Journal of Applied Ecology 2003
40, 423–429

FORUM

Restoring tropical diversity: beating the time tax on species loss

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Summary

1. Fragmentation of tropical forest is accelerating at the same time that already cleared land reverts to secondary growth. Fragments inexorably lose deep-forest species to local extinction while embedded in low-diversity stands of early successional pioneer trees.

2. Pasture matrices undergoing passive secondary succession become a 'pioneer desert' from the vantage of remnant immigration, imposing a 'time tax' of loss of deep-forest plants from forest fragments. However, if seeds of deep-forest trees find pastures, or seedlings are planted there, many will prosper.

3. Bypassing early domination of pioneer trees in regenerating matrices, or enriching matrices with animal-dispersed forest trees, may stem the loss of species from forest fragments and accelerate succession far from the edges of old forest.

4. *Synthesis and applications.* Planting disperser-limited trees that establish in open ground may bypass 30–70 years of species attrition in isolated remnants by attracting animals that encourage normal processes of seed dispersal into and out of the fragments. Development of criteria for selection of persistent, reasonably rapidly growing, animal-dispersed species that are mixed with planted or naturally arriving pioneers will be an important component of enrichment planting.

Key-words: biodiversity, extinction, pioneer matrix, succession, tropical forest restoration.

Journal of Applied Ecology (2003) **40**, 423–429

Introduction

In vast areas of the tropics forest has been displaced by crops and commercial cattle grazing, leaving land devoid of natural vegetation and the soil seed banks, seedling cohorts and suppressed saplings of mature forest trees that might restore it (Quintana-Ascencio *et al*. 1996; Miller 1999). Often forest nuclei remain, but as fragments of a few hectares that inexorably lose species to local extinction (Turner 1996). Where intensive crop production or cattle ranching is unprofitable, restoration of biological diversity in regenerating matrices between fragments has the potential to stem the loss of species from relict forests, and may actually facilitate restoration of natural metapopulation dynamics. This could be done with passive secondary succession, somewhat facilitated natural succession, consciously enriched succession or manipulated succession under exotic monocultures.

We argue that in restoration of biological diversity between forest remnants the vegetation matrix matters. The matrix influences rates of accumulation of organic matter and nutrients (Lugo 1997) and the population and community dynamics of species in the remnants that the matrix surrounds (Vandermeer & Carvajal 2001). Almost any vegetation adds organic matter and nutrients, and retains water, to a greater extend than barren land. However, loss of species from remnants may not be stemmed if land is quickly occupied by one or a few early successional species, followed by what we call the 'pioneer desert' of early and late pioneers that retards the influx of disperser-limited deep-forest trees for a century or more (Finegan 1996). If intensive land use imposes a 'time tax' of soil degradation (Lugo 1988), the 100+ year pioneer matrix imposes another 'time tax' of species loss from remnants, a lost opportunity cost that may be irredeemable.

Loss of mutualists and herbivores may accelerate plant extinctions in forest fragments. A disproportionate number of tropical trees require insects, bats or birds for pollination, and bats, birds, terrestrial or arboreal mammals for seed dissemination (Howe & Westley 1997), and the diversity of recruiting cohorts

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of seedlings is maintained by thinning by ground-foraging mammals (Dirzo & Miranda 1991). An immense array of ecological disruptions occurs if herbivores, predators, dispersal agents and pollinators lack access to forest patches for long intervals (Cordeiro & Howe 2001; Terborgh *et al*. 2001; Wright & Duber 2001; Tewksbury *et al*. 2002). A matrix that accelerates the influx of frugivores and herbivores is an overlooked but important component of forest regeneration.

We argue that loss of tree species continues unabated from forest remnants embedded in a matrix of pioneer species, imposing a time tax of local extinction that will impede future restoration efforts. One remedy is the creation of matrices enriched with large-seeded, animal-dispersed trees that attract dispersal agents that accelerate succession to mature forest, mediate immigration of forest species back into remnant fragments, and augment emigration of trees of relict forests into regenerating matrices.

Natural succession

In rain forests natural disturbances vary in scale, intensity and frequency, and trigger a variety of successional processes. Most disturbances are small branchfalls and treefalls that form canopy gaps of 50–1000 m^2 and close within a few years (Figure 1, Howe 1990), usually filled by deep-forest species already present as seeds, seedlings, saplings, re-sprouts or overhanging canopy trees (Brokaw & Scheiner 1989). Even extensive hurricane blow-downs yield tree species already present as suppressed plants in the understorey or stumps capable of resprouting after damage (Boucher *et al*. 2001). Most natural regeneration in rain forests free from human disturbance comes from established plants, the species composition of which roughly reflects the pre-disturbance community.

