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Recolonizing native wildlife facilitates exotic plant invasion into Singapore's rain forests

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Abstract

Halting biological invasions and rewilding extirpated native fauna are conservation interventions to bolster biodiversity, species interactions, and ecosystems. These actions are often considered separately and the potential for reintroduced wildlife to facilitate invasive plants has been largely overlooked. Here, we investigated the role of Singapore's recolonizing native wild pigs (*Sus scrofa*) in facilitating an invasive weed *Miconia crenata* into tropical rainforests, which are normally highly resistant to invasion. We conducted line-transect surveys in 11 Singaporean rain forests and used generalized linear mixed models to consider the contribution of pigs' soil disturbances, human forest paths, and other environmental covariates, on the density of *M. crenata*. We found that *M. crenata* was more abundant at forest edges and invasion into forest interior was facilitated by pigs, paths, and canopy gaps, but that these effects were all additive, not synergistic (i.e., not multiplicative). These results highlight how modern invasions are driven by multiple disturbances as well as propagule pressure (e.g., urban birds dispersing seeds at forest edges where they establish in pig soil disturbances). Singapore's extensive native forest restoration efforts may have provided plentiful edge and secondary forests that are well suited to pigs and *M. crenata*, which in turn undermine the aims of fostering later-successional native plant communities. To prevent negative externalities, we suggest that plant restoration and rewilding projects consider the potential role of wildlife in facilitating non-native plants, and couple these actions with preliminary screening of unintended consequences and continued monitoring, as well as limiting human-mediated weed invasion to minimize propagule sources.

KEYWORDS
Clidemia, faunal reintroduction, human disturbances, *Miconia crenata*, plant invasion, tropical rain forests, weed management, wild pig

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1 | INTRODUCTION

Calls for rewilding through reintroducing extirpated native wildlife are aimed at restoring degraded habitats and supporting biodiversity and ecosystem services (IPBES, 2019). It is often assumed native animals will disproportionately facilitate natives and have neutral or suppressive effects on exotics (Derham et al., 2018; Law et al., 2017; Parker et al., 2006; Sandom et al., 2013). However, restoration science has few examples of how restored fauna mediate exotic plant populations, but such processes can alter conservation decisions.

Plant invasions in continental tropical rainforests (or land-bridge islands) are scarce despite humans repeatedly introducing propagules (Denslow & DeWalt, 2008; Fine, 2002; Rejmánek, 1996; Teo et al., 2003). There are numerous theories of why continental tropical forests are impervious to invasion (reviewed in Chong et al., 2021), but their resistance is undermined by natural and anthropogenic disturbances (e.g., tree-fall gaps, logging) that can increase resource availability, such as light for plants (Chong et al., 2021; Davis et al., 2000; Denslow & DeWalt, 2008; Rejmánek, 1996). A notable invasion of primary continental tropical rainforests occurred in Asia around the late 1980s to the early 1990s when *Miconia crenata* (formerly *Clidemia hirta*) was first recorded at Pasoh in Peninsular Malaysia and Bukit Timah on the land-bridge island of Singapore (Figure 1a,b; Fujinuma & Harrison, 2012; Peters, 2001; Teo et al., 2003). *M. crenata* is a fast-growing pioneer shrub native to the Neotropics that exploits disturbed areas (Fujinuma & Harrison, 2012; Peters, 2001). It is primarily bird-dispersed, regenerates on bare mineral soil, and — while shade-tolerant — is often associated with higher light environments (Fujinuma & Harrison, 2012; Peters, 2001; Samarasinghe et al., 2022). *M. crenata* was not considered a conservation problem in Singapore in the early 2000s when it was limited only to exposed mineral soils in well-lit and disturbed forest edges, paths, steep slopes and canopy gaps, and was uncommon where leaf litter was undisturbed by humans (Peters, 2001; Teo et al., 2003). However,

M. crenata imposes negative effects on native plants in its invasive range and has been listed as one of the 100 world's most invasive species (IUCN, 2022). For instance, it has threatened endemic plants in Hawaii and the flora on Silhouette Island, Seychelles, to local extinction (Gerlach, 1993; Wester & Wood, 1977). Also in Seychelles on Mahé Island, it has recently been shown to compete with native plants for seed dispersal services from native frugivores, which may in turn negatively impact native frugivore and plant fitness (Costa et al., 2022). In Sri Lanka and Malaysia, its dominance in tree-fall gaps was suggested to outcompete native canopy gap specialists and alter forest succession (Peters, 2001; Tomimura et al., 2012). Understanding *M. crenata's* spread in Singapore's regenerating forests has clear conservation importance.

Human paths (roads and trails) can facilitate the spread of *M. crenata* by exposing bare mineral soil establishment sites and providing conduits for dispersal from humans themselves, and also birds and other animals including pigs, that use paths as flyways and travel corridors, respectively (Allwin et al., 2015; Blake et al., 2017; Botella et al., 2022; Downing, 2020; Le et al., 2018; Liedtke et al., 2020; Mitchell & Mayer, 1997). Indeed, Le et al. (2018) found *M. crenata*'s distribution in Endau Rompin National Park in Peninsular Malaysia was associated with paths. Paths are prevalent in the forests of highly populated Singapore and are used for recreation (e.g., hiking and biking) or to allow access for certain vehicles (e.g., maintenance, military training) (Chatterjea, 2014). *M. crenata* seeds are very small (<2 mm), and thus propagules could be stuck in shoes, clothes, equipment, or vehicles, that are attached during the trampling of its fruits (Metcalfe & Turner, 1998).

