Producing wood at least cost to biodiversity: integrating Triad and sharing–sparing approaches to inform forest landscape management

Matthew G. Betts[1]* , Benjamin T. Phalan[2,8], Christopher Wolf[1], Susan C. Baker[3], Christian Messier[4], Klaus J. Puettmann[1], Rhys Green[5], Scott H. Harris[1], David P. Edwards[6], David B. Lindenmayer[7] and Andrew Balmford[5]

[1]*Forest Biodiversity Research Network, Department of Forest Ecosystems and Society, Oregon State University, Corvallis, OR, 97331, U.S.A.*
[2]*Instituto de Biologia, Universidade Federal da Bahia, Salvador, 40170-115, BA, Brazil*
[3]*School of Natural Sciences and ARC Centre for Forest Value, University of Tasmania, Private Bag 55, Hobart, TAS, 7001, Australia*
[4]*Département des Sciences Biologiques, Université du Québec à Montréal, Montréal, QC, H3C 3P8, Canada*
[5]*Conservation Science Group, Department of Zoology, University of Cambridge, Cambridge, CB2 3EJ, U.K.*
[6]*Department of Animal and Plant Sciences, University of Sheffield, Sheffield, S10 2TN, U.K.*
[7]*Fenner School of Environment and Society, The Australian National University, Canberra, ACT, 2601, Australia*
[8]*Parque das Aves, Av. das Cataratas, 12450 - Vila Yolanda, Foz do Iguaçu, PR, 85855-750, Brazil*

ABSTRACT

Forest loss and degradation are the greatest threats to biodiversity worldwide. Rising global wood demand threatens further damage to remaining native forests. Contrasting solutions across a continuum of options have been proposed, yet which of these offers most promise remains unresolved. Expansion of high-yielding tree plantations could free up forest land for conservation provided this is implemented in tandem with stronger policies for conserving native forests. Because plantations and other intensively managed forests often support far less biodiversity than native forests, a second approach argues for widespread adoption of extensive management, or 'ecological forestryl', which better simulates natural forest structure and disturbance regimes – albeit with compromised wood yields and hence a need to harvest over a larger area. A third, hybrid suggestion involves 'Triad' zoning where the landscape is divided into three sorts of management (reserve, ecological/extensive management, and intensive plantation). Progress towards resolving which of these approaches holds the most promise has been hampered by the absence of a conceptual framework and of sufficient empirical data formally to identify the most appropriate landscape-scale proportions of reserves, extensive, and intensive management to minimize biodiversity impacts while meeting a given level of demand for wood. In this review, we argue that this central challenge for sustainable forestry is analogous to that facing food-production systems, and that the land sharing–sparing framework devised to establish which approach to farming could meet food demand at least cost to wild species can be readily adapted to assess contrasting forest management regimes. We develop this argument in four ways: (*i*) we set out the relevance of the sharing–sparing framework for forestry and explore the degree to which concepts from agriculture can translate to a forest management context; (*ii*) we make design recommendations for empirical research on sustainable forestry to enable application of the sharing–sparing framework; (*iii*) we present overarching hypotheses which such studies could test; and (*iv*) we discuss potential pitfalls and opportunities in conceptualizing landscape management through a sharing–sparing lens. The framework we propose will enable forest managers worldwide to assess trade-offs directly between conservation and wood production and to determine the mix of management approaches that best balances these (and other) competing objectives. The results will inform ecologically sustainable forest policy and

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* Address for correspondence (Tel: +1 541 737 5814; E-mail: matthew.betts@oregonstate.edu)

management, reduce risks of local and global extinctions from forestry, and potentially improve a valuable sector's social license to operate.

Key words: Triad, sharing–sparing, conservation planning, biodiversity conservation, forest management, extensive management, ecological forestry, forestry, wood production

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I. INTRODUCTION

Forests support the majority (about 70%) of terrestrial biodiversity (International Union for Conservation of Nature, 2017), and forest loss and degradation are primary global drivers of biodiversity decline (Betts *et al.*, 2017). Indeed, many have argued that we are entering a sixth mass extinction, with species extinctions occurring 100–1000 times faster than historical rates (Ceballos *et al.*, 2015). The United Nations Convention on Biological Diversity and subsequent Strategic Plan for Biodiversity (2011 Aichi Biodiversity targets) were significant attempts to address this crisis, but consensus is emerging that the overall objective – halting biodiversity loss by 2020 – has failed (Mehrabi, Ellis & Ramankutty, 2018; Díaz *et al.*, 2019).

Central to the challenge of conserving global biodiversity is an increasingly demanding human population with escalating rates of consumption (Fig. 1; Tilman & Clark, 2014). Use of forest products appears to be no exception, with current roundwood production equal to 3.7 billion m³/year and projected growth in wood demand of 30% by 2050 (Kok *et al.*, 2018; FAOSTAT, 2019*b*). Forests remain of high economic value to humanity, worth over $US 600 billion annually (Duraiappah *et al.*, 2005; Rametsteiner &

Whiteman, 2014) and their value will increase with increased global emphasis on renewable resources in a 'Green Economy' (Eaton & Prins, 2018). As a downside of such trends, increasing wood production threatens other critical values including forest biodiversity and carbon stocks, which are both in rapid decline (Butchart *et al.*, 2010; Saatchi *et al.*, 2011; Ceccherini *et al.*, 2020). Although reducing human consumption of wood resources is the best option from a biodiversity standpoint, there is little evidence that such reduction is happening (Fig. 1).

To meet the world's wood demand, foresters have often adapted the agricultural model of increasing production through intensive, high-input management practices aimed at increased tree growth and management efficiency by simplifying and homogenizing stand structure (Puettmann, Coates & Messier, 2008). This has been quite successful at boosting yields – in some cases as much as 40-fold [25–80 m³/ha/year *versus* 1–2 m³/ha/year in unmanaged natural forests (Sedjo, 1999; Wagner *et al.*, 2005; Couto, Nicholas & Wright, 2011)]. Indeed, plantation forest area has increased by over 105 million ha since 1990, with an average annual increase of 3.6 million ha, and planted forests now account for 7% of the world's forests and 33% of roundwood production (Food and Agriculture Organization of the
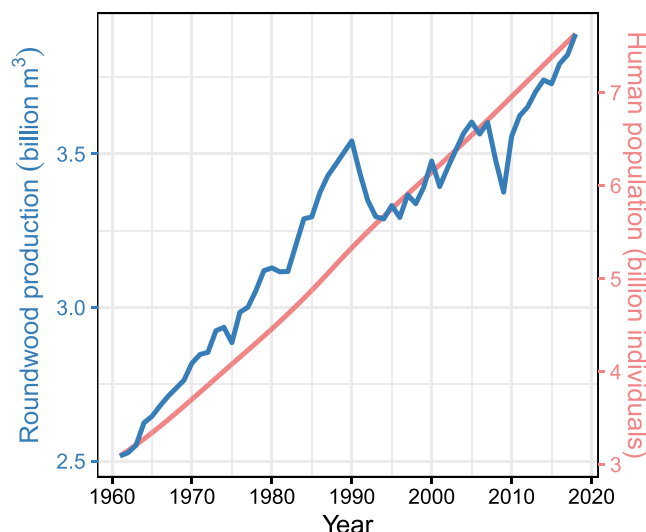
Fig 1. Global roundwood production (blue) and human population size (red). Data sources: FAOSTAT (2019*a*,*b*).

United Nations, 2015). If current trends continue, tree plantations – of either native or non-native species – could provide most of global wood by 2050 (Jürgensen, Kollert & Lebedys, 2014).

Feeding the increasing wood demand through plantations or other intensive management practices has two important implications for biodiversity and carbon conservation. First, management intensification has the potential to reduce harvesting pressure on natural, unmanaged forests (Edwards *et al.*, 2014*a*; Pirard, Dal Secco & Warman, 2016; Runting *et al.*, 2019) and to free up forest land for conservation, provided that appropriate conservation policies are implemented for native forests. Second, however, intensively managed forests, whether of native trees or not, themselves may have relatively low conservation value (Barlow *et al.*, 2007; Brockerhoff *et al.*, 2008; Swanson *et al.*, 2011; but see Yamaura *et al.*, 2019). For this and other reasons, researchers and land managers have proposed and developed various local versions of 'ecological forestry' or extensive management (Pommerening & Murphy, 2004; Franklin & Johnson, 2012; Puettmann *et al.*, 2015; Franklin, Johnson & Johnson, 2018). These techniques typically aim to emulate natural disturbance regimes and vegetation structure, often relying on retention of trees and downed wood during harvest operations (MacLean *et al.*, 2009; Lindenmayer *et al.*, 2012). However, compared to management of homogeneous plantations, profits and yields of extensive forestry approaches are often substantially lower, in part because of the added complexity of management operations (Newton & Cole, 2015); hence meeting any given level of wood production would require extraction over a larger area, thereby reducing the scope for leaving some forests unharvested.

Attempts to reconcile conservation, production, and other objectives have prompted a proposed compromise approach involving forest management in three distinct zones. This 'Triad' zoning divides landscapes into discrete units that emphasize reservation, extensive management, or intensive management (Seymour & Hunter, 1992). Reserve areas are managed for biodiversity conservation, which often means little or no intervention. Extensive forestry operations ('ecological forestry'; Fig. 2) in native temperate forests are typically characterized by partial retention, mixed species, minimal use of external inputs and reliance on natural tree regeneration (Franklin & Donato, 2020), and in tropical forests, by longer harvest rotations, lower timber yields, or stringent restrictions on the number, size and type of individual trees that can be harvested. Practices in the intensive zone can include planting of native or exotic tree species, use of herbicide to control competing vegetation, thinning, and fertilization (Paquette & Messier, 2010), and in tropical forests often involve shorter rotations, lowering of minimum harvesting diameters, and/or and harvesting trees at higher densities (Edwards *et al.*, 2014*a*). The Triad approach is grounded in the idea that producing wood from intensively managed forests can permit more land to be freed up for conservation (Binkley, 1997; Côté *et al.*, 2010; Tittler, Messier & Goodman, 2016) (Fig. 2).

However, the few theoretical (Seymour & Hunter, 1992) and modelling (Tittler, Messier & Fall, 2012; Tittler *et al.*, 2015) studies aimed at determining optimal proportions of different management regimes in the Triad approach (Ward & Erdle, 2015; Tittler *et al.*, 2016) are limited in value due to the absence of sufficient empirical data to identify formally how best to minimize impacts to biodiversity while meeting any given level of demand for wood (Messier *et al.*, 2009; Yoshii *et al.*, 2015; Yamaura *et al.*, 2016; but see Section II). There are still few empirical tests of how differing landscape-level proportions of land under the three Triad compartments alters species' populations and wood yield (Lindenmayer *et al.*, 2012) across entire landscapes. Hence while the Triad approach is now being implemented in several jurisdictions in North America and elsewhere (MacLean *et al.*, 2009; Messier *et al.*, 2009; Paquette & Messier, 2010; Lahey, 2018), the balance of reserves, extensive and intensive forestry operations at landscape scales is typically determined in an *ad hoc* manner. At a time when biodiversity continues to decline and the demands of a resource-hungry human population increase (Ceccherini *et al.*, 2020), it is critical that wood-production strategies are instead based on science-based evaluations of alternatives (Tallis *et al.*, 2018; Runting *et al.*, 2019).