Immense stands of early pioneer trees can develop naturally but the circumstances are limited and rare. Massive mudslides following earthquakes or volcanoes are closed by small-seeded pioneer species with high dispersal capacity (Thebaud & Strasberg 1997). For instance, Garwood, Janos & Brokaw (1979) reported that an earthquake in eastern Panama sloughed an entire watershed into the sea. Much like a large anthropogenic disturbance, the exposed earth was quickly choked with saplings of invasive bird-dispersed *Trema* (Ulmaceae), a common early successional tree that produced fruits within 4 years. Large natural disturbances that remove vegetation over several to hundreds of hectares involve quite different processes of succession than simple closure of canopy gaps or even revegetation after damage by wind or fire that leaves many seeds, seedlings and older plants alive and ready to respond to the increased light and soil resources.

Arriving and surviving in unnatural landscapes

Landscape features influence the arrival and survival of tree species after major disturbances (Tewksbury *et al*. 2002). In the tropics, abandoned croplands and pastures do not have seed banks of forest species, nor are there seedling or sapling cohorts waiting to respond to opportunity. Low rates of colonization and emergence, and high mortality of seeds and seedlings, result in low densities and diversities of tree juveniles and saplings (Uhl, Buschbacher & Serrao 1988; Nepstad *et al*. 1996; Zimmerman, Pascarella & Aide 2000). Under such conditions dispersal becomes a limiting factor in the rate of forest regeneration (Quintana-Ascencio *et al*. 1996; Holl 1999; Miller 1999), and the size and distribution of remnant sources of forest seeds becomes an important determinant of seed dispersal and seedling recruitment. Even when small pastures experience substantial seed rain from late-successional trees in nearby mature forest, they always receive different seed input from small gaps within the mature rain forest (Purata 1986; Martínez-Garza & González-Montagut 1999, 2002). It is not realistic to expect early large-scale colonization of open land by large-seeded bird-, bat- or primate-dispersed tree species even tens of metres, much less hundreds of metres, from a forest edge (Hooper, Condit & Legendre 2002; Ingle 2003). Unsuccessful intensive farming and ranching have made such large tracts of thoroughly disturbed land commonplace, and coincidentally made the dispersal limitation that is characteristic of such situations the rule rather than the exception throughout much of the neo- and palaeotropics. Only part of the problem is what can establish and grow under the canopy of such pioneers; much of the problem is what can get there.

Examples from the neotropics illustrate the issues. A few early pioneers such as *Cecropia* (Moraceae), *Croton* (Euphorbiaceae), *Trema* and *Vismia* (Guttiferae), hold ground for 20–30 years, to be replaced by such longer-lived late pioneers as *Cordia* (Boraginaceae), *Goupia* (Goupiaceae), *Guazuma* (Sterculiaceae), *Laetia* (Flacourtiaceae), *Rollinia* (Annonaceae), *Spondias* (Anacardiaceae), *Stryphnodendron* (Fabaceae) and *Vochysia* (Vochysiaceae) (Uhl & Jordan 1984; Finegan 1996; Mesquita *et al*. 2001). In a mix of successional forests, species richness and diversity may approach that of mature forest in 100 years, but species composition does not resemble mature forest; dominants of primary forest, if present, are rare (Finegan 1996; Aide *et al*. 2000). A century of revegetation after intensive grazing or farming produces forests that restore most ecosystem function but the new forests do not have, for many years, if ever, the same species of trees that were present before the cow or plough. Such a ‘pioneer desert’ does not supply stands of remnant mature forest with propagules of deep-forest species, nor provides genetic diversity from pollen for isolated relict trees, for at least several decades. Ecosystem function may return but much of the biological function of a mature forest does not.

A useful irony is that many disperser-limited deep-forest species do well in open pastures, if they get there. In Panama, Hooper, Condit & Legendre (2002) found

> 70% survival of large-seeded, shade-tolerant tree seedlings in pastures, where *per capita* survival of seedlings of pioneers is < 0·1%. In Costa Rica, seedlings of large-seeded *Octoea glaucosericea* Rowher, *Octoea whitei* Woodson (Lauraceae) and *Calophyllum brasiliense* Cambess. (Guttiferae) have greater than 50% survival when planted in pastures (Loik & Holl 1999), while this *Calophyllum* and deep-forest trees *Virola koschnyi* Warb. (Myristicaceae), *Dipteryx panamensis* (Pittier) Record & Mell (Fabaceae), *Pithecellobium elegans* Ducke (Fabaceae), and *Genipa americana* L. (Rubiaceae) experience 60–98% survival when planted as seedlings in other abandoned pastures (Montagnini *et al.* 1995). Evidence is mounting that many deep-forest species can survive in pastures.