In the early 2010s, native pigs (*Sus scrofa*, commonly referred to as wild boars and hereafter just "pigs") were identified as a possible facilitator of *M. crenata* invasion in Peninsular Malaysia due to pigs' soil disturbances created when they forage for underground materials (known as rooting) (Figure 1c,d; Fujinuma & Harrison, 2012; Peters, 2001). Pigs can also act as seed dispersers
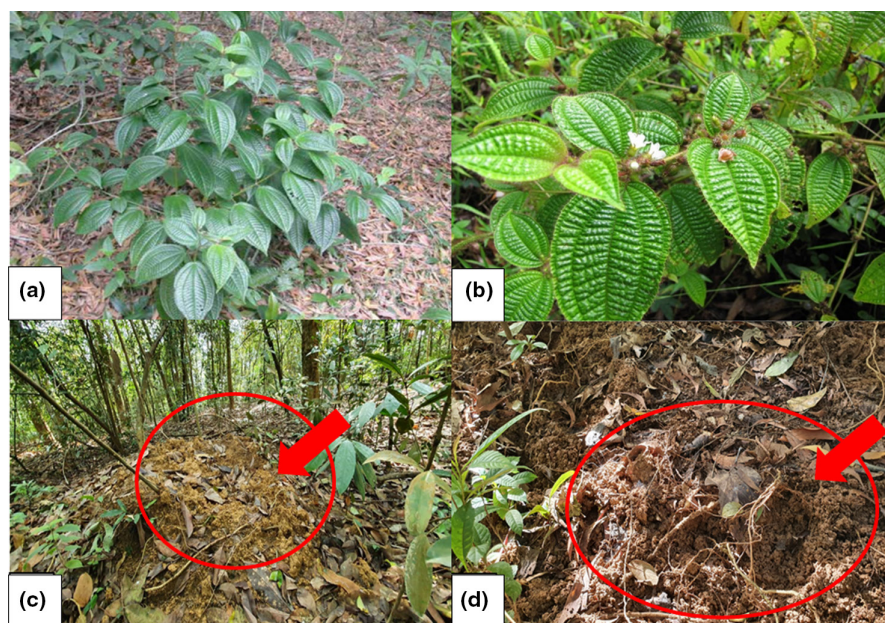

FIGURE 1 Images of the invasive plant *Miconia crenata* and native wild boar (*Sus scrofa*) soil disturbances in Singaporean tropical rainforests. Panel (a) shows an adult *Miconia crenata* approximately 1 m tall and panel (b) shows a reproductively active individual with fruits and flowers (images from Breaden et al., 2012; Jackson and Deesh, 2016). Panels (c, d) show signs of wild pig rooting with characteristic overturned soil, no leaf litter, and exposed roots (circled in red and indicated with red arrow; photos from Yong et al., 2022).

as they are attracted to *M. crenata* fruits, whose seeds can survive pigs' gut passage and germinate in pig dung, while seeds can also attach to their skin and fur (Smith, 1992). Pigs are native to Singapore but were extirpated in the 1950s on mainland Singapore and only persisted in small numbers on offshore islands including Pulau Ubin and Pulau Tekong (Corlett, 1992; Yong et al., 2010). However, they have recolonized without human assistance (i.e., not directly reintroduced by humans) in the early 2000s from nearby Peninsular Malaysia (Lamperty et al., 2023). Their recolonization has been facilitated by forest restoration efforts in Singapore aiming to restore its degraded biodiversity and ecosystems, which have provided increasing secondary forest cover and thus suitable habitats for pigs (Lamperty et al., 2023; Shono et al., 2006). Singapore's pigs have slowly spread across most parts of the island and have reached high densities in some early recolonized forests (Khoo et al., 2021; Lamperty et al., 2023). Pig densities are expected to rise given the hunting ban, lack of predators, and food subsidies from crops and urban areas, and their accumulated soil and vegetation disturbances can become deleterious to the local forest ecology (Amir et al., 2022; Luskin et al., 2019, 2021; Moore et al., 2023).

It is possible that recolonizing pigs and human paths may act additively or synergistically to increase *M. crenata's* invasion because they are both associated with the creation of bare soil establishment sites and dispersal mechanisms, which increases resource availability and propagule pressure for *M. crenata* invasion (Catford et al., 2021). However, the role of pigs and paths on *M. crenata's* invasion has so far been studied separately and not in the same forests (Table 1 and Le et al. (2018) which focused on *M. crenata's* invasion along human paths), limiting our understanding of the multifaceted and evolving invasion pathways present in most contemporary forests (Sharma et al., 2005; Theoharides & Dukes, 2007). Identifying multiple factors contributing to invasion is also important for effective weed management programs (Hobbs & Humphries, 1995).

