

Biodiversity and ecosystem services: lessons from nature to improve management of planted forests for REDD-plus

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Abstract Planted forests are increasingly contributing wood products and other ecosystem services at a global scale. These forests will be even more important as carbon markets develop and REDD-plus forest programs (forests used specifically to reduce atmospheric emissions of CO₂ through deforestation and forest degradation) become common. Restoring degraded and deforested areas with long-rotation planted forests can be accomplished in a manner that enhances carbon storage and other key ecosystem services. Knowledge from natural systems and understanding the functioning novel of

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ecosystems can be instructive for planning and restoring future forests. Here we summarize information pertaining to the mechanisms by which biodiversity functions to provide ecosystem services including: production, pest control, pollination, resilience, nutrient cycling, seed dispersal, and water quality and quantity and suggest options to improve planted forest management, especially for REDD-plus.

Keywords Biodiversity · REDD-plus · Ecosystem services · Planted forest · Forest management · Plantation

Introduction

The estimated rate of decline of global natural forest area is 13 million ha/year. Despite this loss, the area of planted forests¹ has increased annually by an average of 5 million ha, between 2000 and 2010, and now represents ~7 % (264 million ha) of the total global forest (FAO 2010). A significant proportion of these planted forests are plantations,² which may be distinguished from other planted forests by the objectives for their establishment and intensity of management; so those managed primarily for timber and other wood products as opposed to planted forests with many objectives such as sustainability, recreation, food, and carbon storage (Brockerhoff et al. 2008). The extent of plantation forests has been increasing in area by ca. 2 % annually between 1990 and 2005, to an estimated 140.8 million ha, or ca. 4 % of the global forest area (FAO 2010). At present, about 75 % of the world's plantations are comprised of native species and 25 % use exotic species (FAO 2010). Exotic species plantations (typically pines, eucalypts, acacias, and teak) are most common in South America, Southeast Asia, and Oceania and much of the plantation area is through afforestation.

As a result of a high rate of deforestation over the past 40 years (FAO 2010), planted forests have become increasingly important as sources of wood products. Carle and Holmgren (2008) estimated that plantation forests will increase by an additional 32 % (vs. area in 2005) and supply 53 % of global roundwood by 2030. More recently, climate change mitigation, through enhancement of forest carbon sequestration and avoided deforestation, has begun through private initiatives for carbon credits. REDD-plus mechanisms, a form of payment for ecosystem services from forests (Parrotta et al. 2012; Pawson et al. 2013), will soon become a major focus for reforestation and recovery of degraded lands, especially in tropical areas. REDD-plus is a climate mitigation mechanism agreed to under the UN framework convention on climate change (UNFCCC) to reduce carbon emissions from deforestation and degradation and to enhance forest carbon stocks, especially in developing countries. As climate continues to change, however, it is important for managers to consider ways to adapt planted forests to sustain their mitigation value in the future.

Ecosystem processes, or functions, are the many actions performed by species in ecosystems, such as photosynthesis, respiration, decomposition, water purification, mutualism, competition, and predation (Cardinale et al. 2011; Parrotta et al. 2012). These processes transfer energy and nutrients across food webs (Polis and Strong 1996). Ecosystem

¹ Forests predominantly composed of trees established through planting and deliberate seeding (FAO 2010).

² Forest of introduced species and in some cases native species, established through planting or seeding mainly for production of wood or non-wood forest products (FAO 2010).

processes of direct value to humans are referred to as ‘ecosystem services’ and include provisioning, regulating, supporting, and cultural services, for example, carbon storage, pollination, pest reduction, food, and recreation (Diaz et al. 2005). Ecosystem functioning can increase with the amount of biodiversity in an ecosystem (Balvanera et al. 2006), although some processes may be dominated by the most functional species (Diaz and Cabido 2001; Petchey and Gaston 2002; Hoehn et al. 2008). The relationship between biodiversity and ecosystem functioning is complex however, and at high species levels, it may be obscured by competition for limiting resources and climate change effects (Mittelbach et al. 2001; Traill et al. 2010; Laliberté and Tylianakis 2012). Some ecosystem services are more dependent on biodiversity (or specific species) than others, and many biodiversity-related services result primarily in local benefits as opposed to benefits at larger scales (Guariguata and Balvanera 2009).

Ecosystem processes and services are reduced or lost from natural ecosystems, as a result of disturbances (mostly anthropogenic), through hierarchical nested thresholds that reflect species declines at various trophic levels (Dobson et al. 2006). At low trophic levels, most ecosystem functioning is controlled by a relative few common species, but there is a high level of redundancy among species (Diaz and Cabido 2001; Petchey and Gaston 2002). Therefore, some loss of species at low trophic levels may not necessarily be catastrophic to ecosystem functioning. At high trophic levels, however, predators are often relatively rare and have little or no redundancy (Terborgh et al. 2001; Estes et al. 2011). Losses of predators can have large consequences for ecosystems owing to a loss in regulation of herbivores, many of which become forest pests (Estes et al. 2011). Sufficient species loss at any level, especially of keystone species, can produce a change in the ecosystem state (Groffman et al. 2006) and in changing environments, species diversity provides a buffer against the loss of processes (Isbell et al. 2011).