Similar success occurs in the Old World. Hardwick *et al.* (1997) found that in abandoned agricultural land in northern Thailand, seedlings of animal-dispersed *Beilschmiedia* spp. (Lauraceae) with large seeds (6–7 g), and *Prunus cerasoides* D. Don (Rosaceae) with seeds of moderate size (0·23 g), have survival rates in weedy pastures of 93% and 70%, respectively. Pioneers colonize pastures but only because small (< 10 mg) seeds are present in immense numbers. Far from a forest edge even pioneer arrival may be very slow. However, if deep-forest trees with large seeds find pastures, or are planted there, seedlings of many species prosper.

Attrition of species from fragments in alien matrices

Forest fragments excised from continuous forest and embedded in alien matrices lose many species of animals and plants over 20–100 years (Turner 1996). The proximity of fragments to sources of dispersal agents influence which species are vulnerable to local extinction in remnants. The source landscape and the quality of surrounding matrices, will probably determine which species are most vulnerable in a given area.

Very low densities of most species make tropical forest fragments particularly vulnerable to high rates of local extinction (Maina & Howe 2000). Species number is positively associated with size of habitat patches, while population densities of all but the dominants are inversely correlated with richness (Preston 1948; MacArthur 1972). Recent studies have shown that seedlings and juveniles of many rain forest species suffer declines in fragments (Cordeiro & Howe 2001; Githiru, Bennun & Lens 2002) and some island communities show dramatic losses through older juvenile and sapling stages (Leigh *et al.* 1993). With adult tropical trees dying at a rate of roughly 1% per year in mature forest (Brokaw 1985; Sukumar *et al.* 1998), the less representative the matrix is of mature forest, the more rapidly small populations of dispersal agents and trees with reduced recruitment will be lost from remnants. Maina & Howe (2000) argue that tree species most vulnerable to local extinction from small forest remnants are those at the moderately abundant to rare end of the species abundance distribution. These species lose pollinators or dispersal agents in small fragments, while those most likely to persist are highly vagile weeds, augmented by successional pioneer deserts, and ‘always rare’ species that function as successful metapopulations.

Records from old fragments of forest in East Africa have borne out these expectations (Cordeiro & Howe 2001). In the East Usambara Mountains of Tanzania, a rain forest of largely animal-dispersed trees (23% endemic) was fragmented into < 1–600-ha patches around a remnant of 3500 ha, within a matrix of tea plantations 60–90 years old. Interior forest bird and primate populations disappeared or were much reduced in small fragments. Preliminary censuses showed that densities of seedlings and juveniles of 31 animal-dispersed tree species were more than three times greater in continuous forest and in large (> 30 ha) than small (< 10 ha) forest fragments, whereas recruitment of eight wind- and gravity-dispersed trees of the forest interior was unaffected. Recruitment of 10 endemic animal-dispersed tree species was 40 times lower in small fragments than in continuous forest or large fragments. Even in this system, with far fewer species than many forests of South America or East Asia, many tree species were represented by 1–5 adult individuals per fragment, far fewer than necessary to maintain viable populations. In such situations restoration of the matrix is a race against time.

Restoring the matrix: beating the time tax on diversity

Restoring matrix diversity encourages natural processes of immigration and integration among nuclei of forest remnants. One management strategy is planting buffers, corridors and stepping-stone stands around and between remnants (Janzen 1988; Lamb *et al.* 1997; Tewksbury *et al.* 2002). Another method of restoring matrix diversity after release from intensive agriculture is to upgrade or eliminate the 100-year pioneer desert by encouraging late-successional trees long before they would passively arrive of their own accord. This in turn should attract vertebrate dispersal agents that accelerate the process of seed dispersal into and out of forest fragments.