Here we quantified *M. crenata*'s invasion across Singaporean forests with and without pigs and along and off human paths. We examined the contribution of pig soil disturbances and human paths on *M. crenata*'s density, while accounting for known associations of *M. crenata* with forest edges, light and other exposed soil establishment sites, as well as examining potential interactions among all these factors (Peters, 2001; Teo et al., 2003). We hypothesized that (i) *M. crenata* would be more abundant along paths and where pigs have disturbed soils but that there would not be a synergistic effect as each provides relatively similar establishment opportunities (soil disturbance and potential dispersal); (ii) *M. crenata* would also be positively associated with canopy openness due to its preference for higher light environments, which, together with pigs and paths, shape *M. crenata's* invasion in forest interiors; and (iii) *M. crenata* would also be more abundant at forest edges because these areas are closer to propagule sources originating outside of forests, and pigs, paths and canopy openness may provide further suitable conditions for its establishment at forest edges.

2 | METHODS

2.1 | Site description

We conducted fieldwork in 11 rainforest patches in Singapore (1°21″07.6″N, 103°49″11.3″E) from February 2019 to January 2020, including (1) the Dairy Farm and (2) Hindhede area of the Bukit Timah Nature Reserve (BTNR), (3) the MacRitchie in the Central Catchment Nature Reserve (CCNR), (4) Bukit Batok Nature Park, (5) East Coast Park, (6) Mandai Park, (7) the Fort Siloso area of Sentosa, (8) Telok Blangah, (9) Kent Ridge Park, (10) Clementi Forest, and (11) Pulau Ubin Island (Table S1; Figure 2). We conducted vegetation transects (see more below) on and off human paths in all forests and at the time of sampling, pigs had not recolonized (or were absent from) Sentosa, Telok Blangah, and East Coast Park.

Singapore retains less than 1% of its primary vegetation (e.g., lowland dipterocarp rain forest; (Yee et al., 2011)), but secondary forest vegetation covers approximately 50% of the island (Yee et al., 2016). Secondary rain forests in Singapore are defined as having a continuous canopy layer but have reduced structure and species composition compared to primary forests. They vary in their successional stages (early-successional or young vs. late-successional or tall) and dominant vegetation types (native vs. exotic trees) (Yee et al., 2019). There are old native-dominated secondary rain forests established >50 years in BTNR and CCNR and patches of young native-dominated secondary forests established <10 years that are often dominated by *Adinandra dumosa* trees (Yee et al., 2019). As succession progresses, late-successional species accrue, often from the genera *Calophyllum L.*, *Elaeocarpus L.*, *Garcinia L.*, and *Syzygium P.Browne ex Gaertn*. Exotic-dominated secondary rainforests are often regrowth from abandoned plantations or kampungs (villages) and have a high cover of commercial tree species like rubber (*Hevea brasiliensis*), fruit trees (e.g., *Durio* spp.), or exotic timber species (Yee et al., 2019).

2.2 | Study species

Miconia crenata is a densely branching woody shrub native to the humid tropics of Central and South America and the islands of the West Indies and has invaded tropical areas in Africa and Asia and many tropical islands (DeWalt et al., 2004; Wester & Wood, 1977). It is often 1–2 m in height but can reach 5 m in the subcanopy (Smith, 1992). They produce fruits year-round and large plants can produce 500 fruits a season, which are sweet, pulpy bluish-black berries 6–8 mm long, each containing 200–900 seeds that are most often dispersed by frugivorous birds (Peters, 2001; Smith, 1992). They flower and undergo sexual reproduction and apomixis but not vegetative clonal reproduction (Le et al., 2018; Mendes-Rodrigues et al., 2008). *M. crenata's* success as an invader may be due to its fecundity and dispersal paired with rapid germination, high growth rates, and shade-tolerance, even though it prefers well-lit environments (Chong et al., 2021; Fujinuma & Harrison, 2012; Peters, 2001).

TABLE 1 Prior work investigating the role of pig (*Sus scrofa*) soil disturbance (rooting) on *Miconia crenata* invasion and other non-native plant invasions.

Location and habitat	Study design	*S. scrofa* invasive?	*M. crenata* involved?	Facilitate invasion?	Summary of key results	Reference
Tropical rainforest in Peninsular Malaysia	Observational; soil density comparison	Native	Yes	Yes	Observable signs of pig rooting disappear quickly over time, but can leave behind longer lasting effects of increased soil density at depth, so earlier pig rooting might have facilitated *M. crenata* establishment in areas without observable signs of pig rooting.	Peters (2001)
Tropical rainforest in Peninsular Malaysia	Observational; line transects	Native	Yes	Yes	*M. crenata* abundance was correlated with pig rooting and reached >1 km into forest interior.	Fujinuma and Harrison (2012)
Coastal dune ecosystem in North America, including Georgia	Observational, disturbed–undisturbed plot comparison (no exclosure)	Invasive	No	Yes	Repeated pig rooting resulted in the promotion and maintenance of invasive yellow nutsedge (*Cyperus esculentus*).	Oldfield and Evans (2016)
Coastal forest mostly in southeastern USA	Review	Invasive	No	Yes	Pig rooting facilitated exotic plants by reducing native species cover and dispersing seeds of exotic weeds.	Bradley and Lockaby (2021)
Temperate forest and shrubland of South America, including Patagonia	Experimental; fenced exclosures with no-rooting, artificial rooting, and pig-rooting	Invasive	No	Yes	Pig rooting is the driver for the invasion of seven invasive weed species.	Barrios-Garcia and Simberloff (2013)
Grassland of North America, including San Francisco area	Observational; plots with pig disturbance of varying ages AND Experimental; fenced exclosures	Invasive	No	Yes (but transient)	Exotic grasses and forbs recover faster than natives after rooting, but native grasses and forbs did recover and increased over time.	Tierney and Cushman (2006)
Tropical rain forest in Hawaiian islands	Experimental; before-after pig eradication	Invasive	No	Depends on species	Pig eradication reduced the cover for most of most invasive plants established and spread due to pig rooting including rooting, but three were able to continue to spread even after pig eradication.	Tunison (1999)
Montane rain forest in Hawaiian islands	Observational; line transects	Invasive	No	Depends on species	Some invasive plants were associated with pig rooting, but others show negative or no association.	Aplet (1990)

