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Invasive alien species in relation to edges and forest structure in tropical rainforest fragments of the Western Ghats

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Abstract: The impact of invasive alien species on native ecosystems is a major conservation issue in the tropics. This study in the rainforest fragments of Anamalai hills, in the Western Ghats biodiversity hotspot, assessed the effects of distance from edges and forest structure on the occurrence and abundance of three invasive alien species (*Chromolaena odorata, Lantana camara*, and *Maesopsis eminii*). Replicate line transects were laid from the edges into the interiors of four fragments varying in disturbance level and area (32 ha - 200 ha). Densities of alien species in the protected site were lower than in the three disturbed fragments. *Maesopsis eminii* occurred at highest density (382 trees ha^{-1}) in the highly disturbed site where it also showed prolific regeneration (1510 saplings ha^{-1}). The invasive alien species showed no clear edge-to-interior pattern, instead their abundance appeared to be localized and related in a site-specific manner to disturbances such as presence of *Eucalyptus* plantation, canopy openings, and trails.

Resumen: El impacto de las especies exóticas invasoras en los ecosistemas nativos es un problema grande de conservación en los trópicos. Este estudio, realizado en los fragmentos de selva tropical de las colinas Anamalai, en el hotspot de biodiversidad de los Ghats Occidentales, evaluó los efectos de la distancia alborde y de la estructura del bosque sobre la presencia y la abundancia de tres especies exóticas invasoras (*Chromolaena odorata, Lantana camara* y *Maesopsis eminii*). Se establecieron transectos lineales replicados desde los bordes hacia el interior de los cuatro fragmentos, los cuales varían en nivel de perturbación y área (32 ha - 200 ha). Las densidades de las especies exóticas en el sitio protegido fueron menores que en los tres fragmentos perturbados. *Maesopsis eminii* tuvo la densidad más alta (382 árboles ha^{-1}) en el sitio fuertemente perturbado, donde también mostró una regeneración prolífica (1510 plantones ha^{-1}). Las especies exóticas invasoras no mostraron un patrón claro de borde a interior;más bien sus abundancias parecieron ser muy localizadas, y estar relacionadasenforma específica del sitio con alteraciones tales como la presencia de plantaciones de *Eucalyptus*, aperturasen el dosel, y senderos.

Resumo: O impacto de espécies exóticas invasoras em ecossistemas nativos é uma questão importante da conservação nos trópicos. Este estudo, nos fragmentos de floresta tropical de chuvas nas colinas de Anamalai, umponto quente da biodiversidade nos Gates Ocidentais, avaliou os efeitos da distância das bordas e estrutura da floresta na ocorrência e abundância de três espécies exóticas invasoras (*Chromolaena odorata*, *Lantana camara* e *Maesopsis eminii*). Transeptos replicados foram estabelecidas a partir das bordas para o interior de quatro fragmentos variando em nível de perturbação e de área (32 ha - 200 ha). As densidades de

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espécies exóticas na estação protegida foram mais baixas do que nos três fragmentos disturbados. A *Maesopsis eminii* ocorreu em maior densidade (382 árvores ha^{-1}) na estaçãofortemente disturbada, onde ela também mostrou uma regeneração prolífica (1.510 plântulas ha^{-1}). As espécies exóticas invasoras não apresentaram nenhum padrão claro da borda para o interior, se bem que a sua abundância parecia estar localizada e relacionada, de uma maneira específica,com os distúrbios na estação tal como a presença da plantação de *Eucalyptus*, aberturas de dossel, e trilhos.

Key words: Anamalai hills, *Chromolaena odorata, Eucalyptus,* disturbance, fragmentation, *Lantana camara, Maesopsis eminii,* plantations, plant invasive.

Introduction

Around the world's tropics, a range of human activities such as agriculture, deforestation for plantations of economically important plant species, timber logging, and construction of roads and dams, and urbanisation have resulted in the fragmentation of tropical rainforests (Laurance *et al.* 2000; Zhang *et al.* 2001). Habitat fragmentation is now well recognised as a major cause of species extinction and loss of biological diversity in tropical forests (Laurance *et al.* 1997). Edge effects, the result of interaction between two adjacent ecosystems separated by an abrupt transition (Murcia 1995), isolation of forest populations, and spread of invasive alien species may all increase as a consequence of habitat fragmentation in tropical forests, leading to deleterious impacts on native biological diversity (Denslow *et al.* 2001; Laurance *et al.* 1997; Sakai *et al.* 2001). On a global scale the potential damage by invasive alien species to native species and ecosystems may be as severe as the impact due to habitat loss and degradation (IUCN 2000).