In general, in forest regeneration of large areas of abandoned agricultural land or pasture, passive succession cannot stem the loss of species from forest remnants. Isolated trees attract dispersal agents, and artificially positioned perches likewise increase the seed rain of animal-dispersed species (Guevara *et al.* 1991; Miriti 1998), but recruitment is slow and remains unrepresentative of mature forest (Holl 1999). We doubt that passive succession, or succession encouraged with perches, will effectively counter the time tax of loss from remnants except for edges close to mature forest. Encouraging disperser activity in this minimal way may be more appropriate for buffering edges of remnants (Janzen 1988) than for bypassing the pioneer desert.

We suggest that beating the time tax on biodiversity is possible if the natural succession of pioneers is actively enriched with plantings of late-successional and deep-forest animal-dispersed tree species. Pioneers arrive of their own accord close to forest edges, or may be planted far from edges in the largest deforestations. In some cases valuable timber species may be mixed in plantings for later commercial harvest, a conservation measure that has been attempted in Australia (Lamb & Lawrence 1993). We suggest that criteria should include a mix capable of growing in xeric conditions of open ground or capable of growing under exotic grasses, should be capable of establishing under the inevitable pioneer canopy, and when mature should be capable of attracting animal dispersal agents that accelerate the process. Tucker & Murphy (1997) demonstrated enhanced regeneration of animal-dispersed species in enriched successions in tropical Queensland, where dispersal agents and the trees that they use are far more common with plantings of late-successional trees than in control plots of the pioneer matrix. Criteria for selection of those late-successional species most likely to accelerate succession to complex forests should become an important facet of enrichment plantings.

At some sites, exotic plantation monocultures may admit deep-forest species native to surrounding forests. Lugo (1997) makes the interesting point that plantation monocultures of some short-lived exotics cast enough shade to suppress pioneers, but admit invasion by deep-forest species at least as well as pioneers and better than other plantation crops. This variation on passive succession would permit a cash crop and cost little. Whether such a method would create unintended consequences, be a superior strategy to enrichment of early and late pioneer stands, or simply be the only option in regions used for plantation crops, should be a matter of debate.

The evidence indicates that the feasibility of using plantations of exotic monocultures to promote late-successional indigenous species depends on the species used and the location. In Brazil, *Leucaena leucocephala* (Lam.) De Wit (Fabaceae) plantations admitted more native forest species than *Casuarina* plantations (Parrotta 1995). In Hawaii, plantations of *Eucalyptus saligna* Sm. (Myrtaceae) and *Flindersia brayleyana* F. V. Muell. (Rutaceae) from Australia and *Fraxinus uhdei* (Wenzig) Lingelsh (Oleaceae) from Mexico established in the 1950s and 1960s fostered very different regeneration pathways (Harrington & Ewel 1997). *Eucalyptus saligna* strongly favoured exotics and *Flindersia braylenana* replaced itself, while *Fraxinus uhdei* favoured two dominants of surrounding mature forest, *Cibotium glaucum* (Sm.) Hook. & Arnott (Dicksoniaceae) and *Metrosideros polymorpha* Gaud. (Myrtaceae). Various pines and eucalypts in South Africa admitted a few common animal- and wind-dispersed forest canopy species, which appear to represent late pioneer species (Geldenhuys 1997). In the Congo, eucalypt plantations admit a number of native forest species, especially close (< 50 m) to the forest edge, with strong representation of wind-dispersed species that show especially rapid regrowth after clear-cutting of the plantation crop (Loumeto & Huttel 1997). With some exceptions, such as *Leucanea* in Brazil and *Fraxinus* in Hawaii, forests developing under plantation monocultures resemble a pioneer desert produced by passive regeneration of unnaturally extensive abandoned agricultural land, or admit even fewer species than natural successions if exotics replace themselves.

Another option might be the planting of native monocultures or mixed stands (Guariguata, Rheingans & Montagnini 1995; Haggar, Wightman & Fisher 1997; Murcia 1997). Monocultures or mixed stands of native species admit the invasion of other native species, but success also depends on which species are planted and the objectives of restoration. For instance, in Costa Rica establishment of forest trees is favoured under monocultures of *Vochysia guatemalensis* (Donn.Sm.) Standl. (Vochysiaseae) but plant growth is slower than under *Jacaranda copaia* (Aubl.) D. Donn. (Bignoniaceae) monocultures (Guariguata, Rheingans & Montagnini 1995). In the Colombian Andes recruitment of forest species is lower in plantations of *Alnus acuminata* (Kunth) Kuntze (Betulaceae) than in the natural regenerated forest (Murcia 1997). As in natural successions, few of the species that recruit under the plantations belong to the mature forest (Haggar, Wightman & Fisher 1997; Murcia 1997). These planted overstorey trees are wind-dispersed, which would not draw dispersal agents as effectively as animal-dispersed species.

