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Brewing trouble: coffee invasion in relation to edges and forest structure in tropical rainforest fragments of the Western Ghats, India

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Abstract While the conservation impacts of invasive plant species on tropical biodiversity is widely recognised, little is known of the potential for cultivated crops turning invasive in tropical forest regions. In the Western Ghats biodiversity hotspot, India, fragmented rainforests often adjoin coffee plantations. This study in the Anamalai hills assessed the effects of distance from edges and forest structure on the occurrence and abundance of shade-tolerant coffee (Arabica *Coffea arabica* and Robusta *C. canephora*) in four fragments (32–200 ha) using replicate line transects laid from the edges into the interiors. The coffee species cultivated in adjoining plantations was more abundant than the other coffee species inside study fragments, showing a clear decline in stem density from edge (0 m) to interior (250 m), suggesting the influence of propagule pressure of adjoining plantations, coupled with edge effects and seed dispersal by animals. Significant positive correlations of coffee density with canopy cover indicate the potential threat of coffee invasion even in closed canopy rainforests. Stem density of *Coffea arabica* (150–1,825 stems/ha) was higher in more disturbed fragments, whereas *Coffea canephora* had spread in disturbed and undisturbed sites achieving much higher densities (6.3–11,486 stems/ha). In addition, a negative relationship between *C. canephora* and native shrub density indicates its potential detrimental effects on native plants.

Keywords Fragmentation · Plantations · Shade tolerance · Invasive alien species · Anamalai hills · *Coffea arabica* · *Coffea canephora*

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Introduction

Human activities such as deforestation for plantations of economically important crops, logging, and developmental activities have resulted in widespread fragmentation of tropical rainforests, with resulting loss and alteration of biological diversity (Laurance et al. 1997; Benitez-Malvido and Martinez-Ramos 2003). Major consequences of tropical forest fragmentation include changes in the extent and configuration of natural and altered habitats in the landscape, increased isolation of forest populations, increased edge effects, and invasions by non-indigenous species, all of which can have deleterious impacts on native biological diversity (Laurance et al. 1997; Denslow et al. 2001; Sakai et al. 2001). The sharp increase in the amount of edge following fragmentation, in particular, may negatively affect many mature forest species and ecological processes. Studies have shown that the artificial edges created by forest fragmentation create favourable conditions for the appearance of invasive alien species (Denslow et al. 2001; Fine 2002). According to the World Conservation Union (IUCN), the potential damage by invasive species to native species and ecosystems on a global scale is considered as important as the impact due to habitat degradation making it a serious conservation issue (IUCN 2000; Soulé and Orians 2001).

Earlier studies have shown significant changes in biological diversity and increased prevalence of invasive species at or near forest fragment edges (Saunders et al. 1991; Sisk and Margules 1993). This may be linked to disturbance and edge-related micro-climatic changes such as increase in temperature and light and reduction in humidity in fragments (Saunders et al. 1991; Laurance 2000). In addition, variables of forest structure and surrounding landscape matrix may also influence the distribution of non-indigenous species (Whitmore 1997; Denslow et al. 2001). Within fragments, disturbances such as canopy openings and changes to the soil surface may also enhance the likelihood of establishment of light-demanding or disturbance-adapted invasive alien species (Whitmore 1997; Denslow et al. 2001; McNeely et al. 2001).

The rainforests in the Western Ghats of India, a hill range recognised as a global biodiversity hotspot (Mittermeier et al. 2004), face threats similar to those faced by tropical forests in other parts of the world. Much of the Western Ghats rainforests now exists as fragments surrounded by plantations, mostly of non-indigenous plant species such as coffee (*Coffea* spp.), *Eucalyptus*, and tea (Kumar et al. 2004). Studies in one such fragmented landscape, the Valparai plateau in the Anamalai hills, have indicated the occurrence of non-indigenous species in many rainforest fragments (Muthuramkumar et al. 2006; Mudappa and Raman 2007). These include two species of coffee (Arabica *Coffea arabica* and Robusta *C. canephora*) that are shade-tolerant tropical understorey crops, *Maesopsis eminii*, an African tree species used as shade tree in coffee plantations, and other understorey weeds common in tropical south and south-east Asia such as *Lantana camara* and *Chromolaena odorata*.

The need to assess coffee as a potential invasive in tropical forests becomes significant because, globally, around 11 million hectares are under coffee cultivation, almost entirely in tropical forest regions (Clay 2004). With an annual value of over $100 billion, coffee is also the second highest traded commodity in international trade after oil, making assessment of its impacts on biodiversity an imperative (Donald 2004). Clearing new areas of tropical forest for coffee cultivation has also been a matter of recent conservation concern (Rappole et al. 2003). Frequently, coffee plantations adjoin protected conservation reserves or contain embedded forest remnants known to be significant for conservation of biological diversity (Somarriba et al. 2004). Considerable recent research has addressed the biodiversity values of coffee plantations, especially shade-grown coffees (Rappole et al. 2003; Mas and Dietsch 2004), and the economic benefits of biodiversity to coffee farms (Ricketts et al. 2004; Philpott et al. 2007). However, little attention has been paid on the effects of coffee plantations on adjoining tropical forests. A study in New South Wales has reported the spread of coffee (*C. arabica*) as a weed inside rainforest fragments and noted its potential threat to rainforest regeneration (Lymburner et al. 2006).

This study was designed to assess the distribution and abundance of coffee species in relation to the distance from fragment edges and forest structural variables in tropical rainforest fragments on the Valparai plateau. We also compared the patterns of distribution and abundance of the two major coffee species, *C. arabica* and *C. canephora*. The results are discussed in the context of the potential for a widely-cultivated crop to spread as an invasive and thereby affect tropical forest conservation.