Understanding the distribution and abundance patterns of invasive alien species in fragmented landscapes can assist in planning and targeting management and control strategies. Many earlier studies have shown that disturbances such as canopy openings in tropical forests may also enhance the likelihood of establishment of invasive alien species, many of which are light-demanding (Benitez-Malvido & Martinez-Ramos 2003; Denslow *et al.* 2001; McNeely *et al.* 2001; Prasad 2011). Human-induced disturbances also alter soil properties, thereby affecting recruitment of tropical plants that have low dormancy and are intolerant of adverse soil conditions, while creating opportunities for alien species invasions (Colon & Lugo 2006). A disturbance that affects native flora may reduce the uptake of available resources such as light, water and nutrients, making the surplus resource available to alien invasive species and the site vulnerable to invasion (Davis *et al.* 2012).

Disturbance, edge density, and alien species' dispersal potential and mode of dispersal may have interactive effects on alien species invasion. Disturbances may fragment continuous forests into smaller patches with high forest-edge density. Depending on their structural characteristics and microenvironment, forest edges may facilitate or inhibit species' dispersal and the flow of propagules. Most invasive alien plant species are known as good dispersers. Forest edges may trap their airborne propagules and facilitate invasion (Brothers & Spingarn 1992). Thus, areas with many small patches or high edge density are expected to be more prone to invasion by alien plant species (Kumar *et al.* 2006). In addition, some studies report that animal dispersed alien species may pose a significant invasion threat even to undisturbed forests (Cordeiro *et al.* 2004; Joshi *et al.* 2009; Mudappa *et al.* 2010).

Here we report a study from the Anamalai hills of the Western Ghats of India on three plant species known to have serious invasive potential in tropical forests. This included two understorey species native to tropical America that are listed among 100 of the world's worst invasive alien species (Lowe *et al.* 2000)... *Chromolaena odorata* (Siam weed) and *Lantana camara*... both of which are known to often establish under disturbed or open canopies in tropical forests (Duggin & Gentle 1998; Kohli *et al.* 2006; Sharma *et al.* 2005) and are commonly noted as understorey invasives in tropical South and Southeast Asian forests (Lowe *et al.* 2000; Matthews 2004). Studies in tropical dry forests of southern India have documented that thickets of *Lantana camara* could alter plant community composition by affecting the establishment of native tree seedlings (Ramaswami & Sukumar 2011; Prasad 2010). The third species, *Maesopsis eminii*, is a tree species native to Africa, noted to be an early successional tree usually spreading through dispersal by animals (Cordeiro *et al.* 2004). Often used as a shade tree in coffee plantations, *M. eminii* grows well under forest canopy openings (Binggeli & Hamilton 1993; Cordeiro *et al.* 2004; Viisteensaari *et al.* 2000). We also separately consider the abundance of *Clerodendrum viscosum*, a native pioneer occurring commonly as a shrub and growing into small-sized trees under favourable conditions usually related to edges, gaps, light availability and disturbance. The presence and size of *C. viscosum* has been used as an indicator of age of forest gaps and successional or disturbance status of sites (Chandrashekara & Ramakrishnan 1993; Raman *et al.* 2009).

Substantial areas of tropical rainforests in India's Western Ghats, a series of hill ranges recognised as a global biodiversity hotspot (Mittermeier *et al.* 2004), have been historically lost and the forest now exists as fragments surrounded by plantations, mostly of non-indigenous plant species such as coffee, *Eucalyptus*, and tea (*Camellia sinensis*) (Kumar *et al.* 2004). Our earlier studies in one such fragmented landscape, the Valparai plateau in the Anamalai hills, indicated the occurrence of non-indigenous species in many rainforest fragments, including two species of coffee (Arabica *Coffea arabica* and Robusta *C. canephora*) that are shade-tolerant tropical understorey crops, besides *M. eminii*, *L. camara*, and *C. odorata* (Muthuramkumar *et al.* 2006; Mudappa & Raman 2007). We conducted a study to assess the invasion of these non-indigenous species in rainforest fragments of Anamalai hills. Based on information on invasion of these species from other regions, we expected that the proximity to human-made fragment edges and magnitude of disturbance would positively influence the abundance of alien invasive species in rain-forest fragments in Anamalai hills of the southern Western Ghats. While we report on invasion by the two coffee species in a parallel publication (Joshi *et al.* 2009), here we specifically address the following questions: (a) what is the pattern of change in density of trees (all, native, *C. viscosum*, and alien) across fragments of varying sizes, (b) how does the distribution and abundance of the three invasive alien species (*C. odorata, L. camara,* and *M. eminii*) vary across fragments and in relation to the distance from fragment edges and forest structural variables. We discuss the influence of these variables on the occurrence of these invasive species in rainforest fragments on the Valparai plateau and its implications for conservation in the region.

