Conservation Science and Practice
Open Access
A journal of the Society for Conservation Biology

Meta-analysis of management effects on biodiversity in plantation and secondary forests of Japan

Journal:	*Conservation Science and Practice*
Manuscript ID	CSP2-18-0069.R1
Wiley - Manuscript type:	Contributed Paper
Date Submitted by the Author:	n/a
Complete List of Authors:	Spake, Rebecca; University of Southampton, Biological Sciences Yanou, Sakiko Yamaura, Yuichi; Forestry and Forest Products Research Institute, Department of Forest Vegetation Kawamura, Kazuhiro Kitayama, Kanehiro; Kyoto University, Forest Sciences Doncaster, C. Patrick; University of Southampton, Biological Sciences
Search Terms:	coppice, richness, satoyama, synthesis, thinning, traditional management.
Abstract:	Conservation of temperate forest biodiversity has historically focused on natural old-growth. Less than 3% of the world's temperate forests remain unmodified by humans, however, and much of temperate-forest biodiversity is held in the predominating planted and secondary forests. Japan provides a widely applicable model for examining how to maximize biodiversity in managed temperate forests, due to its richness of forestry research generated from its vast forest area, albeit largely in Japanese, and the wide practice of its dominant management interventions across the northern temperate zone. Management for plantations include thinning, extended rotation cycles and clear-cutting. For secondary forests regenerating from past clearance, traditional management varies in its intensities, from clear-cutting as coppices to small-scale understorey clearance. Here we provide a first synthesis of published research on biodiversity in planted and secondary forests of Japan, relevant to management of these forest types in northern temperate forests. Systematic review and meta-analyses of papers published in English and Japanese quantified management impacts on species richness and abundance of several taxa, in relation to moderator variables including stand age and management intensity. Plantation thinning substantially increases the richness and abundance of several taxa. Effect sizes decline with time since thinning for the abundance of regenerating saplings and seedlings, necessitating repeated thinning treatments every six years to sustain this positive effect. Taxonomic groups exhibit variable relationships with stand age in both planted and secondary forests, indicating a need to include both young and old forest stands in managed forest mosaics. We find an insufficient evidence base is available to allow for a meaningful synthesis of low intensity management effects in historically managed secondary forests, with

studies varying widely in scale and reported outcomes. We outline an agenda for the research community to achieve a systematic evaluation of scale-dependent effects of traditional forest management on biodiversity.

R. Spake

Geography and Environmental Science

University of Southampton

Southampton

SO17 1BJ

Editorial Office

Conservation Science and Practice

Dear Sir/Madam,

RE: Resubmission of manuscript ID CSP2-18-0069

We appreciate the opportunity to resubmit a major revision of our article "Meta-analysis of management effects on biodiversity in plantation and secondary forests of Japan" to *Conservation Science and Practice*. We have addressed the comments made by the editor-in-chief, associate editor and two reviewers.

We have incorporated all of the suggestions made by the editor-in-chief, which we think has improved the manuscript greatly. In particular, we have focussed the discussion so that it now i) identifies the management bodies with responsibility for managing forests in Japan, and makes practical recommendations for practitioners, and ii) outlines future research needs for achieving a systematic evaluation of the scale-dependent effects of traditional forest management on biodiversity. The latter is now more clearly targeted to the research community.

We have included a more detailed discussion of these points in a separate document. Thank you in advance for reconsidering our manuscript.

Yours faithfully,

Rebecca Spake

Response to reviewer comments on manuscript ID CSP2-18-0069

Editor-in-chief

Comment 1

You will see below two diametrically opposed reviews and a synthesis by the handling editor, Dr. Luciano Bosso. I endorse and second his recommendation, as stated below. I would like to request, however, that you also consider three additional issues.

Response

Thank you for the opportunity to revise our manuscript and for your suggested improvements. We agree with them all, and have addressed them in the manuscript.

Comment 2

1. If, as Reviewer 2 suggests, this is a minor step forward ("... yet another meta-analysis..."), could you spend a couple of sentences comparing the general findings from this study to what other met-analyses have found in examining forest management practices on biodiversity (and are there major management differences that might drive different outcomes). I realize that this may invite some level of speculation from you. That is ok, as long as it is clearly couched as speculation. Also, I note that "minor step forward" may indicate a review criteria, but CSP does not include novelty as a review criteria, so please do not worry about that. Replication of attempts to understand forest management impacts on biodiversity is a valuable contribution to our broader understanding of forest management practices, in our view.

Response

We now compare our results to previous meta-analyses in the discussion (L354-356 and L424-426). We also now highlight that our synthesis goes beyond previous quantitative syntheses that have quantified differences between broad categories of managed and unmanaged forest stands (L328-333).

Comment 3

2. Conservation Science and Practice tries to appeal to practitioners. Anything that you can say about steps forward with respect to forest management would be appreciated. Just generally, your "Caveats and future directions" is very academically oriented. Inasmuch as climate is changing, I would wager that forest management practices are changing (they are most everywhere else), can you look at this through the lens of the practitioner and say something in these final paragraphs?

Response

We agree this is important. We now divide the discussion into three sections: i) 'Effects of plantation management on biodiversity'; ii) 'Effect of traditional secondary forest management on biodiversity'; and iii) 'Ensuring the maintenance of forest biodiversity within Japan's managed forests: a research agenda'. The first two sections are now more clearly oriented towards practitioners. We now open these sections with a brief description of the management bodies with responsibility for managing *managed forests in Japan (L342-352 and L406-417). In the subsequent paragraphs of these sections, we discuss our results and provide guidance for such practitioners. The final section outlines future directions for forest research in Japan, and is now more clearly targeted to researchers (440-489).*

Comment 4

3. Line 433. In summary we call for..... This is the kind of statement that we academics often make. I find it to be very hollow. Who are you calling, specifically? Who would do this? I am going to bet that (a) whoever could make that happen won't see this paper unless you hand it to them, and (b) won't recognize this as something to be done unless you make a very specific effort to convince them (and a lot of other people) that this effort is a priority. So, what are you really asking for? Are you asking for academics to research differently, managers to manage differently, or regulatory agencies to regulate differently (ie, require mandatory biodiversity monitoring)? The more specific you can be, the more resonance this will have. I do not know what you should do, but I recognize what will be a hollow call for action (yes, I have done that plenty myself over my career). I encourage you to think a little harder about who would actually have the authority to change the world in a way that would be better for forest biodiversity in Japan. (I think you could ditch the entirety of lines 405 -440 and re-focus the conclusion to the issue of forest management practices and regulatory responsibility for assuring the maintenance of forest biodiversity within managed forests).

Response

We agree that this statement lacked focus and utility. For both plantation and secondary forest management, we have restructured the discussion, with sections that now clearly address the relevant practitioners (see above) and clarify who is responsible for managing particular forest types. The following paragraphs in these sections demonstrate how our results provide some guidance to these practitioners.

The lack of an evidence base supporting the recent return of low intensity traditional management practices requires that the government stops promoting the biodiversity benefits of such management by local communities, at least until the completion of a systematic evaluation of traditional management impacts at a range of intensities and scales (Spake et al., 2019). We now clarify this in the manuscript (L435-438), and frame this latter point as an applied research agenda for Japan (final section of the discussion). In this section, we now suggest that the scale-dependent effects of traditional forest management on not only biodiversity, but ecosystem functioning, need to be understood before practicable recommendations for this management intervention can be given.

Associate editor

Comment 1

Thank you for submitting your manuscript "Meta-analysis of management effects on biodiversity in plantation and secondary forests of Japan" (CSP2-18-0069) to Conservation Science and Practice. I have received two opposite reviews. The full set of comments is pasted below.

As you will see below, reviewer 1 is broadly happy with the work. However, reviewer 2 recommended rejection of your ms because he/she finds that your study is too narrow to be of global interest. I do not agree with her/his point of view because I find your study very interesting and well done. Having said that, I would like to invite you to reply both the revisions (ref 1 and ref 2) because I am curious to know how you reply at the critical points carried out by reviewer 2.

Thanks again. I wish you good luck with your work.

Response

Thank you for the opportunity to revise our manuscript. We are pleased that you think the work is interesting and well realised.

Reviewer 1

Comment 1

This paper provides meta-analysis results about how richness and abundance of multiple taxa respond to forest management. The authors found that thinning in plantations enhance richness and abundance of plants and insects (Fig. 1). The abundance of seedlings and saplings increased with thinning intensity, and the authors found that this positive effect of thinning on abundance diminished with the elapsed time after thinning (Fig. 2). The associations between stand age and richness and abundance varied across taxa in both planted (Fig. 4) and secondary forests (Fig. 5). The data was analyzed in the results were discussed in logical manners. I find that the topic and content of the paper matches well with the aim of Conservation Science and Practice. I feel that this manuscript can be published in the current form (after correcting one typo in line 373; Susuki -> Suzuki).

Response

We thank the reviewer for their considered review, and are pleased that they feel it is ready for publication. We have now corrected the typo (L398).

Reviewer 2

Comment 1

Here is yet another of those meta-analysis claiming to report something new and valuable, highlighting how important the study region is and how the conclusions from this region can be adopted worldwide. I feel there the scope of the study is too narrow to justify publication in an international journal of repute.

Response

We thank the reviewer for taking time to review our manuscript. In rebutting his/her reasons for recommending rejection, we hope to have pre-empted the possibility of other readers rejecting the validity of our work. Although Conservation Science and Practice “does not insist on criteria of generality or novelty”(Schwartz, Gottlieb, Masuda, & Runge, 2018), in this paper we demonstrate variable and non-linear responses across taxa to important management covariates (time since thinning, thinning intensity, stand age). These are not typically treated by other meta-analyses, which tend simply to compare ‘managed’ and ‘unmanaged’ forests (e.g. Chaudhary, Burivalova, Koh, & Hellweg, 2016; Paillet et al., 2010; Verschuyl, Riffell, Miller, & Wigley, 2011). This is now emphasised on new lines 328-329.

Comment 2

1. The geographical scope is limited to Japan only which is already doing good in terms of biodiversity conservation and a lot of regional/local research has already been done. There is no point in now translating all that into English and repeat its publication.

Response

The reviewer is misinformed in asserting that Japan is succeeding in biodiversity conservation. Japan's fourth Red List (Ministry of the Environment 2013) identifies 3,597 species as threatened with extinction, corresponding to over 30% of the reptile and amphibian species, over 20% of the mammal and vascular plant species and over 10% of the bird species inhabiting Japan. Japan's National Biodiversity Strategy 2012-2020 considers the underuse of the nation's forest resources as a main driver responsible for what has been called a 'biodiversity crisis' (Ministry of the Environment, 2010). A more recent assessment, 'The Report of Comprehensive Assessment of Biodiversity and Ecosystem Services in Japan' (Ministry of the Environment, 2016), reports that that the biodiversity outlook for Japan has not improved since 2010, with biodiversity continuing to decline due to continued underuse.

We should always strive to make more widely available the large amount of excellent research published only in Japanese, in keeping with the global agenda to make science openly accessible to all. Most papers and datasets published in the Japanese language are not effectively compiled or used in global studies (Amano, González-Varo, & Sutherland, 2016). The Intergovernmental Panel on Biodiversity and Ecosystem Services advocated the need for quantitative methods to specify the level of human interaction needed to manage biodiversity sustainably in satoyama landscapes (IPBES 2012). In this respect, the fact that "a lot of regional/local research has already been done" is what presents us with the opportunity to get beyond linguistic translation to a quantitative synthesis. Our work has tested for relationships that occur amongst studies (e.g., the thinning intensity employed, the taxonomic group), thereby extending the scope of each individual study (Bender, Contreras, Fahrig, Ecology, & Mar, 1998). We have now clarified these points on lines 328-333.

Comment 3

2. Even within Japan, the number of publication and species richness/abundance comparisons compiled in this meta-analysis are too few (just 65 richness comparisons for thinning impact!!).

Response:

We were careful to perform quantitative analysis only on datasets with sufficient sample sizes and appropriate data structures to make precise estimates. For example, we did not quantify the effect of moderator variables (e.g. thinning intensity) on insect abundance, due to the relatively low sample size of this group for this particular management intervention (L256-259).

Comment 4

3. The taxonomic scope is also too narrow and the number of comparisons for each taxa is not sufficient to enable meaningful conclusions (as acknowledged by authors themselves on line 363 and the section on caveats.

Response:

We consider our taxonomic scope to be broad (Table 1). The reviewer misreads our note in L361: "We note that low sample sizes for some taxonomic groups led to low precision in effect sizes". As stated, *this was true for only* some *taxonomic groups, including fungi, moths and climbing plants. This is now clarified on L388.*

Table 1. Taxonomic groups that were quantitatively analysed for each management intervention in our manuscript.

Management intervention	Taxonomic groupings
Effects of plantation thinning on richness and abundance	Saplings and seedlings Ground layer plants Insects
Effects of plantation age on species richness and abundance	Bees Soil invertebrates Birds Moths Terricolous invertebrates Fungi Climbing plants Shrubs and trees
Effects of traditional management of secondary forests on richness and abundance	Bees and wasps Birds Butterflies and moths Terricolous invertebrates Ground-layer plants

Comment 5

4. A lot of recent global meta-analysis already provide impact of various management practices on different metrics of biodiversity, the most prominent one being the PREDICTS database (three levels of management intensities for mature, intermediate and young secondary forests). Therefore I don't see much need or value in results generated by current study using a very limited amount of data.

Response:

The PREDICTS database only collates others' data to make them available for meta-analysis. It currently includes just three studies in total from Japan, despite the existence of a much larger number of relevant articles revealed by our systematic review.

Comment 6

5. Finally, the temperate managed forests and biodiversity in temperate countries is already doing good, the major issue is with tropical low income nations where the species densities are huge and the rate of biodiversity loss is immense. Therefore I see little relevance and contribution of this study in temperate region to ongoing global biodiversity conservation/Aichi Biodiversity target discussions. Given above concerns, I think the current study is of little importance to global audience and therefore doesn't deserve a space in this international journal.

Response:

The reviewer's assertion that "temperate managed forests and biodiversity in temperate countries is already doing good" is, again, vague and misinformed. Temperate zones are the regions of the world most uniformly and extensively altered by human activities (L36-39 in our paper), so restoring the lost biodiversity and preserving what remains is a central challenge facing humanity.

Each analysis in our manuscript relates to specific Aichi objectives, which we refer to throughout the introduction. The Strategic Plan for Biodiversity 2011-2020 and Aichi Biodiversity Targets explicitly advocate the implementation conservation measures within planted and secondary forests, the forest types that our systematic review has focussed on. Indeed, planted forest area is increasing globally, having risen from 4% to 7% of total forest area between 1990 and 2015, and the largest *increases have occurred in the temperate zone. Aichi Target 7 advocates their sustainable management in support of biodiversity, so our analyses of thinning and age effects in plantation forests are relevant. Aichi Target 15 calls for the restoration at least 15% of degraded areas through conservation and restoration activities. Our analysis of biodiversity responses to traditional management of secondary forests, which represents passive restoration (recovery of forest communities regenerating following clearcutting), is therefore relevant.*

References

Amano, T., González-Varo, J. P., & Sutherland, W. J. (2016). Languages Are Still a Major Barrier to Global Science. *PLoS Biology*, *14*(12), e2000933. https://doi.org/10.1371/journal.pbio.2000933

Bender, D. J., Contreras, T. A., Fahrig, L., Ecology, S., & Mar, N. (1998). Habitat Loss and Population Decline : A Meta-Analysis of the Patch Size Effect. *Ecology*, *79*(2), 517–533. https://doi.org/10.2307/176950

Chaudhary, A., Burivalova, Z., Koh, L. P., & Hellweg, S. (2016). Impact of Forest Management on Species Richness : Global Meta- Analysis and Economic Trade-Offs. *Nature Publishing Group*, 1–10. https://doi.org/10.1038/srep23954

Ministry of the Environment, 2010. "Fifth National Report of Japan to the Convention on Biological Diversity." Accessed January 2019. https://www.cbd.int/doc/world/jp/jp-nr-05-en.pdf [Google Scholar]

Ministry of the Environment. 2016. "Japan Biodiversity Outlook 2." Accessed January 2019. http://www.biodic.go.jp/biodiversity/activity/policy/jbo2/jbo2/index.html. [Google Scholar]

Paillet, Y., Bergès, L., HjÄltén, J., Ódor, P., Avon, C., Bernhardt-Römermann, M., … Virtanen, R. (2010). Biodiversity differences between managed and unmanaged forests: Meta-analysis of species richness in Europe. *Conservation Biology*, *24*(1), 101–112. https://doi.org/10.1111/j.1523-1739.2009.01399.x

Schwartz, M. W., Gottlieb, S., Masuda, Y. J., & Runge, M. C. (2018). A vision for documenting and sharing knowledge in conservation. *Conservation Science and Practice*, *1*, 1–2. https://doi.org/10.1002/csp2.1

Spake, R., Bellamy, C., Graham, L., Watts, K., Wilson, T., Norton, L., … Eigenbrod, F. (2019). An analytical framework for spatially targeted management of natural capital. *Nature Sustainability*.

