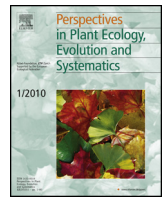




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Review

Balancing the environmental benefits of reforestation in agricultural regions



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ABSTRACT

Reforestation is an important tool for reducing or reversing biodiversity loss and mitigating climate change. However, there are many potential compromises between the structural (biodiversity) and functional (carbon sequestration and water yield) effects of reforestation, which can be affected by decisions on spatial design and establishment of plantings. We review the environmental responses to reforestation and show that manipulating the configuration of plantings (location, size, species mix and tree density) increases a range of environmental benefits. More extensive tree plantings (>10 ha) provide more habitat, and greater improvements to carbon and water cycling. Planting a mixture of native trees and shrubs is best for biodiversity, while traditional plantation species, generally non-native species, sequester C faster. Tree density can be manipulated at planting or during early development to accelerate structural maturity and to manage water yields. A diversity of habitats will be created by planting in a variety of landscape positions and by emulating the patchy distribution of forest types, which characterized many regions prior to extensive landscape transformation. Areas with shallow aquifers can be planted to reduce water pollution or avoided to maintain water yields. Reforestation should be used to build forest networks that are surrounded by low-intensity land use and that provide links within regions and between biomes. While there are adequate models for C sequestration and changes in water yields after reforestation, the quantitative understanding of changes in habitat resources and species composition is more limited. Development of spatial and temporal modelling platforms based on empirical models of structural and functional outcomes of reforestation is essential for deciding how to reconfigure agricultural regions. To build such platforms, we must quantify: (a) the influence of previous land uses, establishment methods, species mixes and interactions with adjacent land uses on environmental (particularly biodiversity) outcomes of reforestation and (b) the ways in which responses measured at the level of individual plantings scale up to watersheds and regions. Models based on this information will help widespread reforestation for carbon sequestration to improve native biodiversity, nutrient cycling and water balance at regional scales.

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1. Introduction

Extensive areas of native forest ecosystems have been cleared and converted to other land uses, such as agriculture, plantation forestry and cities, a trend that will continue with increasing human populations. Forest area is estimated to have decreased by a third over the past three centuries in China, the Middle East, North Africa, the eastern United States of America and Southeast Asia (Ramankutty and Foley, 1999). Deforestation has substantial and widespread negative impacts on climate, hydrology, soils and biodiversity, with consequent impacts on societies and economies (Meyfroidt and Lambin, 2011). A considerable proportion of the remaining native forests has been severely degraded to produce primary resources. In their current restricted and degraded state, the remaining native forests face the potentially rapid and extreme stress of climate change and increased climate variability (Dale et al., 2001). In recent years, there have been several important agreements that suggest there will be extensive reforestation to address this issue (CBD, 2010; GPFLR, 2013; UN, 2014; UNEP, 2014).

It is imperative that the environmental impacts of global deforestation are mitigated by a combination of active (i.e. tree planting) and passive (i.e. regrowth following land abandonment) reforestation. Here, we focus on active reforestation, which we define as the planting of forests on lands that historically had forests but that have since been converted to other land uses (IPCC, 2007). This excludes afforestation of areas that were formerly native grasslands or shrublands, which generally is detrimental to biodiversity (Bremer and Farley, 2010; Gerstner et al., 2014). Land has been reforested actively for many reasons including for plantations for timber, riparian plantings to reduce stream pollution, upland plantings to reduce soil erosion and salinity, and to increase habitat for native species (Jackson et al., 2005). Reforestation may improve links among existing remnant forest patches, increasing movement, gene flow and effective population sizes of native species (Gilbert-Norton et al., 2010). Re-establishing forests can restore biogeochemical cycling of carbon, oxygen and nutrients among the atmosphere, biomass, pedosphere and hydrosphere (Arneeth et al., 2010). Reforestation of agricultural land can improve biodiversity, which can result in increased primary production, reduced susceptibility to invasion by exotic species and increased ecological resistance to pressures such as climate change (Hooper et al., 2005).

Restoration of forest ecosystems could directly mitigate climate change by sequestering atmospheric carbon, both above- and below-ground. Trees sequester and retain more atmospheric carbon in their biomass than do crops or pastures (Pan et al., 2011). Under carbon trading or carbon emission reduction schemes (e.g. United Nations REDD+ programme), it is possible that widespread reforestation will become economically viable (Bradshaw et al., 2013). Increasing uncertainties in crop yields with climate change may encourage landholders to diversify into other investments such as 'carbon farming'. Reforestation could provide an important tool for mitigating climate change in the short-term while fostering

a low-carbon economy and improving environmental conditions jointly in the long-term (Mackey et al., 2013).

How reforestation is approached has long-term consequences with compromises between the structure and function of the forest. The number of trees and the types of tree species planted (exotic vs native, mixed vs single species) and whether shrubs are included are key decisions. Plantations of fast-growing production species can sequester carbon faster than native mixed-species plantings but often have little biodiversity value (Lindenmayer et al., 2003). Reforestation of riparian zones can lead to larger increases in biodiversity but greater reductions in stream flow than reforestation in upslope areas (Scott, 1999; Palmer and Bennett, 2006). Permanent restoration plantings are likely to provide more environmental benefits than harvested plantations (Kanowski et al., 2005).

Issues associated with passive reforestation or land abandonment have been covered in depth by other reviews (e.g. Bowen et al., 2007; Rey-Benayas et al., 2007; Meyfroidt and Lambin, 2011). Here, we explore the range of potential responses of ecosystem structure and function to active reforestation of agricultural land. *Structure* includes the diversity of species in an area, including animals, plants, fungi and bacteria, and the spatial arrangement of these components from the planting (<0.1 km², e.g. canopy strata) to the regional scale (10⁵–10⁶ km², e.g. forest networks). *Function* includes the biogeochemical processes resulting from interactions between species and the physical environment, such as production, decomposition and nutrient dynamics. We outline how the benefits of reforestation may be maximized by practitioners in agricultural regions given the potential compromises between structure and function, and current spatial and temporal constraints. Extensive reforestation of agricultural land is limited by social, economic and political obstacles, which are covered elsewhere by a growing literature (e.g. Barr and Sayer, 2012; Knight et al., 2010). We finish by presenting a modelling framework, and the knowledge required, that would allow land managers to quantify the compromises among structure (biodiversity) and function (carbon and water) under different reforestation scenarios and hence balance the environmental benefits of widespread reforestation in agricultural regions.

2. Structural changes following reforestation

2.1. Development of forest structure

Mature native forests contain strata of different-sized trees, shrubs and a ground layer, which create a range of microhabitats and microclimates beneath the canopy (Oliver and Larson, 1996; Franklin et al., 2002). The structural complexity of a forest includes the density, spatial arrangement, size and height distribution, species richness (see following sections on diversity), canopy cover, canopy strata and debris of trees (McElhinny et al., 2005). Forest structure and the associated habitat resources take decades to centuries to develop following reforestation. The expected sequence

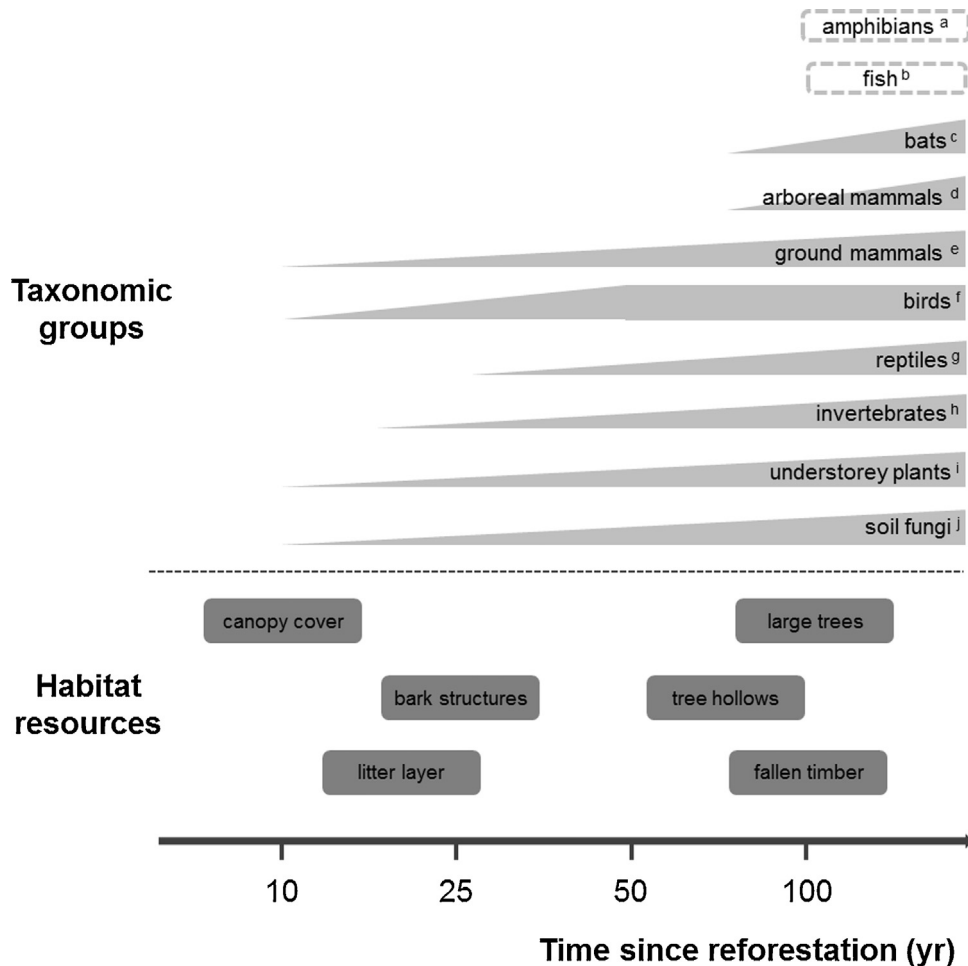


Fig. 1. Conceptual model of temporal development of ecosystem structure (habitat resources and taxonomic groups) following reforestation at the patch scale. The expected time for resources to develop (square boxes) and the richness of native species from different taxonomic groups to increase (wedges) are indicated. Taxonomic groups that may not respond to reforestation are denoted by dashed borders. Times for habitat resources to develop will differ among forest types and with manipulation of stand structure. These were calculated from the following studies of temperate forests: ^aMac Nally et al., 2009; ^bHarding et al., 1998 and Sutherland et al., 2002; ^{c,d}Vesk et al., 2008; ^{e,f}Eyre et al., 2010; ^gKanowski et al., 2006; ^hWatts and Gibbs, 2002; ⁱBrunet, 2007; ^jMacDonald et al., 2009.

of structural development after reforestation is illustrated in Fig. 1. Tree plantings may not develop the full structural complexity of a mature native forest, or they may take a long time for natural recruitment and senescence processes to generate that structure.