Materials and methods

Study area

The Western Ghats hill range along India's west coast (7° N to 21° N), along with Sri Lanka, is recognised as one of the world's 34 biodiversity hotspots (Kumar *et al.* 2004). The Anamalai hills, located south of the Palghat gap (11° N), had large tracts of tropical rainforest that were extensively clear-felled between the 1860s and 1930s for cultivation of tea and coffee, and for teak and *Eucalyptus* plantations as in the Valparai plateau (Congreve 1942). The Valparai plateau (at 700 m - 1400 m altitude), where this study was carried out, is surrounded by Anamalai Tiger Reserve (958 km^2, 10°12′ N to 10°35′ N and 76°49′ E to 77°24′ E) in Tamil Nadu, and other protected areas and reserved forests in Kerala. Extensive areas of private plantations of tea (150 km^2), coffee (28 km^2), cardamom, and *Eucalyptus* spread over an area of 220 km^2 on the Valparai plateau (Mudappa & Raman 2007). Following habitat fragmentation due to the establishment of plantations as well as roads, hydroelectric dams, reservoirs and logging, rainforests today occur as over 40 fragments varying in area from 1 to 2500 ha, often surrounded by monoculture plantations, particularly of tea, amidst a human population of about 90,000 people on the Valparai plateau (Mudappa & Raman 2007). The natural vegetation of this region is mid-elevation tropical wet evergreen rain forest of the *Cullenia exarillata - Mesua ferrea - Palaquium ellipticum* type (Pascal 1988). The average annual rainfall recorded at Injipara estate of Valparai plateau over a period of ten years (1989-1998) was 3497 mm. The southwest monsoon (June to September) contributes about 70 percent of the total rainfall. The daytime temperature ranges between 19 °C and 34 °C.

The study was carried out between April and June 2006. As one of the aims was to assess the spread of coffee into fragments, we selected four sites that adjoined coffee plantations and had coffee established in the rainforest understorey (Joshi *et al.* 2009). The sites varied in area and degree of disturbance as indicated in Table 1 (see also Joshi *et al.* 2009; Muthuramkumar *et al.* 2006; Mudappa & Raman 2007).

Field methods

In each fragment under study, vegetation was sampled systematically and uniformly using quadrats distributed along seven replicate line transects spaced 60 m apart and parallel to each other. The line transects started from the edge of the fragment adjoining the coffee plantation into the interior in a direction perpendicular to the edge. The fragment edge adjoining coffee plantation was considered as a forest edge as periodic human activities for agricultural operations are carried out along that edge. This edge was considered significant to assess the edge effect on the distribution of alien invasive species inside the fragment. Along each line transect, 12 quadrats of size 10 m × 10 m were laid. The first quadrat was located at the fragment edge and the next nine quadrats were laid 10 m apart from each other along the line transect. Given the non-linear trend in influence of edge effects as shown in numerous studies (Ewers & Didham 2006; Ewers *et al.* 2007; Ries *et al.* 2004), and to assess the abundance of focal invasive species well inside the fragment from the edge, the eleventh and twelfth quadrats were laid at intervals of 25 m from the tenth and from each other. The sampling effort was uniform and sample size identical across all sites except the moderately disturbed fragment, Tata Finlay. In this fragment, along one of the seven transects, the location of the last quadrat happened to be at the opposite edge of the fragment and adjoined a *Eucalyptus* plantation. Therefore, we did not place a quadrat at the location. Except for a few quadrats in this fragment (Tata Finlay), the nearest edge for all quadrats was the fragment edge from where the transects began. However, even in Tata Finlay, for those quadrats that were an exception, the nearest edge happened to be an old *Eucalyptus* plantation that had not been subjected to any felling or other disturbance related to regular human activity for several years (personal observation).

For tree density and basal area, all trees ≥ 30 cm girth at breast height (GBH, at 1.3 m) in the 10 m x 10 m quadrat were counted and their GBH was measured. The non-indigenous trees (*M. eminii, Eucalyptus* sp.) were recorded separately. In the case of multi-stemmed species, the sum of the GBH of all stems was taken to be the GBH of that individual. We measured three canopy structure variables in each 10 m × 10 m quadrat. Although the three measures of canopy structure are correlated, all were measured because they provide information regarding different aspects of vegetation structure: canopy cover indicates density of overhead foliage; canopy overlap reveals whether overhead canopy is comprised of single or multiple tree individuals; and vertical layers gives an idea of age or maturity of vegetation. Canopy cover was measured as average of spherical densiometer measurements taken in four directions at the centre of the quadrat; canopy overlap was measured on a 0 (open) to 3 (fully closed) scale; and number of vertical layers present were recorded for the foliage directly overhead at the centre of the quadrat (the different vertical layers constituted foliage at heights of 1-5, 5-10, 10-20, 20-30, 30-40 and > 40 m). Unlike fragment edge, human-made trails inside the fragment may not induce microclimatic changes as they did not disrupt canopy structure to the same extent as edges. However, presence of trails indicates periodic human movement and extraction of resources such as fuelwood from inside the fragments. Therefore, we considered the presence of human-made trails inside fragments as disturbance to native biodiversity, which might favour invasive species establishment and recorded closest distance to human-made trail from each quadrat (further details in Joshi *et al.* 2009).