This challenge in forestry is analogous to the 'land sharing–sparing' question in food-production systems (Balmford, Green & Scharlemann, 2005; Phalan *et al.*, 2011*b*) (Table 1). Land sharing involves (in a parallel with extensive forestry) producing food and supporting wildlife in the same parts of the landscape, by maintaining or restoring the conservation value of the farmed land itself (Puettmann *et al.*, 2015). By contrast, land sparing (analogous to intensive forestry plus reservation) consists of increasing yields on farmed land while at the same time sparing remaining habitat elsewhere in the landscape (Balmford, Green & Phalan, 2015). One other, recently
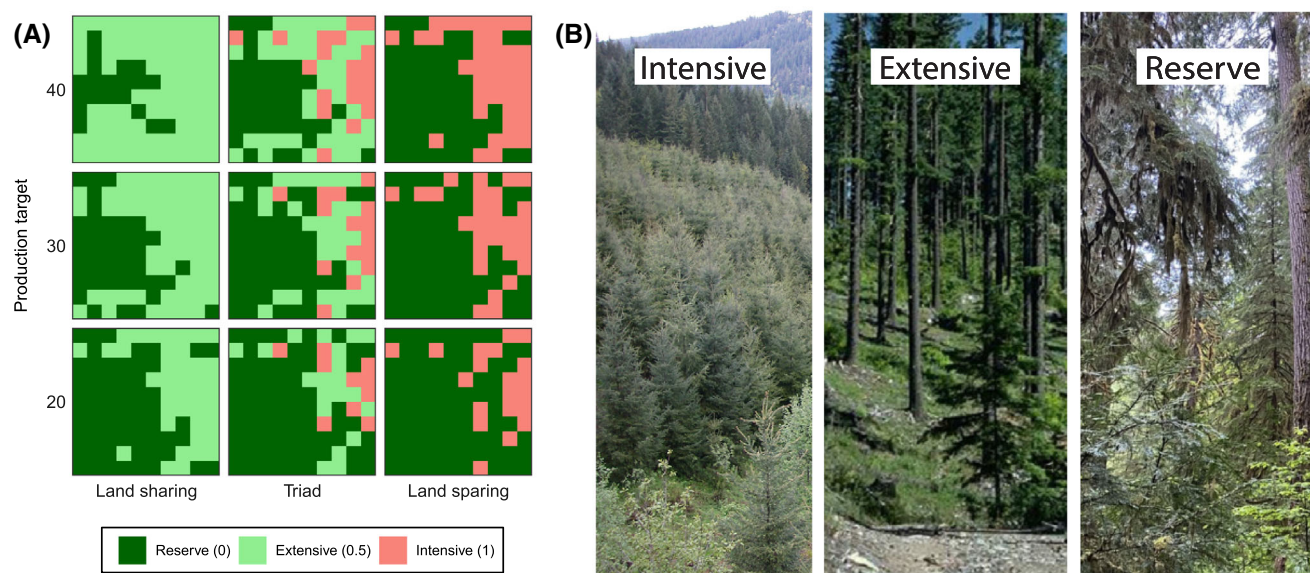
Fig 2. Conceptual illustration of contrasting approaches to managing landscapes for timber production and biodiversity conservation in mixed-wood yield landscapes along a land sparing (reserve + intensive) to sharing (reserve + extensive) continuum, where the intermediate strategies reflect Triad forestry. In A, each of the nine panels is a schematic map of a region with unmanaged habitat (also termed 'reserve', dark green; 0 units of production per pixel), ecological forestry (also termed 'extensive management', light green; 0.5 units/pixel), and high-yield forestry (also termed 'intensive management', coral; 1 unit/pixel). Region maps in the same row all produce the same quantity of wood, but use different proportions of forest management approaches to provide the production target. The three rows show results for low (20), medium (30) and high production targets (40) (after Balmford et al., 2015). In B, examples of each type of management are shown for the west coast of North America: intensive management (native forest plantation), ecological forestry (variable retention harvesting in native forest), and unmanaged, protected old growth (reserve). Photograph credits: M. Betts.

developed approach – which echoes Triad – extends this simple two-compartment sparing model by assigning some of the land spared from highest-yield production to low-yielding farmland (Finch et al., 2019). The sparing–sharing framework provides a basis for assessing the implications for biodiversity of management approaches by combining simple region-wide scenarios of land use – each of which, critically, produces the same total amount of food – with empirical information on how the abundance of each of a large number of species responds to changing yield. Biodiversity outcomes can then be compared across scenarios to identify which combination of management regimes achieves a given overall level of production at least cost to biodiversity [for more details see Green et al. (2005) and Phalan et al. (2011b)]. Recent work has applied the same framework to examining the efficacy of land-use strategies for carbon storage (Gilroy et al., 2014; Williams et al., 2018). An increasing number of studies have successfully applied this framework to examine the merits of a range of approaches to meeting food demand, along a continuum from sharing to sparing (Phalan, 2018). By contrast, in forestry, although the Triad topic has been around for decades (Seymour & Hunter, 1992), field data to assess the efficacy of various Triad scenarios remain sparse (Table 2).

The objectives of this review are fourfold. First, we seek to compare concepts from the land sharing–sparing literature with those of the Triad approach to determine the degree to which the framing and methods deployed to understand biodiversity responses to different intensities of agricultural production can be translated into a forestry context. Second, we provide research design recommendations for establishing field-based empirical Triad studies based on lessons learned from recent sharing–sparing studies and the few modelling studies that address Triad. Third, we present hypotheses to test in new studies. Finally, we discuss potential pitfalls and opportunities in conceptualizing landscape management under the Triad approach, as revealed through a sharing–sparing lens. As forests occupy an enormous land area globally (45.5 million km^2 versus 15 million km^2 of croplands and 28 million km^2 of pastures) (Ramankutty et al., 2008; Runting et al., 2019), quantifying the benefits and trade-offs involved in different forest management strategies has the potential to have major implications for biodiversity conservation, climate change mitigation and wood production.

II. EXISTING EXAMPLES OF SHARING–SPARING STUDIES IN FORESTS

Although still rare, several forest studies have used empirical data to test the relative merits to biodiversity conservation of intensive management with reserves versus ecological forestry (Edwards et al., 2014a; França et al., 2017; Montejo-Kovacevich et al., 2018; Mestre et al., 2020; Table 2). Two

Table 1. Similarities and differences between typical agricultural and forestry settings relevant to quantifying trade-offs and synergies and identifying land allocations that minimize trade-offs between conservation and production

Variable	Resource production setting	
	Agriculture	Forest management
Land-use gradient	Intact habitat, to low-yielding farmland, to high-yielding farmland	Primary forest, to managed native forest, to multi-species plantations, to monoculture plantations
Putative wildlife-friendly extensive practices	Agroforestry; flower strips; hedges; agroecological farming; rotations and fallow cycles	Selective cutting; retention forestry; continuous cover forestry; reduced-impact logging
Topography and soils	Often in level areas with deep, fertile soils	Often on slopes and poor soils (not suitable for agriculture)
Vegetation structure	Typically dissimilar to native vegetation	More similar to native vegetation
Species composition	Typically dissimilar to that in native vegetation	More similar to that in native vegetation
Size of land ownership parcels	Variable, often small (<1 to 100s ha)	Highly variable, but often large (100000s ha) in the case of public land or industrial ownership
Natural disturbance processes	Heavily suppressed	Present to some extent; some practices attempt to emulate natural disturbance
Timescale for field/stand management	1 to 30 years	10 to >100 years
Ownership	Mostly private	Private (both industrial and smallholder) and public
Main ecosystem service expectations	Food production; aesthetic; cultural; some hunting; carbon storage; nutrient cycling; recreation; water flow regulation	Fibre and wood production; wildlife habitat; hunting and trapping; nutrient cycling; freshwater regulation; recreation; carbon storage; aesthetic; cultural

field-based studies (Edwards *et al.*, 2014*a*; França *et al.*, 2017) found that sparing approaches relying on reserves and more intensive management were most effective at maintaining native biodiversity (Table 2). Two other tropical studies, both based on simulation models, indicated that the optimal strategy was contingent either on land tenure security (Griscom *et al.*, 2018) or whether 'improved management' occurred (e.g. reduced-impact logging, enforcement of protected areas) (Runting *et al.*, 2019).

Several studies moved beyond two-compartment models to examine Triad scenarios of at least three management types (Côté *et al.*, 2010; Tittler *et al.*, 2015). Using a spatially explicit simulation model, Côté *et al.* (2010) tested the outcomes of a Triad approach to those of *status quo* management in Quebec, Canada (2% reserve, 0% plantation, 98% extensive forestry). Although they did not examine biodiversity directly, they showed that several Triad scenarios (e.g. 14% intensive, 12% conservation, 74% extensive) outperformed the *status quo*, both in terms of the area of forest with old characteristics (a biodiversity proxy) and wood supply.

III. PARALLELS AND CONTRASTS BETWEEN SHARING–SPARING AND TRIAD

The land-sparing–sharing framework and Triad zoning are both ways of addressing complex trade-offs in land

management to balance production for human needs with the conservation of biodiversity and ecosystem services. Both frameworks consider a range of land management systems, along a gradient from those which most closely mimic natural vegetation, to those which rely most heavily on monocultures, artificial inputs, and mechanization. Broadly, we can expect those systems which most closely mimic natural vegetation to be most hospitable to the wild species that originally occurred in an area, but at the same time to be characterized by reduced yields of food or wood. Conversely, high-yielding systems tend to be the least hospitable for most original species (Gabriel *et al.*, 2013; Chaudhary *et al.*, 2016; Holt *et al.*, 2016). However, these broad patterns are not absolute; excessive use of pesticides, for example, can reduce efficiency of pest control, e.g. by killing natural enemies or resulting in herbicide resistance. In some situations, combining multiple crop or tree species can generate higher yields than monocultures (Liu *et al.*, 2018). Populations of certain species of conservation interest can sometimes be maintained within production systems without greatly compromising yields. Some groups of species will show greater sensitivity to management than others. For example, species dependent on forest cover continuity, large trees and dead wood are especially prone to decline in managed forests (Paillet *et al.*, 2010).

However, agriculture and forestry also differ from each other in important respects:

Table 2. Summary of existing studies on land sharing *versus* sparing in forests. Four studies rely on empirical field data to test land-sharing *versus* sparing or Triad approaches. Two of the studies found that land sparing tended to be best, which is consistent with our hypotheses for the tropics (see Section V). The two temperate studies showed evidence for both increased wood yield and biodiversity under mixed (Triad) scenarios. However, the two other studies found that improvements to either harvesting practices themselves (Runting *et al.*, 2019) or land tenure security Griscom *et al.*, 2018) were more important than whether harvest impact was distributed (i.e. sharing) or concentrated (i.e. sparing). 'Number of compartments' refers to the number of landscape-level treatments (e.g. reserve, intensive, extensive) considered

Study	Location	Number of compartments	Finding	Taxon	Method
França *et al.* (2017)	Tropical, Brazil	Two	Sparing best	Dung beetles	Examination of threshold response to degrees of selective harvesting
Edwards *et al.* (2014*a*)	Tropical, Malaysia	Two	Sparing best	Birds, dung beetles, ants	Logging intensity (once *versus* twice logged, and reserves)
Runting *et al.* (2019)	Tropical, Indonesia	Two, but with 'improved management' within each (e.g. reduced-impact logging, protected area enforcement)	'Improved management' superior to sharing or sparing	Carnivores, primates, bats	Expert-driven knowledge of species responses to treatments + simulation modelling
Griscom *et al.* (2018)	All tropical	Two, but with differing degrees of land tenure security and deforestation risk	Sharing best, but only under conditions when secure land tenure reduces deforestation; otherwise, sparing best	All species (species–area curves), carbon	Simulation modelling with models parameterized from the literature
Côté *et al.* (2010)	Temperate boreal	Three	Triad scenarios outperformed *status quo* (with minimal reserve or intensive management)	Old forest used as a biodiversity proxy	Spatial simulation model
Tittler *et al.* (2015)	Temperate boreal	Three	Spatial clumping of Triad components increased conservation of old forest, landscape connectivity, and maximized wood volume	Old forest used as a biodiversity proxy, habitat connectivity	Spatial simulation model
Montejo-Kovacevich *et al.* (2018)	Tropical	Five	Sharing is best, but some species benefited most from sparing	Butterflies	Empirical data and simulation model
Mestre *et al.* (2020)	Tropical	Two stand-level treatments and conclusions about landscape-level effects were hypothesized	Intermediate strategy best, with primarily sharing, but with reserves	Birds	Empirical data

(1) In terms of vegetation structure and species composition, managed forests and plantations typically resemble areas of natural habitat more closely than does farmland (Phalan *et al.*, 2011*b*; Kroll *et al.*, 2017). When mid-aged or mature, plantations – especially of native tree species – may also be more permeable to dispersing forest organisms than most farmland (Brotons *et al.*, 2003; Smith, Forbes & Betts, 2013; Root & Betts, 2016). These differences suggest that land sharing may be helpful for a larger proportion of species in forestry than it is in agriculture (Baker *et al.*, 2016), although some degree of land sparing is

likely to be needed for species dependent on primary and/or unmanaged forests (Gibson *et al.*, 2011; Kormann *et al.*, 2018; Lennox *et al.*, 2018).