Materials and methods

Study area

The Western Ghats is a chain of mountains running almost parallel to the west coast of India from 7° to 21° N. The 1600 km stretch is interrupted only by the 30 km wide Palghat gap (11° N). High levels of biodiversity and endemism are its prominent characteristics, with about 5,000 flowering plant species, of which 1,700 species are endemic (Kumar et al. 2004). The forests of the Western Ghats include representative non-equatorial tropical wet evergreen forests of high conservation priority (Menon et al. 2001). This region, along with Sri Lanka, has been recognised as a global biodiversity hotspot (Kumar et al. 2004).

The Anamalai hill range, located to the south of the Palghat gap, had one of the largest contiguous tracts of tropical rainforest in the Western Ghats until the mid-nineteenth century. It was extensively clear-felled between the 1860s and 1930s for cultivation of tea and coffee, and later for teak and *Eucalyptus* plantations (Congreve 1942; Muthiah 1993). The establishment of plantations in addition to other forces of landscape change such as roads, hydroelectric dams, reservoirs, and logging led to fragmentation of the rainforest. As a consequence, the majority of the rainforest in the region today is comprised of approximately 40 fragments, varying in area from 1 to 2,500 ha. These fragments are often surrounded by monoculture plantations, particularly by tea *Camellia sinensis*, amidst a human population of around 100,000 people on the Valparai plateau (Mudappa and Raman 2007).

The Valparai plateau at 700–1,400 m above sea level is surrounded by Indira Gandhi Wildlife Sanctuary and National Park (987 km^2, 10°12′–10°35′ N and 76°49′–77°24′ E) in Tamil Nadu and other protected areas and reserved forests in Kerala (Fig. 1). Extensive areas of private plantations of tea (150 km^2), coffee (28 km^2), cardamom (7 km^2), and *Eucalyptus* spread over an area of 220 km^2 on the Valparai plateau (Thomas 2003; Mudappa and Raman 2007). The natural vegetation of this region is mid-elevation tropical wet evergreen 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 10 years (1989–1998) was 3,497 mm. The southwest monsoon (June–September) contributes about 70% of the total rainfall. The daytime temperature ranges between 19 and 24°C.

The rainforest fragments on the Valparai plateau are located close to human settlements and are degraded due to fuel wood collection and felling for timber and a few have been partly under-planted with coffee or cardamom in the past and then abandoned. Most of the large fragments (>200 ha) are protected within the Indira Gandhi Wildlife Sanctuary (Mudappa and Raman 2007).

Intensive study sites

The study was carried out between April and June 2006. The study sites were selected on the basis of a preliminary survey that was carried out to broadly assess the disturbance levels of the fragments and the surrounding landscape. We selected four sites that adjoined coffee plantations and varied in area and degree of disturbance based on our prior research and familiarity with the area over the last decade (Mudappa and Raman 2007). Degree of disturbance was semi-quantitatively assessed by summing scores assigned for disturbance factors such as illegal timber felling, girdling, fuel-wood collection, past logging, presence of enclaves, hunting, incidence of fire and livestock grazing (for details, see Muthuramkumar et al. 2006; Mudappa and Raman 2007). Three of the selected sites were privately-owned rainforest

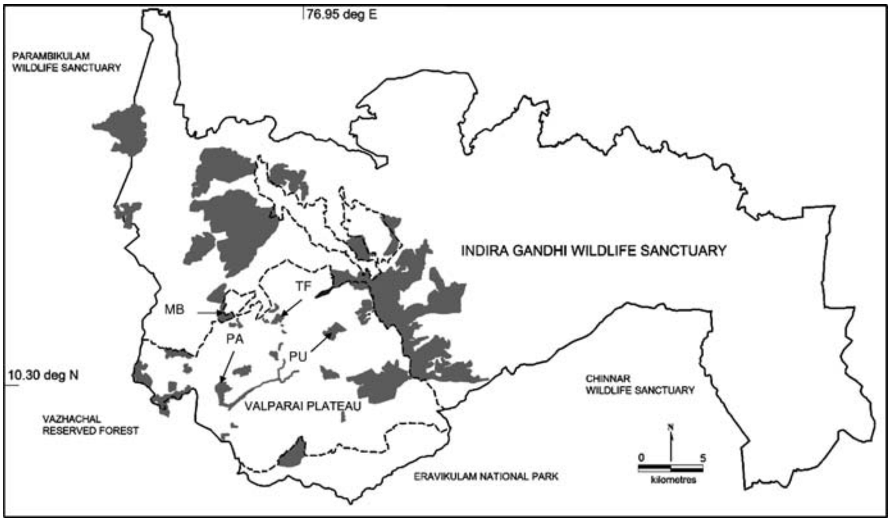

Fig. 1 Map of the Indira Gandhi Wildlife Sanctuary (*continuous line*) indicating plantations on the Valparai plateau (within *dashed lines*) and surrounding protected areas. Rainforest fragments in the region are shown (*grey*) with fragments where the study was carried out indicated by *arrows* (*MB* Manamboli, *PA* Pannimade, *PU* Puthuthottam, *TF* Tata Finlay)

Fig. 2 Boundary between coffee plantation and rainforest fragment, Tata Finlay (*above*); Robusta coffee (*C. canephora*) growing in the understorey of the protected site, Manamboli (*below*, photo courtesy: Kalyan Varma)

fragments, two of which were adjacent to *C. arabica* plantation: Pannimade (less disturbed, 87 ha) and Tata Finlay (moderately disturbed, 32.6 ha). The third fragment, Puthuthottam (highly disturbed, 92 ha), was adjacent to abandoned plantations of *C. arabica* and *C. canephora*. In addition, we selected a relatively undisturbed site, the Manamboli rainforest fragment within the Indira Gandhi Wildlife Sanctuary (referred to as protected site, 200 ha), which adjoins a *C. canephora* plantation (Fig. 1). As a part of the Wildlife Sanctuary, this fragment has legal protection under the Wildlife Protection Act since 1976. This forest fragment is relatively undisturbed compared to all other privately owned rainforest fragments (Muthuramkumar et al. 2006). All sites had a clear boundary with coffee plantations and were found to have coffee established in the rainforest understorey (Fig. 2).

