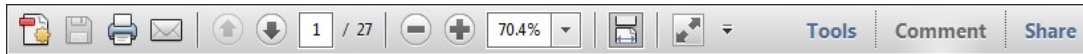
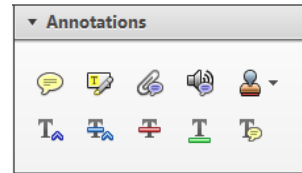


Once you have Acrobat Reader open on your computer, click on the [Comment](#) tab at the right of the toolbar:



This will open up a panel down the right side of the document. The majority of tools you will use for annotating your proof will be in the [Annotations](#) section, pictured opposite. We've picked out some of these tools below:



1. Replace (Ins) Tool – for replacing text.

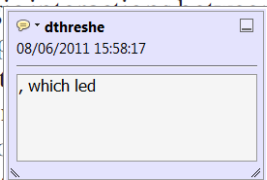


Strikes a line through text and opens up a text box where replacement text can be entered.

How to use it

- Highlight a word or sentence.
- Click on the [Replace \(Ins\)](#) icon in the Annotations section.
- Type the replacement text into the blue box that appears.

standard framework for the analysis of microeconomic behavior. Nevertheless, it also led to the development of a new paradigm of strategic behavior. The number of competitors in the industry is that the structure of the industry is a main component of the competitive level, are explained by the important works on entry by Cournot (henceforth) we open the 'black b



2. Strikethrough (Del) Tool – for deleting text.



Strikes a red line through text that is to be deleted.

How to use it

- Highlight a word or sentence.
- Click on the [Strikethrough \(Del\)](#) icon in the Annotations section.

there is no room for extra profits as mark-ups are zero and the number of firms (net) values are not determined by Blanchard ~~and Kiyotaki~~ (1987), perfect competition in general equilibrium of aggregate demand and supply in the classical framework assuming monopoly. An exogenous number of firms

3. Add note to text Tool – for highlighting a section to be changed to bold or italic.



Highlights text in yellow and opens up a text box where comments can be entered.

How to use it

- Highlight the relevant section of text.
- Click on the [Add note to text](#) icon in the Annotations section.
- Type instruction on what should be changed regarding the text into the yellow box that appears.

dynamic responses of mark-ups consistent with the VAR evidence

sation by Markov and Bellotti and on the number of competitors to a standard also with the demand-



4. Add sticky note Tool – for making notes at specific points in the text.



Marks a point in the proof where a comment needs to be highlighted.

How to use it

- Click on the [Add sticky note](#) icon in the Annotations section.
- Click at the point in the proof where the comment should be inserted.
- Type the comment into the yellow box that appears.

and supply shocks. Most of the literature on the number of firms in the industry is that the structure of the sector



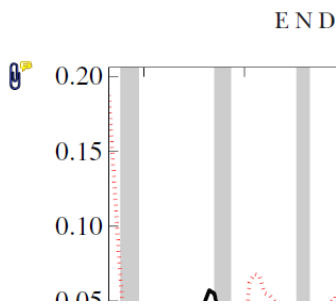
5. Attach File Tool – for inserting large amounts of text or replacement figures.



Inserts an icon linking to the attached file in the appropriate place in the text.

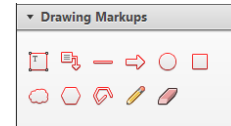
How to use it

- Click on the **Attach File** icon in the Annotations section.
- Click on the proof to where you'd like the attached file to be linked.
- Select the file to be attached from your computer or network.
- Select the colour and type of icon that will appear in the proof. Click OK.



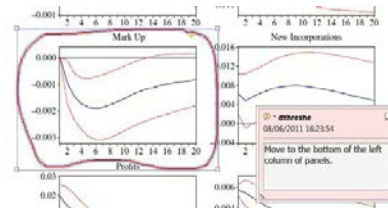
6. Drawing Markups Tools – for drawing shapes, lines and freeform annotations on proofs and commenting on these marks.

Allows shapes, lines and freeform annotations to be drawn on proofs and for comment to be made on these marks.



How to use it

- Click on one of the shapes in the Drawing Markups section.
- Click on the proof at the relevant point and draw the selected shape with the cursor.
- To add a comment to the drawn shape, move the cursor over the shape until an arrowhead appears.
- Double click on the shape and type any text in the red box that appears.



Roles of non-native species in large-scale regeneration of moist tropical forests on anthropogenic grassland

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ABSTRACT

This paper presents a new synthesis of the role of native and non-native species in diverse pathways and processes that influence forest regeneration on anthropogenic grassland in the moist tropics. Because of altered species composition, abiotic conditions and landscape habitat mosaics, together with human interventions, these successional pathways differ from those seen in pre-clearing forests. However, representation of different functional life forms of plant (tree, vine, grass, herb and fern) and animal (frugivorous seed disperser, granivorous seed predator, seedling herbivore and carnivore) shows consistent global variation among areas of pasture, intact forest, and post-grassland regrowth. Biotic webs of interaction involve complex indirect influences and feedbacks, which can account for wide observed variation in regeneration trajectories over time. Important processes include: limitation of tree establishment by dense grasses; recruitment and growth of pioneer pasture trees (shading grasses and facilitating bird-assisted seed dispersal); and smothering of trees by vines. In these interactions, species' functional roles are more important than their biogeographic origins. Case studies in eastern Australia show native rain forest plant species diversity in all life forms increasing over time when pioneer trees are non-native (e.g., *Cinnamomum camphora*, *Solanum mauritianum*), concurrent with decreased grass and fern cover and increased abundance of trees and vine tangles. The global literature shows both native and non-native species facilitating and inhibiting regeneration. However conservation goals are often targeted at removing non-native species. Achieving large-scale tropical forest restoration will require increased recognition of their multiple roles, and compromises about allocating resources to their removal.

Key words: alien; dispersal; functional group; rain forest; restoration; secondary forest; succession; trophic interaction.

ONE OF THE MOST VALUED PROPERTIES OF MOIST TROPICAL FORESTS is their high and globally significant but threatened indigenous diversity, yet its further decline is inevitable unless a substantially greater regional-scale cover of moist tropical forest habitat, capable of supporting diverse native biota, can be rapidly restored (Chazdon *et al.* 2009, Laurance *et al.* 2012). Tropical reforestation is also important to maintain climatic suitability for species, ecosystems and human livelihoods (Locatelli *et al.* 2015). Areas of disused anthropogenic grassland provide significant opportunities for forest restoration, especially since a main product of tropical deforestation has been livestock pasture (Asner *et al.* 2004). Grasslands can also develop on abandoned crop plantations (Gunaratne *et al.* 2010, Cesar *et al.* 2014), and when areas of small-scale cultivation on formerly forested land undergo reduced fallow periods, frequent burning and more intensive use (Albers & Goldbach 2000, Chazdon 2014).


Ecological succession provides an important framework for forest restoration (Walker *et al.* 2007, Elliott *et al.* 2013). However, previously documented successional trajectories and endpoints are likely to have limited reliability as ecological analogs to inform restoration in the 21st century, given the prevalence

of unprecedented combinations of ambient environmental conditions and ecological relationships (Hobbs *et al.* 2009). Massive changes in fundamental abiotic conditions of post-pastoral landscapes include altered regimes of temperature, rainfall, soil texture (e.g., increased compaction), soil chemistry (such as depletion of some elements or enrichment with others), and soil moisture (Myers & Robbins 1991, Ganade 2007, Holl 2007, Paul *et al.* 2010, Nesper *et al.* 2015). Biotic changes are even greater, and include local replacement of the original diverse forest biota with grassland species, as well as the frequent loss of nearby dispersal sources for potential regeneration, that in partially cleared landscapes are provided by areas of remnant native vegetation (Guariguata & Ostertag 2001, Holl 2007, Chazdon 2014, Chazdon & Guariguata 2016). Functionally important larger bodied native vertebrate species are often lost from both the modified and remnant habitats (Wright *et al.* 2007). Biotic additions include non-native pasture grasses and legumes (Teitzel 1992, Asner *et al.* 2004, Knoke *et al.* 2014), grazing livestock, and unassisted invasions by a wide range of species from other geographic regions (Low 1997, Mack *et al.* 2000, D'Antonio & Meyerson 2002).

Some non-native invasive species have undesirable and costly environmental impacts, and consequently a frequent goal of ecological restoration efforts worldwide has been to eradicate

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1 non-native species, aiming to recover purely indigenous species
 2 and ecosystems, also at considerable cost (D'Antonio & Meyer-
 3 son 2002, Simberloff *et al.* 2013). However, it is sometimes possi-
 4 ble for both abiotic ecosystem services and habitat for native
 5 species to be provided by novel or hybrid ecosystems in which
 6 non-native species are mixed with native species, or by human-
 7 constructed ecosystems in which non-natives are dominant (Ewel
 8 & Putz 2004, Lamb *et al.* 2005, Paul *et al.* 2010, Schlaepfer *et al.*
 9 2011). Understanding the extent to which non-native species may
 10 play negative, neutral, or positive roles in contemporary human-
 11 influenced ecosystems is an unresolved and contentious issue
 12 (D'Antonio & Meyerson 2002, Ewel & Putz 2004, Hobbs *et al.*
 13 2009, Simberloff *et al.* 2013).

14 This paper develops a new synthesis of functionally impor-
 15 tant biotic interactions that influence early stages of self-organized
 16 regeneration on anthropogenic grassland in the moist tropics, as
 17 a basis for re-examining the roles of native and non-native spe-
 18 cies (henceforth also 'NAT' and 'NN', respectively) in accelerat-
 19 ing or retarding forest redevelopment during the first five
 20 decades. The desired trajectory is toward establishing a forest-like
 21 structure, associated with increasing similarity to mature indige-
 22 nous forest, in species' diversity, composition, and functional
 23 roles. The focus is on tropical or subtropical regions that once
 24 supported extensive moist forest (rain forest) vegetation, which
 25 then experienced decades or more of extensive deforestation and
 26 conversion into agricultural (especially livestock) production, fol-
 27 lowed by retirement of some areas from intensive land use. Such
 28 areas are widespread globally, and have often become dominated
 29 by NN species (Florentine & Westbrooke 2004, Cesar *et al.* 2014,
 30 Chazdon 2014). I argue that species' functional roles are more
 31 important to regeneration trajectories than their biogeographic
 32 origins.

33 First, without regard to species' origins, I use a wide variety
 34 of published information to consider how land conversions
 35 between intact forest, pasture and regrowth influence functionally
 36 important biotic life forms, and how their complex webs of inter-
 37 action respond to external and starting conditions to either facili-
 38 tate or inhibit forest regrowth. Case study examples from eastern
 39 Australia are then used to illustrate some details of these pro-
 40 cesses, and in particular how invasive NN trees can potentially
 41 facilitate post-pastoral regeneration of rain forest diversity. The
 42 global literature is then used to more generally explore and dis-
 43 cuss the independence of NAT or NN status of certain plant
 44 genera with their positive or negative ecological roles, during
 45 post-grassland regeneration across continents. The ecological
 46 roles of fauna are briefly considered, along with ways in which
 47 their facilitative or inhibitory roles in multi-trophic interactions
 48 can determine trajectories of forest regeneration indepent of spe-
 49 cies' origins. Finally, I consider management interventions, the
 50 associated dilemmas and conflicts, and in particular the need for
 51 scientifically informed compromises about removing non-native
 52 species that are common in early-stage regeneration, if the goal is
 53 to cost-effectively establish trajectories toward recovery of indige-
 54 nous forest diversity over large areas.

