman.2009.08.002

Nakamura, N., & Nemoto, M. (1993). Allelopathic potential of *Eupatorium odoratum* in abandoned shifting cultivation fields in the tropics. *Weed Research (Tokyo)*, *38*(2), 103–108.

Nathan, R., Schurr, F. M., Spiegel, O., Steinitz, O., Trakhtenbrot, A., & Tsoar, A. (2008). Mechanisms of long-distance seed dispersal. *Trends in Ecology & Evolution*, *23*(11), 638–647. https://doi.org/10.1016/j.tree.2008.08.003

Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Stevens, M. H. H., Oksanen, M. J., & Suggests, M. (2007). The vegan package. *Community Ecology Package*, *10*, 631–637.

Pallewatta, N., Reaser, J. K., & Gutierrez, A. T. (2003). *Invasive alien species in South-Southeast Asia: National reports and directory of resources*. Cape Town, South Africa: Global Invasive Species Programme.

Peh, K. S. H. (2010). Invasive species in Southeast Asia: The knowledge so far. *Biodiversity and Conservation*, *19*(4), 1083–1099. https://doi.org/10.1007/s10531-009-9755-7

Peters, H. A. (2001). *Clidemia hirta* invasion at the Pasoh Forest Reserve: An unexpected plant invasion in an undisturbed tropical forest. *Biotropica*, *33*(1), 60–68. https://doi.org/10.1646/0006-3606(2001)033[0060:CHIATP]2.0.CO;2

Potapov, P., Hansen, M. C., Laestadius, L., Turubanova, S., Yaroshenko, A., Thies, C., … Esipova, E. (2017). The last frontiers of wilderness: Tracking loss of intact forest landscapes from 2000 to 2013. *Science Advances*, *3*(1), e1600821. https://doi.org/10.1126/sciadv.1600821

Procheş, Ş., Wilson, J. R. U., Richardson, D. M., & Rejmánek, M. (2008). Searching for phylogenetic pattern in biological invasions. *Global Ecology and Biogeography*, *17*(1), 5–10. https://doi.org/10.1111/j.1466-8238.2007.00333.x

Pütz, S., Groeneveld, J., Alves, L. F., Metzger, J. P., & Huth, A. (2011). Fragmentation drives tropical forest fragments to early successional states: A modelling study for Brazilian Atlantic forests. *Ecological Modelling*, *222*(12), 1986–1997. https://doi.org/10.1016/j.ecolmodel.2011.03.038

Pyšek, P., & Richardson, D. M. (2006). The biogeography of naturalization in alien plants. *Journal of Biogeography*, *33*(12), 2040–2050. https://doi.org/10.1111/j.1365-2699.2006.01578.x

Pyšek, P., & Richardson, D. M. (2008). Traits associated with invasiveness in alien plants: Where do we stand? In W. Nentwig (Ed.), *Biological invasions* (pp. 97–125). Berlin, Germany: Springer.

R Core Team. (2019). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.r-project.org/

Reinhart, K. O., & Callaway, R. M. (2006). Soil biota and invasive plants. *New Phytologist*, *170*(3), 445–457. https://doi.org/10.1111/j.1469-8137.2006.01715.x

Rejmánek, M. (1996). Species richness and resistance to invasions. In G. Orians, R. Dirzo, & J. H. Cushman (Eds.), *Biodiversity and ecosystem processes in tropical forests* (pp. 153–172). Berlin, Germany: Springer.

Rejmánek, M., & Richardson, D. M. (1996). What attributes make some plant species more invasive? *Ecology*, *77*(6), 1655–1661. https://doi.org/10.2307/2265768

Rembold, K., Mangopo, H., Tjitrosoedirdjo, S. S., & Kreft, H. (2017). Plant diversity, forest dependency, and alien plant invasions in tropical agricultural landscapes. *Biological Conservation*, *213*, 234–242. https://doi.org/10.1016/j.biocon.2017.07.020

Reynolds, G., Payne, J., Sinun, W., Mosigil, G., & Walsh, R. P. D. (2011). Changes in forest land use and management in Sabah, Malaysian Borneo, 1990–2010, with a focus on the Danum Valley region. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1582), 3168–3176. https://doi.org/10.1098/rstb.2011.0154