The less disturbed (Pannimade) rainforest fragment contains fairly undisturbed tropical evergreen forest vegetation, but with a portion containing degraded secondary vegetation under scattered plantation of *Eucalyptus* trees. A perennial stream separates the coffee plantation from the fragment. The Sholayar reservoir limits the fragment on two sides. The moderately disturbed fragment (Tata Finlay), the smallest among the four sites, is limited by the reservoir on one side and coffee and *Eucalyptus* plantation on the other sides, with a clear border between the coffee plantation and the fragment. The highly disturbed rainforest fragment (Puthuthottam) is surrounded by tea estates on two sides, *C. arabica* plantation on one side (poorly maintained and mostly abandoned) and abandoned plantation of *C. canephora* on the other side. The *C. arabica* plantation was planted with *Maesopsis eminii* (a non-indigenous species of African origin) as a shade tree along with other species such as *Erythrina* sp. and *Artocarpus heterophyllus*. The abandoned *C. canephora* plantation contained mainly mixed native tree species canopy. This fragment also has substantial naturally-regenerated *Maesopsis eminii* trees, especially along the *C. arabica* edge; this species has been noted to be invasive in forests (Cordeiro et al. 2004). The fragment is highly disturbed due to high fuel-wood collection and its proximity to the Valparai town. The protected site (Manamboli) contains an estate enclave (an estate located within the boundary of wildlife sanctuary) with an extensive area under *C. canephora* forming a clear border with the fragment.

Study plant species

Arabica coffee (*C. arabica*) and robusta coffee (*C. canephora*) are the two major coffee species under cultivation, originating from Africa (Clay 2004). Arabica is a native understorey species of Ethiopian tropical forests growing at elevations between 1,600 and 2,800 m in its native range (DaMatta 2004). Robusta coffee grows as a native mid-storey tree in its native range in the dense equatorial forests of the Congo basin between sea level and 1,200 m (DaMatta 2004). While arabica is cultivated at elevations of 500–2,000 m in different parts of the world (Clay 2004), it is mostly grown between 1,000 and 1,500 m in India (Peter 2002). Robusta is generally cultivated at elevations below 1,000 m (Clay 2004; Peter 2002). The montane origin of arabica as compared to the lowland origin of robusta translates into key differences between the two species in terms of their ecology and requirements for cultivation. Arabica, in comparison with robusta, requires lower optimum temperature (18–21°C vs. 22–30°C), lower humidity (70–80% vs. 80–90%), and is cultivated on gentle to moderate slopes whereas robusta is cultivated on gentle slopes to fairly level lands (Peter 2002; DaMatta 2004). Shade requirements also differ, with arabica generally requiring more shade (medium to light shade) as compared to uniformly thin shade for robusta (Peter 2002; DaMatta 2004). Given this requirement, arabica tends to be shade-grown while robusta is grown under full-sun, although varieties of arabica that tolerate full-sun and of robusta that can grow in shade are also known (Clay 2004; DaMatta 2004). Studies have indicated that coffee grown in full sun tends to have yields that alternate between years of high and low yield resulting in a biennial production pattern (DaMatta 2004), while coffee grown under shade has more sustained annual yields (DaMatta 2004) as well as greater vegetative growth (van Kanten and Vaast 2006). As arabica is a smaller shrub than robusta, it is generally planted at closer spacing resulting in higher densities of c. 3,000–4,000 stems/ha in plantations when compared to robusta (750–1,000 stems/ha) in southern India. Yields of the two species typically range between 1,000 and 1,500 kg/ha for arabica and 1,300 and 2,000 kg/ha for robusta. Thus, individual robusta plants may produce over four times more fruits than individual arabica plants (A. Savarkar and B. P. Mudappa, personal communications). From the perspective of invasion potential, this suggests that robusta is likely to produce a higher number of seeds per hectare and a much higher number of seeds per individual than arabica plantations/individuals. The fruit type of both the coffee species is drupe of 10–12 cm diameter. Each fruit typically contains two seeds (coffee beans). Coffee seeds are known to be dispersed by mammals; in the study area the main dispersers of coffee are the brown palm civet *Paradoxurus jerdoni*, Asian elephant *Elephas maximus,* lion-tailed macaque *Macaca silenus*, and sloth bear *Melursus ursinus* (Mudappa 2001; Muthuramkumar et al. 2006).

Vegetation sampling

In each fragment under study, vegetation was sampled systematically and uniformly using quadrats distributed along replicate line transects. Starting from the edge of the fragment adjoining the coffee plantation into the interior, line transects were marked in a direction perpendicular to the edge. In each fragment, seven line transects were marked, spaced 60 m apart from and parallel to each other. Along each line transect, 12 quadrats of size 10 m $\times$ 10 m were laid. The first quadrat was marked at the fragment edge and the next nine quadrats were laid 10 m apart from each other along the line transect. The 11th and 12th quadrats were laid at intervals of 25 m. In the four corners of each 10 m $\times$ 10 m quadrat, 2 m $\times$ 2 m sub-quadrats were laid to count stems of native shrubs, coffee, *Clerodendrum viscosum* (a native pioneer shrub to large tree) and other focal plant species (data not included here). All stems that were at least 30 cm in height or with girth at breast height (GBH, 1.3 m) >1 cm and <30 cm were counted in these sub-quadrats.