In summary, enrichment of successional plots with seedlings of a variety of animal-dispersed tree species would appear to be the most feasible means of beating the time tax on species loss from remnants embedded in secondary successions (Tucker & Murphy 1997). Variations on passive succession, unattended or under overstoreys of exotic or native trees, may offer a means of restoring ecosystem function, but they do not avoid the equivalent of the pioneer desert: forest remnants remaining surrounded by low-diversity matrix. Adding perches for birds may or may not speed succession near forest edges, and planting animal-dispersed monocultures might attract birds and mammals that eat fruits and disperse other seeds in the process. The risk in any variation of passive succession is embedding remnant forests in alien matrices for unnecessarily long periods of time. In our view, useful factors to consider as criteria for enrichment plantings of late-successional trees include both attributes of growth and survival of the tree species, and their role in dispersal dynamics.

Not all deep-forest species can survive in xeric pasture conditions or prosper under a thick cover of exotic grasses or exotic or native weeds. Some deep-forest species are more likely to survive in the open than others, and some species grow more rapidly than others (Hooper, Condit & Legendre 2002). High mortality and very slow growth could admit weedy herbaceous grasses and forbs, thereby delaying succession. Pioneer trees will arrive of their own accord near forest edges (Martínez-Garza & González-Montagut 1999, 2002; Ingle 2003) but animal-dispersed pioneers such as *Cecropia*, *Cordia*, *Ficus* and *Trema* could usefully be planted far (> 100 m) from source forests edges to secure soil, provide shade and initiate the process of frugivore assembly. Maury-Lechon (1993) has found that the growth plasticity of juvenile stages of trees is a predictor of growth rate in secondary succession. We found that variation (coefficient of variation) in an easily measured leaf character, specific leaf weight, is a reasonable predictor of growth rate and survival of deep-forest trees in a 5-year-old planting in southern Mexico (Martínez-Garza & Howe 2002). Given a pool of dozens to hundreds of moderate- to large-seeded species in the vicinity of almost any tropical forest, the high survival rate of those mature forest species that have been planted in open pastures, and an increasing understanding of easily detected attributes that are correlated with high growth rates and persistence, we are confident that plant functioning will not limit enrichment.

Besides having a reasonable capacity for survival, species used in enrichment plantings should also serve other purposes. Species chosen might represent rare species logged out of many remnants and could therefore serve a conservation function (Lamb & Lawrence 1993). A more general tactic is to select those species that, once mature, will attract birds, primates, bats or other fruit-eating animals that accelerate seed dispersal of late-successional species into and out of forest remnants. Because the greater majority of tree species in many tropical forests bear fruits adapted for animal dispersal (Howe & Westley 1997), a wide range of species appealing to both generalist and specialist species is likely to be available and otherwise suitable for planting as seedlings. With refined criteria for inclusion of components of the mature forest community, Tucker & Murphy's (1997) approach could be the basis for a model for effective revegetation in most tropical regions of the world.

Synthesis and applications

Planting seedlings of interior forest species after land abandonment should sharply accelerate the process of revegetation of complex communities. Two to 10 years may be lost in slower growth of some trees but decades will be saved in total community recovery. Bypassing acute dispersal limitation with plantings that accelerate the re-occupation of land far from remnants by herbivorous and fruit-eating animals may subtract 30–100 years of the time tax on diversity imposed by a low-diversity pioneer matrices. The effects of enrichment between forest remnants will be strongest where matrices are dominated by wind-dispersed trees, where plantation exotics self-seed easily, and in deforested areas far (> 100 m) from forest edges. Pioneer stands or plantation monocultures may be enriched with seeds or even better with seedlings of late-successional animal-dispersed trees, or initial plantings could be mixes of late-successional and pioneer species. Whatever enrichment is used, it will almost certainly do more to beat the time tax on species loss from remnants than passive secondary succession or minimal encouragement with artificial perches for birds.