Climate change also alters ecosystem processes at small and large scales, through changes in temperature, moisture, fertilisation effects, and increased severe weather events (e.g. Parrotta et al. 2012). These factors alter the most fundamental processes of photosynthesis, decomposition, and respiration, with consequences for ecosystem assembly and services in the future (Traill et al. 2010). Climate change has become a major cause of global species loss, often as a synergistic effect with direct anthropogenic effects (Thomas et al. 2004; Brook et al. 2008; Hellmann et al. 2008) and enhancing existing mortality factors (Allen et al. 2010). These effects, coupled with variability among species responses to climate change, result in a high level of uncertainty about consequences for ecosystems. Nevertheless, species are already responding through altered ranges with consequences for ecosystems and this process will be exacerbated as organisms respond to further climate and habitat changes (Davis and Shaw 2001). Increased successful invasions by exotic species are also predicted (Brook et al. 2008; Traill et al. 2010) and are already occurring for many pest species that are altering ecosystems, including trees, mammals, and insects (Mack et al. 2000; Van Wilgen et al. 2001; Tompkins et al. 2013). Changes in species and conditions have important implications for planning REDD-plus forests with respect to maintaining desired services.

We summarise key linkages between biodiversity and ecosystem services that forest managers should consider in planted forests, especially to enhance long-term carbon storage, including productivity, soil processes, pest control services, pollination, resilience, and water quality and quantity (see Supplementary material). We use a reductionist approach to discuss individual mechanisms and then take a broader ecosystem approach to relate how these mechanisms could be used to improve the provision of ecosystem services. We pose the question: under a changing climate, can an understanding of the

ecosystem functions that are related to biodiversity be used to improve the likelihood that planted forests will achieve REDD objectives of maximising carbon storage, while enhancing the provision of other ecosystem services? We specifically distinguish industrial short-rotation (or fastwood) ‘plantations’, typified by their low species richness, few management objectives (i.e., mostly for wood products), and short rotation lengths, typically <10 year for *Eucalyptus* spp. and <25 year for *Pinus* spp., from the much longer rotation of ‘planted forests’, where management maintains many characteristics of natural forest ecosystems for multiple objectives (Pawson et al. 2013). Fastwood forest types are not developed as functional ecosystems and so will store less carbon than planted forests that are intended to be managed sustainably over longer rotations, with carbon stored in trees, soils, dead wood, and ground covers including litter (Guo and Gifford 2002; He et al. 2013). We suggest practices to use or avoid in plantations and planted forests for REDD-plus (Table 1), given the certainty of climate change effects on forests, including more or less rainfall, increased fire, extreme weather events, fertilisation effects, altered pest species regimes, and increased soil respiration (Pawson et al. 2013).

Ecosystem services and forest management

Production

The relationship between biodiversity and productivity in natural and managed ecosystems has been the focus of ecological research for more than two decades, but interest in this relationship goes back to the late 18th century, with debate over the relative merits of single-versus mixed-species silviculture (Pretzsch 2005 referring to von Cotta from 1828). The relationship between biodiversity, species richness, and net primary productivity is complex, governed by many abiotic factors such as climate, precipitation and temperature regimes, soil properties, limiting nutrients, and by biotic feedback (Willig 2011). Research in temperate grassland systems has demonstrated positive diversity-productivity effects (Mittelbach et al. 2001). In forests, however, the few studies have not been as conclusive (Waide et al. 1999; Thompson et al. 2009; Vilà et al. 2013) due to the structural complexity of forest ecosystems and the longevity, size, and diversity of trees (Leuschner et al. 2009). Further, at a landscape scale, ecosystem processes can be affected by fragmentation and edge effects that exacerbate species losses and population declines that, in turn, affect ecosystem functioning (Laurance et al. 2007).

Current theory and increasing empirical evidence suggests that biodiversity promotes net primary productivity in forests and other terrestrial ecosystems via three main mechanisms. The first is niche complementarity (Loreau et al. 2001), whereby different species use different resources or the same resources in different ways, resulting in enhanced resource use and reduced competition (Cardinale et al. 2004; Tylianakis et al. 2008; Zhang et al. 2011). Complementarity depends on species performing functions in different ways, thus, the strongest increase in functioning is observed when species have different functional traits (Diaz and Cabido 2001; Fontaine et al. 2006; Hoehn et al. 2008). Furthermore, there is evidence that turnover of species among regions (Loreau et al. 2003) and evenness in abundances of several species also promote ecosystem functioning, including productivity (Zhang et al. 2012).

The second mechanism is facilitation, whereby species provide resources, or alter the environment, enabling other species to perform better (Cardinale et al. 2002; Forrester et al. 2006; Kelty 2006). For example, many studies have demonstrated the facilitative

Table 1 Examples of practices to use in plantations and planted forests that will enhance the ecosystem services and for planted forest results in increased carbon storage

Ecosystem service	Fastwood exotic	Semi-natural planted or assisted natural
Production	Increase species mix; encourage understory	Improve soils using multi-species; plant close to natural forest; use reduced impact logging
Pest control	Plant close to natural forest; enhance landscape connectivity	Plan to maintain predator habitat; allow dead wood to stand; avoid congener proximity
Nutrient cycling and decomposition	Leave residual deadwood and encourage litter accumulation	Leave residual deadwood and encourage litter accumulation; inoculate soils as required; plant near natural forest
Seed dispersal	N/A	Plant close to natural forest; consider habitat availability for seed dispersing species
Pollination	N/A	Plant close to natural forest; foster habitats for local pollinators
Water quality and quantity	Reduce use of species with high water demand; reduce spacing; leave and accumulate litter and branches; use mixed species; use 2 or 3 pass harvesting	Use selection harvesting and reduced impact logging; increase litter quality; avoid riparian zones
Resilience	N/A	Base harvesting plan on natural ecosystem dynamics; improve habitats for top predators; plan for stand and landscape heterogeneity; understand and avoid thresholds

N/A not applicable: plantations are planted and so require no seed dispersal or pollination, and as they are logged and replanted, they have no resilience

effect of planting nitrogen-fixing species with non-nitrogen fixing trees (Forrester et al. 2006). Nitrogen limitation may be exacerbated as a result of climate-change-related reduced soil moisture (Groffman et al. 2012). Facilitation is also often used as a silvicultural tool to grow desired shade-tolerant tree species beneath faster growing pioneer tree species. The final mechanism is the ‘sampling effect’, whereby there is a higher probability that a highly productive species will be included in a large group of species compared to a smaller group (Cardinale et al. 2006).