Verschuyl, J., Riffell, S., Miller, D., & Wigley, T. B. (2011). Verschuyl J , Riffell S , Miller D , Wigley TB .. Biodiversity response to intensive biomass production from forest thinning in North American forests-a meta- Forest Ecology and Management Biodiversity response to intensive biomass production from forest . *Forest Ecology and Management*, *261*(2), 221–232. https://doi.org/10.1016/j.foreco.2010.10.010

Meta-analysis of management effects on biodiversity in plantation and secondary forests of Japan

Rebecca Spake[1,2], Sakiko Yanou[3], Yuichi Yamaura[4,5], Kazuhiro Kawamura[6], Kanehiro Kitayama[3] and C. Patrick Doncaster[2]

[1] School of Geography and Environmental Science, University of Southampton, Highfield Campus, Southampton, SO17 1BJ, U.K.

[2] School of Biological Sciences, University of Southampton, Highfield Campus, SO17 1BJ, U.K.

[3] Laboratory of Forest Ecology, Graduate School of Agriculture, Kyoto University, Sakyoku Kyoto, Japan.

[4] Department of Forest Vegetation, Forestry and Forest Products Research Institute, 1 Matsunosato, Tsukuba, Ibaraki, Japan.

[5] Fenner School of Environment and Society, Australian National University, Canberra, ACT, 2601, Australia

[6] Graduate School of Agriculture, Hokkaido University, Nishi 9, Kita 9, Kita-ku, Sapporo, Hokkaido 060-8589, Japan.

Corresponding author: Rebecca Spake; R.Spake@soton.ac.uk; +44(0)7595670038; School of Geography and Environmental Science, Building 44, Highfield Campus, University of Southampton, Southampton, SO17 1BJ, U.K.

Article type: Contributed paper

Running head: Forest management in Japan

Article impact statement: A quantitative synthesis of Japan's biodiversity research can guide management to enhance the biodiversity of disturbed forests across the temperate zone

Keywords: coppice, richness, satoyama, synthesis, thinning, traditional management.

Acknowledgements: RS was funded by the Japan Society for the Promotion of Science and the UK Biotechnology and Biological Sciences Research Council (grant number BB/H531935/1). We thank all authors who contributed their data to this analysis, and all members of the Laboratory of Forest Ecology at Kyoto University for informative discussions of forestry in Japan.

Abstract

Conservation of temperate forest biodiversity has historically focused on natural old-growth. Less than 3% of the world's temperate forests remain unmodified by humans, however, and much of temperate-forest biodiversity is held in the predominating planted and secondary forests. Japan provides a widely applicable model for examining how to maximize biodiversity in managed temperate forests, due to its richness of forestry research generated from its vast forest area, albeit largely in Japanese, and the wide practice of its dominant management interventions across the northern temperate zone. Management for plantations include thinning, extended rotation cycles and clear-cutting. For secondary forests regenerating from past clearance, traditional management varies in its intensities, from clear-cutting as coppices to small-scale understorey clearance. Here we provide a first synthesis of published research on biodiversity in planted and secondary forests of Japan, relevant to management of these types of forest in northern temperate forests. Systematic review and meta-analyses of papers published in English and Japanese quantified management impacts on species richness and abundance of several taxa, in relation to moderator variables including stand age and management intensity. Plantation thinning substantially increases the richness and abundance of several taxa. Effect sizes decline with time since thinning for the abundance of regenerating saplings and seedlings, necessitating repeated thinning treatments every six years to sustain this positive effect. Taxonomic groups exhibit variable relationships with stand age in both planted and secondary forests, indicating a need to include both young and old forest stands in managed forest mosaics. We find an insufficient evidence base is available to allow for a meaningful synthesis of low intensity management effects in historically managed secondary forests, with studies varying widely in scale and reported outcomes. We outline an agenda for the research community to achieve a systematic evaluation of scale-dependent effects of traditional forest management on biodiversity.

Introduction

Natural old-growth forests are considered irreplaceable biodiversity resources due to their long continuity and high structural diversity (e.g. Gibson et al. 2011). Whilst their strict protection represents a conservation priority in the face of forest loss and degradation worldwide, the biodiversity potential of disturbed planted and secondary forests is widely acknowledged (Putz et al., 2012). Empirical studies measuring biodiversity in forests under varying intensities of disturbance have proliferated in recent decades (Spake & Doncaster, 2017). Although several syntheses of this vast literature exist, they have limited potential for practicable recommendations across a range of contexts, due to their tendency towards narrative synthesis over quantitative meta-analysis and to focus on charismatic taxa and tropical regions (Spake et al. 2015), or their inclusion of studies published only in English (Amano et al. 2016). Human-disturbed forests particularly merit valuation in the temperate zone, where planted and secondary forests predominate following millennia of exploitation, to the extent that only 1-2% of natural old-growth forest remains intact in unharvested remnants (Currie & Bergen, 2008). Existing quantitative syntheses, however, typically measure the biodiversity value of disturbed forests by their comparison to natural, old-growth forests as a reference. This conventional set up yields inference of limited practicable value to managers and conservationists in temperate nations where little old-growth remains, and has resulted in the exclusion of much research from pan-global syntheses (Spake & Doncaster, 2017). Consequently, the efficacy of forest management practices for biodiversity conservation remains poorly understood for much of the temperate zone (Lindenmayer et al. 2015).

The Strategic Plan for Biodiversity 2011-2020 and Aichi Biodiversity Targets, adopted by the Convention on Biological Diversity in 2010 explicitly advocate implementing conservation measures within planted and secondary forests. Planted forest area is increasing globally, having risen from 4% to 7% of total forest area between 1990 and 2015. The largest increases have occurred in the temperate zone, and regionally in East Asia, Europe and North America, for diverse purposes including production, soil protection and carbon sequestration (Payn et al. 2015). Plantations generally lack the continuity and structural attributes typical of old-growth forests, giving rise to the moniker of ‘green deserts’ (Koh and Gardner 2010); however, their habitat quality can vary in relation to management activities (Humphrey, 2005). Aichi Target 7 advocates their sustainable management in support of biodiversity. Principal management interventions for enhancing biodiversity in temperate plantations include disturbance by stand thinning to enhance the natural regeneration of native trees, and rotation age extension, on the premise that many species are dependent on later successional stages (Spake et al. 2015).

Aichi Target 15 calls for the restoration at least 15% of degraded areas through conservation and restoration activities. Secondary forests arise from both assisted restoration, and unassisted forest regeneration following human disturbance or land abandonment (Chazdon, 2008). Several options are available for their management, with traditional management receiving mounting interest due to potential benefits for biodiversity, biomass, and climate change mitigation (Müllerová et al. 2015). Throughout the northern temperate zone, broadleaved forests that border human settlements have been managed over millennia for fuelwood, fertiliser and food (Takeuchi, 2010). Stands of trees were cut in rotations of 15-30 years, while less intensive practices included litter removal, understorey clearance and tree thinning to provide fertiliser, fuel, livestock feed and bedding (Kirby & Watkins, 1998). Worldwide, traditional secondary forest management largely ceased during the mid-1900s, as fossil fuels and chemical fertilisers become widely available (Kirby & Watkins, 1998). Abandonment of traditional management is widely regarded as a driver of biodiversity loss, due to reduced habitat suitability for early successional species requiring open habitats or vegetation structures that are reduced under heavy shade (Takeuchi, 2015). Interest is mounting in a return to traditional management at varying intensities across the temperate zone for 'abandoned' public, private and even protected forests. For example, the global Satoyama Initiative (http://satoyama-initiative.org/), launched concurrently with the Strategic Plan for Biodiversity in 2010, advocates the value of traditional management not only in Japan but globally. Moreover, understorey clearance is traditionally practiced in urban woodlands in Europe and Japan, in compliance with recreational and aesthetic values (Heyman, 2010).

The nation of Japan provides a valuable opportunity to assess the impacts of planted and secondary forest management on biodiversity in the northern temperate zone (Appendix A). Forest covers approximately 25 million hectares in Japan, constituting two thirds of the total land area (Forestry Agency, 2009), but very little is pristine (Yamaura et al. 2012). Plantations occupy more than 40% of total forest area, principally as monocultures of Japanese cedar (*Cryptomeria japonica*), Hinoki cypress (*Chamaecyparis obtusa*), and larch (*Larix kaempferi*), with the rest comprising secondary forests dominated by evergreen and deciduous oaks (*Quercus* sp.), and red pine (*Pinus densiflora*), naturally regenerating from past coppicing and selective cutting at varying intensities (Forestry Agency, 2009). Japan's vast forest area and interest in conservation has generated copious empirical research on biodiversity responses to forest management interventions (Higuchi & Primack, 2009). The northern temperate forestry community stands to benefit from a synthesis of this rich literature, due to the wide practice and history throughout the temperate zone of management interventions exemplified by Japanese forest management. For example, just as for Japan the majority of Central European forests are restricted to mountain areas, and have been exploited by clearcutting and coppicing for millennia (Hilmers et al. 2018; Washitani, 2003). Interest in the revival of active management within 'abandoned' secondary forests is increasing in Japan, as also in the UK and Europe (Takeuchi, 2003), while clearcutting of plantations that predominates in North America and northern Europe (Rosenvald and Lohmus, 2008) is also increasing in Japan amidst plans to increase domestic wood supply (Forest Agency, 2017). Effective conservation strategies for temperate forests experiencing such a range of disturbance intensities require a comprehensive and quantitative understanding of how different trophic groups vary across a wide range of successional stages and management intensities (Hilmers et al. 2018). With its forests at various successional stages following a diversity of management practices, Japan's empirical literature offers the possibility of such understanding. Many of Japan's forestry studies, however, are published only in Japanese (Nagaike, 2012), reflecting the major barrier that language still presents to the global compilation and application of scientific knowledge (Amano et al. 2016). Indeed, given the extent of its forest area and richness of empirical research, it is apparent that Japanese studies are underrepresented in synthetic studies of forest management impacts. Although several narrative syntheses exist (Inoue, 2005; Nagaike, 2012; Yamaura et al., 2012), a robust systematic and quantitative synthesis is lacking.

Here we synthesise and quantitatively assess the effects on biodiversity of coniferous and broadleaved forest management practices in Japan which are widely promoted to conserve biodiversity across the northern temperate zone. Specifically, we examine impacts on the species richness and abundance of a range of taxonomic groups from four management interventions: i) plantation thinning; ii) extended rotation cycles (plantation age); iii) traditional management of secondary forests (secondary forest age); and iv) lower intensity traditional management of natural and abandoned secondary forests (thinning, understory clearance and/or litter removal). By synthesising the Japanese forestry literature published in English and Japanese, we aim to provide practicable recommendations to inform policy-making in Japan, and to similarly managed forests across the northern temperate zone, due to the wide practise of the management interventions we synthesise.

Materials and methods

Literature search and data extraction

We followed standard systematic review methods (Pullin and Stewart, 2006) to collate published empirical studies on the focal management interventions. Following recommendations of Amano et al. (2016), we conducted extensive literature searches in both English and Japanese, using Web of Science, Google Scholar and J-Stage (the largest platform for publishing electronic journals in Japan; https://www.jstage.jst.go.jp/). We sought studies conducted in Japan using search terms relating to the country, forest management interventions, and biodiversity (search queries in Appendix B). Additional literature was identified by 'snowballing': searching for references within retrieved articles and reviews. We used the R package 'metagear' (Lajeunesse, 2016), to screen retrieved abstracts.

Relevant studies compared biodiversity in planted or secondary forest with appropriate controls, given in Table 1. In order to produce data relevant to the management decisions affecting forest management actions in Japan and the rest of the temperate zone, we compared the biodiversity value of forests in their current state (control groups of low disturbance relative to treatment groups), compared to a plausible alternative state (treatment groups of managed forests; Table 1; Spake & Doncaster, 2017). Species richness was used as a proxy for biodiversity, being most widely used biodiversity measure (Magurran, 2004). We note here that authors measuring "species richness" in primary studies were actually measuring species density, the number of species per unit area (Gotelli and Colwell, 2001), wherein richness is standardized against area or sampling effort across treatments. We use the term species richness to avoid confusion with abundance, which is often measured as density (number of individuals per unit area). We evaluate the implications of this diversity metric in our discussion.

Meta-analysis of plantation thinning effects on biodiversity

To ensure meaningful comparisons across studies, we sought publications that compared thinned treatment to unthinned control stands with the same canopy dominant and age. For each comparison of species richness and/or abundance, the effect size of log response ratio (ln*R*) was calculated, as:

$$lnR = ln\,(\bar{x}_T) - ln\,(\bar{x}_C)\ , \qquad (1)$$

where $\bar{x}_T$ is the mean species richness or abundance in treatment forest stands and $\bar{x}_C$ is the mean value for control stands. The ln*R* describes the proportional difference in species richness or abundance between control and treatment groups. The natural log transformation of the response ratio linearizes the metric, treating deviations in the denominator and the numerator as equal, and normalises its otherwise skewed distribution (Hedges et al., 1999). Abundance measures included values of cover, biomass, and number of individuals. If an article reported single abundance values for a number of different species within the same taxonomic group (e.g. within understorey plants), we calculated the combined effect size for the group (Borenstein et al. 2009).

We extracted data on the following moderator variables: taxon (understory plants, saplings and seedlings, invertebrates), thinning stand age, years since thinning and thinning intensity (percentage volume of trees removed). We used linear mixed models to investigate variation in effect size with the moderator variables. We included quadratic or $\log_{10}$ relationships with thinning intensity to test for possible nonlinear relationships. Study quality varied widely regarding replication and spatial interspersion of treatments. Meta-analyses conventionally weight effect sizes by the inverse of study variance to account for differences in sampling effort. With forest biodiversity studies however, the variance of replicate means is often i) unreported, ii) unavailable because sample size is one, or iii) not meaningful because studies varied widely in their design, with a high prevalence of pseudoreplicated designs (Spake and Doncaster, 2017). We accounted for differences in study quality by weighting effect sizes based on their true sample sizes, following Mayerhofer et al. (2013) and Doncaster and Spake (2017), with the relative weights estimated as:

$$wt = (N_C N_T)/(N_C + N_T)\ , \qquad (2)$$

where N_C and N_T are the true sample sizes of the unthinned control and thinned treatments, respectively, identifying the number of spatially interspersed replicates of forest treatments (Halme et al. 2010). See Appendix C for this weighting rationale.

Where articles reported separate values for two or more study locations, canopy dominants or taxonomic groups, we regarded each as an independent observation. Study was included as a random effect to accommodate studies with multiple effect-size estimates based on a common control stand. Just one study was omitted from the abundance analysis, due to a zero abundance that precluded calculation of a response ratio. All possible additive models were constructed by maximum likelihood methods using packages lme4 (Bates et al., 2014), and MuMIn (Barton, 2013). Akaike's Information Criterion (AIC) with small sample correction (AICc) was used to identify a candidate set (Burnham and Anderson, 2004). We performed model averaging when multiple models were plausible (ΔAICc < 4), but selected a single model if the next best model had ΔAICc > 4. Goodness of model fits was estimated by the marginal R^2 (Nakagawa and Schielzeth, 2013).

Meta-analysis of extended rotation cycles for plantations and high-intensity traditional management of secondary forest

Studies investigating the impact of extended rotation cycles typically measure biodiversity in plantations of varying ages (Appendix D). Studies investigating the impact of high intensity traditional management typically measure secondary stands of varying ages following clearance (Appendix E). We here define secondary forests *sensu lato* as any forests regenerating naturally from a stand-level clearance event, following high intensity coppicing or clearcutting. For plantations, we included studies that used a control group of overmature plantations beyond 50 years of age (median reference stand age: 76 years), reflecting the Japanese convention to harvest at ~50 years old (Forestry Agency, 2017). For traditional secondary forests, we included studies that used at least one reference stand exceeding 100 years in age (median age: 128 years).

Whilst all studies of stand age-biodiversity relationships included a common reference stand, studies varied in treating stand age as either a continuous or categorical variable. When treated as continuous, researchers sampled forest plots across a stand-age gradient, whereas when treated as categorical, researchers sampled plots replicated within grouped age classes. We therefore adopted the meta-analytical approach of previous stand-age biodiversity syntheses by Curran et al. (2014) and Martin et al. (2013), which synthesised pair-wise comparisons between single treatment stands and either replicated or unreplicated reference stands. We calculated ln*R* as the effect size for abundance and richness comparisons. We grouped taxa into the following groups: butterflies and moths, bees and wasps, terricolous invertebrates (beetles, spiders and ants sampled above the soil), soil invertebrates (collembola and mites sampled from within soil), fungi and ground-layer plants (including groups termed as vascular, shrub or herb species).