Active enrichment of successions or plantations with a variety of animal-dispersed species appears to be the best method for recruiting a variety of mature forest trees in and from remnants, with some care in selection of trees bearing fruits for consumption and dispersal by different animal guilds. Enrichment of plantations, when possible by animal-dispersed species, has the advantage of adjusting overstorey densities enough to suppress pioneers but not so much as to suppress mature-forest species planted underneath. A challenge will be to establish criteria for selecting candidates for enrichment projects and in some cases for overstoreys. The mix should include species that are able to grow in xeric open pastures in some cases and under shade of trees or grasses in others (Hooper, Condit & Legendre 2002). Species should be animal-dispersed to harness most effectively the natural processes of dissemination into and out of remnant forests, and should represent a variety of fruit sizes and attractiveness to the birds, primates, bats and other arboreal and terrestrial mammals that will mediate the process.

Acknowledgements

We are grateful N. Cordeiro, P. Fine, B. Finegan, N. Ingle, J. Klock, G. Nuñez, S. Saha, A. Sullivan, B. Zorn-Arnold and one anonymous referee for comments on the manuscript, and to the Lincoln Park Zoo Neotropic Foundation, CONACyT of Mexico, and the National Science Foundation of the United States for support of research leading to these insights.

References

Aide, T.M., Zimmerman, J.K., Pascarella, J.B., Rivera, L. & Marcano-Vega, H. (2000) Forest regeneration in a chronosequence of tropical abandoned pasture: implications for restoration ecology. *Restoration Ecology*, **8**, 328–338.

Boucher, D.H., Vandermeer, J.H., Granzoa de la Cerda, I., Mallona, M.A., Perfecto, I. & Zamora, N. (2001) Post-agriculture versus post-hurricane succession in southeastern Nicaraguan rain forest. *Plant Ecology*, **156**, 131–137.

Brokaw, N.V.L. (1985) Gap-phase regeneration in a tropical forest. *Ecology*, **66**, 682–687.

Brokaw, N.V.L. & Scheiner, S.M. (1989) Species composition in gaps and structure of a tropical forest. *Ecology*, **70**, 538–541.

Cordeiro, N. & Howe, H.F. (2001) Low recruitment of trees dispersed by animals in African forest fragments. *Conservation Biology*, **15**, 1733–1741.

Dirzo, R. & Miranda, A. (1991) Altered patterns of herbivory and diversity in the forest understorey: a case study of the possible consequences of contemporary defaunation. *Plant–Animal Interactions: Evolutionary Ecology in Tropical and Temperate Regions* (eds P. Price, T. Lewingston, G. Fernandes & W. Benson), pp. 273–287. John Wiley & Sons, New York, NY.

Finegan, B. (1996) Pattern and process in neotropical secondary rain forests: the first 100 years of succession. *Trends in Ecology and Evolution*, **11**, 119–124.

Garwood, N.C., Janos, D. & Brokaw, N. (1979) Earthquake-caused landslides: a major disturbance to tropical forests. *Science*, **205**, 997–999.

Geldenhuys, C.J. (1997) Native forest regeneration in pine and eucalypt plantations in Northern Province, South Africa. *Forest Ecology and Management*, **99**, 101–115.

Githiru, M., Bennun, L. & Lens, L. (2002) Regeneration patterns among bird-dispersed plants in a fragmented Afrotropical forest, south-east Kenya. *Journal of Tropical Ecology*, **18**, 143–149.

Guariguata, M.R., Rheingans, R. & Montagnini, F. (1995) Early woody invasion under tree plantations in Costa Rica: implications for forest restoration. *Restoration Ecology*, **3**, 252–260.

Guevara, S., Meave del Castillo, J., Moreno-Casasola, P. & Laborde, J. (1991) Floristic composition and structure of vegetation under isolated trees in neotropical pastures. *Journal of Vegetation Science*, **3**, 655–664.

Haggar, J., Wightman, K. & Fisher, R. (1997) The potential of plantations to foster woody regeneration within a deforested landscape in lowland Costa Rica. *Forest Ecology and Management*, **99**, 55–64.

Hardwick, K., Healey, J., Elliott, S., Garwood, N. & Anusarnsunthorn, V. (1997) Understanding and assisting natural regeneration processes in degraded seasonal evergreen forests in northern Thailand. *Forest Ecology and Management*, **99**, 203–214.

Harrington, R.A. & Ewel, J.J. (1997) Invasibility of tree plantations by native and non-native indigenous plant species in Hawaii. *Forest Ecology and Management*, **99**, 153–162.

Holl, K.H. (1999) Factors limiting tropical rain forest regeneration in abandoned pastures: seed rain, seed germination, microclimate and soil. *Biotropica*, **31**, 229–242.

Hooper, E., Condit, R. & Legendre, P. (2002) Responses of 20 native tree species to reforestation strategies for abandoned pastures in Panama. *Ecological Applications*, **12**, 1626–1641.

