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Relative Roles of Disturbance and Propagule Pressure on the Invasion of Humid Tropical Forest by *Cordia alliodora* (Boraginaceae) in Tanzania

Ezekiel Edward, Pantaleo K. T. Munishi

Department of Forest Biology, Faculty of Forestry and Nature Conservation, Sokoine University of Agriculture, P.O. Box 3010 Morogoro, Tanzania

and

Philip E. Hulme[1]

National Centre for Advanced Bio-Protection Technologies, P.O. Box 84, Lincoln University, Lincoln 7647, Canterbury, New Zealand

ABSTRACT

Current understanding of the vulnerability of tropical forests to plant invasion is limited but is widely believed to increase where forests: (1) suffer marked natural or man-made disturbance; and/or (2) are exposed to high propagule pressure of alien species. This study aimed, for the first time, to address the importance of propagule pressure and disturbance by examining the spread of an introduced tree, *Cordia alliodora*, from a single plantation into a surrounding mosaic of humid forest in the East Usambara Mountains, Tanzania. By assessing vulnerability to invasion along transects radiating from the plantation, the effects of distance (measure of propagule pressure), and disturbance could be discerned. For all life stages, distance from source population was the strongest correlate of density. A marked influence of disturbance was only evident for *C. alliodora* seedlings. Spatial variation in the densities of later life stages may be a function of past disturbances, less easy to assess from current surveys, especially following the marked self-thinning between seedling and adult densities. Nevertheless, the evidence suggests that propagule pressure is a more important determinant of *Cordia* density than disturbance. If this is true for other alien tree species in tropical forests, controlling for introduction effort is essential to assess the drivers of plant invasion. Given an annual population growth rate of *ca* 3.5 percent, equivalent to the population doubling every 20 yr, *C. alliodora* poses a significant threat to the East Usambaras as well as other humid forests where it is promoted for agroforestry.

Key words: alien; dispersal; East Africa; exotic; naturalization; regeneration.

INVASIVE ALIEN PLANT SPECIES POSE SIGNIFICANT CHALLENGES to the management and conservation of indigenous biodiversity in natural ecosystems (Rejmánek *et al.* 2005). Invasive plants can transform ecosystems by establishing viable populations with growth rates high enough to displace elements of the native biota or they may modify disturbance regimes, thereby potentially transforming ecosystem structure and functioning (Levine *et al.* 2003, Hulme 2006). Although regarded as a significant threat to global biodiversity, current understanding of the vulnerability of tropical forests to invasion or the factors that lead to alien species becoming invasive in the tropics is limited (Lugo 2004, Dawson *et al.* 2008). Compared to other biomes, tropical forest ecosystems appear more resistant to invasions by alien plants, at least judged by the number of naturalized taxa in floras (Rejmánek 1996). The presence of fast-growing multilayered vegetation has been proposed as the main mechanism by which undisturbed tropical forests are resistant to invasions (Rejmánek *et al.* 2005).

An emerging consensus view (*e.g.*, Whitmore 1991, Rejmánek 1996, Fine 2002, Denslow 2003) is that to be vulnerable to plant invasions, tropical forests should: (1) suffer marked natural or man-made disturbance; (2) be fragmented and have a high perimeter to core ratio; (3) comprise low species or functional richness; and/or (4) be exposed to high propagule pressure of alien species. These drivers are not mutually exclusive nor do they often occur in isolation and thus disentangling their relative importance can be a challenge. However, while the effects of disturbance (*e.g.*, Colon & Lugo 2006), fragmentation (*e.g.*, Muthuramkumar *et al.* 2006), and species richness (*e.g.*, Zimmerman *et al.* 2008) on invasion can often be assessed *post-hoc*, the effects of propagule pressure are often difficult to discern since knowledge of the original numbers of individuals introduced is usually not known or difficult to estimate. Few studies, particularly in the tropics, have been able to account for propagule pressure when assessing the drivers of plant invasion. To address this challenge, this study uses a unique natural experiment to assess the spread of an introduced tree from a single plantation into a surrounding mosaic of differentially disturbed humid forest. By assessing vulnerability to invasion along transects radiating from the plantation, the importance of propagule pressure (as measured by distance from the plantation) relative to other potential correlates of invasion success, *e.g.*, disturbance could be discerned.