In each 10 m $\times$ 10 m quadrat, canopy cover, canopy overlap, number of vertical layers, tree density, basal area, and closest distance to human trail from the quadrat were recorded as the forest structure variables. To calculate tree density and basal area, trees $\geqslant$30 cm GBH were counted and their GBH measured with tape. The non-indigenous trees (*Maesopsis 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. Canopy cover was measured at the centre of each 10 m $\times$ 10 m quadrat in four directions using a spherical crown densiometer (Forestry Suppliers) and the average of readings was recorded as percentage canopy cover. Canopy overlap, number of vegetation layers, and the closest distance from human trail were ranked and recorded by ocular estimation at the centre of each 10 m $\times$ 10 m quadrat. Canopy overlap was ranked as 0 (when there was no tree canopy overhead), 1 (tree canopies present but not touching each other), 2 (tree canopies overlapping with the sky visible through the leaves), and 3 (tree canopies overlapping and sky not visible through the leaves). The presence or absence of woody vegetation directly overhead was recorded for the following vertical layers: 1–5, 5–10, 10–20, 20–30, 30–40, >40 m. The closest distance from human trail was recorded as 0 (within quadrat), 2.5 (0–5 m distance), 7.5 (5–10 m), and 15 m (10–20 m).

Analysis

For each site, averages of measured vegetation variables (and corresponding standard errors) were calculated from measurements across all replicate quadrats sampled in the site. To obtain a measure of coffee stem density (*C. arabica* and *C. canephora,* considered separately) 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. A similar procedure was used for shrub density, although this is represented as stems per 16 m^2. As transects were nested within sites, statistical differences in vegetation variables and coffee density across sites were assessed by nested analysis of variance (ANOVA) of quadrat data with site as the main effect and transect within site as error term, followed by Tukey HSD multiple comparison tests (Zar 1999; Crawley 2007).

To model the effects of site and distance from coffee plantation edge on the density of coffee in the fragments we used a linear mixed model approach (Quinn and Keough 2002; Crawley 2007). Fixed effects in the model included site (categorical) and distance from coffee plantation edge to individual quadrats (continuous covariate), while transects nested within site were treated as random effects on the intercept. The analysis was carried out using the lmer function implemented in the lme4 package (Bates et al. 2008) in the R statistical and computing environment (R Development Core Team 2008, version 2.7.2). Interactions between the fixed effects were assessed by graphical exploration of data followed by likelihood ratio significance tests of models with and without the interaction estimated using maximum likelihood (Crawley 2007). Due to the presence of significant interactions, we report coefficients for intercept and slope for the four different sites in the model. To graphically illustrate the edge-to-interior pattern, the stem density in quadrats at each distance from the edge was averaged across the replicate line transects within a site and expressed as stems per 16 m^2. In the highly disturbed site, that adjoined *C. arabica* and *C. canephora* plantations, distance from plantation edge referred to distance from the edge of the respective plantation in the analysis for each species.

Within each site, the interactive influence of distance from the plantation edge and other variables of forest structure on the density of coffee stems was assessed using multiple linear regression. We used the backward stepwise method for variable selection (Zar 1999) using the computer programme SPSS (Bryman and Cramer 1997).

Results

Forest structure and coffee abundance

Among the study sites, the protected rainforest fragment had the highest tree basal area (47.85 m^2) and native rainforest tree density (450 trees/ha), decreasing along the gradient to the highly disturbed site that had the lowest tree basal area (4.17 m^2/ha) and lowest native tree density (132 trees/ha, Table 1). The density of the indigenous pioneer *Clerodendrum viscosum* trees and shrubs was least in the protected site and higher in the moderately and highly disturbed sites, with the latter having an overall *C. viscosum* density of 3155 stems/ha (combining tree and shrub densities, Table 1). Similarly, the non-indigenous tree species (*Eucalyptus* sp., *Maesopsis eminii*) were absent in the protected site and occurred at highest densities in the highly disturbed site (382 trees/ha), although density was slightly higher in the less disturbed site (49/ha) as compared to moderately disturbed site (7/ha, Table 1). The *Eucalyptus* trees were all planted individuals, whereas *Maesopsis eminii* included older planted trees as well as numerous smaller naturally-regenerated trees.

Both coffee species, *C. arabica* and *C. canephora*, were found in all four sites. The respective coffee species that was cultivated in the adjacent coffee plantation was most abundant inside the fragment. The coffee species that was not cultivated in the adjoining plantation occurred in lower abundance throughout the corresponding fragment (Fig. 3). The highly disturbed fragment adjoining plantations of both *C. arabica* and *C. canephora* showed high abundance of both coffee species.

The stem density of *C. arabica* varied significantly across sites (nested ANOVA $F_{3,24} = 10.6$, $P < 0.0001$) in relation to disturbance, increasing by an order of magnitude from an average of 150 stems/ha in the protected site to 1,825 stems/ha in the highly disturbed site (Fig. 3). In contrast, *C. canephora* occurred at significantly higher density in both sites adjoining the plantation, the protected site and the highly disturbed rainforest fragment, as compared to the other two sites (ANOVA $F_{3,24} = 69.6$, $P < 0.0001$, Fig. 3). In the highly disturbed rainforest fragment that adjoined abandoned plantations of both coffee species, the stem density of *C. canephora* (11,475 stems/ha) was much higher than that of *C. arabica* (1,825 stems/ha, Fig. 3).

