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REVIEW: FOREST BIODIVERSITY AND ECOSYSTEM SERVICES

Biodiversity and ecosystem services in forest ecosystems: a research agenda for applied forest ecology

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Summary

1. Given the substantial contributions of forest biodiversity and ecosystem services to society, forest sciences have a large potential to contribute to the integrity and sustainability of our future. This is especially true when the roles of biodiversity for sustaining ecosystem services are considered.

2. The rapid expansion of sustainable forest management (SFM) has resulted in the adoption of various forest management frameworks intended to safeguard biodiversity. Concurrently, the importance of forest ecosystem services has been increasingly recognized. Although some initiatives aimed at conserving both biodiversity and ecosystem services are emerging, knowledge gaps still exist about their relationships and potential trade-offs in forests. Given recent advancements, increasing opportunities and some lags in forest ecology, further research on biodiversity, ecosystem functions and services will play substantial roles in the development of SFM practices.

3. Here, we identified key issues including (i) relationships between biodiversity and ecosystem function as a foundation of ecological integrity, (ii) resilience thinking to better prepare for and adapt to environmental changes, (iii) social–ecological perspectives that facilitate real-world conservation and management and (iv) theory-driven restoration that bridges science and practice. Thus, we illustrate priorities and future possibilities in applied ecology studies in forests, which will help society and ecosystems to build capacity and resilience to face uncertainty in the changing environment.

4. *Synthesis and applications*. Under substantial human influences, forests are highly likely to be largely altered, potentially leading to the emergence of novel ecosystems or alternative stable states. Management thus needs more flexible, novel measures to address the significant uncertainty this generates. Resilience-based approaches are important to respond adaptively to future changes and cope with surprises, potentially providing multiple options. Although challenges exist, theory should play an important role in managing, conserving and restoring forest ecosystems. The issues discussed here should receive further attention in the context of the multiple goals of sustainable forest management.

Key-words: alternative stable states, biodiversity–ecosystem functioning, novel ecosystems, response diversity, restoration, social–ecological system, sustainable forest management, theory and practice

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Introduction

Increasing concern and demand for biodiversity conservation world-wide has arisen from substantial contemporary declines in biodiversity at various spatial, temporal and biological scales (Tittensor *et al.* 2014). Concurrently, a growing body of scientific evidence indicates that biodiversity does not merely respond to environmental changes but is also a predictor of various ecosystem functions and services that are essential for sustaining human welfare (Cardinale *et al.* 2012). Although much remains to be learned about the relationships between biodiversity and ecosystem functionality, this knowledge is already playing a critical role in informing policy at multiple legislative scales. The latest examples include a new assessment body of the Intergovernmental Science–Policy Platform on Biodiversity and Ecosystem Services (IPBES; http://www.ipbes.net/), which is now undertaking multiple tasks to synthesize cutting-edge knowledge on the science of biodiversity–ecosystem services. As exemplified in the formation of the IPBES, biodiversity issues are no longer merely 'of concern' but rather 'in demand' for the sake of humanity.

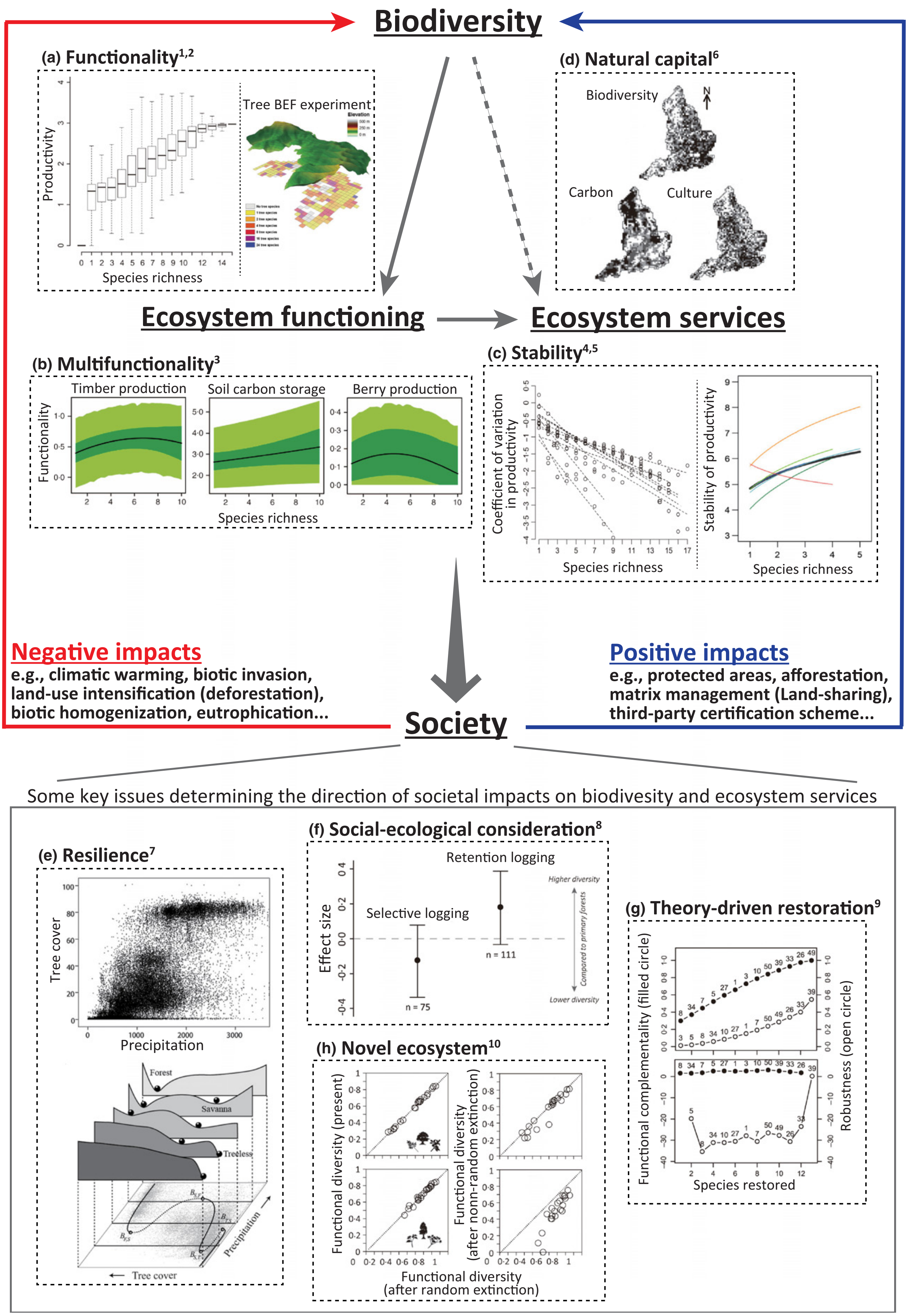
A number of successful frameworks for safeguarding biodiversity have appeared in the forestry sector associated with the rapid expansion of sustainable forest management (SFM) (Tittensor *et al.* 2014). Recent methodological advancements have improved the assessment of distributions, synergies and trade-offs of various ecosystem services at different spatiotemporal scales (Raudsepp-Hearne, Peterson & Bennett 2010; Andrew, Wulder & Nelson 2014). Considering the substantial contributions of forest ecosystem services to global society (e.g. carbon sequestration, water regulation and erosion control; Thompson *et al.* 2011) and the wide biodiversity that forests support (e.g. about three quarters of terrestrial taxa; CPF 2008), forest sectors including practitioners and scientists have significant responsibility for the integrity and sustainability of future societies.