Canopy closure is an important developmental step because it reduces irradiance, soil temperature and wind speed beneath the canopy (Vetaas, 1992). Plantings of many species reach canopy closure within two decades (Fig. 1, Oliver and Larson, 1996). Fast-growing tree species, particular in the tropics, can be planted to accelerate canopy closure in plantings (Haggar et al., 1997). To develop forest-interior conditions beneath the canopy, plantings must be large (>100 m wide and >10 ha) because the effect of agricultural land on microclimate can extend >50 m into a forest (Murcia, 1995). Reforestation along streams must be longitudinally extensive to reduce water temperatures, which are influenced by the amount of shading several kilometres upstream (Allan, 2004).

Most habitat resources are slow to develop, with temperate trees often taking 50 years to produce substantial floral resources and at least a century to become large trees (Fig. 1, Vesk et al., 2008). The inclusion of shrubs in the initial planting accelerates the availability of floral resources, including seeds and nectar. Plant litter is an important structural component of forests and thick layers can accumulate within two decades when taxa such as *Eucalyptus* are planted (Cunningham et al., 2012). Reforestation may take >30 year to increase fallen timber on forest floors, which

is a key resource for many taxa (Harmon et al., 1986), and centuries to attain levels in streams similar to those within mature forests (Davies-Colley et al., 2009).

Large trees with large branches and reiterated trunks are significant structural features of mature forests, which provide distinct habitat resources (e.g. hollows, Franklin et al., 2002). Many tree species take over a century to develop these characteristics (Fig. 1, Humphrey, 2005), so planting trees around focal remnant trees can provide these resources while the planting develops (Lindenmayer and Hobbs, 2004). Within plantings, tree hollows can be simulated by artificial structures and some trees can be intentionally wounded to promote tree-hollow development (Gibbons and Lindenmayer, 2002).

The development of structural complexity after reforestation depends on which tree species are planted and the age of the planting. Wood plantations (including agroforestry) have less structural complexity than mature remnant forests or than naturally regenerating forests of equivalent age due to the more uniform spatial and temporal establishment of plantations (Aubin et al., 2008). When left to mature (>50 years), wood plantations can develop similar canopy cover, litter mass and strata to remnant forests (Kanowski et al., 2003). Planting a mixture of tree and shrub species provides a higher structural complexity than plantations of production tree species (Kanowski et al., 2003) and can lead to the diverse-size structure associated with a mature forest faster (Munro et al., 2009).

Manipulating tree density is an important tool for accelerating the development of many habitat resources. Tree plantings typically are planted at high densities (ca 1000 trees ha⁻¹, [Smith et al., 1996](#)) to ensure adequate recruitment rates but dense thickets often form that restrict structural development due to stagnating growth. Active thinning of dense stands during early decades can accelerate the development of the remaining trees, make them less vulnerable to drought ([Horner et al., 2009](#)) and windthrow ([Wilson and Oliver, 2000](#)), while the retention of cut stems provides some fallen timber, which is a key habitat component. Planting trees at lower densities allows trees to develop wide crowns and branches faster, and shrubs and understorey taxa to establish between trees ([Oliver and Larson, 1996](#)).

Reforestation should mimic the heterogeneity of stand structures found within native forests by planting a mosaic of different mixtures of tree species and tree densities over an area. Plantings should aim to have a similar richness of trees to surrounding remnant forests but we recognize that this would not be practical for highly diverse forests of the subtropics and tropics. More importantly, plantings should contain representative species from the different functional types found in remnant forests. Alternatively, the 'framework species' approach developed in tropical Australia ([Goosem and Tucker, 1995](#)) uses local knowledge to choose species that have high survival and growth rates on cleared land, rapidly produce dense canopy to control competing vegetation and produce fruits and flowers that attract seed-dispersing animals to promote establishment of new species ([Elliott et al., 2003](#)).

Appropriate species for the current and future environmental conditions should be planted. There needs to be awareness that species that occurred prior to land clearance may not successfully develop into mature forests due to climate change. Tree species within a planting should include fast-growing species to rapidly ameliorate the microclimate and long-lived species to provide the structure of mature forests ([Haggar et al., 1997](#)). Manipulating tree density at planting or during early development creates a range of stand structures from thickets for shelter to wide spacing for understorey establishment ([Oliver and Larson, 1996](#)), and accelerates the development of some habitat structures (e.g. [Horner et al., 2010](#)).

2.2. Diversity of understorey plants

The development of a native plant understorey within tree plantings is dependent on dispersal from local sources because native seed banks usually are impoverished on agricultural land ([Cramer et al., 2008](#)). Understorey species richness of plantings decreases with distance from the nearest remnant forest ([Brunet, 2007](#)). The abundance of seed in plantings decreases from wind-dispersed, bird-dispersed to heavy seeds ([Battaglia et al., 2008](#)). Many understorey species need to be planted because the nearest source forest often is too distant or too degraded to provide seeds.

Establishment of native plant species commonly is limited by the existing cover of exotic species or the nutrient enrichment of soils associated with long-term agricultural management ([Prober et al., 2005](#)). Agricultural weeds may be controlled using herbicides and targeted grazing but these actions can be detrimental to native species. Canopy closure increases competition for soil moisture and light, generally favouring native species over agricultural weeds a decade after reforestation ([Brunet, 2007, Fig. 1](#)). Canopy openings are needed to recruit native shrubs ([Oliver and Larson, 1996](#)) and to maintain cover of aquatic macrophytes in riparian plantings ([Broadmeadow and Nisbet, 2004](#)).

Reforestation commonly develops a plant composition that is intermediate between the adjacent field and remnant forest, but plantings may not become native forest. Although species richness of older (>80 years) planted forests may be similar to that of remnant forests ([Brunet, 2007](#)), many forest and woodland species are

missing from the understorey of tree plantings a century after reforestation ([Harmer et al., 2001](#)). Consequently, there may be lower diversity of plants among older (ca 70 years) planted woodlands than among nearby remnant woodlands ([Dzwonko and Gawronski, 1994](#)).

The native diversity of the understorey is determined partly by which tree species are planted. Plantations of single production species usually contain a similar number of native understorey species to adjacent fields, and more exotic and fewer native species than native forests ([Felton et al., 2010](#)). Within a region, plantations of some forest types (e.g. broadleaf) increase α -diversity (understorey richness within plantings) more than others (e.g. conifer). However, each forest type promotes a distinct understorey flora ([Pensa et al., 2008](#)), helping to increase both β -diversity (among plantings) and γ -diversity (regional).

Increasing the structural complexity of reforestation, by planting several species within a planting, and a range of tree species and tree densities across a region, is likely to increase the diversity of understorey plant species that become established ([Brockerhoff et al., 2013](#)). Tree plantings must provide conditions favourable for the establishment of native plants, including growing space and appropriate nutrient levels, to develop a diverse native understorey. Many native plant species need to be actively planted, due to a lack of local seed sources ([Finn and Vellend, 2005](#)). Planting the full diversity of forest understoreys is not practical, especially for highly diverse tropical forests, so planted species should be chosen to provide specific strata and resources (e.g. perch trees).

2.3. Diversity of terrestrial animals

The response of terrestrial animals to reforestation differs among taxonomic groups ([Fig. 1](#)). Species richness usually is higher in tree plantings than in surrounding fields for mammals (e.g. [Christian et al., 1998](#)), birds (e.g. [Loyn et al., 2007](#)) and reptiles (e.g. [Kanowski et al., 2006](#)) but lower than in remnant forests. The composition (but not richness) of beetles changes with reforestation, with plantings having compositions more similar to remnants than to fields ([Watts and Gibbs, 2002; Gollan et al., 2011](#)). Amphibians and bats have similar richness, composition and activity in developing plantings (<30 years) to surrounding agriculture ([Kavanagh et al., 2005; Law and Chidel, 2006](#)). Tree plantings typically are dominated by animal species that are already abundant on agricultural land ([Christian et al., 1998](#)).