3 ECOLOGICAL ROLES AND PROCESSES 4 DURING FOREST-PASTURE CONVERSIONS

Wide global variation in the species composition of diverse tropi-
 cal forests complicates any search for general patterns in their
 post-grassland regeneration. However, if species are grouped into
 broad life forms of functional importance, published reviews of
 the ecological processes that drive regeneration dynamics in rem-
 nant old growth forests, anthropogenic grasslands and post-grass-
 land regeneration in the moist tropics reveal considerable global
 functional similarities despite many regional differences in species
 identity (Holl *et al.* 2000, Erskine *et al.* 2007, Holl 2007, Wright
et al. 2007, Zimmerman *et al.* 2007, Chazdon *et al.* 2008, Dalling
 & Burslem 2008, Elliott *et al.* 2013, Ganade 2007, Martínez-
 Garza *et al.* 2013, McConkey *et al.* 2012, Reid & Holl 2013, Shoo
 & Catterall 2013, Chazdon 2014, Corlett 2014). Based on these
 and other sources, Fig. 1 and Table 1 describe and summarize
 important interactions among different plant and animal life
 forms; how their frequencies or abundances are changed in
 actively used livestock pasture and in regrowth forest, compared
 with old growth forest, and how these processes also respond to
 external and starting conditions to determine a site's likely trajec-
 tory of vegetation development over time. A site is considered to
 be an area of land in a given location.

Relatively few studies of community development during
 tropical forest succession have quantified the roles of plants other
 than trees (Chazdon 2008, here denoting all woody-stemmed
 freestanding plants, including shrubs). However, the ecological
 roles played by different plant life forms (grasses, herbs, ferns,
 vines, and trees) are nevertheless well recognized (Ewel & Bige-
 low 1996). By comparison, scientific knowledge of the roles
 played by animal species and life forms during forest regrowth is
 rudimentary, aside from growing knowledge of the significant role
 played by frugivore-assisted seed dispersal (McConkey *et al.*
 2012). Fauna also influence tree regeneration through predation
 on seeds and seedlings (Erskine *et al.* 2007, Ganade 2007, Holl
 2007). Here, animal life forms are categorized as: frugivorous
 seed dispersers, granivores (seed predators), browsers/grazers
 (seedling predators), and larger carnivores (Fig. 1; Table 1), as in
 McAlpine *et al.* (2016). A variety of physical properties (soil and
 climate) may further influence how processes of forest regenera-
 tion differ among sites (Guariguata & Ostertag 2001, Holl 2007),
 but the focus here is on potential within-site trajectories of vege-
 tation development.

Trees and vines dominate both the vegetative structure and
 species diversity of indigenous moist tropical forests (Chazdon
 2008, Letcher & Chazdon 2009), including many fleshy-fruited
 species that are dispersed by birds or mammals (McConkey *et al.*
 2012). Grasses, herbs, and ferns are relatively uncommon, being
 suppressed by competition from the tree and vine canopy, except
 in cases of local disturbance such as the light gaps created by
 storms (Chazdon 2014). When people cut down and burn large
 areas of forest vegetation, altered physical conditions (especially
 high light availability) enable the growth of a range of different

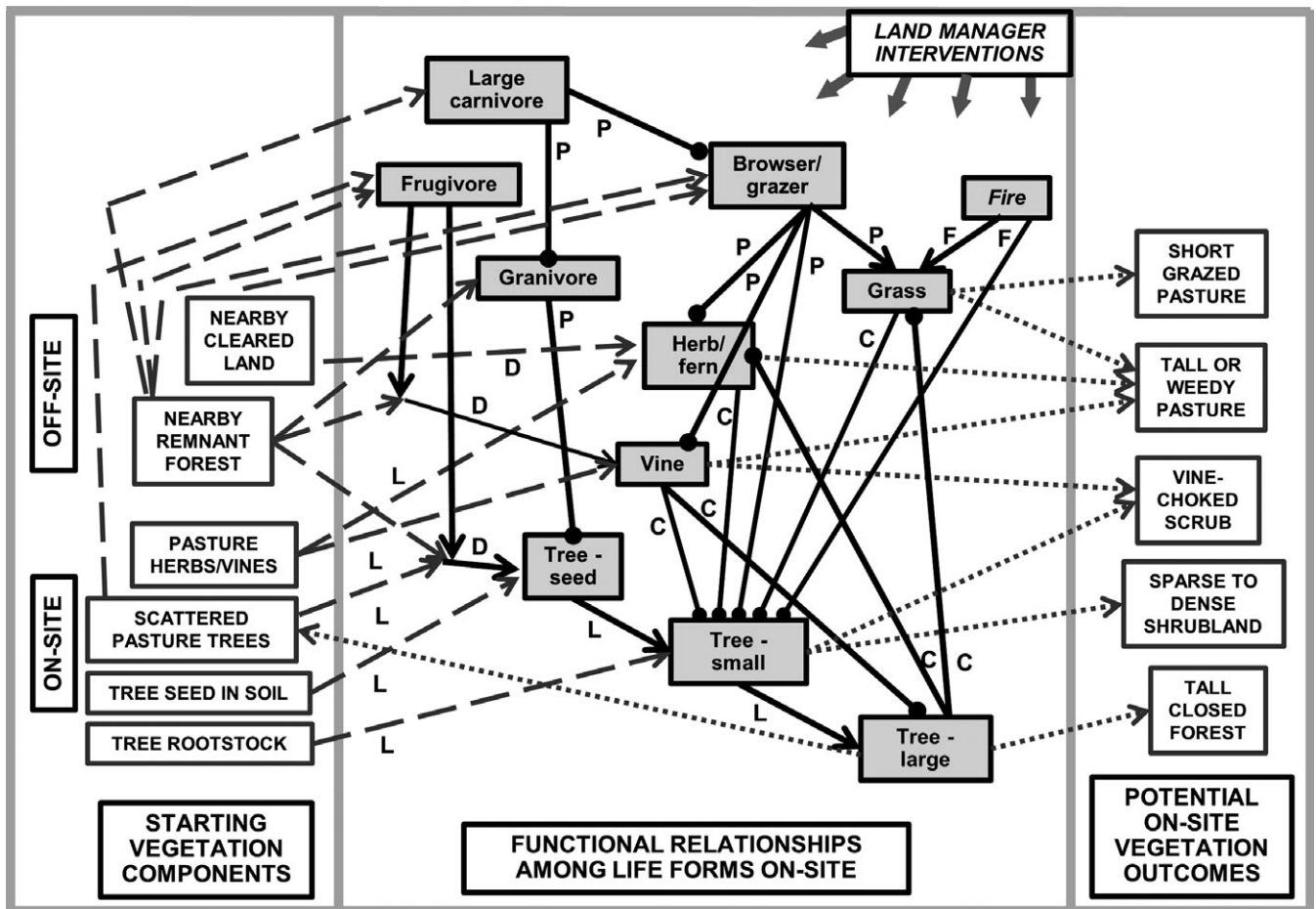


FIGURE 1. Functional relationships important to early stages of forest redevelopment on anthropogenic grassland in the moist tropics. The right hand section shows the ecologically significant starting components (on and off-site); the left-hand section shows the potential range of final on-site vegetation outcomes; these are determined by the ecological interactions among life forms shown in the central section. Life forms are gray-shaded boxes, and described in Table 1 (“Tree” includes shrubs and is here separated into three growth stages); biotic interactions are solid black lines, where arrows or round endings indicate direct positive or negative effects, respectively. Gray-dashed lines show main influences of external or starting factors; gray-dotted lines show important pathways to vegetation outcomes. Time progresses during the transition from left to right sections, and is implicit in ecological interactions. Letters L = life history processes, D = seed dispersal, P = predation, C = competition, F = fire effects. A species’ identity (irrespective of native or non-native origin) will determine how much it contributes to a particular process at a location. Edaphic (soil-related) factors and local climate may also influence the outcomes, and other interactions may also occur (such as competition among grasses, herbs, ferns, and vines). Active land manager interventions on-site affect many life forms, and include: addition (by sowing seed) of both grasses and nitrogen-fixing herbs and leguminous vines; addition and removal of grazing livestock; addition of fertilizers or other growth promoters; burning; removal of unwanted plant species in all life forms (including with herbicides); and removal of carnivorous mammals.

species of grass, herb, fern, and vine (Fig. 1; Table 1) which can form dense ground-covering mats (Holl 2007, Chazdon 2014). However, to sustain profitable livestock densities, landholders must subsequently undertake a sustained set of complex and dynamic interventions aimed at maintaining a high cover and growth rate of desired pasture grasses (Teitzel *et al.* 1992, Jank *et al.* 2014, Knoke *et al.* 2014), which variously include: sowing the seeds of NN grass cultivars selected for nutritional value and rapid growth; adding nutrients (especially N and P); sowing the seeds of N-fixing leguminous herbs or vines (often NN species); and actively removing (mechanically or with herbicide) non-woody species that are unpalatable or toxic to livestock, as well

as any emerging woody saplings; repeated burning may also be involved. Livestock grazing also tends to remove any recruited tree seedlings.

In the absence of grass-maintaining interventions, even a few years of livestock production tend to deplete soil nutrient stocks and reduce grass growth, so that livestock densities must decrease (Buschbacher 1986, Myers & Robbins 1991, Ganade 2007). This shift in abiotic and biotic conditions can favor recruitment of some woody seedlings, which then grow to shade and further reduce the cover of pasture grasses (Fig. 1, Table 1; see also Asner *et al.* 2004), leading to feedback processes that promote the initial stages of forest regeneration. Alternatively, in

TABLE 1. *Macroscopic life forms that play notable functional roles in forest-pasture transitions—a generalized description of their characteristics and changes during forest regeneration in the moist tropics. See also Fig. 1. NAT = native, NN = non-native species.*

Life form ^a	Role ^b	Intact forest, other than small fragments	Productive pasture	Regenerating post-pasture forest ^c
Tree/shrub	Free standing and woody stemmed; can grow large; many together form complex 3-D physical structures and diverse microhabitats, shading the ground and modifying micro-climates.	Dominant structuring life form; multiple stem diameters; form a dense multi-layered canopy; diverse species and families; many are large-seeded and dispersed by frugivores.	Rare or sparse; size distribution biased away from seedlings and saplings.	Density varies, mostly small stem diameters; modest diversity; species functionally biased toward pioneer traits, including small seeds.
Vine	Twining climbers, sometimes woody; can form dense tangles of foliage at various heights (depends on support), shading lower growing plants. “Liana” when large diameter, woody.	Important and diverse forest canopy component of forest; multiple stem diameters.	Rare or sparse unless sown nitrogen-fixing vine legumes.	Varying densities, small-diameter creepers and twiners may sometimes blanket the ground or cover small trees.
Herb/fern	Low growing; some species form dense mats in well-lit conditions, shading or inhibiting smaller plants.	Diverse but not structurally dominant.	Rare to variably common typically mixed with pasture grasses.	May form dense patches up to 2 m tall; tend to dieback beneath emerging trees.
Grass	Low growing but some species form dense swards up to 2–3 m tall unless suppressed (<i>e.g.</i> , by shade or grazing mammals); may outcompete seedlings of other life forms; some species are tolerant of fire and moisture deficits.	Rare except in well-lit gaps or ecotones with more open vegetation; C3 grasses predominant.	Dominant structuring life form, forming dense short layer; C4 grasses predominant.	May be dominant and tall (to 2 m+) and very dense, or interspersed with patches of vines, herbs, or ferns; tend to dieback beneath emerging trees.
Frugivore (seed disperser)	Regeneration of most rain forest trees and vines depends on dispersal by fruit-eating birds and mammals which pass or regurgitate seeds undigested; larger species can disperse a wider range of plant species.	Seed-dispersing birds and mammals of large and small body sizes are diverse and common.	Seed-dispersing fauna are uncommon (grasses are dispersed by wind or grazing mammals).	Variable occurrence of seed dispersers; species biased toward small habitat generalist birds.
Granivore (seed predator)	Regeneration of most plants can be limited if seeds are eaten by the larvae of insects, or by mammals (especially ground-active rodents).	A wide range of insects and small mammals consume seeds in the canopy and on the forest floor.	Often uncommon (except sometimes, small rodents or insects); desiccation also kills seeds.	Variable occurrence of seed predators; poorly studied.
Browser/grazer	Regeneration of most plants can be limited if their seedlings or saplings are eaten by herbivores; catastrophic consumption is most likely for large and medium mammalian herbivores.	Large and medium-sized browsing mammals consume leaves of tree seedlings and saplings, herbs and vines.	Grazing livestock consume most of the grass productivity, along with seedlings of other life forms.	Grazing livestock absent or rare; medium-sized browsing mammals may be locally common and consume tree seedlings; poorly studied.
Large carnivore	Local effects of seed predators, foliage browsers, and some seed dispersers can be reduced by predation or behavioral avoidance of large carnivorous mammals, thereby increasing forest regeneration.	Medium to large mammal carnivores are diverse; may exert strong top-down influence on seed and seedling predators; not rare unless hunted.	Rare except for domestic dogs.	Large mammal carnivores may become more common, with variable potential influence; poorly studied

(continued)

TABLE 1. (continued)

Life form ^a	Role ^b	Intact forest, other than small fragments	Productive pasture	Regenerating post-pasture forest ^c
Land manager (human)	Harvests resources; controls other life forms and alters nearby habitats and propagule sources.	Limited to negligible (selective hunting and harvesting).	Dominant presence.	Limited but variable.