METHODS

STUDY AREA.—The East Usambara submontane rain forests in northeastern Tanzania are one of the most valuable conservation areas in Africa and constitute one of the world centers of plant diversity (Sayer *et al.* 1992). The vegetation belongs to the Zanzibar-Inhambane submontane rain forest type and has floristic affinity particularly to the Guineo-Congolian flora of West and Central Africa (Lovett 1989). The forests are known for their exceptionally high levels of regional and local endemism; at least 100 species of plants are strictly endemic to the Usambaras, and the forests are noteworthy for several rare and near-endemic species of birds and

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[1] Corresponding author; e-mail: hulmep@lincoln.ac.nz

reptiles (Iversen 1991, Sayer *et al.* 1992). This study was conducted in the Amani Nature Reserve (ANR) located between 5°14′10″–5°04′30″ S and 38°30′34″–38°40′06″ E in the East Usambara Mountains. Rainfall averages 1900 mm annually and as a result the soils are leached and rather acidic, and the mineral soil under the thin organic layer is poor in nutrients (Hamilton 1989). The mean annual temperature is 20.6°C (Binggeli *et al.* 1989). Amani Nature Reserve has in the past suffered a range of localized anthropogenic disturbance events from the establishment of alien tree plantations, timber removal, pit-sawing activities as well as cutting of poles for firewood (Frontier Tanzania 2001). As a result, the forest is a fine mosaic of differentially disturbed areas.

The study site was centered on the single original plot of *Cordia alliodora* (Ruiz & Pav.) Oken (Boraginaceae) planted during the establishment of the Amani Botanical Garden (Greenway 1934). The study site was *ca* 50 ha in area at 598–855 m asl within a matrix of home gardens, plantations and secondary forests. The original plantation occupied *ca* 0.2 ha and records at the time suggest only 210 trees were established. The tree has now become locally dominant in areas of secondary forest and abandoned plantations and it is suggested that the species has potential to spread rapidly and replace native pioneer species (Dawson *et al.* 2008).

SPECIES DESCRIPTION.—*Cordia alliodora* (hereafter referred to as *Cordia*) is a fast-growing tropical hardwood tree native to Central America. It is distributed widely in the Neotropics and extends from Central Mexico through Central and South America to Paraguay, southern Brazil to northern Argentina and the islands of the Caribbean (Liegel & Stead 1990). In its native range, *Cordia* grows under a wide variety of ecological conditions, varying from seasonally dry to very wet (600–6000 mm annual precipitation). It grows best on well-drained, medium-textured soils from lowland to highland forests (0–1500 m) where mean annual rainfall exceeds 2000 mm and the mean annual temperature is *ca* 24°C (Boshier 2002). It is a light-demanding species though survives under light shade, and is common in undisturbed dry forest where it is found in natural and human-made gaps, forest edges or roadsides, secondary vegetation, as well as degraded and abandoned areas once used for crops, pasture, or shifting cultivation (Liegel & Stead 1990). *Cordia* may commence flowering at 2 yr, but trees usually reach sexual maturity at 4–10 yr (Boshier 2002). Heights of reproductively mature trees are 12–20 m though under optimum growing conditions it may reach > 40 m and > 1 m dbh (Hummel 2000). Coppicing and epicormic branching on injured young trees has been reported in Costa Rica and sprouting was seen from lateral roots in Trinidad (Liegel & Stead 1990). Individual trees produce 2–8 kg of seeds at 42,000–100,000 seeds/kg, which are wind dispersed (Boshier 2002). It has been widely planted in other tropical regions including Africa and, the Pacific region and has been reported to naturalize and/or become invasive in Vanuatu, Tonga, Samoa and the Galapagos islands (Haysom & Murphy 2003).