FIGURE 2 Sampling design for *M. crenata* in Singaporean rain forests. In panel (a), the pink dots show where our transects occurred. The inset panel (b) illustrates the "on path" transects that followed existing human trails or roads through the forest, while panel (c) shows the "off path" transects running from the forest edge directly to the forest center. We recorded *M. crenata* and several biotic and environmental variables along all transects, which are illustrated in panels (b, c) (e.g., pig rooting and canopy gaps). Note the actual line transects varied in length based on total forest size but the unit of analysis was density per 40 m² segment. Map GIS layers were adapted from Yee et al. (2011).
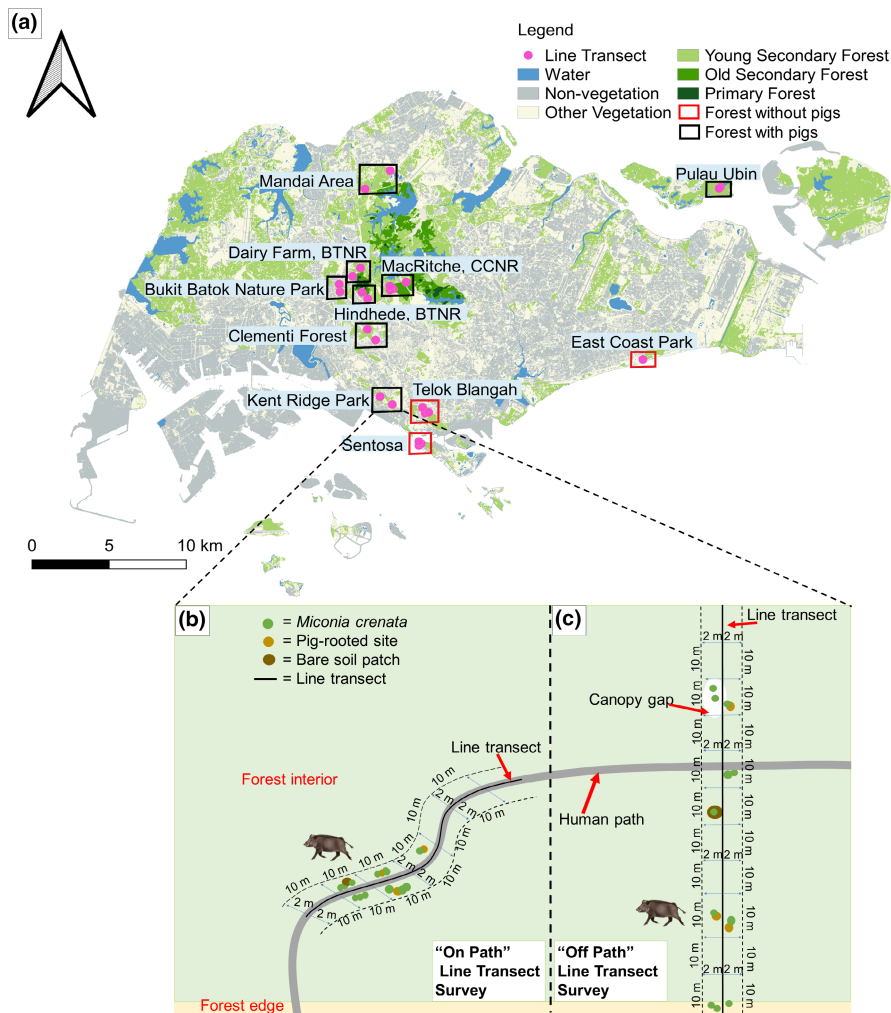
Wild pigs (*Sus scrofa*) are omnivorous and opportunistic and often forage in the soil (known as rooting) for underground materials like tubers, roots, and invertebrates (Fujinuma & Harrison, 2012). Bearded pigs (*Sus barbatus*) have not recolonized (Ke & Luskin, 2019; Luskin & Ke, 2017). This leaves behind uneven surfaces of loose bare soil and altered leaf litter and vegetation (Fujinuma & Harrison, 2012). Singapore does not have any other animals that disturb the soil in this particular manner (Dehaudt et al., 2022; Nursamsi et al., 2023). Pigs were restricted to the areas north of the Pan-Island Expressway in Singapore until 2012 and now have dispersed further south but have yet to reach Telok Blangah, Sentosa or the East Coast Park (Amir et al., 2022; Lamperty et al., 2023; Koh et al., 2018).