^aHerbs and ferns are here grouped due to their similar ecological roles in this context (see text). Within some groups, there may be many species whose roles differ from those described here, but these are generally less functionally significant in forest-pasture transitions. Other plant groups which can be important in regrowth are bamboos (functionally like tall grasses) and rattans (*Calamus*; functionally like vines).

^bGeneralized; the importance of listed taxa may vary regionally, and functional supplementation or substitution may be involved, for example, ants are more significant as leaf browsers in the Neotropics; mammals are less significant dispersers in Australia and on islands; herbivorous insects may also kill young plants through defoliation.

^cHigh variability is associated with both regeneration age and a range of environmental factors, including interactions among species with different functional roles.

other situations, well-established low growing mats of grass, herb, fern, or vine may suppress recruitment of tree seedlings, either through competition (Cohen *et al.* 1995, Sun & Dickinson 1996, Holl *et al.* 2000, Hooper *et al.* 2005, Zimmerman *et al.* 2007, Elgar *et al.* 2014) or through their fire-encouraging properties (Erskin *et al.* 2007, Dalling & Burslem 2008). Then, the outcome may be a persistent quasi-stable state, in which forest regeneration is greatly inhibited (Zahawi & Augspurger 1999, Mack *et al.* 2000, Hartig & Beck 2003, Gunaratne *et al.* 2010, Knoke *et al.* 2014); in this situation low-intensity grazing by livestock can further reinforce a state of non-forest (Gunaratne *et al.* 2010). Even when some regenerating trees do establish, vines may grow to smother them (Kanowski *et al.* 2009, Paul & Yavitt 2011).

In any given region, the variety and complexity of potential functional inter-relationships (Fig. 1) can lead to cycles of either positive or negative feedback, ultimately promoting or enhancing forest regeneration. The many potential pathways of indirect effect will lead to a high potential for variability and unpredictability in vegetative outcomes, influenced by circumstances such as nearby seed sources, seed-dispersing fauna, the on-site presence of enduring tree resprouts, or scattered pioneers, the feeding preferences and abundance of wild browsing mammals (which may advantage either ground vegetation or young trees), and the flammability of grasses (Fig. 1; Table 1). Accordingly, the potential short-term outcomes range from a rapidly developed tree cover similar to that seen in disturbed remnant forest to persistent low-growing thickets of tall grass, perhaps intermixed with ferns, herbs, vines, or shrubs (Fig. 1). Indeed, studies of regeneration trajectories after various forms of anthropogenic disturbance have reported great variation, even at a local scale, especially when human impact has been high (Uhl *et al.* 1988, Guariguata & Ostertag 2001, Chazdon 2003, 2008, Holl 2007, Norden *et al.* 2015).

These complex interactions also provide opportunities for species from either NAT or NN origin to have functional roles that either accelerate or retard regeneration. For example, shading by mature trees will suppress the growth of pasture grasses

irrespective of whether either is NAT or NN in origin, while the strength of this effect depends on species-specific functional attributes such as the canopy density of the tree and the shade tolerance of the grass. The important “tree” category subsumes varied functional characteristics, such as those which distinguish the first colonizers (pioneer species *sensu lato*, with many small widely dispersed seeds, and fast growing shade-intolerant seedlings) from the greater diversity of later-successional species, often having large seeds and seedlings that tolerate shade and grow slowly (Holl 2007, Dalling & Burslem 2008, Martínez-Garza *et al.* 2013, Chazdon 2014).

Successional processes and functional traits of pioneer trees in light gaps within old growth moist tropical forests have been extensively studied (Chazdon 2014). Although these share some characteristics with regeneration processes on anthropogenic grasslands, there are also many respects in which they differ (Table 2). Successful tree recruitment in the latter case requires a somewhat different set of functional properties than those associated with success in forest light gaps; such as a capacity for dispersal across open landscapes, ability to establish in exposed or nutrient-depleted substrates, competitiveness with mat-forming grasses, herbs or ferns; and resistance to livestock grazing. Consequently, a different suite of tree pioneer species could be expected. Accordingly, in the Neotropics, *Cecropia* (Urticaceae) is a common NAT pioneer genus in treefall gaps, and immediately after forest clear-felling, but is less common in post-pasture regrowth compared with NAT species of *Vismia* (Clusiaceae) and *Solanum* (Solanaceae) (Uhl 1988, Mequita *et al.* 2001). The ecological properties of the novel grasslands in human-dominated regions also create colonization opportunities for invasive NN trees that are uncommon in undisturbed old growth forest, as discussed in the next section.

CASE STUDIES OF POST-PASTURE REGROWTH IN NORTHERN AUSTRALIA

Ecological studies of rain forest regrowth on disused pastures in the Australian upland tropics and lowland subtropics provide case

TABLE 2. Differing ecological contexts of succession on anthropogenic grasslands compared with forest light gaps, in the moist tropics.

Ecological factor	Anthropogenic grassland	Forest light gap
Soil ^a	Modified variously: compacted; may be eroded; nutrients could be depleted or enriched.	Similar to forest soil.
Exposure	High insolation and exposure to wind.	Some adjacent tree shade; sheltered from wind.
Agricultural flora	Pasture grasses and legumes abundant and form dense ground cover.	Mat-forming grasses and legumes uncommon.
Tree seed sources ^a	Few scattered remnant or regrowth trees sometimes present.	Many adjacent mature NAT trees.
Tree seed dispersers ^{a,b}	Often few seed dispersers (larger seeds affected most severely).	Many and diverse seed dispersers (of all seed sizes).
Tree seed predators ^b	Few/small rodents, but may vary greatly.	Common/diverse species.
Tree seed bank	Few persistent species.	Wider range of species (but mostly pioneers).
Tree seedlings initially present	Absent or rare.	Diverse species.
Tree seedling predators	Abundant large livestock; few species.	Common and diverse species.
Tree seedling competitors ^c	Mat-forming agricultural flora.	Adjacent tree shade.

^aAlso noted by Corlett (1991).

^bAlso noted by Janzen (1990), who also suggested higher seed predation in post-grassland regeneration.

^cSmall seeds especially vulnerable to competition (Doust *et al.* 2008, Hooper *et al.* 2005).

studies that illustrate the diverse functional roles of both NAT and NN species. These two regions share similar climates and many plant and animal genera and species; both once supported large areas of indigenous closed-canopy rain forest around 30 m tall, containing diverse tree species of many families (including Euphorbiaceae, Lauraceae, Myrtaceae, Rutaceae, and Sapindaceae), with fire-prone eucalypt-dominated forests in drier adjacent areas, sometimes interspersed with the rain forest and demarcated by abrupt ecotonal boundaries (Erskine *et al.* 2007).

Extensive deforestation of level land on basaltic soils occurred with European settlement during the late nineteenth and early twentieth centuries (Erskine *et al.* 2007); an initial phase of selective logging was followed by small-scale agriculture and then widespread conversion into cattle pasture, including sowing NN grasses and a variety of legumes, together with fertilization, especially phosphorous addition (Teitzel 1992). While steep mountain slopes remained forested, any level areas became large expanses of short pasture grass containing few scattered trees, together with some patches of remnant forest (*e.g.*, Fig. 2). Dominant pasture grasses are NN species, including signal grass (brachiaria: *Urochloa decumbens*) guinea grass (*Megathyrsus maximus*) and setaria (*Setaria sphacelata*); in the moist subtropics kikuyu (*Pennisetum clandestinum*) is more common. Pasture development has also incorporated NN vine legumes such as glycine (*Neonotia wightii*), desmodium (*Desmodium intortum*) and siratro (*Macroptilum atropurpureum*). Commencing in the mid-twentieth century, changed economic circumstances in the dairy industry coupled with increasing community interest in conservation and alternative lifestyles resulted in increasing reduction or removal of livestock grazing, subdivision of farms, and transfer to landholders who derived part or all of their income from off-farm sources, including some focused on conservation and restoration rather than primary production (Erskine *et al.* 2007, Parkes *et al.* 2012, Goosem & Tucker 2013). By the end of the twentieth century, areas of regrowth forest had therefore developed on many farms in both the tropics (*e.g.*, Fig. 2) and subtropics (Neilan *et al.* 2006).

In the tropical uplands, Shoo *et al.* (2016) investigated rates of recovery in NAT plant diversity during post-pasture regrowth on basaltic soils, using a multi-site 1–59 yr chronosequence, across an area of some 900 km². Across these sites, the structural components of canopy cover and stem density had reached forest-like levels within about two and four decades, respectively, while both the species richness of NAT trees, and their resemblance to old growth forest in species composition, reached about one-third of the mean value across old growth reference forest sites after 60 yr (Shoo *et al.* 2016). However, NN species and their roles in developmental trajectories were largely excluded from these analyses, as were life forms other than trees and vines (Shoo *et al.* 2016). Figure 3 now shows the temporal pattern of development in both total cover (or density) and the relative representation of NAT versus NN species, for each functionally important life form in this same regrowth chronosequence, together with mean values in old growth forest sites. The age of a site is the number of years since early regrowth was visible in historical aerial photography (Shoo *et al.* 2016; but here excluding sites aged <5 yr, where regrowth may not have established).

In five active pasture sites that were also surveyed, the average grass cover was 92 percent (range 68–99%), and dominated by the NN species *U. decumbens* and *M. maximus*; average cover of herbs and ferns was 7 and 0 percent, respectively, and there were no vine tangles or trees (woody stems >2.5 cm diameter). By the time regrowth had become visible in aerial photographs for about 5 years, the grass cover was reduced to about 50 percent (Fig. 3), with NN grasses still predominant, but now comprising mainly *Melinis minutiflora* and *S. sphacelata*. In progressively older sites, grass cover was further reduced to near zero in about five decades (resembling reference forest values), and the species composition shifted to almost entirely NAT. Fern cover showed a variable increase in not only young regrowth (maximum 16% in one 24-yr old site), but also reduced to near zero after about five decades (similar to forest values; Fig. 3). All fern species were NAT, including the initially dominant bracken (*Pteridium*