(2) In terms of spatial scale, land management units in forestry landscapes are typically much larger than those in agricultural landscapes. Forest ownership includes public lands managed by either state agencies or private concessions, often occupying contiguous parcels of thousands or millions of hectares. Regional or federal governments may have legal mandates to maintain biodiversity and non-wood forest values, and public expectations that they should do so are likely greater in the case of forest management than agriculture (Stevens & Montgomery, 2002). Conservation requirements vary regionally and with land tenure and certification status, typically being more stringent in native forests, on public land, and in certified forests. These differences in the scale and objectives of ownership may mean that large-scale adoption of conservation measures is often more feasible in forestry lands than in many agricultural systems. In particular, the larger spatial scales inherent in forest management may be closer to those needed to incorporate natural disturbance processes such as fires, insect outbreaks and storms.

(3) In terms of temporal scale, agricultural harvesting cycles are typically short, from less than a year to a few decades (for some perennial crops). By contrast, forest management usually operates over timescales from several decades to much longer intervals. Some forest management systems also involve periodic but ecologically important interventions such as pruning, thinning, or partial stand harvests, often spaced over relatively long time intervals, before final stand harvest occurs. Further, both partial (e.g. insect damage) and stand-replacing (e.g. fire, blowdown) disturbances often occur even in the absence of human intervention. Thus, native species have evolved associations with particular stages of succession, including recently disturbed forests (Hansen *et al.*, 1995; Drapeau *et al.*, 2016). Measuring different biodiversity outcomes across successional stages is a critical, but challenging, aspect of understanding the costs and benefits of Triad approaches.

IV. DESIGN CONSIDERATIONS FOR EVALUATING ALTERNATIVE FORESTRY REGIMES USING THE SHARING–SPARING FRAMEWORK

Many of the key design features for conducting sharing–sparing studies in forestry carry over directly from farming studies, but some of the differences between agriculture and forestry (Section II; Table 1) mean that applying the framework to wood production raises additional challenges. The core data, for forestry as for farming studies (Phalan *et al.*, 2011*a*), are replicated, spatially coupled estimates of

(*i*) the abundance of large numbers of species; and (*ii*) yield across sites which are biophysically similar and representative of the region (and so could support very similar biota) but which differ as widely as possible in management practices. In the case of forestry, management regimes should include a range of conventional harvesting regimes, reduced-impact logging/variable-retention harvesting or ecological forestry (Franklin *et al.*, 2018), plantations of native and/or exotic species in monocultures or mixtures, and entirely unharvested stands. Some regions may include a variety of these contrasting practices, while other regions may simply include a range of intensity of a particular harvesting regime compared to unlogged controls [e.g. variable lengths of harvest rotations, or different numbers of harvest entries (Edwards *et al.*, 2014*a*; França *et al.*, 2017)].

A central challenge in research design in many parts of the world will be an association between ecosystem productivity (which also affects biodiversity distributions) and forest management treatments (Grau, Kuemmerle & Macchi, 2013). Often those areas managed most intensively for wood production are concentrated on the most fertile ground, with reserves relegated to lower productivity sites (Lindenmayer & Laurance, 2012). The less-productive areas may have reduced value for many biodiversity elements than might old-growth or intact stands in more productive areas (Scott & Tear, 2007; Lindenmayer & Laurance, 2012). Conversely, several studies have placed reserves in locations where they are likely to have the highest conservation outcomes (Côté *et al.*, 2010, Tittler *et al.*, 2012). It will be vital for researchers to avoid, but where necessary quantify and account for, such potential biases as much as possible. Of course, the strongest Triad research design would be one that decouples this inherent confounding factor by starting with unharvested landscapes, then randomly attributing harvest treatments at the landscape level (i.e. extensive, intensive, and reserve in varying proportions).

Choice of study taxa will be influenced by available knowledge and expertise, but we recommend assessing all species in one or more reasonably speciose but tractable groups, including some that are thought likely to be particularly sensitive to differences in management practices. We emphasize the importance of measuring biodiversity responses to management in terms of the absolute or relative abundance of individual species, or better still, population trajectories over longer time periods (Fischer *et al.*, 2014). Other, simpler metrics (such as species richness) may be much easier to obtain but say little or nothing about the likely viability of populations present, and may treat as equivalent the presence of scarce specialists and common (even non-native) generalists. Indeed, in agricultural analyses, degrading abundance-level data to species richness scores has been shown to generate opposite, and incorrect, insights into the relative merits for biodiversity of land sharing *versus* sparing approaches to food production (Balmford *et al.*, 2015). As in farming studies, data on biodiversity in different forest sites need to be accompanied by data on the yield of those sites, which might be expressed in biophysical units (such as m³/ha/yr) or profit

(e.g. \$US/ha/yr, net of all startup as well as recurrent costs and subsidies), or both.

Field campaigns to inform sharing–sparing analyses of forestry also need to reflect two critical ways in which forestry differs from most forms of agriculture. First, as noted above, production cycles are much longer than in farming (where they are often annual), so the biodiversity value of all management regimes of interest needs to be assessed across representative stages of the cycle (from immediately pre-harvest, through early to late re-growth). Similar sampling will be needed to account for the dynamics of unharvested forest reserves (from old growth through the stages of succession from prevailing natural disturbance regimes). Species' population density values can then be averaged or summed across successional stages.

Second, farming studies to date have typically characterized the diversity of management regimes in a region using 20–30 1-km^2 study sites (ideally embedded in larger areas under similar management, to limit spillover effects; e.g. Phalan *et al.*, 2011*b*). By contrast, in forestry, areas of similarly homogeneous management are sometimes considerably smaller (on the order of 10 ha or less). There are two ways to address this. One is to select small study sites such as individual managed stands. Challenges include the need for large numbers of sites and the consideration of whether the the scale of sample sizes matches the scales perceived by the organisms under study. However, increasing the number of sites also offers the potential for possible covariates of species abundance (such as the presence of habitat edges, streams, or landscape context) to be recorded and accounted for in subsequent analysis. An alternative approach, that mirrors what has been done in agricultural systems, is to sample within broad-scale study sites, each containing representative proportions of different stages of the successional or harvesting cycle. An advantage of this latter approach is that it more readily enables researchers to address questions about the effects of differing Triad proportions at the landscape scale. For instance, does intensive forest management limit the capacity of late-successional species to disperse between patches, thereby eroding the efficacy of reserves (Root & Betts, 2016)?

The resulting field data can then be used to assess the biodiversity consequences of contrasting management approaches *via* two main steps. The response of each species to variation in forestry practices can be assessed by modelling abundance estimates (adjusted for detectability) across differently managed forests, as quantified by their wood yield (e.g. Royle, Dawson & Bates, 2004). Models can incorporate any relevant covariates. Inspection of the shapes of the resulting relationships (termed 'density–yield curves') can be used to infer the degree to which a species is affected positively, negatively or not at all by various forestry practices over the duration of a rotation cycle. These curves can be used to calculate the expected population size for each species under different sharing–sparing or Triad scenarios [Fig. 3; see Runting *et al.* (2019) and Green *et al.* (2005)], for any given level of total production.

The consequences for biodiversity of contrasting management regimes can then be estimated by combining density–yield curves with a series of spatially explicit scenarios for achieving a given target level of production (in m^3 or \$US profit per year) across the region, which specify where different practices might take place. These could include extreme sharing scenarios (i.e. no reserves), extreme sparing ones (i.e. only reserves and intensive management), and various intermediate scenarios, including three-compartment Triad-style solutions (Tittler *et al.*, 2012, 2015; Feniuk, Balmford & Green, 2019). Applying data from density–yield curves to these contrasting land-use compositions (and taking into account not just management regime, but also any significant effects of edges, streams, etc.) then allows estimation of region-wide population sizes of each species assessed. Note that similar results can be achieved without full parameterization of density–yield curves, simply by statistical estimation of how each species' population density varies with local management regimes [see Williams *et al.* (2017) for an example].

Results can then be expressed relative to some baseline. Baselines might be estimated region-wide species' populations under present-day land use, or those estimated for the region in the absence of forestry but with natural disturbances (Seymour & Hunter, 1999). Summary results can be extracted separately for each major study taxon, or for subsets of particular interest (e.g. endemic or threatened species, or cohorts such as saproxylic or late-seral affiliates). Summaries might use an average across species, e.g. the geometric mean of each species' population size relative to baseline (Fig. 4), or number of species with more than a threshold probability of being committed to regional extinction. The effects on biodiversity of differences in demand can be investigated by re-running the models for a range of region-wide targets for forestry production.

Lastly, it is worth noting that a similar field and analytical design can be followed for assessing the region-wide impacts of different forestry scenarios on outcomes other than biodiversity. This is especially relevant as forests are typically expected to deliver a wide array of economic benefits and ecosystem services including carbon storage, freshwater regulation and multiple forms of recreation (Table 1). Such landscape-scale studies also allow investigation of several potential negative externalities, such as soil erosion or downstream eutrophication. Fieldwork designs could be modified to incorporate measurement of how these outcomes vary across sites with differing management regimes, with the results then applied to contrasting region-wide land-use configurations. Such impacts could be considered alongside production and biodiversity outcomes when deciding which land-use strategy to adopt (Balmford *et al.*, 2018).