While biodiversity-productivity relationships in complex natural forests remain somewhat obscure, studies of forest systems involving two or more planted tree species have found positive relationships between species richness and evenness, and above-ground productivity (Healy et al. 2008; Nadrowski et al. 2010; Potvin et al. 2011), especially at small scales. Tree plantations may achieve higher production for a range of species combinations, if species mixes involve complementary resource use and facilitation of growth of one species by another (Piotto 2008; Forrester et al. 2006; Kelty 2006). A meta-analysis of 54 studies of single-species and mixed plantations by Zhang et al. (2012) found an average of 23.7 % higher productivity in forest polycultures than in monocultures. The latter analysis indicated that evenness and heterogeneity of shade tolerance explained 63 % of the observed variation in productivity, while species richness and stand age explained an additional 28 %.

Support is emerging for the idea that the coexistence of functionally different species increases forest productivity especially in low production, high stress environments. In more productive environments, dominant and highly productive species competitively dominate and so complementary effects are smaller or less frequent (Potter and Woodall 2013). Interactions between a given pair of species will change spatially and temporally as resource availabilities and climatic conditions change (Forrester 2014). Further, for a given species, complementarity can increase as growing conditions improve, such as when species interactions improve light-use efficiency (Forrester 2014). Interactions that improve nutrient or water availability could become increasingly useful, and improve complementary effects, as nutrient and water availability declines, respectively (Forrester 2014). These dynamics may explain why biodiversity-productivity relationships have been difficult to observe in some studies (e.g. Forrester et al. 2006; Thompson et al. 2009; Vilà et al. 2013). For example, no relationship was found between species richness and either above-ground or below-ground biomass or litter in naturally regenerating conifer stands in China, ranging from 5 to 310 years (Zhang et al. 2011). Similarly, Firm et al. (2007) found a negative relationship between overstory plant diversity and productivity in 23–72-year-old planted forests of various native and introduced timber species in Australia, where natural regeneration of native woody species had already enriched the plantations. Hence, knowledge of local ecosystems is required to understand species interactions.

Conclusions for REDD planted forest managers

Management decisions that influence both biodiversity and productivity will play a key role in determining outcomes of REDD-plus strategies for enhancement of forest carbon stocks. Many deforested sites can naturally revert to highly productive species-rich secondary forest if the pressures on them (such as biomass harvesting, grazing, fire, etc.) are lifted, particularly those that are located in proximity to biodiversity-rich native forests, and if they retain some residual trees, seedling banks, and soil seed stores of native species (Parrotta et al. 1997; Carnus et al. 2006; Brockerhoff et al. 2008).

Planted forests provide an alternative to restore ecosystem productivity and enhance carbon sequestration on sites that do not meet the above criteria, for example where soils and local biota have been severely degraded, such as in abandoned agricultural landscapes that have become dominated by fire-prone grasses. Productivity (and carbon sequestration) is highly likely to be increased in mixed-species forest, relative to plantation monocultures, if mixes result in complementary resource use and facilitation among species (Piotto et al. 2003; Kelty 2006). Species mixtures may also eliminate the need for expensive fertilization. For planted forests, key management decisions include (a) the choice of appropriate species mixtures considering the adaptability to local site conditions of soils, aspect, climatic tolerances, and species interactions and (b) intensity of management, including site preparation, pre-harvest management, rotation lengths (which may have short term and longer-term positive or negative effects on productivity), and practices that either encourage or discourage enrichment of planted forest flora (and biota of other trophic levels) via natural in-filling by non-planted species, such as reduced impact logging. Whether the planted species are native or exotic does not necessarily have a direct influence on productivity, instead site adaptability and possible complementarity and facilitation relationships are the main determinants. Longer rotation native planted forests harbour greater biodiversity (at different trophic levels) and so should be less susceptible to productivity losses due to insects and diseases, than simpler systems with few tree species (Jactel and Brockerhoff 2007).

Fastwood exotic plantations are typically highly productive but low in species richness relative to other planted forest types. Since a significant proportion of the production is lost at short intervals via harvests, their value for directly meeting REDD-plus objectives is limited. Nevertheless, short-term productivity in plantations may be enhanced by applying ecological principles, including judicious use of mixed species plantings and management practices that favour even short-term biodiversity development within plantations. Such forests can be used to offset some logging in primary forests, increasing positive REDD-plus benefit, and so better growth offsets more logging of primary forests.

Nutrient cycling and decomposition

Nutrient cycling is an important, primarily bottom-up, process that strongly affects soil fertility by making nutrients from dead plant material biologically available to green plants (Harris 2009; Sylvain and Wall 2011). Nutrient cycling is affected by temperature, moisture, and soil type (Vitousek and Sanford 1986) and is largely performed by animals, bacteria, moulds, and fungi in the soil and detritus. Nutrient cycling includes a complex food-web of herbivores, fungivores, and carnivores with diverse processes. For example, termites and fungi, which are sensitive to the extent and severity of forest disturbances, play an important role in wood litter decomposition, and require that dead wood be supplied or left on the forest floor (Davies et al. 1999; Schuurman 2005). Similarly, detritivores require the presence of a permanent litter layer (Harris 2009). Restoring these processes in degraded soils may take active management, including the use of N-fixing plants, because soil community recovery is slow and depends on the level of forest degradation (Davies et al. 1999; Macedo et al. 2008; Amazonas et al. 2011).