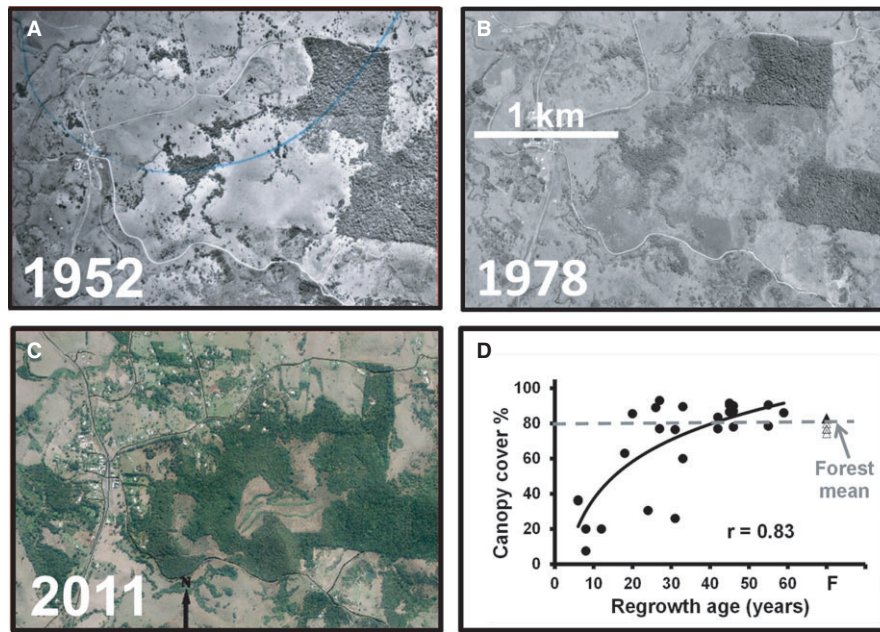


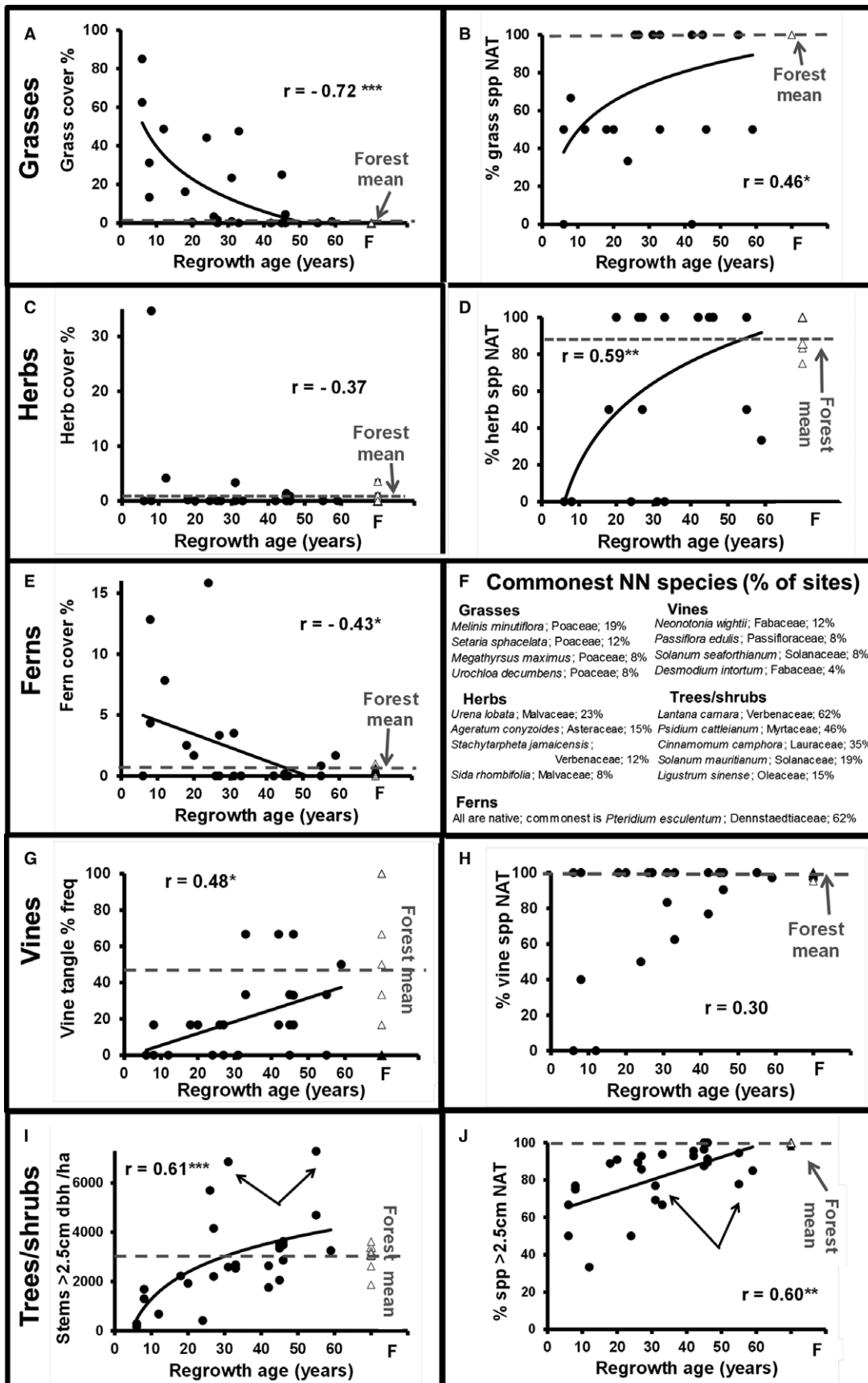
FIGURE 2. Forest regrowth in the moist tropical uplands of northeast Australia (Tazrali region, Atherton Tablelands). (A), (B), (C) show changes in forest cover across six decades during which the grazing industry declined; the dark patches in (A) are remnant rain forest and the mid-grey areas in (B) are early regrowth. In (C), these have formed established closed-canopy forest regrowth 30+ years old. (D) shows the development of canopy cover in a more broadly distributed 5–59 yr old site chronosequence ($N = 26$, including five Tazrali sites).

esculentum). Herb cover was always low, as in reference forest (aside from 35% in one 8-yr old site dominated by the NN *Urena lobata*), however, the herb species mix shifted across the different regrowth ages, from entirely NN to entirely NAT for most sites (Fig. 3). The frequency of vine tangles increased progressively with regrowth age, while mostly remaining below the mean reference forest value (greatly exceeding it in three sites aged 33–46 yr; Fig. 3). The vine species mix of NN and NAT was initially very variable (some sites being dominated by the NN pasture legume *N. wightii*), but shifted toward almost completely NAT in older regrowth.

The density of tree stems increased rapidly in the first three decades (Fig. 3); subsequently often exceeding mean forest values (associated with dominance by relatively small stem diameters). In the first decade, about 25–50 percent of species were NN (particularly frequent species were *Lantana camara*, *Psidium cattleianum*, *Cinnamomum camphora*, and *Solanum mauritianum*, all dispersed by birds), but after four decades all sites had <25 percent NN species (Fig. 3). This shift over time is a consequence of substantially increased density and species richness of NAT stems, with little change in density or richness of NN stems (Shoo *et al.* 2016). In the first decade, 41 percent of stems on average were NN (SD = 27, $N = 4$ sites), while after four decades this had dropped to 4.5 percent of stems (SD = 5.4, $N = 10$ sites; excluding one 55-yr old site with 58 percent NN, because of multi-stemmed individuals of *P. cattleianum*). While such chronosequence data may not always correspond with real time changes within sites, scrutiny of the early historical aerial photography of this study's older regrowth sites indicated that the NN scrambling

shrub lantana (*L. camara*) had initially been common at many sites. During field sampling, tall and straggly remnant stems from former lantana thickets were observed in a state of dieback beneath the native tree overstory of some older sites. Previous longitudinal studies of rain forest succession in the subtropics have also shown that reduced *L. camara* cover accompanied tree canopy development (Webb *et al.* 1972). Slow return of larger seeded species (>1 cm diameter) was a main factor limiting the recovery of NAT tree diversity in these sites (Shoo *et al.* 2016), a factor which must be due at least in part to likely dispersal deficits for large seeds as observed in NAT regrowth worldwide (McConkey *et al.* 2012, Reid *et al.* 2015), and also reported by Yeo and Fensham (2014) for regrowth sites dominated by NAT *Acacia* species (about 5–100 yr old) on less fertile soils in the Australian moist tropical uplands.

Although some former grazing areas in the tropical uplands were dominated by regrowth shrubland or forest (Fig. 2), other properties acquired for conservation purposes in the early 2000s have retained a persistent dense tall cover of pasture grasses with little sign of transition toward trees during a decade or more. At three sites on two such properties, the roles of the tall and dense pasture grasses, and of scattered pasture trees, were experimentally tested in 0.64-ha plots adjacent to old growth forest, using herbicides chosen and applied in a manner designed to kill the grasses but not any emerging woody shrubs and trees (Elgar *et al.* 2014). At the two older sites (20 months after commencement), herbicide-induced grass suppression alone stimulated substantial woody stem recruitment (density of seedlings >10 cm tall = 3316 stems/ha, compared with 5 stems/ha in untreated grassland;



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FIGURE 3. Relationship between regrowth age, life form abundance, and extent to which species are mainly native (NAT) or non-native (NN), across a 5–59 yr old site chronosequence in the moist tropical uplands of northeast Australia. (A), (C), (E), (G), and (I), respectively, show abundance measures of grasses, herbs, ground ferns, vine tangles and tree stems (>2.5 m diameter, excluding a few species not fully identified). (B), (D), (H), and (J), respectively, show the percent of identified species that are NAT. (F) lists the most commonly occurring NN species within each life form. Regrowth sites ($N = 26$) are closed circles, forest reference sites ($N = 8$) are open triangles, gray-dashed lines show mean forest values. See Shoo *et al.* (2016) for methods and site details; samples were 100 m \times 10 m plots, with some components subsampled. Arrowed sites in (I) and (J) contained many multi-stemmed individuals of *Psidium cattleianum*. Lines show best significant fit from either linear or logarithmic relationship (Pearsons r ; * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

Elgar *et al.* 2014). While 99 percent of the recruited stems were a single NN species, *S. mauritianum* (from South America), the recruitment of NAT tree seedlings was also significantly increased by grass suppression (260 seedlings/ha, compared with zero in the untreated grassland), and the other 14 of the 15 commonest species were NAT. Furthermore, the strongest response of NAT tree recruitment occurred beneath scattered pre-existing trees and shrubs, at 7460 NAT seedlings/ha (Elgar *et al.* 2014). Both *S. mauritianum* and 93 percent of the 28 regenerating NAT tree species recorded in this study were bird-dispersed.

These findings demonstrate two important processes: first, suppression of tree regeneration by dense pasture, consistent with Sun and Dickinson's (1996) experimental greenhouse results in the same region; and second, facilitation of further tree recruitment by scattered pasture trees, as also described in the subtropics by Toh *et al.* (1999). Furthermore, this same role was played by both NAT tree species and NN *L. camara* and *S. mauritianum*, both having been initially present pre-treatment (Elgar *et al.* 2014). Therefore, in the apparently stalled retired pasture, a series of pulsed interventions to suppress the grass facilitated a successional feedback in which abundant recruitment of NN *S. mauritianum* (from soil-stored seed) was initially stimulated, together with some NAT species; this could then catalyze further recruitment of diverse NAT species beneath the newly emerging canopy, thereby shifting the state of the site toward forest regeneration with NN species as the dominant pioneers. Furthermore, dominance by *S. mauritianum* is likely to be temporally transient, due to its functional properties of short stature (around 4 m) and (as for *L. camara*) an inability to recruit and grow in shaded situations (Elgar *et al.* 2014), which mean that it can be readily overtopped as taller NAT forest recruits grow. In the Australian subtropics, *S. mauritianum* declines over time during forest succession (Webb *et al.* 1972) and also with decreased light levels following closure of canopy gaps in New Zealand forests (Enright *et al.* 1993).

A taller bird-dispersed NN tree species, camphor laurel (*Cinnamomum camphora*, Lauraceae, growing to 20 m or more and originating from eastern Asia) is also well represented in the tropical regrowth (Fig. 2). In the subtropics, *C. camphora* has become a very dominant component of forest regrowth. For example, in the Big Scrub region, some 750 km² of original rain forest was converted to pasture or cropland in the late 1880s across over 99 percent of the area, but by the early 2000s about one-quarter of this landscape had re-acquired a closed-canopy forest cover several decades old, in which *C. camphora* was often strongly

dominant (Neilan *et al.* 2006, Kanowski *et al.* 2008, Parkes *et al.* 2012). Ecological studies indicate that *C. camphora* is functioning in retired pastures of this region as a tree pioneer, attracting a diversity of seed-dispersing birds, and accumulating NAT rain forest seedlings and saplings beneath its canopy (Woodford 2000, Neilan *et al.* 2006, Kanowski *et al.* 2008, Kanowski *et al.* 2009, Paul *et al.* 2012).