2.3 | Vegetation transects

We established 2–5 linear "off path" transects spaced >200 m apart randomly in each forest, extending 30–200 m from the forest edge to the center, depending on the size of the forest (Figure 2b; Table S1). We observed *M. crenata* and covariates along 10 m-long contiguous segments along these transects, within a 2 m observation window on both sides, forming 40 m² plots (Figure 2b). We surveyed 1–2 human paths in each forest, by establishing non-linear "on

path" transects following human paths, extending 60–220 m along the paths (Figure 2b; Table S1). We observed *M. crenata* and covariates along 10 m-long contiguous segments, within a 2 m observation window perpendicular to the path edges (left or right side, occasionally both sides), forming 20 m² plots on either side and grouped these into 40 m² plots. Our unit of analysis was density per 40 m² in all cases (Figure 2b; Table S1).

We recorded the following variables in each plot along the line transects: (1) number of *M. crenata* plants 40 m⁻², (2) percentage of canopy openness (% of the plot area), (3) canopy height (m), (4) pig soil disturbance (% of the plot area), (5) exposed soil without leaf litter that was not induced by pigs (hereafter, bare soil, measured as % of the plot area), and (6) distance to a forest edge (m), which was recorded at the starting point of each 10-m contiguous segment for "off path" transects (Table S2). To ensure correct identification based on characteristic leaves, only *M. crenata* stems 10 cm or taller were counted, and each stem emerging from the soil was considered an individual plant, regardless of its potential connectedness to other stems underground. In choosing our sampling approach, we faced a trade-off between sampling feasibility versus the ideal metric for estimating invasion severity (e.g., abundance vs. biomass). We opted to use the abundance of stems and acknowledge this may not scale linearly with *M. crenata* biomass or area coverage. This is one limitation of the study design.

We collected data on leaf litter because it has been previously shown to inhibit the germination of small-seeded shade-tolerant plants including *M. crenata* (Metcalfe & Turner, 1998; Samarasinghe et al., 2022; Teo et al., 2003). Prior work suggested Singaporean secondary forests have a thick leaf litter layer formed from slowly decomposing leaves from dominant trees and shrubs (Chua et al., 2013).

Pig disturbances result in distinctive overturned soil and broken stems, which is easily identifiable (e.g., Figure 1c,d; Luskin et al., 2017). The environmental covariates were estimated to the nearest 5% by dividing the $20\,m^2$ plots on either side of the transect into $1\,m^2$ sections and counting the proportion of affected. The canopy height was estimated at 2.5m increments.

2.4 | Statistical analysis

We fit generalized linear mixed-effects models (GLMMs) with zero-inflated negative binomial (ZINB) distributions and included forest ID and transect ID as a nested random effect to account for non-independence of nearby observations, using the "glmmTMB" R package (Brooks et al., 2017). Our models included *M. crenata* density (plants $40\,m^{-2}$) as the response variable, and various additive combinations of explanatory variables shown above (on or off path (binary dummy variable), canopy openness, canopy height, pig soil disturbance, bare soil, and distance to forest edge). We explored interactions and non-linear relationships by fitting quadratic terms. To test if forests with pigs have more *M. crenata* overall, we used a similar ZINB GLMM but replaced pig soil disturbance with a binary dummy variable denoting forests with and without pigs. We did not detect multicollinearity with variance inflation factor tests using the "performance" R package (Lüdecke et al., 2021). All explanatory covariates were centered and standardized prior to modelling to make their coefficients comparable. We used Akaike information criteria (AIC) to select the most parsimonious model and conducted all analyses in R v4.2.1.

3 | RESULTS

We observed 4018 *M. crenata* plants along 46 transects containing 624 plots in 11 Singaporean secondary forests. Along human paths (12 transects containing 238 plots), we observed a mean number of 25.45 plants per $40\,m^2$ (median=10 plants $40\,m^{-2}$; Table 2). Off paths

(i.e., in more natural forest areas, 34 transects containing 386 plots), we observed a mean number of 2.57 plants per $40\,m^2$ (median=0 stems $40\,m^{-2}$; Table 2). *M. crenata* density in forests recolonized by pigs was 1.05–1.8 times higher than in forests uncolonized by pigs (Table 2) but this was not statistically significant (effect size=0.048, p=.93; Table S3). In pig-recolonized forests, pigs rooted more frequently along paths than off-paths, of which 83% of the on-path plots and 53% of the off-path plots had pig soil disturbances (Figure S1). Pig soil disturbances were positively associated with distance away from forest edge in recolozined forests (effect size=0.20, p=.009; Figure S1). However, it showed a significant quadratic trend away from forest edge, which peaked at around 150m away from the forest edge(effect size=−0.12, $p<$.001; Figure S1).

The best model explaining *M. crenata* invasion included pig soil disturbances, human paths (on or off path binary), canopy openness, and distance from forest edge, which had a significant interaction with human paths, and there were no other interaction terms in the best model (Table 3). In particular, the best model did not have an interaction term between pig soil disturbances and paths, suggesting pigs and paths have an additive effect instead of a synergistic effect on *M. crenata* invasion (Table 3). The coefficients from the best model supported our hypotheses that *M. crenata* density was significantly positively associated with pig soil disturbances (effect size=0.60, p=.003), but there was a significant quadratic effect (effect size=−0.16, p=.031), suggesting pigs' facilitation of *M. crenata* peaks when approximately 50% of the sampled area is disturbed (Figure 3a, Table 4). *M. crenata* density was significantly higher along paths than off-paths suggesting humans also contribute to invasion (effect size=3.09, $p<$.001) (Figure 3a, Table 4). *M. crenata* also significantly increased with canopy openness (effect size=0.28, $p<$.001; Figure 3c, Table 4) and significantly declined with distance away from forest edges (effect size=−0.44, p=.007; Figure 3b, Table 4). However, there was a significant interaction between distance away from forest edge and human paths, suggesting *M. crenata* density decreased more substantially away from forest edges when off-paths than along paths (effect size=0.38, p=.0470; Figure 3b, Table 4).

