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RESEARCH ARTICLE

Tropical forest regeneration following land abandonment is driven by primary rainforest distribution in an old pastoral region

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Abstract

Context Tropical forest regeneration is increasingly prominent as agro-pastoral lands are abandoned. Regeneration is characterised as favouring 'marginal' lands; however, observations of its drivers are often coarse or simple, leaving doubt as to spatial dynamics and causation.

Objectives We quantified the spatial dynamics of forest regeneration relative to marginality and remnant forest cover in a 3000 km^2 pastoral region in northern tropical Australia.

Methods Classification and regression trees related the extent and distribution of regeneration to soil agricultural potential, land-cover history, terrain slope, distance to primary forest, and primary forest fragment size, as defined by aerial photography.

Results Secondary forest extent and distribution overwhelmingly reflect the proximity and size of primary forest fragments. Some 85 % of secondary forest area occurs <1 km of primary forest, and 86 % of secondary forest patches >50 ha are <400 m from primary forest and coincident with historic primary forest fragments. Where primary forest fragments are >8.5 ha, secondary forest area declines less rapidly with increasing distance from primary forest up to 1.5 km. Marginality inferred by soil potential and slope had no bearing on regeneration, except at the coarsest of spatial scales where regeneration is a proxy for primary forest cover.

Conclusion Findings underline the need to conserve even modest rainforest patches as propagule reservoirs enabling regeneration. Marginality per se may have a limited role in regeneration. As most secondary forest was an extension of primary forest, its unique conservation value relative to that of primary forest may likewise merit reconsideration.

Keywords Reforestation · Regeneration · Succession · Forest transition · Marginal · Abandonment · Remnant forest · Recruitment · Biodiversity

Introduction

Deforestation has been and continues to be the predominant trend in tropical forest change (Williams 2003; FAO 2010; Hansen et al. 2013). While spontaneous forest regeneration has always accompanied tropical deforestation to some degree, novel and relatively-pronounced recent secondary forest expansion in many tropical regions following large-scale

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shifts in human settlement and agricultural activity is increasingly a trend of interest (Meyfroidt and Lambin 2011). In some regions forest recovery marks a nascent departure from a history of deforestation—many Latin American regions are experiencing net increases in forest cover, for example (Rudel 2005 Hecht and Saatchi 2007; Aide et al. 2013; Sloan 2015). Forest regeneration also marks a new means to conserve biodiversity and sequester atmospheric carbon (Wright and Muller-Landau 2006; Asner et al. 2009; Chazdon et al. 2009b; Letcher and Chazdon 2009; Rudel et al. 2009; Sloan and Pelletier 2012), leading some authors to contemplate *The Promise of Tropical Forest Regeneration in an Age of Deforestation* (Chazdon 2014). Interest has consolidated around the tropical forest transition (Rudel 2005)—a loose empirical model whereby socio-economic shifts encourage agriculturalists on marginal lands to 'rest' and ultimately abandon their lands and, thus, allow forests to reclaim them via natural succession. In the context of tropical Australia, we qualify the role of 'marginality' in forest regeneration as a proxy for remnant forest cover, which we find to determine the area and distribution of forest regeneration following abandonment almost exclusively.

The tropical forest transition is predicated on an association between agro-economic marginality and the propensity to abandon agricultural activity following major socio-economic shifts like urbanisation (Mather and Needle 1998). Agriculturalists on marginal lands are presumed to be foremost in abandoning their lands because they are under-productive and/or because socio-economic shifts offer enticing alternatives to continued agricultural production. Such is the centrality of marginality that 'core-periphery' models—originally designed to describe spatial variation in land use as a function of market access—have been applied to agricultural contraction and forest expansion at the margins of production (Angelsen 2007). Large-scale surveys of forest recovery sustain the role of 'marginality' in fomenting regeneration by characterising regeneration contexts via the shorthand geographical adjectives 'upland' or 'peripheral' (Thomlinson et al. 1996; Rudel et al. 2000; Rudel 2005; Asner et al. 2009; Crk et al. 2009; Redo et al. 2012; Sloan and Pelletier 2012; Timms et al. 2012; Aide et al. 2013). Aide et al. (2013), for example, show that whereas deforestation over 2000–2010 concentrated at <250 m above sea level within Latin America's tropical moist forest biome, forest cover expansion concentrated at 300–1000 m, with the implication that these uplands are more marginal for production. Similarly, Rudel's (2005) meta-analysis of South East Asian case studies of forest-cover change suggests that spontaneous reforestation there concentrates in the peripheral fringes of fertile, intensively-cultivated valleys, with the implication that a transfer of labour and investment from the fringes to the valleys drives land abandonment and reforestation.

The relationship between abandonment, tropical forest recovery, and agricultural marginality remains unclear, however. While there are certainly examples of forest regeneration being relatively likely in 'marginal' contexts or correlating with its proxies, such as topographical elevation, climate, and distance from population centers (Rudel et al. 2000; Perz and Skole 2003b; Rudel 2005; Crk et al. 2009; Redo et al. 2012; Rudel 2012), there remains reasons to scrutinise the role of marginality. The term 'marginality' is understood to denote lands that are underproductive or otherwise unattractive for agriculture, but it has rarely been well defined, instead being implied by proxies spanning an array of economic and biophysical factors. Such characterisations say little of the actual dynamics promoting regeneration on the ground (Sloan 2011), particularly in contexts dominated by pastoral activities resilient to unfavourable biophysical conditions and scarce labour (Hecht and Saatchi 2007; Preston 1998). Such characterisations similarly may fail to recognise that marginality is relative to the opportunity costs of continued agricultural production and to different land uses, all of which may change independently of biophysical conditions. The *degree* of 'marginality' beyond which abandonment and regeneration are likely is similarly rarely specified. Rather, marginality is often inferred only in *relative* terms, with the all-important referent typically being cleared lands *not* experiencing regeneration. Supposedly 'marginal' lands undergoing forest regeneration may therefore not be agro-ecologically limited per se, except relative to still-cultivated lands, and the differences between these lands may be slight in practice.

Further, ecological fallacies are problematic in light of the coarse scales at which regeneration has been surveyed (Perz and Skole 2003a; Perz and Skole 2003b; Redo et al. 2012; Aide et al. 2013 especially

Sloan 2015; Wright and Samaniego 2008). Regeneration may concentrate due to factors only partially related to apparent marginality. 'Uplands', for example, very often host relatively extensive remnant forest that may 'seed' regrowth following abandonment, accelerating recovery relative to comparable flatter lands. Various case studies of the distribution of secondary forests observe upwards of 80 % of their area to be adjacent to a dominant remnant forest fragment, which typically occupies the top of a mount (Endress and Chinea 2001; Lugo 2002; Thomlinson et al. 1996; Helmer et al. 2008; Timms et al. 2012). Historically light land usage and favourable landscape matrices are similarly prominent in broadly marginal regions and known to facilitate regeneration but seldom considered by landscape surveys (Uhl et al. 1988; Brown and Lugo 1990; Thomlinson et al. 1996; Endress and Chinea 2001; Chazdon 2003; Crk et al. 2009; Brancalion et al. 2013; Pereira et al. 2013; Chazdon 2014). Accordingly, one may infer that lands in marginal regions are potentially relatively *amenable* to extensive and rapid regeneration if abandoned.