DATA COLLECTION.—Data were collected through a fine scale survey focusing on the area where *Cordia* was originally introduced. Between September and December 2006, 67 concentric nested circular plots (De Vries 1986) were systematically established at 50-m intervals in eight cardinal directions to a maximum distance of 650 m (though several transect were shorter since they extended to settlements or cliffs) radiating away from the original point of *Cordia* introduction. The following life stages of all trees were counted and identified to species level for each nested circular plot: all seedlings (< 30 cm tall, > 30 cm but < 1 cm dbh) within a 2 m radius of the plot; all saplings (≥ 1 cm dbh but < 5 cm dbh) within a 5 m radius; all sub-adults (≥ 5 cm but < 20 cm dbh) within a 10 m radius and all adult trees with dbh ≥ 20 cm within a 15 m radius. These data were used to calculate stem density and basal area of trees. A simple, quantitative regeneration index (RI) was calculated using the number of naturally regenerated seedlings N_{se} and saplings N_{sa} as a proportion of the number of adults N_a (Hulme 1996): $RI = (N_{se} + N_{sa})/ N_a$

A single value for canopy density, elevation, litter depth, and a disturbance index was recorded for each series of nested plots. Although disturbance is widely credited as important in plant invasions it is difficult to quantify (Hulme 2006) and thus more than one measure of disturbance was assessed. Canopy density was measured to the nearest percent using a concave (Model C) spherical densiometer (Lemmon 1957) held at a height of 1 m. Four readings were taken over each plot (one facing each of the four cardinal directions) and averaged for the plot. The species richness of native adult trees was used as an indicator of the intactness of the forest while the richness of alien adult trees was assumed to be a measure of historical disturbance. Finally, a more subjective measure of disturbance was derived by scoring plots (within a 15-m radius) as experiencing mild, intermediate, or high disturbance, based on forest physiognomy, presence of tracks and trails, treefalls, evidence of timber/pole removal etc. Litter was assessed since it may play an important role in plant invasions; often its depth may limit or reduce the establishment of alien tropical trees (Ellsworth *et al.* 2004, Garcia Robledo & Murcia 2005). Furthermore, some studies have revealed changes in litter depth following anthropogenic forest disturbance (Olander *et al.* 2005, Dezzeo & Chacon 2006, Villela *et al.* 2006, Negrete Yankelevich *et al.* 2007).

DATA ANALYSIS.—One-way ANOVA and correlations were used to describe basic trends in forest and population structure. Multiple regression analysis (using backward elimination) examined the influence on *Cordia* life-stage densities ($\log x + 1$ transformed) of elevation, propagule pressure (distance from source) and the various measures of disturbance, *e.g.*, canopy cover (angular transformation), litter depth, disturbance index, and richness of alien and native adult trees ($\log x + 1$ transformed). To compare the importance of disturbance variables relative to propagule pressure on the establishment of *Cordia* lifestages, the model that best explained the data with a minimum of free parameters was identified for each life stage using the Akaike Information Criterion (AIC). The relative goodness of fit of models taking account of elevation and either only distance or only the disturbance variables was compared to the minimum model. The difference (Δ_i) in the Akaike Information Criterion (AIC) between the minimum model and the individual distance or disturbance models was used to identify their relative

TABLE 1. *Main environmental attributes and* Cordia alliodora *densities recorded (mean ± SE) in plots exhibiting different levels of disturbance surveyed in Amani Nature Reserve, East Usambaras, Tanzania.*