We used linear mixed models to investigate variation in effect size (ln*R*) with stand age and other moderator variables. Just one study was omitted from the abundance analysis, due to a zero abundance. Moderator variables included taxon, stand age, and their interaction. We included quadratic or $\log_{10}$ relationships with stand age to test for possible nonlinear biodiversity recovery, and we weighted by sample size as described above. Study was included as a random effect to accommodate publications with multiple effect-size estimates using a common control. To identify important moderators of effect size differences across studies, we used model selection as described above. All quantitative analyses were performed using R (R Core Team, 2017).

Review of lower intensity traditional management impacts on biodiversity in natural and secondary forests

We compiled studies that assessed the influence on biodiversity in secondary forests of traditional management practices that are lower in intensity than clearcutting in terms of the amount of biomass removed (Appendix F). Such practices include tree thinning, understorey clearance and litter removal (Shibuya et al. 2008). We selected studies that compared forest sites described as recently unmanaged, abandoned or natural to forest sites that were either currently or recently actively managed (within 20 years). To control for stand age and canopy-dominant effects on biodiversity, we sought studies with similar control and treatment stands in these attributes. Each study was described according to the following moderator variables: taxonomic group, stand age, years since management, and management type (thinning/understorey removal/litter removal) and intensity (e.g. volume of trees removed, area of understorey cleared). Descriptions of management actions were often vague, with inconsistent reporting of intensity and stand age. Insufficient replication and crossing at the level of management intervention by taxonomic group precluded meaningful quantitative summaries. We therefore synthesised these results narratively.

Results

Effects of plantation thinning on richness and abundance

Twenty-six publications were retrieved (Appendix C) comparing biodiversity in thinned and unthinned plantations, spanning a range of thinning intensities and taxonomic groups on widely distributed studies across Japan. Plantations in all but one study were planted as monocultures. One study was retrieved on birds (Toyoshima et al. 2013), and one on below-ground mite communities (Takasaki et al. 2010). Studies on insects comprised Hymenoptera, Coleoptera, Diptera and Lepidoptera. Data were sufficient for meta-analysis of saplings and seedlings, ground-layer plants and insects (pooling across Orders), totalling 65 richness and 134 abundance comparisons.

Subgroup analysis showed that plantation thinning substantially increased the richness of tree saplings and seedlings, ground-layer plants and insects by 227%, 60% and 38% respectively ($P < 0.05$; Figure 1a). Thinning also increased abundance of the studied groups, by 330%, 177% and 63% respectively ($P < 0.05$; Figure 1b). Effect sizes were heterogeneous amongst studies, due to study-wise variation in stand ages and thinning intensities. Collinearity between taxonomic group, stand age and thinning intensity restricted our mixed effects modelling of abundance effect sizes to broadleaved saplings and seedlings and ground-layer plants only. Moderator collinearity precluded mixed-effects analysis of species richness effect sizes. The most important predictors of sapling and seedling abundance were thinning intensity, time since thinning and their interaction (Appendix C, marginal $R^2 = 0.42$ for minimum adequate model). Impacts of thinning on abundance depended on both the volume of trees removed and time since thinning (Figure 2a). In recently thinned stands, the impacts increased linearly with increasing volume of trees removed. This effect declined with the time elapsed since thinning (Figure 2b), with no effect detectable after ~6 years (Figure 2c; Appendix C). Effect sizes of ground-layer plant abundance increased with both thinning intensity and plantation stand age, with a thinning intensity of about 66% resulting in a doubling of ground-layer plant abundance (Figure 3; Appendix C, marginal $R^2 = 0.23$ for minimum adequate model).

Effects of plantation age on species richness and abundance

We retrieved 15 publications (Appendix D) describing species richness or abundance differences between younger planted and reference overmature planted forest stands, yielding 115 richness and 68 abundance comparisons. One study was excluded from the quantitative synthesis because of its outlying age of 20-250 year-old stands (Suzuki et al. 2005). The minimum adequate models selected to explain differences in species richness and abundance between extended rotation and younger planted forest stands included taxonomic group (species richness: $F_{1,85} = 5.99$; $P < 0.001$; abundance: $F_{1,66} = 11.63$; $P < 0.001$), $\log_{10}$ stand age (species richness: $F_{1,88} = 4.11$; $P = 0.046$; abundance: $F_{1,66} = 0.02$; $P = 0.875$), and their interaction (specie richness: $F_{1,90} = 3.85$; $P < 0.001$; abundance: $F_{1,66} = 7.77$; $P < 0.001$). These models had marginal R^2 values of 0.54 and 0.55 for effect sizes of species richness and abundance respectively, and both had ΔAIC >4 to the next best model. Climbing plants, and terricolous invertebrates exhibited consistently higher species richness and abundance levels in younger planted stands than overmature planted stands, while fungi were consistently richer and more abundant in overmature stands (Fig. 4). The interaction reflects taxon-specific relationships of species richness and abundance with stand age (explaining the absence of a detectable stand-age main effect). Birds, shrubs and trees demonstrated positive relationships, whilst flying and terricolous invertebrate and ground layer plant richness had declining abundance with stand age (Fig.5). Fungi richness and abundance did not vary detectably with stand age (Fig.4).

Effects of traditional management of secondary forests on richness and abundance

We retrieved 25 publications describing species richness or abundance in secondary forest stands regenerating from clearcutting, in comparison to a reference secondary forest stand >100 years old (Appendix E), yielding 141 richness and 105 abundance comparisons. Prior to modelling the relationship between richness recovery and stand age across taxonomic groups, we removed studies on trees, epiphytic plants (climbers and vines) and Diptera, because treatment forest sites from these studies did not present a stand age gradient. For the same reason, we removed studies of ground-layer plants when modelling abundance effect sizes. The minimum adequate models selected to explain species richness and abundance differences between abandoned older and younger secondary forest contained taxonomic group (species richness: $F_{5,58} = 5.67$; $P = <0.001$; abundance: $F_{5,50} = 6.44$; $P = <0.001$), stand age (species richness: $F_{1,82} = 0.31$; $P = 0.575$; abundance: $F_{1,66} = 0.33$; $P = 0.566$), and their interaction (species richness: $F_{4,82} = 7.20$; $P = <0.001$; abundance: $F_{4,66} = 4.15$; $P = <0.01$). These models had marginal R^2 values of 0.35 and 0.38 for species richness and abundance effect sizes respectively, and both had ΔAIC > 4 to the next best model. The interaction reflects a balanced opposition of stand-age effects amongst taxonomic groups (explaining the absence of detectable main effects; Fig. 6). Flying invertebrates and ground-layer plant richness benefited from early successional conditions and declined with stand age, whilst soil invertebrates and birds exhibited lower richness levels in younger secondary forest relative to older abandoned forest and tended to increase with stand age (Fig. 6).

Effects of lower intensity traditional management of secondary forests on biodiversity

We retrieved 27 publications that investigated the impact of low intensity forest management on biodiversity by comparing unmanaged and managed forest (Appendix F). Wide variation in study variables including management intensity, taxonomic group and forest ages precluded a quantitative synthesis; we instead report the results narratively, in detail in Appendix F. Broadly, management interventions comprised tree thinning at varying intensities, understorey removal and litter removal, and various combinations of these interventions. The majority of studies were observational, with researchers selecting forest sites already subjected to management by voluntary citizens or the prefectural government for purposes including compost production, mushroom production, recreation and biodiversity conservation, with few studies performing controlled experiments (but see Shibuya et al. 2008). Studies varied widely in scale, in terms of the sizes of forest stands and the observational plots for management and biodiversity measurement (Table F1), and such scale information was typically not reported.

Discussion

Our meta-analysis of relatively large sets of published studies from Japan demonstrates that diverse stand-level factors influence the impacts on biodiversity of management interventions that are widely practised in planted and secondary forests across the northern temperate zone. Quantitative synthesis, which allows the testing of relationships between individual study outcomes and their characteristics, have allowed us to demonstrate variable and non-linear responses amongst taxa to important management covariates (time since thinning, thinning intensity, stand age). These are not typically treated by other meta-analyses, which tend simply to compare ‘managed’ and ‘unmanaged’ forests (e.g. Chaudhary et al., 2016; Paillet et al., 2010; Verschuyl et al. 2011). Broadly, our results demonstrate that both young and old stands must be present in managed forest mosaics to support multiple taxonomic groups. Our comprehensive review has revealed the need for a stronger evidence base to evaluate the impacts on biodiversity of traditional low-intensity management strategies for northern secondary temperate forests. Here we discuss the relevance of our results to forestry practitioners for maintaining biodiversity in temperate forests managed on principles similar to the Japanese model. We go on to outline an agenda for the research community if biodiversity is to be preserved effectively in these types of managed temperate forests.

Effects of plantation management on biodiversity

Under the Forest and Forestry Revitalisation Plan to increase Japan’s timber self-sufficiency (Nagasaka et al. 2016), mature plantations are increasingly subject to clearcutting in many parts of Japan including Kyushu and eastern Hokkaido. In topographically complex areas that preclude commercial management, a range of groups under municipal control, including voluntary NGOs and private companies, funded by a national Forest Environment Tax to be introduced this year (Forestry Agency, 2017), conducts plantation thinning. The aim of such management is to enhance ecosystem services that benefit the public, including watershed conservation, mitigation of climate change in addition to and biodiversity conservation, and the assisted regeneration of natural broadleaved forest (Forestry Agency, 2017). Here we discuss our results of plantation forest age and thinning impacts in biodiversity, to provide guidance to practitioners conducting such management.

Plantation thinning positively affected species richness and abundance of invertebrates, ground layer plants and saplings and seedlings (Fig.1), which is consistent with a synthesis of thinning impacts on several taxa, including birds mammals and invertebrates, in North American forests (Verschuyl et al. 2011). Thinning substantially increased sapling and seedling abundance and richness. The response of sapling and seedling abundance to thinning intensity depended on the time since thinning; effect sizes increased with thinning intensity in recently thinned plantations, but no effect of intensity was detectable in stands thinned ~6 years previously (Figure 2; Appendix C).This finding suggests repeated thinning at such intervals is required to ensure the survival of regenerated seedlings. The effect of thinning on understorey plant abundance increased linearly with stand age (Fig. 3b), demonstrating a larger effect in older stands with more closed canopies, suggesting such stands could be prioritised for thinning efforts. Effect size relationships with thinning intensity and stand age for saplings/seedlings and understorey plants did not plateau, suggesting an absence of generally applicable thresholds for maximising positive effects on species richness or abundance.

Our explanatory power was low for models explaining understorey abundance with thinning intensity and stand age, and previous research has shown that thinning resulted in almost no increase in understory vegetation. Such instances are attributed to grazing by deer (Tamura and Yamane, 2017), and so the effectiveness of thinning in Japan and other northern temperate nations that similarly are experiencing high deer densities (Cote, 2004), will likely depend on local deer densities and grazing management.

Timber harvesting in Japan has conventionally used a rotation age of between 40 and 60 years (Masaki et al. 2006), similar to other northern temperate nations (Benkman, 1993; Macdonald et al. 2010). However, extended rotation ages >70 years are becoming increasingly widespread, to hedge against fluctuations in timber prices with a larger, more valuable stock (Masaki et al. 2006). This review has shown that the richness and abundance of birds, shrubs and trees increases nonlinearly with planted stand age (Fig. 5), likely attributable to the combined effects of time favouring colonisation by dispersal-limited species, and structural diversification as forests age (Norden and Appelqvist, 2001). The richness of several taxonomic groups, including ground-layer plants and soil and terricolous invertebrates, declined with stand age, however. With different taxonomic groups exhibiting contrasting species richness levels in different successional stages, our results from Japan support recommendations for both young and old forest stands to be included in plantation forest mosaics for invertebrate and ground-layer plant conservation (Viljur and Teder 2016).

We note that low sample sizes for some taxonomic groups led to low precision in effect sizes for these groups, including the climbing plants, moths and fungi. Although functional groups within broad taxonomic groupings vary in their responses to forest management impacts (Spake et al. 2015), low sample sizes forced their grouping into broad taxonomic classifications, which may have obscured differences in responses of finer classifications. Richness and abundance relationships with stand age revealed little difference between the biodiversity value of 50- and ~70-year-old (control) plantations. Extending the conventional rotation age to > 70 years may therefore not offer a win-win for economic return and biodiversity conservation. However, it is important to understand patterns of biodiversity variation beyond 70 years, because a large quantity of planted stands are likely to remain unharvested in Japan. We retrieved one study of hinoki cypress plantations from 20 to 250 years old. Suzuki et al. (2005) found that stands >200 years old differed in species compositions to stands <100 years-old, having developed multi-layered canopies with broadleaved species occupying the lower canopy. The authors state that canopy openings were a product of both past logging and natural stand dynamics, and suggest that much older planted forests stands may require thinning.

Effect of traditional secondary forest management on biodiversity

The Satoyama Initiative promotes the revival of traditional management at a range of intensities, based on presumed benefits to biodiversity and ecosystem services (Takeuchi, 2010). This includes the return of more traditional interventions, with secondary forests managed by clear-cutting, in addition to more commonly practised contemporary interventions that include thinning, undergrowth clearance and leaf-litter removal applied at smaller extents (Shibuya et al. 2008). Contemporary satoyama management practices reflect shifting sociocultural and resource needs. Although the original primary function of satoyama was for production, interest is mounting in the value of satoyama for delivering a range of other ecosystem services. In particular, the cultural and aesthetic opportunities inherent in the woodland management process are motivating community-based management, with subsidies from municipal governments (Yokohari & Bolthouse, 2011; Tatsui & Fujii, 2007). Here we set the results of our analyses of secondary-forest management in the context of future research needs that are required to effectively guide local community groups in maintaining secondary forest biodiversity.

We have shown that species richness and abundance relationships with stand age (a proxy for high intensity traditional management) varied according to taxonomic group in secondary forests. Flying invertebrates and ground-layer plants benefited from more open, early-successional conditions and tended to decline with stand age while the abundance and richness of birds and soil invertebrates increased with stand age. Late successional secondary forests are needed to support mature forest-specialists, but are scarce in southern Japan and much of Europe due to the long history of forest usage (Totman 1989; Currie & Bergen, 2008). Our results accord with the taxon-specific responses to stand age found in Europe and

North America (Spake et al. 2015), and also suggest that managed mosaics should contain secondary forests that remain set-aside to mature.

The studies retrieved by our review of low intensity traditional management varied widely in taxonomic group (plants, invertebrates and fungi), the particular combination of management interventions and their intensity (amount of biomass removed), scale of management and study design; with positive, negative and neutral effects of management on a range of biodiversity metrics reported (Table S1). Due to this variation, it is difficult to make clear generalisations on the effect of low intensity traditional management on forest biodiversity. It can only be concluded that impacts are highly heterogeneous and context-specific, with positive, negative or neutral management effects on a range of biodiversity metrics. We therefore caution against the promotion by governments of the biodiversity value in traditional forest-management practices, such as through the Satoyama Initiative, until an understanding of the effects of scale-dependent management interventions is achieved (Spake et al. 2019). We note however, that management can provide other benefits including the enhancement of cultural ecosystem services.

Ensuring the maintenance of forest biodiversity within Japan's managed forests: a research agenda

Effect sizes were estimated from species density, as opposed to species richness, which is typically estimated by using abundance or incidence distributions to model the number of undetected species (Gotelli and Colwell, 2001). It is therefore possible that species density differences could have been partly driven by effects on overall abundance of individuals. Additionally, using species density can potentially underestimate the true biodiversity difference between e.g. >100-year-old secondary and younger secondary forests; higher intrinsic richness in older forests could lead to a systematic under-sampling bias that misses more species per site than in younger secondary sites when sampling is standardised by area or sampling effort (Spake and Doncaster, 2017). Moreover, use of species density or richness alone does not account for compositional differences between forest stands, and ignores the incidence of rare or functionally important species, and important attributes such as invasiveness. Much research into biodiversity–ecosystem functioning relationships has shown that biodiversity (including taxonomic, functional and phylogenetic diversity) affects the functioning of ecosystems (e.g. primary production, decomposition, nutrient cycling, trophic interactions and so on) and consequently a range of ecosystem services (e.g. food production, climate regulation, pest control, pollination etc; Cardinale et al. 2012). An important next step is to use biodiversity data from forests to give practical advice for enhancing ecosystem functioning and ecosystem services (Mori et al., 2017).

The studies included in our meta-analysis varied widely in scale, in terms of the size of the individual sampling plots (grain), the area of inference represented by each data point (e.g. whether a forest stand), the scale at which a mean is calculated (the focus), and the size of the study area (extent; Gerstner et al., 2017). While grain was frequently reported, focus and extent were often missing, or descriptions did not allow clear distinctions among the spatial scale components, precluding an analysis of the scale-dependence of effect sizes. We follow Gerstner et al. (2017) in urging studies to report such information in the future to allow for an understanding of the importance of management and study scale of the effects of forest management on biodiversity. We see a need for researchers to conduct more systematic field studies of the impacts of different traditional management practices on biodiversity across Japan. This can be achieved by evaluations of practices piecemeal (thinning, understorey clearance and litter removal), and in combination across a network of well-replicated sites across Japan. There is a particular need to consider and report the extent of the area managed, and the effect of the intensity of management practices (e.g. volume of trees removed), so that thresholds may be identified to guide management practices.