Case studies have not fully described the spatial dynamics of forest regeneration in relation to marginality and facilitating factors such as remnant forest cover. They have generally been confined to smaller contexts, often centered around a single remnant forest block, and overwhelmingly in Puerto Rico or Costa Rica (Thomlinson et al. 1996; Helmer 2000; Endress and Chinea 2001; Helmer et al. 2008; Crk et al. 2009). Their approaches offer only a partial perspective on the spatial dynamics of regeneration given spatial variations in underlying conditions including remnant forest cover. For example, models predicting the probability of forest regrowth at a given point have little bearing on the actual extent of regrowth or of its patches (Helmer 2000; Etter et al. 2005; Helmer et al. 2008; Crk et al. 2009). Similarly, remnant forest extent, distribution, and proximity have often been observed simplistically, e.g., as the area of remnant forest within 100 m of a point (Helmer 2000; Etter et al. 2005; Helmer et al. 2008; Crk et al. 2009; Brancalion et al. 2013; Pereira et al. 2013). The models have also simplified the spatial dynamics of interest. Most have been 'global' and linear (Helmer 2000; Etter et al. 2005; Helmer et al. 2008; Crk et al. 2009; Freitas et al. 2010) and therefore ill-suited for the spatially-variable, non-linear, interactive relationships that unfold *across* a landscape (Foody 2004, 2005). Still others have deemed observed spatial relationships as 'significant' insofar as they depart from random (Endress and Chinea 2001), which is a questionable referent for ecological phenomena (Pontius and Millones 2011). Consequently, expectations that regeneration responds to 'marginality' and facilitative landscape factors have not translated into a clear spatial profile of that response.

In a pastoral region in tropical north Australia this article examines the affinity between secondary forest extent and distribution with indicators of marginality and the proximity and size of remnant forest fragments. The findings highlight the primacy of remnant forest as a driver of regeneration. It concludes with a critical discussion of the debate over the conservation value of primary and secondary forest and the role of marginality in regeneration.

Methods

Study area

The study area comprises the Atherton and Evelyn Tablelands (17°18′ S, 145°29′ E to 17°36′ S, 145°44′ E) in tropical north-eastern Australia, a mid-elevation (600–900 m) plateau spanning 3000 km^2 and bordered by peaks reaching 1370 m. Rainfall is 1800–3000 mm per annum and is marked by a pronounced dry season from July to September during which monthly rainfall is <100 mm. Soil parent material is predominantly basalt but granitic and metamorphic substrates are also common (Willmott and Stephenson 1989). The area hosts tropical rainforest locally classified as complex mesophyll and notophyll vine forests as well as sclerophyll forests in its drier western reaches (Tracey 1987).

Following European settlement in the 1870s rainforests were widely logged and cleared for grazing. A dairy industry was established by the 1920's in most areas (Gilmore 2005) and by the 1960's in the south-east (Frawley 1987). Forest clearing ultimately removed at least 76,000 ha so that primary rainforest now survives largely in contiguous upland tracts and, to a lesser degree, as remnant fragments of <3600 ha (Winter et al. 1987; Laurance and Laurance 1999). The dairy industry began contracting in the early 1970s (Statham 1998; Gilmore 2005) when subsidies were removed, and again from 2000 following industry deregulation. Between 1959 and 2005 the number of dairy farms declined by 91.5 %, from ~600 to 51 (Gilmore 2005). Although some of dairy farms may have transitioned to beef cattle or undergone consolidation overall there has been widespread abandonment of grazing, which has in turn allowed secondary forests to expand.

Spatial data on forest cover and landscape attributes

We derived spatial data on forest type and successional status from 1:25,000 aerial photography of 2002 as interpreted by expert local botanists and geologists (P. Stanton and D. Stanton) and updated via field verifications in 2005. Detailed vegetative typologies including primary and secondary forests (Table S1) were manually delineated on the air photos, which were then digitally geo-registered to a 1:50,000 topographic map (Australian Topographic Survey Map Series R733, registration accuracy ±12 m) and orthorectified. The original line work on the photos was digitally extracted to constitute the GIS dataset analysed here (WTMA 2009). The accuracy of the vegetation attribute typology is estimated at 95 %. In the study region, we observed 2491 secondary forest fragments spanning 11,158 ha (Table 1). Secondary forest is defined as a range of rainforest successional complexes with the occasional presence of sclerophyll species (e.g. *Acacia* spp.) (Table 1). In focusing on the wetter regions of the Tablelands, we exclude areas of drier eucalypt-dominated forests situated to the far west and north-west, although small pockets of sclerophyll communities may be included in our estimates.

Spatial data on key landscape attributes influencing agro-pastoral abandonment and forest regeneration were defined as follows:

- Biophysical potential of the soil for sustained and productive cultivation and grazing was delineated using aerial photography (Malcolm et al. 1999). Initial patterns in soil, landform, vegetation, and lithography were first defined using 1:25,000 photography as per McDonald et al. (1990). Soil profile classes were then developed based on Laffan (1988), and a free survey technique (Reid 1988) entailing 2500 ground sites (approximately 1 site per 60 ha) mapped the soil-potential classes at 1:50,000. Seven ordinal classes were defined (Table 2).
- Terrain slope in degrees was measured using a digital terrain model of 25-m pixel resolution and <25-m horizontal locational error (DNRM 2006).
- Land cover in 1992 was mapped and ground-truthed by one of the authors (SL) using 1:25,000 aerial photography of 1992. The land-cover classes are: Primary Rainforest, *Acacia*-Dominated Forest, Mixed Regrowth Forest, Sclerophyll Communities (rare), Streamside Vegetation, and Lesser Vegetation Communities [Cleared Lands (predominantly), Plantations (few), Swamp Communities (rare)]. Both *Acacia*-Dominated Forest and Mixed Regrowth Forests are secondary forest covers, differentiated from each other by the degree of canopy dominance of *Acacia spp*., which may persist for at least 50 years following early succession (Tracey 1987).

Soil potential and slope are indicators of agro-ecological marginality. Poorer soils (e.g., classes B1, B2, C2, D) and steeper slopes (e.g., >10°) would host significantly greater areas of secondary forests if marginality were a significant factor of secondary forest extent. Land use and the opportunity costs thereof are generally uniform across the region and so do not vary the interpretation of these two variables. Other potential aspects of marginality, such as distance to major roads, distance to population centers, precipitation, and elevation, were not considered because they are relatively uniform or uninfluential to land use across the region. Various measures of primary and secondary patch areas and their extents at varying distances from each other were also estimated, as described below.