In the four corners of each 10 m × 10 m quadrat, 2 m × 2 m sub-quadrats were laid. For understorey species, all stems that were at least 30 cm in height or with GBH between 1 cm and 30 cm were counted in these sub-quadrats. Among these, the number of stems was noted species-wise for the three invasive species, *L. camara*, *C. odorata*, and *M. eminii*.

Analysis

As a portion of the less-disturbed rainforest fragment contained planted *Eucalyptus* trees, with the associated more-disturbed environment, we post-stratified this site into less disturbed + *Eucalyptus* (3 transects) and less disturbed rainforest (4 transects). This yielded five strata across the four sites. For each stratum, mean basal area and mean tree density (and corresponding standard errors) were calculated across replicate quadrats. To obtain a measure of stem density of the three invasive alien species for each site, we summed stem counts within the sub-quadrats and averaged across the replicate quadrats within the site and expressed this as stems per hectare.

Table 1. Details of intensive study fragments in the Valparai plateau, Anamalai hills.

Rainforest fragment	Disturbance	Area (ha)	Altitude (m asl)	Ownership	Surrounding landscape
Manamboli	Protected, relatively undisturbed	200	760-1120	Anamalai Tiger Reserve	Plantations of *Coffea arabica, C. canephora*, and *Elettaria cardamomum* (cardamom)
Pannimade	Less disturbed	87	1080	Tata Coffee Limited	*Coffea arabica, Eucalyptus*, *Camellia sinensis* (tea), Sholayar Reservoir
Tata Finlay	Moderately disturbed	32.6	980-1200	Tata Coffee Limited	*Coffea arabica, Eucalyptus*
Puthuthottam	Highly disturbed	92	1000-1100	Puthuthottam Estates Limited	Tea, *Coffea arabica, C. canephora,* Valparai town

Statistical analyses were carried out using R statistical and programming environment (version 2.13.2, R Development Core Team 2011). The data appeared to meet the assumptions of independence and homoscedasticity, with minor variations. Statistical differences in tree density variables and stem density of *L. camara*, *C. odorata*, and *M. eminii* across sites were assessed by linear mixed effects models of quadrat data of each of these variables with strata as the fixed effect and transect as random effect using the lme function in package nlme (Crawley 2007; Zar 1999). This was followed by Tukey multiple comparisons tests to assess pair-wise differences among sites at $P < 0.05$ (using glht function in package multcomp in R (Hothorn *et al*. 2008). To assess the edge-to-interior pattern, the stem density in quadrats at each distance from the edge was averaged across the replicate line transects and expressed as stems per 16 m^2 and plotted against, and correlated to, distance from the edge. The interactive effects of distance from the fragment edge and other forest structure variables (canopy cover, canopy overlap, number of vegetation layers, distance from human-made trail, tree basal area, native rainforest tree density, native shrub density, *Clerodendrum viscosum* tree density and *C. viscosum* shrub density) on the distribution of the focal invasive alien species across each of the study fragments were assessed using multiple linear regression (with backward stepwise method for variable selection, Zar 1999).

Results

Although the overall tree density did not vary substantially across sites, there were notable differences among native and alien species tree densities (Table 2). Across sites, native rainforest tree densities were highest in the protected site (450 stems ha^{-1}) and decreased along the disturbance gradient to the highly disturbed site (166 stems ha^{-1}, Table 2). The quadrats in the protected site did not have any alien tree species and no tree-sized individuals of *C. viscosum*, a native species of pioneer shrub that established as small trees (> 30 cm girth at breast height, GBH) in the other sites. Overall, alien trees were absent in the protected site, highest in the *Eucalyptus* portion of the less disturbed site and in the highly disturbed site, being intermediate elsewhere. *Eucalyptus* trees occurred only in a portion of the less disturbed site at a density of 81 trees ha^{-1}. *M. eminii* trees occurred at high densities (382 ha^{-1}) in the highly disturbed site. The girth-class distributions of the native pioneer *C. viscosum* and the alien tree species *M. eminii* in the highly disturbed site indicated a preponderance (69 %) of stems of GBH < 75 cm in the case of the latter. In comparison, only 48 % of the stems of other (native) trees were < 75 cm GBH (Fig. 1).