It is conceivable that climate could moderate forest management impacts on biodiversity. For example, the importance of plantation thinning for increasing sapling abundance could depend on variables such as temperature and solar radiation, with a certain level of canopy cover required to buffer against climatic extremes. Testing for both additive and interactive effects of climatic variables on effect sizes (management impacts) would require a larger sample size than is currently available, and represents a future research opportunity for Japan.

In conclusion, we call for a coordinated research agenda to achieve a systematic evaluation of traditional management impacts, at a range of intensities and scales, on forest biodiversity and ecosystem functioning in Japan. Future studies of all forests should measure community attributes other than species richness that capture ecosystem function, in addition to reporting attributes of scale and the topographic and regional climatic context, to permit testing for interacting effects. Japan presents an ideal opportunity to test for such cross-scale interactions (Peters et al. 2007), due to its wide climatic and topographic gradients that could potentially modify biodiversity responses to the management of its vast forest estate (Yamaura et al. 2011; Spake et al. 2019).

Literature cited

Amano, T., González-Varo JP, Sutherland WJ (2016) Languages Are Still a Major Barrier to Global Science. PLoS Biol 14(12): e2000933

Barton, K. 2013. MuMIn: multi-model inference. http://cran.r-project.org/web/packages/MuMIn/index.html.

Bates, D., Maechler, M., Bolker, B. & Walker, S. 2014. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7.

Benkman, C.W. (1993) Logging, Conifers, and the Conservation of Crossbills, Conservation Biology, 7(3) 473-479.

Burnham, K.P. & Anderson, D.R. 2004. Multimodel inference- understanding AIC and BIC in model selection. Sociological Methods & Research, 33:261-304.

Borenstein, M., Hedges, L.V., Higgins, J.P.T., Rothstein, H.R. 2009. Introduction to meta-analysis. John Wiley & Sons Ltd, New York.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P. et al. (2012) Biodiversity loss and its impact on humanity. Nature, 486, 59–67.

Chazdon, R. 2008. Beyond Deforestation: Restoring Forests and Ecosystem Services on Degraded Lands. Science, 32:1458-1460.

Curran, M., Hellweg, S. Beck, J. 2014. Is there any empirical support for biodiversity offset policy? Ecological Applications, 24:617-632.

Currie, W.S., Bergen, K.M. (2008) Temperate Forest. In *Ecosystem Ecology.* SE. Jorgenson, (eds). Elsevier, Amsterdam.

Doncaster, C.P. Spake, R. 2017. Correction for bias in meta-analysis of little-replicated studies. Methods in Ecology and Evolution. 9:634-644.

Forestry Agency (2009) State of Japan's Forests and Forest Management. Ministry of Agriculture, Forestry and Fisheries, Tokyo.

Forestry Agency. (2017). Annual Report on Forest and Forestry in Japan Fiscal Year 2017. Retrieved from http://www.rinya.maff.go.jp/j/kikaku/hakusyo/29hakusyo/index.html

Gerstner, K., Moreno-Mateos, D., Gurevitch, J., Beckmann, M., Kambach, S., Jones, H.P. and Seppelt, R. 2017. Will your paper be used in a meta-analysis? Methods in Ecology and Evolution. doi:10.1111/2041-210X.12758

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-.

Gill, R.M.A. (1992) A review of damage by mammals in North temperate forests. 3. Deer. Forestry, 65, 145–169.

Gotelli, N.J., Colwell, R.K. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters, 4:379–391.

Halme, P., Toivanen, T., Honkanen, M., Kotiaho, J.S., Monkkonen, M., Timonen, J. 2010. Flawed Meta-Analysis of Biodiversity Effects of Forest Management. Conservation Biology, 24:1154-1156.

Hedges, L.V., Gurevitch, J., Curtis, P.S. 1999. The meta-analysis of response ratios in experimental ecology. Ecology, 80:1150-1156.

Heyman, E. 2010. Clearance of understory in urban woodlands: Assessing impact on bird abundance and diversity. Forest Ecology and Management. 260:125-131.

Higuchi, H., Primack, R.B. 2009. Conservation and management of biodiversity in Japan: An introduction. Biological Conservation, 142:1881-1883.

Hilmers, T., Friess, N., Bässler, C., Heurich, M., Barandl, R., Pretzsch, H., Seidl, R., Müllerm J. (2018) Biodiversity along temperate forest succession. Journal of Applied Ecology, DOI: 10.1111/1365-2664.13238.

Humphrey, J.W. 2005. Benefits to biodiversity from developing old-growth conditions in British upland spruce plantations: a review and recommendations. Forestry, 78:33-53.

IPBES 2012. Japan Satoyama Satoumi Assessment (JSSA). Catalogue of Assessments on Biodiversity and Ecosystem Services. Available at: http://catalog.ipbes.net/assessments/62

Inoue, T. 2005. Causes of butterfly decline in Japan. Japanese Journal of Entomology, 8:43-64.

Kirby, K.J. & Watkins, C. 1998. The Ecological History of European Forests. CAB International, Wallingford, UK.

Koh, L. P. and T. A. Gardner 2010. Conservation in human-modified landscapes. In: Conservation biology for all. N. S. Sodhi and P. R. Ehrlich (Eds). Oxford, Oxford University Press. Pp. 236-261.

Lajeunesse, M.J. 2016. Facilitating systematic reviews, data extraction, and meta-analysis with the metagear package for R. Methods in Ecology and Evolution, 7:323-330.

Lindenmayer D, Messier C, Paquette A, Hobbs RJ 2015. Managing tree plantations as novel socioecological systems: Australian and North American perspectives. Canadian Journal of Forest Research 45:1427–1433

Macdonald, E. Gardiner, B., Mason, W. (2010) The effects of transformation of even-aged stands to continuous cover forestry on conifer log quality and wood properties in the UK. 83, 1–16.

Magurran A.E. (2004) Measuring biological diversity. Blackwell, Oxford

Martin, P.A., Newton, A.C., Bullock, J. M. 2013. Carbon pools recover more quickly than plant biodiversity in tropical secondary forests. Proceedings of the Royal Society B-Biological Sciences, 280: DOI: 10.1098/rspb.2013.2236.

Masaki, T., Mori, S., Kajimoto, T., Hitsuma, G., Sawata, S., Mori, M., Osumi, K., Sakurai, S., Seki, T. 2006. Long-term growth analyses of Japanese cedar trees in a plantation: neighborhood competition and persistence of initial growth deviations. Journal of Forest Research, 11:217-225.

Mayerhofer, M.S., Kernaghan, G. & Harper, K.A. 2013. The effects of fungal root endophytes on plant growth: a meta-analysis Mycorrhiza 23:119.

Mori A.S., Lertzman, K., Gustafsson, L. (2017) Biodiversity and ecosystem services in forest ecosystems: a research agenda for applied forest ecology. Journal of Applied Ecology 54: 12-27.

Müllerová, J., Hédl, R., Szabó, P. 2015. Coppice abandonment and its implications for species diversity in forest vegetation. Forest Ecology and Management, 343:88-100.

Nagaike, T. 2012. Review of plant species diversity in managed forests in Japan. ISRN Forestry, http://dx.doi.org/10.5402/2012/629523 (Article ID 629523).

Norden, B. & Appelqvist, T. 2001. Conceptual problems of Ecological Continuity and its bioindicators. Biodiversity and Conservation, 10:779-791.

Nakagawa, S. & Schielzeth, H. 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods in Ecology and Evolution, 4:133-142.

Payn,T., Kollert, W., Liu, S., Rodriguez, L., Neves-Silva, L., Wingfield, M., MichelCarnus, J., Orazio, C., Freer-Smith, P., 2015. Changes in planted forests and future global implications. For. Ecol. Manage. 352:57–67.

Peters, D. P. C., Bestelmeyer, B. T. & Turner, M. G. (2007) Cross-scale interactions and changing pattern-process relationships: Consequences for system dynamics. Ecosystems 10, 790–796.

Pullin, A., Stewart, G.B. (2006) Guidelines for Systematic Review in Conservation and Environmental Management. Conservation Biology, 20:1647-1656

Putz, F.E., Zuidema, P.A., Synnott, T., Pena-Claros, M., Pinard, M. A., Sheil, D., Vanclay, J.K., Sist, P., Gourlet-Fleury, S., Griscom, B., Palmer, J. & Zagt, R. 2012. Sustaining conservation values in selectively logged tropical forests: the attained and the attainable. Conservation Letters, 5:296-303.

R Core Team 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.

Shibuya, S., Kubota, K., Kikvidze, Z., Ohsawa, M., 2008. Differential sensitivity of ground beetles, Eusilpha japonica and Carabidae, to vegetation disturbance in an abandoned coppice forest in central Japan. Eurasian Journal of Forest Research, 11:61–72.

Spake, R., Martin, P.M., Ezard, T.H.G., Newton, A.C., Doncaster, C. P. 2015. A meta-analysis of functional group responses to forest recovery outside of the tropics. Conservation Biology. 29:1695-703.

Spake, R., Doncaster, C.P. 2017. Use of meta-analysis in forest biodiversity research: key challenges and considerations. Forest Ecology and Management, 40:429-437.

Spake, R., Bellamy, C., Graham, L.J., Watts, K., Norton, L.R., Wood, C.M., Schmucki, R., Bullock, J.M., Eigenbrod, F. (2019) *Nature Sustainability*, in press.

Suzuki, W., Suzaki, T., Okumura, T., Ikeda, S, 2005. Aging induced development patterns of *Chamaecyparis obtusa* plantations. Journal of the Japanese Forestry Society, 87;27–35.

Takasaki T., Takenaka, C., Yoshida, T. (2010) The effect of thinning on the community structure and densities of soil animals in a Chamaecyparis obtusa plantation. Journal of the Japanese Forest Society, 92:67-170.

Takeuchi, K. 2010. Rebuilding the relationship between people and nature: the Satoyama Initiative. Ecological Research, 25:891-897.

Tamura, A., Yamane, M. 2017. Response of understory vegetation over 10 years after thinning in an old-growth cedar and cypress plantation overgrazed by sika deer in eastern Japan. Forest Ecosystems, 4:1. DOI: 10.1186/s40663-016-0088-

Totman, C. 1989. The green archipelago: forestry in pre-industrial Japan. Ohio Univ Press, Athens.

Toyoshima, Y., Yamaura, Y., Yabuhara, Y., Nakamura, F. (2013). A preliminary study on the effects of line and selective thinning on bird communities in Hokkaido, northern Japan. Journal of Forestry Research, 24:553-559.

Verschuyl, J., Riffell, S., Miller, D., & Wigley, T. B. (2011). Biodiversity response to intensive biomass production from forest thinning in North American forests-a meta-analysis. Forest Ecology and Management, 261(2), 221–232.

Viljur, M-L., Teder, T. 2016. Butterflies take advantage of contemporary forestry: Clear-cuts as temporary grasslands. Forest Ecology and Management, 376:118-25.

Yamaura, Y., Amano, T., Kusumoto, Y., Nagata, H., Okabe, K. (2011) Climate and topography drives macroscale biodiversity through land-use change in a human-dominated world. Oikos, 120:427-451.

Yamaura, Y., Oka, H., Taki, H., Ozaki, K., Tanaka, H. 2012. Sustainable management of planted landscapes: lessons from Japan. Biodiversity and Conservation, 21:3107-3129.

Tables

Table 1. Descriptors of treatment and control groups used in our systematic review of the impact of four forest management interventions on biodiversity in Japan.

Management intervention	Treatment group	Control group	Moderator variables considered in quantitative synthesis
Plantation forest			
Thinning	Thinned plantation	Unthinned plantation	Taxon, stand age, taxon, thinning intensity, canopy dominant, thinning intensity.
Extended rotation cycles (stand age)	Young plantation (1-50 years, median age 21 years)	Overmature plantation beyond economic felling age (typically >65 years)	Taxon, treatment stand age, canopy dominant.
Secondary forests			
High intensity traditional management of secondary forests (stand age)	Secondary forests regenerating from stand-level clearance such as through coppicing	Unmanaged secondary forest that has not been cleared for >100 years	Taxon, treatment stand age, canopy dominant
Lower intensity traditional management of natural and secondary forests	Natural or secondary forest that has undergone recent thinning, understory removal and/or litter removal.	Recently unmanaged or “abandoned” secondary or natural forest	-

Figure legends and embedded figures

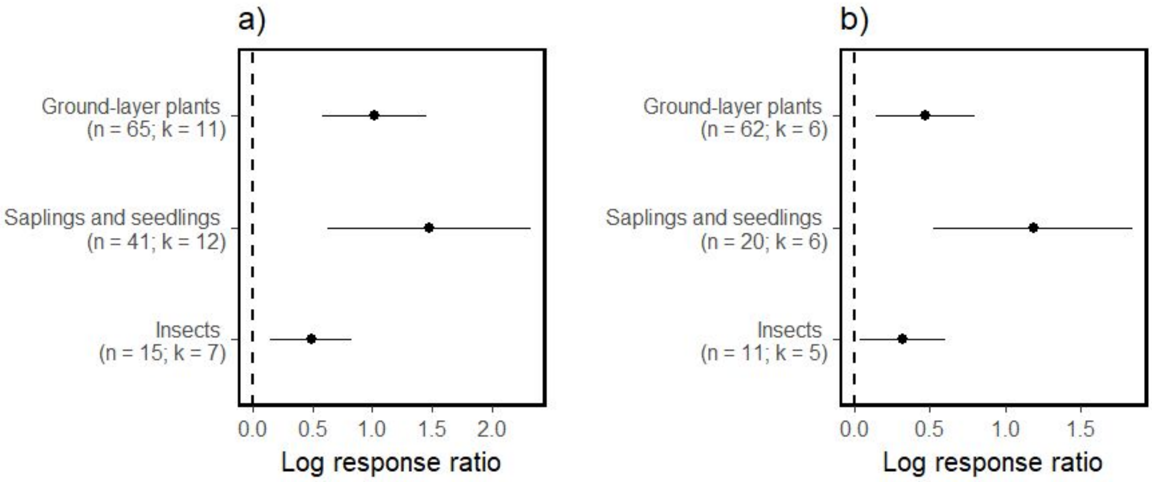

Figure 1. Summary mean effects and confidence intervals of plantation thinning on a) abundance and b) species richness of biotic communities, from *n* studies at *k* study sites.

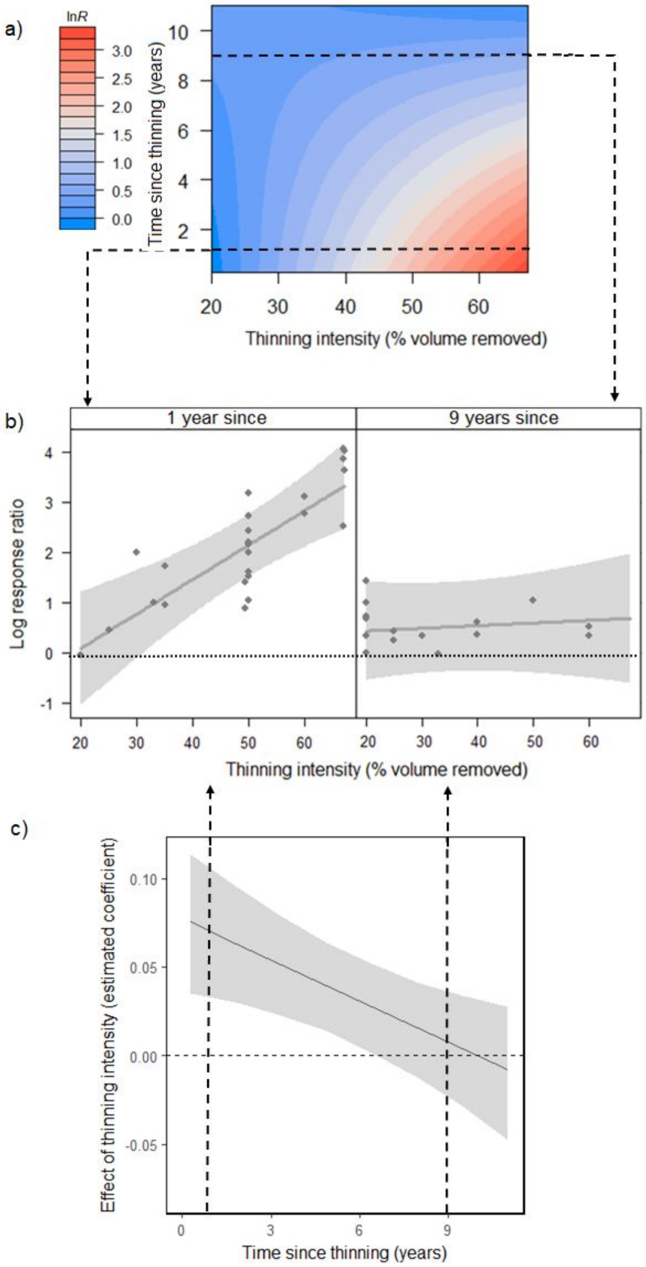

Figure 2. Impacts of plantation thinning on abundance of saplings and seedlings as dependent on time since thinning. a) Countour plot showing abundance differences (ln*R*) between thinned and unthinned forest stands as a function of thinning intensity and time since thinning. Dashed arrows point to sections through the plot at 1 and 9 years, illustrated in part b below. b) Influence of thinning intensity on abundance differences at 1 and 9 years since thinning, showing grey-shaded 95% CI in the regression based on between-study uncertainty in fixed effects only; values above horizontal dotted line signify higher abundance in thinned than unthinned stands. c) Marginal effect of thinning intensity, conditional on years since thinning; shading as for part b. Dashed arrows at 1 and 9 years show effects corresponding to response ratios in part b above. No effect of thinning intensity is detectable after six years. Regression used coefficients of the minimum adequate model.