Currently, there is a rapid advancement in our understanding of the relationships among biodiversity, ecosystem functions and services in forest ecosystems. An important example is research on biodiversity–ecosystem functioning in forests. Biodiversity effects on ecosystem functions have been traditionally evaluated in other systems such as grasslands and aquatic systems, and thus the relative lag in forest ecology domain is of great concern (Nadrowski, Wirth & Scherer-Lorenzen 2010). Early syntheses of this topic in forests (CBD 2009; Aerts & Honnay 2011) thus largely relied on knowledge from systems other than forests. For the last several years, theoretical and experimental initiatives on functional biodiversity research have been rapidly emerging in forests (e.g. Hector *et al.* 2011; Morin *et al.* 2011; Baeten *et al.* 2013; Bruelheide *et al.* 2014; Verheyen *et al.* 2015). Although a large knowledge gap still exists in forests compared to better-studied systems, a growing research agenda on forest biodiversity–ecosystem functioning is expected to play a substantial role in mitigating future environmental change (e.g. climate change mitigation; Hulvey *et al.* 2013; Poorter *et al.* 2015). Another point of interest that exemplifies the need for further studies on forest biodiversity and ecosystem services can be inferred from the marked difference in framing socio-economic perspectives on biodiversity conservation between agriculture and forestry sciences. For agriculture, detailed strategic plans have often been proposed for sustaining food production while reducing the environmental impacts of land use (e.g. Foley *et al.* 2011; Tilman *et al.* 2011). No equivalent, global synthesis has yet been provided for forestry, possibly reflecting the difficulty in assessing trade-offs among different biodiversity indicators and multiple ecosystem services. Again, a number of tools and information have increasingly become available to estimate the distributions of both biodiversity and ecosystem services in various biomes including forests (Nagendra, Reyers & Lavorel 2013; Duncan, Thompson & Pettorelli 2015), further suggesting the potential of applied forest ecology.

In view of recent advancements, knowledge gaps and the future significance of research on forest biodiversity and ecosystem services, we outline several key research priorities addressing the need to build capacity and resilience for social and ecological systems to face uncertainty in the changing environment (Fig. 1). Based on an extensive literature review, we envision a research agenda that will be fruitful for scholars as well as practitioners.

Forest biodiversity, ecosystem functions and services

A series of biodiversity–ecosystem functioning (BEF) studies (Cardinale *et al.* 2012) have revealed that biodiversity (including taxonomic, functional and phylogenetic diversity) promotes the functionality of ecosystems (e.g. primary production, decomposition, nutrient cycling, trophic interactions and so on) and consequently supports a broad range of ecosystem services (e.g. food production, climate regulation, pest control, pollination and numerous others). The development of BEF theory has mainly arisen from experimental and theoretical work, with a central contribution from experimental manipulation of plant assemblages in grassland ecosystems over the last several decades (e.g. Hautier *et al.* 2014; Isbell *et al.* 2015a). The knowledge coming from these biodiversity experiments has been widely used to make inferences about other systems, as it is often difficult to set up equivalent experiments elsewhere. This is especially true for forests, which are characterized by higher structural complexity, longer life cycles of the dominant taxa and larger-scale spatiotemporal dynamics than grassland communities (Scherer-Lorenzen 2014). Knowledge gaps in the discipline of forest ecology have been therefore largely



Biodiversity
(a) Functionality[1,2]
Productivity
Species richness
Tree BEF experiment
(d) Natural capital[6]
Biodiversity
Carbon
Culture
Ecosystem functioning
Ecosystem services
(b) Multifunctionality[3]
Timber production
Soil carbon storage
Berry production
Functionality
Species richness
(c) Stability[4,5]
Coefficient of variation in productivity
Species richness
Stability of productivity
Species richness
Negative impacts
e.g., climatic warming, biotic invasion, land-use intensification (deforestation), biotic homogenization, eutrophication...
Positive impacts
e.g., protected areas, afforestation, matrix management (Land-sharing), third-party certification scheme...
Society
Some key issues determining the direction of societal impacts on biodivesity and ecosystem services
(e) Resilience[7]
Tree cover
Precipitation
Forest
Savanna
Treeless
Tree cover
Precipitation
(f) Social-ecological consideration[8]
Retention logging
Selective logging
Effect size
n = 111
n = 75
Higher diversity
Compared to primary forests
Lower diversity
(g) Theory-driven restoration[9]
Functional complementality (filled circle)
Robustness (open circle)
Species restored
(h) Novel ecosystem[10]
Functional diversity (present)
Functional diversity (after nonn-random extinction)
Functional diversity (after random extinction)

Fig. 1. Linkages from biodiversity to ecosystem services and the societal impacts on the relationships. Biodiversity may support ecosystem services directly (dashed grey arrow) and indirectly through ecosystem functions (solid grey arrows). Numbers indicate papers cited below. (a) A study framework of biodiversity–ecosystem functioning (BEF) is rapidly expanding in forests, with some notable examples of tree diversity effects on above-ground productivity (1, Morin *et al.* 2011). Tree BEF experiments have been recently launched in some regions (2, Bruelheide *et al.* 2014). (b) To obtain benefits from natural systems, society needs to consider the relationships between biodiversity and ecosystem multifunctionality (3, Gamfeldt *et al.* 2013). (c) To ensure the roles of biodiversity to deliver ecosystem services, the stability of ecosystem functioning is also important. Some studies have started to elucidate underlying mechanisms of the biodiversity–stability relationships using simulation (4, Morin *et al.* 2014) and using a retrospective approach (5, Jucker *et al.* 2014). (d) In addition to the local-scale evaluation, the assessment of ecosystem service provisions at the large scale (i.e. regional scale) is important to help resource management and decision-making (6, Eigenbrod *et al.* 2010). There are some key issues that can determine the direction of societal impacts on biodiversity and on ecosystem services in turn (negative and positive impacts are illustrated with red and blue arrows, respectively). (e) Terrestrial systems may undergo regime shifts in response to precipitation changes, determining the degree of ecological resilience in a changing climate (7, Hirota *et al.* 2011). (f) Social-ecologically sustainable forestry can potentially provide a win-win solution to reconcile the trade-offs and conflicts between conservation and commodity production (8, Mori & Kitagawa 2014). (g) In theory, the order of species reintroduction affects restoration outcomes measured with functional complementarity and redundancy, determining the restoration outcomes for ecosystem functions (9, Devoto *et al.* 2012). (h) While local communities can buffer the impact of random loss of species to maintain the fundamental functionality, non-random (realistic) loss of species can substantially alter functional characteristics of communities, leading to the emergence of novel communities (10, Mori *et al.* 2015b). [Colour figure can be viewed at wileyonlinelibrary.com]

complemented by studies in other systems such as grasslands, aquatic systems and bacterial microcosms. Now, global meta-analyses and syntheses are also available for diversity–functioning relationships in forests (e.g. Piotto 2008; Zhang, Chen & Reich 2012; Chisholm *et al.* 2013), indicating some progresses in this research field in forest ecology. An important next step is to use biodiversity data from forests to give practical implications for SFM (Table 1).