Spatial analyses of forest regeneration

We determined the spatial relationships between secondary forest extent, landscape attributes, and primary forest cover using classification and regression tree analyses. These approaches are well suited to uncovering complex, non-linear relationships and their heterogeneity over space (Fig. S1) (Foody

Table 1 Secondary forest types and their respective contribution to total and analysed secondary forest observations

Basic classification	Detailed classification	Contribution to total secondary forest observations				Contribution to secondary forest in the CTA			
		Total Ha.	No. patches	Mean Ha.	SD Ha.	Total Ha.	No. Patches	Mean Ha.	SD Ha.
Rainforest secondary successional complexes	Variable rainforest secondary successional forest complex. Very wet to dry lowlands to highlands on a variety of geologies	9,851.9	2,251	4.4	16.5	7,813.0	447	17.5	34.3
Rainforest secondary successional complexes	Vine-dominated secondary successional communities: *Merremia peltata*, *Entada phaseoloides* + *Cissus spp.*, *Calamus spp.* Moist to very wet foothills mostly on granites and metamorphics	2.5	3	0.8	0.4	0	0	–	–
Rainforest secondary successional complexes	Variable sclerophyll derived secondary successional forest and woodland complex. Very wet to dry lowlands to highlands on a variety of geologies	1,293.8	228	5.7	10.6	1020.7	75	13.6	15.7
Sclerophyll forest and woodland complexes	Variable communities of native vegetation with a significant component of exotic species in the canopy, understorey and/or ground cover. Wet and moist lowlands on a variety of geologies	10.2	9	1.1	1.2	0.6	1	–	–
Total		11,158.7	2491	4.5	16,1	8,834.4	523	16.9	32.3

Source WTMA (2009)

Vegetation typologies are classified at five levels of detail (Table S1). The above show the two most detailed levels

SD standard deviation

2004, 2005; Muñoz and Felicísimo 2004; Berk 2008; Moisen 2008; Loh 2011). Each approach partitioned our region into subsets describing the local extent and distribution of secondary forests on the basis of local attributes and the extent and distribution of primary forests. The approaches are largely free of problematic assumptions concerning the nature of the data since they uncover relationships by recursively 'mining' data rather referencing parametric assumptions, e.g., independence of observations. Correspondingly, we were able to analyse the entirety of our spatial data rather than a small sample thereof and so observe both the area and distribution of secondary forests. The classification and regression tree analyses adopt complementary spatial units of observation (Fig. 1). This helped highlight key dynamics by triangulating insights from each analysis. The following summaries these analyses, and additional details are given in Text S1.

Classification tree analysis by secondary forest fragment

We accounted for secondary-forest patch size as a function of the slope, soil potential, historical land-cover class, and distance to primary forest of each patch using the classification-tree approach (CTA) of Breiman et al. (1984) (see also Biggs et al. 1991). For this analysis each secondary forest patch assumed its predominant soil potential and historical vegetation cover classes and its mean slope and distance-from-primary forest (Fig. 1a). Distance from primary forests was measured at a 30-m pixel resolution.

The response variable, secondary forest patch size, was categorised as 0–5, 5–10, 10–25, 25–50, or >50 ha (Table 3), with size classes reflecting natural breaks in the patch-size distribution. The CTA partitioned the initial pool of secondary forest patches into smaller pools of patches or 'nodes' following 'if–then'

Table 2 Soil agricultural potential classes

Class label	Description
A1	Suitable for cropping or grazing, with negligible limitations due to soil, climate, and topography, requiring basic management practices to sustain production and soil integrity
A2	Suitable for cropping or grazing, with minor limitations due to soil, climate, and topography, which either reduce productivity or require more active management practices than for A1
A4	Suitable for cropping or grazing, with severe limitations due to soil, climate, and topography, making it doubtful whether the inputs/investments required for sustain cropping would outweigh the long-term benefits
B1	Suited for limited cropping or sustained grazing, being marginal or unsuitable for most crops due to severe soil, climatic, or topographical limitations requiring minor engineering and/or agronomic improvements, but allowing grazing with negligible improvements
B2	Suited for limited cropping or sustained grazing, being marginal or unsuitable for most crops due to severe soil, climatic, or topographical limitations, which either reduce productivity or require more active engineering and/or agronomic improvements than for B1, but allowing grazing with only minor improvements
C2	Suitable for grazing only, with minor limitations due to soil, climate, and topography, allowing short-term ground disturbance for pasture establishment with active management practices
D	Marginal and unsuited for agriculture or grazing due to severe soil, climatic, or topographical limitations or local environmental value, e.g., endangered habitat

Source Deparmet of Primary Industries (1993) and Malcolm et al. (1999)

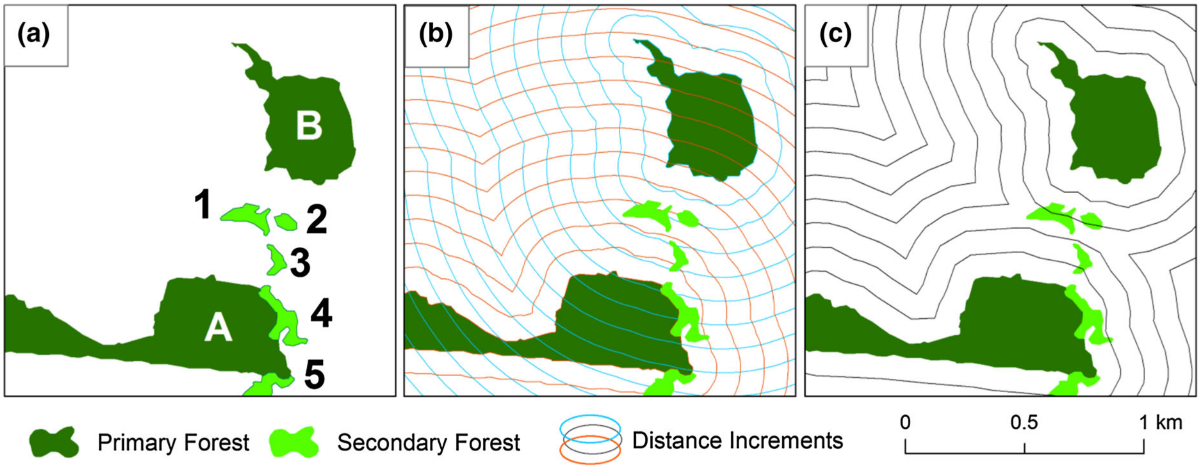

Fig. 1 Complementary approaches to observing and partitioning the landscape: a by Secondary forest patch, b by distance from individual primary forest fragments, and c by distance from primary forest cover. *Note* in a, predictor variables values including distance to the nearest primary forest fragment A or B are summarised for each secondary forest patch 1–5 individually. This is the basis for the CTA. In b, c variable values are summarised for each distance increment, including the proportional areas of all secondary and/or primary forest cover. In b, a 'set' of distance increments extends from each of primary forest fragments A and B, shown in *red* and *blue* respectively, with the increments from fragment A encompassing fragment B and vice versa. This is the basis of the RTA. In c a single set of distance increment extends from fragments A and B combined. These increments are not progressively concentric, but rather define mutually-exclusive distance 'bands'. This is the basis of Eq. 1, Figs. 2, S2

thresholds of a given predictor variable, e.g., if predictor variable $A < x$ then patches go to Node 1, if $A > y$ then patches go to Node 2, if $A = [x,y]$ then patches go to Node 3 (Berk 2008, Chap. 3; Witten and Frank 2005; Biggs et al. 1991). Node partitioning continues recursively, producing a hierarchical tree of

Table 3 Number of secondary forest patches by size in study area

	Patch size class (ha)					Total
	0–5	5–10	10–25	25–50	>50	
Total patches	2138	154	124	38	37	2491
Patches in CTA	170	154	124	38	37	523

nodes (pools of patches) and branches (thresholds producing nodes). Each node hosts fewer patches than the preceding and generally has more homogeneous patch size distribution.