Quantitative assessments of present-day floristic composition and size distributions of trees at 24 camphor-dominated regrowth sites (aged about 20–50 yr; average canopy cover and height 58%, 25 m respectively) showed that among adult trees NAT species comprised 25 percent of stems and 85 percent of species, compared with 47 and 97 percent, respectively, among younger recruits (>0.5 m tall and <2.5 cm diameter; Neilan *et al.* 2006). Furthermore, 93 and 79 percent of recruited individuals and species respectively were dispersed by birds, and concurrent bird surveys revealed frequent visitation by 16 NAT bird species capable of effective seed dispersal (Neilan *et al.* 2006). Seed bank assessments in this region (Paul *et al.* 2012) showed that germinable seeds of NAT trees and shrubs in soils from camphor regrowth and old growth reference forest were, respectively, sixfold and 17-fold greater than in pasture sites, belonging mainly to pioneer species. Among all germinable seeds, the most common species in both pasture and camphor regrowth soils were NN *C. camphora* (and *S. mauritianum*), but these species were uncommon in soil from old growth forest (Paul *et al.* 2012).

From a functional perspective, *C. camphora* readily recruits into pasture, unlike many common NAT rain forest trees. The mechanisms that promote this are unclear, although its seeds are larger than those of many NAT pioneer trees (about 7–8 mm), which may increase its ability to compete with grass, since in general larger seeds produce seedlings that compete better with grasses (Hooper *et al.* 2005, Doust *et al.* 2008). Its seedlings can develop lignotuber-like structures (Schenk 2009), which increases their ability to withstand herbivore damage, and they are moderately fast growing, and relatively drought and frost tolerant (Kanowski *et al.* 2008). Mature camphor trees shade out pasture grasses, and their large fruit crops attract feeding visits by NAT frugivorous birds that widely disperse the seeds of both *C. camphora* and NAT rain forest trees (Woodford 2000, Neilan *et al.* 2006); this fruit supply has also been credited with rescuing some NAT specialist frugivorous birds from deforestation-induced decline (Date *et al.* 1996). On the other hand, *C. camphora* seeds suffer heavy predation by forest fauna (Stewart 2000, Woodford 2000, G. Palmer unpubl. data), and its seedlings appear to be

relatively shade-intolerant (Neilan *et al.* 2006). Therefore, it does not strongly invade closed-canopy remnant rain forest, and as a post-pasture regrowth pioneer, it tends to create conditions that do not favor its own regeneration (Neilan *et al.* 2006, Kanowski *et al.* 2008). However, *C. camphora* adults are also long lived, and so the accumulating understory collection of NAT trees may be slow to replace the mostly NN canopy.

Conservation managers and restoration practitioners vigorously debate how to manage this camphor-dominated regrowth, with many land managers wishing to control or eliminate *C. camphora* because of its NN origin (Kanowski *et al.* 2008, Kanowski *et al.* 2009, Paul 2012). However, some practitioners have developed techniques of intervening more selectively, to accelerate a successional transition toward NAT canopy trees in stands of established camphor regrowth. Herbicide is used to kill the mature *C. camphora* trees, and when the canopy dies and sunlight reaches the ground there is a large flush of new germination and growth of both NAT and NN (especially *C. camphora*) seedlings. A sequence of selective herbicide sprays during the following 1–5 yr then controls the *C. camphora* seedlings while preserving the seedlings of NAT rain forest pioneers, which rapidly grow to shade the ground, after which further *C. camphora* regeneration is reduced (Kanowski *et al.* 2008, Paul *et al.* 2012). During the next decade, the treated sites rapidly become more similar to mature reference forest in both structure (Sanger *et al.* 2008) and floristic composition (Kanowski *et al.* 2008), although different sites vary considerably, associated with variation in factors such as forest proximity, climatic conditions during initial treatment, and abundance of seed predators and herbivores (Woodford 2000, Kanowski *et al.* 2008). This approach differs fundamentally from herbicide-based biocontrol, because its success depends on tolerating the initial establishment of a tree canopy of fruiting *C. camphora*, rather than removing the early tree colonizers to re-establish pasture.

POSITIVE AND NEGATIVE FUNCTIONS OF NATIVE AND NON-NATIVE PLANT SPECIES

Beyond the specific Australian case studies, a much wider range of ecological roles may be filled by either NAT or NN species, depending on location and context (Fig. 1), raising the questions of which of these roles would be desirable (facilitative) or undesirable (inhibitory) for achieving large-scale reforestation, and to what extent some roles may be typically occupied by either NAT or NN species.

Among plants, the most frequently noted inhibitory function shared by grasses, herbs, ferns, and vines is competitive suppression of tree seedlings, as previously discussed. Dense grasses which do this are frequently NN, since most developed pastures in moist tropical landscapes worldwide were sown with very similar suites of NN cultivars, often of African origin, including species of *Brachiaria*/*Urochloa*, *Cynodon*, *Melinis*, *Panicum*/*Megathyrsus*, *Pennisetum*, and *Setaria*, (Uhl *et al.* 1988, Sun & Dickinson 1996, Toh *et al.* 1999, Asner *et al.* 2004, Elgar *et al.* 2014, Jank *et al.* 2014, Knoke *et al.* 2014). Large-scale NAT pastures are less common in the

moist tropics (unlike the drier tropics). Prior to human domination there was little grass (comprising mainly physiologically shade-tolerant species) in indigenous moist forest vegetation; NAT tropical pasture species have expanded or been introduced from other environments after reduction in the forest canopy. However, both NAT and NN grasses can suppress tree regeneration. For example, NAT *Imperata brasiliensis* and NN *Melinis minutiflora* have functionally similar inhibitory roles in southeastern Brasil (Cesar *et al.* 2014); *Imperata cylindrica* and *Saccharum spontaneum* both inhibit tree regeneration as NAT species across tropical Asia (Shono *et al.* 2007, Elliott *et al.* 2013); and *S. spontaneum* does so as a NN species in central America (Hooper *et al.* 2005).

When ferns form mats that similarly suppress tree regeneration in retired pasture or degraded agricultural land in the moist tropics, this typically involves NAT species of two cosmopolitan genera: *Dicranopteris*/*Gleichenia* and *Pteridium* (Robinson *et al.* 2010, Martínez-Ramos *et al.*, this issue). Descriptions of their impact and management are broadly similar to those for grasses and herbs, with which they may grow interspersed (Hartig & Beck 2003, Shono *et al.* 2007, Robinson *et al.* 2010, Chazdon 2014, Knoke *et al.* 2014).

A diverse range of both NAT and NN herbs can become locally dominant in retired pasture or agricultural land, and can inhibit tree recruitment. For example, in the variously re-named group of genera *Chromolaena*/*Eupatorium*/*Ageratina* (Asteraceae; originating from the Americas), several NN low-growing species do this (Elliott *et al.* 2013) in the Asia-Pacific region. Their ecological roles in the native range are largely undocumented, although the depauperate flora of apparently stalled vegetation on degraded farmland in southern Ecuador includes NAT species within both *Eupatorium* and *Ageratina*, the latter being able to patchily overgrow *Pteridium* ferns (Hartig & Beck 2003). In abandoned pastures of northern Ecuador, a NAT *Baccharis* (Asteraceae) species growing densely at 1–2 m tall was associated with apparently arrested succession (Zahawi & Augspurger 1999). Overall, it seems that some herb species, both NAT and NN, can have an inhibitory role whereas for other species (or other situations) their interactions may be either neutral or more complex.

The inhibitory tree-smothering roles of vines may also be played by either NAT or NN species. The N-fixing (and mostly NN) legumes that were initially sown to promote the productivity of pasture grasses have in some cases expanded to become more generalized problems when they overgrow trees in remnant forest (Low 1997). More broadly, overgrowth of trees by a wide range of NAT and NN vines has been most frequently described in the context of disturbed remnant forest (Catterall *et al.* 2008, Schnitzer & Bongers 2011). Interestingly, several studies of forest regrowth in moist tropical landscapes have noted that NAT vines have not formed a major component of the vegetation, and may initially recruit into disused anthropogenic grasslands less effectively than do trees (Corlett 1991, Reid *et al.* 2015, Shoo *et al.* 2016).

Trees (including shrubs) that are pioneer colonizers of former pasture or farmland generally facilitate forest regeneration, especially through grass suppression and seed disperser attraction, which are more effective in combination than alone in assisting

1 further recruitment of tree seedlings (Hooper *et al.* 2005, Holl
2 2007, Gunaratne *et al.* 2010, Shoo & Catterall 2013). Both these
3 roles can be filled by NAT or NN species; even NAT pioneer
4 trees in pasture are likely to include species that are scarce or
5 absent in old growth forest tracts, being derived from drier, more
6 open habitats in the region (Corlett 1991, Zimmerman *et al.*
7 2007). *Solanum mauritianum* is considered an important NAT pio-
8 neer species in Brazil (Martins & Engel 2007), and has a similar
9 role when NN in Australia (Fig. 3; Elgar *et al.* 2014). In Puerto
10 Rico, the NN *Spathodea campanulata* (from Africa) is a significant
11 post-agricultural pioneer; it suppresses grass growth while
12 enabling recruitment of NAT forest species, but then declines
13 over time because it is shade-intolerant (Lugo 2004, Zimmerman
14 *et al.* 2007). *Spathodea campanulata* may perhaps also have this role
15 in Fiji (Keppel & Watling 2011).

16 In contrast, a growing number of cases show where invasive
17 NN tree species within successional or disturbed woody vegetation
18 are strongly implicated as inhibitors of NAT regeneration. For
19 example, seedlings of NN forest species that are shade-tolerant will
20 be less suppressed by a tree canopy, and such species are therefore
21 likely to occur more frequently as invaders in intact forest, as well
22 as potentially persisting long-term as a major component of regen-
23 erating forests. Early colonizing NN species in the Australian case
24 studies that have greater shade tolerance as seedlings include *Ligus-*
25 *trum lucidum* (from China) and *Psidium cattleianum* (from south Amer-
26 ica), both of which are common NN species in secondary tropical
27 forests of other regions globally (Lichstein *et al.* 2004, Meyer 2004,
28 12 Tng *et al.* 2016). For such species, a capacity to outcompete other
29 young trees when growing in forest conditions would shift their
30 ecological role from positive or neutral to negative.

31 However, the ecological role of successional inhibitor during
32 certain phases of post-agricultural redevelopment of moist tropi-
33 cal forest is not confined to NN tree species. For example,
34 Ganade (2007) noted that NAT post-pasture tree pioneers com-
35 petitively inhibited recruits of later-successional species in the
36 Amazon basin, and recommended canopy thinning as a manage-
37 ment action to accelerate succession. In a review of tropical sec-
38 ondary forest succession, Chazdon (2008) noted that established
39 NAT regrowth stands one to three decades old, which tend to
40 have high densities of even-aged stems, lack the light gaps which
41 provide important opportunities for establishment and growth of
42 a diversity of rain forest tree seedlings in old growth forest. In
43 the Australian case study context, Erskine *et al.* (2007) noted the
44 potential for dominance by NAT *Acacia* tree species to retard or
45 arrest post-pasture succession.

46 Attributes that profile useful NN facilitator tree species
47 could include: short lifespan; high fecundity; seeds capable of
48 wide dispersal across cleared landscapes; seeds predated by forest
49 fauna (but not pasture fauna); seedlings that can outcompete pas-
50 ture plants and grow rapidly in sunlight, but which are also
51 shade-intolerant; and adult trees that are both attractive to seed-
52 dispersing fauna and not strongly competitive with seedlings or
53 saplings of desired later-successional NAT species. Among the
54 Australian case study examples, *S. mauritianum* and *L. camara* pos-
55 sess most of these attributes. *Cinnamomum camphora* differs in

being long lived, yet it still assists rain forest to establish in pas-
ture, as described previously. However, a particular species' role
would also be context-dependent. For example, seedling growth
is sensitive to soil conditions and other abiotic factors; wide dis-
persal depends on dispersal agents; and seed predation depends
on the fauna community. Accordingly, in Australia *L. camara* can
act as a facilitating pioneer in post-pasture regeneration of moist
rain forest (Webb *et al.* 1972, Elgar *et al.* 2014), but in remnant
drier forest *L. camara* promotes degradation through increased fire
frequency (Berry *et al.* 2011).