TREE DIVERSITY AND PRODUCTIVITY

As observed in other systems, examining biomass production is probably one of the greatest opportunities to

Table 1. Key messages, tools and early examples used to inform biodiversity–ecosystem functioning studies in forest ecology. Numbers indicate associated references. Appendix S1 in Supporting Information provides the list of references

Aspects of research on biodiversity, ecosystem functioning and services	Key message for research	Tools/Early results
Given the limitations in establishing experiments and making data available to test biodiversity–ecosystem functioning relationships in forests		
A need exists to have experimental frameworks specific for biodiversity–ecosystem functions in forest ecosystems	Develop biodiversity experiments	BEF China[1], Sabah Biodiversity Experiment[2]
Methodological advancement, including statistical approaches that can control for the effects of confounding variables in a heterogeneous environment, is necessary to improve the use of data from naturally assembled communities (i.e. unmanipulated communities)	Develop analytical methods	Bayesian models[3,4], Null models[5-7]
Existing study plots have a strong potential for demonstrating the role of tree biodiversity in naturally functioning forest ecosystems	Continue to use existing data collection projects	Long-term monitoring sites[4,8], CTFS-ForestGEO[9], National forest inventories[3,10,11]
A large amount of uncertainty exists if multifunctionality that is crucial for society can be supported by biodiversity in forests, as observed for experimental systems	Test diversity multifunctionality	Multiple analytical methods[5,12] Results for fungal diversity[6]
Facets of diversity other than trees should be further assessed to gain a better picture of the flow from forest biodiversity and ecosystem function to ecosystem services.	Explore different taxa	Results for fungal diversity[6]
Once new platforms for tree diversity research (such as TreeDivNet[13], FunDivEUROPE[14]) are established		
Finding a better combination of tree species for mixed plantations with the goal of enhancing ecosystem functions and services becomes important	Find a best mix	Mono vs. two-species forest stands[10]
Disentangling the possible functional roles of biodiversity becomes possible by benefitting from the uniqueness of tree diversity experiments	Take advantage of tree diversity experiments	A focus on three-dimensional forest structure[15]
Research related to the genetic engineering of trees could be informed by diversity studies	Learn from a different discipline	Diversity and selection[16]

disentangle the underlying mechanisms of diversity–function linkages in forests (e.g. Morin *et al.* 2011; Jucker *et al.* 2014, 2016; Lasky *et al.* 2014; Jucker, Bouriaud & Coomes 2015). Although higher productivity cannot necessarily be translated directly into higher levels of provision services (i.e. timber production, bioenergy and so on) (Chisholm *et al.* 2013), it is likely to contribute to some services, such as carbon sequestration and storage (Hector *et al.* 2011; Hulvey *et al.* 2013; Poorter *et al.* 2015). Analogous to biodiversity experiments in grasslands, tree experiments have been established world-wide (Verheyen *et al.* 2015). There are potential strengths of tree experiments. For example, Jucker, Bouriaud & Coomes (2015) focused on the three-dimensional structure of forests and the plasticity of individual trees to explain the complementary mechanisms among species that support positive diversity–function relationships. Furthermore, it is feasible to control the number of individuals in tree plantations, providing a greater experimental control over 'true diversity indices' (*sensu* Jost 2007) compared to grassland experiments. This approach allows one to rigorously quantify how contributions to different ecosystem functions and services scale across ecological levels (i.e. the individual, species and community). Knowledge of scaling effects of biodiversity on ecosystem function is still largely limited (Mori *et al.* 2016), and thus, an important frontier in BEF studies is tree diversity experiments.

Another issue that needs attention is that tree diversity–function relationships may be confounded by variables other than tree diversity, such as tree density, biomass, age, edaphic conditions and other environmental factors (Toïgo *et al.* 2015; Jucker *et al.* 2016). For these reasons, new experimental frameworks such as BEF China (Bruelheide *et al.* 2014; Fig. 1a) and TreeDivNet (Verheyen *et al.* 2015) are emerging in forests. However, results from experimental settings specific for forest BEF studies are still scarce (Schuldt *et al.* 2015), mainly because of the long life span nature of trees. Furthermore, compared to grasslands, there are generally high levels of difficulties to manipulate environmental factors (e.g. water, nutrients and so on). Given these limitations, it has been necessary and continues to be important to rely on data from inventory plots that have not been primarily designed for BEF studies. To use data from these non-experimental tree communities, methodological advancements such as statistical approaches that can control for the confounding effects of the other explanatory variables on diversity–productivity relationships are an important research priority (e.g. Healy, Gotelli & Potvin 2008). Notably, other research platforms, such as FunDivEUROPE (Baeten *et al.* 2013), which combine both experimental and inventory platforms, are also emerging. To date, the research field of tree diversity–ecosystem function relationships has a primary focus on biomass production, but these new platforms and initiatives will and should play further important functions and services beyond the focus on productivity (Gamfeldt *et al.* 2013).

As such, tree diversity studies are still at the early stage of development, and thus, a large amount of knowledge can be gleaned from the comparatively mature field of biodiversity studies in grasslands. For example, a recent grassland experiment of Zuppinger-Dingley *et al.* (2014) may have application not only to the agriculture sector but also to the forestry sector. They suggested that using varieties that have been selected in diverse planting regimes may increase (timber) productivity. Given the long history of genetic engineering in forestry (Harfouche, Meilan & Altman 2011), their implication is intriguing. Their conclusion may be especially applicable when intensification in a given allotment of land (to avoid extensification and leakage to other lands) is important to secure both commodity production and environmental integrity, as is often discussed in the agriculture sector (Tilman *et al.* 2011; Loos *et al.* 2014). Given the increasing pressure to allocate more lands for nature reserves as proposed under the CBD framework, the use of multiple species provenances may provide an alternative solution in the context of SFM. However, testing this potential is far from easy. Theory suggests a high likelihood of natural enemy attacks when conspecific cohorts are grown densely (negative density dependence, or the so-called Janzen–Connell hypothesis), which is one of the rationales for encouraging mixtures rather than monocultures to enhance productivity (Maron *et al.* 2011; Schnitzer *et al.* 2011). A meta-analysis that compared insect herbivory between mono- and mixed plantations also supports the tree diversity effects to reduce the risk of damage by pests (Jactel & Brockerhoff 2007). For these reasons, a hidden risk may exist for tree monocultures. Finding a better combination of tree species for mixed plantations aimed at enhancing ecosystem functions and services has been one of the main focuses in the forest BEF studies (Baeten *et al.* 2013; Toïgo *et al.* 2015; Verheyen *et al.* 2015). Research on genetic engineering for trees could be informed from these diversity studies in forests.