V. RESEARCH AND IMPLEMENTATION CHALLENGES ASSOCIATED WITH TRIAD AND LAND SHARING–SPARING IN FORESTS

One of the greatest challenges to the implementation and testing of the Triad approach lies in establing the appropriate
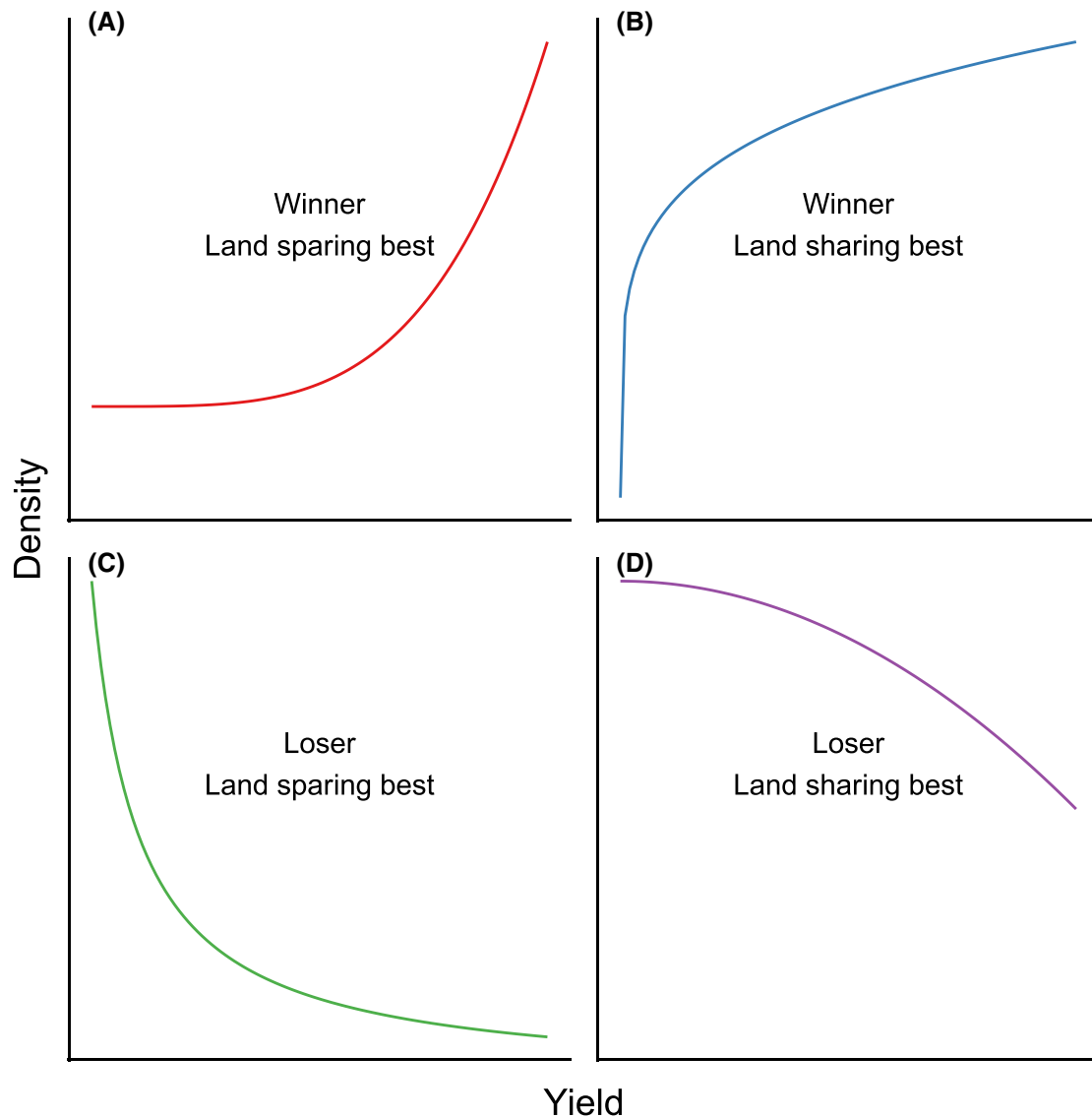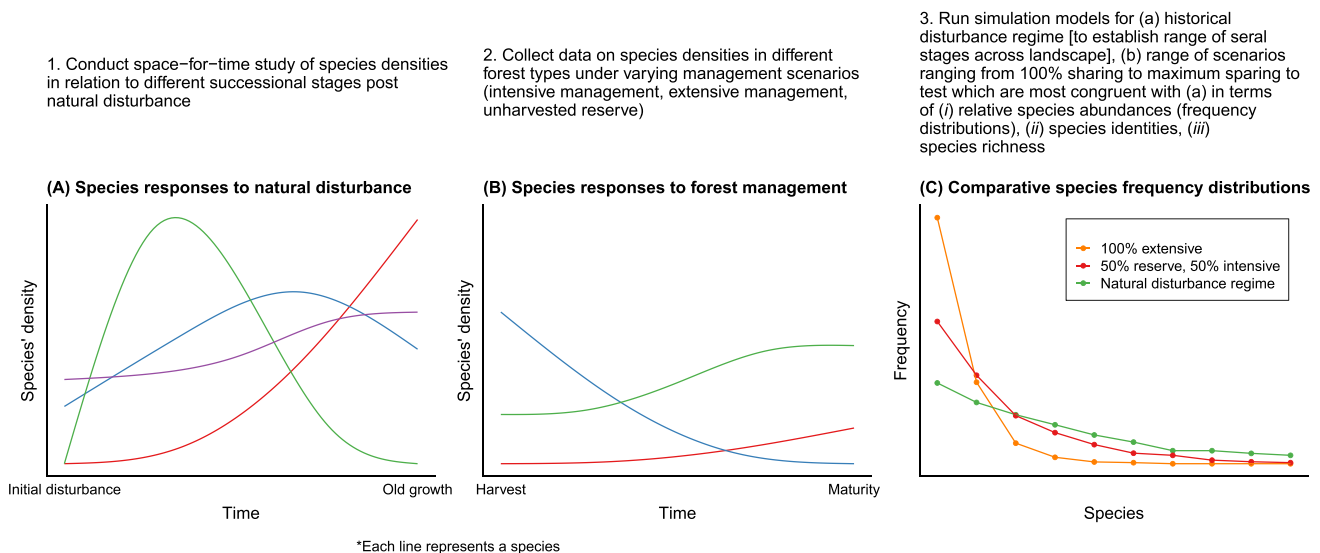
Fig 3. Examples of species density–yield functions that can be estimated from empirical field data in land sharing–sparing studies. (A, B) Species with population densities that are a positive function of yield are 'winner' species. In instances where curves are concave, sharing is a better strategy, whereas when curves are convex, sparing will be better. (A) Land sparing is best (reserves + intensive management). (B) Species are favoured by land sharing (extensive, softer management with lower yields). (C, D) 'Loser' species – showing negative relationships between density and yield – are of greater conservation concern. Species with densities that decline dramatically at even low yields (C) tend to be favoured by a land-sparing approach (i.e. *via* reserves, with all production *via* intensive management). Species with populations that are resilient to low-yield production (D) do best under a land-sharing scenario. After Phalan *et al.* (2011*b*).

baseline for comparison of contrasting management approaches. Clearly, the overall objective should be maintaining as much as possible of the biodiversity present before wood extraction, but at what densities, total population abundances, and at what scales? One approach in ecological forest management has been to attempt to mimic, *via* silviculture, the historical range of variation (HRV) (Swanson & Franklin, 1992; Seymour & Hunter, 1999) or the 'natural' range of variation (NRV) (Spies *et al.*, 2007) in the frequency, spatial pattern, and extent of natural disturbance. This

approach is based on the notion that native species evolved to tolerate such disturbance regimes. Thus, if management practices approximate these, is it more likely that native biodiversity will be conserved (Nonaka & Spies, 2005; Kuuluvainen & Grenfell, 2012). This type of 'coarse-filter' approach has been criticized on numerous grounds, including lack of sufficient data on historical disturbance regimes, challenges associated with determining the appropriate timeline for the definition of 'historical', and the fact that past conditions may not be an adequate guide to the future (Keane

Adopting historical range of variation as a baseline in TRIAD management

1. Conduct space−for−time study of species densities in relation to different successional stages post natural disturbance

2. Collect data on species densities in different forest types under varying management scenarios (intensive management, extensive management, unharvested reserve)

3. Run simulation models for (a) historical disturbance regime [to establish range of seral stages across landscape], (b) range of scenarios ranging from 100% sharing to maximum sparing to test which are most congruent with (a) in terms of (*i*) relative species abundances (frequency distributions), (*ii*) species identities, (*iii*) species richness

(A) Species responses to natural disturbance

Species' density

Initial disturbance — Old growth
Time

(B) Species responses to forest management

Species' density

Harvest — Maturity
Time

*Each line represents a species

(C) Comparative species frequency distributions

Frequency

— 100% extensive
— 50% reserve, 50% intensive
— Natural disturbance regime

Species

Fig 4. Adopting historical range of variation as a baseline in Triad management. Sampling regimes and modelling approaches to determine the relative biodiversity gain from differing sharing/sparing/Triad approaches in relation to a baseline based on historical range of variation. One challenge in forest systems is to determine the appropriate baseline for comparison with managed landscapes. Completely unmanaged landscapes are still prone to natural disturbances, and many species are adapted to forests as they succeed such disturbances. Therefore, establishing only mature forest baselines will often be inappropriate. We propose that species abundance be quantified in space-for-time studies representing initial disturbance through forest maturity (A). This can then be compared to similar data collected for temporal gradients following different forest management treatments, each with a different estimated yield (e.g. intensive plantation management, as shown in B). Finally, dynamic landscape-scale models can be applied (*sensu* Ward & Erdle, 2015) to test the effect of different Triad scenarios (e.g. 50:50 reserve/intensive management, 100% extensive management) and compared to forest structure under a modelled natural disturbance regime. Species abundances and frequency distributions (C) under each scenario would be parameterized from steps A and B. In this hypothetical case, note that the species frequency distribution under the natural disturbance regime (green) has fewer common species, but a fatter tail (rare species are more abundant) than either the extensive or mixed strategy (red, yellow).

et al., 2009; Puettmann *et al.*, 2015). The extent to which silvicultural practices can adequately mimic natural disturbance processes has been a frequent point of debate and conflict in forest conservation (e.g. Lindenmayer & McCarthy, 2002; Hanson, Bond & Lee, 2018; Mikusiński *et al.*, 2018).

The most rigorous approach to establishing a baseline in sharing–sparing studies in forests would involve quantifying species abundances in space-for-time studies representing initial (natural) disturbance through forest maturity (Fig. 4A). This can then be compared to similar data collected for temporal gradients following different forest management treatments [e.g. intensive plantation management (Fig. 4B), selection cutting, thinning, etc.], each corresponding to an estimated wood yield. Finally, dynamic landscape-scale models can be applied (*sensu* Ward & Erdle, 2015) to test the effect of different sharing–sparing scenarios (e.g. 50:50 reserve/intensive management; equal-thirds reserve/intensive/extensive; 100% extensive management) and compared to forest structure under a modelled natural disturbance regime. Species population sizes and frequency distributions (Fig. 4C) under each scenario would be parameterized from steps A and B. Of course, reliable data on disturbance regimes and native species' associations with forest age

classes may be unavailable – perhaps due to long-term human settlement in a region (as is the case for most of western Europe for example). In these cases, appropriate baseline comparators will need to be determined using different criteria – such as habitat amount criteria for indicator species – with a minimum expectation that regional extirpations do not occur.

A second issue – addressed in the land sharing–sparing literature (Green *et al.*, 2005) but nonetheless a continuing source of criticism – is that situating land sparing in opposition to land sharing institutes a false dichotomy (Kremen, 2015) and that some land-sharing methods can be implemented without yield penalties and thus without compromising the area of land that can be spared. A similar criticism could be levelled at the Triad approach. However, it is important to recognize that both frameworks (Triad, sharing–sparing) make no assumptions about the methods used to boost yields. To the extent that wildlife-friendly practices can be introduced without compromising yields or profits, those should be researched and encouraged where possible. There are many such opportunities in forestry. For instance, plantations can be softened by reduced use of herbicide, planting native species, planting mixtures of

species, and some retention of dead wood (Messier *et al.*, 2009; Lindenmayer *et al.*, 2019; Runting *et al.*, 2019) without necessarily incurring yield penalties (Kormann *et al.*, in press). Extensive forestry can be improved by careful road planning and reducing logging damage to remaining trees, and protected areas can be rendered more effective with enhanced enforcement and monitoring. Indeed, using an expert-driven approach combined with simulation modelling, Runting *et al.* (2019) found that such 'improved management' outperformed traditional versions of sharing and sparing in a tropical forest region. In the context of agricultural practices, there has also been heightened interest in 'sustainable intensification' whereby undesirable externalities are much reduced while maintaining high yields (Pretty *et al.*, 2018). It is essential to test (rather than assume) the merits of such intermediate solutions. This presents a challenge to research efforts because it substantially increases the number of possible treatments to examine, which in turn, will require greater overall sample sizes.

Active management (silviculture) of post-harvest forest restoration *via* cutting of competing vines, herbs or early-successional trees, or planting of harvestable saplings, can also play key roles in facilitating recovery times and in shifting the optimal balance between land-sharing and land-sparing logging (Cerullo & Edwards, 2019). Such timber enrichment activities are likely to take a more central role in tropical forests given potential emerging roles of carbon markets *via* reduced impact logging for climate change mitigation (RIL-C), and sustainable forestry and carbon enhancements under REDD+ (Reducing Emissions from Deforestation and Forest Degradation).

We suggest that initial Triad research should compare 'best management practices' across all treatments rather than confounding silvicultural pratices in Triad with other elements of timber extraction. For example, one should ideally not compare extensive forestry that happens to have a badly designed road layout and construction, to intensive forestry that utilizes a well-designed road system. Of course, if one regime is *necessarily* associated with poor practices, such practices cannot be disentangled and should be considered a legitimate source of differences among the regimes.