In partitioning a given node *n* into up to five ‘daughter’ nodes the procedure considered an exhaustive series of potential threshold values for each predictor variable, all of which are ‘binned’. For the continuous variables, slope and distance, bins were in 1-degree and 100-m intervals, respectively. The threshold(s) ultimately selected to partition node *n* corresponds to the particular grouping of categorical values of a given predictor variable that ‘fits’ the distribution of secondary forest patch sizes at node *n* most significantly according to its χ^2 score (Text S1). The partitioning of a given node stops when one of three criteria are met: (i) no potential threshold achieves a χ^2 significance of $p < 0.05$, (ii) the node hosts fewer than 50 secondary forest patches, or (iii) a daughter node that would be produced would host fewer than 30 patches.

Most secondary forest patches in the region are very small, with 86 % of the 2491 patches being <5 ha and accounting for only 22 % of the area of secondary forests (11,158 ha) (**Table 3**). This skewness heavily biased preliminary analyses towards smaller patches (cf. Baptista and Rudel 2006; Berk 2008). A CTA on the full dataset of 2491 resulted in a highly complex classification tree largely reflecting the ubiquitousness of patches <5 ha rather than more substantive spatial patterns in secondary forest succession. Therefore, the CTA considered all patches > 5 ha and a random 8 % sample of patches < 5 ha (Table 3). This adjusted dataset of 523 secondary forest patches has a more balanced frequency distribution and still accounts for 80 % of total secondary forest area. The CTA performed on the adjusted dataset clearly focuses on substantive secondary forest distributions. A CTA on the full dataset of 2491 patches (Table S2) is also briefly discussed.

Regression tree analysis by distance from primary forest fragment

We determined how the extent of secondary forest varies as a function of primary forest fragment size at varying distances from primary forest using the regression-tree approach (RTA) (Breiman et al. 1984). Spatial units of analysis are 100-m distance increments extending from each of the 473 primary forest fragments in the region, to a maximum distance of 3 km (Fig. 1b). Since each of the 473 ‘sets’ of increments are particular to a given primary forest fragment it was possible to infer the effect of the size of that fragment on secondary forest extent over varying distances. The units are progressively concentric, meaning that the unit defined by a given distance from a given primary forest fragment is encompassed by the unit of the next greatest distance for the same fragment, and so on. The RTA considered the entirety of forest regrowth (i.e., 11,158 ha) since it is concerned with aggregate secondary forest area rather than secondary forest patch size frequency. Of 14,190 total units, we considered those 9871 that contained secondary forest. We developed the tree using a random 75 % sample of these units and validated it with the remaining 25 % ‘hold-out’ sample.

The response variable, secondary forest extent as a proportion of a unit’s area, was regressed on the distance from the primary forest fragment, the size of that primary forest fragment, and the area of all other primary forest exclusive of the primary forest fragment in question as a proportion of a unit’s area (Fig. 1b). The latter variable accounts for the potentially confounding tendency for primary fragments to cluster spatially. The RTA partitions the initial pool of units into a hierarchical tree of increasingly smaller and more homogenous daughter nodes on the basis of local relationships between the response and predictor variables. A given node *n* is partitioned into two daughter nodes at the threshold value of the predictor variable that minimises the sum of squared errors (SSE) in the two daughter nodes (Text S1). As with the CTA, all values of all predictor variables are candidates for partitioning, and daughter nodes are mutually exclusive.

Nodes were partitioned wherever doing so reduced the SSE of node *n* by >0.0001 (Text S1; Eq. 1), a small so-called ‘improvement value’ meant to over grow the

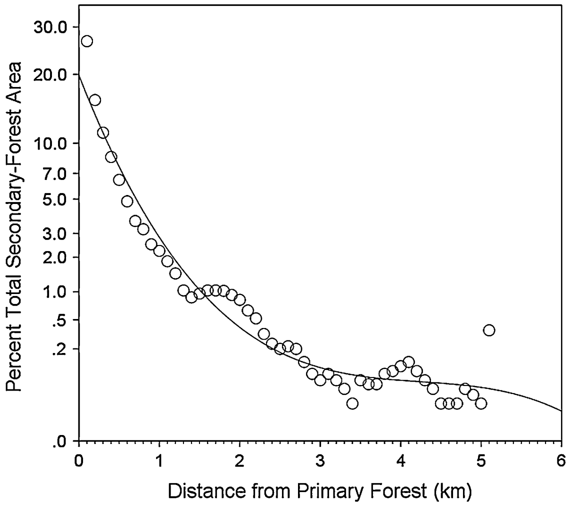

Fig. 2 Percent total secondary forest area by distance from primary forest. *Note* graphed data pertain to all 2491 secondary forest patches. Distance from primary forest is measured at 100-m intervals as per Fig. 1c. *Y axis* labels reflect actual data values, but the axis' gradations reflect a power function of 0.3 as per Eq. 1. The curve-of-best fit is defined by Eq. 1. The final distance interval actually spans 5.1–10.5 km from primary forest, containing only 0.37 % of total secondary forest area. Whereas 10.5 km is the maximum possible distance from a primary forest within the study site the greatest observed distance from primary forest for any secondary forest patch is 6.15 km

initial tree. Partitioning ceased where this criterion could not be met, a node had <200 units, or its partitioning would have yielded a daughter node with <100 units. The initial tree was then 'pruned' by collapsing partitions in inverse order of their improvement values to form the smallest possible sub-tree with an overall residual SSE within one standard unit of that of the initial tree, following Breiman et al. (1984) (see also Wu et al. 2008: 32). The importance of a given predictor variable was defined as the sum of all improvement values for partitions directly attributable to the variable and for which the variable qualified as a surrogate variable (Text S1).

Successional forest plots by distance to primary forest

We also examined the relationship between proximity to primary forest and the temporal lag in forest succession via a historical air-photo analysis of 66 successional forest plots ranging between 9 and 72 years since abandonment. Some 31 of these plots are long-term research plots clustered around Tarzali and Millaa Millaa townships and representative of the southern Atherton Tablelands. A further 35 plots were randomly selected from a pool of 90 secondary forest sites dispersed around these townships. All plots are ~500 m^2.

For each plot, the years elapsed since the abandonment of grazing and the commencement of forest succession were estimated by inspecting 1:25,000 aerial photography for 1943, 1951, 1952, 1961, 1964, 1977, 1978, 1983, 1986, 1992, 1994, 1997, 2000, 2003, 2004, 2008 and 2011. High-resolution satellite imagery for 2002-2012 was also consulted using Google Earth. The year of abandonment is defined as the mid-point between successive photos in which pasture was succeeded by another vegetation type, e.g. shrubs. The year at which forest succession commenced is defined as the mid-point between successive photos in which forest >5 m in height was visually estimated as having canopy closure of ≥70 % in the more recent photo, as per McDonald et al. (1990). Forest height was determined via parallax analysis using stereoscopic photo pairs for 1943, 1952, 1978, 1992, 1997, and 2000, and by visual analysis of forest texture, shadow, and scale for other years as informed by the photo-pair analysis. Field data for 42 of our plots indicate that our estimates of forest height are within 10 % of actual average forest height.

Linear distances were measured from each plot to the nearest primary forest (continuous forest and remnant forest fragments). Primary forests were observed in the aerial photography for all years of the time series, and were verified as primary forest using the ground-truthed GIS dataset (WTMA 2009). All of the nearest fragments and most of the nearest continuous forest tracts had been selectively logged in the past.