Tree plantings must provide appropriate physical and biotic requirements (habitat) for foraging, shelter and nesting for animals to colonize. Animals often require different habitat or habitat resources for these activities and the needs of animals can differ seasonally and through the life cycle ([Law and Dickman, 1998](#)). Many animals are associated with particular plant species ([Koh et al., 2004](#)) or stand structures ([Sullivan et al., 2001](#)), so planting a representative range of native plant species and densities should increase the richness of native animals colonizing tree plantings. Habitat value of reforestation is determined partially by landscape position. For example, birds are more abundant in gullies than ridges due to taller trees with hollows and possibly higher nectar availability ([Mac Nally et al., 2000](#)), while reptiles can be more abundant on rocky ridges ([Michael et al., 2011](#)). Plantings, while lacking some habitat resources, provide more habitat around remnants, which is particularly beneficial during some seasons (e.g. overwintering or migration) and following disturbance events in remnants (e.g. fire).

Colonization of tree plantings by native animals is restricted by the temporal development of their required habitat resources ([Fig. 1](#)). After a decade, a tree planting provides adequate canopy cover, particularly if shrubs are planted, for some native birds and ground-dwelling mammals ([Eyre et al., 2010](#)). Ground-foraging

insects increase 20 years after reforestation after which a substantial litter layer has accumulated (Watts and Gibbs, 2002). Hollow-dependent animals, such as birds, arboreal mammals and bats, may colonize when trees are mature enough to develop hollows (>75 years, Vesik et al., 2008). The presence of reptiles depends on the availability of specific microhabitats, with some species using bark features that develop after a few decades while others require large rocks, which will not be provided by reforestation (Kanowski et al., 2006). Amphibians may respond more to the characteristics of water-bodies than to the presence of trees per se (MacNally et al., 2009).

Native animals may colonize plantings but this may not lead to the establishment of successful breeding populations. Breeding success rarely is measured in tree plantings and information largely has been limited to birds (e.g. Sergio and Bogliani, 2000). In a long chronosequence (9–111 years) of tree plantings in south-eastern Australia, breeding activity was dominated by open-country species, with breeding by declining woodland species only evident in plantings >100 years (Selwood et al., 2009). There is a need for comparisons of a range of taxa among tree plantings, agricultural land and remnant forests to determine the degree to which reforestation induces breeding because we currently have little idea of whether plantings are 'sinks' rather than 'sources' for declining species.

Reforestation must create a diversity of habitats and resources within them to maximize colonization by native animals. A range of forest types and landscape positions needs to be restored in a region, ideally with a mixture of native trees and shrubs within a planting. The area of plantings should be large enough to provide sufficient habitat for 'interior species' (>100 m wide and >10 ha, Murcia, 1995). Many habitat resources are slow to develop, particularly in temperate areas (Vesik et al., 2008, Fig. 1), although some can be accelerated by reducing tree density (e.g. Horner et al., 2010), and others are absent (e.g. fallen timber), needing to be added to encourage colonization by animal species.

2.4. Diversity of freshwater animals

Given the expected changes in microclimate (reduced irradiance and water temperature) and increased resource inputs (e.g. litter, Allan, 2004), reforestation along stream-banks is likely to change assemblages of freshwater animals substantially. Recently reforested (<25 years) streams can have a similar richness of macroinvertebrates to agricultural streams (Parkyn et al., 2003), and can have distinct macroinvertebrate compositions and lower γ -diversity compared with forested streams (Becker and Robson, 2009). Streams in mature forests have higher richness and more pollution-sensitive species than agricultural streams (Harding et al., 1998), suggesting a long-term potential for reforestation. Trends for fish are equivocal, with forested reaches having either a higher (Sutherland et al., 2002) or lower (Harding et al., 1998) abundance and richness than agricultural reaches, which may depend on the location of potential source populations.

Colonization by native freshwater animals following reforestation would be improved by concurrently restoring habitat resources within stream channels (Lake et al., 2007). Fallen timber, which provides habitat and food for many freshwater animals, may take a century to accumulate in streams following reforestation (Davies-Colley et al., 2009) and needs to be supplemented. Clearance of forests for agriculture generally increases sedimentation, clogging stream channels and crevices, which are used by many freshwater animals (Burcher et al., 2008). Riparian reforestation promotes an herbaceous layer that increases interception of sediment (Broadmeadow and Nisbet, 2004), while accumulated sediment loads in the stream channel need to be removed actively or by high-flow events.

The longitudinally connected nature of stream networks restricts the potential for small-scale (<0.1 km²) reforestation to improve native species diversity of individual reaches (Lake et al., 2007). Composition of stream assemblages often is more strongly related to the amount of upstream forest cover than to the extent of local riparian vegetation (Thomson et al., 2012). Past land use can be a stronger predictor of fish and macroinvertebrate assemblages than current land use, suggesting long-term 'legacy effects' of agriculture on streams (Harding et al., 1998). Restoration of native stream assemblages will be most successful when several kilometres of a stream are replanted and surrounding agricultural practices are changed to minimize negative impacts.

2.5. Physical and biological structure of soils

Soil structure is a primary determinant of water and air movement, stability of organic matter, root growth, seedling establishment and erosion (Lal, 1991). Agricultural practices alter soil structure due to regular disturbance breaking soil aggregates and filling pore spaces, compaction from machinery and livestock, and irrigation dissolving aggregates (Young and Young, 2001). Reforestation is likely to improve soil structure because forest soils have higher aggregate stability due to larger litter inputs and reduced soil disturbance, lower bulk density (less compacted) and higher porosity than agricultural soils (Lichtfouse et al., 2011). However, reforestation may not lead to a substantial decrease in bulk density within the first three decades (Lima et al., 2006).

Forest soils tend to have more diverse soil assemblages than agricultural soils (Bardgett et al., 2005). Soils are very biodiverse predominantly due to soil microbes (fungi, bacteria, archaea and viruses), but there are also protozoa, nematodes, microarthropods, enchytraeids, earthworms, termites and millipedes (Andre et al., 2002). Soil animals and microbes play a key role in ecosystems, affecting plants directly through parasitism, pathogens, herbivory and symbioses and indirectly by cycling nutrients from soil organic matter (Wardle, 2002). Reforestation of agricultural fields is likely to increase the heterogeneity of soil resources, which usually increases the species richness of soil assemblages (Bardgett et al., 2005), because trees redistribute resources through uptake from their extensive root systems and deposition of leaf, stem and root material.

Soil fauna and microbes show rapid changes in abundance and biomass within a few years after cropping has ceased (Kardol et al., 2005). Compositional changes in soil assemblages after reforestation may be slower, with changes in fungi seen after a decade (MacDonald et al., 2009, Fig. 1) and in earthworms after three decades (Pizl, 2001). A shift towards a fungal-dominated assemblage following reforestation of pasture (MacDonald et al., 2009) is associated with changes in plant litter quality (e.g. C:N ratio), cessation of cultivation, fertilizer addition and grazing (Six et al., 2006). Establishment of a diverse, native soil assemblage may be slow following reforestation due to limitations of dispersal, resource availability or abiotic factors (e.g. pH, Lauber et al., 2008).

Distinct soil microbial communities are associated with forest types (Hackl et al., 2005) and trees species (Ushio et al., 2008). Consequently, planting a range of mixed-species plantings is likely to increase the heterogeneity of physico-chemical properties of the soil and hence the diversity of soil assemblages. Inoculation of tree species with symbiotic bacteria can overcome dispersal limitations and double establishment success (Thrall et al., 2005).

2.6. Increasing regional (γ)-diversity of agricultural regions

Reforestation is constrained by present land use, making the area, configuration and habitat quality of forest patches critical to species use of, and movement through, regions (Fig. 2, Bennett et al.,