A further critique of the land-sparing framework requiring consideration in the context of forestry is that although biodiversity may benefit from spared landscapes and intensified production, various less-quantifiable externalities might reduce the estimated benefits of land sparing. The widespread application of chemical pesticides to control plant competition and insect damage is a controversial example (Brockerhoff *et al.*, 2008; Betts *et al.*, 2013). The impacts of such chemicals on human health and biodiversity are still not well known due to the potential for cumulative, long-term effects and the challenge of researching multiple, interacting stressors. Other externalities include risks of long-term declines in productivity across multiple intensive rotations (Bi *et al.*, 2007).

The outcomes of land sparing *versus* land sharing debates also have a strong socio-economic component. First, there is often variation in community acceptability of different forms of harvesting. For example, in New Zealand all wood production is from plantations – in part because of social conflict (which lies outside the scope of this review), partly due to very slow growth rates of many native tree species, but also because of the extent that prior forest clearing eliminated options other than a land-sparing approach. In other jurisdictions, the intensification of wood production *via* plantations may be socially unacceptable. In the tropics, intensification might also require high establishment costs relative to logging (timber 'mining') in natural forest that cannot be borne by some tropical countries or by smaller, local actors.

Wood quality from plantations may be inferior and unsuitable for certain end uses compared to those available in natural forests under extensive harvesting regimes (Fisher, Edwards & Wilcove, 2014). Thus, while revenues from natural forests and plantations might be equivalent and substitutable when making low-value wood products [e.g. cardboard, medium density fibreboard (MDF); Runting *et al.*, 2019], net returns on prized hardwoods can be large and cannot be substituted with plantation wood (e.g. Ipe-amarelo and Ipe-roxo sell at ~US\$1500 per m^3 in Rondonia, Brazilian Amazon, with substantial added value after finishing for the EU flooring market; D.P. Edwards, personal communication). For a full assessment, Triad scenarios should therefore be compared not just in terms of total wood volume and biodiversity value, but in terms of the products available, jobs generated, and overall economic impact. Clearly, future research on the Triad approach should concentrate not only on biodiversity and wood growth responses, but also attempt rigorously to quantify externalities, social needs, and economic outcomes across the spectrum from extensive to intensive management; frameworks are already in place do so (Balmford *et al.*, 2018, 2019).

To an even greater extent than with agriculture, research in forest systems must take time into account. Wood production cycles can last decades. This makes studying the effects of management decisions difficult, because changes in biodiversity and yields may take decades to manifest. Longitudinal studies that track stands subjected to well-defined management combinations are of immense value, but current incentives and funding structures make such studies difficult to establish and maintain. Added complications include dealing with potential changes in growing conditions due to, for example, global change or wind and fire disturbances, changes in market preferences, management technologies, and social and legal settings. For these reasons, space-for-time studies are likely to remain the most common approach for measuring trade-offs and synergies in forest landscapes. Wood yields and profits can be estimated using tree-growth models and averaged over the rotation length, but these models are subject to a range of uncertainties about future economic conditions and non-linear responses to a changing climate, for example, *via* insect outbreaks and altered fire regimes.

A final research challenge for deploying sharing–sparing approaches for forestry relates to governance and other

mechanisms to ensure the intended functioning of selected systems. For instance, if biodiversity conservation and wood production are optimized under sparing, strict zoning and enforcement of reserves may be required to ensure that plantation areas are not further expanded to meet society's increasing demand for forest products (Kremen, 2015; Phalan *et al.*, 2016). A variety of mechanisms have been proposed for addressing this challenge in agricultural systems, including land-use zoning [an approach that is already in place in many managed forests (Noble & Dirzo, 1997; Paquette & Messier, 2010)], payments, tax incentives and subsidies for conserved land, and standards and certification (Phalan *et al.*, 2016). The success of these sorts of initiatives may differ between food and wood production, so we anticipate considerable scope for identifying, implementing and evaluating new ideas in forestry systems.

VI. HYPOTHESES ON THE APPLICATION OF TRIAD AND SHARING–SPARING FRAMEWORKS TO FORESTS

Given the lack of empirical data on the relative merits of strategies along the sharing–sparing continuum for forestry (Edwards *et al.*, 2014a), it is timely to present *a priori* hypotheses on how wood production can be maintained at the least cost to nature. We emphasize that these are hypotheses and predictions to be tested – ideally in broad-scale studies across multiple forest biomes, and over the long term.

(1) Hypothesis 1: the relative merits of sharing and sparing will depend on the exposure of native forests to disturbance over evolutionary time

Species' evolutionary histories shape their capacity to deal with novel stressors (Betts *et al.*, 2019). Theory predicts that species that have evolved in, and survived in, high-disturbance environments should be more likely to persist in the face of analogous contemporary disturbances, including those of habitat loss and fragmentation (Balmford, 1996). Disturbances often create edges, and in environments with frequent and large-scale disturbances, persistent species are likely to be adapted to edge habitats and to dispersing across unsuitable habitats. This 'extinction filter' hypothesis has been suggested for forest (Drapeau *et al.*, 2016) and grassland systems (Balmford, 1996). We therefore predict that species inhabiting forests that have been prone to frequent canopy-removing natural disturbances should be more amenable to forestry operations, and hence more likely to fare better under sharing rather than sparing strategies – as long as wood harvesting approximates the severity and spatial extent of past disturbances (Seymour & Hunter, 1992). Indeed, because many species in disturbance-prone forest systems may be disturbance adapted, it may be *necessary*, if natural disturbance regimes have been dampened by human suppression of fires, floods

or megaherbivores, to create early successional habitat *via* wood harvest (Franklin & Johnson, 2012) – although restoring large mammal populations, fire regimes, insect outbreaks, or natural river dynamics could also be options. Of course, natural disturbances do occur in reserves, but these are frequently suppressed in the interest of safety, or conserving old forests, and are particularly difficult to maintain when reserves are small and isolated (Pereira *et al.*, 2012). Conversely, species inhabiting regions where stand-replacing disturbances are rare may be more effectively conserved *via* reserves. This is particularly likely to be the case for species prone to strong negative effects of disturbances, such as those benefiting from closed-canopy conditions for reproduction or dispersal (Fredericksen & Putz, 2003). Such species are more likely to be prevalent in the tropics, due to the relative paucity of severe disturbances in such regions (Betts *et al.*, 2017, 2019).

(2) Hypothesis 2: sharing (and management for early seral stages) is more likely to be favourable in regions with a long history of forestry

The corollary to natural disturbances acting as extinction filters is that long-term anthropogenic disturbances *via* wood harvesting or agriculture might also result in a biota which fares better under land sharing. This effect could take effect through extirpation of sensitive species, increases in abundance of and colonization by insensitive species, and adaptation of remaining species to forestry practices. A long land-use history clearly has implications for conservation efforts (Whitlock *et al.*, 2018). For example, humans have managed and deforested the landscape extensively in central and southern Europe for millennia. Much of the remaining forest was heavily degraded in the 16th to 18th century and modern silviculture techniques have led to more intensive management over the past two centuries. Similar processes apply to other regions of the world, e.g. the northeastern USA, which was nearly completely deforested during the 1700s (Thompson *et al.*, 2013). An important caveat is that such a history may have shifted the baselines used to evaluate the merits of strategies along the sharing–sparing continuum, for example by the extirpation of old-growth specialists from much of the region (Müller *et al.*, 2013). If such species are not globally extinct, it will be important to consider them in the evaluation of different forest management options.

(3) Hypothesis 3: advantages of sparing may depend on the proportion of intensive management in the landscape, with benefits diminishing at high proportions of high-yield forestry

Theory predicts that species may decline precipitously once habitat has declined below a threshold (Andren & Angelstam, 1993), particularly if the intervening matrix is inhospitable to movement (With & Crist, 1995). Given that intensive silviculture may reduce the functional connectivity of forest landscapes (Villard & Haché, 2012; Smith

et al., 2013), if substantial proportions of the landscape are occupied by less-permeable matrix (i.e. intensive management), viability of native populations may be impaired (Root & Betts, 2016). For this hypothesis to be supported, a species would need to be able to persist, albeit at low densities, in 'ecological forestry', but do best in large patches of 'sparing'. At high levels of intensive management, area sensitivity would cause local extirpation from small reserve patches, without recolonization due to impermeability of intensive forest management zones. Options exist to increase the permeability of such intensively managed landscapes (Tittler *et al.*, 2012; MacLean *et al.*, 2015) using reserves connected *via* lower impact (extensive) forestry may be a fruitful way of reducing such fragmentation effects. Again, the optimal proportion of reserve/intensive/extensive forestry in a landscape is likely to depend heavily on species' life-history characteristics – particularly dispersal capacity through different silvicultural approaches, as well as their capacity to handle low-intensity disturbance (ecological forestry). This hypothesis would only be relevant in cases where the difference in timber yield between ecological and intensive management is small. Otherwise, production from any given area of ecological forestry could in principle be replaced with a much smaller area of intensive management and most forest in the landscape could be spared in unharvested reserves.

(4) Hypothesis 4: a greater proportion of species will be favoured by a land-sharing approach in forest management systems as compared to agricultural systems, but this pattern will be context dependent

Most forest operations result in stands that have lower contrast with remaining unmanaged forest, compared with the differences between agricultural regimes and the natural habitat they replace. Higher vegetation cover facilitates the survival and movement of some species during dispersal (Vitz & Rodewald, 2010) and residual trees in more ecological approaches to forestry – such as variable retention – could still facilitate dispersal through the matrix (Haché, Bayne & Villard, 2014; Geoffroy *et al.*, 2019). Further, although the initial effect of light forest management treatments may be negative, results from experimental studies show that over the long term such treatments may increase densities of late-successional species (Cahall, Hayes & Betts, 2013; Yegorova *et al.*, 2013, Baker *et al.*, 2016). By contrast, although an intensively managed matrix might be more permeable than agricultural land (Edwards *et al.*, 2014*b*), it might still filter animal movements (Villard & Haché, 2012), and may not serve as habitat for late-successional species (Pedley *et al.*, 2019).

(5) Hypothesis 5: land sparing will yield the greatest benefit to biodiversity when implemented at broad spatial scales

At extremely fine spatial scales where unmanaged forest and high-yield forestry areas are adjacent to each other in very small stands, the situation is essentially akin to land sharing (Daily, Ehrlich & Sanchez-Azofeifa, 2001), and benefits of sparing for sensitive species are likely to be limited. By contrast, for species that require intact, unmanaged habitat, sparing at broad scales (e.g. 100s–10000s of hectares) can help to ensure that areas are sufficiently large to minimize edge effects, reduce issues such as illegal hunting, and maximize landscape connectivity. We therefore predict that the performance of sparing relative to sharing will increase with the size of the patches being spared, and for this effect to be particularly pronounced for tropical species, which seem more sensitive to habitat fragmentation (Betts *et al.*, 2019).

(6) Hypothesis 6: in tropical forests, land sparing will leave forests less vulnerable to other impacts in the long term than will land sharing

Both land-sharing and land-sparing logging are likely to exacerbate threats to long-term forest and biodiversity integrity, but in different ways. Land sparing leaves behind unlogged areas containing high-value timber species; these areas could be subjected to illegal logging. However, the fact that more area is under production under land sharing means these forests are likely to have a more extensive road network. Thus, there are again substantial risks from illegal loggers, as well as hunters that threaten large-bodied vertebrates and their dispersal of the seeds of late-successional trees (Peres *et al.*, 2016). Additionally, given the spectre of more severe climate change-induced droughts, a more extensive road network generates canopy fragmentation and dry conduits over a large area that could promote and spread fire. On balance, therefore, we predict that the retention of primary forest reserves offers the best long-term chance of biodiversity protection and, in turn, sources for recolonization into logged forest areas.