Results

Regrowth and proximity to primary forest

Secondary forests displayed a marked spatial affinity with primary rainforest. Upon defining 100-m distance intervals from all primary forest as simple distance bands (Fig. 1c) a relationship between distance from primary rainforest and the percentage of the total secondary forest area (11,158 ha) within a given interval fits an exponentially decreasing curve with an exceptionally high predictive accuracy (r^2) of 95 % to a maximum distance of ~6.5 km, this being the greatest distance observed between primary and secondary forest (Fig. 2). At any given distance interval D_i, the percentage of total secondary forest area in the region is predicted by the following function:

$$\%\ \text{Total secondary forest}^{0.3} = 2.45 - 1.376 * D_i + 0.315 * D_i^2 - 0.025 * D_i^3 \qquad (1)$$

Thus across the region 68 % of the total secondary-forest area occurs within 500 m of primary forests, 85 % within 1 km, and 91 % within 1.5 km. A similar cubic relationship of a comparable accuracy was observed between distance from primary forest and the percentage area of each distance interval occupied by secondary forest (Fig. S2).

The CTA affirms the primacy of proximity to remnant forest as a driver of forest regrowth. Secondary forest patches >50 ha are distinguished from others by their coincidence with primary forest, acacia-dominated patches, or (rarely) sclerophyll communities in 1992 and their immediate proximity (125–395 m) to primary forest (Fig. 3, Nodes 6 and 7). These thresholds correctly identify 84 % of the 37 patches >50 ha, although they also inevitably capture many adjacent mid-sized and smaller 'satellite' patches. A CTA performed on the full dataset of 2491 patches (Table S2) suggests that these classification rules may actually be simplified while increasing classification accuracy for patches >50 ha. The

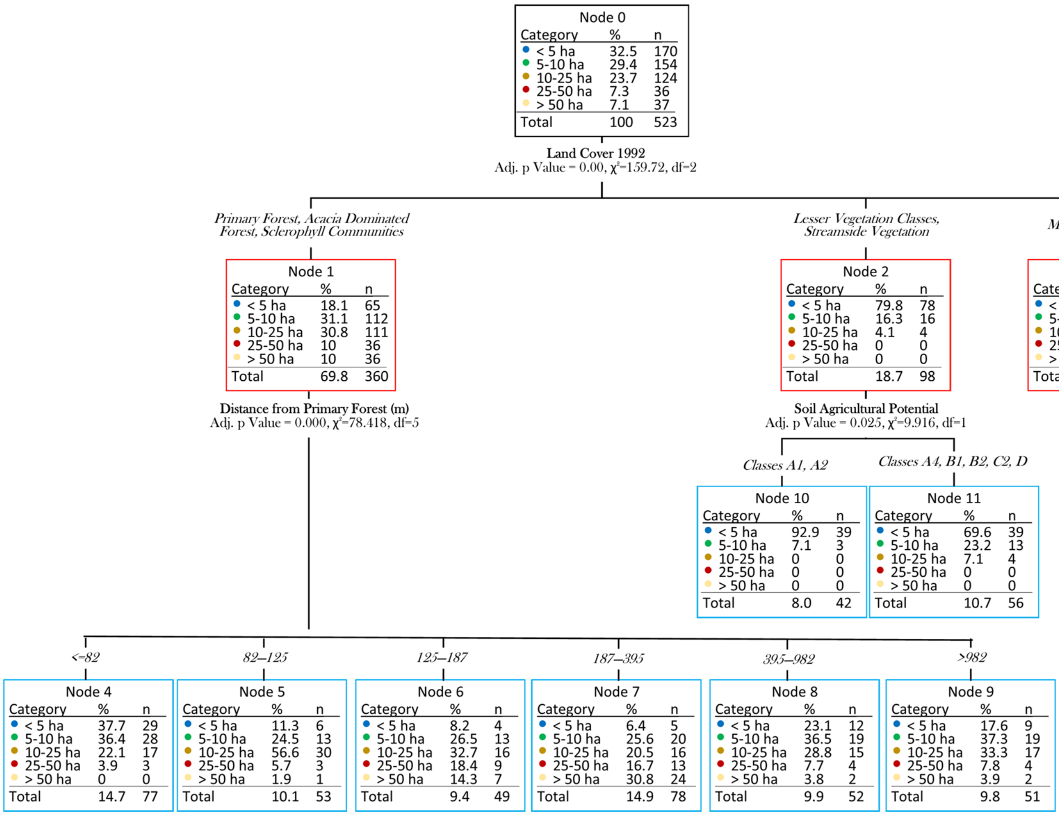

Fig. 3 Classification tree: secondary forest patch size as a function of the historical land cover, proximity to primary forests, soil potential, and slope of individual secondary Forest patches. *Notes* n = 523 secondary forest patches. Classification accuracies according to the terminal nodes and with respect to the total number of patches of a given size class are as follows: <5 ha, 79 %; 5–10 ha, 25 %; 10–25 ha, 37 %; 25–50 ha, 0 %; >50 ha, 65 %; Overall classification accuracy with respect to total number of patches: 46 %; Overall classification accuracy with respect to total secondary forest area, 49 %. Terrain slope did not define any partitions in the classification tree

Table 4 Mean distances from primary forest for nodes defining smaller secondary forest patches in CTA

Node	Predominant class size of node (ha)	Mean distance from primary forest (m)	Standard deviation of distance from primary forest (m)
3	<5	803	525
2	<5	1178	1084
10	<5	1025	659
11	<5	1292	1304
9	5–10	1537	224

Nodes and the number of patches in each are as defined in Fig. 3

Table 5 Classification tree accuracy when slope or soil agricultural potential are forced to define first partition

Variable defining first CTA partition	% Total secondary forest area correctly classified according to target class of terminal nodes	% Secondary forest patches >50 ha correctly classified according to target class of terminal nodes
Slope	17	0
Soil agricultural potential	17	0
Distance from primary forest	47	65

Note: n = 523 secondary forest patches

presence of primary forest in 1992 and a distance-from-contemporary-primary-forest of 68–397 m alone capture 86 % of patches >50 ha, as well as 63 and 55 % of patches 25–50 and 10–25 ha, respectively (Table S2, Nodes 19 and 20).

In contrast, patches <10 ha and particularly <5 ha are more widely and unevenly dispersed. While most commonly occurring closer to primary forests they are the dominant size class at greater distances. For example, Nodes 2 and 3 of the CTA collectively capture 62 % of patches <5 ha and 45 % of patches <10 ha and have respective average distance-from-primary-forest measures of 0.8 and 1.2 km (Fig. 3). While the CTA does not explicitly define these nodes with reference to distance from primary forest, it is evident that their average distance is orders of magnitude greater than that of nodes describing patches >10 ha, for which distance thresholds are explicit, e.g., Nodes 5–7 at 82–395 m (Table 4; Fig. 3). The leading edge of secondary forest expansion is apparently represented by Node 3, the patches of which are coincident with secondary forests in 1992 (Mixed Regrowth), relatively distant from primary forest, and relatively heterogeneous with respect to size class. In contrast, areas of arrested succession are identified by Node 2, the patches of which are almost entirely <5 ha and situated on long-exploited lands with limited scope for further regeneration, e.g., in gullies and river banks.

Neither slope nor agricultural potential are clearly related to the distribution of secondary forests patch sizes across our regional landscape according to the CTA. The CTA did not call upon slope to partition nodes and it called upon agricultural potential only once, and only then to make a subtle distinction between two comparable nodes concerning very small patches (no.. 10 and 11). Correspondingly, much lower classification accuracies were attained in two CTAs for which slope and agricultural potential were forced to define the first partition (Figs. S5, S6). This was true with respect to both the total area of secondary forest and the number of secondary forest patches >50 ha (Table 5).