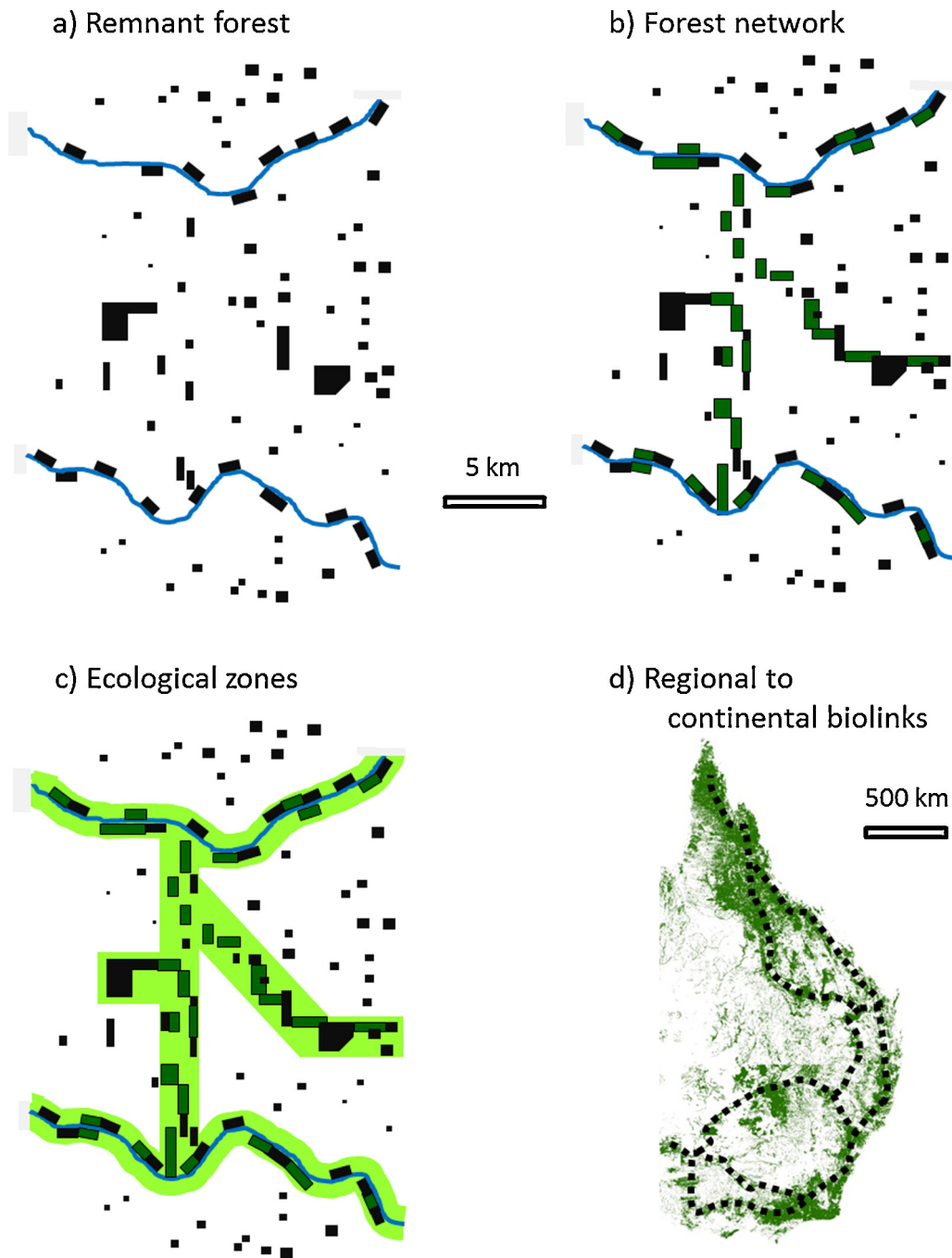


Fig. 2. Planting configurations to maximize species dispersal across areas showing (a) distribution of remnant forests, (b) forest network, (c) ecological zones and (d) continental biolinks. 'Forest networks' are areas in which reforestation is used to increase the forest extent and to decrease the isolation among forest patches. 'Ecological zones' are areas the extent of native vegetation is increased and the intensity of land use is reduced. 'Biolinks' are focal zones for reforestation that extend across regions and continents. The area includes remnant forests (black), rivers (blue lines), reforestation (dark green) and ecological zones (light green). At the continental scale, remnant forests (grey) and potential biolinks (dashed) are shown for eastern Australia. (For interpretation of the references to color in this legend, the reader is referred to the web version of the article.)

2006). γ -Diversity of forest-dependent animals decreases rapidly below a forest cover of 10–30% within an area (Radford et al., 2005; Swift and Hannon, 2010). A pragmatic approach is to concentrate reforestation in areas within existing moderate forest cover (>30%) and potentially higher remnant diversity. However, clearance has focused on specific areas and forest types, typically those on the more fertile and well-watered lowlands, so that focused reforestation of these areas may maintain or provide higher γ -diversity (Vesk and Mac Nally, 2006).

Reforestation (including restoration plantings and wood plantations) can be used to improve connectivity among remnant

forests by creating a 'forest network' (Fig. 2b), which although not forming a continuous corridor increases the extent of forest and reduces the isolation of patches in an area. The effectiveness of a forest network of remnants and reforestation depends on the quality of habitat provided for taxa. The spread of individual native plant species through such a network may be restricted by soil type, moisture and nutrient availability, and the presence of other species (Dzwonko and Gawronski, 1994). Many remnant forests are degraded, with depauperate understories, impoverished seed banks and few animals (Prober et al., 2005), and need to be restored to ensure the viability of native populations. The structure of tree

plantings, including tree density and size distribution, determines whether animals move through a forest network. Currently, most restoration plantings are too young (<30 years) to provide many habitat resources (Fig. 1, Vesik et al., 2008) and some resources may need to be supplied (e.g. nest boxes). Agroforestry presents an economic solution to increasing forest cover in agricultural regions but their typically small areas and harvest during early development provides limited habitat resources (Bhagwat et al., 2008).

The location of tree plantings relative to the nearest source population of native taxa is an important factor in producing advantageous reforestation outcomes (Lindenmayer and Hobbs, 2004; Brunet, 2007). Mobile taxa, such as birds, can disperse through networks of forest fragments. However, the dispersal ability of most other taxa is poor, with woodland herbs moving <2 m year⁻¹ (Singleton et al., 2001). Although adult forms of freshwater macroinvertebrates can disperse more than a kilometre along a stream, many macroinvertebrates usually do not move between streams (Parkyn and Smith, 2011). Tree plantings adjoining remnant forests have higher species richness and augment habitat area, potentially improving the chances of colonization by native species and reducing the adverse effects of surrounding land uses on remnants (Lindenmayer and Hobbs, 2004). Riparian plantings are most likely to be effective when located downstream of existing remnants because freshwater animals are much influenced by upstream processes and degradation (Lake et al., 2007).

Reforestation can overcome dispersal limitations by creating 'forest corridors' or linkages that connect patches of remnant forest (Fig. 2b). Dispersal of plants, invertebrates and non-avian vertebrates was higher, while that of birds was unaffected, with forest corridors in a meta-analysis of 78 paired comparisons with and without corridors (Gilbert-Norton et al., 2010). Wider forest corridors were more effective, with richness of tropical rainforest birds and mammals increasing rapidly up to corridor widths of 500 m (Lees and Peres, 2008). Although wood plantations provide fewer habitat resources than restoration plantings, they may provide functional forest corridors (Lindenmayer and Hobbs, 2004). Poor dispersers can be introduced to reforested patches once appropriate habitat resources and environmental conditions have been created or developed.

β and γ diversities are products of the heterogeneity of habitats at all scales, from microhabitats within patches (<1 ha) to physiographic regions (10⁵–10⁶ km²), which are associated with variation in nutrients (e.g. soil type), water availability and disturbance history (Tews et al., 2004). Forest networks should emulate this spatial heterogeneity by establishing a variety of native mixed-species plantings in different landscape positions to increase the γ -diversity of agricultural regions. Targeted reforestation of more productive locations, such as floodplains (Vesik and Mac Nally, 2006), has the potential for higher gains in species richness, but other locations support distinct assemblages that together would increase γ -diversity of a region. Reforestation needs to account for the different habitat requirements of animals (i.e. forest types), and the time taken for mature forests to develop. Optimization procedures can be used to guide scheduling of reforestation in space and time to avoid future population bottlenecks caused by delayed provision of critical resources (Thomson et al., 2009).

Forest networks based on wide belts (>500 m) of native trees through areas would be ideal because such belts substantially increase the dispersal of native species (Lees and Peres, 2008). Several extensive reforestation programmes have been initiated recently, with China's Grain for Green Programme establishing 24 million ha of plantations in less than a decade (Chen et al., 2009). More typically, reforestation is small scale (<5 ha, e.g. Bhagwat et al., 2008; Cunningham et al., 2014), discontinuous, and along roadsides or riparian zones (Fig. 2b). This forms 'stringy' networks of small patches that do not support most native species, especially

interior species and large animals (Turner, 1996), and may facilitate the exclusion of small animals by aggressive native animals (Maron et al., 2013). The design of forest networks may be best informed by the needs of 'umbrella species' (e.g. apex predators) that have the largest area requirement for habitat (Lambeck, 1997).

Semi-natural vegetation, such as clumps of remnant trees, scrub or abandoned fields, can provide useful resources for some forest species (Humphrey, 2005). Similarly, planting small 'tree islands' (<0.01 ha) in fields can improve the recruitment of native trees by altering the immediate microclimate and attracting seed-dispersing birds (Zahawi and Augspurger, 2006). One approach to increasing the effective size of forest networks is to create 'ecological zones' in which the extent of native vegetation is increased and the intensity of land use is reduced concurrently (Fig. 2c, sensu Bennett, 1999). This could be achieved through the maintenance and restoration of habitat resources within remnants, creating new habitats with reforestation (active and passive) and reducing the intensity of land use (harvesting, cultivating and chemical additions) in the surrounding agricultural land (Fig. 2c). This would not necessarily exclude reforestation of areas of high-intensity land use or degraded condition outside these ecological zones.

For reforestation to increase the dispersal of native species and to improve γ -diversity of a region, reforestation preferably should include plantings that provide sufficient habitat for interior species (>100 m wide and >10 ha, Murcia, 1995), aspire to create extensive habitat fragments for umbrella species (>50 ha, Ray et al., 2005), cover a large extent (>30% of historical extent, Swift and Hannon, 2010), are functionally connected and are allowed to mature (not harvested) to offer an adequate range of habitats and resources. A functionally connected forest network may be developed by increasing the extent of forest and concurrently reducing the impact of surrounding agriculture on native species within 'ecological zones'. Such ecological zones could form part of a larger network that provides 'biolinks' among biomes of a continent (Fig. 2d, sensu Brereton et al., 1995), which may allow native species to migrate as climates change.