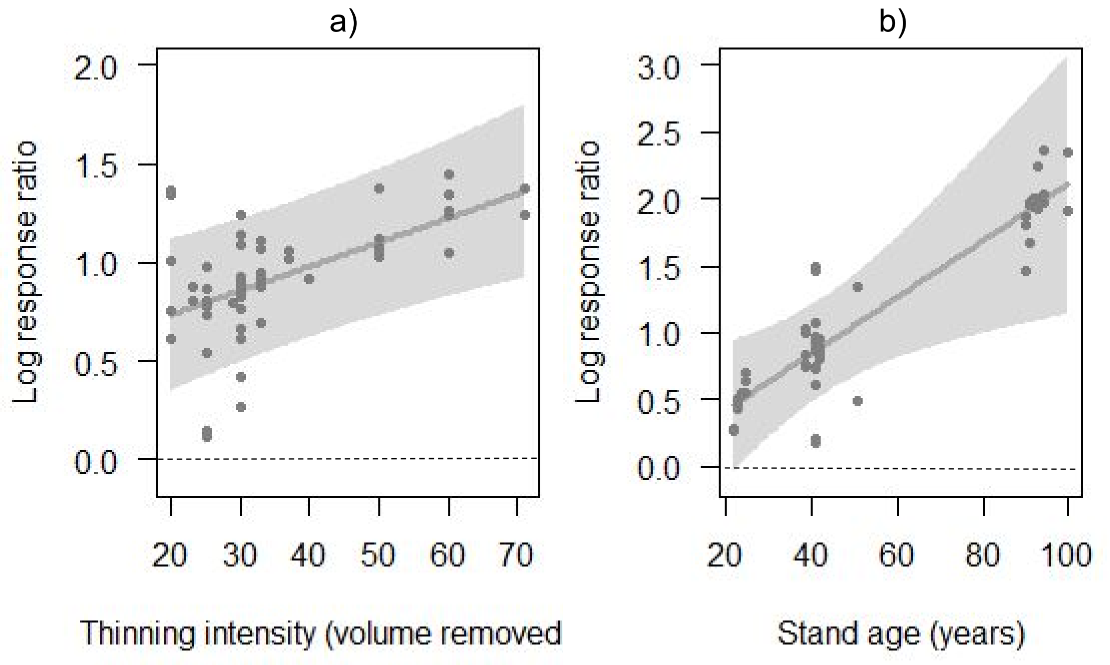

Figure 3. Influence of a) thinning intensity and b) stand age on abundance differences between thinned and unthinned plantation stands for understorey plants (horizontal dashed line means no difference). Regression used coefficients of the minimum adequate model. Grey shading shows 95% prediction intervals based on between-study uncertainty in fixed effects only.

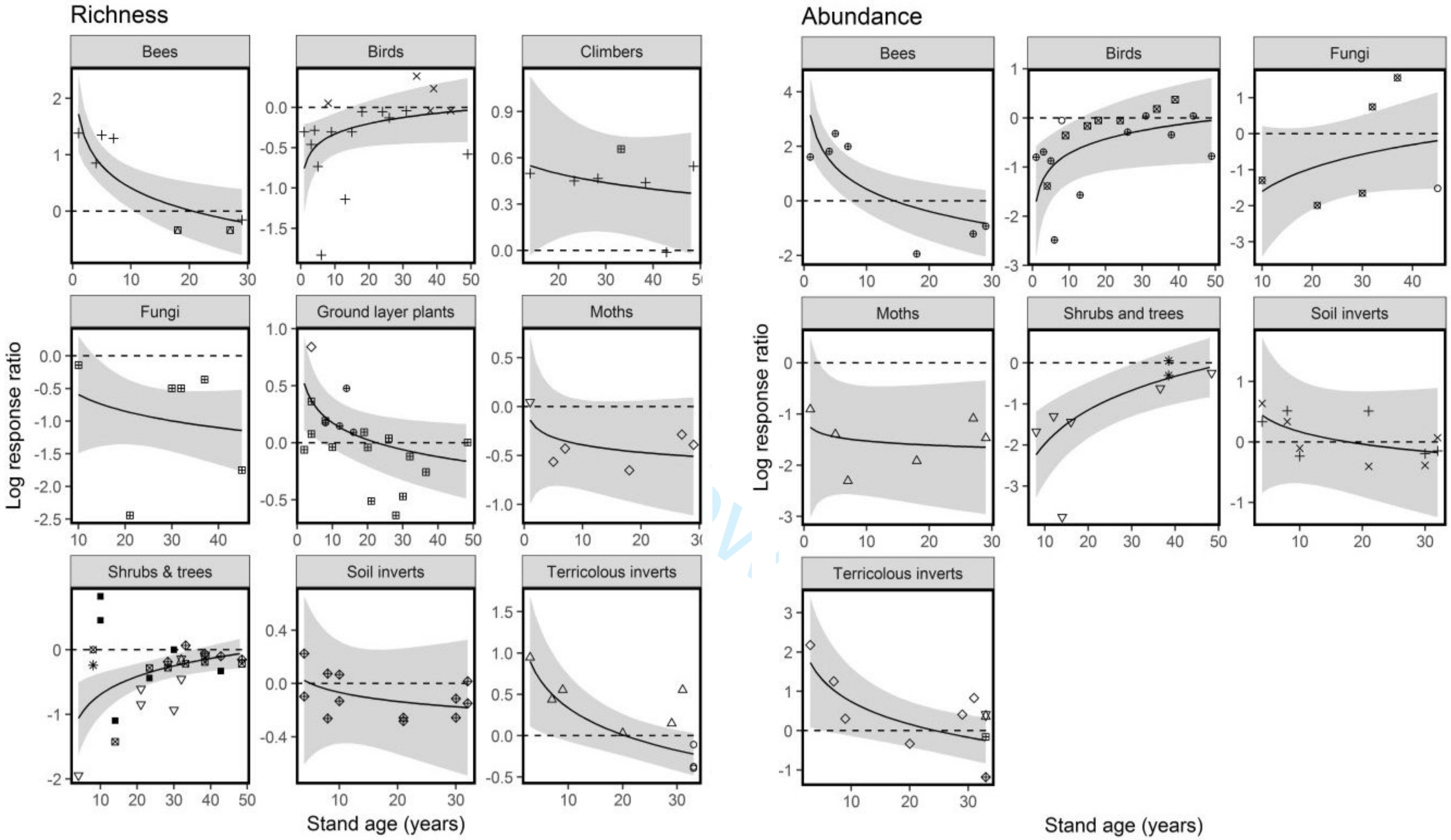

Figure 4. Influence of stand age on species richness and abundance effect sizes in planted stands relative to extended rotation planted stands. The horizontal dashed lines reference zero difference between extended rotation and younger treatment forest stands. Regressions used coefficients of the minimum adequate model. Grey shading shows 95% prediction intervals based on between-study uncertainty in fixed effects only. Different symbols correspond to different publications.

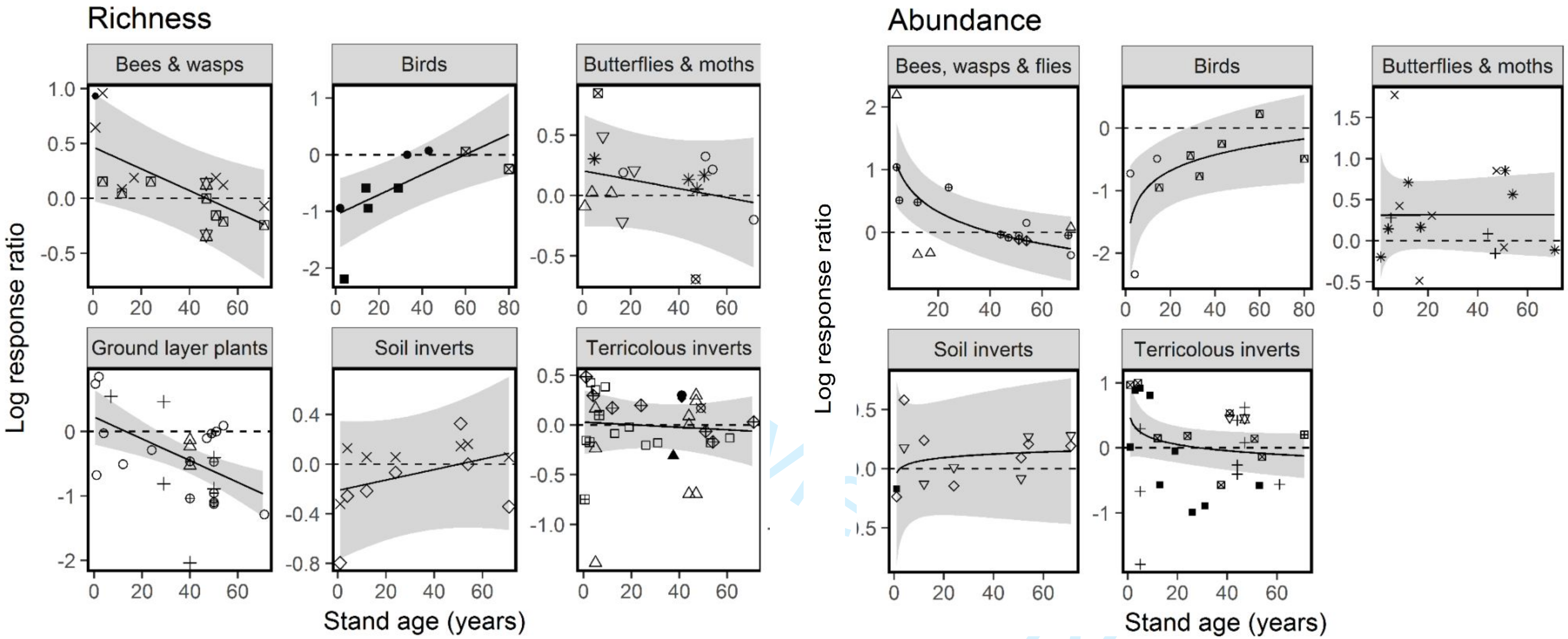

Figure 5. Influence of stand age on species richness effect sizes in younger secondary forest stands relative to older (>100-yr) abandoned forest stands. The horizontal dashed lines reference zero difference between extended rotation and younger treatment forest stands. Regressions used coefficients of the minimum adequate model. Grey shading shows 95% prediction intervals based on between-study uncertainty in fixed effects only. Different symbols correspond to different publications.

Abstract

Conservation of temperate forest biodiversity has historically focused on natural old-growth. Less than 3% of the world's temperate forests remain unmodified by humans, however, and much of temperate-forest biodiversity is held in the predominating planted and secondary forests. Japan provides a widely applicable model for examining how to maximize biodiversity in managed temperate forests, due to its richness of forestry research generated from its vast forest area, albeit largely in Japanese, and the wide practice of its dominant management interventions across the northern temperate zone. Management for plantations include thinning, extended rotation cycles and clear-cutting. For secondary forests regenerating from past clearance, traditional management varies in its intensities, from clear-cutting as coppices to small-scale understorey clearance. Here we provide a first synthesis of published research on biodiversity in planted and secondary forests of Japan, relevant to management of these types of forest in northern temperate forests. Systematic review and meta-analyses of papers published in English and Japanese quantified management impacts on species richness and abundance of several taxa, in relation to moderator variables including stand age and management intensity. Plantation thinning substantially increases the richness and abundance of several taxa. Effect sizes decline with time since thinning for the abundance of regenerating saplings and seedlings, necessitating repeated thinning treatments every six years to sustain this positive effect. Taxonomic groups exhibit variable relationships with stand age in both planted and secondary forests, indicating a need to include both young and old forest stands in managed forest mosaics. We find an insufficient evidence base is available to allow for a meaningful synthesis of low intensity management effects in historically managed secondary forests, with studies varying widely in scale and reported outcomes. We outline an agenda for the research community to achieve a systematic evaluation of scale-dependent effects of traditional forest management on biodiversity.

Introduction

Natural old-growth forests are considered irreplaceable biodiversity resources due to their long continuity and high structural diversity (e.g. Gibson et al. 2011). Whilst their strict protection represents a conservation priority in the face of forest loss and degradation worldwide, the biodiversity potential of disturbed planted and secondary forests is widely acknowledged (Putz et al., 2012). Empirical studies measuring biodiversity in forests under varying intensities of disturbance have proliferated in recent decades (Spake & Doncaster, 2017). Although several syntheses of this vast literature exist, they have limited potential for practicable recommendations across a range of contexts, due to their tendency towards narrative synthesis over quantitative meta-analysis and to focus on charismatic taxa and tropical regions (Spake et al. 2015), or their inclusion of studies published only in English (Amano et al. 2016). Human-disturbed forests particularly merit valuation in the temperate zone, where planted and secondary forests predominate following millennia of exploitation, to the extent that only 1-2% of natural old-growth forest remains intact in unharvested remnants (Currie & Bergen, 2008). Existing quantitative syntheses, however, typically measure the biodiversity value of disturbed forests by their comparison to natural, old-growth forests as a reference. This conventional set up yields inference of limited practicable value to managers and conservationists in temperate nations where little old-growth remains, and has resulted in the exclusion of much research from pan-global syntheses (Spake & Doncaster, 2017). Consequently, the efficacy of forest management practices for biodiversity conservation remains poorly understood for much of the temperate zone (Lindenmayer et al. 2015).

The Strategic Plan for Biodiversity 2011-2020 and Aichi Biodiversity Targets, adopted by the Convention on Biological Diversity in 2010 explicitly advocate implementing conservation measures within planted and secondary forests. Planted forest area is increasing globally, having risen from 4% to 7% of total forest area between 1990 and 2015. The largest increases have occurred in the temperate zone, and regionally in East Asia, Europe and North America, for diverse purposes including production, soil protection and carbon sequestration (Payn et al. 2015). Plantations generally lack the continuity and structural attributes typical of old-growth forests, giving rise to the moniker of ‘green deserts’ (Koh and Gardner 2010); however, their habitat quality can vary in relation to management activities (Humphrey, 2005). Aichi Target 7 advocates their sustainable management in support of biodiversity. Principal management interventions for enhancing biodiversity in temperate plantations include disturbance by stand thinning to enhance the natural regeneration of native trees, and rotation age extension, on the premise that many species are dependent on later successional stages (Spake et al. 2015).

Aichi Target 15 calls for the restoration at least 15% of degraded areas through conservation and restoration activities. Secondary forests arise from both assisted restoration, and unassisted forest regeneration following human disturbance or land abandonment (Chazdon, 2008). Several options are available for their management, with traditional management receiving mounting interest due to potential benefits for biodiversity, biomass, and climate change mitigation (Müllerová et al. 2015). Throughout the northern temperate zone, broadleaved forests that border human settlements have been managed over millennia for fuelwood, fertiliser and food (Takeuchi, 2010). Stands of trees were cut in rotations of 15-30 years, while less intensive practices included litter removal, understorey clearance and tree thinning to provide fertiliser, fuel, livestock feed and bedding (Kirby & Watkins, 1998). Worldwide, traditional secondary forest management largely ceased during the mid-1900s, as fossil fuels and chemical fertilisers become widely available (Kirby & Watkins, 1998). Abandonment of traditional management is widely regarded as a driver of biodiversity loss, due to reduced habitat suitability for early successional species requiring open habitats or vegetation structures that are reduced under heavy shade (Takeuchi, 2015). Interest is mounting in a return to traditional management at varying intensities across the temperate zone for ‘abandoned’ public, private and even protected forests. For example, the global Satoyama Initiative (http://satoyama-initiative.org/), launched concurrently with the Strategic Plan for Biodiversity in 2010, advocates the value of traditional management not only in Japan but globally. Moreover, understorey clearance is traditionally practiced in urban woodlands in Europe and Japan, in compliance with recreational and aesthetic values (Heyman, 2010).