These results seemingly contrast those from 'global' analyses comparing slope and agricultural potential values between secondary forests and cleared lands at broader scales. However, equivalent findings could also be drawn from our data. Upon randomly sampling ~ 10,000 points within secondary forests and cleared lands and then comparing their respective frequency distributions for slope and agricultural potential (Fig. 4), slope was found to be significantly greater under secondary forests than under cleared lands ($p < 0.001$, random-effects ANOVA with 1000 bootstrapped iterations; $p < 0.01$, Kruskal–Wallis test; $n = 19{,}984$), and agricultural potential was likewise found to be significantly less under secondary forests than under cleared lands ($p < 0.001$, Kruskal–

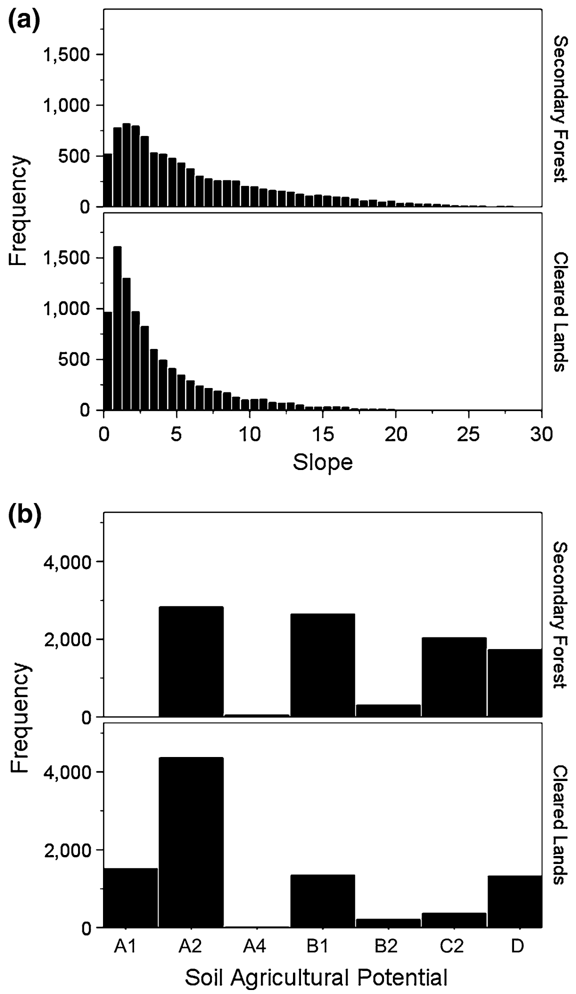

Fig. 4 Frequency distributions for **a** slope, in degrees and **b** agricultural potential classes, within secondary forest and cleared lands. *Notes* frequency distributions defined by two random samples of n = ~10,000 points in secondary forests and in cleared lands. Refer to Table 2 for descriptions of soil agricultural potential classes

Wallis test). Equivalent comparative analyses of the distribution of slope and agricultural potential between primary and secondary forests similarly observes significantly greater slope and lesser agricultural potential under primary forests than secondary forests ($p < 0.01$, n = 14,646).

These comparative, broad-scale observations confirm the supposed positive effect of marginality on the presence of secondary and primary forests. Yet when considered in conjunction with the CTA they also suggest that the role of marginality is over-stated with respect to the extensiveness of forest succession. We reconcile these observations with the CTA by recognising that the CTA concerns the *area* of secondary forest whereas the point data concern only the *incidence* of secondary forest; that the statistically-significant effects observed for the point data indicate merely statistically *non-nil* relationships, which may have little aerial importance; that these apparent effects are detectable only at coarser, all-of-landscape scales at which 'significant' effects are likely due to scale effects (Wrigley et al. 1996) and at which the distribution of secondary forests become a proxy for the presence of nearby, relatively marginally-situated primary forests; and that at finer scales of observation more commensurate with patterns of forest regrowth the actual magnitude and consistency of the supposed effects do not readily reflect patterns of regrowth. Indeed, given the comparability of secondary forests and cleared lands on measures of slope and agricultural potential (Fig. 4), it is debatable whether most lands hosting secondary forests are truly 'marginal', except relative to cleared lands. Therefore while regrowth may apparently favour areas with relatively greater slopes and poorer agricultural potential at broad regional scales, it is principally the extent and distribution of primary forests in such contexts, and not 'marginality', that determine the extent and distribution of secondary forests.

Regrowth and primary forest fragment size

The regression tree analysis (RTA) confirms the effect of distance from primary forest on secondary forest extent and also observes an interactive effect between the distance from a given primary forest fragment and the size of that fragment. In general, for any given spatial unit of analysis (Fig. 1b), the proportional area of secondary forest decreased with distance from the corresponding primary forest fragment, as above, and the rate of decrease was significantly less when the size of the corresponding primary forest fragment was larger. In other words, at a given distance from a given primary forest fragment, the proportional area of secondary forest was greater where the corresponding primary forest fragment was larger.

The regression tree summarises these relationships (Fig. 5). At distances <250 m, primary forest fragment size has no observable effect on the proportional area of secondary forest. Between 250 and 650 m,