Judgments concerning the likely role of particular NN spe-
cies could be aided by the development and refinement of eco-
logical classifications which use functional traits to better predict
how species will perform and interact during forest re-establish-
ment on anthropogenic grasslands in the tropics (*e.g.*, Lohbeck
et al. 2013, Friday *et al.* 2015, Ostertag *et al.* 2015). Such
approaches could also be usefully applied to non-tree life forms.
However, given the context-specificity of species' ecological roles,
together with limited current knowledge about the predictive
capacity of trait-based approaches, the most effective way of
determining the role of a given NN species in successional
dynamics within a region may be to empirically assess it. But dis-
tinguishing among facilitation, inhibition, and neutrality from
observational data can be difficult. For example, an observation
that increased tree density of an invasive NN species is correlated
(across multiple sites) with decreased native tree species diversity
may occur either if NN pioneers facilitate subsequent coloniza-
tion and recruitment of diverse NAT species, or if invasion of
regrowth forest by NN species reduces NAT diversity. To disen-
tangle cause and effect requires historical or long-term data sets,
and/or experimental interventions, with scientifically robust repli-
cation (given multiple potential causal factors) and monitoring at
appropriate spatial scales.

All plant life forms have further potential abiotic roles of
stabilizing or destabilizing soil, and of modifying its physical
and chemical properties. Attributes related to these roles could
also make particular species either desirable or undesirable in
the context of forest restoration, in a manner unrelated to
species' origin.

Finally, landscape context sets an important context for
propagule sources of both NN and NAT plant species, and for
use of a site by NN and NAT animals. Indeed, the presence of
old growth forest communities within a feasible dispersal distance
must set an ultimate hard constraint to the potential for many
NAT species to recolonize any site, although the evidence for
exactly how landscape-scale forest cover influences recolonization
is mixed (Martínez-Ramos *et al.* 2016). In the case of the Aus-
tralian camphor laurel regrowth forests, bird-dispersed NAT rain
forest tree recruits (taller than 0.5 m with diameter <2.5 cm) with
large seeds (>1 cm) were twice as abundant, with twice as many
species, at sites <1 km from a large source area of old growth
forest than in more distant sites (Kanowski *et al.* 2008), and dis-
tance to mature forest was a significant predictor of estimated
richness of all trees and vines >2.5 cm diameter in rain forest
regrowth sites in the Australian wet tropical uplands (Goosem

1 *et al.* 2016). Development of rain forest bird communities in
 2 restored post-grassland sites is likewise affected by context (Reid
 3 *et al.* 2014, Freeman *et al.* 2015). However, studies in central
 4 America and elsewhere have found negligible effects of landscape
 5 forest cover on seed rain (Reid *et al.* 2015).

7 FAUNA, TROPHIC CASCADES, AND 8 COMPLEXITIES

10 Animal species influence tree regeneration either directly (as seed
 11 dispersers or predators of seeds and seedlings) or indirectly
 12 through trophic cascades involving higher level predators (Wright
 13 *et al.* 2007, McAlpine *et al.* 2016); although many of these pro-
 14 cesses have been infrequently researched outside of old growth
 15 forest. For example, mammalian browsers could facilitate forest
 16 regeneration if they preferred the grass, herb, or vine species that
 17 would otherwise suppress tree seedlings, but alternatively they
 18 could inhibit this regeneration if they preferred to consume the
 19 emerging leaves of tree seedlings (Fig. 1). As with plant life
 20 forms, the nature of animals' functional roles is unrelated to spe-
 21 cies origin. For example, a NN murid rodent species will not
 22 necessarily show more divergence in its patterns of seed preda-
 23 tion than the amount of variation that already occurs among sev-
 24 eral coexisting species of NAT murid rodent. A NN invader
 25 whose functional attributes are novel in its new context could
 26 have unprecedented ecological effects, but this will depend on its
 27 functional properties rather than its origin *per se*.

28 Moreover, forest regrowth on disused pasture often involves
 29 interlinked functional networks that incorporate both NAT and
 30 NN species across several trophic levels. In Mexico, experimental
 31 regeneration of NAT trees in areas dominated by a tall NN grass
 32 (*Cynodon plectostachyus*) was inhibited when seedlings were con-
 33 sumed by a NAT vole (*Microtus quasiater*), whereas areas domi-
 34 nated by a shorter NAT grass (*Panicum glutinosum*) supported
 35 fewer voles, but enabled higher tree seedling survival (Ortega-
 36 Pieck *et al.* 2011). In the Australian subtropics, NAT marsupial
 37 browsers (*Thylogale* spp.) aggregate at rain forest edges, where they
 38 feed in the adjacent NN pasture, preferring grasses and vines,
 39 and thus potentially facilitating regeneration (Wahungu *et al.*
 40 1999); their selective browsing at some sites likewise functions to
 41 inhibit dense growth of the NN herb *Ageratina riparia*, which
 42 otherwise can suppress tree regeneration (Zancola *et al.* 2000).
 43 However, if the NN grass growth is experimentally suppressed
 44 using herbicide, browsing by *Thylogale* on NAT pioneer seedlings
 45 reduces the potential for forest regeneration (Elgar *et al.* 2014).
 46 There is anecdotal evidence that the amount of *Thylogale* browsing
 47 can be reduced by behavioral avoidance responses to a quasi-
 48 native predator (the dingo *Canis lupus*), but dingos are persecuted
 49 by farmers seeking to protect their livestock.

50 There is increasing interest in 'rewilding' of reserved old
 51 growth ecosystems, by reintroducing large bodied and function-
 52 ally important vertebrates to reinstate ecosystem processes, which
 53 often involve such cascading interactions (McConkey *et al.* 2012,
 54 Louys *et al.* 2015). For globally extinct species, their 'ecological
 55 replacement' requires planned introductions of ecologically similar

NN vertebrates (Louys *et al.* 2015). These ideas also have clear
 potential application to forest restoration (McConkey *et al.* 2012,
 McAlpine *et al.* 2016). In some situations, maintaining suitably
 managed densities of NN domestic livestock may likewise be use-
 ful in facilitating forest recovery, when their grazing assists in
 suppressing grasses or other life forms which otherwise inhibit
 tree regeneration (Shoo & Catterall 2013). Interventions aimed at
 simply removing NN fauna can lead to unexpected and perverse
 outcomes, as in the case where removal of grazing livestock
 releases NN grasses or herbs which competitively suppress NAT
 tree seedlings (Zavaleta *et al.* 2001), or whose growth increases
 the risk of fire, killing NAT tree seedlings.

Conversely, in the case of seed dispersal, 'invasional melt-
 down' scenarios have been described, in which NN vertebrates
 and NN plants have become assembled into webs of positive
 feedback that reinforce each other (especially on islands); but
 there are other cases in which NAT vertebrate seed dispersers
 are initially supported by NN plants, and then are able to more
 widely disperse seeds of NAT plants (Buckley *et al.* 2006, Neilan
et al. 2006). In diverse moist tropical regrowth, it can be a signifi-
 cant challenge to disentangle the actual functional roles of NN
 and NAT vertebrates because of the many altered factors that
 occur concurrently, such as NAT seed bank depletion, loss of
 NAT dispersers, competition from NN grasses and herbs, and
 the presence of NN vertebrate seed predators or carnivores.

MANAGEMENT INTERVENTIONS, DILEMMAS, AND CONFLICTS

Land managers are faced with a suite of potential decisions about
 on-site interventions. In large areas of pasture or other anthro-
 pogenic grassland, a 'no intervention' option still requires deci-
 sions about livestock removal, burning, and fencing. Active
 interventions in situations of woody regrowth are typically aimed
 at either: (1) maintaining or restoring pasture-based production
 (thereby suppressing tree recruitment); or (2) accelerating tree
 recruitment into stalled grassland (or herbland/fermland/shrub-
 land/vine thicket) to achieve forest restoration; or (3) suppressing
 or eradicating non-native species from regenerating forest to
 restore an all-native ecosystem (considering common NN species
 to be an indicator of dysfunction). Each of these options involves
 financial and environmental costs and benefits, which lead to sig-
 nificant trade-offs involved in making a choice.

Restoration practitioners in regions where there is ubiquitous
 regrowth retardation (due to low tree seed input coupled with
 seedling suppression by pasture species) have often looked to tree
 planting as an obvious pathway to reforestation (Erskine *et al.*
 2007, Ganade 2007). Rearing and planting young saplings at a
 stage where they can compete successfully with pasture species
 bypasses many of the inhibitory processes (Dalling & Burslem
 2008, Holl & Aide 2011). If only NAT seedlings or saplings are
 planted, this method also accords with a viewpoint that equates
 "restoration" with conversion into purely NAT species. However,
 to limit the risk of failure, tree planting with a high diversity of
 NAT species requires careful planning and intensive inputs,

making it unlikely to be a cost-effective solution for large-scale restoration of diverse forest (Lamb *et al.* 2005, Shono *et al.* 2007, Shoo *et al.* 2016).

Accordingly, others have turned their attention to potential intervention techniques that may accelerate or catalyze tree recruitment and growth in the face of the retarding processes, although few of these have been adequately costed (Shoo & Catterall 2013). Some involve actions to suppress pasture grasses and associated life forms, and it is likely that in some regions the result will be the emergence of NN trees, as in the Australian case study (Elgar *et al.* 2014). Such an outcome runs directly contrary to the considerable financial and human resources also allocated, through the independent logic of biocontrol, to achieving restoration through attempted eradication of invasive NN species (Mack *et al.* 2000, Simberloff *et al.* 2013). On the other hand, the endpoint of efforts to eradicate NN pioneer trees may be the maintenance of NN pasture ecosystems, which runs contrary to the goal of forest recovery. Furthermore, the case studies demonstrate that a post-pasture regrowth trajectory which begins with NN species' dominance may of itself transition toward dominance by NAT species.

An alternative approach is to focus on the speed and trajectory of forest regeneration, rather than the early-stage presence or absence of NN species. Component actions would be to first identify currently established invasive NN tree species likely to have appropriate ecological pioneer attributes; then to tolerate or encourage their growth in disused grassland, up to a stage where a native tree seedling bank could accumulate (perhaps requiring decades); and then to make an informed judgment about whether there is a trajectory toward increased NAT species representation, whether any persisting NN trees are inhibiting further ecological development, and if so to consider what interventions could be both useful and cost-effective. This approach is increasingly being acknowledged within restoration menus for the Australian subtropics and tropics (Parkes *et al.* 2012, Goosem & Tucker 2013) and elsewhere (Keppel & Watling 2011). The potentially facilitative functional roles of self-recruited pioneer NN trees are similar to those of planted NN 'nurse trees' advocated for greater cost-effectiveness in active restoration (Lamb *et al.* 2005, Friday *et al.* 2015), but the approach is even more economical as it does not require raising and planting of nursery-grown seedlings. On small remote oceanic islands, where limited seed sources for endemic old growth species may be coupled with relatively sparse native forest canopies, as well as numerous animal species' extinctions and invasions, particular caution will be required (Meyer 2004).

To achieve restoration of moist tropical forests on the scale needed, conservation ecologists will need to make compromises about goals of regaining purely native ecosystems, at least in the short term: the nature and cost-effectiveness of management interventions would be improved by incorporating a greater focus on species' ecological roles rather than using their origins as a surrogate cue for restoration decisions. The paradox for conservation managers is that, to reach a point of "recovered native biodiversity" it may often be useful to tolerate (or even encourage) some early developmental stages of functionally useful non-native biodiversity.

High cover or abundance of a non-native species does not necessarily mean that its removal will facilitate forest restoration.