(7) Hypothesis 7: specialists and restricted-range species are those that could benefit most from land-sparing forestry

In agricultural systems, there is evidence that restricted-range and specialist species are those most likely to benefit from land sparing, while the smaller set of species that would benefit from land sharing are more widespread generalists (Balmford *et al.*, 2015; Phalan, 2018). We hypothesize a similar finding in forest management systems. The mechanism is that harvesting systematically depletes certain resources from the landscape, such as older trees, specific tree species, undisturbed understorey, and large-diameter dead wood. Species whose niches are associated with these resources will struggle to persist outside of unharvested areas. Given that most species globally are relatively restricted in range, rare and specialized (Forister *et al.*, 2015), and that such species are disproportionately likely to be declining (Clavel, Julliard & Devictor, 2011), evidence for or against this hypothesis would have an important bearing on conservation priorities.

VII. CONCLUSIONS

(1) Given a rapid escalation in world demand for wood and continued high rates of deforestation worldwide, it is surprising that relatively little research has focused on how to meet wood demand with the least impact on biodiversity and carbon storage. Although there are now several field-based empirical tests of land sharing, land sparing, and various intermediate options in agricultural settings, there has been very limited analogous research in forestry.

(2) We suggest that the framework developed for agriculture offers promise for addressing this gap, outline modifications to the farm-focused protocol, and provided specific, testable predictions. The utility of this approach will best be explored (as in agriculture) through the targeted collection of empirical field data, replicated across many regions.

(3) We urge researchers to collaborate with forest managers to design predictive models and empirical studies – particularly experiments where data are collected on species abundances, management inputs, **economic benefits,** and wood production over the long term. Such collaborations could be facilitated by the establishment of a global working group that maintains a registry of ongoing studies in this area, detailed sampling and measurement protocols, and a database of results in a standardized format. This could aid future research that combines studies from very different landscapes to build predictive models for the relative performance of sharing–sparing or Triad management.

(4) It is our hope that such results will not only advance understanding of dynamics of forest ecosystems worldwide (e.g. by testing our hypotheses, and those developed by others), but improve forest management decisions for the benefit of biodiversity, climate, the forestry sector, and society at large.

VIII. ACKNOWLEDGEMENTS

IX. REFERENCES

ANDREN, H. & ANGELSTAM, P. (1993). Moose browsing on scots pine in relation to stand size and distance to forest edge. *Journal of Applied Ecology* **30**, 133–142.

BAKER, S. C., HALPERN, C. B., WARDLAW, T. J., KERN, C., EDGAR, G. J., THOMSON, R. J., BIGLEY, R. E., FRANKLIN, J. F., GANDHI, K. J. K., GUSTAFSSON, L., JOHNSON, S., PALIK, B. J., SPIES, T. A., STEEL, E. A., WESLIEN, J., et al. (2016). A cross-continental comparison of plant and beetle responses to retention of forest patches during timber harvest. *Ecological Applications* **26**, 2493–2504.

BALMFORD, A. (1996). Extinction filters and current resilience: the significance of past selection pressures for conservation biology. *Trends in Ecology & Evolution* **11**, 193–196.

BALMFORD, A., AMANO, T., BARTLETT, H., CHADWICK, D., COLLINS, A., EDWARDS, D., FIELD, R., GARNSWORTHY, P., GREEN, R., SMITH, P., WATERS, H., WHITMORE, A., BROOM, D. M., CHARA, J., FINCH, T., et al. (2018). The environmental costs and benefits of high-yield farming. *Nature Sustainability* **1**, 477–485.

BALMFORD, A., GREEN, R. & PHALAN, B. (2015). Land for food & land for nature? *Daedalus* **144**, 57–75.

BALMFORD, A., GREEN, R. E. & SCHARLEMANN, J. P. (2005). Sparing land for nature: exploring the potential impact of changes in agricultural yield on the area needed for crop production. *Global Change Biology* **11**, 1594–1605.

BALMFORD, B., GREEN, R. E., ONIAL, M., PHALAN, B. & BALMFORD, A. (2019). How imperfect can land sparing be before land sharing is more favourable for wild species? *Journal of Applied Ecology* **56**, 73–84.

BARLOW, J., GARDNER, T. A., ARAUJO, I. S., ÁVILA-PIRES, T. C., BONALDO, A. B., COSTA, J. E., ESPOSITO, M. C., FERREIRA, L. V., HAWES, J., HERNANDEZ, M. I. M., HOOGMOED, M. S., LEITE, R. N., LO-MAN-HUNG, N. F., MALCOLM, J. R., MARTINS, M. B., et al. (2007). Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. *Proceedings of the National Academy of Sciences of the United States of America* **104**, 18555–18560.

BETTS, M. G., VERSCHUYL, J., GIOVANINI, J., STOKELY, T. & KROLL, A. J. (2013). Initial experimental effects of intensive forest management on avian abundance. *Forest Ecology and Management* **310**, 1036–1044.

BETTS, M. G., WOLF, C., PFEIFER, M., BANKS-LEITE, C., ARROYO-RODRÍGUEZ, V., RIBEIRO, D. B., BARLOW, J., FARIA, D. JR., FLETCHER, R. J., HADLEY, A. S., HAWES, J. E., HOLT, R. D., KLINGBEIL, B., KORMANN, U., et al. (2019). Extinction filters mediate the global effects of habitat fragmentation on animals. *Science* **366**, 1236–1239.

BETTS, M. G., WOLF, C., RIPPLE, W. J., PHALAN, B., MILLERS, K. A., DUARTE, A., BUTCHART, S. H. M. & LEVI, T. (2017). Global forest loss disproportionately erodes biodiversity in intact landscapes. *Nature* **547**, 441–444.

BI, J., BLANCO, J., SEELY, B., KIMMINS, J., DING, Y. & WELHAM, C. (2007). Yield decline in Chinese-fir plantations: a simulation investigation with implications for model complexity. *Canadian Journal of Forest Research* **37**, 1615–1630.

BINKLEY, C. S. (1997). Preserving nature through intensive plantation forestry: the case for forestland allocation with illustrations from British Columbia. *The Forestry Chronicle* **73**, 553–559.

BROCKERHOFF, E. G., JACTEL, H., PARROTTA, J. A., QUINE, C. P. & SAYER, J. (2008). Plantation forests and biodiversity: oxymoron or opportunity? *Biodiversity and Conservation* **17**, 925–951.

BROTONS, L., MÖNKKÖNEN, M., HUHTA, E., NIKULA, A. & RAJASÄRKKÄ, A. (2003). Effects of landscape structure and forest reserve location on old-growth forest bird species in northern Finland. *Landscape Ecology* **18**, 377–393.

BUTCHART, S. H. M., WALPOLE, M., COLLEN, B., VAN STRIEN, A., SCHARLEMANN, J. P. W., ALMOND, R. E. A., BAILLIE, J. E. M., BOMHARD, B., BROWN, C., BRUNO, J., CARPENTER, K. E., CARR, G. M., CHANSON, J., CHENERY, A. M., CSIRKE, J., et al. (2010). Global biodiversity: indicators of recent declines. *Science* **328**, 1164–1168.

CAHALL, R. E., HAYES, J. P. & BETTS, M. G. (2013). Will they come? Long-term response by forest birds to experimental thinning supports the "Field of dreams" hypothesis. *Forest Ecology and Management* **304**, 137–149.

CEBALLOS, G., EHRLICH, P. R., BARNOSKY, A. D., GARCÍA, A., PRINGLE, R. M. & PALMER, T. M. (2015). Accelerated modern human–induced species losses: entering the sixth mass extinction. *Science Advances* **1**, e1400253.

CECCHERINI, G., DUVEILLER, G., GRASSI, G., LEMOINE, G., AVITABILE, V., PILLI, R. & CESCATTI, A. (2020). Abrupt increase in harvested forest area over Europe after 2015. *Nature* **583**, 72–77.

CERULLO, G. R. & EDWARDS, D. P. (2019). Actively restoring resilience in selectively logged tropical forests. *Journal of Applied Ecology* **56**, 107–118.

CHAUDHARY, A., BURIVALOVA, Z., KOH, L. P. & HELLWEG, S. (2016). Impact of forest management on species richness: global meta-analysis and economic trade-offs. *Scientific Reports* **6**, 23954.

CLAVEL, J., JULLIARD, R. & DEVICTOR, V. (2011). Worldwide decline of specialist species: toward a global functional homogenization? *Frontiers in Ecology and the Environment* **9**, 222–228.

Côté, P., Tittler, R., Messier, C., Kneeshaw, D. D., Fall, A. & Fortin, M.-J. (2010). Comparing different forest zoning options for landscape-scale management of the boreal forest: possible benefits of the TRIAD. *Forest Ecology and Management* **259**, 418–427.

Couto, L., Nicholas, I. & Wright, L. (2011). *Short Rotation Eucalypt Plantations for Energy in Brazil*, p. 17. IEA Bioenergy. https://www.ieabioenergy.com/wp-content/uploads/2018/01/IEA_Bioenergy_Task43_PR2011-02.pdf

Daily, G. C., Ehrlich, P. R. & Sanchez-Azofeifa, G. A. (2001). Countryside biogeography: use of human-dominated habitats by the avifauna of southern Costa Rica. *Ecological Applications* **11**, 1–13.

Díaz, S., Settele, J., Brondízio, E., Ngo, H. T., Guèze, M., Agard, J., Arneth, A., Balvanera, P., Brauman, K., Butchart, S., Chan, K., Garibaldi, L., Ichii, K., Liu, J., Subramanian, S. M., et al. (2019). Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the intergovernmental science-policy platform on biodiversity and ecosystem services. In *Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*, p. 56. IPBES Secretariat, Bonn.

Drapeau, P., Villard, M.-A., Leduc, A. & Hannon, S. J. (2016). Natural disturbance regimes as templates for the response of bird species assemblages to contemporary forest management. *Diversity and Distributions* **22**, 385–399.

Duraiappah, A. K., Naeem, S., Agardy, T., Ash, N. J., Cooper, H. D., Diaz, S., Faith, D. P., Mace, G., McNeely, J. A., Mooney, H. A., Oteng-Yeboah, A. A., Pereira, H. M., Polasky, S., Prip, C., Reid, W. V., et al. (2005). *Ecosystems and Human Well-Being: Biodiversity Synthesis; a Report of the Millennium Ecosystem Assessment*, p. 137. Washington, DC: World Resources Institute.

Eaton, D. & Prins, C. (2018). *Measuring the Value of Forests in a Green Economy*, p. 27. United Nations, New York.

Edwards, D. P., Gilroy, J. J., Woodcock, P., Edwards, F. A., Larsen, T. H., Andrews, D. J. R., Derhā, M. A., Docherty, T. D. S., Hsu, W. W., Mitchell, S. L., Ota, T., Williams, L. J., Laurance, W. F., Hamer, K. C. & Wilcove, D. S. (2014a). Land-sharing versus land-sparing logging: reconciling timber extraction with biodiversity conservation. *Global Change Biology* **20**, 183–191.

Edwards, D. P., Tobias, J. A., Sheil, D., Meijaard, E. & Laurance, W. F. (2014b). Maintaining ecosystem function and services in logged tropical forests. *Trends in Ecology & Evolution* **29**, 511–520.

FAOSTAT (2019a). *FAOSTAT Database on Agriculture*. Food and Agriculture Organization of the United Nations, Rome. http://faostat.fao.org/ accessed 26 August 2019.

FAOSTAT (2019b). *Forestry Production and Trade Database*. Food and Agriculture Organization of the United Nations, Rome. http://www.fao.org/faostat/en/#data/FO.

Feniuk, C., Balmford, A. & Green, R. E. (2019). Land sparing to make space for species dependent on natural habitats and high nature value farmland. *Proceedings of the Royal Society B: Biological Sciences* **286**, 20191483.

Finch, T., Gillings, S., Green, R. E., Massimino, D., Peach, W. J. & Balmford, A. (2019). Bird conservation and the land sharing-sparing continuum in farmland-dominated landscapes of lowland England. *Conservation Biology* **33**, 1045–1055.