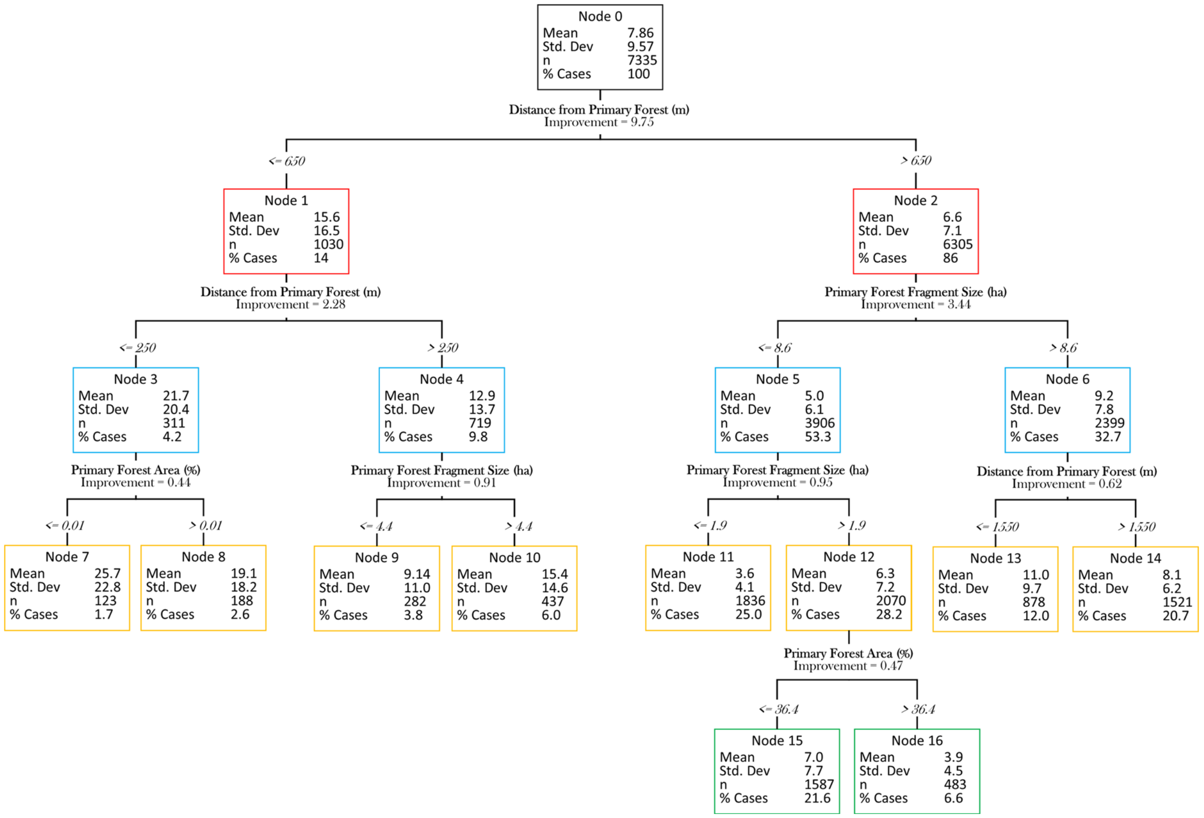

Fig. 5 Regression tree: proportional area of secondary forest as a function of proximity to nearest primary forest fragment, size of nearest primary forest fragment, and proportional area of primary forest. *Note* $r^2 = 21$ %, $n = 7335$. For the hold-out sample: $r^2 = 21$ %, $n = 2536$. Proportional areas of primary and secondary are with respect to the spatial units of observation of Fig. 1b

primary fragments >4.4 ha have nearly double the proportional area of secondary forest than fragments <4.4 ha, at 15 % versus 9 %, respectively (Nodes 9 and 10). Beyond 650 m, greater primary forest fragment sizes are needed to have the same 'doubling' effect. For instance, fragments >8.5 ha correspond to 9 % secondary forest cover, compared to 5 % for fragments <8.5 ha (Nodes 5 and 6). The 650 m distance threshold appears critical, as nodes beneath this threshold almost unanimously host greater proportional areas of secondary forest than those above it, regardless of primary forest fragment size. Interactions between distance and primary forest fragment size are not observed beyond 1550 m, nor interestingly are they defined for primary forest fragments >8.5 ha despite there being 145 such fragments with occasionally much larger areas (Table 3). Interactions were apparent despite the inclusion of the variable defining the proportional area of primary forest within a given unit of analysis, and indeed interactions remained largely unchanged when this variable was forced to define the first partition in an alternative RTA (Fig. S5), indicating the importance of the interactions to the overall distribution of secondary forests.

The RTA explained 21 % of the variance in the proportional area of secondary forest cover for the 7335 units of analysis—an appreciable amount, considering the focus on regrowth area within small spatial units spanning a variable and sizeable landscape. The distance measure again is most important, explaining 13.0 % of variance in the data. Primary forest fragment size was just less than half as important (5.4 %), and the proportional area of primary forest one-third as important (3.9 %). However, the importance of the proportional area of primary forest variable falls to ~0.9 % while remaining stable for the other variables if variable importance is estimated only with respect to partitions directly attributable to a variable, thus ignoring partitions for which a variable is the ‘next-best’ surrogate. The regression tree validated well when applied to the ‘hold-out’ sample. There was no reduction to its explanatory power and discrepancies between the expected and observed proportional areas of secondary forest were <1 % for all 16 nodes (Fig. S6).

Temporal lags in succession by distance to primary forest

Our successional-forest plot data underscore the enhancement of forest regrowth by extant primary forest cover. We observed an increase in the temporal lag between land abandonment and 70 % successional canopy closure with increasing distance between a plot and primary forest (Fig. 6). In general, for plots 2500 m from primary forest the lag is ∼8 years more than for plots 100 m distant, with respective mean lag periods of ∼19 and ∼11 years (Fig. 6). The effect of distance on lag is significant despite appreciable variation in the plot-level data ($p < 0.05$, OLS bootstrap regression with 3000 iterations).

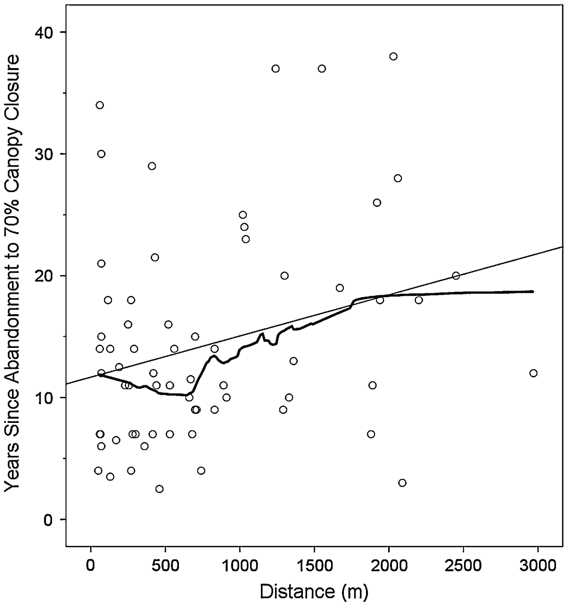

Fig. 6 Temporal lag between land abandonment and successional canopy closure, by minimum distance to primary forest. *Notes* distance measures reflect the minimum distance to remnant or continuous primary forest cover. Measures of years elapsed between abandonment and canopy closure are approximate only. The line-of-best fit is defined by linear regression, while the curve of best fit is defined by iteratively-weighted lest-squares Epanechnikov loess function robust to outliers (Jacoby 2000)

The increase in the temporal lag between abandonment and succession with greater distance from primary forest does not alone explain the markedly uneven spatial distribution of forest regeneration described above. Considering that succession has been ongoing for up to 40 years and that almost all secondary forest patches are <1.5 km from primary forest (Fig. 2) and thus near enough that differences in their respective lag periods would be <5 years on average (Fig. 2), it is reasonable to assume that any effects of differential lags on the current distribution of secondary forest are now very modest. Given the preceding, it is plausible that the uneven distribution of interest is mostly attributable to greater recruitment and accelerated rates of patch expansion nearer to primary forest generally and larger primary forest fragments particularly.

Discussion

The extent and rate of secondary forest regeneration in our region was associated principally with interactions between proximity to primary rainforest and the area of primary forest fragments. Some 70 % of secondary forest occurred within 500 m of primary forest, and 85 % occurred within 1 km, in keeping with small-scale observations from other tropical regions (Thomlinson et al. 1996; Endress and Chinea 2001; Timms et al. 2012). The distribution of secondary forest relative to primary forest was so regular that a cubic exponential relationship fit it with a predictive accuracy of 95 %. Proximity to primary forest of <650 m and primary forest fragment area of >8.5 ha appear to constitute thresholds for relatively extensive regeneration, although we stress that the phenomenon exists along an uneven continuum. In contrast, agro-ecological marginality as measured by soil agricultural potential and slope had no particular association with the extent and distribution of secondary forests across the region. Whereas forest plot-level studies have suggested that regeneration in abandoned pastoral regions may be delayed due to the paucity of seeds in soils and the isolation of forest seed banks (Uhl et al. 1988; Holl 1999; Chazdon 2003, 2014), our regional observations more pointedly indicate that, where remnant forests are scarce, widespread abandonment may yield only limited secondary forests even 40 years after abandonment.