Table 1 Variation in forest structure variables across the study sites

Variable	Protected	Less disturbed	Moderately disturbed	Highly disturbed	ANOVA $F_{3,24}$
Canopy cover (%)	92.49^{b} (0.36)	85.68^{a} (1.30)	85.77^{a} (1.92)	$87.07^{a,b}$ (0.53)	4.80**
Canopy overlap index	1.89^{b} (0.03)	1.77^{b} (0.05)	1.54^{a} (0.07)	1.81^{b} (0.05)	10.20**
Distance from trail (m)	15.24^{b} (1.72)	2.14^{a} (0.60)	2.47^{a} (0.43)	1.31^{a} (0.32)	20.01***
Number of vegetation layers	4.36^{c} (0.10)	3.20^{a} (0.09)	2.83^{a} (0.10)	3.68^{b} (0.08)	39.59***
Tree basal area (m^2/ha)	47.85^{b} (4.20)	30.21^{b} (3.19)	41.35^{b} (5.85)	4.17^{a} (0.25)	17.67***
Native rainforest tree density (stems/ha)	450^{b} (20)	444^{b} (24)	371^{b} (25)	167^{a} (18)	24.98***
Non-native tree density (stems/ha)	0^{a}	49^{a} (10)	7^{a} (3)	382^{b} (32)	78.86***
Clerodendrum viscosum tree density (stems/ha)	0^{a}	$25^{a,b}$ (7.6)	$67^{a,b}$ (12.5)	36^{b} (8.9)	6.22**
Clerodendrum viscosum shrub density (stems/16 m^2)	0.05^{a} (0.03)	$1.01^{a,b}$ (0.15)	2.45^{b} (0.33)	4.99^{c} (0.34)	28.37***
Native shrub density (stems/16 m^2)	19.69^{a} (0.91)	$24.77^{a,b}$ (1.22)	28.76^{b} (1.60)	18.76^{a} (0.98)	4.44*

Corresponding standard error is given in parentheses. Nested analysis of variance (ANOVA) was used to test for significance of difference across sites followed by Tukey HSD multiple comparisons tests (means with different superscripted alphabets differ from each other significantly)

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

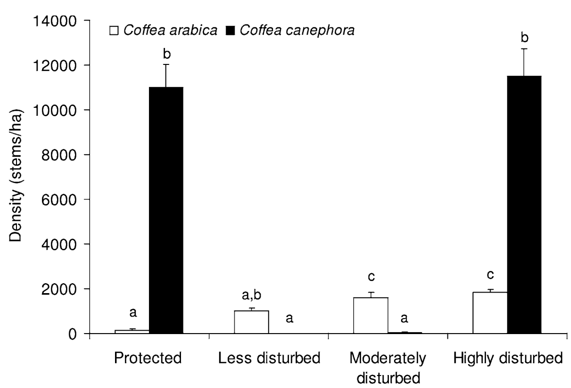

Fig. 3 Density of the two coffee species across rainforest fragment sites in the Anamalai hills. Sites sharing the same alphabet do not differ significantly from each other in density of *Coffea arabica* or *C. canephora* (Tukey HSD multiple comparison test for each species separately)

Effects of edge and forest structure on coffee density

Both coffee species showed significant variation in density across sites as well as in relation to distance from plantation edges (Fig. 4). The edge to interior pattern appeared to depend on site as evidenced by the significantly better fit of linear mixed models that included interaction between the factors (site × distance from plantation edge) compared to models without the interaction term using the Akaike Information Criterion (AIC) and likelihood ratio tests (*C. arabica*: AIC = 1440 vs. 1479, $\chi^2 = 44.8$, $df = 3$, $P < 0.0001$; *C. canephora*: AIC = 2497 vs. 2561, $\chi^2 = 70.8$, $df = 3$, $P < 0.0001$). The stem density of the coffee species cultivated in the adjacent plantation showed a sharp decline (negative slope) with the distance from plantation edge up to around 100 m, with the exception of the less disturbed rainforest fragment (Table 2, Fig. 4).

Multiple regression analyses were carried out to examine the effects of edge and other forest structure variables on the density of coffee and other focal plant species (Table 3). *C. arabica* density in moderately disturbed and highly disturbed rainforest fragments was significantly negatively related to distance from the plantation edge (Fig. 4, Table 3). None of the other variables had a significant effect on *C. arabica* density and the overall proportion of the variation explained by distance from edge was moderate in both sites (highly disturbed: $R^2 = 0.29$, moderately disturbed: $R^2 = 0.24$, Table 3). In contrast, the protected fragment and the less disturbed fragment did not show any pattern in distribution of *C. arabica* in relation to distance from the edge of the plantation (Fig. 4). In these sites, although some forest structural parameters (canopy cover, tree density, basal area) were correlated to *C. arabica* density, the predictors explained a very small proportion of the total variation in these two sites ($R^2 < 0.10$, Table 3).