The nation of Japan provides a valuable opportunity to assess the impacts of planted and secondary forest management on biodiversity in the northern temperate zone (Appendix A). Forest covers approximately 25 million hectares in Japan, constituting two thirds of the total land area (Forestry Agency, 2009), but very little is pristine (Yamaura et al. 2012). Plantations occupy more than 40% of total forest area, principally as monocultures of Japanese cedar (*Cryptomeria japonica*), Hinoki cypress (*Chamaecyparis obtusa*), and larch (*Larix kaempferi*), with the rest comprising secondary forests dominated by evergreen and deciduous oaks (*Quercus* sp.), and red pine (*Pinus densiflora*), naturally regenerating from past coppicing and selective cutting at varying intensities (Forestry Agency, 2009). Japan’s vast forest area and interest in conservation has generated copious empirical research on biodiversity responses to forest management interventions (Higuchi & Primack, 2009). The northern temperate forestry community stands to benefit from a synthesis of this rich literature, due to the wide practice and history throughout the temperate zone of management interventions exemplified by Japanese forest management. For example, just as for Japan the majority of Central European forests are restricted to mountain areas, and have been exploited by clearcutting and coppicing for millennia (Hilmers et al. 2018; Washitani, 2003). Interest in the revival of active management within ‘abandoned’ secondary forests is increasing in Japan, as also in the UK and Europe (Takeuchi, 2003), while clearcutting of plantations that predominates in North America and northern Europe (Rosenvald and Lohmus, 2008) is also increasing in Japan amidst plans to increase domestic wood supply (Forest Agency, 2017). Effective conservation strategies for temperate forests experiencing such a range of disturbance intensities require a comprehensive and quantitative understanding of how different trophic groups vary across a wide range of successional stages and management intensities (Hilmers et al. 2018). With its forests at various successional stages following a diversity of management practices, Japan's empirical literature offers the possibility of such understanding. Many of Japan's forestry studies, however, are published only in Japanese (Nagaike, 2012), reflecting the major barrier that language still presents to the global compilation and application of scientific knowledge (Amano et al. 2016). Indeed, given the extent of its forest area and richness of empirical research, it is apparent that Japanese studies are underrepresented in synthetic studies of forest management impacts. Although several narrative syntheses exist (Inoue, 2005; Nagaike, 2012; Yamaura et al., 2012), a robust systematic and quantitative synthesis is lacking.

Here we synthesise and quantitatively assess the effects on biodiversity of coniferous and broadleaved forest management practices in Japan which are widely promoted to conserve biodiversity across the northern temperate zone. Specifically, we examine impacts on the species richness and abundance of a range of taxonomic groups from four management interventions: i) plantation thinning; ii) extended rotation cycles (plantation age); iii) traditional management of secondary forests (secondary forest age); and iv) lower intensity traditional management of natural and abandoned secondary forests (thinning, understory clearance and/or litter removal). By synthesising the Japanese forestry literature published in English and Japanese, we aim to provide practicable recommendations to inform policy-making in Japan, and to similarly managed forests across the northern temperate zone, due to the wide practise of the management interventions we synthesise.

Materials and methods

Literature search and data extraction

We followed standard systematic review methods (Pullin and Stewart, 2006) to collate published empirical studies on the focal management interventions. Following recommendations of Amano et al. (2016), we conducted extensive literature searches in both English and Japanese, using Web of Science, Google Scholar and J-Stage (the largest platform for publishing electronic journals in Japan; https://www.jstage.jst.go.jp/). We sought studies conducted in Japan using search terms relating to the country, forest management interventions, and biodiversity (search queries in Appendix B). Additional literature was identified by 'snowballing': searching for references within retrieved articles and reviews. We used the R package 'metagear' (Lajeunesse, 2016), to screen retrieved abstracts.

Relevant studies compared biodiversity in planted or secondary forest with appropriate controls, given in Table 1. In order to produce data relevant to the management decisions affecting forest management actions in Japan and the rest of the temperate zone, we compared the biodiversity value of forests in their current state (control groups of low disturbance relative to treatment groups), compared to a plausible alternative state (treatment groups of managed forests; Table 1; Spake & Doncaster, 2017). Species richness was used as a proxy for biodiversity, being most widely used biodiversity measure (Magurran, 2004). We note here that authors measuring "species richness" in primary studies were actually measuring species density, the number of species per unit area (Gotelli and Colwell, 2001), wherein richness is standardized against area or sampling effort across treatments. We use the term species richness to avoid confusion with abundance, which is often measured as density (number of individuals per unit area). We evaluate the implications of this diversity metric in our discussion.

Meta-analysis of plantation thinning effects on biodiversity

To ensure meaningful comparisons across studies, we sought publications that compared thinned treatment to unthinned control stands with the same canopy dominant and age. For each comparison of species richness and/or abundance, the effect size of log response ratio (ln$R$) was calculated, as:

$$lnR = ln\,(\bar{x}_T) - ln\,(\bar{x}_C)\ , \qquad (1)$$

where $\bar{x}_T$ is the mean species richness or abundance in treatment forest stands and $\bar{x}_C$ is the mean value for control stands. The ln$R$ describes the proportional difference in species richness or abundance between control and treatment groups. The natural log transformation of the response ratio linearizes the metric, treating deviations in the denominator and the numerator as equal, and normalises its otherwise skewed distribution (Hedges et al., 1999). Abundance measures included values of cover, biomass, and number of individuals. If an article reported single abundance values for a number of different species within the same taxonomic group (e.g. within understorey plants), we calculated the combined effect size for the group (Borenstein et al. 2009).

We extracted data on the following moderator variables: taxon (understory plants, saplings and seedlings, invertebrates), thinning stand age, years since thinning and thinning intensity (percentage volume of trees removed). We used linear mixed models to investigate variation in effect size with the moderator variables. We included quadratic or $\log_{10}$ relationships with thinning intensity to test for possible nonlinear relationships. Study quality varied widely regarding replication and spatial interspersion of treatments. Meta-analyses conventionally weight effect sizes by the inverse of study variance to account for differences in sampling effort. With forest biodiversity studies however, the variance of replicate means is often i) unreported, ii) unavailable because sample size is one, or iii) not meaningful because studies varied widely in their design, with a high prevalence of pseudoreplicated designs (Spake and Doncaster, 2017). We accounted for differences in study quality by weighting effect sizes based on their true sample sizes, following Mayerhofer et al. (2013) and Doncaster and Spake (2017), with the relative weights estimated as:

$$wt = (N_C N_T)/(N_C + N_T)\ , \qquad (2)$$

where N_C and N_T are the true sample sizes of the unthinned control and thinned treatments, respectively, identifying the number of spatially interspersed replicates of forest treatments (Halme et al. 2010). See Appendix C for this weighting rationale.

Where articles reported separate values for two or more study locations, canopy dominants or taxonomic groups, we regarded each as an independent observation. Study was included as a random effect to accommodate studies with multiple effect-size estimates based on a common control stand. Just one study was omitted from the abundance analysis, due to a zero abundance that precluded calculation of a response ratio. All possible additive models were constructed by maximum likelihood methods using packages lme4 (Bates et al., 2014), and MuMIn (Barton, 2013). Akaike's Information Criterion (AIC) with small sample correction (AICc) was used to identify a candidate set (Burnham and Anderson, 2004). We performed model averaging when multiple models were plausible (ΔAICc < 4), but selected a single model if the next best model had ΔAICc > 4. Goodness of model fits was estimated by the marginal R^2 (Nakagawa and Schielzeth, 2013).

Meta-analysis of extended rotation cycles for plantations and high-intensity traditional management of secondary forest

Studies investigating the impact of extended rotation cycles typically measure biodiversity in plantations of varying ages (Appendix D). Studies investigating the impact of high intensity traditional management typically measure secondary stands of varying ages following clearance (Appendix E). We here define secondary forests *sensu lato* as any forests regenerating naturally from a stand-level clearance event, following high intensity coppicing or clearcutting. For plantations, we included studies that used a control group of overmature plantations beyond 50 years of age (median reference stand age: 76 years), reflecting the Japanese convention to harvest at ~50 years old (Forestry Agency, 2017). For traditional secondary forests, we included studies that used at least one reference stand exceeding 100 years in age (median age: 128 years).

Whilst all studies of stand age-biodiversity relationships included a common reference stand, studies varied in treating stand age as either a continuous or categorical variable. When treated as continuous, researchers sampled forest plots across a stand-age gradient, whereas when treated as categorical, researchers sampled plots replicated within grouped age classes. We therefore adopted the meta-analytical approach of previous stand-age biodiversity syntheses by Curran et al. (2014) and Martin et al. (2013), which synthesised pair-wise comparisons between single treatment stands and either replicated or unreplicated reference stands. We calculated ln$R$ as the effect size for abundance and richness comparisons. We grouped taxa into the following groups: butterflies and moths, bees and wasps, terricolous invertebrates (beetles, spiders and ants sampled above the soil), soil invertebrates (collembola and mites sampled from within soil), fungi and ground-layer plants (including groups termed as vascular, shrub or herb species).

We used linear mixed models to investigate variation in effect size (ln*R*) with stand age and other moderator variables. Just one study was omitted from the abundance analysis, due to a zero abundance. Moderator variables included taxon, stand age, and their interaction. We included quadratic or $\log_{10}$ relationships with stand age to test for possible nonlinear biodiversity recovery, and we weighted by sample size as described above. Study was included as a random effect to accommodate publications with multiple effect-size estimates using a common control. To identify important moderators of effect size differences across studies, we used model selection as described above. All quantitative analyses were performed using R (R Core Team, 2017).

Review of lower intensity traditional management impacts on biodiversity in natural and secondary forests

We compiled studies that assessed the influence on biodiversity in secondary forests of traditional management practices that are lower in intensity than clearcutting in terms of the amount of biomass removed (Appendix F). Such practices include tree thinning, understorey clearance and litter removal (Shibuya et al. 2008). We selected studies that compared forest sites described as recently unmanaged, abandoned or natural to forest sites that were either currently or recently actively managed (within 20 years). To control for stand age and canopy-dominant effects on biodiversity, we sought studies with similar control and treatment stands in these attributes. Each study was described according to the following moderator variables: taxonomic group, stand age, years since management, and management type (thinning/understorey removal/litter removal) and intensity (e.g. volume of trees removed, area of understorey cleared). Descriptions of management actions were often vague, with inconsistent reporting of intensity and stand age. Insufficient replication and crossing at the level of management intervention by taxonomic group precluded meaningful quantitative summaries. We therefore synthesised these results narratively.

Results

Effects of plantation thinning on richness and abundance

Twenty-six publications were retrieved (Appendix C) comparing biodiversity in thinned and unthinned plantations, spanning a range of thinning intensities and taxonomic groups on widely distributed studies across Japan. Plantations in all but one study were planted as monocultures. One study was retrieved on birds (Toyoshima et al. 2013), and one on below-ground mite communities (Takasaki et al. 2010). Studies on insects comprised Hymenoptera, Coleoptera, Diptera and Lepidoptera. Data were sufficient for meta-analysis of saplings and seedlings, ground-layer plants and insects (pooling across Orders), totalling 65 richness and 134 abundance comparisons.

Subgroup analysis showed that plantation thinning substantially increased the richness of tree saplings and seedlings, ground-layer plants and insects by 227%, 60% and 38% respectively (P <0.05; Figure 1a). Thinning also increased abundance of the studied groups, by 330%, 177% and 63% respectively (P <0.05; Figure 1b). Effect sizes were heterogeneous amongst studies, due to study-wise variation in stand ages and thinning intensities. Collinearity between taxonomic group, stand age and thinning intensity restricted our mixed effects modelling of abundance effect sizes to broadleaved saplings and seedlings and ground-layer plants only. Moderator collinearity precluded mixed-effects analysis of species richness effect sizes. The most important predictors of sapling and seedling abundance were thinning intensity, time since thinning and their interaction (Appendix C, marginal $R^2 = 0.42$ for minimum adequate model). Impacts of thinning on abundance depended on both the volume of trees removed and time since thinning (Figure 2a). In recently thinned stands, the impacts increased linearly with increasing volume of trees removed. This effect declined with the time elapsed since thinning (Figure 2b), with no effect detectable after ~6 years (Figure 2c; Appendix C). Effect sizes of ground-layer plant abundance increased with both thinning intensity and plantation stand age, with a thinning intensity of about 66% resulting in a doubling of ground-layer plant abundance (Figure 3; Appendix C, marginal $R^2 = 0.23$ for minimum adequate model).

Effects of plantation age on species richness and abundance

We retrieved 15 publications (Appendix D) describing species richness or abundance differences between younger planted and reference overmature planted forest stands, yielding 115 richness and 68 abundance comparisons. One study was excluded from the quantitative synthesis because of its outlying age of 20-250 year-old stands (Suzuki et al. 2005). The minimum adequate models selected to explain differences in species richness and abundance between extended rotation and younger planted forest stands included taxonomic group (species richness: $F_{1,85} = 5.99$; $P < 0.001$; abundance: $F_{1,66} = 11.63$; $P < 0.001$), $\log_{10}$ stand age (species richness: $F_{1,88} = 4.11$; $P = 0.046$; abundance: $F_{1,66} = 0.02$; $P = 0.875$), and their interaction (specie richness: $F_{1,90} = 3.85$; $P < 0.001$; abundance: $F_{1,66} = 7.77$; $P < 0.001$). These models had marginal R^2 values of 0.54 and 0.55 for effect sizes of species richness and abundance respectively, and both had ΔAIC >4 to the next best model. Climbing plants, and terricolous invertebrates exhibited consistently higher species richness and abundance levels in younger planted stands than overmature planted stands, while fungi were consistently richer and more abundant in overmature stands (Fig. 4). The interaction reflects taxon-specific relationships of species richness and abundance with stand age (explaining the absence of a detectable stand-age main effect). Birds, shrubs and trees demonstrated positive relationships, whilst flying and terricolous invertebrate and ground layer plant richness had declining abundance with stand age (Fig.5). Fungi richness and abundance did not vary detectably with stand age (Fig.4).

Effects of traditional management of secondary forests on richness and abundance

We retrieved 25 publications describing species richness or abundance in secondary forest stands regenerating from clearcutting, in comparison to a reference secondary forest stand >100 years old (Appendix E), yielding 141 richness and 105 abundance comparisons. Prior to modelling the relationship between richness recovery and stand age across taxonomic groups, we removed studies on trees, epiphytic plants (climbers and vines) and Diptera, because treatment forest sites from these studies did not present a stand age gradient. For the same reason, we removed studies of ground-layer plants when modelling abundance effect sizes. The minimum adequate models selected to explain species richness and abundance differences between abandoned older and younger secondary forest contained taxonomic group (species richness: $F_{5,58} = 5.67$; $P = <0.001$; abundance: $F_{5,50} = 6.44$; $P = <0.001$), stand age (species richness: $F_{1,82} = 0.31$; $P = 0.575$; abundance: $F_{1,66} = 0.33$; $P = 0.566$), and their interaction (species richness: $F_{4,82} = 7.20$; $P = <0.001$; abundance: $F_{4,66} = 4.15$; $P = <0.01$). These models had marginal R^2 values of 0.35 and 0.38 for species richness and abundance effect sizes respectively, and both had ΔAIC > 4 to the next best model. The interaction reflects a balanced opposition of stand-age effects amongst taxonomic groups (explaining the absence of detectable main effects; Fig. 6). Flying invertebrates and ground-layer plant richness benefited from early successional conditions and declined with stand age, whilst soil invertebrates and birds exhibited lower richness levels in younger secondary forest relative to older abandoned forest and tended to increase with stand age (Fig. 6).

Effects of lower intensity traditional management of secondary forests on biodiversity

We retrieved 27 publications that investigated the impact of low intensity forest management on biodiversity by comparing unmanaged and managed forest (Appendix F). Wide variation in study variables including management intensity, taxonomic group and forest ages precluded a quantitative synthesis; we instead report the results narratively, in detail in Appendix F. Broadly, management interventions comprised tree thinning at varying intensities, understorey removal and litter removal, and various combinations of these interventions. The majority of studies were observational, with researchers selecting forest sites already subjected to management by voluntary citizens or the prefectural government for purposes including compost production, mushroom production, recreation and biodiversity conservation, with few studies performing controlled experiments (but see Shibuya et al. 2008). Studies varied widely in scale, in terms of the sizes of forest stands and the observational plots for management and biodiversity measurement (Table F1), and such scale information was typically not reported.