	Disturbance index		
	High	Intermediate	Low
Number of plots	34	22	11
Distance from source (m)	162 ± 25.5	350 ± 40.7	273 ± 71.5
Elevation (m)	734 ± 10.1	727.0 ± 15.0	672 ± 15.0
Canopy cover (%)	70.7 ± 1.8	72.7 ± 2.2	76.4 ± 1.1
Litter depth (cm)	3.8 ± 0.4	3.0 ± 0.4	3.4 ± 0.7
Native adult tree richness (per plot)	1.91 ± 0.29	3.77 ± 0.36	8.64 ± 1.03
Alien adult tree richness (per plot)	2.15 ± 0.21	1.95 ± 0.20	1.27 ± 0.30
Proportion alien trees (per plot)	0.59 ± 0.04	0.38 ± 0.05	0.14 ± 0.04
Cordia seedling density (per ha)	25,113 ± 5434	36,958 ± 11,073	11,049 ± 4516
Cordia sapling density (per ha)	1768 ± 526	2002 ± 673	760 ± 349
Cordia subadult density (per ha)	542 ± 74.4	535 ± 145	285 ± 129
Cordia adult density (per ha)	179 ± 27.8	95.4 ± 29.1	69.1 ± 35.5

importance with models having $\Delta_i < 2$ viewed as equivalent to the minimum model, those with $\Delta_i > 4$ and < 7 having considerably less support, while $\Delta_i > 10$ has essentially no support (Burnham & Anderson 2002). All statistical analyses were undertaken using SAS 8.0 (Statistical Analysis System Institute Inc. 1999).

RESULTS

POPULATION STRUCTURE.—A total of 136 tree species (of which 28 were alien) from 45 plant families were encountered within the area surveyed in ANR (Table 1). Across all plots, irrespective of life stage, the density of *Cordia* was higher than any other species with on average 26,693 seedlings, 1680 saplings, 497 sub-adults, and 133 adults found per hectare. The high number of individuals close to the original plantation is to be expected, since many of the original plantation trees were still extant. Nevertheless, comparisons both near (< 250 m) and far (> 250 m) from the original source highlight that seedlings, saplings, sub-adults, and adults of *Cordia* were found at higher densities than either native or other alien species (Table 2). The RI was high both near (RI = 139) and especially far (692) from the original source plantation (Table 2). These data suggest that *Cordia* has considerable potential to expand and regenerate beyond the original plantation.

The disturbance index corresponded to gradients adult richness of both native and alien trees. Species richness of adult trees varied markedly across disturbance categories in relation to species status ($F_{2,128} = 37.3$, $P < 0.001$). Alien richness increased with intensity of disturbance while native trees revealed the opposite pattern, with the result that almost 60 percent of species were alien in highly disturbed forest (Table 1). There were no significant relationships, however, between alien and native species richness for seedling, sapling, subadult, or adult trees. Although a gradient existed in average canopy cover across disturbance index categories, with increasingly more open canopies as disturbance intensity increased, overall there was no significant difference across the three categories ($F_{2,64} = 1.45$, $P > 0.05$; Table 1). Mildly disturbed forest plots were at a significantly lower elevation than plots in either of the other two disturbance categories, though on average by only 60 m ($F_{2,64} = 4.42$, $P < 0.05$; Table 1).

In general for all life stages, *Cordia* density was highest where disturbance was scored as high with relatively little difference found between mild and intermediate disturbance categories (Table 1). Furthermore, the regeneration of *Cordia* in high (150), intermediate (408), and mild (171) disturbed forest all indicated regular and sustained recruitment of seedlings into larger size classes and that sites experiencing intermediate disturbance were most vulnerable to invasion.