C. canephora occurred in a plantation adjoining the protected forest and also in the abandoned plantation in

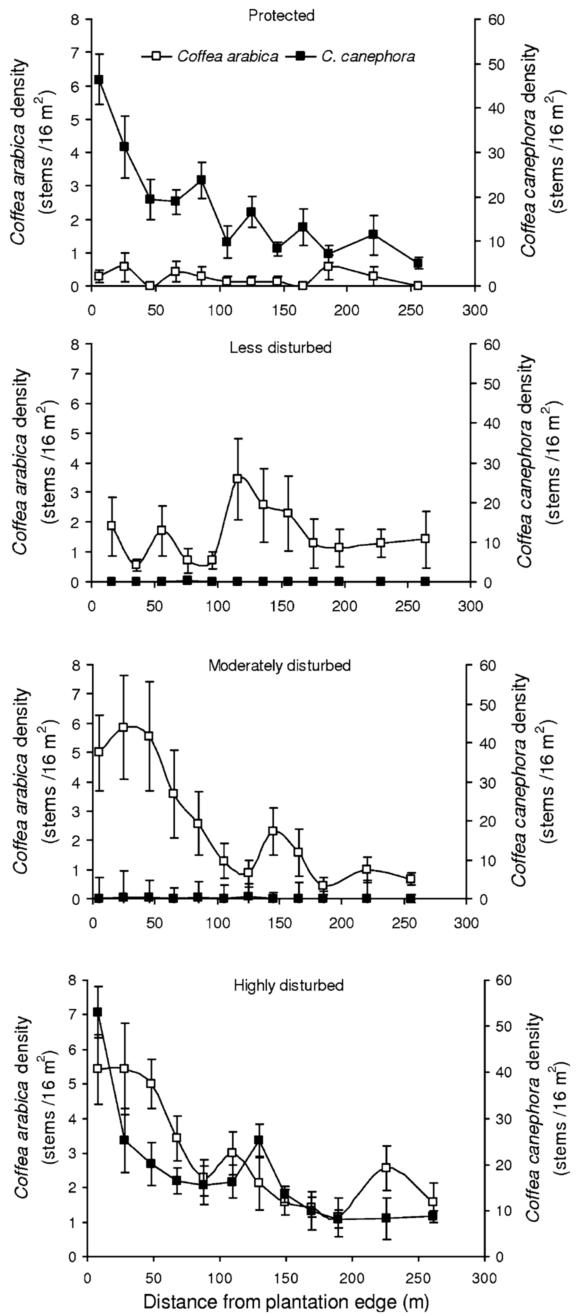

Fig. 4 Density of the two coffee species in relation to distance from fragment edges across the four sites in the Anamalai hills

the highly disturbed rainforest fragment. *C. canephora* stem density declined with distance from the plantation in both these sites (Fig. 4, Table 3). Along with distance from plantation edge, the density of *C. canephora* was also negatively related to native shrub density in protected rainforest fragment (Table 3). In the highly disturbed rainforest fragment, other variables showing significant positive influence on the density of *C. canephora* were distance from trail, canopy cover, canopy overlap, whereas basal area and native shrub density were negatively correlated. In the two other sites that did not adjoin *C. canephora* plantations, its stem density did not show any significant relationship with the distance from plantation edge or any of the other variables (Table 3).

Discussion

This study clearly demonstrates the extent to which coffee invades into rainforest fragments that adjoin plantations, with stems occurring even at the largest distance class (>250 m) from the edge. A major limitation of the study in exploring the influence of disturbance is, however, the lack of replicate sites for each disturbance level. This was a limitation due to logistics as there were no other rainforest fragments that adjoined coffee plantations in the Valparai plateau to place comparable sets of edge-to-interior transects. With this limitation as a caveat, the patterns of invasion nevertheless appear related to the disturbance levels in fragments as well as the coffee species cultivated in the adjoining plantation. The categorisation of disturbance levels across the selected sites appear reasonable given the trends in rainforest tree density, basal area, and abundance of the pioneer rainforest plant species *Clerodendrum viscosum*. The trend in non-indigenous tree species density across sites also seems to indicate that the establishment of these species is positively related to disturbance level, as noted in an earlier study (Muthuramkumar et al. 2006).

Effects of edge and forest structure on coffee in rainforest fragments

The results showed a clear edge-to-interior decline in coffee stem density in all sites except the less disturbed rainforest fragment, Pannimade, possibly for reasons explained below. In the highly disturbed rainforest fragment that adjoined *C. canephora* and *C. arabica* plantations, the stem density of each coffee species decreased with increasing distance from the respective plantation edge into the fragment interior. Overall, the study indicates that coffee

Table 2 Results of linear mixed effects models assessing effects of site and distance from coffee plantation edge on stem density of *Coffea arabica* and *Coffea canephora* in the Anamalai hills

	Coefficient	SE	*t* Value
Coffea arabica			
Fixed effects			
Site			
Protected	0.33	0.473	0.70
Less disturbed—protected	1.37	0.750	1.83
Moderately disturbed—protected	4.92	0.671	7.33
Highly disturbed—protected	5.43	0.727	7.48
Distance to coffee plantation edge			
Protected	−0.0007	0.0028	−0.26
Less disturbed—protected	0.0001	0.0039	0.02
Moderately disturbed—protected	−0.0214	0.0040	−5.31
Highly disturbed—protected	−0.0171	0.0040	−4.30
Random effect	SD		
Transect within site (intercept)	0.6502		
Residual	1.9445		
Coffea canephora			
Fixed effects			
Site			
Protected	32.65	2.027	16.11
Less disturbed—protected	−32.64	3.237	−10.08
Moderately disturbed—protected	−32.54	2.872	−11.33
Highly disturbed—protected	5.13	3.190	1.61
Distance to coffee plantation edge			
Protected	−0.1237	0.0142	−8.72
Less disturbed—protected	0.1237	0.0191	6.47
Moderately disturbed—protected	0.1234	0.0202	6.11
Highly disturbed—protected	0.0021	0.0199	0.11
Random effect	SD		
Transect within site (intercept)	0.0003		
Residual	9.7506		

Tabled fixed effect coefficients (site intercepts and slopes in relation to distance from plantation edge) are values estimated for the protected site and differences between coefficients of other sites and the protected site, along with corresponding standard errors and *t* values estimated by the lmer function in R (see "Materials and methods")

density in fragments is mostly related to proximity to coffee plantations.