Some types of tropical soils are notably poor and so a rapid rate of nutrient cycling is necessary for trees to grow. On these soils, the replacement of mixed species forests with fastwood plantations has severe consequences for productive capacity because much of the nutrients are stored in autotroph biomass (DeAngelis et al. 1989), especially phosphorus that is limiting in most tropical systems (Vitousek 1984; Cleveland et al. 2011). A detritus compartment can buffer and increase the resilience to disturbances on living components in soils, and systems are slow to recover from perturbations affecting the detritus (Ewel et al. 1991; Laliberté et al. 2010). Individual species effects are important in reducing nutrient leaching (Ewel and Bigelow 2011) and Macedo et al. (2008) found that the use of leguminous tree species restored C and N cycling in depleted tropical soils. Tree diversity, in part, is important for maintaining the N and P pools in tropical plantations (Zeugin et al. 2010) but depends initial site conditions (Redondo-Brenes and Montagnini 2006), making it difficult to generalise about nutritional interactions among tree species (Rothe and Binkley 2001). Nutrient levels are also affected by plant species richness, with reduced species numbers leading to nutrient limitations (e.g. Firn et al. 2007; Inagaki et al. 2010). For example, Ewel et al. (1991) showed that poor soils developed under monoculture forests in Costa Rica. Similarly, fertilisation is required to maintain growth rates in many *Eucalyptus* plantations, where soils readily become depleted (Smethurst et al. 2004; Laclau et al. 2010).

The amount and rate of nutrient cycling is partly affected by herbivores through litterfall and dung (Fonte and Schowalter 2005). Insect herbivores can increase soil N and P fluxes by as much as 30 % in tropical rainforests through their frass (Schowalter et al. 2011) and defecation by monkeys and other vertebrate herbivores, with further processing by dung beetles, contributes to improving soils, ultimately affecting carbon storage in these forests (Feeley and Terborgh 2005; Neves et al. 2010). Elevated decomposer performance reflects

high plant diversity and likely enhances autotrophic production, contributing to a positive relationship between plant diversity and ecosystem functioning (Eisenhauer et al. 2012).

Ectomycorrhizal fungi are important symbionts on many tree species that improve root nutrient uptake and enhance growth rate (Allen et al. 2005). Loss of these fungi through poor management is responsible for declines tree productivity, as reported for *Eucalyptus* production in Australia (Horton et al. 2013). Fungi are primarily dispersed by wind but spores produced underground are dispersed by small mammals and arthropod fungivores (Johnson 1995; Lilleskov and Bruns 2005). Dispersal is severely limited by fragmentation and poor soil quality (Peay et al. 2010), absence of fungal dispersers in degraded forests (Nunez et al. 2009), and soil desiccation following disturbances (Ashton and Kelliher 1996), which can be related to open canopy cover (Ingleby et al. 1998).

Conclusions for REDD planted forest managers

REDD-plus forest development will need to consider soil improvement and redevelopment of soil food webs to maximise production and carbon storage. Under climate change, tropical forests may become drier, reducing soil processes even further and intensive use of many types of tropical sites will lead to nutrient depletion. Avoiding soil degradation is possible by planting multiple tree species, fostering understory species and ground covers, and eliminating fire, in part, by recovering moist soils. If soil litter is recalcitrant, inoculating with soil fauna and flora from natural forests will enhance decomposition (Allen et al. 2005). Planting REDD-plus forests near to existing natural forest can take advantage of multiple biodiversity-related mechanisms for soil improvement through dispersal and invasion by soil biota and herbivores from the natural forest. Better landscape connectivity, reduced fragmentation, and a higher percentage of forest on a landscape will lead to persistent occupation of planted forests by species than can help fertilize soils via dung input and disperse fungi. The use of N-fixing ground cover plants can assist restoration on sites where nitrogen has become limiting. Managers should be aware that most fastwood forests will eventually require nutrient input, but that employing mechanisms to support soil functions can reduce this requirement.

Pest and disease reduction

Plant diversity can decrease the rate of herbivory on focal plants through associational resistance to herbivores (Barbosa et al. 2009). Similarly, forest trees are less prone to pest insect damage when grown in mixed species stands rather than in monocultures (Brown and Ewel 1987; Jactel and Brockerhoff 2007; Castagneyrol et al. 2014). Although less studied, the same positive relationship exists between tree species diversity and resistance to diseases (Pautasso et al. 2005; Hantsch et al. 2013). Several mechanisms have been proposed to explain the pest and disease regulation service provided by tree species diversity. Bottom-up processes operate through tree to tree interactions. In host and non-host tree mixtures, the amount of available food for insect herbivores decreases with increasing tree diversity through resource dilution (Hambäck et al. 2000; Giffard et al. 2012) and reduced host tree apparency (Endara and Coley 2011; Dulaurent et al. 2012; Castagneyrol et al. 2013). Further, non-host tree volatiles can also disrupt olfactory-guided host choice by specialist herbivores (Zhang and Schlyter 2004; Jactel et al. 2011). The presence of non-host trees around focal trees may also slow the spread of root rot fungi through the interruption of root contact (Linden and Vollbrecht, 2002) and the spread of invasive pest at the landscape scale (Rigot et al. 2014). Schweizer et al. (2013) reported

that planting young trees near conspecific old trees resulted in reduced survival, higher levels of herbivory and diseases and slow growth rate, related to pests and diseases harboured by the older trees (Castagneyrol et al. 2014).