Across the four fragments sampled during this study, *C. odorata* was present in all, whereas *L. camara* and *M. eminii* were absent in the samples from the protected rainforest site (in supplementary observations, *L. camara* was noted in this site at several locations, particularly along roads and along a large water pipeline from the Sholayar reservoir to Manamboli hydroelectric powerhouse). Stem density of all three invasive alien species were found to be significantly different across five selected strata: protected, less disturbed, less

Table 2. Differences in densities of tree-sized stems (> 30 cm girth at breast height) of alien and native tree species in selected study strata in the Anamalai hills, analysed with linear mixed effects models followed by Tukey HSD multiple comparisons tests (within each variable, means with different superscripted letters differ from each other significantly).

Variable / Strata	Mean density (stems ha^{-1})	Mixed model (lme) results			
		Value* (SE)	T (DF)	*P*	Random effect
All trees					
Protected (intercept)	450.0^{a}	450.0 (34.5)	13.05 (307)	< 0.001	SD = 55.1
Less disturbed	512.5^{a,b}	62.5 (57.2)	1.09 (23)	0.286	Residual = 251.9
Less disturbed + Euc	525.0^{a,b}	75.0 (63.0)	1.19 (23)	0.246	
Moderately disturbed	445.8^{a}	-4.7 (48.9)	-0.10 (23)	0.924	
Highly disturbed	583.3^{b}	133.3 (48.8)	2.73 (23)	0.012	
All native					
Protected (intercept)	450.0^{a}	450.0 (26.9)	16.73 (307)	< 0.001	SD = 43.7
Less disturbed	460.4^{a}	10.4 (44.6)	0.23 (23)	0.817	Residual = 194.6
Less disturbed + Euc	422.2^{a}	-27.8 (49.1)	-0.57 (23)	0.577	
Moderately disturbed	371.1^{a}	-79.2 (38.1)	-2.08 (23)	0.049	
Highly disturbed	165.5^{b}	-284.5 (38.0)	-7.48 (23)	< 0.001	
Clerodendrum viscosum					
Protected (intercept)	0.0^{a}	0.0 (10.7)	0.00 (307)	1.000	SD = 17.8
Less disturbed	41.71^{a,b}	41.7 (17.7)	2.36 (23)	0.027	Residual = 75.8
Less disturbed + Euc	2.8^{a}	2.8 (19.5)	0.14 (23)	0.888	
Moderately disturbed	67.5^{b}	67.3 (15.1)	4.45 (23)	< 0.001	
Highly disturbed	35.7^{a,b}	35.7 (15.1)	2.37 (23)	0.027	
All alien					
Protected (intercept)	0.0^{a}	0.0 (18.9)	0.00 (307)	1.000	SD = 24.7
Less disturbed	10.4^{a,b}	10.4 (31.3)	0.33 (23)	0.743	Residual = 150.7
Less disturbed + Euc	100.0^{b}	100.0 (34.5)	2.89 (23)	0.008	
Moderately disturbed	7.2^{a,b}	7.20 (26.8)	0.27 (23)	0.790	
Highly disturbed	382.1^{c}	382.1 (26.7)	14.3 (23)	< 0.001	
Eucalyptus					
Protected (intercept)	0.0^{a}	0.0 (5.28)	0.00 (307)	1.000	SD = 11.4
Less disturbed	0.0^{a}	0.0 (8.76)	0.00 (23)	1.000	Residual = 28.1
Less disturbed + Euc	80.6^{b}	80.6 (9.65)	8.35 (23)	< 0.001	
Moderately disturbed	0.0^{a}	0.0 (7.48)	0.00 (23)	1.000	
Highly disturbed	0.0^{a}	0.0 (7.47)	0.00 (23)	1.000	
Maesopsis eminii					
Protected (intercept)	0.0^{a}	0.0 (17.8)	0.00 (307)	1.000	SD = 20.1
Less disturbed	10.4^{a}	10.4 (29.5)	0.35 (23)	0.728	Residual = 147.6
Less disturbed + Euc	19.4^{a}	19.4 (32.5)	0.60 (23)	0.556	
Moderately disturbed	7.2^{a}	7.2 (25.2)	0.29 (23)	0.778	
Highly disturbed	382.1^{b}	382.1 (25.2)	15.2 (23)	< 0.001	

*Values are density in protected site and differences of each strata from protected site.