4 | DISCUSSION

Rewilding can restore important ecosystem processes, but scientists have also warned of unintended negative consequences

TABLE 2 *Miconia crenata* densities on and off paths in forests with and without pigs and sample size.

	M. crenata on paths ($40\,m^{-2}$)		*M. crenata* off paths ($40\,m^{-2}$)	
	Mean	Median	Mean	Median
All forests (n=11)	25.45	10	2.57	0
	(12 transects, 238 plots)		(34 transects, 386 plots)	
Forests with pigs (n=8)	25.7	12	2.83	0
	(9 transects, 187 plots)		(24 transects, 305 plots)	
Forests without pigs (n=3)	24.51	6	1.56	0
	(3 transects, 51 plots)		(10 transects, 81 plots)	

TABLE 3 Factors shaping *M. crenata* invasion in Singaporean rainforests. Model selection from GLMMs with zero-inflated negative binomial distribution and nested random effects for transects within sites.

Model	AIC	K	ΔAIC	AICwt
~ Path*Edge + Canopy_openness + Pig + Pig^2	2971.78	11	0	0.34
~ Path*Canopy_openness + Edge + Pig + Pig^2	2973.74	11	1.96	0.13
~ Edge + Canopy_openness + Path + Pig + Pig^2	2973.72	10	1.96	0.13
~ Pig*Edge + Canopy_openness + Pig^2	2973.95	11	2.17	0.12
~ Path*Edge + Canopy_openness + Pig	2974.37	10	2.6	0.09
~ Pig*Canopy_openness+ Edge + Path + Pig^2	2975.33	11	3.56	0.06
~ Pig*Path + Edge + Canopy_openness + Pig^2	2975.46	11	3.68	0.05
~ Edge + Canopy_openness + Path + Pig	2975.87	9	4.1	0.04
~ Edge + Canopy_openness + Pig + Path + Bare_soil	2976.70	10	4.92	0.03
~ Pig*Edge + Pig*Path + Pig*Canopy_openness + Path*Edge + Path*Canopy_openness + Bare_soil + Canopy_ht	2982.03	16	10.26	0
Null/reduced model	3010.13	5	38.35	0

Note: "Path" is a binary dummy variable (on or off path, of which off path is the reference category), "Edge" is the distance from a forest edge, "Canopy_openness", "Pig (pig soil disturbances)" and "Bare_soil" were estimated as a percentage (% of area), with the latter implying the absence of leaf litter without evidence of pig disturbance. Canopy_ht is the height of the canopy. The "*" denotes an interaction in addition to each term included separately in the models and "^2" denotes a non-linear relationship. Null/reduced model did not include any fixed effects but only included the nested random effect.

(Nogués-Bravo et al., 2016; Pearson et al., 2022). In Singapore, restoration efforts have largely focused on native forest cover recovery, which paved the way for recolonizing wildlife (Lamperty et al., 2023). This was particularly beneficial for edge-adapted and human commensal generalist species like pigs which in turn, cause soil disturbances (Lamperty et al., 2023). We showed that a non-native plant invasion was associated with this native faunal recolonization. This result is consistent with invasion theories that suggest disturbances can undermine the normal resistance of tropical rainforests (Chong et al., 2021; Denslow & DeWalt, 2008; Fine, 2002; Rejmánek, 1996; Teo et al., 2003; Waddell et al., 2020). This plant invasion counteracts Singapore's longer-term objectives of achieving late-successional native rainforest plant communities (Chua et al., 2013; Yee et al., 2019). Therefore, decisions around rewilding and reintroductions should thus consider the potential facilitation of non-native species, interactions with people, and management required to avoid negative externalities (Pearson et al., 2022). This challenge can be addressed using the decision tools presented by Clark-Wolf et al. (2022) and Pearson et al. (2022).

The invasion of *M. crenata* into Singaporean rainforests was associated with human paths and with soil disturbances from pigs' normal foraging behavior. It is noteworthy that pig soil disturbance's effect size was larger than previously described environmental factors associated with *M. crenata* establishment including light availability and leaf litter cover. Pig rooting creates microsites for *M. crenata*'s colonization by additionally removing native plants reducing root competition and altering the soil's physical and chemical properties, which potentially favor *M. crenata*'s establishment over native plants (Barrios-Garcia et al., 2022; Fujinuma & Harrison, 2012). By turning over the soil, pigs may also bring up buried *M. crenata* seeds in the soil to the surface, exposing them to

sunlight for germination, further benefiting their invasion (Metcalfe & Turner, 1998).

Previous studies on *M. crenata*'s invasion mechanisms suggest generalist birds that travel between forest and non-forest areas may be important dispersers (Fujinuma & Harrison, 2012; Peters, 2001; Waddell et al., 2020). Urban-adapted generalist birds (both native and exotic) are abundant in Singapore and prefer more open habitats at forest fringes (Lim et al., 2003; Lok et al., 2013; Schneiberg et al., 2020). These birds may provide higher propagule pressure and explain the higher densities of *M. crenata* at forest edges.