Tree species diversity can enhance insect pest control through the provision of suitable resources and habitats for predators. The species richness of insect predators is positively correlated with the number of plant and herbivore species (Castagneyrol and Jactel 2012). Generalist insect predators and parasitoids benefit from alternative herbivore prey associated with multiple tree species in mixed forests (Siemann et al. 1998; Jactel et al. 2006). Tree mixtures are also more likely to provide habitat for nectar-rich plants supplying insect parasitoids with complementary foods (Syme 1975; Hougardy and Grégoire 2000). Similarly, the persistence and richness of vertebrate predators depends on sufficient habitat. Habitats can be degraded at a landscape scale via fragmentation and habitat loss (Vié et al. 2009; Koh et al. 2010), or at a local scale through structural and compositional simplification of the forest (Lewis 2009) resulting in the loss of niche space. Loss of keystone predators can have large consequences for a system through cascading effects of expansion of herbivore populations (Estes et al. 2011). For example, birds are important predators of pest insects at chronic levels (Morrison and Lindell 2012; Giffard et al. 2012) and Bridgeland et al. (2010) showed that bird predation on herbivores improved tree growth by 20 % for *Populus* spp. Similarly, bat predation reduces insect herbivory in tropical forests (Kalka et al. 2008; Morrison and Lindell 2012). Mixtures of tree species can also provide more suitable habitat to antagonistic fungi that control fungal pathogens (Fedorov and Poleschuk 1981; Murray 1987).

Loss of predators can also have cascading effects on other functions within the ecosystem, such as nutrient cycling and plant community assemblage (Dunham 2007; Fornara and Du Toit 2007), including altered ecosystem state (Terborgh et al. 2001; Didion et al. 2009). Reduction in key predators leads to trophic cascades resulting in altered arboreal insect and soil faunas (Dyer and Letourneau 1999; Dunham 2007). Other studies, however, have shown predator inability to limit herbivores in some forests, especially during severe outbreaks (Strong et al. 2000; Schwenk et al. 2010) but none has quantified tree growth parameters as a response variable.

Mutualisms occur in complex forest ecosystems, such as between native trees and ants in tropical forests, and benefit the trees through reduced herbivory and resultant increased production (Floren et al. 2002; Gaume et al. 2005). Such mutualisms are often lacking in plantations where there can be a high incidence of pests (Kirton and Cheng 2007; Lombardero et al. 2008). The incidence of insect pests may be lower in exotic tree plantations (Zas et al. 2011; Lombardero et al. 2012) but this advantage may be offset by increased fungal attack, as for example on exotic pines (Zas et al. 2011) and eucalypts (Wingfield 2003). Braganca et al. (1998) found that *Eucalyptus* plantations harboured higher levels of lepidopteran pests than heterogeneous native forests in Brazil. Powers (1999) and Gadgil and Bain (1999) noted that some exotic plantations had low incidences of pests or diseases, which they attributed to the lack of native insect pests to attack phylogenetically isolated trees.

Although in a majority of cases, trees in mixed stands suffer lower losses to herbivory than those in pure stands (Brown and Ewel 1987; Jactel and Brockerhoff 2007), there are some reported cases of associational susceptibility (White and Whitham 2000), i.e., more herbivory damage in mixed forests. This mainly occurs when polyphagous insect herbivores first develop on preferred host trees and then spill over onto neighbouring tree species (Jactel and Brockerhoff 2007; Schuldt et al. 2010).

Forests can play an important role in providing alternative hosts and prey to maintain potential natural enemies (insects, spiders, and birds) of agricultural pests on broad landscapes (Bianchi et al. 2006). Resource and landscape heterogeneity positively affect insect natural enemies of agricultural insect pests, both at the landscape level (Tylianakis et al. 2008) and at the stand level (Langellotto and Denno 2004; Bisseleua et al. 2013). At the landscape scale, pest reduction service (and pollination) that can be expected for agricultural crops from nearby forests is directly related to total forest area and patch size (Tscharntke et al. 2008).

Conclusions for REDD planted forest managers

Avoiding disease and pest damage is crucial in recovering forests, maintaining ecosystem stability, and to maintain ecosystem services. A lower incidence of pests and diseases can be achieved by designing mixed species plantations and also through favouring the natural regeneration of diverse tree species in planted forests. At a landscape scale, interspersing plantations and planted forests would enable pest reduction services into the plantations from the planted longer rotation forests. The composition of the mixture for planted and plantation forests is often more important than the number of tree species per se. Even two species mixed plantations can improve forest resistance. To enhance bottom-up processes affecting pest regulation, managers can work to reduce host tree apparency by intermixing crop trees with fast growing ‘nurse’ species, which can then be removed selectively as a first fastwood crop. To favour top-down control by natural enemies, associated plant species providing complementary foods or shelter (e.g., cavities) should be preferred and attention to providing and maintaining habitat for key predators is important. In both cases, associated tree species that are phylogenetically distinct from the important crop species are of highest benefit and congeners should not be planted under existing trees of the same species. For example, mixtures of conifers and broadleaved trees are more likely to be resistant to a wide array of pests and pathogens. The relative share of species needs to be adjusted according to trade-offs between different planned ecosystem services.

Pollination

Pollination is a service that is strongly related to biodiversity that has been well-studied for agricultural production near forest ecosystems (e.g. Dobson et al. 2006). Approximately 87.5 % of flowering plants require animal pollination, including 78 % in temperate zone and 94 % in tropics (Ollerton et al. 2011), and pollination accounts for 35 % of global crop production (Klein et al. 2007). The value of pollination has been estimated to be billions of dollars, including for important crops such as coffee and cacao in the tropics (Costanza et al. 1997; Ricketts et al. 2004). No estimates have been made for pollination of forest trees.