PROPAGULE SUPPLY AND DISTURBANCE.—The primary variable underpinning variation in the density of all four *Cordia* life stages was distance from the original plantation (Table 3). The density of seedlings, saplings, sub-adults, and adults decreased with increasing distance from the original plantation. A less significant, but consistent explanatory variable was elevation, with densities increasing at higher elevations. Variables associated with aspects of forest disturbance were the only significant determinants of seedling densities. Seedlings occurred at higher densities in plots with a high disturbance index, where native tree richness was low but alien richness was high (Table 3). Canopy cover and litter depth were nonsignificant in all models. The explanatory power of the regression models varied with life stage, being highest for adult densities and lowest for saplings. Elevation was significantly correlated with several of the disturbance variables (alien richness $r = 0.26$, $P < 0.05$; native richness $r = -0.33$, $P < 0.01$, canopy cover $r = -0.34$, $P < 0.01$; disturbance index $r = 0.31$, $P < 0.05$, all df 65). To assess whether elevation reflected disturbance gradients, models were rerun excluding this variable. Models for seedlings and adults were

TABLE 2. *Mean density (number of individuals/ha), SE and regeneration index (RI) of four life stages of the five most abundant native and alien tree species at a distance of* < *250 m and* > *250 m from the* Cordia alliodora *plantation in Amani Nature Reserve, East Usambaras, Tanzania. Nomenclature follows Iversen (1991).*

	Life stage				
Species	Seedlings	Saplings	Sub-adults	Adults	RI
< 250 m from plantation					
Cedrela odorata[a]	3141 ± 1548	60 ± 24	13 ± 5	16 ± 7	205
Maesopsis eminii[a]	128 ± 108	4 ± 4	3 ± 2	1 ± 1	168
Cordia alliodora[a]	28,654 ± 5640	1406 ± 284	593 ± 73	216 ± 27	139
Artocarpus heterophyllus[a]	21 ± 21	4 ± 4	1 ± 1	0	64
Castilla elastica[a]	0	18 ± 11	11 ± 9	3 ± 2	6
Funtumia africana	449 ± 138	151 ± 35	23 ± 12	5 ± 2	128
Trilepisium madagascariense	363 ± 299	105 ± 38	7 ± 2	4 ± 2	109
Bombax rhodognaphalon	43 ± 30	11 ± 6	3 ± 2	4 ± 2	12
Sapium ellipticum	21 ± 21	0	8 ± 5	5 ± 2	5
Makharmia lutea	0	18 ± 7	7 ± 5	4 ± 2	4
> 250 m from plantation					
Cordia alliodora[a]	24,417 ± 7810	1997 ± 685	386 ± 108	38 ± 11	692
Cedrela odorata[a]	4169 ± 1387	90 ± 40	76 ± 30	37 ± 9	114
Castilla elastica[a]	25 ± 25	0	1 ± 1	0	55
Maesopsis eminii[a]	422 ± 276	110 ± 39	43 ± 16	19 ± 7	29
Artocarpus heterophyllus[a]	74 ± 55	8 ± 6	2 ± 1	4 ± 1	20
Funtumia africana	794 ± 275	355 ± 119	45 ± 14	4 ± 2	281
Bridelia micrantha	546 ± 311	86 ± 53	17 ± 8	8 ± 3	82
Trichilia dregeana	347 ± 204	78 ± 26	9 ± 3	6 ± 3	67
Celtis gomphophylla	99 ± 99	33 ± 12	15 ± 6	4 ± 2	32
Sapium ellipticum	74 ± 55	29 ± 15	15 ± 6	9 ± 3	11

[a] Indicates alien species.

unaffected by dropping elevation, but for both saplings and sub-adults, a negative term for native adult richness was included in the best-fit models ($P < 0.05$ in both cases). Thus there is weak evidence for a hidden effect of elevation on life-stage densities.

Since in many studies of invasion, the influence of propagule pressure cannot be quantified, analyses were repeated without the distance variable. For all life stages, significant models could be produced (though lower fit than corresponding models with distance). In each model, a negative term for native adult richness was the most significant parameter ($P < 0.01$). Only for adult *Cordia* densities was another variable, canopy cover, included in the best-fit model ($P < 0.05$). Thus, without explicit information on propagule pressure it would be possible to conclude that disturbance, expressed as a measure of forest intactness, was the primary barrier to invasion.