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LITERATURE CITED

- ALBERS, H. J., AND M. J. GOLDBACH. 2000. Irreversible ecosystem change, species competition, and shifting cultivation. *Resour. Energy Econ.* 22: 261–280.
- ASNER, G. P., A. J. ELMORE, L. P. OLANDER, R. E. MARTIN, AND A. T. HARRIS. 2004. Grazing systems, ecosystems responses, and global change. *Annu. Rev. Environ. Resour.* 29: 261–299.
- BERRY, Z. C., K. WEVILL, AND T. J. CURRAN. 2011. The invasive weed *Lantana camara* increases fire risk in dry rainforest by altering fuel beds. *Weed Res.* 51: 525–533.
- BUCKLEY, Y. M., S. ANDERSON, C. P. CATTERALL, R. T. CORLETT, E. ENGEL, C. R. GOSPER, R. NATHAN, D. M. RICHARDSON, M. SETTER, O. SPIEGEL, G. VIVIAN-SMITH, F. S. VOIGT, J. E. S. WEIR, AND D. A. WESTCOTT. 2006. Management of plant invasions mediated by frugivore interactions. *J. Appl. Ecol.* 43: 848–857.
- BUSCHBACHER, R. J. 1986. Tropical deforestation and pasture development. *Bioscience* 36: 22–28.
- CATTERALL, C. P., S. MCKENNA, J. KANOWSKI, AND S. D. PIPER. 2008. Do cyclones and forest fragmentation have synergistic effects? A before–after study of rainforest vegetation structure at multiple sites. *Austral Ecol.* 33: 471–484.
- CESAR, R. G., R. A. G. VIANI, M. C. SILVA, AND P. H. S. BRANCALION. 2014. Does a native grass (*Imperata brasiliensis* Trin.) limit tropical forest restoration like an alien grass (*Melinis minutiflora* p. Beauv.)? *Trop. Conserv. Sci.* 7: 639–656.
- CHAZDON, R. L. 2003. Tropical forest recovery: legacies of human impact and natural disturbances. *Perspect. Plant Ecol. Evol. Syst.* 6: 51–71.
- CHAZDON, R. L. 2008. Chance and determinism in tropical forest succession. In W. Carson, and S. A. Schnitzer (Eds.). *Tropical forest community ecology*, pp. 384–408. Wiley-Blackwell Publishing, Oxford, UK.
- CHAZDON, R. L. 2014. *Second growth: the promise of tropical forest regeneration in an age of deforestation*. University of Chicago Press, Chicago, Illinois.
- CHAZDON, R. L., AND M. R. GUARIGUATA. 2016. Natural regeneration as a tool for large-scale forest restoration in the tropics: prospects and challenges. *Biotropica* 48: ?????–?????
- CHAZDON, R. L., C. A. HARVEY, O. KOMAR, D. M. GRIFFITH, B. G. FERGUSON, M. MARTÍNEZ-RAMOS, H. MORALES, R. NIGH, L. SOTO-PINTO, M. van BREUGEL, AND S. M. PHILPOTT. 2009. Beyond reserves: a research agenda for conserving biodiversity in tropical human-modified landscapes. *Biotropica* 41: 142–153.
- COHEN, A. L., B. M. P. SINGHAKUMARA, AND P. M. S. ASHTON. 1995. Releasing rainforest succession: a case study in the *Dicranopteris linearis* fernlands of Sri Lanka. *Restor. Ecol.* 3: 261–270.

- CORLETT, R. T. 1991. Plant succession on degraded land in Singapore. *J. Trop. For. Sci.* 4: 151–161.
- CORLETT, R. T. 2014. The ecology of tropical east Asia, (2nd Edition). Oxford University Press, Oxford.
- DALLING, J. W., AND D. F. R. P. BURSLEM. 2008. Anthropogenic disturbance in tropical forests: toward a functional understanding of seedling responses. *In* M. A. Leck, V. T. Parker, and R. L. Simpson (Eds.). *Seedling ecology and evolution*, pp. 332–351. Cambridge University Press, New York, New York.
- D'ANTONIO, C., AND L. A. MEYERSON. 2002. Exotic plant species as problems and solutions in ecological restoration: a synthesis. *Restor. Ecol.* 10: 703–713.
- DATE, E. M., H. F. RECHER, H. A. FORD, AND D. A. STEWART. 1996. The conservation and ecology of rainforest pigeons in northeastern New South Wales. *Pac. Conserv. Biol.* 2: 299–308.
- DOUST, S. J., P. D. ERSKINE, AND D. LAMB. 2008. Restoring rainforest species by direct seeding: tree seedling establishment and growth performance on degraded land in the wet tropics of Australia. *For. Ecol. Manage.* 256: 1178–1188.
- ELGAR, A. T., K. FREEBODY, C. L. POHLMAN, L. P. SHOO, AND C. P. CATTERALL. 2014. Overcoming barriers to seedling regeneration during forest restoration on tropical pasture land and the potential value of woody weeds. *Front. Plant Sci.* 5/200: ???–???. doi: 10.3389/fpls.2014.00200.
- ELLIOTT, S. D., D. BLAKESLEY, AND K. HARDWICK. 2013. Restoring tropical forests: a practical guide. Royal Botanic Gardens, Kew.
- ENRIGHT, N. J., R. M. BARTLETT, AND C. R. De FREITAS. 1993. Patterns of species composition, recruitment, and growth within canopy gaps in two New Zealand kauri (*Agathis australis*) forests. *N. Z. J. Bot.* 31: 361–373.
- ERSKINE, P. D., C. P. CATTERALL, D. LAMB, AND J. KANOWSKI. 2007. Old field vegetation succession in the Neotropics. *In* R. J. Hobbs, and K. N. Suding (Eds.). *New models for ecosystem dynamics and restoration*, pp. 163–194. Island Press, Washington, District of Columbia.
- EWEL, J. J., AND S. W. BIGELOW. 1996. Plant life-forms and tropical ecosystem functioning. *In* G. H. Orians, R. Dirzo, and J. H. Cushman (Eds.). *Biodiversity and ecosystem processes in tropical forests*, pp. 101–126. Springer-Verlag, Berlin.
- EWEL, J. J., AND F. E. PUTZ. 2004. A place for alien species in ecosystem restoration. *Front. Ecol. Environ.* 2: 354–360.
- FLORENTINE, S. K., AND M. E. WESTBROOKE. 2004. Restoration on abandoned tropical pasturelands – do we know enough? *J. Nat. Conserv.* 12: 85–94.
- FREEMAN, A. N. D., C. P. CATTERALL, AND K. FREEBODY. 2015. Use of restored habitat by rainforest birds is limited by spatial context and species' functional traits but not by their predicted climate sensitivity. *Biol. Cons.* 186: 107–114.
- FRIDAY, J. B., S. CORDELL, C. P. GIARDINA, F. INMAN-NARAHARI, N. KOCH, J. J. LEARY, C. M. LITTON, AND C. TRAUERNICHT. 2015. Future directions for forest restoration in Hawai'i. *New Forest.* 46: 733–746.
- GANADE, G. 2007. Processes affecting succession in old fields of Brazilian Amazonia. *In* R. J. Hobbs, and K. N. Suding (Eds.). *New models for ecosystem dynamics and restoration*, pp. 75–92. Island Press, Washington, District of Columbia.
- GOOSEM, M., C. PAZ, R. FENSHAM, N. PREECE, S. GOOSEM, AND S. G. LAURANCE. 2016. Forest age and isolation affect the rate of recovery of plant species diversity and community composition in secondary rain forests in tropical Australia. *J. Veg. Sci.* 27: 504–514.
- GOOSEM, S., AND N. I. J. TUCKER. 2013. *Repairing the rainforest*, (2nd Edition). Wet Tropics Management Authority and Biotropica Pty. Ltd, Cairns, Queensland.
- GUARIGUATA, M. R., AND R. OSTERTAG. 2001. Neotropical secondary forest succession: changes in structural and functional characteristics. *For. Ecol. Manage.* 148: 185–206.
- GUNARATNE, A. M. T. A., C. V. S. GUNATILLEKE, I. A. U. N. GUNATILLEKE, H. M. S. P. MADAWALA WEERASINGHE, AND D. F. R. P. BURSLEM. 2010. Barriers to tree seedling emergence on human-induced grasslands in Sri Lanka. *J. Appl. Ecol.* 47: 157–165.
- HARTIG, K., AND E. BECK. 2003. The bracken fern (*Pteridium arachnoideum* (Kaulf.) Maxon) dilemma in the Andes of Southern Ecuador. *Ecotropica* 9: 3–13.
- HOBBS, R. J., E. HIGGS, AND J. A. HARRIS. 2009. Novel ecosystems: implications for conservation and restoration. *Trends Ecol. Evol.* 24: 599–605.
- HOLL, K. D. 2007. Old field vegetation succession in the Neotropics. *In* R. J. Hobbs, and K. N. Suding (Eds.). *New models for ecosystem dynamics and restoration*, pp. 93–117. Island Press, Washington, District of Columbia.
- HOLL, K. D., AND T. M. AIDE. 2011. When and where to actively restore ecosystems? *For. Ecol. Manage.* 261: 1558–1563.
- HOLL, K. D., M. E. LOIK, E. H. V. LIN, AND I. A. SAMUELS. 2000. Tropical montane forest restoration in Costa Rica: overcoming barriers to dispersal and establishment. *Restor. Ecol.* 8: 339–349.
- HOOPER, E., P. LEGENDRE, AND R. CONDITT. 2005. Barriers to forest regeneration of deforested and abandoned land in Panama. *J. Appl. Ecol.* 42: 1165–1174.
- JANK, L., S. C. BARRIOS, C. B. DO VALLE, R. M. SIMEÃO, AND G. F. ALVES. 2014. The value of improved pastures to Brazilian beef production. *Crop Pasture Sci.* ?????-?????. doi:10.1071/CP13319.
- JANZEN, D. H. 1990. An abandoned field is not a tree fall gap. *Vida Silvestre Neotrop.* 2: 64–67.
- KANOWSKI, J., C. P. CATTERALL, AND W. NEILAN. 2008. Potential value of weedy regrowth for rainforest reforestation. *Ecol. Manage. Restor.* 9: 88–99.
- KEPPEL, G., AND D. WATLING. 2011. Ticking time bombs—current and potential future impacts of four invasive plant species on the biodiversity of lowland tropical rainforests in south-east Viti Levu, Fiji. *South Pacific J. Nat. Appl. Sci.* 29: 43–45.
- KNOKE, T., J. BENDIX, P. POHLE, U. HAMER, P. HILDEBRANDT, K. ROOS, A. GERIQUE, M. L. SANDOVAL, L. BREUER, A. TISCHER, AND B. SILVA. 2014. Afforestation or intense pasturing improve the ecological and economic value of abandoned tropical farmlands. *Nat. Commun.* 26: 5612.
- LAMB, D., P. D. ERSKINE, AND J. A. PARROTTA. 2005. Restoration of degraded tropical forest landscapes. *Science* 310: 1628–1632.
- LAURANCE, W. F., D. C. USECHE, J. RENDEIRO, M. KALKA, C. J. BRADSHAW, S. P. SLOAN, S. G. LAURANCE, M. CAMPBELL, K. ABERNETHY, P. ALVAREZ, AND V. ARROYO-RODRIGUEZ. 2012. Averting biodiversity collapse in tropical forest protected areas. *Nature* 489: 290–294.
- LETCHER, S. G., AND R. L. CHAZDON. 2009. Lianas and self-supporting plants during tropical forest succession. *For. Ecol. Manage.* 257: 2150–2156.
- LIHSTEIN, J. W., H. R. GRAU, AND R. ARAGON. 2004. Recruitment limitation in secondary forests dominated by an exotic tree. *J. Veg. Sci.* 15: 721–728.
- LOCATELLI, B., C. P. CATTERALL, P. IMBACH, C. KUMAR, R. LASCO, E. MARÍN-SPIOTTA, B. MERCER, J. POWERS, N. SCHWARTZ, AND M. URIARTE. 2015. Tropical reforestation and climate change: Beyond carbon. *Restor. Ecol.* 23: 337–343.
- LOHBECK, M., L. POORTER, E. LEBRIJA-TREJOS, M. MARTÍNEZ-RAMOS, J. A. MEAVE, H. PAZ, E. A. PÉREZ-GARCÍA, I. E. ROMERO-PÉREZ, A. TAURO, AND F. BONGERS. 2013. Successional changes in functional composition contrast for dry and wet tropical forest. *Ecology* 94: 1211–1216.
- LOUYS, J., R. T. CORLETT, G. J. PRICE, S. HAWKINS, AND P. J. PIPER. 2015. Rewilding the tropics, and other conservation translocations strategies in the tropical Asia-Pacific region. *Ecol. Evol.* 4: 4380–4398.
- LOW, T. 1997. Tropical pasture plants as weeds. *Trop. Grassl.* 31: 337–343.
- LUGO, A. E. 2004. The outcome of alien tree invasions in Puerto Rico. *Front. Ecol. Environ.* 2: 265–273.
- MACK, R. N., D. SIMBERLOFF, W. M. LONSDALE, H. EVANS, M. CLOUT, AND F. A. BAZZAZ. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol. Appl.* 10: 689–710.