BIODIVERSITY AND ECOSYSTEM FUNCTIONS

In addition to the potential importance of higher productivity in mixed stands, there are other reasons why tree diversity may be important (Scherer-Lorenzen 2014). Tree diversity is often linked with major properties in forests, including the possible enhancement of diversity of other forest assemblages (Schuldt *et al.* 2014) and potential contribution to other functions, such as litter decomposition (Handa *et al.* 2014). Notably, these kinds of connections can have significant uncertainty. For example, the former issue needs caution as tree richness does not necessarily promote the diversity of other organism groups (Donoso, Johnston & Kaspari 2010). The latter issue also has limitations as diversity–decomposition relationships have been primarily tested for evaluating the effects of litter diversity (Gessner *et al.* 2010), and the effects of tree diversity have been inferred indirectly. For the last several years, an increasing number of studies have demonstrated that tree diversity is important for sustaining various ecosystem functions provided by natural forests simultaneously, so-called multifunctionality (e.g. Gamfeldt *et al.* 2013; Mori *et al.* 2016), an emergent motif among BEF studies (Lefcheck *et al.* 2015). Considering how forests are more structurally complex than grasslands, a higher dimensionality of functional space is expected. Issues of multifunctionality in forests (Fig. 1b), which are critical for real-world situations (Lefcheck *et al.* 2015), thus need further investigation. Overall, independent of BEF contexts, there is an enormous accumulation of tree community data that cover large spatial and temporal scales in natural, semi-natural and planted forests (e.g. at various Long-Term Ecological Research (LTER) sites across the globe). It is critical that these data be used to demonstrate the possible roles of tree biodiversity in naturally functioning forest ecosystems (e.g. Paquette & Messier 2011; Chisholm *et al.* 2013; Gamfeldt *et al.* 2013; Ruiz-Benito *et al.* 2014). In sum, different data bases and platforms that are currently available are expected to jointly play important roles in disentangling the underlying processes of diversity–functioning relationships and thus further advancing functional biodiversity research.

So far, we have described the present context of the forest BEF studies, with a primary focus on tree assemblages. Apart from trees, knowledge gaps exist between forest science and other domains. For example, while the importance of forests as a habitat for conserving pollinator communities – a critical component of sustained crop production – has been well studied (e.g. Garibaldi *et al.* 2011; Mitchell *et al.* 2014), the reverse relationship (the functional roles of pollinators for forest ecosystems) has been relatively little covered. Furthermore, while the functional consequences of non-random, realistic loss of diversity on trophic structure have been recently demonstrated for grassland and aquatic systems (e.g. Zavaleta & Hulbey 2004; Bracken *et al.* 2008; Karp, Moeller & Frishkoff 2013), this issue has been rarely visited in forest ecosystems (but see Barnes *et al.* 2014). Thus, in understanding the contributions of forest biodiversity to ecosystem functions and services, a large amount of uncertainty still exists not only for trees but also for other groups of organisms. These issues undoubtedly need to be continually tested, in addition to the focus on trees, to gain a full picture of the flow from biodiversity and ecosystem functions to ecosystem services. However, considering the fundamental roles that trees play both directly and indirectly (via other facets of diversity in a given system) to support the overall functionality of forest ecosystems, the high likelihood that trees determine the assemblage structures of other taxa, and the fact that different silvicultural practices and land-use modifications directly alter tree diversity, tree diversity–function studies represent a most promising frontier for the improvement of SFM practices.

Forest resilience for facing uncertainty

High levels of biodiversity are effective and often essential for ecosystems to endure environmental changes and retain their fundamental functionality, largely contributing to the maintenance of resilience in ecosystems (Elmqvist *et al.* 2003; Mori, Furukawa & Sasaki 2013). Here, ecological resilience is defined as the capacity of a system for absorbing changes to maintain fundamental controls on function and structure (Chapin, Kofinas & Folke 2009; Gunderson, Allen & Holling 2009). Ecological resilience is the modern concept of facing uncertainty, unpredictability, nonlinearity and changeability in a system to be managed (Standish *et al.* 2014). Furthermore, resilience thinking can act as a bridge between science and society under severe uncertainty (Polasky *et al.* 2011). Taken together, resilience thinking should be further embedded in the biodiversity sciences to ensure ecosystem functions and services are maintained in this era of biodiversity crisis (Table 2).

DIVERSITY RESPONSES UNDER ENVIRONMENTAL FLUCTUATIONS

An important issue in considering resilience is how to secure the fundamental functionality of a focal system. In this regard, the insurance hypothesis (Yachi & Loreau 1999) deserves further attention. The insurance hypothesis predicts that ecosystem function is stabilized in species-rich communities where the redundancy of species contributes to the same function and thus reduces fluctuations in that function over space or time. That is, high diversity may ensure the high resiliency of a system. The concept of 'response diversity' adds more inference to the insurance effects of biodiversity (see Mori, Furukawa & Sasaki 2013). Briefly, in addition to the number of functionally redundant species, the intraspecific variation in responses to environmental fluctuations is also critical; if this variation is reduced, a fundamental control on ecosystem function could be lost from local communities in the face of environmental change (Elmqvist *et al.* 2003; Mori, Furukawa & Sasaki 2013). To date, empirical evidence of response diversity is still scarce, especially for forest ecosystems. Notably, Karp *et al.* (2011) explicitly demonstrated the importance of response diversity in forest communities (bird assemblages) for sustaining ecosystem services (pest control, seed dispersal and pollination). Potentially important mechanisms for enhancing response diversity include interspecific asynchrony of population dynamics and temporal niche differentiation among species, both of which lead to functional compensation under environmental fluctuations (Mori, Furukawa & Sasaki 2013). However, difficulty exists in assessing these processes, especially in naturally assembled communities in which long-term monitoring data are often needed to quantify intraspecific variation. Some studies have relied on different methodological approaches, such as space–

Table 2. Key messages, tools and early examples used to inform resilience studies in forest ecology. Numbers indicate associated references. Appendix S1 provides the list of references