Comparison of Δ_i values highlighted that, with the exception of seedlings, a model including elevation and distance was substantially equivalent ($\Delta_i < 2$) to the best-fit model for the three other life stages (Table 4). For seedlings, the minimum model also included the disturbance index, as well as native and alien adult richness. The finding that adding elevation into the disturbance model made no impact on the goodness of fit supports the view that elevation and disturbance are associated. These results are entirely consistent with the multiple regression analyses. Models including distance were consistently better than those with disturbance variables alone. Thus, the evidence suggests that propagule pressure is a more important determinant of *Cordia* density than disturbance.

SPATIAL SPREAD AND DISTANCE FROM SOURCE.—Adult trees (dbh > 20 cm) were found at least 600 m from the original plantation. Although wind dispersed, there was no significant difference in life-stage densities among the eight radial transects (seedlings $F_{7,14} = 2.01$, $P > 0.05$; saplings $F_{7,14} = 0.32$, $P > 0.05$; sub-adults $F_{7,14} = 0.56$, $P > 0.05$; adults $F_{7,14} = 0.96$, $P > 0.05$). Given the densities of trees at different distances, it is likely that more than half the *Cordia* trees were found at distances > 200 m from the original plantation. When the sizes of all trees were examined there was no indication that trees further away were significantly smaller ($F_{1,633} = 1.21$, $P > 0.05$; Fig. 1), which suggests frequent colonization events at > 600 m from the plantation. However, examination of the five largest trees found at each distance revealed a negative relationship between size and distance ($F_{1,51} = 33.7$, $P < 0.001$; Fig. 1). The relationship appears to reveal a disjoint distribution with trees possessing a dbh > 45 cm found only within 300 m of the plantation while those < 45 cm were found further away. Either side of 300 m from the plantation there appears little relationship between tree size and distance.

TABLE 3. *Results of multiple regressions examining the influence of distance from source (m), elevation (m), alien tree richness, native tree richness, disturbance index, canopy density (angular transformed percentage), and litter depth (cm) on the mean density (number of individuals/ha) of four different life stages of* Cordia alliodora *in Amani Nature Reserve, East Usambaras, Tanzania. Best-fit models were assessed using backward elimination. The table displays the goodness-of-fit statistics for the best-fit model for each life stage and the parameter values for all significant terms in the best-fit model.*

	Life-stage			
	Seedlings	Saplings	Sub-adults	Adults
Adjusted R^2	0.41	0.27	0.50	0.61
F	10.3	13.1	34.5	53.3
Distance	−0.0067****	−0.0041****	−0.0046****	−0.004****
Elevation	0.0088*	0.0077**	0.0067***	0.0036**
Alien richness	3.18*	–	–	–
Native richness	−2.03*	–	–	–
Disturbance index	0.812*	–	–	–
Canopy cover	–	–	–	–
Litter depth	–	–	–	–

Statistical significance of model terms is illustrated as follows: $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$, and $^{****}P < 0.0001$.

DISCUSSION

DISTURBANCE AND INVASION.—Disturbance is widely implicated as a major driver of plant invasions (D'Antonio *et al.* 1999). Discerning which suite of environmental and biological parameters is sufficiently altered by human impacts to facilitate invasions is rarely simple (Hulme 2006). In this study, disturbance was characterized by several different variables assumed to encompass both recent and historical disturbance events. The influence of disturbance was only evident for *Cordia* seedling density. This is probably a reflection of seedlings being the more responsive life stage to changes in current environmental conditions.