Successful pollination rates increase with pollinator species richness (Kremen et al. 2002; Tylianakis et al. 2008). Vertebrate pollination by bats, rodents, monkeys, and birds is common in tropical regions, while insect pollination by bees, butterflies, beetles, and other arthropods is most common in the temperate zone (Bawa 1990). Many animals that pollinate flowers have specific relationships with certain plant species, mediated by morphology and phenology that have co-evolved (Stebbins 1970; Bawa 1990). Therefore, local extinction of pollinators often results in the eventual extinction of the plants that they pollinated (Biesmeijer et al. 2006). Moreover, because the distance between habitats of pollinators and agricultural fields affects success of seed set, local conservation of pollinators and their high quality forest habitats is crucial (Klein et al. 2003; Kennedy et al.

2013). For instance, the honey bees *Apis* spp. tend to nest in tree cavities that are more abundant in natural forests than in plantations. Therefore, distance to natural forest rather than plantation affects honey bee abundance and the amount of the seed set in crops (Ricketts et al. 2008; Taki et al. 2011). (Aizen and Feinsinger 1994) found a negative relationship between pollination services and forest fragmentation and reduced size of remnant fragment. On the other hand, Winfree et al. (2007) found that moderately disturbed landscapes with extensive forest still maintained most bee species and Taki et al. (2013) found that a range of stand ages was needed to maintain all bee species in a temperate forest landscape.

Conclusions for REDD planted forest managers

Local habitat conservation for pollinators is essential to maintain pollination services for planted forest ecosystems and associated agricultural fields, and keeping forest as a large percentage of the landscape will help ensure a high level of pollination by animals. This is important for REDD-plus forests where multiple services are desired, but unimportant for fastwood plantations. Specifically, maintaining several old and large trees with cavities per ha in planted stands could help to maintain social bee populations, thereby improving set in local crops. Many flowers in tropical forests tend to have co-evolved plant-pollinator relationships, both with arthropods and vertebrates, and so habitat conservation for nesting and feeding by pollinators at the landscape level is also important. A range of forest ages may be required to maintain bee species and local knowledge is needed to understand pollinator ecology. Further work is needed to determine the optimal amount of forest in a mixed forest and agriculture landscape.

Seed dispersal

Seed dispersal is an important process in planted forests where natural regeneration is expected to contribute to the tree density. Although seeds of many tree species are wind dispersed, many other tree and other plant seeds are only dispersed by herbivores and frugivores, especially in tropical forests. For example, in Mexico, Cortes-Flores et al. (2013) reported that 68 % of tree species were dispersed through zoochory. An absence or reduced populations of seed dispersing animals results in poor to no dispersal, especially for large-seeded trees (Anzures-Dadda et al. 2011; Brodie and Aslan 2012; Beaune et al. 2013). Also, because dispersal distances and food preferences differ among dispersers, it is the local suite of animals that is important to maintaining plant communities (Garcia and Martinez 2012; Gonzalez-Varo et al. 2013). The rate of seed germination for some species is enhanced by passage of seeds through mammalian endozoochory (Traveset 1998; Campos-Arceiz and Blake 2011). Absence of dispersal processes results in a homogenisation of forest plant species (Terborgh et al. 2008; Lehouck et al. 2009; Markl et al. 2012).

Proximity of seed sources affects seed dispersal processes to adjacent areas, and so habitat connectivity can improve the influx of animal-dispersed seeds, influencing the composition and structure of forests (LeHouck et al. 2009; Jesus et al. 2012). Animal species that simply drop seeds have effective distances of generally under 0.5 km (Wehncke and Dominguez 2007) but dispersal distances by seed-eaters is often many kilometres (Beaune et al. 2013). Available suitable forest habitat for the disperser species is important to supporting their populations (e.g. Anzures-Dadda et al. 2011; Uriarte et al. 2011). Although many ecosystem functions have functional redundancy among species, most evidence suggests that frugivores often provide complementary services (Gonzales et al. 2009). Hence, the loss of the seed

dispersers ultimately means a decline in local or regional tree species richness (Lehouck et al. 2009; Beaune et al. 2013; Bueno et al. 2013). Gonzales et al. (2009) found that, while that birds and bats competed for fruits in the dry season in the Philippines, both were important for ectozoochory of different plant species throughout the year. Seidler and Plotkin (2006) concluded that seed dispersal by mammals is a major process maintaining tree community structure over the long term in tropical forests and is a key mechanism explaining the pattern of low aggregation of conspecifics on tropical forest plots.

Conclusions for REDD planted forest managers

Protection of plant reproductive processes involves consideration of stand and landscape level context for planted forests, and the presence of persistent populations of seed dispersers sufficiently near to use the planted forests. For example, isolated stands in a fragmented landscape will suffer limited seed dispersal by animals and reduced tree species recruitment. In areas where large wildlife species populations have been eliminated, supplemental planting of tree species is needed to enable large-seeded tree species to survive, and only the longer-term reintroduction of frugivore populations into sufficient habitat will sustain these species (Brodie and Aslan 2012). Seed dispersal mechanisms provide models for how community assembly can be achieved in planted forests, for aspects such as tree species density and complementarity between species. Landscape connectivity and attention to increasing total forest area are important to maintaining dispersal processes in planted forests.