Aspects of research on biodiversity, ecosystem functioning and services	Key message for research	Tools/Early results
Given that resilience thinking that is based on system variability and changeability is increasingly important for resource management in the era of global environmental change		
Assessment of the mechanisms of forest biodiversity–stability relationships is important to secure the provisioning of ecosystem services under environmental fluctuations, and will likely lead to helping to develop ecological resilience in forests	Assess diversity–stability relationships	Results from FunDivEUROPE[17], FORCLIM[16]
Rigorous assessment of response diversity, which is important to ensure ecosystem resilience, is required to better understand the linkages between functional traits and ecosystem processes under environmental fluctuations	Develop and explore response diversity	TRY data base[18] for quantifying response and effect traits of plants Results from bird communities[19] and a trait-based approach[20]
To attain sustainable forest management, participating in the debate related to dominance vs. diversity is crucial to ensure the resiliency of ecosystem functions. No consensus currently exists related to which types of planting regimes (e.g. monocultures vs. mixed culture) are most beneficial to multipurpose forestry that is aimed at maintaining both forest commodity production and the delivery of other forest ecosystem services	Test dominance vs. diversity	Testing alternative hypotheses for tree mixture effects[21]
Further evaluations are necessary if tree diversity is maintained to help buffer the effects of acute environmental perturbations (e.g. climate extremes)	Test the buffering effects of diversity	In contrast to grasslands[22], diversity has few effects on the resistance of forests to disturbance[23]
Cross-scale resilience that focuses on the effects of biodiversity on the integrity of ecological systems at different scales has received less attention. In practice, it is important to know how large-scale properties such as landscape connectivity and heterogeneity affect resilience	Focus on multiple scales	Several syntheses for this topic[24,25]

time substitution (Winfree & Kremen 2009; Karp *et al.* 2011) and theoretical modelling (Wang & Loreau 2014). At this juncture, ongoing accumulation of long-term monitoring data for forest communities including plants and animals, which are increasingly archived in the public domain (open data), will give opportunities to demonstrate whether diversity in responses among species exists and how this ensures the functionality of ecosystems. Notably, most existing studies on the variety of responses among different species have relied on trait-based approaches (e.g. Laliberte *et al.* 2010). That is, instead of quantifying a rate of ecosystem process (e.g. annual crop production), they indirectly inferred a potential of supporting the functionality using functional traits. More rigorous assessments to ensure ecosystem resilience would evaluate direct linkages between functional traits and ecosystem processes.

DIVERSITY EFFECTS TO STABILIZE ECOSYSTEM FUNCTIONS

Experimental and theoretical studies have suggested that biodiversity has the potential not only to generate but also to stabilize ecosystem functions (Tilman, Reich & Knops 2006; Hautier *et al.* 2014; Morin *et al.* 2014; Isbell *et al.* 2015a). Although a number of theoretical explanations have been given to resolve the mechanisms of biodiversity–stability relationships, large uncertainty still surely exists regarding how and when biodiversity contributes to stabilizing and (consequently) ensuring the vital functionality of ecosystems (Hautier *et al.* 2015). However, given the prominence of environmental stability for determining the development, prosperity and security of human society (Hsiang, Burke & Miguel 2013), the potential of biodiversity is of practical importance (Isbell *et al.* 2015a).

As we stressed earlier, primary productivity is one of the greatest concerns in forests. Recent studies using a process-based model (Morin *et al.* 2014) and a retrospective approach (Jucker *et al.* 2014) have shown that species asynchrony in tree species assemblages can stabilize aboveground productivity (Fig. 1c). Both studies have suggested that while interspecific segregation of functional traits (e.g. shade tolerance and leaf display) can drive complementary effects in tree mixtures (implying temporal niche differentiation) as often observed in grasslands, species asynchrony remains important but is weaker in tree communities than herbaceous communities. This evidence suggests that while the commonly observed relationship between diversity and stability in other ecosystems is applicable to forests, the underlying mechanisms are not necessarily the same in different ecosystems. This evidence again emphasizes the importance of having specific frameworks for forest ecosystems. For instance, the mass ratio hypothesis (Grime 1998), which proposes that traits of dominant species are critical in determining ecosystem functioning, has been proposed as an alternative explanation for supporting biomass production in herbaceous plant communities (e.g. Sasaki & Lauenroth 2011). Given the importance of dominant tree species in supporting numerous ecosystem functions and services in forests (e.g. foundation species; Ellison *et al.* 2005), tree diversity may be of limited use for predicting productivity. Jucker *et al.* (2014) suggested a limitation of asynchrony among tree species due to the long-lived nature of trees. Similarly, Morin *et al.* (2014) suggested that interspecific asynchrony occurs in tree communities, independent of environmental fluctuations. These findings imply that tree diversity may have limitations when buffering the impacts of large and unpredictable environmental changes (e.g. climate extremes and insect outbreaks; Conner, Bunnell & Gill 2014; Grossiord *et al.* 2014); that is, there may be no direct contribution of tree diversity to forest ecosystem resistance and resilience. Forest ecologists thus need to further investigate the issue of dominance vs. diversity. Such debates may potentially determine the future direction of SFM, as there is no current consensus over which types of planting regimes (e.g. monocultures vs. mixed cultures) best maintain both forest commodity production and the delivery of other forest ecosystem services.

CROSS-SCALE RESILIENCE

In addition to the individual-, species- and community-level responses to environmental change, large-scale properties also determine the resilience of ecological systems (Peterson, Allen & Holling 1998; Cumming *et al.* 2013; Reyer *et al.* 2015). This is because, while biodiversity effects on the functionality and stability of ecosystem function are especially significant at the local scale (Pasari *et al.* 2013), biodiversity responses, including response diversity (Laliberte *et al.* 2010), are often affected by landscape properties (Tscharntke *et al.* 2005). In a human-modified landscape, Fischer, Lindenmayer & Manning (2006) and Standish *et al.* (2014) similarly emphasized the importance of connectivity and heterogeneity of habitat patches as the major properties that determine ecosystem resilience. A diverse array of structurally complex patches connected by corridors and stepping stones can harbour higher levels of biodiversity that likely contribute to a system's resilience to external forces (i.e. disturbance) (Fischer, Lindenmayer & Manning 2006) by fostering post-disturbance recovery (engineering resilience) of vegetation from remnant patches of surviving trees and also by potentiating recovery to an alternative stable state. This is an important feature of ecological resilience (Seidl, Rammer & Spies 2014). Peterson, Allen & Holling (1998) presented an early conceptual model in which they proposed the importance of cross-scale resilience. Despite this early recognition, processes that reinforce resilience at the local scale and at the landscape scale have been explored in parallel. Considering the fundamental significance of the scale issues in forest ecosystems in particular, research that can assess forest resilience at different scales is necessary to inform policy and management (Mori 2011).

RESILIENCE THINKING

Overall, the present evidence for biodiversity as a source of forest resilience is largely limited, although such potential has sometimes been inferred (e.g. CBD 2009; Ghazoul *et al.* 2015; Seidl *et al.* 2015). Resilience thinking has been often argued to be less applicable to real-world decision-making and conservation situations (Polasky *et al.* 2011; Curtin & Parker 2014). In forests, a limited understanding of the potential linkages between biodiversity and system states limits the use of resilience-based approaches for helping SFM. Importantly, possible nonlinearity, changeability, thresholds (tipping points), regime shifts and alternative stable states, all of which are primary focuses of system characteristics in resilience thinking (Chapin, Kofinas & Folke 2009; Gunderson, Allen & Holling 2009), are inherently difficult to be tested in forest ecosystems characterized by long-term dynamics. To overcome this difficulty, some approaches such as space–time substitution (e.g. Hirota *et al.* 2011; Fig. 1e) and palaeoecological reconstruction (e.g. Cole, Bhagwat & Willis 2014) have proven useful. Along with studies using these new approaches, we emphasize the importance of further observational, experimental and theoretical works that quantify the potential roles and limitations of biodiversity for sustaining forest resilience. Studies on the biodiversity–stability and the biodiversity–functionality relationships have especially large potential to provide the requisite knowledge for informed, meaningful and successful ecosystem management to be achieved (Mori, Furukawa & Sasaki 2013).