The densities of later life stages may be a function of past disturbances, less easy to assess from current surveys especially following the likely marked self-thinning between *Cordia* seedling and adult densities. Light availability (assessed as canopy cover) plays an important role in determining regeneration success of pioneer species (such as *Cordia*) in the tropics (Dalling & Hubbell 2002, Makana

TABLE 4. *Differences (Δ_i) in the Akaike Information Criterion (AIC) between the minimum model and individual distance or disturbance models. The minimum model was the model that best explained the data with a minimum of free parameters for each life stage. The pool of variables from which the minimum model could be generated included: distance from source (m), elevation (m), alien tree richness, native tree richness, disturbance score, canopy density (angular transformed percentage), and litter depth (cm). The relative goodness of fit of models taking account of elevation and either only distance or only the disturbance variables was compared to this minimum model. The relative importance of models can be gained by the magnitude of Δi with $\Delta_i < 2$ viewed as equivalent to the minimum model, those with $\Delta_i > 4$ and < 7 having considerably less support, while $\Delta_i > 10$ has essentially no support.*

	Life stage			
Δ_i	Seedlings	Saplings	Sub-adults	Adults
Distance	11.7	7.02	11.0	7.15
Disturbance	22.7	12.1	37.7	52.5
Elevation	31.8	19.2	44.8	63.7
Distance + Elevation	3.75	0.00	1.41	0.00
Disturbance + Elevation	22.7	12.1	37.7	52.5

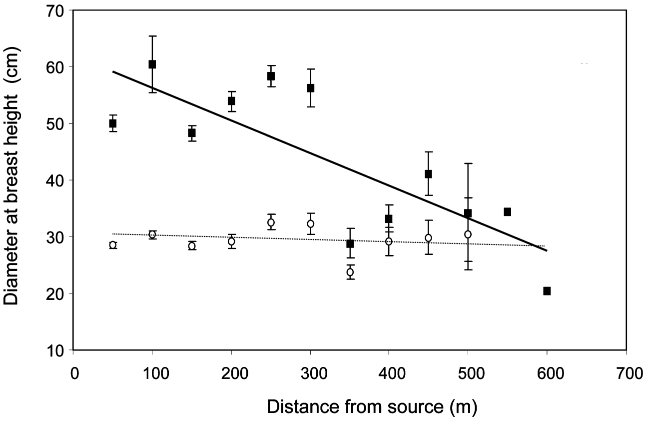

FIGURE 1. The relationship between mean dbh (cm) of *Cordia alliodora* adult trees with increasing distance from the original plantation in the surveyed area in Amani Nature Reserve, Tanzania. Data include the relationship drawn from the means of all trees (empty circles; $y = -0.004x + 29.0$, $R^2 = 0.001$, $P > 0.05$) and the mean of the five largest trees (full squares; $y = -0.056x + 61.6$, $R^2 = 0.40$, $P < 0.001$) at each distance.

& Thomas 2005) and is often increased under anthropogenic forest disturbance. Thus, the limited significance of canopy cover on densities of any life stage, but especially seedlings, is surprising given that *Cordia* prefers full light (Boshier 2002) but is consistent with some studies that have found reasonable survival under shade (Somarriba *et al.* 2001). Habitat structure, as quantified by the richness of native trees (a measure of forest intactness) and alien trees (a measure of past disturbance) also influenced *Cordia* seedling densities.

DISTURBANCE AND PROPAGULE PRESSURE.—For all life stages, distance from the source population was the most consistent variable correlated with *Cordia* density. A large *Cordia* adult tree may produce as many as one million seeds in a single year and combined with a hermaphrodite reproductive strategy, high germination rates, early age of reproduction, and long life span (individuals from the original plantings are still extant after 100 yr) represents considerable propagule pressure (Boshier 2002). Once established, *Cordia* mortality rates are generally low (< 2%), even in densely stocked plantations that undergo self-thinning (Somarriba *et al.* 2001). Furthermore, the evidence of large adult trees established at least 300 m away from the original plantation is indicative that wind dispersal, particularly given the height the species can achieve at maturity (*ca* 30–40 m), is an effective mechanism for disseminating propagules over a large area.