Water quantity and quality

Water is an important output from forest systems and water retention in forest soils is necessary for many processes including decomposition and nutrient cycling. Forests are important for maintaining water quantity and quality for domestic, agricultural, and industrial uses, and for flood and flow regulation. The process and mechanisms of both are similar; water vapour (fog and cloud) and precipitation becomes surface runoff and ground water with flows infiltrated through vegetation and soils, or is taken up by plants, and surface water and water in plants evaporates or is transpired (see Fig. 4 in Brauman et al. 2007). Although annual and long term change in water quantity is thought to be affected by climate change and deforestation, the degree of the effect from deforestation is not clear because many factors affect flows, such as irregular cyclic patterns of rainfall under quasi-biennial oscillation, El Niño occurrences, sunspot activity, equatorial heat transport, and human activities and the time lag between when an event and the output occurs at a regional scale (Bruijnzeel 2004; Oki and Kanae 2006). Differences in scale among the various factors and local water quantity makes assessing the direct effects of deforestation alone unclear (Bruijnzeel 2004). There are both positive and no correlation between a decrease of rainfall and loss of vegetation cover in the same region (Dirmeyer and Shukla 1994 in Amazon and Kanae et al. 2001 in Thailand for positive correlations; Costa et al. 2003 in cerrado in Brazil, for no effect). In Chile, the area of short-rotation plantations in small watersheds reduced water quantity and provided irregular flows relative to larger and more stable outputs from natural forest cover (Lara et al. 2009; Little et al. 2009). Similarly, in Panama, Sprenger et al. (2013) found that a mixture of tree species maintained a steady water flow compared to flows through monoculture stands. However, in Australia, Brown et al. (2007) found no relation between plantation establishment and the availability of water downstream. At a landscape scale, there was no effect of reforestation on water

flows where <20 % of a catchment basin was forested (Zhang et al. 2006), suggesting that forest restoration to affect water flow must be accomplished at a large scale.

Generally, ecosystem water use increases with ecosystem productivity (Law et al. 2002) and fast-growing species are often used in plantations and are therefore more likely to use more water negatively affecting local ground water supply and stream volume, such as acacias in South Africa (van Wilgen et al. 2001). Treatments for faster growth rates (fertilisation, thinning, etc.) can improve water-use efficiency (Binkley 2012). For example, *Eucalyptus* and *Acacia* mixtures produced 73 and 243 % more biomass than *Eucalyptus* and *Acacia* monocultures, respectively, but only transpired (annually) 17 and 93 % more water than the monocultures, respectively (Forrester et al. 2010). These species mixtures, on this site, produced the same stand biomass using 54 % of the land area and about two-thirds of the water that *Eucalyptus* monocultures would use (Forrester et al. 2010). The mixtures dried the soil more, however, and so any treatment that increases water use, regardless of efficiency, could potentially increase the susceptibility of the plantation to drought.

Water quality is related to both physical and chemical processes: purification by filtration, and detoxification, respectively (Neary et al. 2009). Biological detoxification is effective because it converts chemical pollutants to less toxic substances or removes them entirely (Pimentel et al. 1997) and maintaining this ecosystem service costs far less than treating water (Brauman et al. 2007). Although water quality is particularly important for drinking water at the lower reaches of a river, the water is purified at a small scale, generally in the upper level streams. Riparian and watershed deforestation has resulted in reduced stream habitat and less water purification that results from channel narrowing and too rapid runoff with high levels of silt (Sweeney et al. 2004; Postel and Thompson 2005; Little et al. 2009). Hence upper stream and riparian protection with REDD-plus forests will result in multiple ecosystem services.

Conclusions for REDD planted forest managers

Forest cover is clearly superior to bare ground for improving soil moisture levels and reducing run-off, although total water availability will decline from evapo-transpiration from forests (Vanclay 2008). Water availability is predicted to be a major concern under climate change (Malhi et al. 2008) owing to reductions in regional precipitation and forest drying as management fragments forests. Several mechanisms to alleviate the problem include ensuring a closed canopy to reduce evaporation from soils, avoiding large plantations of species that have high water requirements, and planning to maintain cover along riparian zones. Because ecosystem services related to water are primarily provided by upper streams, but delivered at the lower reaches of rivers, planning and assessment must be conducted at the watershed scale (Little et al. 2009). A balance then needs to be sought among the desired ecosystem services. If a large proportion of the catchment needs to be covered by forests without excessive water use, then clearly it is not advisable to establish plantations; rather, planted forests should be established. However, if fastwood production is a major aim, the most water-use efficient way to do this would be to use very fast growing and water-use efficient plantations, but on a small proportion of the catchment, to minimise water use. Short-rotation plantations will negatively affect water quantity but the effect can be reduced through tree selection and multiple passes over time for harvesting. For example, eucalypts use more water than pines (Scott et al. 2005). Lastly, anthropogenic disturbances, including forest plantations, should be avoided in riparian zones to maintain the water filtration function of natural systems.

Resilience and stability

Resilience is the capacity of forests to recover from large disturbances over space and time (Gunderson 2000) and is important for permanence of carbon storage in REDD-plus forests. Resilience is an emergent ecosystem property conferred through biodiversity, related to genetic diversity, species diversity (especially those that dominate processes), and ecosystem diversity (heterogeneity and beta diversity) across a forest landscape (Thompson et al. 2009). Production, pollination, seed dispersal, nutrient cycling, and pest reduction contribute to resilience in forests.

Several studies have related ecosystem stability to species abundance and response diversity among functional species (Thompson et al. 2009; Isbell et al. 2011; Kuiters 2013). Such observations support the concept that maintaining resilience over time is related to the capacity of species to re-assemble into communities and establish ecosystem functioning. Redundancy is common in ecosystems and contributes to the capacity of systems to resist change and maintain their resilience (Walker 1992). Species in the same functional group often show different responses to disturbances (Laliberté et al. 2010), and hence the value of redundancy. Some individual species perform key functional roles (Walker 1992; Diaz and Cabido 2001) and are highly influential on process rates in the ecosystem; the loss of these species can result in cascading effects that are sufficient to alter the ecosystem state (Koh et al. 2004; Estes et al. 2011). An important related concept is thresholds, which refers to a point where the system has been sufficiently disturbed to result in a change to another state, which may or may not be stable, and is marked by different plant and animal communities. Changes in state are associated with a substantial change in biodiversity and often result in altered (usually reduced) ecosystem services (Groffman et al. 2006; Chazdon 2008; Lewis 2009).