Social–ecological considerations for forest conservation

In the forestry sector across many regions, a wide range of reduced-impact logging is becoming popular, which has largely contributed to the development of SFM (Lindenmayer *et al.* 2012). Among several frameworks, the emergence of retention forestry over the last two decades, which aims to preserve key structural elements of the forest stand during harvesting to ameliorate the post-logging structure over forest generations (Lindenmayer *et al.* 2012), is the most notable case. Recent meta-analyses quantitatively showed that this approach is effective for conserving biodiversity in production landscapes (Fedrowitz *et al.* 2014; Mori & Kitagawa 2014; Fig. 1f). Alternatively, functional zoning is also becoming important to reconsider land use. A study based on landscape models showed that the TRIAD approach, which aims to reduce the impacts of forestry on landscape conditions based on broad-scale zoning, has the potential to reconcile landscape conservation and timber supply over the long term (Côté *et al.* 2010). As such, different tools and options are

Table 3. Key messages, tools and early examples used to inform social–ecological studies in forest ecology. Numbers indicate associated references. Appendix S1 provides the list of references

Aspects of research on biodiversity, ecosystem functioning and services	Key message for research	Tools/Early results
Considering that the increasing recognition of the need for conservation has led to increased emphasis on multipurpose forestry practices such as reduced-impact logging, reconversion to mixed-species stands from mono-species plantations and the expansion of reserve systems		
A further exploration is required to find better land-use schemes for conserving biodiversity and ecosystem services in forests	Consider land-use allocation	Land sharing vs. Land sparing[26], Zoning (e.g. TRIAD)[27]
Socio-economic evaluations need to be expanded, especially those including estimations of the costs and financial benefits associated with conservation activities	Analyse costs and benefits of conservation strategies	Coupled ecological–economic models[28,29]
Future studies related to multipurpose forestry should consider the provisioning of and trade-offs among multiple ecosystem services as a result of ecological set-asides that are designed for biodiversity conservation	Evaluate effectiveness of set-aside strategies on multifunctionality	Coupled ecological–economic model[29]
It is important to infer how conserved or lost biodiversity that is caused by human influences and is associated with forestry will have positive or negative consequences on ecosystem services	Consider functional consequences of diversity change	Coupled ecological–economic model[30]
Considering the future uncertainty of environmental changes including climate change and land-use change and so on		
Future plans should consider ongoing change related to social–ecological conditions. In particular, different agents of environmental change may have synergetic effects on biodiversity and ecosystem services	Anticipate multiple and synergetic changes	Coupled human–natural system models[31] Results from European forests using EFISCEN model[32]

available to facilitate land management and allotment (Table 3). Future studies that account for social–ecological processes will further assist policy formation and decision-making (Table 3).

LAND SHARING AND LAND SPARING

Land-use change is one of the strongest drivers that has caused declines in biodiversity, in particular at large spatial scales. To reconcile different (and often conflicting) objectives of both biological conservation and commodity demands on the same land, 'land sparing' and 'wildlife-friendly farming (land sharing)' have been actively debated as two alternative approaches in the agriculture sector (Fischer *et al.* 2008). Forestry approaches aimed at reducing the negative impacts of logging on biodiversity are tightly linked with the latter idea of land sharing in agriculture (Lindenmayer *et al.* 2012). In agricultural settings, advocates for land-sharing approaches have provided various quantitative models based on social–ecological and socio-economic scenarios, including cost–benefit calculations over future decades (e.g. Phelps *et al.* 2013). Criticisms surely exist for land-sharing approaches; critics argue that land sparing, which aims to maximize commodity production on a given allotment of land while the remaining land is set aside and reserved for biodiversity conservation (Fischer *et al.* 2008), is more promising (e.g. Phalan *et al.* 2011). A context dependency between the two land allocation schemes has also been quantified in agriculture settings (e.g. a trade-off exists between them depending on the proximity to natural habitats; Gilroy *et al.* 2014). In contrast, although some opinions have been advanced (Edwards *et al.* 2014), forestry science has not yet reached the point of having a clear discussion equivalent to the land-sharing vs. land-sparing debate in the agricultural domain. Despite multifunctional forestry becoming popular in response to the increasing demand for SFM, rigorous socio-economic evaluations including monetary estimations of the costs and the benefits (incentive) associated with reduced logging for biodiversity conservation are still scarce, and thus, further studies are needed (Tittler, Messier & Fall 2012; Messier *et al.* 2015). Considering the rich body of ecological economics models in the conservation sciences (Eppink & van den Bergh 2007) along with a long history of models designed for optimal harvesting (including considerations for both timber production and conservation) being used in the forestry sector (e.g. Nalle *et al.* 2004), it should be possible to seek cost-effective strategies that optimize modern forestry for multiple social–ecological bottom lines.

ECOSYSTEM SERVICES PERSPECTIVE FOR MULTIFUNCTIONAL FORESTRY

Biodiversity conservation has traditionally tended to focus on a subset of biodiversity that includes iconic and/or endangered species, and rather ignored the functional roles of biodiversity as a driver and source of ecosystem functions and services (Mace, Norris & Fitter 2012). A series of approaches for forestry aimed at conserving biodiversity has had a tendency to adopt that traditional perspective, and little explicit consideration has been given to multiple ecosystem functions and services so far. Yet there is great potential in conserving forest taxa from the perspective of ecosystem services, as conserved taxa in forest patches may contribute to providing and sustaining the functionality of forested ecosystems (see Karp *et al.* 2013 for an example in agriculture). The potential benefits include biogeochemical processes supported by soil biodiversity retained in the stand, pest control and pollinations as a result of conserving trophic interactions, and water retention and erosion control by understorey plant communities. These services are likely maintained in forests with high diversity in their assemblages, including those of microbes, invertebrates, vertebrates and plants (Thompson *et al.* 2011), although expectations of such potential have not been rigorously tested in production forests managed with conservation approaches. The next generation of multifunctional forestry studies should take into account ecosystem services provided as a result of conservation actions in forestry and the trade-offs made by this practice.

BIODIVERSITY AND ECOSYSTEM SERVICES

Social–ecological models evaluating the cost-effectiveness of conserving biodiversity and several ecosystem services (e.g. commodity production and carbon sequestration), such as seen in issues surrounding REDD+ (e.g. Koh & Ghazoul 2010), have been recently developed to reconsider land use; however, relevant case studies are still in short supply. Land-use models are often useful for considering trade-offs between biodiversity conservation and ecosystem service conservation. Scenarios and policy options gained from these models would be fundamentally beneficial for decision-making. However, models considering the synergies between biodiversity and ecosystem services are relatively scarce; that is, both tend to be considered as distinct and unlinked response variables affected by human activities. The functional consequences of biodiversity conservation on ecosystem services have not been well integrated into these models so far (Isbell *et al.* 2015b). In this regard, ecosystem services models that can also account for biodiversity conservation, such as the InVEST (Integrated Valuation of Environmental Services and Tradeoffs) model (Kareiva *et al.* 2011), have great potential to inform SFM. To date, while numerous tools are available, the conceptual flow from biodiversity to the functionality and services of ecosystems has consequently been rarely integrated into models and analyses of forest ecosystems.