While the coffee species cultivated in the adjoining plantation showed the edge-to-interior trend, the other species did not show this trend and tended to occur in lower density throughout the fragment (Table 2, Fig. 4). Both coffee species are cultivated in the region and are capable of spreading into fragments, however any given estate is usually dominated by one species that consequently occurs in higher densities in fragments as may be expected from its abundance.

Germinated seedlings are often seen around coffee bushes, apparently from fallen berries (most berries are normally collected in well-maintained plantations). The growth and eventual reproduction of these seedlings could be one mechanism for the gradual spread of coffee away from plantation edges. Another possible cause for the spread of coffee noted in an earlier study on plant community structure of the rainforest fragments is dispersal of coffee seeds by mammals such as elephants, primates, and civets (Muthuramkumar et al. 2006). The lack of edge-to-interior trend in stem density of *C. arabica* in the less disturbed fragment (Pannimade) may have been due to the perennial stream separating the fragment and coffee plantation, which may act as a barrier for movement of small mammals and reduce seed dispersal and spread of coffee into the fragment. In other sites, the density of the coffee species (*C. arabica* and *C. canephora*) cultivated in the adjoining plantation

Table 3 Multiple regression analysis of *Coffea arabica* and *Coffea canephora* density in rainforest fragments in the Anamalai hills

Site	Dependent variable	Constant/predictors	Regression coefficients (SE)	$t(P)$	Regression $F(P)$	*df* (regression, residual)	Adjusted R^2
Protected	*C. arabica* density	Constant	0.393 (0.176)	2.233 (0.028)	2.50 (0.088)	2, 81	0.04
		Tree density	−0.0808 (0.044)	−1.840 (0.070)			
		Basal area	0.004353 (0.002)	2.090 (0.04)			
	C. canephora density	Constant	39.650 (3.519)	11.268 (<0.001)	31.52 (<0.001)	2, 81	0.42
		Distance from plantation edge	−0.115 (0.017)	−6.756 (<0.001)			
		Native shrub density	−0.423 (0.153)	−2.761 (0.007)			
Less disturbed	*C. arabica* density	Constant	−3.618 (1.753)	−2.064 (0.042)	8.976 (0.004)	1, 81	0.09
		Canopy cover	0.06071 (0.20)	2.996 (0.004)			
	C. canephora density	–	–	–	–	–	NS
Moderately disturbed	*C. arabica* density	Constant	5.158 (0.587)	8.795 (<0.001)	27.07 (<0.001)	1, 81	0.24
		Distance from plantation edge	0.022 (0.004)	−5.203 (<0.001)			
	C. canephora density	NS	NS	NS	NS		NS
Highly disturbed	*C. arabica* density	Constant	4.950 (0.410)	12.079 (<0.001)	34.01 (<0.001)	1, 81	0.29
		Distance from plantation edge	−0.0165 (0.003)	−5.832 (<0.001)			
	C. canephora density	Constant	−32.908 (28.144)	−1.169 (0.246)	11.493 (<0.001)	6, 77	0.472
		Distance from plantation edge	−0.100 (0.021)	−4.839 (<0.001)			
		Distance from trail	1.568 (0.542)	2.894 (0.005)			
		Canopy cover	0.823 (0.316)	2.602 (0.011)			
		Canopy overlap	7.705 (4.010)	1.921 (0.058)			
		Basal area	−1.885 (0.855)	−2.203 (0.031)			
		Native shrub density	−0.668 (0.177)	−3.782 (0.001)			

declined sharply from the edge of the plantation up to 100 m inside the fragment; beyond this threshold, coffee density is low and does not change substantially further into the interior. The geographical range of seed dispersal by animals is definitely larger than 100 m. For example, the home range of brown palm civet (*Paradoxurus jerdoni*) is between 6 and 57 ha (Mudappa 2001), and that of primates and elephants even larger. Another factor that may significantly influence the spread of coffee and its decline in density from the edge is propagule pressure from the forest-plantation boundary directly due to proximity to fruit-bearing crop plants. Increased availability of propagules is known to increases the chances of establishment, persistence, naturalisation, and invasion of plant species (Rouget and Richardson 2003) and this is likely to be the case for coffee, a fruit crop.

Changes in microclimatic conditions may also influence the density of coffee inside fragments. Earlier research showed that the effects of edge in fragmented landscapes include microclimatic changes such as increase in temperature and light and reduction in humidity (Saunders et al. 1991). Increased perimeter-area ratios and artificial edges created due to habitat fragmentation are known to affect many forest species and ecological processes and favour establishment of non-indigenous species (Saunders et al. 1991; Laurance 2000) as do factors such as canopy gaps (Denslow et al. 2001). Changes in microclimate are generally limited to a zone within 60 m of tropical forest edges, with edge penetration distance of disturbance-adapted plant species being seldom greater than 20 m (Laurance and Vasconcelos 2004). The more extensive spread of coffee is likely due to its shade tolerance and therefore microclimatic changes associated with disturbance may not strongly influence their distribution. In fact, the positive influence of canopy cover on coffee stem density in multiple regression analyses suggests that after factoring the edge-to-interior effect, shade may enhance the likelihood of coffee establishment. The significant positive relationships between coffee stem density and canopy cover in less and highly disturbed fragments indicate the potential threat of coffee invasion in a range of closed canopy forests. In fact, coffee attained higher densities in rainforest fragments than other non-indigenous, light-demanding species such as *Lantana camara and Chromolaena odorata* in this study (data not presented here).