Ricketts, T. H. (2004). Tropical forest fragments enhance pollinator activity in nearby coffee Crops. *Conservation Biology*, *18*(5), 1262–1271. https://doi.org/10.1111/j.1523-1739.2004.00227.x

Royal Botanic Gardens Kew. (2019). *Seed information database (SID)*. Retrieved from http://data.kew.org/sid/

RSPO. (2018). *Roundtable on sustainable palm oil principles & criteria for sustainable palm oil*. Retrieved from https://rspo.org/resources/certification/rspo-principles-criteria-certification

Sargent, R. D., & Ackerly, D. D. (2008). Plant–pollinator interactions and the assembly of plant communities. *Trends in Ecology & Evolution*, *23*(3), 123–130. https://doi.org/10.1016/j.tree.2007.11.003

Schupp, E. W., Howe, H. F., Augspurger, C. K., & Levey, D. J. (1989). Arrival and survival in tropical treefall gaps. *Ecology*, *70*(3), 562–564. https://doi.org/10.2307/1940206

Seebens, H., Essl, F., Dawson, W., Fuentes, N., Moser, D., Pergl, J., … Blasius, B. (2015). Global trade will accelerate plant invasions in emerging economies under climate change. *Global Change Biology*, *21*(11), 4128–4140. https://doi.org/10.1111/gcb.13021

Senior, M. J. M., Brown, E., Villalpando, P., & Hill, J. K. (2015). Increasing the scientific evidence base in the 'high conservation value' (HCV) approach for biodiversity conservation in managed tropical landscapes.

Conservation Letters*, *8*(5), 361–367. https://doi.org/10.1111/conl.12148

Sher, A. A., & Hyatt, L. A. (1999). The disturbed resource-flux invasion matrix: A new framework for patterns of plant invasion. *Biological Invasions*, *1*(2–3), 107–114.

Teo, D. H. L., Tan, H. T. W., Corlett, R. T., Wong, C. M., & Lum, S. K. Y. (2003). Continental rain forest fragments in Singapore resist invasion by exotic plants. *Journal of Biogeography*, *30*(2), 305–310. https://doi.org/10.1046/j.1365-2699.2003.00813.x

van Kleunen, M., Weber, E., & Fischer, M. (2010). Review and synthesis: A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecology Letters*, *13*(2), 235–245. https://doi.org/10.1111/j.1461-0248.2009.01418.x

Veldman, J. W., & Putz, F. E. (2010). Long-distance dispersal of invasive grasses by logging vehicles in a tropical dry forest. *Biotropica*, *42*(6), 697–703. https://doi.org/10.1111/j.1744-7429.2010.00647.x

Waddell, E. H., Banin, L. F., Fleiss, S., Hill, J. K., Hughes, M., Jelling, A., … Chapman, D. S. (2020). Land-use change and propagule pressure promote plant invasions in tropical rainforest remnants. *Landscape Ecology*, *35*(9), 1891–1906. https://doi.org/10.1007/s10980-020-01067-9

Waddell, E. H., Chapman, D. S., Hill, J. K., Hughes, M., Bin Sailim, A., Tangah, J., & Banin, L. F. (2020). *Occurrence of exotic plant species in oil palm dominated landscapes with embedded rainforest remnants in Sabah, Malaysian Borneo, 2019*. NERC Environmental Information Data Centre. https://doi.org/10.5285/372861ee-67c5-4bb3-b765-cf8c03c06199

Weiher, E., & Keddy, P. A. (1995). Assembly rules, null models, and trait dispersion: New questions from old patterns. *Oikos*, *74*(1), 159–164. https://doi.org/10.2307/3545686

Weiher, E., Van Der Werf, A., Thompson, K., Roderick, M., Garnier, E., & Eriksson, O. (1999). Challenging Theophrastus: A common core list of plant traits for functional ecology. *Journal of Vegetation Science*, *10*(5), 609–620. https://doi.org/10.2307/3237076

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.