The role of marginality in regeneration

Our finding that marginality was not a significant determinant of regrowth extent or distribution appears contrary to expectations (Thomlinson et al. 1996; Helmer 2000; Crk et al. 2009; Rudel 2005, 2012). We believe that this finding qualifies, rather than refutes, this expectation. Case studies of the incidence of regeneration at sample points along a spectrum of marginality proxies (Helmer 2000; Etter et al. 2005; Helmer et al. 2008; Crk et al. 2009) have only partially accounted for secondary forest extent and distribution as well as landscape factors like remnant forest cover and favourable landscape matrices. Indeed they have occasionally specified models accounting for the incidence of secondary forests using variables flagging the very contexts most likely to retain extensive remnant forests, e.g., high elevations, high precipitation rates, and widespread coffee cultivation of central Puerto Rico (Rudel et al. 2000). In our study, marginality discriminated secondary forests from cleared lands only once observations were aggregated to a general regional scale and simplified to reflect the incidence, rather than the area, of secondary forest, and then only subtly, suggesting that the explanatory power of 'marginality' is conflated with landscape factors. Large-scale surveys of tropical forest change inferring a phenomelogical relationship between regeneration and the marginality of broad upland or otherwise peripheral contexts (Arroyo-Mora et al. 2005; Asner et al. 2009; Redo et al. 2012; Aide et al. 2013) are not invalidated as such. Observations by Arroyo-Mora et al. (2005) and others of secondary forests favouring poorer soils over large pastoral regions are unambiguous, albeit broad. Accordingly their validity arguably holds largely only at their broad scale of observation (Wrigley et al. 1996).

We reconcile our study with the literature by noting that ours is, to our knowledge, the first to specify non-linear, spatially-explicit models of the extent and distribution of regeneration as well as the first to relate these traits to marginality and landscape factors as continuous variables over large scales. The relationships we observe are arguably most applicable in pastoral landscapes. In predominantly agricultural landscapes or, more specifically, mechanised agricultural landscapes, slope and soil quality probably influence land abandonment and regeneration more directly.

Dynamic biodiversity in larger fragments extends regeneration

The relative extensiveness of secondary forest cover around larger primary forest fragments even after accounting for proximity may signal local effects of biodiversity on recruitment. Smaller forest fragments tend to assume simpler floral and faunal communities, lose critical elements of their biodiversity such as larger mammals, birds, and trees, and do so at a faster rate and to a greater degree than larger fragments (MacArthur and Wilson 1967; Laurance et al. 1997; Laurance et al. 2000; Laurance et al. 2002; Broadbent et al. 2008; Laurance et al. 2006; Gibson et al. 2013). The loss of larger trees from smaller fragments in particular has been observed to negatively affect the presence of larger fauna important for seed dispersal and abundance (Laurance et al. 2000; Benitez-Malvido pers comm.). The corollary is that larger primary fragments may retain a greater capacity to effect tree recruitment over a greater area insofar as they retain functionally influential fauna and flora.

Plot-level studies offer limited support for this argument in observing greater species richness, basal area, and tree abundance in secondary forests surrounded by greater extents of remnant forest (Pereira et al. 2013; Kauano et al. 2013; Chazdon 2014; Yeo and Fensham 2014). The present study goes further by indicating that larger primary forest fragments and proximity thereto also promote greater secondary forest patch area, faster commencement of post-abandonment forest succession, and more extensive secondary forests generally, and that these effects remain detectable up to 1.5 km from primary forest fragments.

Further research is required to elaborate these observations. For instance, whereas primary forest fragments <50 ha are particularly vulnerable to biodiversity degradation (Laurance et al. 2002; Gibson et al. 2013), we still observed regeneration to respond positively e to primary forest fragments >8.5 ha when >650 m distant or indeed >4.4 ha when <650 m distant (Turner and Corlett 1996). Also, while our analysis encompassed many primary forest fragments with considerably greater areas than these thresholds, we observed no other, higher thresholds of primary-fragment area above which secondary forest extent was relatively extensive. Further, while proximate, extensive primary forests are known to promote successional forest species richness (Goosem et al. In Review; Kauano et al. 2013; Yeo and Fensham 2014) and, according to this study, successional forests extensiveness, we stress that any relationship between secondary forest species richness and extensiveness following from nearby primary forests is uncertain and beyond the scope of this study. Further studies should also give attention to fragment connectivity as a means of enhancing this proximity effect amongst smaller primary forest fragments; to variations in this effect amongst a larger sample of fragments >50 ha, given that we somewhat perversely observed effects principally amongst smaller fragments; and to the ecological mechanisms of the effects of primary fragment area and proximity on forest regrowth over space, as we have not directly assessed them here.

Primary versus secondary forest conservation value, revisited

The conservation value of secondary forests has been debated recently given the apparent trends in secondary forest expansion in many tropical regions. On the one hand are arguments that secondary forests tend not to contain endemic, rare, specialised, or 'old-growth' forest species found in comparable primary forests (Barlow et al. 2007; Gardner et al. 2007; Laurance 2007; Chazdon et al. 2009b; Dent and Wright 2009; Gibson et al. 2011). These arguments characterise secondary forests as "no substitute for primary forests"(Gibson et al. 2011) and draw a clear dichotomy between these forest types. On the other hand are arguments that, given enough time and amenable conditions, secondary forest species richness, abundance, and composition may closely approximate those in mature primary forests, including endemics to some degree (Chazdon et al. 2009b; Chai and Tanner 2011; McNamara et al. 2012; Chazdon 2014), and that bias in comparative assessments of primary and secondary forests have discounted the biodiversity of regrowth (Gardner et al. 2009; Chazdon 2014, pp. 229, 311–312).

Two challenges within this debate are relevant to this study. First, the 'baseline' secondary and primary forests compared to one another "tend to occupy different ecological zones, elevations, soil types, slope conditions, and levels of human access" (Chazdon 2014, p. 311), affecting impressions of their respective biodiversity. Second, the ecological quality of regenerating forests depends on the nature of the landscape matrix as much as on forest age or patch size, and as we have noted such landscape factors have not received due attention. Recalling that numerous cases studies observe a marked spatial affinity between secondary forest and remnant primary forest (Thomlinson et al. 1996; Helmer 2000; Endress and Chinea 2001; Etter et al. 2005; Helmer et al. 2008; Crk et al. 2009), if we may generalise our observations that the majority of regeneration in pastoral regions occurs in larger patches in proximity to larger primary forest fragments, then this supposed dichotomy between primary and secondary forests appears less salient than the debate would suggest. At regional scales, much secondary forest may effectively be an extension of remnant primary forest, with primary forest being vital to its extensiveness and rapidity of establishment. Correspondingly, and perversely, extensive secondary forest surrounding extensive primary forests may buffer old-growth species (Chazdon et al. 2009b) but afford less conservation benefit than in more deforested landscapes wherein less extensive regrowth bridges gaps between smaller and fewer remnant forest fragments (Harvey et al. 2008; Chazdon et al. 2009a; van Breugel et al. 2013). Our observations of increasing secondary forest area in relation to primary forest proximity and extent are suggestive of positive effects on species richness, but as we did not survey species richness the above remains speculative. The actual degree of biodiversity recovery and conservation across landscapes with different spatial configurations of secondary and primary forests requires urgent study.

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