Howe, H.F. (1990) Seedling survival in a Central American tree (*Virola surinamensis*): effects of herbivory and canopy closure. *Journal of Tropical Ecology*, **6**, 259–280.

Howe, H.F. & Westley, L.C. (1997) Ecology of pollination and seed dispersal. *Plant Ecology*, 2nd edn (ed. M.J. Crawley), pp. 262–283. Blackwell Science, London, UK.

Ingle, N.R. (2003) Seed dispersal by wind, birds and bats between Philippine montane rainforest and successional vegetation. *Oecologia*, **134**, 251–261.

Janzen, D.H. (1988) Management of habitat fragments in a tropical dry forest: growth. *Annals of the Missouri Botanic Garden*, **75**, 105–116.

Lamb, D. & Lawrence, P. (1993) Mixed species plantations using high value rainforest trees in Australia. *Restoration of Tropical Forest Ecosystems* (eds H. Lieth & M. Lohmann), pp. 101–108. Kluwer Academic Publishers, Dordrecht, the Netherlands.

Lamb, D., Parrotta, J., Keenan, R. & Tucker, N. (1997) Rejoining habitat remnants restoring degraded rainforest land. *Tropical Forest Remnants* (eds W.F. Laurance & R.O. Bierregaard, Jr), pp. 366–385. University of Chicago Press, Chicago, IL.

Leigh, E.G. Jr, Wright, S.J., Herre, E.A. & Putz, F.E. (1993) The decline of tree diversity on newly isolated tropical island: a test of a null hypothesis and some implications. *Evolutionary Ecology*, **7**, 76–102.

Loik, M.E. & Holl, K.D. (1999) Photosynthetic responses to light for rainforest seedlings planted in abandoned pasture, Costa Rica. *Restoration Ecology*, **7**, 382–391.

Loumeto, J., J. & Huttel, C. (1997) Understorey vegetation in fast-growing tree plantations on savanna soils in Congo. *Forest Ecology and Management*, **99**, 65–81.

Lugo, A.E. (1988) The future of the forest: ecosystem rehabilitation in the tropics. *Environment*, **30**, 17–20, 41–45.

Lugo, A.E. (1997) The apparent paradox of establishing species richness on degraded lands with tree monocultures. *Forest Ecology and Management*, **99**, 9–19.

MacArthur, R. (1972) *Geographical Ecology*. Princeton University Press, Princeton, NJ.

Maina, G. & Howe, H.F. (2000) Inherent rarity in community restoration. *Conservation Biology*, **14**, 1335–1340.

Martínez-Garza, C. & González-Montagut, R. (1999) Seed rain from forest fragment into tropical pastures in Los Tuxtlas, Mexico. *Plant Ecology*, **145**, 655–665.

Martínez-Garza, C. & González-Montagut, R. (2002) Seed rain of fleshy-fruited species in tropical pastures in Los Tuxtlas, Mexico. *Journal of Tropical Ecology*, **18**, 457–462.

Martínez-Garza, C. & Howe, H.F. (2002) Growth rates and leaf characteristics in tropical tree species: selection of species for restoration projects. *Abstract of the Association for Tropical Biology Annual Meeting – Tropical Forests: Past, Present and Future* (ed. S.J. Wright), pp. 70–71. Smithsonian Tropical Research Institute, Panama City, Panama.

Maury-Lechon, G. (1993) Biological characters and plasticity of juvenile tree stages to restore degraded tropical forests: a systems framework for site analysis and restoration research. *Restoration of Tropical Forest Ecosystems* (eds H. Lieth & M. Lohmann), pp. 37–46. Kluwer Academic Publishers, Dordrecht, the Netherlands.

Mesquita, R.C.G., Ickes, K., Ganade, G. & Williamson, G.B. (2001) Alternative successional pathways in the Amazon Basin. *Journal of Ecology*, **89**, 528–537.

Miller, P.M. (1999) Effects of deforestation on seed banks in a tropical deciduous forest of eastern Mexico. *Journal of Tropical Ecology*, **15**, 179–188.

Miriti, M.N. (1998) Regeneracao florestal em pastagens abandonadas na Amazonia Central: competicao, predação, e dispersao de sementes. *Floresta Amazonica: Dinamica, Regeneracao E Manejo* (eds C. Gascon, D. Nepstad & P. Moutinho), pp. 179–191. Instituto Nacional de Pesquisa da Amazonia, Manaus, Brazil.