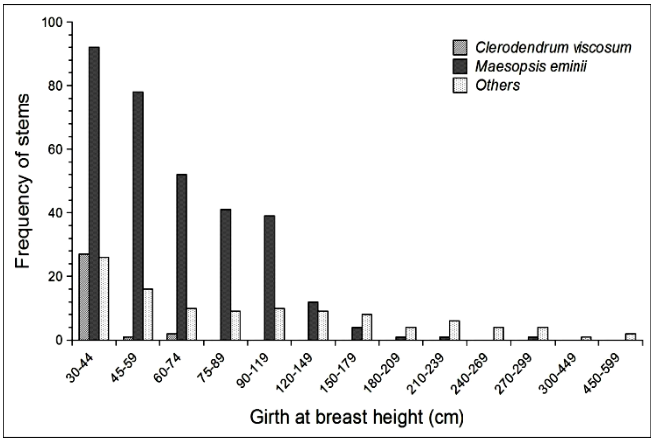

Fig. 1. Tree girth-class distributions of the native pioneer *Clerodendrum viscosum*, alien *Maesopsis eminii*, and other (native) species in the highly disturbed site in the Anamalai hills.

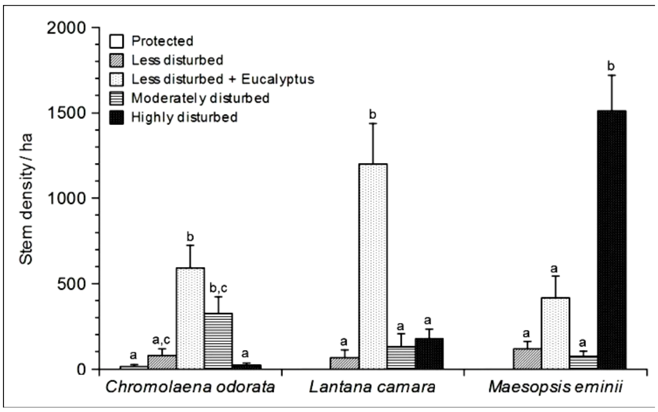

Fig. 2. Density of *Chromolaena odorata*, *Lantana camara,* and *Maesopsis eminii* stems across the selected study strata in the Anamalai hills with Tukey multiple comparisons tests (means with different letters differ from each other significantly).

disturbed - portion with *Eucalyptus,* moderately disturbed, and highly disturbed sites (Fig. 2; strata as fixed effect in linear mixed model analysis using lme function, at $P < 0.05$). Pair-wise differences between sites assessed by Tukey HSD post-hoc tests (Fig. 2) showed that the stem density of *C. odorata* was highest (590 stems ha^{-1}) in the portion with *Eucalyptus* within the less disturbed fragment and in the moderately disturbed rainforest fragment (324 stems ha^{-1}). It was significantly lower in both the protected site (15 stems ha^{-1}) and highly disturbed sites (22 stems ha^{-1}). *L. camara* stem density appeared to be positively related to disturbance, being absent in the protected site (0 stems ha^{-1}) and increasing along the gradient from less disturbed (65 stems ha^{-1}), moderately disturbed (128 stems ha^{-1}), and highly disturbed (179 stems ha^{-1}) sites. Notably, in the portion with planted *Eucalyptus* in the less disturbed site, *L. camara* densities were significantly higher at 1198 stems ha^{-1} (Fig. 2). Similarly, the stem density of *M. eminii* in the understorey was significantly higher in the highly disturbed site (1510 stems ha^{-1}), absent in the protected site and intermediate in the other sites (Fig. 2).

The stem density of *C. odorata*, *L. camara*, and *M. eminii* showed no significant trend in relation to distance from fragment edge (Fig. 3) and was unrelated to this variable in multiple regression analyses (edge distance, Table 3). Instead, analyses showed that *C. odorata* stem densities in the protected site was negatively related to canopy overlap and positively related to distance from trails (adjusted R^2 = 0.124, Table 3). Stem densities in all other cases showed very weak relationships (adjusted $R^2 < 0.08$) with predictor variables, including several weak negative correlations with canopy variables such as cover, overlap, and vertical layers, and positive relationship with edge distance (Table 3).

Discussion

Studies carried out hitherto indicate that alien plant species invasion in tropical forests is largely related to human disturbance and that undisturbed tropical forests tend to have few alien species (Fine 2002). Similarly, the results of this study suggest that the stem density of *C. odorata*, *L. camara*, and *M. eminii* is influenced by the history and extent of disturbance to rainforest vegetation. The protected rainforest fragment showed lowest stem density of all three invasive alien species considered. In the case of *C. odorata*, stem densities were highest in the moderately disturbed site and in the portion of the less disturbed site with *Eucalyptus.* Its low density in the highly disturbed site is, however, anomalous to this pattern for reasons that remain unknown. *L. camara* density also appeared to be broadly related to disturbance at the site level, including disturbance associated with the establishment of *Eucalyptus* planted in a portion of the less disturbed site. Dense thickets of *L. camara* frequently occur in the understorey of *Eucalyptus* plantations