- MARTÍNEZ-GARZA, C., F. BONGERS, AND L. POORTER. 2013. Are functional traits good predictors of species performance in restoration plantings in tropical abandoned pastures? *For. Ecol. Manage.* 303: 35–45.
- MARTÍNEZ-RAMOS, M., A. PINGARRONI, J. RODRÍGUEZ-VELÁZQUEZ, L. TOLEDO CHELALA, I. ZERMEÑO-HERNÁNDEZ, AND F. BONGERS. 2016. Natural forest regeneration and ecological restoration in human modified tropical landscapes. *Biotropica* 48: ????-????.
- MARTINS, A. M., AND V. L. ENGEL. 2007. Soil seed banks in tropical forest fragments with different disturbance histories in southern Brazil. *Ecol. Eng.* 31: 165–174.
- MCALPINE, C., C. P. CATTERALL, R. M. MAC NALLY, D. LINDENMAYER, J. L. REID, K. D. HOLL, A. F. BENNETT, R. K. RUNTING, K. WILSON, R. J. HOBBS, L. SEABROOK, S. CUNNINGHAM, A. MOILANEN, M. MARON, L. SHOO, I. LUNT, P. VESK, L. RUMPF, T. G. MARTIN, J. THOMSON, AND H. POSSINGHAM. 2016. Integrating plant- and animal-based perspectives for more effective restoration of biodiversity. *Front. Ecol. Env.* 14: 37–45.
- MCCONKEY, K. R., S. PRASAD, R. T. CORLETT, A. CAMPOS-ARCEIZ, J. F. BRODIE, H. ROGERS, AND L. SANTAMARIA. 2012. Seed dispersal in changing landscapes. *Biol. Cons.* 146: 1–13.
- MEYER, J.-Y. 2004. Threat of invasive alien plants to native flora and forest vegetation of Eastern Polynesia. *Pac. Sci.* 58: 357–375.
- MYERS, R. J. K., AND G. B. ROBBINS. 1991. Sustaining productive pastures in the tropics 5. Maintaining productive sown grass pastures. *Trop. Grassl.* 25: 104–110.
- NEILAN, W., C. P. CATTERALL, J. KANOWSKI, AND S. MCKENNA. 2006. Do frugivorous birds assist rainforest succession in weed dominated oldfield regrowth of subtropical Australia? *Biol. Cons.* 129: 393–407.
- NESPER, M., E. K. BÜNEMANN, S. J. FONTE, I. M. RAO, J. E. VELÁSQUEZ, J. B. RAMÍREZ, D. HEGGLIN, E. FROSSARD, AND A. OBERSON. 2015. Pasture degradation decreases organic P content of tropical soils due to soil structural decline. *Geoderma* 257–258: 129–133.
- NORDEN, N., H. A. ANGARITA, F. BONGERS, B. FINEGAN, I. GRANZOW DE LA CERDA, E. LEBRIJA-TREJOS, M. MARTÍNEZ-RAMOS, J. MEAVE DEL CASTILLO, R. MESQUITA, M. VAN BREUGEL, J. VANDERMEER, G. B. WILLIAMSON, AND R. L. CHAZDON. 2015. Successional dynamics in Neotropical forests are as uncertain as they are predictable. *Proc. Natl Acad. Sci. USA* 112: 8013–8018.
- ORTEGA-PIECK, A., F. LÓPEZ-BARRERA, N. RAMÍREZ-MARCIAL, AND J. G. GARCÍA-FRANCO. 2011. Early seedling establishment of two tropical montane cloud forest tree species: the role of native and exotic grasses. *For. Ecol. Manage.* 261: 1336–1343.
- OSTERTAG, R., L. WARMAN, S. CORDELL, AND P. M. VITOUSEK. 2015. Using plant functional traits to restore Hawaiian rainforest. *J. Appl. Ecol.* 52: 805–809.
- PARKE, T., M. DELANEY, M. DUNPHY, R. WOODFORD, H. BOWER, S. BOWER, D. BAILEY, R. JOSEPH, J. NAGLE, T. ROBERTS, AND S. LYMBURNER. 2012. Big Scrub: A cleared landscape in transition back to forest? *Ecol. Manage. Restor.* 13: 212–223.
- PAUL, M., C. P. CATTERALL, J. KANOWSKI, AND P. C. POLLARD. 2012. Recovery of rain forest soil seed banks under different reforestation pathways in eastern Australia. *Ecol. Manage. Restor.* 13: 144–152.
- PAUL, M., C. P. CATTERALL, P. C. POLLARD, AND J. KANOWSKI. 2010. Recovery of soil properties and functions in different rainforest restoration pathways. *Forest Ecol. Manage.* 259: 2083–2092.
- PAUL, G. S., AND J. B. YAVITT. 2011. Tropical vine growth and the effects on forest succession: a review of the ecology and management of tropical climbing plants. *Bot. Rev.* 77: 11–30.
- REID, J. L., AND K. D. HOLL. 2013. Arrival = survival. *Restor. Ecol.* 21: 153–155.
- REID, J. L., K. D. HOLL, AND R. K. ZAHAWI. 2015. Seed dispersal limitations shift over time in tropical forest restoration. *Ecol. Appl.* 25: 1072–1082.
- REID, J. L., C. D. MENDENHALL, T. A. ROSALES, R. A. ZAHAWI, AND K. D. HOLL. 2014. Landscape context mediates avian habitat choice in tropical forest restoration. *PLoS ONE* 9: e90573.
- ROBINSON, R. C., E. SHEFFIELD, AND J. M. SHARPE. 2010. Problem ferns: their impact and management. *In* K. Mehlreter, L. R. Walker, and J. M. Sharpe (Eds.). *Fern ecology*, pp. 255–322. Cambridge University Press, New York, New York.
- SANGER, J. C., J. KANOWSKI, C. P. CATTERALL, AND R. WOODFORD. 2008. Restoration of forest structure in managed regrowth at Rocky Creek Dam, Australia. *Ecol. Manage. Restor.* 9: 143–145.
- SCHENK, J. R. 2009. Phytochemistry, allelopathy and the capability attributes of camphor laurel (*Cinnamomum camphora* (L. Ness & Eberm.)). PhD Dissertation, Southern Cross University, Lismore, Australia.
- SCHLAEPPER, M. A., D. F. SAX, AND J. D. OLDEN. 2011. The potential conservation value of non-native species. *Conserv. Biol.* 25: 428–437.
- SCHNITZER, S. A., AND F. BONGERS. 2011. Increasing liana abundance and biomass in tropical forests: emerging patterns and putative mechanisms. *Ecol. Lett.* 14: 397–406.
- SHONO, K., E. A. CADAWENG, AND P. B. DURST. 2007. Application of assisted natural regeneration to restore degraded tropical forestlands. *Restor. Ecol.* 15: 620–626.
- SHOO, L. P., AND C. P. CATTERALL. 2013. Stimulating natural regeneration of tropical forest on degraded land: approaches, outcomes and information gaps. *Restor. Ecol.* 21: 670–677.
- SHOO, L. P., K. FREEBODY, J. KANOWSKI, AND C. P. CATTERALL. 2016. Slow recovery of tropical old field rainforest regrowth and the value and limitations of active restoration. *Conserv. Biol.* 30: 121–132.
- SIMBERLOFF, D., J. MARTIN, P. GENOVESI, V. MARIS, D. A. WARDLE, J. ARONSON, F. COURCHAMP, B. GALIL, E. GARCCIA-BERTHOU, M. PASCAL, P. PYSEK, R. SOUSA, E. TABACCHI, AND M. VILA. 2013. Impacts of biological invasions - what's what and the way forward. *Trends Ecol. Evol.* 28: 58–66.
- STEWART, B. 2000. Camphor Laurel (*Cinnamomum camphora*) seed and seedling ecology in forest and plantation sites near Mullumbimby, NSW. *Ecol. Manage. Restor.* 1: 142–144.
- SUN, D., AND G. R. DICKINSON. 1996. The competition effect of *Brachiaria decumbens* on the early growth of direct-seeded trees of *Alphitonia petriei* in tropical North Australia. *Biotropica* 28: 272–276.
- TEITZEL, J. K. 1992. Sustainable pasture systems in the humid tropics of Queensland. *Trop. Grassl.* 26: 196–205.
- TOH, I., M. GILLESPIE, AND D. LAMB. 1999. The role of isolated trees in facilitating tree seedling recruitment at a degraded subtropical rainforest site. *Restor. Ecol.* 7: 288–297.
- UHL, C., R. BUSCHBACHER, AND E. A. S. SERRAO. 1988. Abandoned pastures in eastern Amazonia. I. Patterns of plant succession. *J. Ecol.* 76: 663–681.
- WAHUNGU, G. M., C. P. CATTERALL, AND M. F. OLSEN. 1999. Selective herbivory by red-necked pademelon *Thylogale thetis* at rainforest margins: factors affecting predation rates. *Aust. J. Ecol.* 24: 577–586.
- Walker, L. R., J. Walker, and R. J. Hobbs (Eds.). 2007. *Linking restoration and ecological succession*. Springer, New York, New York.
- WEBB, L. J., L. G. TRACEY, AND W. T. WILLIAMS. 1972. Regeneration and pattern in the subtropical rain forest. *J. Ecol.* 60: 675–695.
- WRIGHT, S. J., K. E. STONER, N. BECKMAN, R. T. CORLETT, R. DIRZO, H. C. MULLER-LANDAU, G. NUÑEZ-ITURRI, C. A. PERES, AND B. C. WANG. 2007. The plight of large animals in tropical forests and the consequences for plant regeneration. *Biotropica* 39: 289–291.
- YEO, W. L. J., AND R. J. FENSHAM. 2014. Will Acacia secondary forest become rainforest in the Australian Wet Tropics? *For. Ecol. Manage.* 331: 208–217.
- ZAHAWI, R. A., AND C. K. AUGSPURGER. 1999. Early plant succession in abandoned pastures in Ecuador. *Biotropica* 31: 540–552.
- ZANCOLA, B. J., C. WILD, AND J.-M. HERO. 2000. Inhibition of *Ageratina riparia* (Asteraceae) by native Australian flora and fauna. *Austral Ecol.* 25: 563–569.
- ZAVALETA, E. S., R. J. HOBBS, AND H. A. MOONEY. 2001. Viewing invasive species removal in a whole-ecosystem context. *Trends Ecol. Evol.* 16: 454–459.
- ZIMMERMAN, J. K., T. M. AIDE, AND A. E. LUGO. 2007. Implications of land use history for natural forest regeneration and restoration strategies in Puerto Rico. *In* R. J. Hobbs, and K. N. Suding (Eds.). *New models for ecosystem dynamics and restoration*, pp. 51–74. Island Press, Washington, District of Columbia.

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