Discussion

Our meta-analysis of relatively large sets of published studies from Japan demonstrates that diverse stand-level factors influence the impacts on biodiversity of management interventions that are widely practised in planted and secondary forests across the northern temperate zone. Quantitative synthesis, which allows the testing of relationships between individual study outcomes and their characteristics, have allowed us to demonstrate variable and non-linear responses amongst taxa to important management covariates (time since thinning, thinning intensity, stand age). These are not typically treated by other meta-analyses, which tend simply to compare ‘managed’ and ‘unmanaged’ forests (e.g. Chaudhary et al., 2016; Paillet et al., 2010; Verschuyl et al. 2011). Broadly, our results demonstrate that both young and old stands must be present in managed forest mosaics to support multiple taxonomic groups. Our comprehensive review has revealed the need for a stronger evidence base to evaluate the impacts on biodiversity of traditional low-intensity management strategies for northern secondary temperate forests. Here we discuss the relevance of our results to forestry practitioners for maintaining biodiversity in temperate forests managed on principles similar to the Japanese model. We go on to outline an agenda for the research community if biodiversity is to be preserved effectively in these types of managed temperate forests.

Effects of plantation management on biodiversity

Under the Forest and Forestry Revitalisation Plan to increase Japan’s timber self-sufficiency (Nagasaka et al. 2016), mature plantations are increasingly subject to clearcutting in many parts of Japan including Kyushu and eastern Hokkaido. In topographically complex areas that preclude commercial management, a range of groups under municipal control, including voluntary NGOs and private companies, funded by a national Forest Environment Tax to be introduced this year (Forestry Agency, 2017), conducts plantation thinning. The aim of such management is to enhance ecosystem services that benefit the public, including watershed conservation, mitigation of climate change in addition to and biodiversity conservation, and the assisted regeneration of natural broadleaved forest (Forestry Agency, 2017). Here we discuss our results of plantation forest age and thinning impacts in biodiversity, to provide guidance to practitioners conducting such management.

Plantation thinning positively affected species richness and abundance of invertebrates, ground layer plants and saplings and seedlings (Fig.1), which is consistent with a synthesis of thinning impacts on several taxa, including birds mammals and invertebrates, in North American forests (Verschuyl et al. 2011). Thinning substantially increased sapling and seedling abundance and richness. The response of sapling and seedling abundance to thinning intensity depended on the time since thinning; effect sizes increased with thinning intensity in recently thinned plantations, but no effect of intensity was detectable in stands thinned ~6 years previously (Figure 2; Appendix C).This finding suggests repeated thinning at such intervals is required to ensure the survival of regenerated seedlings. The effect of thinning on understorey plant abundance increased linearly with stand age (Fig. 3b), demonstrating a larger effect in older stands with more closed canopies, suggesting such stands could be prioritised for thinning efforts. Effect size relationships with thinning intensity and stand age for saplings/seedlings and understorey plants did not plateau, suggesting an absence of generally applicable thresholds for maximising positive effects on species richness or abundance.

Our explanatory power was low for models explaining understorey abundance with thinning intensity and stand age, and previous research has shown that thinning resulted in almost no increase in understory vegetation. Such instances are attributed to grazing by deer (Tamura and Yamane, 2017), and so the effectiveness of thinning in Japan and other northern temperate nations that similarly are experiencing high deer densities (Cote, 2004), will likely depend on local deer densities and grazing management.

Timber harvesting in Japan has conventionally used a rotation age of between 40 and 60 years (Masaki et al. 2006), similar to other northern temperate nations (Benkman, 1993; Macdonald et al. 2010). However, extended rotation ages >70 years are becoming increasingly widespread, to hedge against fluctuations in timber prices with a larger, more valuable stock (Masaki et al. 2006). This review has shown that the richness and abundance of birds, shrubs and trees increases nonlinearly with planted stand age (Fig. 5), likely attributable to the combined effects of time favouring colonisation by dispersal-limited species, and structural diversification as forests age (Norden and Appelqvist, 2001). The richness of several taxonomic groups, including ground-layer plants and soil and terricolous invertebrates, declined with stand age, however. With different taxonomic groups exhibiting contrasting species richness levels in different successional stages, our results from Japan support recommendations for both young and old forest stands to be included in plantation forest mosaics for invertebrate and ground-layer plant conservation (Viljur and Teder 2016).

We note that low sample sizes for some taxonomic groups led to low precision in effect sizes for these groups, including the climbing plants, moths and fungi. Although functional groups within broad taxonomic groupings vary in their responses to forest management impacts (Spake et al. 2015), low sample sizes forced their grouping into broad taxonomic classifications, which may have obscured differences in responses of finer classifications. Richness and abundance relationships with stand age revealed little difference between the biodiversity value of 50- and ~70-year-old (control) plantations. Extending the conventional rotation age to > 70 years may therefore not offer a win-win for economic return and biodiversity conservation. However, it is important to understand patterns of biodiversity variation beyond 70 years, because a large quantity of planted stands are likely to remain unharvested in Japan. We retrieved one study of hinoki cypress plantations from 20 to 250 years old. Suzuki et al. (2005) found that stands >200 years old differed in species compositions to stands <100 years-old, having developed multi-layered canopies with broadleaved species occupying the lower canopy. The authors state that canopy openings were a product of both past logging and natural stand dynamics, and suggest that much older planted forests stands may require thinning.

Effect of traditional secondary forest management on biodiversity

The Satoyama Initiative promotes the revival of traditional management at a range of intensities, based on presumed benefits to biodiversity and ecosystem services (Takeuchi, 2010). This includes the return of more traditional interventions, with secondary forests managed by clear-cutting, in addition to more commonly practised contemporary interventions that include thinning, undergrowth clearance and leaf-litter removal applied at smaller extents (Shibuya et al. 2008). Contemporary satoyama management practices reflect shifting sociocultural and resource needs. Although the original primary function of satoyama was for production, interest is mounting in the value of satoyama for delivering a range of other ecosystem services. In particular, the cultural and aesthetic opportunities inherent in the woodland management process are motivating community-based management, with subsidies from municipal governments (Yokohari & Bolthouse, 2011; Tatsui & Fujii, 2007). Here we set the results of our analyses of secondary-forest management in the context of future research needs that are required to effectively guide local community groups in maintaining secondary forest biodiversity.

We have shown that species richness and abundance relationships with stand age (a proxy for high intensity traditional management) varied according to taxonomic group in secondary forests. Flying invertebrates and ground-layer plants benefited from more open, early-successional conditions and tended to decline with stand age while the abundance and richness of birds and soil invertebrates increased with stand age. Late successional secondary forests are needed to support mature forest-specialists, but are scarce in southern Japan and much of Europe due to the long history of forest usage (Totman 1989; Currie & Bergen, 2008). Our results accord with the taxon-specific responses to stand age found in Europe and

North America (Spake et al. 2015), and also suggest that managed mosaics should contain secondary forests that remain set-aside to mature.

The studies retrieved by our review of low intensity traditional management varied widely in taxonomic group (plants, invertebrates and fungi), the particular combination of management interventions and their intensity (amount of biomass removed), scale of management and study design; with positive, negative and neutral effects of management on a range of biodiversity metrics reported (Table S1). Due to this variation, it is difficult to make clear generalisations on the effect of low intensity traditional management on forest biodiversity. It can only be concluded that impacts are highly heterogeneous and context-specific, with positive, negative or neutral management effects on a range of biodiversity metrics. We therefore caution against the promotion by governments of the biodiversity value in traditional forest-management practices, such as through the Satoyama Initiative, until an understanding of the effects of scale-dependent management interventions is achieved (Spake et al. 2019). We note however, that management can provide other benefits including the enhancement of cultural ecosystem services.

Ensuring the maintenance of forest biodiversity within Japan's managed forests: a research agenda

Effect sizes were estimated from species density, as opposed to species richness, which is typically estimated by using abundance or incidence distributions to model the number of undetected species (Gotelli and Colwell, 2001). It is therefore possible that species density differences could have been partly driven by effects on overall abundance of individuals. Additionally, using species density can potentially underestimate the true biodiversity difference between e.g. >100-year-old secondary and younger secondary forests; higher intrinsic richness in older forests could lead to a systematic under-sampling bias that misses more species per site than in younger secondary sites when sampling is standardised by area or sampling effort (Spake and Doncaster, 2017). Moreover, use of species density or richness alone does not account for compositional differences between forest stands, and ignores the incidence of rare or functionally important species, and important attributes such as invasiveness. Much research into biodiversity–ecosystem functioning relationships has shown that biodiversity (including taxonomic, functional and phylogenetic diversity) affects the functioning of ecosystems (e.g. primary production, decomposition, nutrient cycling, trophic interactions and so on) and consequently a range of ecosystem services (e.g. food production, climate regulation, pest control, pollination etc; Cardinale et al. 2012). An important next step is to use biodiversity data from forests to give practical advice for enhancing ecosystem functioning and ecosystem services (Mori et al., 2017).

The studies included in our meta-analysis varied widely in scale, in terms of the size of the individual sampling plots (grain), the area of inference represented by each data point (e.g. whether a forest stand), the scale at which a mean is calculated (the focus), and the size of the study area (extent; Gerstner et al., 2017). While grain was frequently reported, focus and extent were often missing, or descriptions did not allow clear distinctions among the spatial scale components, precluding an analysis of the scale-dependence of effect sizes. We follow Gerstner et al. (2017) in urging studies to report such information in the future to allow for an understanding of the importance of management and study scale of the effects of forest management on biodiversity. We see a need for researchers to conduct more systematic field studies of the impacts of different traditional management practices on biodiversity across Japan. This can be achieved by evaluations of practices piecemeal (thinning, understorey clearance and litter removal), and in combination across a network of well-replicated sites across Japan. There is a particular need to consider and report the extent of the area managed, and the effect of the intensity of management practices (e.g. volume of trees removed), so that thresholds may be identified to guide management practices.

It is conceivable that climate could moderate forest management impacts on biodiversity. For example, the importance of plantation thinning for increasing sapling abundance could depend on variables such as temperature and solar radiation, with a certain level of canopy cover required to buffer against climatic extremes. Testing for both additive and interactive effects of climatic variables on effect sizes (management impacts) would require a larger sample size than is currently available, and represents a future research opportunity for Japan.

In conclusion, we call for a coordinated research agenda to achieve a systematic evaluation of traditional management impacts, at a range of intensities and scales, on forest biodiversity and ecosystem functioning in Japan. Future studies of all forests should measure community attributes other than species richness that capture ecosystem function, in addition to reporting attributes of scale and the topographic and regional climatic context, to permit testing for interacting effects. Japan presents an ideal opportunity to test for such cross-scale interactions (Peters et al. 2007), due to its wide climatic and topographic gradients that could potentially modify biodiversity responses to the management of its vast forest estate (Yamaura et al. 2011; Spake et al. 2019).

Literature cited

Amano, T., González-Varo JP, Sutherland WJ (2016) Languages Are Still a Major Barrier to Global Science. PLoS Biol 14(12): e2000933

Barton, K. 2013. MuMIn: multi-model inference. http://cran.r-project.org/web/packages/MuMIn/index.html.

Bates, D., Maechler, M., Bolker, B. & Walker, S. 2014. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7.

Benkman, C.W. (1993) Logging, Conifers, and the Conservation of Crossbills, Conservation Biology, 7(3) 473-479.

Burnham, K.P. & Anderson, D.R. 2004. Multimodel inference- understanding AIC and BIC in model selection. Sociological Methods & Research, 33:261-304.

Borenstein, M., Hedges, L.V., Higgins, J.P.T., Rothstein, H.R. 2009. Introduction to meta-analysis. John Wiley & Sons Ltd, New York.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P. et al. (2012) Biodiversity loss and its impact on humanity. Nature, 486, 59–67.

Chazdon, R. 2008. Beyond Deforestation: Restoring Forests and Ecosystem Services on Degraded Lands. Science, 32:1458-1460.

Curran, M., Hellweg, S. Beck, J. 2014. Is there any empirical support for biodiversity offset policy? Ecological Applications, 24:617-632.

Currie, W.S., Bergen, K.M. (2008) Temperate Forest. In *Ecosystem Ecology.* SE. Jorgenson, (eds). Elsevier, Amsterdam.

Doncaster, C.P. Spake, R. 2017. Correction for bias in meta-analysis of little-replicated studies. Methods in Ecology and Evolution. 9:634-644.

Forestry Agency (2009) State of Japan's Forests and Forest Management. Ministry of Agriculture, Forestry and Fisheries, Tokyo.

Forestry Agency. (2017). Annual Report on Forest and Forestry in Japan Fiscal Year 2017. Retrieved from http://www.rinya.maff.go.jp/j/kikaku/hakusyo/29hakusyo/index.html

Gerstner, K., Moreno-Mateos, D., Gurevitch, J., Beckmann, M., Kambach, S., Jones, H.P. and Seppelt, R. 2017. Will your paper be used in a meta-analysis? Methods in Ecology and Evolution. doi:10.1111/2041-210X.12758

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-.

Gill, R.M.A. (1992) A review of damage by mammals in North temperate forests. 3. Deer. Forestry, 65, 145–169.

Gotelli, N.J., Colwell, R.K. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters, 4:379–391.

Halme, P., Toivanen, T., Honkanen, M., Kotiaho, J.S., Monkkonen, M., Timonen, J. 2010. Flawed Meta-Analysis of Biodiversity Effects of Forest Management. Conservation Biology, 24:1154-1156.

Hedges, L.V., Gurevitch, J., Curtis, P.S. 1999. The meta-analysis of response ratios in experimental ecology. Ecology, 80:1150-1156.

Heyman, E. 2010. Clearance of understory in urban woodlands: Assessing impact on bird abundance and diversity. Forest Ecology and Management. 260:125-131.

Higuchi, H., Primack, R.B. 2009. Conservation and management of biodiversity in Japan: An introduction. Biological Conservation, 142:1881-1883.

Hilmers, T., Friess, N., Bässler, C., Heurich, M., Barandl, R., Pretzsch, H., Seidl, R., Müllerm J. (2018) Biodiversity along temperate forest succession. Journal of Applied Ecology, DOI: 10.1111/1365-2664.13238.

Humphrey, J.W. 2005. Benefits to biodiversity from developing old-growth conditions in British upland spruce plantations: a review and recommendations. Forestry, 78:33-53.

IPBES 2012. Japan Satoyama Satoumi Assessment (JSSA). Catalogue of Assessments on Biodiversity and Ecosystem Services. Available at: http://catalog.ipbes.net/assessments/62

Inoue, T. 2005. Causes of butterfly decline in Japan. Japanese Journal of Entomology, 8:43-64.

Kirby, K.J. & Watkins, C. 1998. The Ecological History of European Forests. CAB International, Wallingford, UK.

Koh, L. P. and T. A. Gardner 2010. Conservation in human-modified landscapes. In: Conservation biology for all. N. S. Sodhi and P. R. Ehrlich (Eds). Oxford, Oxford University Press. Pp. 236-261.

Lajeunesse, M.J. 2016. Facilitating systematic reviews, data extraction, and meta-analysis with the metagear package for R. Methods in Ecology and Evolution, 7:323-330.

Lindenmayer D, Messier C, Paquette A, Hobbs RJ 2015. Managing tree plantations as novel socioecological systems: Australian and North American perspectives. Canadian Journal of Forest Research 45:1427–1433

Macdonald, E. Gardiner, B., Mason, W. (2010) The effects of transformation of even-aged stands to continuous cover forestry on conifer log quality and wood properties in the UK. 83, 1–16.

Magurran A.E. (2004) Measuring biological diversity. Blackwell, Oxford

Martin, P.A., Newton, A.C., Bullock, J. M. 2013. Carbon pools recover more quickly than plant biodiversity in tropical secondary forests. Proceedings of the Royal Society B-Biological Sciences, 280: DOI: 10.1098/rspb.2013.2236.

Masaki, T., Mori, S., Kajimoto, T., Hitsuma, G., Sawata, S., Mori, M., Osumi, K., Sakurai, S., Seki, T. 2006. Long-term growth analyses of Japanese cedar trees in a plantation: neighborhood competition and persistence of initial growth deviations. Journal of Forest Research, 11:217-225.

Mayerhofer, M.S., Kernaghan, G. & Harper, K.A. 2013. The effects of fungal root endophytes on plant growth: a meta-analysis Mycorrhiza 23:119.

Mori A.S., Lertzman, K., Gustafsson, L. (2017) Biodiversity and ecosystem services in forest ecosystems: a research agenda for applied forest ecology. Journal of Applied Ecology 54: 12-27.

Müllerová, J., Hédl, R., Szabó, P. 2015. Coppice abandonment and its implications for species diversity in forest vegetation. Forest Ecology and Management, 343:88-100.

Nagaike, T. 2012. Review of plant species diversity in managed forests in Japan. ISRN Forestry, http://dx.doi.org/10.5402/2012/629523 (Article ID 629523).

Norden, B. & Appelqvist, T. 2001. Conceptual problems of Ecological Continuity and its bioindicators. Biodiversity and Conservation, 10:779-791.

Nakagawa, S. & Schielzeth, H. 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods in Ecology and Evolution, 4:133-142.

Payn,T., Kollert, W., Liu, S., Rodriguez, L., Neves-Silva, L., Wingfield, M., MichelCarnus, J., Orazio, C., Freer-Smith, P., 2015. Changes in planted forests and future global implications. For. Ecol. Manage. 352:57–67.