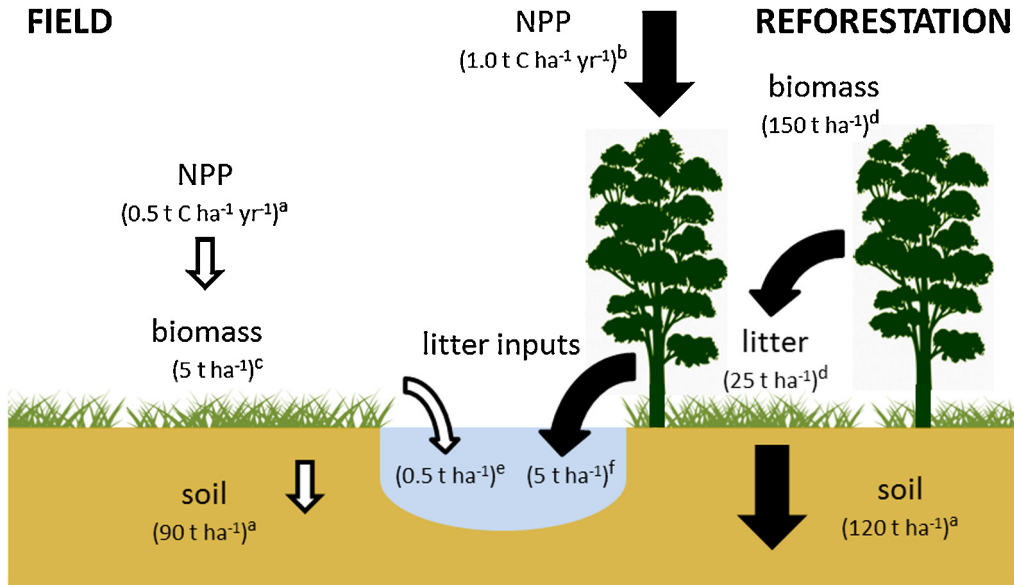
3. Functional changes after reforestation

3.1. Carbon cycling

Net ecosystem production of forests is estimated globally to be 1.0 t C ha⁻¹ year⁻¹ (Pan et al., 2011) while improved pastures and croplands sequester on average 0.5 t C ha⁻¹ year⁻¹ (Lal, 2004). Therefore, reforestation of agricultural land provides an opportunity to sequester substantial amounts of atmospheric carbon (C) and potentially to mitigate climate change (Mackey et al., 2013). Carbon sequestration following reforestation is dependent on the balance between the accumulation of biomass and litter and losses from respiration and decomposition of litter and soil C. This balance can be altered by differences in establishment of plantings (e.g. single- vs mixed-species, Piotta, 2008; Paquette and Messier, 2010) and in previous land uses (e.g. pasture vs cropping, Paul et al., 2002; Laganière et al., 2010).

Tree plantings accumulate large amounts of biomass, with *Pinus* species storing ca 250 t C ha⁻¹ after a century (Fig. 3a, Hooker and Compton, 2003; Thuille and Schulze, 2006). Productivity of forests, and consequently carbon sequestration potential, varies widely among climate zones and forest types (1–30 t C ha⁻¹ year⁻¹, Churkina and Running, 1998). Monocultures of production trees generally accumulate biomass faster than native tree species due to tree breeding and silviculture (Paquette and Messier, 2010). In low-rainfall areas (<800 mm year⁻¹), native species are likely to be equally productive, and less vulnerable to drought and climate change, than production trees due to the trade-off between growth rate and drought tolerance (e.g. Sterck et al., 2011). Limited

a) Carbon cycling



b) Water cycling

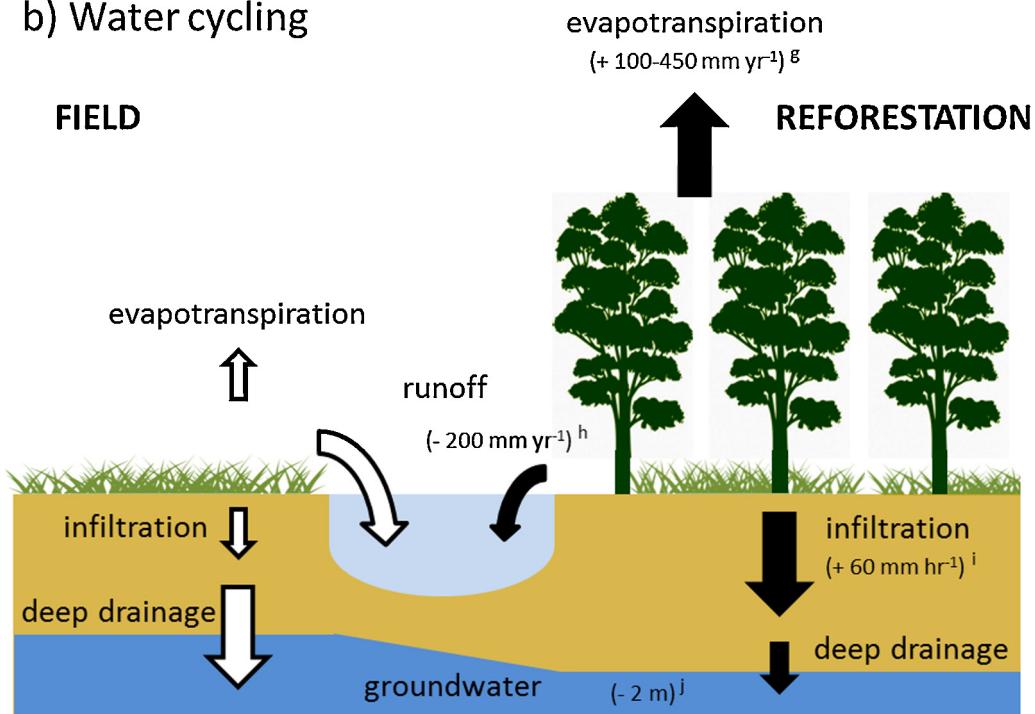


Fig. 3. Conceptual models of (a) carbon cycling and (b) water cycling in fields and after reforestation. Differences in arrow width between an agricultural field (white) and a reforested field (black) indicate the relative increase or decrease in a stock following reforestation. NPP = net primary production. Estimates for stocks and flows of carbon under both land uses are given in brackets whereas only changes in water cycling following reforestation are indicated. These were calculated from the following sources: ^aLal (2004); ^bPan et al. (2011); ^cBondeau et al. (2007); ^dPregitzer and Euskirchen (2004); ^eHagen et al. (2010); ^fBenfield (1997); ^gZhang et al. (2001); ^hJackson et al. (2005); ⁱIlstedt et al. (2007); and ^jGeorge et al. (1999).

meta-analyses (19 studies) suggested that the same species produce more biomass in mixed-species plantings than in monocultures of the individual species because interspecific competition generally is less intense than intraspecific competition, which probably is due to niche differentiation among species (Piotto, 2008; Hulvey et al., 2013). Higher diversity does not generally mean increased productivity because outcomes depend on site

productivity and ecological niche differentiation among species (Pretzsch, 2005). Species choice determines growth rates, with the inclusion of nitrogen-fixing trees (e.g. *Acacia*), as in the above meta-analyses, often increasing productivity during early development (Forrester et al., 2006).

A substantial amount of C accumulates with planting age as leaf and stem litter on the forest floor until a steady state between

deposition and decomposition is reached (Fig. 3a). Afforested streams tend to have higher inputs of litter (Allan, 2004) and larger accumulations of organic matter in the sediment than adjacent agricultural streams (Giling et al., 2013). Litter accumulation differs widely among forest types and species, with 17 t ha^{-1} under a mixed *Eucalyptus* planting after 30 years (Cunningham et al., 2012) and 40 t ha^{-1} under a *Picea abies* planting after 90 years (Thuille and Schulze, 2006), but centuries-old, mixed-deciduous oak forests had only 10 t ha^{-1} (Facelli and Carson, 1991). Such differences in accumulation predominantly reflect disparities in litter incorporation, with slower decomposition rates in evergreen species than for deciduous species (Cornwell et al., 2008), and at lower temperatures and lower rainfall.

Soil generally provides a more stable C store than plant biomass, which is susceptible to catastrophic disturbances, and soil continues to accumulate C after forest maturity (Schulze et al., 2000). Substantial decreases in soil C often follow conversion of forest to agriculture (30%, Murty et al., 2002), so reforestation has much potential for sequestration (Fig. 3a). Estimates of the change in soil C after reforestation range widely (-3% to $+26\%$), reflecting differences in sequestration among climate regions, soil types, forest types and previous land use (Paul et al., 2002; Laganière et al., 2010). Soil C stocks generally show little change until 30 years after reforestation (Hoogmoed et al., 2012) but can increase by 20% within 50 years (Laganière et al., 2010).

Species choice in tree plantings is important to C sequestration in soil, with the largest increases under broadleaf species (27%), intermediate values under eucalypts (12%) and little change under conifers (2%, Laganière et al., 2010). Plantings that include nitrogen-fixing tree species can have higher productivity (Forrester et al., 2006) and higher retention of original soil C stocks (Resh et al., 2002), suggesting that their inclusion may accelerate the accumulation of soil C. Regular addition of fertilizer and water increases productivity of agricultural land over that of the pre-clearance vegetation, such that reforestation may not achieve the same surface soil C content as pastures in some areas (e.g. Trumbore et al., 1995).

Reforestation may increase the stability of the existing soil C stock by changing its physical and molecular form within the soil. Physical (e.g. soil aggregates) and biological protection (e.g. fungal biomass) of soil C may be more important than the chemical structure, with lignin and sugars having the same mean residence time of 10–50 years (Schmidt et al., 2011). Reforestation may not change aggregate stability in the first 20 years (Kasel et al., 2011) but the substantially higher aggregate stability of forest soils compared with agricultural soils (Lichtfouse et al., 2011) suggests that reforestation may increase the protection of soil C in the longer term. Increases in soil C following reforestation are often substantial in the 'light' fraction of partly decayed material (Berthrong et al., 2012). However, increases in the more stable 'heavy' fraction of humic material may occur 20 years after reforestation with deciduous trees (Del Galdo et al., 2003) but have not been found with evergreen trees (Kasel et al., 2011). The C:N ratio of soils often increases after reforestation (e.g. Cunningham et al., 2012), which suggests decreased decomposition and increased stability of soil C. Fungal:bacterial ratios in soil can be 50% higher following reforestation of pastures (MacDonald et al., 2009) implying higher C sequestration (Jastrow et al., 2007).