Though more abundant around the forest edge, *M. crenata* was present in core forest areas >150m from an edge, and this was predominantly where there were disturbances including paths, pig soil disturbances, and canopy gaps coincided. The beneficial effects of pig soil disturbances, paths, and canopy gaps on *M crenata's* invasion are intuitive, based on prior work that identified factors affecting its propagule pressure, establishment sites, and survival of its seedlings (Fujinuma & Harrison, 2012; Le et al., 2018; Peters, 2001; Teo et al., 2003). These factors had additive effects when they were considered together (no synergistic interactions) and in reality, they often co-occur. This suggests *M. crenata's* ability to invade forest interiors may be facilitated by multiple co-occurring factors (birds, pigs, humans, and canopy gaps)—with each factor contributing to *M. crenata*'s successful establishment—which is consistent with other invasions dependent on multiple factors (Aschero et al., 2021; Geppert et al., 2021; Sharma et al., 2005; Speziale et al., 2018). Managers should therefore consider the additive effects of all co-occurring factors when controlling the invasion. These results also support the findings from the primary forest at Pasoh Malaysia, where pigs cause soil and plant disturbances >1km into forests and facilitate *M. crenata* invasion (Fujinuma &
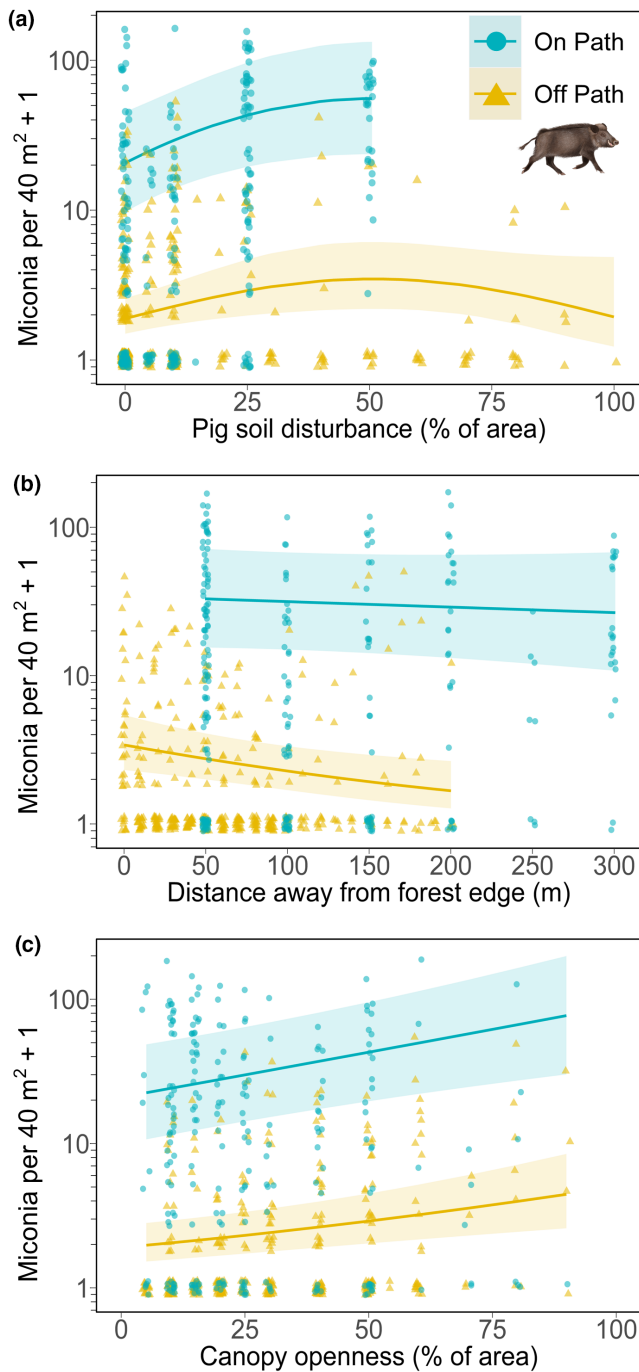
TABLE 4 Coefficients from the top model explaining *M. crenata* invasion in Singapore.

Parameters	Effect size (± SE)	*p*-value
Intercept	0.34 (±0.30)	.26
Distance from forest edge	−0.44 (±0.16)	.0072**
Path (on)	3.09 (±0.49)	<.001***
Pig soil disturbance	0.60 (±0.20)	.003**
Pig soil disturbance^2	−0.16 (±0.07)	.031*
Canopy openness	0.28 (±0.080)	<.001***
Path (on)*distance from forest edge	0.38 (±0.19)	.047*

Note: "Path" is a binary dummy variable with off path being the reference category. The "*" denotes an interaction. Quadratic terms are shown with "^2" and the standard error (SE) is shown in parentheses. The zero-inflation component of the model has an intercept of −0.93 (±0.16) and *p* < .001.

*p < .05; **p < .01; ***p < .001.

crenata plants themselves being killed when there is excessive or extreme pig rooting.