MANAGEMENT IN A CHANGING CLIMATE

In addition to focussing on the current status of forests, different perspectives are also important in this era of a changing environment. Climate change is one of the greatest concerns that can incur additional costs on forest management (Hanewinkel *et al.* 2013). Modelling approaches have identified some key aspects of future forest management approaches that are aimed at mitigating or adapting to changing climate. Duveneck & Scheller (2015) proposed a climate-suitable planting regime in which species from outside the landscape are planted to anticipate a northward shift of the optimal thermal ranges of tree species. However, the study concluded that, because climate change effects often outweigh management actions, this management alternative has a limited ability to enhance the (engineering) resilience. Furthermore, the effects of climate change on forest landscapes can be amplified if further consideration is given to the changing disturbance regime. Using an ensemble of climate change scenarios, Seidl *et al.* (2014) estimated that there is a high likelihood of increasing damage from wildfires, insect outbreak and wind-throws in the coming decades, and this will likely offset management strategies that are aimed at increasing the forest carbon sink. The study concluded that intensifying forest disturbances will not only affect the carbon sink but will also have detrimental influences on different types of ecosystem services. For example, the authors argue that management costs may increase because of fire suppression, pest control, salvage logging and so on, which will very likely affect timber markets. These and other model-based studies have provided an important picture of the future, although these results are largely dependent on various scenarios. To further implement these and other projections into practice, novel approaches such as coupled human–natural system models should be considered in which future changes in ecological and social systems and synergies and feedbacks between these subsystems can be integrated. Such a novel approach will facilitate policy and management by providing multiple options that better deal with future uncertainty.

Theory-driven forest restoration

An increasing number of alarms have been raised about anthropogenic impacts on forest biodiversity (e.g. Gibson *et al.* 2011; Wilcove *et al.* 2013); land-use change associated with deforestation and forest degradation have threatened numerous forest-dependent taxa across many regions. In response to this biodiversity crisis, a large number of studies have described how habitat alteration and destruction have affected and will change forest biodiversity at different spatial, temporal and biological scales (e.g. Newbold *et al.* 2014). Note that human-induced species extinction does not occur at random, but there are instead multiple deterministic factors causing their loss. In this regard, some studies have explicitly demonstrated the underlying mechanisms of non-random loss of forest biodiversity (e.g. Mori *et al.* 2015a; Fig. 1h). Furthermore, recent studies have also quantified the consequences of land-use change on ecosystem services in forest landscapes (e.g. Lavorel *et al.* 2011). Compared to such information about forest degradation, knowledge of the responses of biodiversity and, especially, of ecosystem services to forest restoration is relatively limited (Table 4). However, knowledge on functional consequences of forest restoration has been gradually accumulating (e.g. Lamb 2005; Chazdon 2008; Bullock *et al.* 2011).

Table 4. Key messages, tools and early examples used to inform applied and practical studies in forest ecology. Numbers indicate associated references. Appendix S1 provides the list of references

Aspects of research on biodiversity, ecosystem functioning and services	Key message for research	Tools/Early results
Because knowledge related to the responses of biodiversity and ecosystem services to forest restoration is accumulating but still largely limited		
The ongoing experimental and theoretical frameworks of biodiversity–ecosystem functioning studies in forested lands may yield important implications for the restoration or ecosystem services resulting from land-use improvement (e.g. forest reconversion to multispecies stands)	Assess the roles of biodiversity related to the restoration of ecosystem services	No evidence, but inferred from an opposite possibility[30]
Recent advancements in community ecology may aid restoration activities by providing some guidelines about the identity and the order of species that should be reintroduced in the sites	Apply restoration theory	Trait-based model[33]
Assessing the possibilities of alternate states and hysteresis, a view important in resilience thinking, is often necessary rather than simply taking measures to maintain present conditions	Be flexible to cope with change	Remote sensing (MODIS)[34-36]
Empirical evidence of regime shifts and threshold changes in the ecosystem state are further needed, especially those relevant to local forest restoration activities	Know ecological surprises	Long-term monitoring sites[37], National inventories[37], Data base (DAISIE, IUCN, IPANE)[38], Space–time substitution[39]
A need may exist to prepare for steering novel ecosystems alongside simultaneous efforts to conserve and restore desirable states	Explore and anticipate novelty	Ecosystem function restoration using non-native species[40,41]

RESTORING BIODIVERSITY AND ECOSYSTEM SERVICES

Under SFM frameworks, it is highly encouraged to convert monoculture plantations into stands with multiple tree species in many regions because trees in mixed-species stands are likely to harbour higher biodiversity of other organism groups and provide more multiple ecosystem goods and services than those in monocultures (Knoke *et al.* 2008). However, it is still unclear whether and especially how biodiversity and ecosystem functions respond to forest restoration activities based on re-establishment of multiple tree species. Based on results from BEF experiments and theoretical models, tree communities in restored mixed-species stands are expected to provide higher levels of regulating services (e.g. flood control, erosion control and soil nutrient maintenance), provision services (e.g. timber and other forest products) and cultural services (e.g. recreational use). Although the functional roles of tree diversity in generating these services have not been directly evaluated, some empirical evidence on ecosystem properties in mixed-species stands (Rothe & Binkley 2001; Knoke *et al.* 2008) implies that this potential of ecosystem services restoration (including economic benefits; e.g. Piotto *et al.* 2010) is likely. Ongoing experimental and theoretical BEF studies in forests thus have potential to suggest guidelines for ecosystem services restoration resulting from stand reconversion to mixed-species stands. Furthermore, due to the reduced environmental variation (environmental homogenization) in plantations of a single or a small number of species, such as through the decreased structural complexity of forest canopy and the reduced diversity of plant litter, plantations have a potential to homogenize communities of forest-dwelling taxa (Chazdon 2008; Mori *et al.* 2015a). Note that this biotic homogenization occurs not only taxonomically (taxonomic homogenization) but also functionally (functional homogenization), importantly suggesting that the vital functionality of forest stands supported by forest-dwelling communities can be threatened in mono-species plantations (Mori *et al.* 2015a). Responses of forest communities to the forest reconversion into mixed stands are largely variable among different taxa (Knoke *et al.* 2008). To date, studies of the potential of redifferentiating forest-dwelling communities in terms of both taxonomic and functional characteristics (i.e. recovery from biotic homogenization) have been limited (Mori *et al.* 2015a), and more studies are necessary to inform society on how to restore and conserve forest ecosystem services.