Establishment choices (location, species) determine the C sequestration potential of reforestation. Planting in higher productivity regions leads to faster accumulation of biomass (Paul et al., 2002) while reforestation on degraded soils can double soil C content (Jiao et al., 2012). Evergreen and deciduous trees species have a similar range of biomass accumulation rates (Reich and Bolstad, 2001) while decomposition products of leaves of deciduous species are incorporated faster into stable soil C (Del Galdo et al., 2003). Production species generally accumulate biomass C faster

than native species (Paquette and Messier, 2010), making them desirable if C sequestration were the goal. However, production species are unlikely to provide comparable biodiversity benefits to native species (Lindenmayer et al., 2003), and are likely to be more vulnerable to drought and climate change (e.g. Sterck et al., 2011). An effective strategy would be to plant a mosaic of production-tree monocultures for biomass accumulation, diverse native plantings of trees and shrubs for biodiversity, and mixed plantings of productive native tree species for both carbon and biodiversity.

3.2. Nutrient cycling

Reforestation changes nutrient cycling on agricultural land due to changes in quantity and quality of inputs, and rates of uptake. Plant litter increases on the forest floor and adjacent stream beds after reforestation of fields (Allan, 2004; Thuille and Schulze, 2006). Decomposition of litter and, therefore, the cycling of nutrients are slower after reforestation because of the lignified nature of litter from trees and the shift towards a fungal-dominated assemblage in the soil (MacDonald et al., 2009). The tree species used in a planting affects the breakdown of litter due to differences in quality (e.g. deciduous vs evergreen species, Cornwell et al., 2008). However, environmental differences among plantings (e.g. soil moisture and stream temperatures) may have a larger effect on litter decomposition than the species mix of litter (Lacan et al., 2010). The eventual (>30 years) increase in soil C after reforestation will improve the physical properties of soil, the amount of nutrients, cations and trace elements, and concentration of organic acids that make minerals available and prevent leaching from the system (Leeper and Uren, 1993).

Losses in soil nitrogen (N) are expected after reforestation because concentrations usually are higher on agricultural land than in forests (Garten and Ashwood, 2002) due to the addition of agricultural fertilizers. Soil N decreased by 20% under *Pinus* plantations but not under *Eucalyptus*, other angiosperms or other conifers based on meta-analysis of 153 tree plantings (Berthrong et al., 2009). A century-long chronosequence of reforestation with *Pinus strobus* showed that ecosystem N stocks were conserved by translocation of N from the soil to aboveground biomass (Hooker and Compton, 2003). Changes in soil N after reforestation may depend on site productivity, with losses in high rainfall areas ($>1200 \text{ mm year}^{-1}$) but gains in low-rainfall areas ($<800 \text{ mm year}^{-1}$, Berthrong et al., 2012) and on degraded soils (Jiao et al., 2012).

Reforestation with conifers increases the mineralization and availability of phosphorus compared with agricultural soils (Chen et al., 2008). Some forest types may accumulate soil phosphorus for centuries, with plantings of *Quercus robur* showing substantial increases between 100 and 200 years (Wilson et al., 1997). Other macronutrients, such as calcium, potassium and magnesium, decrease ($>20\%$) in the soil after reforestation because these are translocated to biomass (Berthrong et al., 2009), except on degraded soils, where macronutrients can increase by as much as 70% (Jiao et al., 2012).

The redistribution of base cations (Ca^{2+} , K^{+} , Mg^{2+} , Na^{+}) from the soil to biomass after reforestation with species of *Eucalyptus*, *Pinus* and other conifers acidifies the surface soil (-0.3 pH units , Berthrong et al., 2009). Reforestation with *Picea sitchensis* in Scotland led to substantial decreases in stream pH (-0.7 pH units) once forest cover exceeded 60% of the catchment, with an associated 80% decrease in abundance of native brown trout (Rees and Ribbens, 1995). Similarly, extended use of saline ground water by trees accumulates salt in their biomass, soil or the ground water (Jobbagy and Jackson, 2004). Reforestation can lead to an average increase of 71% in soil Na, with plantings of *Eucalyptus* in some areas increasing soil Na by an average of 250% (Berthrong et al., 2009). Eucalypts are planted to lower saline water tables because of their

rapid growth, but the associated increasing salinization of soil and ground water may reduce the long-term viability of such plantings. Adverse effects of reforestation on nutrient cycling (acidification and salinization) may be avoided by planting native species found under similar environmental conditions and by reducing tree density.

3.3. Stand-scale water cycling

Water falling on the land surface can: (1) return rapidly to the atmosphere through interception by plant canopies and by evaporation from surface soil; (2) infiltrate to deeper soil layers; or (3) run off the surface to provide stream flow (Fig. 3b). Of the water that penetrates to deeper soil layers and the water table, much is taken up by roots and transpired from leaves while the rest contributes to base flows into streams (Waring and Running, 1998). Evapotranspiration (ET), which includes transpiration and interception by plants and evaporation from the soil, can be a substantial proportion of annual rainfall (30–80%, Zhang et al., 2001), giving plants a primary role in cycling water between the land and atmosphere. Trees have a greater potential to influence water cycles than agricultural crops and pastures due to their larger leaf area and extensive root systems (Farley et al., 2005).

Evapotranspiration can be 50% higher from forests than from agriculture (Ellison et al., 2012, Fig. 3b), suggesting reforestation could shift the water budget from a surplus ($ET < \text{rainfall}$), resulting in decreased ground water recharge and runoff (Jobbagy and Jackson, 2004). However, the difference in ET between forest and grassland depends on annual rainfall, with forests having 50% more ET at 2000 mm year⁻¹ and little difference below 500 mm year⁻¹ (Zhang et al., 2001). Many estimates of ET are from short-rotation (<30 years) wood plantations and probably overestimate the long-term water use of tree plantings. ET decreases in older stands, with rates decreasing by a third between 10 and 54 years in *Pinus pinaster* forests (Delzon and Loustau, 2005).

Water use differs widely (10–200 kg day⁻¹ tree⁻¹) among forest types and among tree taxa (Wullschleger et al., 1998). Interception of rainfall by canopies of evergreen coniferous forests is twice that of broadleaf deciduous forests (Komatsu et al., 2011). Tree species appropriate for the local current and future water conditions should be planted in preference to production species, which typically combine high rates of biomass accumulation with high ET (Jackson et al., 2005).

Water infiltration is usually higher beneath trees than in agricultural land due to a large network of macropores in the soil (Fig. 3b, Vetaas, 1992). Clearance of forests for agriculture leads to long-term reductions in infiltration owing to soil compaction (Bruijnzeel, 2004). In tropical regions (850–2500 mm rainfall year⁻¹), infiltration of soils can increase by 60 mm h⁻¹ during early development of reforestation (Ilstedt et al., 2007). However, most undisturbed forest soils have an infiltration rate of 20 mm h⁻¹ (Waring and Running, 1998). Even with increased infiltration after reforestation, the year-round water use of trees leads to lower soil moisture and reduced deep drainage to the water table relative to agriculture (Fig. 3b, Jobbagy and Jackson, 2004).

The increase in ET and infiltration following reforestation of agricultural land suggest decreases in local runoff (Fig. 3b). Fast-growing tree species such as production species are likely to reduce runoff more than slow-growing species (Carnus et al., 2006), and may be more susceptible to drought and climate change (e.g. Sterck et al., 2011). Riparian forest can produce twice the reduction in runoff to an equivalent area of upland forest (Scott, 1999) demonstrating that landscape position is an important determinant of runoff after reforestation. Reductions in local runoff would be achieved by planting trees at lower densities and with species that use less water.

3.4. Water yield of catchments

There is concern that widespread reforestation of agricultural land may lead to substantial reductions in water yields from catchments. A global meta-analysis of 504 catchment observations indicated that stream flow generally was reduced by 50% at 20 years after reforestation (Jackson et al., 2005). Reforestation causes larger proportional reductions in water yields in moderate rainfall areas (–60%, 1000–1250 mm year⁻¹) than in high rainfall areas (–30%, 1250–2000 mm year⁻¹, Farley et al., 2005). In lower rainfall areas (600–1000 mm year⁻¹) where water is more critical, little difference in stream flow has been predicted between forested and agricultural land (van Dijk et al., 2007). Given that stream flow from catchments usually is monitored for a few years and rarely in plantings older than 30 years, the long-term effects of reforestation on water yield are unclear.

The species used in reforestation can have a substantial effect on the water yield of catchments. In a review of 94 catchment studies, a 10% increase in extent of *Eucalyptus* and *Pinus* forest caused a 40 mm decrease in annual stream inputs relative to grasslands, while the decrease in deciduous hardwood forests was 25 mm (Bosch and Hewlett, 1982). In the first decade, *Eucalyptus* plantations induced a larger proportional decrease in stream flow, and more cease-to-flow events than did *Pinus* plantations (Farley et al., 2005). However, these production eucalypts were predominantly planted outside Australia and may cause smaller reductions in their native ranges.

Focusing only on annual water yields following reforestation overlooks the seasonality of flows, which is more important for the life histories of plants and animals. This is especially true in arid areas where base flows determine survival through the dry season. Absolute reductions in yield following reforestation usually are larger during the wet season while proportional reductions are larger during the critical dry season (Brown et al., 2005). How much reforestation reduces base flows during the dry season depends on the access of trees to groundwater systems (Bruijnzeel, 2004). Forest cover seems to have little impact on base flows in tropical catchments, which potentially is explained by the balancing effect of increased evapotranspiration and increased infiltration under forests (Locatelli and Vignola, 2009). The effect of forest cover on storm flows is unclear (Bradshaw et al., 2007; Locatelli and Vignola, 2009).