Forest resilience can be diminished through loss of landscape connectivity, habitat loss, edge effects and fragmentation (Tylianakis et al. 2007; Laliberté et al. 2010). Land use intensity is known to reduce functional diversity among plants (Laliberté et al. 2010). Fastwood plantations have no resilience, because of the intensity of management and low species richness. More complex planted forests, which can be managed sustainably over time using assisted regeneration, can be resilient if planned properly by paying attention to biodiversity at all scales. Recovery of forests after severe degradation requires energy input in the form of active management to enable successful recovery from, for example, a pasture or scrub forest, back to a more natural forest ecosystem (van Wilgen et al. 2001; Griscom and Ashton 2011). Restoring a forest requires an understanding of how to overcome the current stability of the particular ecosystem, through careful selection of tree species and active management to enhance desired forest growth (Griscom and Ashton 2011).

An important aspect of forest resilience involves susceptibility to invasion by pests and pathogens. Diverse forests provide, on average, less of the resources required by particular invader species than a low diversity stand because the resources are increasingly diluted as plant diversity increases. Results from experimental plots confirmed that invasion by alien plants was negatively correlated with plant species richness of plots (Kennedy et al. 2002), probably because species richness results in no available niches and inter-specific competition. For host-specific invaders, such as certain phytophagous insects, a reduction in host apparency (density) directly reduces their ability to locate host plants, thereby reducing invasibility. For example, severity of beech bark disease in North America is inversely related to the basal area of beech at large scales because of the limited dispersal capacity of the disease (Griffin et al. 2003). The relative importance of all these

mechanisms to resilience and the net effects on invasions vary across the spatial scales, although this has only been examined for plant invasions (Fridley et al. 2007).

Conclusions for REDD planted forest managers

Maintaining resilience is an important consideration for REDD-plus forest managers because loss of resilience necessitates considerable effort to recover a forest type over time and the consequent loss of carbon from the forest. Resilience can only be achieved by restoring ecosystems that function fully and provide multiple services, including sustained production, soil quality, and reproduction over time, which requires attention to biodiversity and ecosystem processes. Mixed tree communities may have high resistance to invasion thereby helping to maintain their resilience (Thompson et al. 2009). While native species are usually recommended (Brockerhoff et al. 2008), the use of exotic species may be required owing to an existing ecosystem state that can only be occupied by tree species tolerant of the existing conditions (Griscom and Ashton 2011).

Conclusions for improving plantation forestry for REDD-plus

Several authors have suggested forest practices and silvicultural techniques for planted forests for adaptation to climate change or to enhance biodiversity (Carnus et al. 2006; Parrotta et al. 2012; Pawson et al. 2013). In this review, we illustrate the importance of understanding ecological linkages and ecological functioning within ecosystems, as a means to improving forestry practices in plantations and planted forests to enhance delivery of expected services, including carbon storage. Adapting REDD-plus forests to climate change includes using practices and planning to improve resistance and resilience, such as by increasing functional redundancy among species, promoting a full suite of ecosystem processes by paying attention to biodiversity, improving genetic diversity within key species, and using practices to reduce the negative impacts from pests, diseases, and drying.

In increasingly managed landscapes, however, novel forest assemblages that have developed may not ‘play by the same rules’ as the original ecosystems and knowledge of how these new assemblages function may not be gained for some period of time, resulting in a challenge to our understanding of forest ecology (Hobbs et al. 2006; Gardner et al. 2009). Decoupling and mismatches within processes may result in less successful reproduction, for example, because of inadequate pollination or seed dispersal, resulting in a need for assisted regeneration on a continuous basis. Certainly, it is understood that forest structures and cover can be re-established before much of the biodiversity and the services it provides can be recovered (Brook et al. 2008; Sodhi et al. 2010; Bullock et al. 2011), resulting in low levels of redundancy and processes for some time. Under such circumstances, planning at a very large landscape scale (Chazdon et al. 2009; Gardner et al. 2009) is essential and taking advantage of every opportunity to incorporate remnant forests into larger-scale planning will increase the conservation potential of modified forests (Anand et al. 2010). So, while REDD-plus projects will be carried out on a stand by stand basis, it will be essential to incorporate these efforts into broad landscape-level thinking to achieve success and optimality in terms of carbon and other ecosystem services.

Practices to avoid under climate change are generally the converse of the suggested practices in Table 1. However, for planted forests in particular, careful thought must be given to local predicted future conditions and the ecosystem services expected from a

forest given those possible future scenarios. A main focus of REDD-plus is planted forests, especially on degraded and deforested landscapes. Restoration of forest ecosystems can be accomplished best by understanding the basic ecosystem functions and processes relevant to local circumstances. For example, planning for restoration on peat soils will necessarily differ from that on dry soils. A growing body of evidence suggests that increased levels of biodiversity can play a role in enhancing many of the services that are derived from a planted forests and plantations. Nevertheless, assuming that restoring some level of biodiversity will equate to a certain level of ecosystem services is likely to be incorrect. This is especially true over short time periods because, while planting trees is relatively easy, the recovery of functioning ecosystems takes time and depends considerably on the availability of source populations. Further, certain forest structures, such as dead wood and deep detritus, only redevelop with time. Generally, the full complement of biodiversity is missing from second-growth forests in tropical areas, even in well managed areas (Lewis 2009; Klimes et al. 2012; Putz et al. 2012). There are, however, excellent examples of ecosystem recovery, with high species richness and recovered benefits and services from well-planned forest ecosystems. Examples include the new forests of Puerto Rico (Lamb et al. 2005) and the jarrah forests of western Australia (Koch and Hobbs 2007). We believe that REDD-plus planted forestry can be best accomplished if planning is done in an ecologically holistic manner and considers adapting to future climate, by the development of fully functioning forest ecosystems across large landscapes.

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