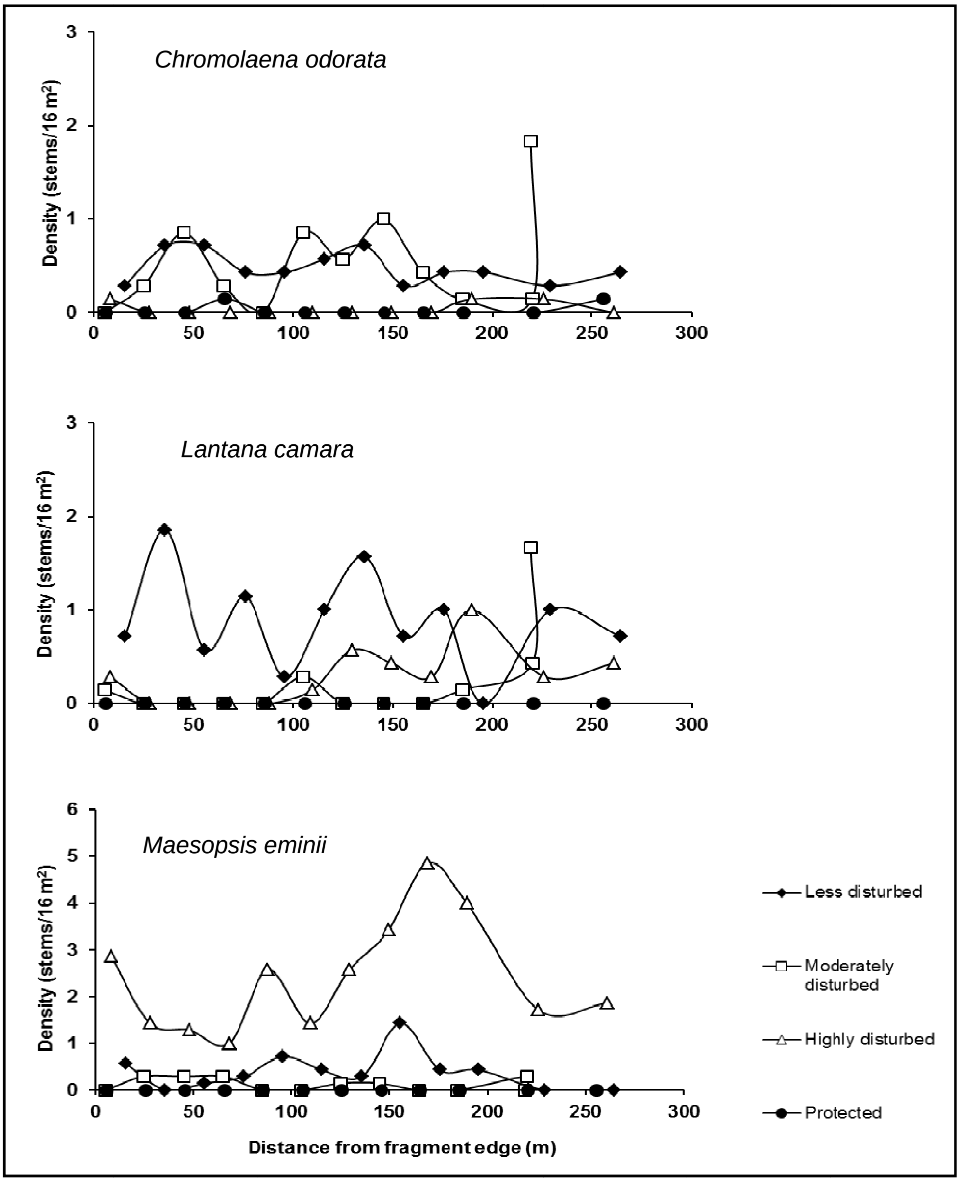

Fig. 3. Density of *Chromolaena odorata*, *Lantana camara,* and *Maesopsis eminii* stems in relation to distance from fragment edges in the Anamalai hills.

in this region, apparently related to the higher disturbance (clearing or opening-up of vegetation during plantation establishment and felling cycles) and sparse canopy associated with this alien tree species (personal observations), and this is consistent with recent studies on *Lantana* invasion (Raizada *et al.* 2008; Sharma & Raghubanshi 2010). Disturbances that create canopy openings and light gaps may stimulate the establishment and growth of light-demanding species (CRC 2003; Denslow *et al.* 2001; Kohli *et al.* 2006). However, only weak relationships with canopy closure were observed in this study.