Increasingly, propagule pressure is being identified as one of the key drivers of biological invasions (Lockwood *et al.* 2005, Colautti *et al.* 2006) and it has been suggested that even where biotic or ecosystem resistance to invasion is high it can be overcome if propagule pressure is high enough (D'Antonio *et al.* 2001). Nevertheless, there are few direct quantifications of its role in plant invasions (Hayes & Barry 2008, Hulme *et al.* 2008). Propagule pressure, as measured by the number of plantations established in Amani Botanic Garden, is a significant correlate of invasion success in 26 introduced woody species in Amani Nature Reserve, (Dawson *et al.* in press). Thus, the spread of *Cordia* is all the more significant given that only one plantation was ever established.

Nevertheless, a fundamental problem is that propagule pressure is often confounded with habitat attributes, such as habitat disturbance, *e.g.*, degraded ecosystems tend to be proximate to human settlements or roads that in themselves facilitate the introduction of alien species. For example, the association of the alien leguminous tree *Leuceana leucocephala* in reforested areas in Puerto Rico (Colon & Lugo 2006) may simply reflect the abundance of the species prior to land abandonment rather than specific successional processes. Similarly, the occurrence of alien trees in disturbed forest fragments of the Western Ghats (Muthuramkumar *et al.* 2006) is likely to reflect how widespread the species have been used as shade trees. In contrast, several studies have found invasion of relatively intact forests by alien species (Peters 2001; Zimmerman *et al.* 2008). This study reveals that not accounting for propagule pressure may easily lead to conclusion that disturbance or forest intactness determines invasion. This is one of the first studies to be able to tease apart these confounding variables and identify the overriding importance of propagule pressure in the invasion of the study site.

CORDIA AND INVASION RISK.—Although *Cordia* has previously been identified as an invasive species in ANR (Sheil 1994), identifying whether an alien plant is invasive or not requires an understanding of underlying species performance, rather than simply evidence of naturalization (Truscott *et al.* 2008). Based on the average *Cordia* adult densities near (< 250 m) and far (> 250 m) from the plantation, a crude estimate of the adult population within the study area is *ca* 6500. Given 210 individuals established in 1909, this provides an annual population growth rate of around 3.5 percent, equivalent to the population doubling every 20 yr. Such an estimate assumes no mortality and a constant rate of increase over the last century. The inverse 'J'-shaped size class distributions and high RI support the idea of a rapidly expanding population. Converting size distributions to age structure is a challenge and although significant relationships between tree size and age exist for *Cordia*, they are highly variable, strongly dependent on local conditions and growth rates decline for large trees (Liegel & Stead 1990, Hummel 2000). However, the coarse size categories used in this study probably do capture the essence of the population structure in ANR.

In addition, over the last century, *Cordia* has spread at least 600 m from the original source, this equates to an annual rate of spread of 60 m and is three times the average local dispersal rate found for a range of invasive tree/shrub species (Pyšek & Hulme 2005). Given that at least one classification of invasive status for taxa spreading by seeds is that there should be spread of more than 100 m in under 50 yr (Richardson *et al.* 2000), it is clear that *Cordia* is an invasive threat to ANR. The occurrence of large trees (dbh > 45 cm) is indicative of early colonization, possibly within 50 yr, of up to 300 m away. This study was unable to gauge the vulnerability of pristine forest in the East Usambaras since none occurred within the study area and it might be expected that such forest would be less vulnerable than semi-natural forest. However, it is likely that even in these habitats, while forest may be more intact, high propagule pressure may present opportunities for *Cordia* invasion (Rejmánek 1989). Thus whereas some authors have suggested that natural succession of native species in degraded habitats will reduce the abundance of alien trees in the East Usambaras (Viisteensaari *et al.* 2000) this will be less likely while significant sources of long-distance dispersed propagules remain within the region. Identifying and managing these sources should be a priority for the managers of ANR (Hulme 2006) and given the promotion of *Cordia* as a suitable agroforestry species (Greaves & McCarter 1990), this study should be taken as a strong counter-argument to its further dissemination in the humid tropics outside of its native range.

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