Our work adds to a growing body of evidence showing tropical forest plant invasions are more common along roads and trails, which includes examples from insular and land-bridge islands, and continental forests (Benitez et al., 2012; Chong et al., 2021; Kudo et al., 2014; Le et al., 2018; Tan et al., 2012; Teo et al., 2003; Waddell et al., 2020). This is not surprising given the disturbance-adapted traits of many invasives and that paths into forests increase the likelihood of seed dispersal from nearby non-forest areas (Ballantyne & Pickering, 2015; Chong et al., 2021; Liedtke et al., 2020; Martin et al., 2009; Moles et al., 2008; Pickering et al., 2011). Human paths therefore often act as starting points for non-native plant invasions into more pristine habitats, which was supported by our results that *M. crenata* was consistently abundant along paths, even further away from forest edges. Paths face recurrent disturbances from maintenance and usage (e.g., human or wildlife trampling and/or vehicle passage) that consistently disturb native vegetation and leaf litter layer, thereby increasing resource availability by exposing bare compact soil, facilitating *M. crenata*'s colonization (Davis et al., 2000; Le et al., 2018; Liedtke et al., 2020; Teo et al., 2003). Humans and wildlife using paths as travel corridors are also important dispersal vectors (Botella et al., 2022; Liedtke et al., 2020; Pickering et al., 2011; Wichmann et al., 2009). Wider paths with increased light availability from greater canopy disturbance may be especially conducive for invasive establishment and—if there is more human and animal traffic—also provides more propagule pressure and disturbance (Campbell & Gibson, 2001; Downing, 2020; Kudo et al., 2014; Lemke et al., 2019; Liedtke et al., 2020; Lonsdale, 1999). Indeed, we found pigs frequently rooted alongside paths and this facilitated *M. crenata*. Pigs' heightened activity around paths could transport propagules and could facilitate further spread (Smith, 1992). As this is a correlative study, we acknowledge that it is possible this pattern could also arise if pigs preferred to forage and root in areas where *M. crenata* was already abundant, such as around human paths.

FIGURE 3 *M. crenata* invasion is associated with native wild pigs, paths, forest edges and canopy gaps in Singapore. Trends in *M. crenata* invasion "on paths" and "off paths" are shown in every panel (see legend). Y-axis was plotted on a log scale. Relationships were plotted from the top model using AIC model selection (presented in Table 3), with shaded areas showing the 95% confidence intervals. Data points were jittered for clarity.

Harrison, 2012; Luskin et al., 2020, 2021; Luskin & Ke, 2017; Yong et al., 2022), whereas in Singaporean secondary forests, pigs preferentially rooted within 150 m away from forest edge. Finally, we note that the facilitation of *M. crenata's* invasion by pig soil disturbances was hump-shaped and slightly decreased at the highest levels of pig soil disturbances, which we posit may be due to *M.*

Future studies are needed to separate the importance of various dispersal agents (e.g., birds, pigs and humans) of *M. crenata* in Singapore through diet analyses, feeding experiments, and dung samples (using methods in e.g., Costa et al., 2022 and Acosta-Rojas et al., 2019). The region's pig diet and movement data is quite limited, inhibiting our inferences on their potential dispersal effectiveness (Cousens et al., 2010). Pigs causal links to *M. crenata*'s invasion should also be experimentally investigated via fenced exclosure experiments (Aplet et al., 1991; Barrios-Garcia & Simberloff, 2013; Williams et al., 2021). The spread of African swine fever has reached Singapore in early 2023, with carcasses found in multiple forested areas, providing rare opportunities to examine how the collapse of pig populations influences forest environments, plant communities, and *M. crenata* invasion dynamics (Luskin et al., 2020, 2023).

The recolonization, reintroduction, and rewilding of extirpated wildlife (or their ecological equivalents) and enhancement of nature parks for humans through creating extensive path networks, are both intended for good purposes, contributing to conservation and human appreciation of nature, respectively (Mohamed et al., 2021; Nogués-Bravo et al., 2016). While the former is often predicted to facilitate the restoration of degraded ecosystems and biodiversity, our results suggest there can be unintended negative consequences, as a result of the presence of non-native plant propagules initially introduced by humans. These externalities may be managed in the small island-city-state of Singapore through direct weed management, but rewilding of larger areas should consider the potential management feasibility and costs. We hope our empirical example can inform conservation managers to conduct a thorough preliminary screening of potential unintended consequences arising from the interactions of reintroduced species with its ecosystem, including biotic, abiotic, and anthropogenic components. Such processes can be challenging due to the lack of systematic tools or guidelines for identifying important potential interactions as well as an insufficiency in quantitative monitoring data and skills for modelling outcomes (Clark-Wolf et al., 2022; Pearson et al., 2022). However, new tools developed in recent years are making such processes more accessible to practitioners. For instance, the community assessment framework, coupled with qualitative modelling in a user-friendly web interface like MPG Matrix (https://matrix.mpgranch.com/#/), will guide conservation managers to systematically map, model and evaluate a lot of the potential interactions and consequences, prior to implementing species introduction programs as well as evaluating real-time trends following the implementation of such programs (Clark-Wolf et al., 2022; Pearson et al., 2022). Finally, given *M. crenata*'s potential to impose negative effects on native plants and frugivores if it further proliferates with pigs' facilitation, we suggest Singaporean park managers continue monitoring pigs and invasive plants and limit propagule sources by limiting trail access into the core areas of the nature reserves, and educating the public about non-native invasive plant species through weed-removal and forest restoration programs (Costa et al., 2022; Peters, 2001).

DATA AVAILABILITY STATEMENT
The data that support the findings of this study are openly available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.612jm648g

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SUPPORTING INFORMATION

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