The spatial arrangement of reforestation in a catchment depends on whether the goal is to minimize reductions in water yield or to mitigate rising water tables. The highest water use of plantations occurs at the bottom of slopes or near streams where soils are deep and water accumulates (Benyon et al., 2007), and these areas should be avoided to maintain water yields. Recharge zones (e.g. slopes and hilltops) should be planted preferentially over discharge zones (e.g. floodplains) to maximize the effectiveness of reforestation for lowering the water table (van Dijk et al., 2007). The impact of tree plantings on water tables is local (<30 m away), so that extensive reforestation (ca 25% forest cover) is required to lower the water table by 1 m across a landscape (10–100 km², George et al., 1999).

Productive species provide fast C sequestration but their widespread planting could lead to substantial reductions in water yields (Jackson et al., 2005). Species that occur in places with similar moisture conditions, preferably native species, need to be planted to avoid unintended negative water-yield effects of reforestation. Reducing tree density either at planting or during early development can reduce the negative effects of reforestation on water yields, particularly in higher precipitation and elevation areas (Zou et al., 2010).

Although reforestation can reduce runoff at the local scale (<2 km²), extensive forest cover at regional to continental scales

(10^5 – 10^7 km²) may increase rainfall and water yields (Ellison et al., 2012). Even pessimistic forecasts of water yields under extensive reforestation for C sequestration in North America were based on very uncertain predictions for mean annual rainfall (Jackson et al., 2005). The high evapotranspiration of forests can stimulate cloud formation by increasing water vapour and aerosols in the atmosphere, and can create areas of low pressure, which attract air currents (Makarieva et al., 2006). Continental evapotranspiration is a major source of annual global rainfall (40%, van der Ent et al., 2010) and of summer rainfall in large river basins (48%, Ellison et al., 2012). Extensive reforestation may substantially increase regional and continental rainfall and potentially outweigh smaller decreases in local runoff.

3.5. Water quality

Agricultural land use increases nutrient inputs into streams relative to native vegetation, with consequent negative effects on macroinvertebrate and fish assemblages (Maloney and Weller, 2011), potentially resulting in toxic algal blooms (Cloern, 2001). Reforestation has the potential to reduce the amount of agricultural pollutants (fertilizer and pesticides) applied to the land, and to filter out sediment and excess nutrients before entering streams (Lowrance et al., 1997; Newbold et al., 2010). Increasing forest cover in a region may reduce saline discharge into streams by lowering rising water tables (Tuteja et al., 2003).

Restoring the ground layer of vegetation reduces soil erosion (Francis and Thornes, 1990) and occurs after reforestation principally by the ending of cultivation and by the removal of livestock. Trees should be planted at densities that provide sufficient light for the development of a ground layer (Broadmeadow and Nisbet, 2004). Riparian plantings can reduce sediment entering streams because vegetation reduces runoff and channelled flow, which increases infiltration and deposition of material (Broadmeadow and Nisbet, 2004). A riparian vegetation buffer of 30 m can capture nearly half the suspended sediment (Newbold et al., 2010). The eventual accumulation of fallen timber in streams decreases transport of sediments along streams (Montgomery, 1997).

Forested reaches reduce N in subsurface water to a greater degree (40–100%) than do agricultural reaches (10–60%). Wide plantings ($\gg 30$ m) over shallow aquifers have the highest potential for reducing nutrient loads in streams, with retention rates of almost 100% possible for N (Osborne and Kovacic, 1993). However, the retention of N by plantings is reduced dramatically after canopy closure and continues to decrease as the growth rate of the trees declines with maturity (Gundersen et al., 2006). The removal of P is less effective because there is no microbial process equivalent to denitrification (Lowrance et al., 1997). At the catchment scale (10^4 – 10^5 km²), nutrient loads are determined mainly by land use, so that extensive reforestation is required to reduce the impact of agriculture and improve water quality (Allan, 2004).

Reforestation can lower local water tables (George et al., 1999) and has the potential to improve water quality of streams in salinized areas. However, extensive reforestation (ca 25% forest cover) is needed for major reductions (ca 25%) in stream salinity (Tuteja et al., 2003). Preferential planting on hill slopes may be much more effective (+50–600%) in reducing stream salinity than haphazard planting across a catchment (van Dijk et al., 2007).

Reforestation of individual reaches has a negligible effect on water quality because pollutants are transported long distances along streams (Parkyn et al., 2003). The effectiveness of riparian plantings in reducing nutrient loads in streams decreases with maturity (Gundersen et al., 2006). Issues of water quality must be addressed at the whole-catchment scale, of which riparian zones are a minor component in terms of total area, with an

understanding of the flow paths of surface and ground water. Sources of pollution (e.g. sediment and salinity) may be more efficiently reduced by reforesting along drainage lines of upland areas instead of relying mainly on riparian zones. Given that reforestation (including restoration and wood plantings) may remain a minor component of most agricultural regions, improving agricultural practices is likely to be a more effective way of improving water quality.

4. Balancing the environmental benefits of reforestation

Reforestation presents many potential compromises in the concurrent management of biodiversity, C sequestration, water yields and water quality (Fig. 4). Plantations of production species sequester C rapidly but have limited biodiversity benefits (Lindenmayer et al., 2003) and may cause substantial reductions in water yields (Jackson et al., 2005). No single type of reforestation can simultaneously maximize all environmental benefits (Fig. 4) but any form of reforestation should provide environmental improvements over agricultural land, with the relative benefits changing as plantings mature.

Our review suggests that practitioners can use different planting configurations (location, size, species mix and tree density) to achieve different environmental outcomes (Fig. 4). To maximize biodiversity outcomes, individual plantings should be as large as possible, given the long-established relationship between area and species diversity (Gaston, 1996), and remain unharvested to allow a range of habitats and resources to develop and mature (Kanowski et al., 2005). The biodiversity of a region could be increased by planting a range of native trees and shrubs at various densities across all landscape positions (Fig. 4). Maximizing carbon sequestration could be achieved by establishing plantations of production species on the most productive land (high rainfall areas and floodplains) at medium densities (Oliver and Larson, 1996). Reductions to water yields could be minimized by planting trees having low water use at low densities and by avoiding landscape positions with access to groundwater; improving water quality could be achieved by the opposite strategies (Carnus et al., 2006; Benyon et al., 2007; Zou et al., 2010).

Reforestation in agricultural regions involves compromises among components of structure and function at the local scale, but the regional benefits will far outweigh local negative effects. This involves a mosaic of reforestation approaches for different outcomes across a region (Fig. 4) and intermediate approaches for combined outcomes (e.g. plantations of productive native tree species for both C sequestration and biodiversity, Lamb et al., 2005). Planting native tree species that grow under similar environmental conditions should avoid adverse functional outcomes. Tree density is a key attribute of tree plantings that practitioners can manipulate to provide different stand structures, habitat resources, water yields and water quality (Oliver and Larson, 1996; Zou et al., 2010).

It is difficult for land managers and policy makers to measure the effects of alternative reforestation scenarios on the structure and function of agricultural regions. For widespread reforestation to be accepted and implemented strategically, land managers and policy makers must be able to predict the balance of risks and benefits. Study of reforestation has only become widespread in recent decades, particularly for mixed-species plantings, so that most understanding is limited to the early development of such forests (Jackson et al., 2005; Laganière et al., 2010). Comparisons of remnant forests and cleared land are used to infer long-term changes after reforestation (e.g. Allan, 2004) but it is unknown whether tree plantings will develop eventually into similar mature forest ecosystems, particularly given changing climates and the timeframes involved. Previous work on reforestation has

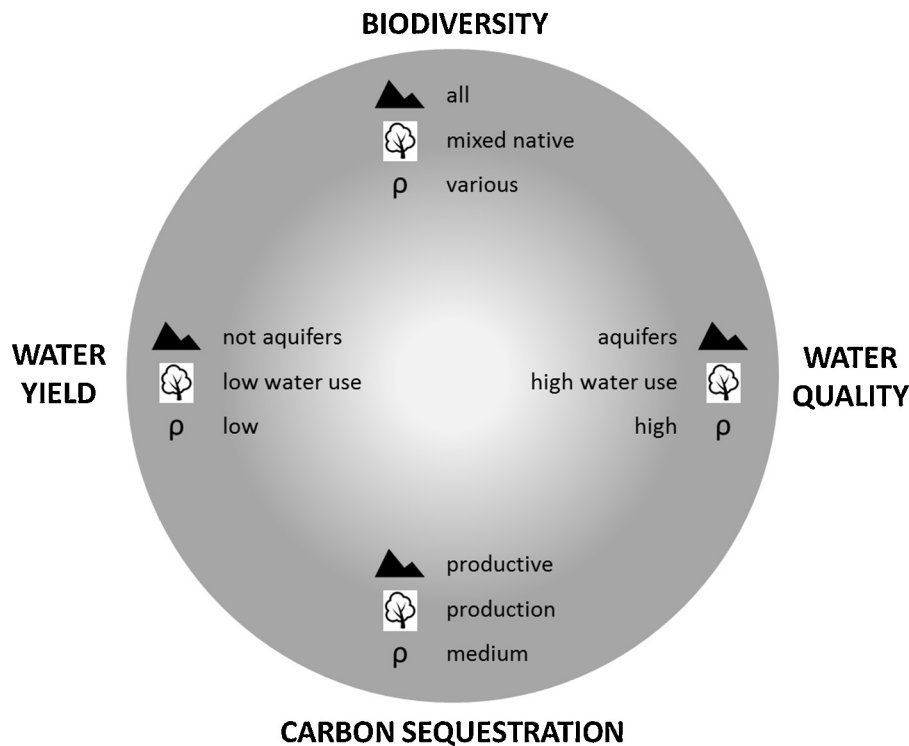


Fig. 4. Conceptual diagram of optimal reforestation for different structural and functional outcomes at a location to illustrate the associated compromises. The type of reforestation is defined by the preferential location (▲), species mix (🌳) and the density (ρ) of trees planted. Compromises among outcomes can be achieved with intermediate reforestation approaches.

focused on specific disciplines and structural or functional effects (e.g. changes to water yields or bird assemblages, Jackson et al., 2005; Selwood et al., 2009). With the expected increase in reforestation, there is increasing exploration of the trade-off between carbon sequestration and biodiversity potential (Hall et al., 2012; Bryan et al., in preparation). However, if effective reforestation programmes are to be developed for agricultural regions, land managers must be able to concurrently evaluate changes in forest structure, composition of a representative range of taxa, nutrient stocks (including C sequestration) and hydrology.