THEORY FOR RESTORATION

A series of theories in functional ecology may guide applied ecologists and practitioners (Laughlin 2014; Ostertag *et al.* 2015), but large uncertainties remain. For instance, there is an increasing number of observational studies of biodiversity in stands managed and conserved under retention or reduced-impact logging forestry; however, the underlying processes of community assembly, which determine the actual responses of biodiversity to environmental alteration in logged stands, have been given little attention so far (but see Bässler *et al.* 2014). Such approaches founded in community ecology, which can give mechanistic understandings of biodiversity responses to human influences (Mouillot *et al.* 2013), should be further employed in future studies of applied ecology (Laughlin 2014). Notably, recent theoretical and experimental studies in community ecology have proved the importance of history (the order of species immigration) in determining community composition (Fukami & Nakajima 2011) and ecosystem function (Fukami *et al.* 2010). Similar findings have also been reported in woodlands in which the importance of plant reintroduction sequences for restoring ecosystem functions supported by plant–pollinator networks was shown (Devoto *et al.* 2012; Fig. 1g). To integrate these latest findings into practice, the order of species reintroduction into restoration sites (e.g. revegetation, enrichment planting and assisted relocation) should not be random, and restoring biodiversity and biodiversity-based ecosystem functions and services should ideally be theory-driven.

NON-EQUILIBRIUM AND ALTERNATIVE STATES

Another important issue related to theoretical implication for ecological restoration is the possibility of alternative stable states (Suding, Gross & Houseman 2004), which have been demonstrated also by recent empirical evidence from different forest biomes (e.g. Hirota *et al.* 2011; Kitzberger *et al.* 2011; Staver, Archibald & Levin 2011; Scheffer *et al.* 2012). The potential of a regime shift into an alternative state suggests that resilience is a key concept for guiding restoration; according to Suding (2011), resilience-based approaches in restoration are a logical extension of current ecosystem-based management practices that build on an improved understanding of the dynamics of thresholds and reinforcing feedbacks. However, in reality, a majority of forest restoration activities have rarely used such a conceptual framework. For restoring forest ecosystem state, many practitioners have traditionally relied on a reference condition, which is also used to quantify the success of short-term restoration activities (Halme *et al.* 2013). Although understanding reference conditions is fundamentally important, caution is necessary. Attempting to define precise reference states may sometimes misguide management due to system variability resulting from human, climatic and vegetational instability (Mori 2011), again suggesting the importance of an approach that does not assume equilibrium, but instead recognizes stochasticity and nonlinearity of ecological systems (Norden *et al.* 2015). Some studies have tried to evaluate forest resilience using an ecological reference (e.g. Norden *et al.* 2009), but such approaches somewhat contradict the concept of ecological resilience, as assuming a reference condition is implicitly based on the idea of a single equilibrium rather than the possibility of alternative stable states. Notably, the existence of alternative stable states also implies the potential for hysteresis, wherein the pathway of degradation differs from recovery (Suding & Hobbs 2009). In grasslands, an experimental study demonstrated the persistence of low diversity in plant communities despite cessation of chronic nutrient enrichment two decades ago (Isbell *et al.* 2013); this study provided important empirical evidence for hysteresis. In forests, although equivalent evidence is lacking, studies based on other approaches such as space–time substitution (e.g. Hirota *et al.* 2011; Scheffer *et al.* 2012) have started to suggest similar potential for hysteresis, which is structured by positive feedbacks between the forest state and environmental variables. Because these possibilities have been observed at relatively coarse spatial resolutions, such as those recognizable using satellite images (i.e. 0·25–1·00 km^2), empirical evidence from finer spatial resolutions, which can be more relevant to local forest restoration activities, is currently desired.

NOVEL ECOSYSTEMS

Lastly, difficulty exists surrounding issues of ecosystem dynamics. Some argue that novel ecosystems, potentially created by threshold crossing, irreversibility and alternative states, are a reality in the Anthropocene (Hobbs, Higgs & Harris 2009), while others consider that the concept of novel ecosystems is ill-defined (Murcia *et al.* 2014). The latter argues that restoration ecology has not yet achieved the scientific maturity to identify the point of no return for an ecosystem and has thus never demonstrated any ecological thresholds that could prevent restoration. Although such criticisms exist, there is an increasing recognition about the potential of altered ecosystem states as a result of anthropogenic influences, irrespective of such states being called novel, no-analogue or something else (Hobbs, Higgs & Harris 2014). In coping with novelty and uncertainty in modern ecosystems in the face of complex human interventions, novel approaches to ecosystem management over and above preventative and reactive measures could be crucial to achieve desired outcomes or trajectories (Seastedt, Hobbs & Suding 2008). The implementation of such active adaptive management in real-world ecosystems has recently started to be recommended. For instance, non-native species may have desirable effects on an ecosystem, including the potential for conserving biodiversity (Schlaepfer, Sax & Olden 2011) and restoring ecosystem functions (Tognetti *et al.* 2010). Reviewing a 15-year forest restoration process in Sri Lanka, Ashton *et al.* (2001) stressed that the establishment of exotic plantations on highly eroded sites was effective to restore soil structure, resulting in an increase in soil carbon storage and water-holding capacity. In Hawaii, Mascaro, Hughes & Schnitzer (2012) also suggested the potential of diversity effects of introduced species to restore below-ground carbon storage after losses of native species diversity. That is, there may be a potential for ecosystem function restoration by virtue of trait identity of invading and introduced species (instead of extinct native species), independent of their origin (Mascaro, Hughes & Schnitzer 2012). However, active usage of non-native species is still largely questionable and continues to be the least desirable option in many cases. Theory and experiment both suggest that underlying mechanisms of diversity effects often differ between native and non-native assemblages (e.g. Wilsey *et al.* 2014). In sum, given the complexity of coupled social–ecological systems due to interactions between modern environmental threats such as climate change, biological invasion and human disturbance, it is necessary to actively manage novel ecosystems, with concurrent efforts to conserve and restore historical conditions where viable (Mori *et al.* 2013).

Conclusion

In this review, we have illustrated the potential of applied ecology to help conserve and restore forest ecosystems (summarized in Tables 1–4). Although there is great potential for SFM to benefit from the efforts and knowledge gained from a series of studies within the sciences of biodiversity and ecosystem services, a knowledge gap still exists in the discipline of forest ecology. In this regard, we argue that synergies and linkages between biodiversity and ecosystem services in forested lands deserve more attention. Under substantial human influence, forests will likely be grossly altered, potentially leading to the emergence of novel ecosystems or switching to alternative stable states. Management thus needs to be more flexible and use novel measures to face such large uncertainties. Resilience-based approaches will be key to foreseeing future changes and coping with surprises. Although the issues that we have addressed are not a complete list for a future research agenda in applied forest ecology, this review emphasizes the interactions and the interdependence between these issues, some of which have tended to be discussed rather superficially, while others have been well studied in disciplines outside the domain of forest ecology. Although it is not easy to bridge the gap between science and practice (Hulme 2014), theory is expected to play a more important role in managing, conserving and restoring forest ecosystems. The issues that we identified as relatively little-studied thus need further study in order to achieve the multiple goals of SFM.

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Data accessibility

Data have not been archived because this article does not contain data.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Supporting references for tables.