The stem density of *M. eminii* could not be clearly attributed to disturbance; instead, it may be related to proximity effects. Its high abundance in the highly disturbed site is probably because this site adjoined a coffee plantation that was planted abundantly with *M. eminii* as a shade tree (33 % of individuals of an estimated tree density of 131 trees ha^{-1}, T. R. S. Raman, unpublished data), and its absence from the protected site is likely because of the absence of *M. eminii* shade trees in the coffee plantation adjoining that site. The intermediate abundance of *M. eminii* in the other two fragments is probably due to this species being

Table 3. Variables influencing stem density of *Chromolaena odorata*, *Lantana camara*, and *Maesopsis eminii* in rainforest fragments: results of multiple regression analysis.

Dependent variable / Site	Constant / Predictors	Regression coefficients (SE)	Adjusted R^2 (%)	*T*	*P*
Chromolaena odorata					
Protected	Constant	0.201 (0.097)	12.4	2.073	0.041
	Trail distance	0.003 (0.001)		3.169	0.002
	Canopy overlap	-0.119 (0.051)		-2.338	0.022
Less disturbed	Constant	2.271 (0.768)	5.2	2.959	0.004
	Canopy cover	-0.021 (0.009)		-2.361	0.021
Moderately disturbed	Constant	0.229 (0.289)	4.5	0.792	0.431
Highly disturbed	Edge distance	0.004 (0.002)	NS	1.925	0.058
	Trail distance	-0.084 (0.41)		-2.021	0.047
Lantana camara					
Less disturbed	Constant	3.093 (0.818)	7.6	3.782	< 0.001
	Layers	-0.426 (0.234)		-1.824	0.072
	Native shrubs	-0.034 (0.017)		-2.006	0.048
Moderately disturbed	Constant	0.220 (0.313)	7.6	0.702	0.485
	Edge distance	0.004 (0.002)		2.434	0.017
	Native shrubs	-0.017 (0.008)		-1.999	0.049
Highly disturbed	Constant	2.807 (1.551)	5.6	1.809	0.074
	Edge distance	0.002 (0.001)		1.918	0.059
	Canopy cover	-0.032 (0.018)		-1.804	0.075
Maesopsis eminii					
Less disturbed	Constant	1.385 (0.703)	5.3	1.968	0.052
	Canopy cover	-0.017 (0.009)		-2.013	0.047
	Native shrubs	0.02 (0.009)		2.150	0.035
Moderately disturbed	Constant	NS	NS	NS	NS
Highly disturbed	Constant	2.042 (0.354)	6.5	5.770	< 0.001
	Trail distance	0.286 (0.110)		2.610	0.011

used as a shade tree only in coffee fields some distance away (> 200 m) from the edge of those fragments.

Maesopsis eminii is dispersed by mammals such as macaques, civets, bears, and elephants, besides birds such as hornbills (D. Mudappa & T. R. S. Raman, personal observations) and this may explain its pattern of spread into adjoining fragments, as in the case of coffee (Joshi *et al.* 2009; Mudappa *et al.* 2010). Concerns have been expressed over the dispersal-mediated invasive potential of *M. eminii* in tropical forests of Africa (Binggeli & Hamilton 1993; Cordeiro *et al.* 2004), although *M. eminii* may eventually decline in the regeneration 45 - 50 years after planting if mature closed-canopy forest of native tree species is allowed to recover in sites protected from further disturbances and canopy gaps (Viisteensaari *et al.* 2000). The density attained by *M. eminii* in the highly disturbed site (1510 stems ha^{-1} on average with a maximum around twice as high in patches) appears higher than densities reported from African forests invaded by this species (< 200 stems ha^{-1}), although the data are not strictly comparable due to differences in girth classes and sampling protocols used. Nevertheless, the relatively high density and girth class distribution showing a preponderance of young but reproductively mature trees indicates a significant invasion threat by this species. If this is to be curtailed in the site, it needs to be protected from further disturbance such as fuelwood collection and occasional girdling and felling of trees that are continuing because of the proximity of this site to the densely populated Valparai town (Mudappa & Raman 2007).

We found no clear pattern of invasive species distribution in relation to distance from edge. This is consistent with earlier reports that edge penetration distance of disturbance-adapted plant species is seldom greater than 20 m (Laurance & Vasconcelos 2004). Instead, distribution of these weeds may be localised in relation to canopy gaps resulting from disturbances such as tree falls, human-made trails, and illicit felling. It also contrasts strongly with the patterns of strong edge-effects and deep penetration (> 200 m) and much higher abundance attained by a shade-tolerant alien species, coffee (particularly Robusta *Coffea canephora*), in the same area (Joshi *et al.* 2009).

A major lacuna of this study is the use of only a few sites, with no replicates for various disturbance and fragment size categories; thus the conclusions may be taken as preliminary and indicative. Nevertheless, the study presents useful information on the occurrence and abundance of invasive species in fragments and will, we hope, stimulate further research on linkages between rainforest fragmentation and invasive species in the region.

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