The first step in evaluating regional effects of reforestation is for scientists to develop quantitative models of how reforestation affects structure, function and their interactions at the planting scale (<0.1 km², Fig. 5a) over relevant time scales (decades to centuries). There are adequate models for short-term (<50 years) predictions of C sequestration (Brack and Richards, 2002; Kurz et al., 2009) and changes in water yields (Zhang et al., 2001; Sun et al., 2005) after reforestation. However, quantitative understanding of changes in habitat resources and species composition with planting age is limited in temporal, taxonomic and geographic scope (e.g. Thompson et al., 2003; Vesik et al., 2008). An important part of model development is to quantify differences among alternative establishment methods (active vs passive reforestation, single vs mixed-species plantings), plant functional types and previous land use (pasture, cropping). All models of reforestation could be improved by focused research, particularly in more mature (>50 years) plantings where these exist. Given the urgency of reforestation, expert opinion might be used to develop models when quantitative knowledge is unavailable. Close collaborations between researchers and land managers could help design reforestation trials to fill knowledge gaps while increasing the area of forest.

Second, these planting-scale response models must be scaled up to catchment and regional scales (10⁴–10⁶ km², Fig. 5b). Scaling up

requires spatial and temporal modelling methods that can predict the aggregated effect of reforestation on structure and function at larger scales. Development of large-scale modelling programmes, advanced modelling techniques (Lehmann et al., 2002), geographic information systems and remote sensing technologies (Venier et al., 2004), make such modelling feasible. The main spatial challenges for scientists are quantifying the largely unknown interactions among adjacent land uses (e.g. Willi et al., 2005) and how to scale up structure and function, which are likely to have non-linear relationships with area replanted and spatial arrangements (Wu et al., 2006).

The integration of fine-scale understanding of processes with regional-scale modelling is a key step towards being able to predict effects of widespread reforestation on catchments and regions. With such large-scale spatial and temporal models, it will be possible to investigate the full range of plausible future scenarios, including potential changes in climate (e.g. increased drought), and social (e.g. changing human populations and attitudes to land-use change), economic (e.g. developing carbon markets, commodity prices) and political (e.g. incentives and levies) determinants of reforestation (Fig. 5c). Such models could be used by land managers to reveal and to avoid potential deleterious planting scenarios (e.g. drastic reductions in stream flow, widespread tree mortality, Fig. 5d), and to develop spatial configurations, including different types of reforestation, that concurrently maximize biodiversity, carbon and water management in a region.

Spatial and temporal modelling platforms based on empirical models of structural and functional outcomes of reforestation are essential for deciding how to reconfigure agricultural regions. Such platforms provide a substantial advance on current attempts to predict the environmental impacts of reforestation (e.g. Jackson et al., 2005; Hall et al., 2012) by (a) including and comparing biodiversity, carbon and water concurrently, (b) accounting for the temporal development of plantings, (c) including spatial

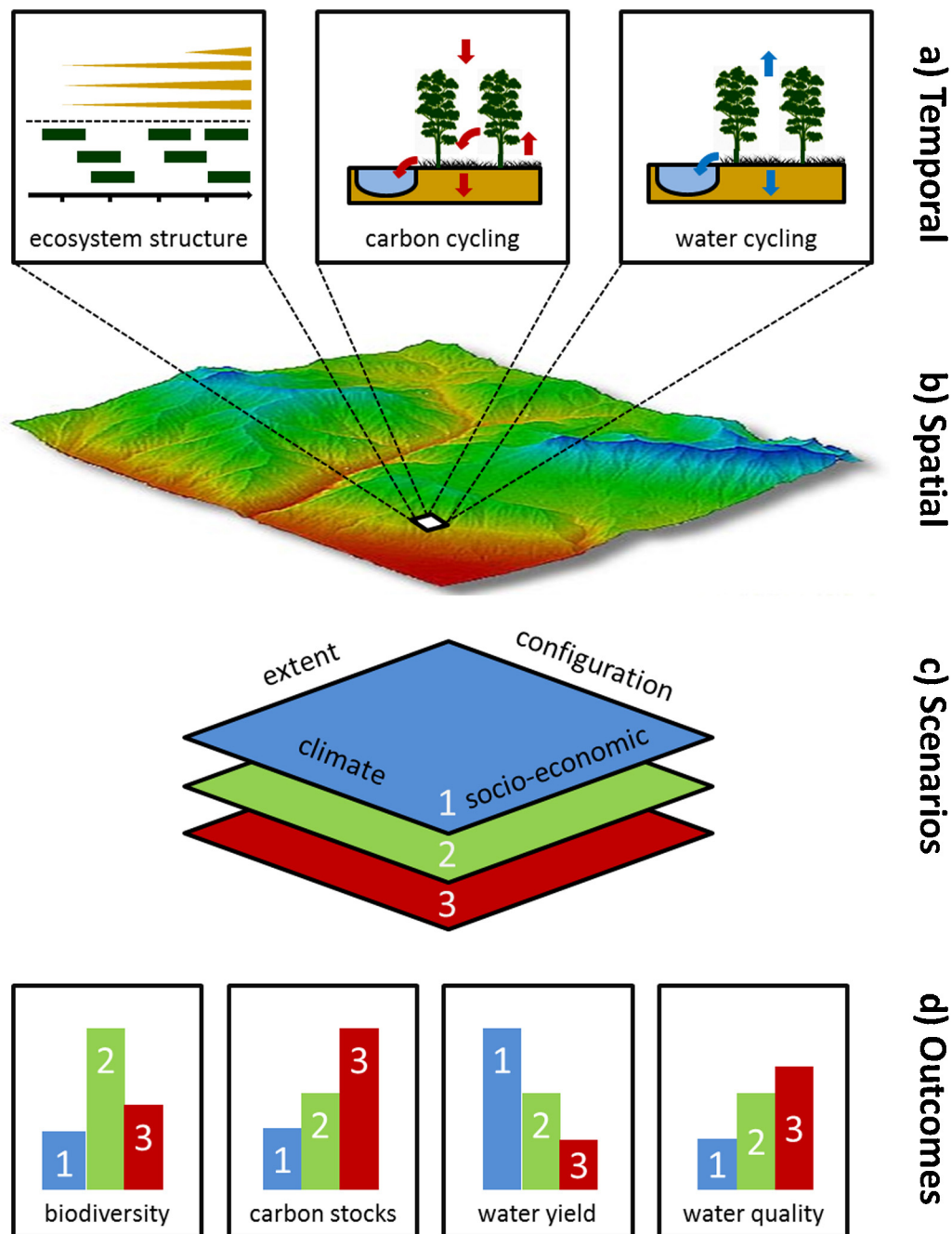


Fig. 5. Conceptual diagram of the spatio-temporal model needed to predict the aggregated effect of different reforestation scenarios across large regions. The model includes temporal models of ecosystem structure, carbon cycling and water cycling responses to reforestation (a). These temporal models are scaled up to a whole region (b) allowing future reforestation scenarios (1, 2 and 3) to be explored (c). The outcomes of these scenarios on biodiversity, carbon stocks and water yield of a region can then be compared concurrently (d).

interactions among locations and land uses, and (d) incorporating complex scenarios of extent and configuration, and future climate and socio-economic conditions. If the impacts of widespread reforestation are to be predicted, we must: (1) quantify the effect of previous land uses, establishment methods, species mixes and interactions with adjacent land uses on the environmental outcomes of reforestation and (2) determine how these responses measured at individual plantings can be scaled up to watersheds and regions. It is important that our understanding from the available developing (<50 years) plantings is supplemented by complementary studies of older forests. Models based on this information will help to ensure that widespread reforestation driven

by carbon sequestration helps to improve biodiversity, nutrient cycling and water balance across regions. The success of any reforestation programme will be determined by the support of human society, which includes political will and economic incentives but most importantly tangible benefits of reforestation to landholders. The failure of past reforestation programmes due to the further concentration of resources among powerful political and economic groups and not to forest-dependent communities (Barr and Sayer, 2012) has led to the development of 'forest landscape restoration', which considers both conservation and development to achieve a balance between the social and environmental needs of a region (Mansourian et al., 2005). Widespread reforestation must happen

now to reverse the substantial environmental impacts of past deforestation but it must be designed with an integrated understanding to avoid deleterious environmental and social impacts.

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