Montagnini, F., González, E., Porras, C. & Rheingans, R. (1995) Mixed and pure forest plantations in the humid neotropics: a comparison of early growth, pest damage and establishment costs. *Commonwealth Forest Review*, **74**, 306–314.

Murcia, C. (1997) Evaluation of Andean alder as a catalyst for the recovery of tropical cloud forest in Colombia. *Forest Ecology and Management*, **99**, 163–170.

Nepstad, D.C., Uhl, C., Pereira, C.A. & Cardoso Da Silva, J.M. (1996) A comparative study of tree establishment in abandoned pasture and mature forest of eastern Amazonia. *Oikos*, **76**, 25–39.

Parrotta, J.A. (1995) Influence of overstorey composition on understorey colonization by native species in plantations on a degraded tropical site. *Journal of Vegetation Science*, **6**, 627–636.

Preston, F. (1948) The commonness and rarity of species. *Ecology*, **29**, 254–283.

Purata, S. (1986) Floristic and structural changes during old-field succession in the Mexican tropics in relation to site history and species availability. *Journal of Tropical Ecology*, **2**, 257–276.

Quintana-Ascencio, P.F., Gonzales-Espinoza, M., Ramírez-Marcial, N., Dominguez-Vázquez, G. & Martínez-Icó, M.

(1996) Soil seed banks and regeneration of tropical rain forest from milpa fields at the Selva Lacandona, Chiapas, Mexico. *Biotropica*, **28**, 192–209.

Sukumar, R., Suresh, S., Dattaraja, H.S. & Joshi, N.V. (1998) Dynamics of a tropical deciduous forest: population changes (1988 through 1993) in a 50-ha plot at Mudumalai, southern India. *Forest Biodiversity, Research Monitoring and Modelling* (eds F. Dallmeier & J. Comiskey), pp. 495–506. Man and Biosphere Series, V. 20. UNESCO and the Parthenon Publishing Group, NY, USA.

Terborgh, J.T., Lopez, L., Nuñez, P., Rao, M., Shahabuddin, G., Orihuela, G., Riveros, M., Ascanio, R., Adler, G.H., Lambert, T.D. & Balbas, L. (2001) Ecological meltdown in predator-free forest fragments. *Science*, **294**, 1923–1926.

Tewksbury, J.J., Levey, D.J., Haddad, N.M., Sargent, S., Orrock, J.L., Weldon, A., Danielson, B.J., Brinkerhoff, J., Damschen, E.I. & Townsend, P. (2002) Corridors affect plants, animals, and their interactions in fragmented landscapes. *Proceedings of the National Academy of Sciences, USA*, **99**, 12923–12926.

Thebaud, C. & Strasberg, D. (1997) Plant dispersal in fragmented landscapes: a field study of woody colonization in rain forest remnants of the Mascarenie Archipelago. *Tropical Forest Remnants* (eds W.F. Laurance & R.O. Bierregaard, Jr), pp. 321–332. University of Chicago Press, Chicago, IL.

Tucker, N.I.J. & Murphy, T.M. (1997) The effects of ecological rehabilitation on vegetation recruitment: some observations from the wet tropics of North Queensland. *Forest Ecology and Management*, **99**, 133–152.

Turner, I.M. (1996) Species loss in fragments of tropical rain forests: a review of the evidence. *Journal of Applied Ecology*, **33**, 200–209.

Uhl, C. & Jordan, C.F. (1984) Succession and nutrient dynamics following forest cutting and burning in Amazonian. *Ecology*, **65**, 1476–1490.

Uhl, C., Buschbacher, R. & Serrao, E.A.S. (1988) Abandoned pastures in Eastern Amazonia. I. Patterns of plant succession. *Journal of Ecology*, **76**, 663–681.

Vandermeer, J. & Carvajal, R. (2001) Metapopulation dynamics and the quality of the matrix. *American Naturalist*, **158**, 211–220.

Wright, S.J. & Duber, H.C. (2001) Poachers and forest fragmentation alter seed dispersal, seed survival, and seedling recruitment in the palm *Attalea butyraceae*, with implications for tropical tree diversity. *Biotropica*, **33**, 583–595.

Zimmerman, J.K., Pascarella, J.B. & Aide, T.M. (2000) Barriers to forest regeneration in an abandoned pasture in Puerto Rico. *Restoration Ecology*, **8**, 350–360.

Received 29 July 2002; final copy received 7 February 2003