Fischer, J., Abson, D. J., Butsic, V., Chappell, M. J., Ekroos, J., Hanspach, J., Kuemmerle, T., Smith, H. G. & von Wehrden, H. (2014). Land sparing versus land sharing: moving forward. *Conservation Letters* **7**, 149–157.

Fisher, B., Edwards, D. P. & Wilcove, D. S. (2014). Logging and conservation: economic impacts of the stocking rates and prices of commercial timber species. *Forest Policy and Economics* **38**, 65–71.

Food and Agriculture Organization of the United Nations (2015). *Global Forest Resources Assessment 2015: How Are the World's Forests Changing?* p. 244. Food and Agriculture Organization of the United Nations, Rome.

Forister, M. L., Novotny, V., Panorska, A. K., Baje, L., Basset, Y., Butterill, P. T., Cizek, L., Coley, P. D., Dem, F., Diniz, I. R., Drozd, P., Fox, M., Glassmire, A. E., Hazen, R., Hrcek, J., et al. (2015). The global distribution of diet breadth in insect herbivores. *Proceedings of the National Academy of Sciences of the United States of America* **112**, 442–447.

França, F. M., Frazão, F. S., Korasaki, V., Louzada, J. & Barlow, J. (2017). Identifying thresholds of logging intensity on dung beetle communities to improve the sustainable management of Amazonian tropical forests. *Biological Conservation* **216**, 115–122.

Franklin, J. F. & Donato, D. C. (2020). Variable retention harvesting in the Douglas-fir region. *Ecological Processes* **9**, 1–10.

Franklin, J. F. & Johnson, K. N. (2012). A restoration framework for federal forests in the Pacific northwest. *Journal of Forestry* **110**, 429–439.

Franklin, J. F., Johnson, K. N. & Johnson, D. L. (2018). *Ecological Forest Management*, p. 688. Waveland Press, Long Grove.

Fredericksen, T. S. & Putz, F. E. (2003). Silvicultural intensification for tropical forest conservation. *Biodiversity and Conservation* **12**, 1445–1453.

Gabriel, D., Sait, S. M., Kunin, W. E. & Benton, T. G. (2013). Food production vs. biodiversity: comparing organic and conventional agriculture. *Journal of Applied Ecology* **50**, 355–364.

Geoffroy, C., Fiola, M.-L., Bélisle, M. & Villard, M.-A. (2019). Functional connectivity in forest birds: evidence for species-specificity and anisotropy. *Landscape Ecology* **34**, 1363–1377.

Gibson, L., Lee, T. M., Koh, L. P., Brook, B. W., Gardner, T. A., Barlow, J., Peres, C. A., Bradshaw, C. J. A., Laurance, W. F., Lovejoy, T. E. & Sodhi, N. S. (2011). Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature* **478**, 378–381.

Gilroy, J. J., Woodcock, P., Edwards, F. A., Wheeler, C., Medina Uribe, C. A., Haugaasen, T. & Edwards, D. P. (2014). Optimizing carbon storage and biodiversity protection in tropical agricultural landscapes. *Global Change Biology* **20**, 2162–2172.

Grau, R., Kuemmerle, T. & Macchi, L. (2013). Beyond 'land sparing versus land sharing': environmental heterogeneity, globalization and the balance between agricultural production and nature conservation. *Current Opinion in Environmental Sustainability* **5**, 477–483.

Green, R. E., Cornell, S. J., Scharlemann, J. P. & Balmford, A. (2005). Farming and the fate of wild nature. *Science* **307**, 550–555.

Griscom, B. W., Goodman, R. C., Burivalova, Z. & Putz, F. E. (2018). Carbon and biodiversity impacts of intensive versus extensive tropical forestry. *Conservation Letters* **11**, e12362.

Haché, S., Bayne, E. M. & Villard, M.-A. (2014). Postharvest regeneration, sciurid abundance, and postfledging survival and movements in an ovenbird population. *The Condor* **116**, 102–112.

Hansen, A. J., McComb, W. C., Vega, R., Raphael, M. G. & Hunter, M. (1995). Bird habitat relationships in natural and managed forests in the west cascades of Oregon. *Ecological Applications* **5**, 555–569.

Hanson, C. T., Bond, M. L. & Lee, D. E. (2018). Effects of post-fire logging on California spotted owl occupancy. *Nature Conservation* **24**, 93–105.

Holt, A. R., Alix, A., Thompson, A. & Maltby, L. (2016). Food production, ecosystem services and biodiversity: we can't have it all everywhere. *Science of the Total Environment* **573**, 1422–1429.

International Union for Conservation of Nature. (2017). The IUCN Red List of Threatened Species. Version 2016.3. http://www.iucnredlist.org.

Jürgensen, C., Kollert, W. & Lebedys, A. (2014). *Assessment of Industrial Roundwood Production from Planted Forests*, p. 41. FAO, Rome.

Keane, R. E., Hessburg, P. F., Landres, P. B. & Swanson, F. J. (2009). The use of historical range and variability (HRV) in landscape management. *Forest Ecology and Management* **258**, 1025–1037.

Kok, M. T. J., Alkemade, R., Bakkenes, M., van Eerdt, M., Janse, J., Mandryk, M., Kram, T., Lazarova, T., Meijer, J., van Oorschot, M., Westhoek, H., van der Zagt, R., van den Berg, M., van der Esch, S., Prins, A.-G., et al. (2018). Pathways for agriculture and forestry to contribute to terrestrial biodiversity conservation: a global scenario-study. *Biological Conservation* **221**, 137–150.

Kormann, U. G., Hadley, A. S., Tscharntke, T., Betts, M. G., Robinson, W. D. & Scherber, C. (2018). Primary rainforest amount at the landscape scale mitigates bird biodiversity loss and biotic homogenization. *Journal of Applied Ecology* **55**, 1288–1298.

Kormann, U. G., Stokely, T. D., Verschuyl, J., Kroll, A. J., Harris, S. H., Maguire, D. A., Mainwaring, D. B., Rivers, J. W. & Betts, M. G. (in press). Reconciling biodiversity with timber production and revenue. *Ecological Applications*.

Kremen, C. (2015). Reframing the land-sparing/land-sharing debate for biodiversity conservation. *Annals of the New York Academy of Sciences* **1355**, 52–76.

Kroll, A. J., Verschuyl, J., Giovanini, J. & Betts, M. G. (2017). Assembly dynamics of a forest bird community depend on disturbance intensity and foraging guild. *Journal of Applied Ecology* **54**, 784–793.

Kuuluvainen, T. & Grenfell, R. (2012). Natural disturbance emulation in boreal forest ecosystem management—theories, strategies, and a comparison with conventional even-aged management. *Canadian Journal of Forest Research* **42**, 1185–1203.

Lahey, W. (2018). *An Independent Review of Forest Practices in Nova Scotia*, p. 61. Dalhousie University, Halifax.

Lennox, G. D., Gardner, T. A., Thomson, J. R., Ferreira, J., Berenguer, E., Lees, A. C., Mac Nally, R., Aragão, L. E. O. C., Ferraz, S. F. B., Louzada, J., Moura, N. G., Oliveira, V. H. F., Pardini, R., Solar, R. R. C., Vaz-de Mello, F. Z., et al. (2018). Second rate or a second chance? Assessing biomass and biodiversity recovery in regenerating Amazonian forests. *Global Change Biology* **24**, 5680–5694.

Lindenmayer, D. B., Blanchard, W., Westgate, M. J., Foster, C., Banks, S. C., Barton, P., Crane, M., Ikin, K. & Scheele, B. C. (2019). Novel bird responses to successive, large-scale, landscape transformations. *Ecological Monographs* **89**, e01362.

Lindenmayer, D. B., Franklin, J. F., Lõhmus, A., Baker, S. C., Bauhus, J., Beese, W., Brodie, A., Kiehl, B., Kouki, J., Pastur, G. M., Messier, C., Neyland, M., Palik, B., Sverdrup-Thygeson, A., Volney, J., et al. (2012). A

major shift to the retention approach for forestry can help resolve some global forest sustainability issues. *Conservation Letters* **5**, 421–431.

LINDENMAYER, D. B. & LAURANCE, W. F. (2012). A history of hubris–cautionary lessons in ecologically sustainable forest management. *Biological Conservation* **151**, 11–16.

LINDENMAYER, D. B. & McCARTHY, M. A. (2002). Congruence between natural and human forest disturbance: a case study from Australian montane ash forests. *Forest Ecology and Management* **155**, 319–335.

LIU, X., TROGISCH, S., HE, J.-S., NIKLAUS, P. A., BRUELHEIDE, H., TANG, Z., ERFMEIER, A., SCHERER-LORENZEN, M., PIETSCH, K. A., YANG, B., KÜHN, P., SCHOLTEN, T., HUANG, Y., WANG, C., STAAB, M., et al. (2018). Tree species richness increases ecosystem carbon storage in subtropical forests. *Proceedings of the Royal Society B: Biological Sciences* **285**, 20181240.

MacLEAN, D., SEYMOUR, R., MONTIGNY, M. & MESSIER, C. (2009). Allocation of conservation efforts over the landscape: the TRIAD approach. In *Setting Conservation Targets for Managed Forest Landscapes* (eds M. A. VILLARD and B. G. JONSSON), pp. 283–303. Cambridge University Press, Cambridge 426 p.

MacLEAN, D. A., DRACUP, E., GANDIAGA, F., HAUGHIAN, S. R., MacKAY, A., NADEAU, P., OMARI, K., ADAMS, G., FREGO, K. A., KEPPIE, D., MOREAU, G. & VILLARD, M.-A. (2015). Experimental manipulation of habitat structures in intensively managed spruce plantations to increase their value for biodiversity conservation. *The Forestry Chronicle* **91**, 161–175.

MEHRABI, Z., ELLIS, E. C. & RAMANKUTTY, N. (2018). The challenge of feeding the world while conserving half the planet. *Nature Sustainability* **1**, 409–412.

MESSIER, C., TITTLER, R., KNEESHAW, D. D., GÉLINAS, N., PAQUETTE, A., BERNINGER, K., RHEAULT, H., MEEK, P. & BEAULIEU, N. (2009). TRIAD zoning in Quebec: experiences and results after 5 years. *The Forestry Chronicle* **85**, 885–896.

MESTRE, L. A. M., COSSET, C. C. P., NIENOW, S. S., KRUL, R., RECHETELO, J., FESTTI, L. & EDWARDS, D. P. (2020). Impacts of selective logging on avian phylogenetic and functional diversity in the Amazon. *Journal of Zoology* **23**, 725–740.

MIKUSIŃSKI, G., BUBNICKI, J. W., CHURSKI, M., CZESZCZEWIK, D., WALANKIEWICZ, W. & KUIJPER, D. P. (2018). Is the impact of loggings in the last primeval lowland forest in Europe underestimated? The conservation issues of Białowieża Forest. *Biological Conservation* **227**, 266–274.

MONTEJO-KOVACEVICH, G., HETHCOAT, M. G., LIM, F. K. S., MARSH, C. J., BONFANTTI, D., PERES, C. A. & EDWARDS, D. P. (2018). Impacts of selective logging management on butterflies in the Amazon. *Biological Conservation* **225**, 1–9.

MÜLLER, J., BRUNET, J., BRIN, A., BOUGET, C., BRUSTEL, H., BUSSLER, H., FÖRSTER, B., ISACSSON, G., KÖHLER, F., LACHAT, T. & GOSSNER, M. M. (2013). Implications from large-scale spatial diversity patterns of saproxylic beetles for the conservation of European beech forests. *Insect Conservation and Diversity* **6**, 162–169.

NEWTON, M. & COLE, L. (2015). Overstory development in Douglas-fir-dominant forests thinned to enhance late-seral features. *Forest Science* **61**, 809–816.

NOBLE, I. R. & DIRZO, R. (1997). Forests as human-dominated ecosystems. *Science* **277**, 522–525.

NONAKA, E. & SPIES, T. A. (2005). Historical range of variability in landscape structure: a simulation study in Oregon, USA. *Ecological Applications* **15**, 1727–1746.