While disturbance-adapted weeds that proliferate under open or early successional conditions are more commonly known in degraded and secondary tropical forests, the invasive potential of shade-tolerant species is also increasingly being noticed (Fine 2002). Examples include the neotropical shrub *Clidemia hirta* (Melastomataceae) found to be invasive in tropical lowland forests of Hawaii (DeWalt et al. 2004) and in Pasoh, Peninsular Malaysia (Peters 2001). Shade tolerance alone may not be responsible for *Clidemia hirta* invasion success, as release from natural enemies (DeWalt et al. 2004) and adaptation to small-scale disturbances associated with gaps and the activity of wild pigs (Peters 2001) have also been implicated. Other examples of shade-tolerant invasives in tropical forests such as *Cinnamomum verum*, *Miconia calvescens* and *Musa ornata* are also known (Fine 2002; Kueffer et al. 2007). Coffee, primarily *Coffea arabica*, has found mention as a potential weed in Australia (Lymburner et al. 2006) and as a 'moderate invader' on Pacific islands (Meyer 2000). There is a mention of *C. canephora* having spread into additional areas and edges of lowland (<700 m altitude) and submontane (>700 m) rainforest fragments adjoining the Amani Botanical Garden in Tanzania (Dawson et al. 2008). Besides these reports, we have been unable to trace any research on coffee as an invasive species in tropical forests and its effects on native vegetation, particularly of robusta coffee *C. canephora*. In an earlier study from the Valparai plateau, Western Ghats, the high abundance of *C. canephora* (around 25% of the individuals among understorey plants) in the protected rainforest site, Manamboli, was noted (Muthuramkumar et al. 2006).

Invasion by *Coffea arabica* and *Coffea canephora*: comparative analysis

Where it was cultivated adjoining fragments, *C. canephora* attained much higher densities in these fragments than *C. arabica*. The density of *C. arabica* inside the rainforest fragments adjoining *C. arabica* plantations tended to be positively related to disturbance, being highest in the highly disturbed rainforest fragment and least in the less disturbed fragment. In contrast, the level of disturbance did not appear to affect density of *C. canephora* inside fragments adjoining *C. canephora* plantations. The protected fragment and the highly disturbed fragment had similarly high *C. canephora* density. This indicates the potential threat of *C. canephora* even to relatively undisturbed rainforest but it needs to be confirmed by the data from replication of sites with different levels of disturbance.

Density of *C. canephora* was also negatively related to native shrub density in the two rainforest fragments that adjoined *C. canephora* plantations. It is possible that the high density of *C. canephora* acts to suppress the germination and growth of native plant species by occupying space and competing for shared resources. However, this needs to be verified by experimental study. A study from Australia reports better regeneration of native rainforest plant species after removal of weeds including *C. arabica* (Lymburner et al. 2006). Unlike *C. canephora*, no negative relationship was noted in the present study between *C. arabica* density and native shrub density, probably due to it not attaining high densities (at fragment edges, densities attained by *C. arabica* are an order or magnitude lower than densities attained by *C. canephora*, Fig. 4). These results suggest that, although both coffee species are capable of spreading into rainforests, *C. canephora* may quantitatively have a greater adverse impact as an invasive species than *C. arabica* in this region.

Conservation implications

At a broad level, the potential for agricultural crops to become invasive appears to have received less attention than invasive alien species that are pests of agriculture, horticultural escapes, weeds of disturbed areas, or timber tree species (for example, Matthews 2004). Concern has been expressed regarding escape of genetically-modified crops and hybridisation or gene transfer with closely-related wild species in specific studies such as a report on crops that have gone 'feral' in Europe (Sukopp and Sukopp 1993) or more generally in agricultural landscapes in various parts of the world (McNeely and Scherr 2003). In this context, coffee needs urgent attention as it is the most traded global agricultural commodity, cultivated in over 11 million hectares mainly in tropical countries around the world.

The occurrence and spread of coffee in tropical rainforests that are globally recognised repositories of biodiversity is a matter of conservation concern: 'Coffee—a weed of the future?' as Lymburner et al. (2006) cautiously put it. This study indicates that coffee is very much an invasive weed of the present in the Western Ghats tropical rainforests. A related concern in the Western Ghats, as in other tropical regions, is the increasing prevalence of *C. canephora* (robusta) plantations, which are replacing *C. arabica* in large areas (Clay 2004; Donald 2004; Coffee Board 2007). *C. canephora* currently accounts for one-fourth of the world's production (Clay 2004) and nearly two-thirds of coffee production in India (Coffee Board 2007). In India, area under coffee production increased from 92,523 ha in 1950 to 270,821 ha in 1990 with a concurrent increase in the proportion under *C. canephora* from 27% to 53%; area under coffee continued to increase to 381,085 ha in 2007, but the percentage of area under *C. canephora* appears to have stabilized at around 53% (Coffee Board 2007). *C. canephora,* being usually grown under little shade tree canopy, offers a poorer habitat for wildlife in plantations (Raman 2006), besides being of greater invasive potential in adjoining forests (this study).

There is a need to generate greater awareness among conservation organisations, coffee certification agencies, coffee consumers, and land managers about the invasive potential of coffee, especially *C. canephora*, in tropical forests. A second need is experimental research to establish the effects of coffee on native plant diversity and regeneration. A final, urgent need is applied research to determine management and control methods for coffee and ways to restore tropical forest vegetation in areas that have been negatively impacted by its spread.

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