PAILLET, Y., BERGÈS, L., HJÄLTÉN, J., ÓDOR, P., AVON, C., BERNHARDT-RÖMERMANN, M., BIJLSMA, R.-J., DE BRUYN, L., FUHR, M., GRANDIN, U., KANKA, R., LUNDIN, L., LUQUE, S., MAGURA, T., MATESANZ, S., et al. (2010). Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe. *Conservation Biology* **24**, 101–112.

PAQUETTE, A. & MESSIER, C. (2010). The role of plantations in managing the world's forests in the Anthropocene. *Frontiers in Ecology and the Environment* **8**, 27–34.

PEDLEY, S. M., BARBARO, L., GUILHERME, J. L., IRWIN, S., O'HALLORAN, J., PROENÇA, V. & SULLIVAN, M. J. P. (2019). Functional shifts in bird communities from semi-natural oak forests to conifer plantations are not consistent across Europe. *PLoS One* **14**, e0220155.

PEREIRA, P., MIERAUSKAS, P., ÚBEDA, X., MATAIX-SOLERA, J. & CERDA, A. (2012). Fire in protected areas-the effect of protection and importance of fire management. *Environmental Research, Engineering and Management* **59**, 52–62.

PERES, C. A., EMILIO, T., SCHIETTI, J., DESMOULIÈRE, S. J. M. & LEVI, T. (2016). Disperser overkill erodes tropical forest carbon. *Proceedings of the National Academy of Sciences of the United States of America* **113**, 892–897.

PHALAN, B. (2018). What have we learned from the land sparing-sharing model? *Sustainability* **10**, 1760.

PHALAN, B., BALMFORD, A., GREEN, R. E. & SCHARLEMANN, J. P. (2011a). Minimising the harm to biodiversity of producing more food globally. *Food Policy* **36**, S62–S71.

PHALAN, B., GREEN, R. E., DICKS, L. V., DOTTA, G., FENIUK, C., LAMB, A., STRASSBURG, B. B., WILLIAMS, D. R., ZU ERMGASSEN, E. K. & BALMFORD, A. (2016). How can higher-yield farming help to spare nature? *Science* **351**, 450–451.

PHALAN, B., ONIAL, M., BALMFORD, A. & GREEN, R. E. (2011b). Reconciling food production and biodiversity conservation: land sharing and land sparing compared. *Science* **333**, 1289–1291.

PIRARD, R., DAL SECCO, L. & WARMAN, R. (2016). Do timber plantations contribute to forest conservation? *Environmental Science & Policy* **57**, 122–130.

POMMERENING, A. & MURPHY, S. (2004). A review of the history, definitions and methods of continuous cover forestry with special attention to afforestation and restocking. *Forestry* **77**, 27–44.

PRETTY, J., BENTON, T. G., BHARUCHA, Z. P., DICKS, L. V., FLORA, C. B., GODFRAY, H. C. J., GOULSON, D., HARTLEY, S., LAMPKIN, N., MORRIS, C., PIERZYNSKI, G., VARA PRASAD, P. V., REGANOLD, J., ROCKSTRÖM, J., SMITH, P., et al. (2018). Global assessment of agricultural system redesign for sustainable intensification. *Nature Sustainability* **1**, 441–446.

PUETTMANN, K. J., COATES, K. D. & MESSIER, C. C. (2008). *A Critique of Silviculture: Managing for Complexity*, 1st Edition, p. 207. Washington, DC: Island Press.

PUETTMANN, K. J., WILSON, S. M., BAKER, S. C., DONOSO, P. J., DRÖSSLER, L., AMENTE, G., HARVEY, B. D., KNOKE, T., LU, Y., NOCENTINI, S., PUTZ, F. E., YOSHIDA, T. & BAUHUS, J. (2015). Silvicultural alternatives to conventional even-aged forest management-what limits global adoption? *Forest Ecosystems* **2**, 8.

RAMANKUTTY, N., EVAN, A. T., MONFREDA, C. & FOLEY, J. A. (2008). Farming the planet: 1. Geographic distribution of global agricultural lands in the year 2000. *Global Biogeochemical Cycles* **22**, GB1003.

RAMETSTEINER, E. & WHITEMAN, A. (2014). *State of the World's Forests; Enhancing the Socio-Economic Benefits from Forests*, p. 126. FAO, Rome.

ROOT, H. T. & BETTS, M. G. (2016). Managing moist temperate forests for bioenergy and biodiversity. *Journal of Forestry* **114**, 66–74.

ROYLE, J. A., DAWSON, D. K. & BATES, S. (2004). Modeling abundance effects in distance sampling. *Ecology* **85**, 1591–1597.

RUNTING, R. K., GRISCOM, B. W., STRUEBIG, M. J., SATAR, M., MEIJAARD, E., BURIVALOVA, Z., CHEYNE, S. M., DEERE, N. J., GAME, E. T., PUTZ, F., WELLS, J. A., WILTING, A., ANCRENAZ, M., ELLIS, P., KHAN, F. A. A., et al. (2019). Larger gains from improved management over sparing–sharing for tropical forests. *Nature Sustainability* **2**, 53–61.

SAATCHI, S. S., HARRIS, N. L., BROWN, S., LEFSKY, M., MITCHARD, E. T., SALAS, W., ZUTTA, B. R., BUERMANN, W., LEWIS, S. L., HAGEN, S., PETROVA, S., WHITE, L., SILMAN, M. & MOREL, A. (2011). Benchmark map of forest carbon stocks in tropical regions across three continents. *Proceedings of the National Academy of Sciences of the United States of America* **108**, 9899–9904.

SCOTT, J. M. & TEAR, T. H. (2007). What are we conserving? Establishing multiscale conservation goals and objectives in the face of global threats. In *Managing and Designing Landscapes for Conservation: Moving from Perspectives to Principles*, pp. 494–510. Blackwell Publishing, Oxford.

SEDJO, R. A. (1999). Planted forests: contribution to the quest for sustainable societies. *New Forests* **17**, 339–359.

SEYMOUR, R. S. & HUNTER, M. L. (1992). *New Forestry in Eastern Spruce-Fir Forests: Principles and Applications to Maine*, p. 41. College of Forest Resources, University of Maine, Orono.

SEYMOUR, R. S. & HUNTER, M. L. (1999). Principles of ecological forestry. In *Maintaining Biodiversity in Forest Ecosystems*, pp. 22–61. Cambridge University Press, Cambridge.

SMITH, M. J., FORBES, G. J. & BETTS, M. G. (2013). Landscape configuration influences gap-crossing decisions of northern flying squirrel (*Glaucomys sabrinus*). *Biological Conservation* **168**, 176–183.

SPIES, T. A., McCOMB, B. C., KENNEDY, R. S., McGRATH, M. T., OLSEN, K. & PABST, R. J. (2007). Potential effects of forest policies on terrestrial biodiversity in a multi-ownership province. *Ecological Applications* **17**, 48–65.

STEVENS, J. A. & MONTGOMERY, C. A. (2002). *Understanding the Compatibility of Multiple Uses on Forest Land: A Survey of Multiresource Research with Application to the Pacific Northwest*. Gen. Tech. Rep. PNW-GTR-539, p. 44. US Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland.

SWANSON, F. J. & FRANKLIN, J. F. (1992). New forestry principles from ecosystem analysis of Pacific northwest forests. *Ecological Applications* **2**, 262–274.

SWANSON, M. E., FRANKLIN, J. F., BESCHTA, R. L., CRISAFULLI, C. M., DELLASALA, D. A., HUTTO, R. L., LINDENMAYER, D. B. & SWANSON, F. J. (2011). The forgotten stage of forest succession: early-successional ecosystems on forest sites. *Frontiers in Ecology and the Environment* **9**, 117–125.

TALLIS, H. M., HAWTHORNE, P. L., POLASKY, S., REID, J., BECK, M. W., BRAUMAN, K., BIELICKI, J. M., BINDER, S., BURGESS, M. G., CASSIDY, E., CLARK, A., FARGIONE, J., GAME, E. T., GERBER, J., ISBELL, F., et al. (2018). An attainable global vision for conservation and human well-being. *Frontiers in Ecology and the Environment* **16**, 563–570.

THOMPSON, J. R., CARPENTER, D. N., COGBILL, C. V. & FOSTER, D. R. (2013). Four centuries of change in northeastern United States forests. *PLoS One* **8**, e72540.

TILMAN, D. & CLARK, M. (2014). Global diets link environmental sustainability and human health. *Nature* **515**, 518–522.

TITTLER, R., FILOTAS, E., KROESE, J. & MESSIER, C. (2015). Maximizing conservation and production with intensive forest management: it's all about location. *Environmental Management* **56**, 1104–1117.

TITTLER, R., MESSIER, C. & FALL, A. (2012). Concentrating anthropogenic disturbance to balance ecological and economic values: applications to forest management. *Ecological Applications* **22**, 1268–1277.

TITTLER, R., MESSIER, C. & GOODMAN, R. C. (2016). Triad forest management: local fix or global solution. In *Ecological Forest Management Handbook*, pp. 33–45. CRC Press, Boca Raton.

VILLARD, M.-A. & HACHÉ, S. (2012). Conifer plantations consistently act as barriers to movement in a deciduous forest songbird: a translocation experiment. *Biological Conservation* **155**, 33–37.

VITZ, A. C. & RODEWALD, A. D. (2010). Movements of fledgling ovenbirds (*Seiurus aurocapilla*) and worm-eating warblers (*Helmitheros vermivorum*) within and beyond the natal home range. *The Auk* **127**, 364–371.

WAGNER, R. G., LITTLE, K. M., RICHARDSON, B. & MCNABB, K. (2005). The role of vegetation management for enhancing productivity of the world's forests. *Forestry* **79**, 57–79.

WARD, C. & ERDLE, T. (2015). Evaluation of forest management strategies based on Triad zoning. *The Forestry Chronicle* **91**, 40–51.

WHITLOCK, C., COLOMBAROLI, D., CONEDERA, M. & TINNER, W. (2018). Land-use history as a guide for forest conservation and management. *Conservation Biology* **32**, 84–97.

WILLIAMS, D. R., ALVARADO, F., GREEN, R. E., MANICA, A., PHALAN, B. & BALMFORD, A. (2017). Land-use strategies to balance livestock production,

biodiversity conservation and carbon storage in Yucatán, Mexico. *Global Change Biology* **23**, 5260–5272.

WILLIAMS, D. R., PHALAN, B., FENIUK, C., GREEN, R. E. & BALMFORD, A. (2018). Carbon storage and land-use strategies in agricultural landscapes across three continents. *Current Biology* **28**, 2500–2505.

WITH, K. A. & CRIST, T. O. (1995). Critical thresholds in species' responses to landscape structure. *Ecology* **76**, 2446–2459.

YAMAURA, Y., LINDENMAYER, D., YAMADA, Y., GONG, H., MATSUURA, T., MITSUDA, Y. & MASAKI, T. (2019). A spatially explicit empirical model of structural development processes in natural forests based on climate and topography. *Conservation Biology* **34**, 195–206.

YAMAURA, Y., SHOJI, Y., MITSUDA, Y., UTSUGI, H., TSUGE, T., KURIYAMA, K. & NAKAMURA, F. (2016). How many broadleaved trees are enough in conifer plantations? The economy of land sharing, land sparing and quantitative targets. *Journal of Applied Ecology* **53**, 1117–1126.

YEGOROVA, S., BETTS, M. G., HAGAR, J. & PUETTMANN, K. J. (2013). Bird-vegetation associations in thinned and unthinned young Douglas-fir forests 10 years after thinning. *Forest Ecology and Management* **310**, 1057–1070.

YOSHII, C., YAMAURA, Y., SOGA, M., SHIBUYA, M. & NAKAMURA, F. (2015). Comparable benefits of land sparing and sharing indicated by bird responses to stand-level plantation intensity in Hokkaido, Northern Japan. *Journal of Forest Research* **20**, 167–174.