Peters, D. P. C., Bestelmeyer, B. T. & Turner, M. G. (2007) Cross-scale interactions and changing pattern-process relationships: Consequences for system dynamics. Ecosystems 10, 790–796.

Pullin, A., Stewart, G.B. (2006) Guidelines for Systematic Review in Conservation and Environmental Management. Conservation Biology, 20:1647-1656

Putz, F.E., Zuidema, P.A., Synnott, T., Pena-Claros, M., Pinard, M. A., Sheil, D., Vanclay, J.K., Sist, P., Gourlet-Fleury, S., Griscom, B., Palmer, J. & Zagt, R. 2012. Sustaining conservation values in selectively logged tropical forests: the attained and the attainable. Conservation Letters, 5:296-303.

R Core Team 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.

Shibuya, S., Kubota, K., Kikvidze, Z., Ohsawa, M., 2008. Differential sensitivity of ground beetles, Eusilpha japonica and Carabidae, to vegetation disturbance in an abandoned coppice forest in central Japan. Eurasian Journal of Forest Research, 11:61–72.

Spake, R., Martin, P.M., Ezard, T.H.G., Newton, A.C., Doncaster, C. P. 2015. A meta-analysis of functional group responses to forest recovery outside of the tropics. Conservation Biology. 29:1695-703.

Spake, R., Doncaster, C.P. 2017. Use of meta-analysis in forest biodiversity research: key challenges and considerations. Forest Ecology and Management, 40:429-437.

Spake, R., Bellamy, C., Graham, L.J., Watts, K., Norton, L.R., Wood, C.M., Schmucki, R., Bullock, J.M., Eigenbrod, F. (2019) *Nature Sustainability*, in press.

Suzuki, W., Suzaki, T., Okumura, T., Ikeda, S, 2005. Aging induced development patterns of *Chamaecyparis obtusa* plantations. Journal of the Japanese Forestry Society, 87;27–35.

Takasaki T., Takenaka, C., Yoshida, T. (2010) The effect of thinning on the community structure and densities of soil animals in a Chamaecyparis obtusa plantation. Journal of the Japanese Forest Society, 92:67-170.

Takeuchi, K. 2010. Rebuilding the relationship between people and nature: the Satoyama Initiative. Ecological Research, 25:891-897.

Tamura, A., Yamane, M. 2017. Response of understory vegetation over 10 years after thinning in an old-growth cedar and cypress plantation overgrazed by sika deer in eastern Japan. Forest Ecosystems, 4:1. DOI: 10.1186/s40663-016-0088-

Totman, C. 1989. The green archipelago: forestry in pre-industrial Japan. Ohio Univ Press, Athens.

Toyoshima, Y., Yamaura, Y., Yabuhara, Y., Nakamura, F. (2013). A preliminary study on the effects of line and selective thinning on bird communities in Hokkaido, northern Japan. Journal of Forestry Research, 24:553-559.

Verschuyl, J., Riffell, S., Miller, D., & Wigley, T. B. (2011). Biodiversity response to intensive biomass production from forest thinning in North American forests-a meta-analysis. Forest Ecology and Management, 261(2), 221–232.

Viljur, M-L., Teder, T. 2016. Butterflies take advantage of contemporary forestry: Clear-cuts as temporary grasslands. Forest Ecology and Management, 376:118-25.

Yamaura, Y., Amano, T., Kusumoto, Y., Nagata, H., Okabe, K. (2011) Climate and topography drives macroscale biodiversity through land-use change in a human-dominated world. Oikos, 120:427-451.

Yamaura, Y., Oka, H., Taki, H., Ozaki, K., Tanaka, H. 2012. Sustainable management of planted landscapes: lessons from Japan. Biodiversity and Conservation, 21:3107-3129.

Tables

Table 1. Descriptors of treatment and control groups used in our systematic review of the impact of four forest management interventions on biodiversity in Japan.

Management intervention	Treatment group	Control group	Moderator variables considered in quantitative synthesis
Plantation forest			
Thinning	Thinned plantation	Unthinned plantation	Taxon, stand age, taxon, thinning intensity, canopy dominant, thinning intensity.
Extended rotation cycles (stand age)	Young plantation (1-50 years, median age 21 years)	Overmature plantation beyond economic felling age (typically >65 years)	Taxon, treatment stand age, canopy dominant.
Secondary forests			
High intensity traditional management of secondary forests (stand age)	Secondary forests regenerating from stand-level clearance such as through coppicing	Unmanaged secondary forest that has not been cleared for >100 years	Taxon, treatment stand age, canopy dominant
Lower intensity traditional management of natural and secondary forests	Natural or secondary forest that has undergone recent thinning, understory removal and/or litter removal.	Recently unmanaged or “abandoned” secondary or natural forest	-

Figure legends and embedded figures

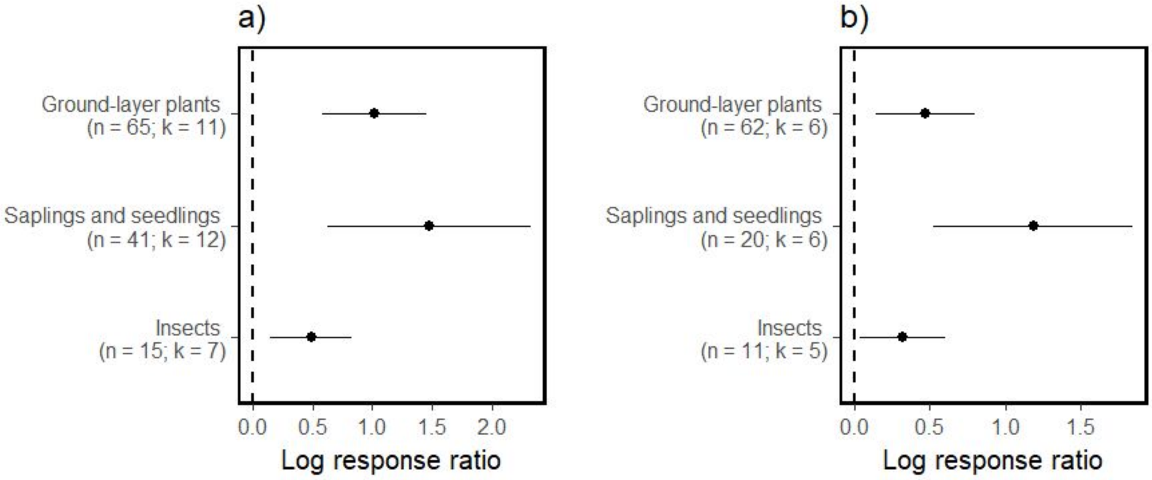

Figure 1. Summary mean effects and confidence intervals of plantation thinning on a) abundance and b) species richness of biotic communities, from *n* studies at *k* study sites.

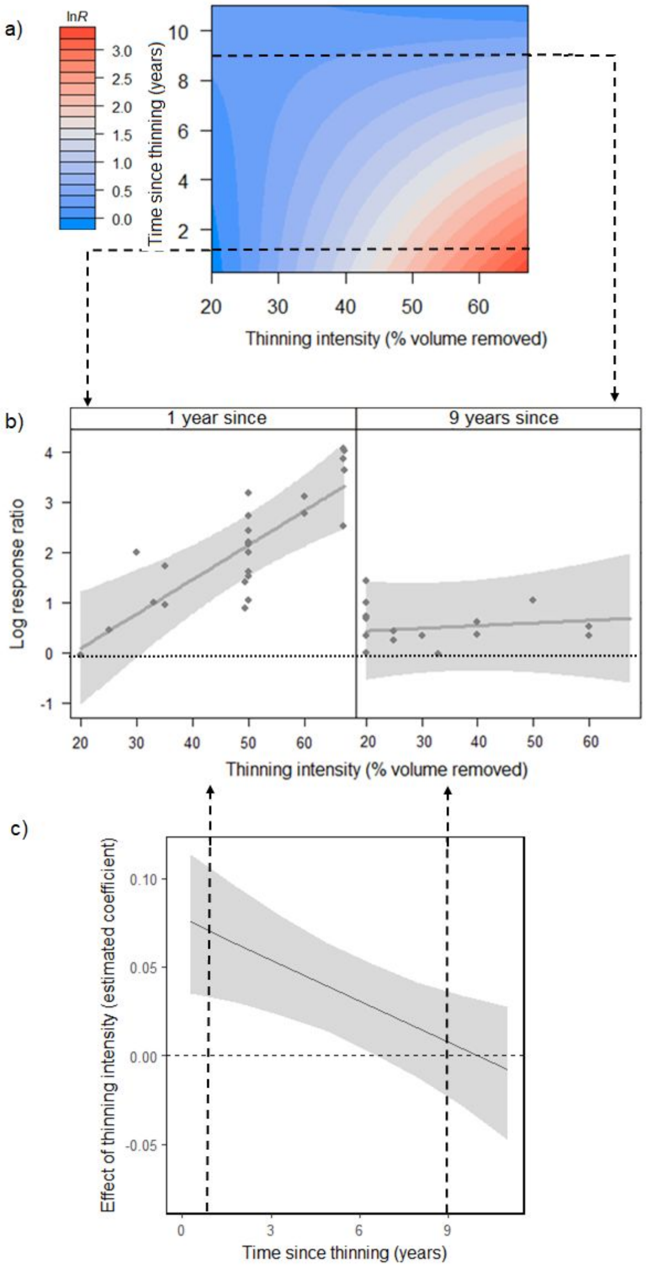

Figure 2. Impacts of plantation thinning on abundance of saplings and seedlings as dependent on time since thinning. a) Countour plot showing abundance differences (ln*R*) between thinned and unthinned forest stands as a function of thinning intensity and time since thinning. Dashed arrows point to sections through the plot at 1 and 9 years, illustrated in part b below. b) Influence of thinning intensity on abundance differences at 1 and 9 years since thinning, showing grey-shaded 95% CI in the regression based on between-study uncertainty in fixed effects only; values above horizontal dotted line signify higher abundance in thinned than unthinned stands. c) Marginal effect of thinning intensity, conditional on years since thinning; shading as for part b. Dashed arrows at 1 and 9 years show effects corresponding to response ratios in part b above. No effect of thinning intensity is detectable after six years. Regression used coefficients of the minimum adequate model.

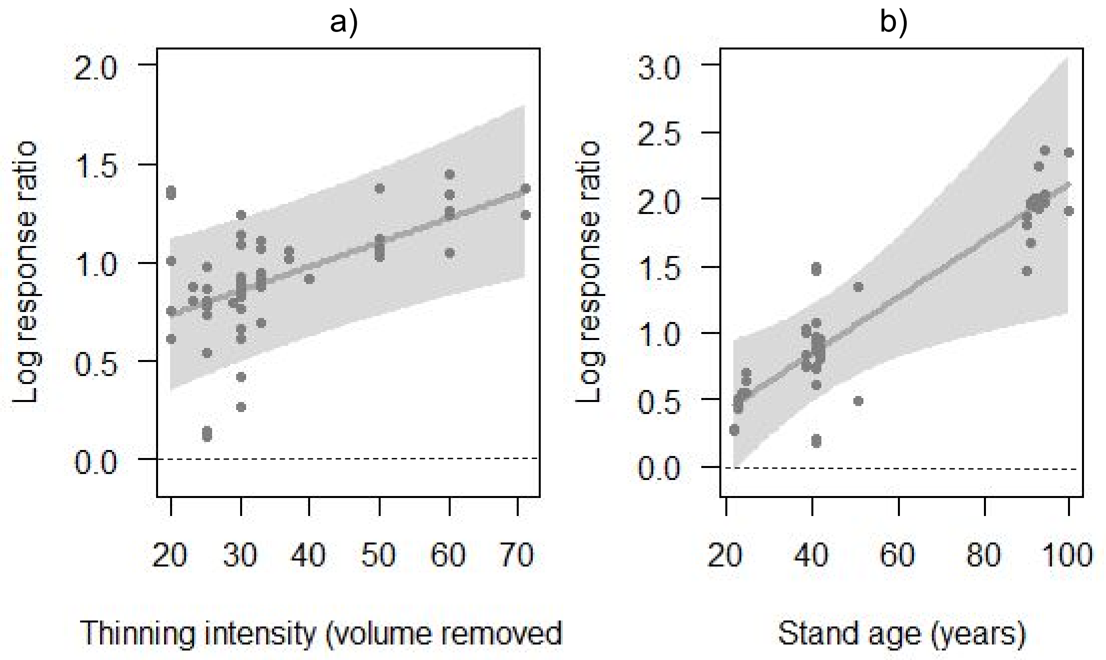

Figure 3. Influence of a) thinning intensity and b) stand age on abundance differences between thinned and unthinned plantation stands for understorey plants (horizontal dashed line means no difference). Regression used coefficients of the minimum adequate model. Grey shading shows 95% prediction intervals based on between-study uncertainty in fixed effects only.

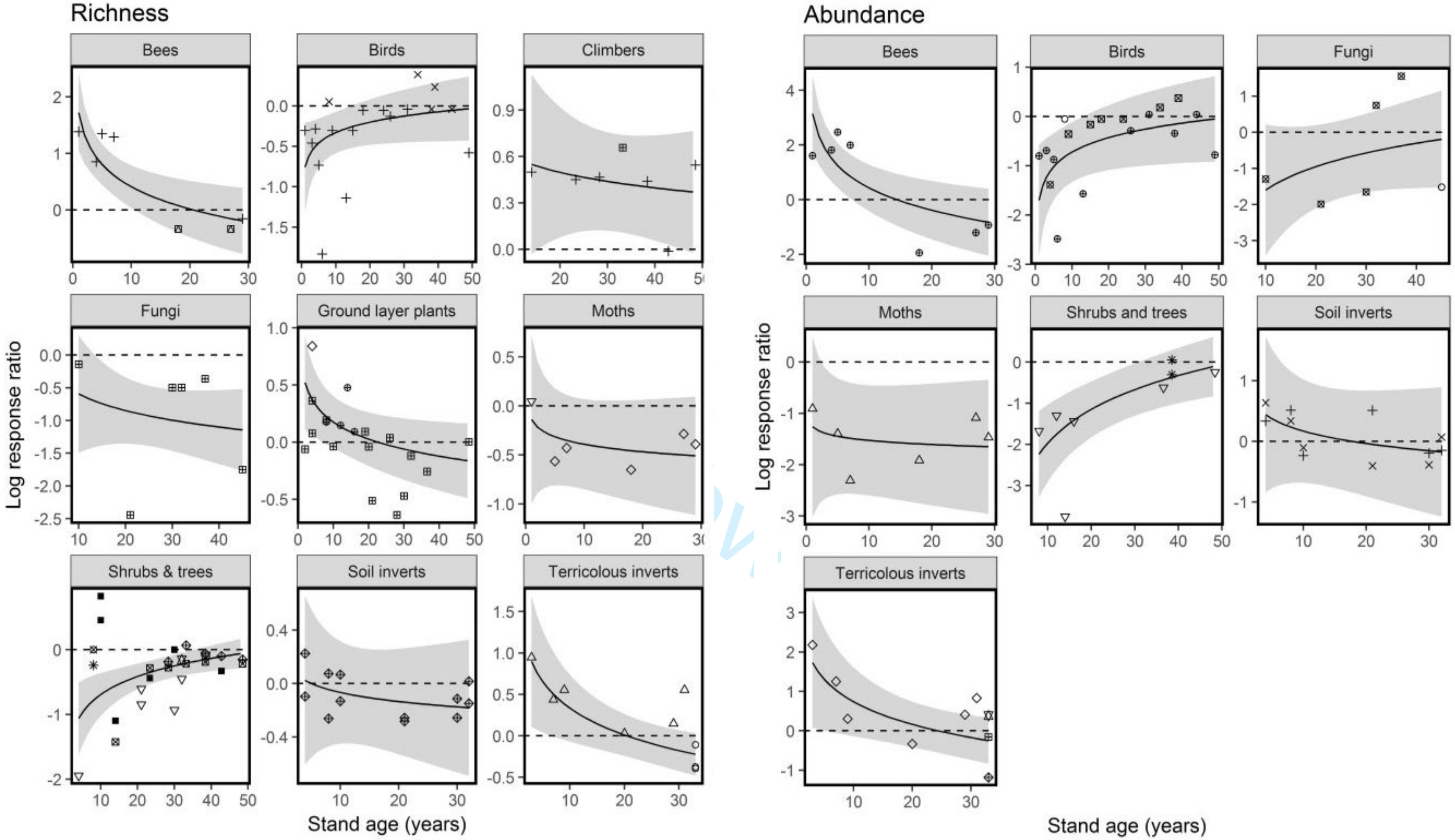

Figure 4. Influence of stand age on species richness and abundance effect sizes in planted stands relative to extended rotation planted stands. The horizontal dashed lines reference zero difference between extended rotation and younger treatment forest stands. Regressions used coefficients of the minimum adequate model. Grey shading shows 95% prediction intervals based on between-study uncertainty in fixed effects only. Different symbols correspond to different publications.

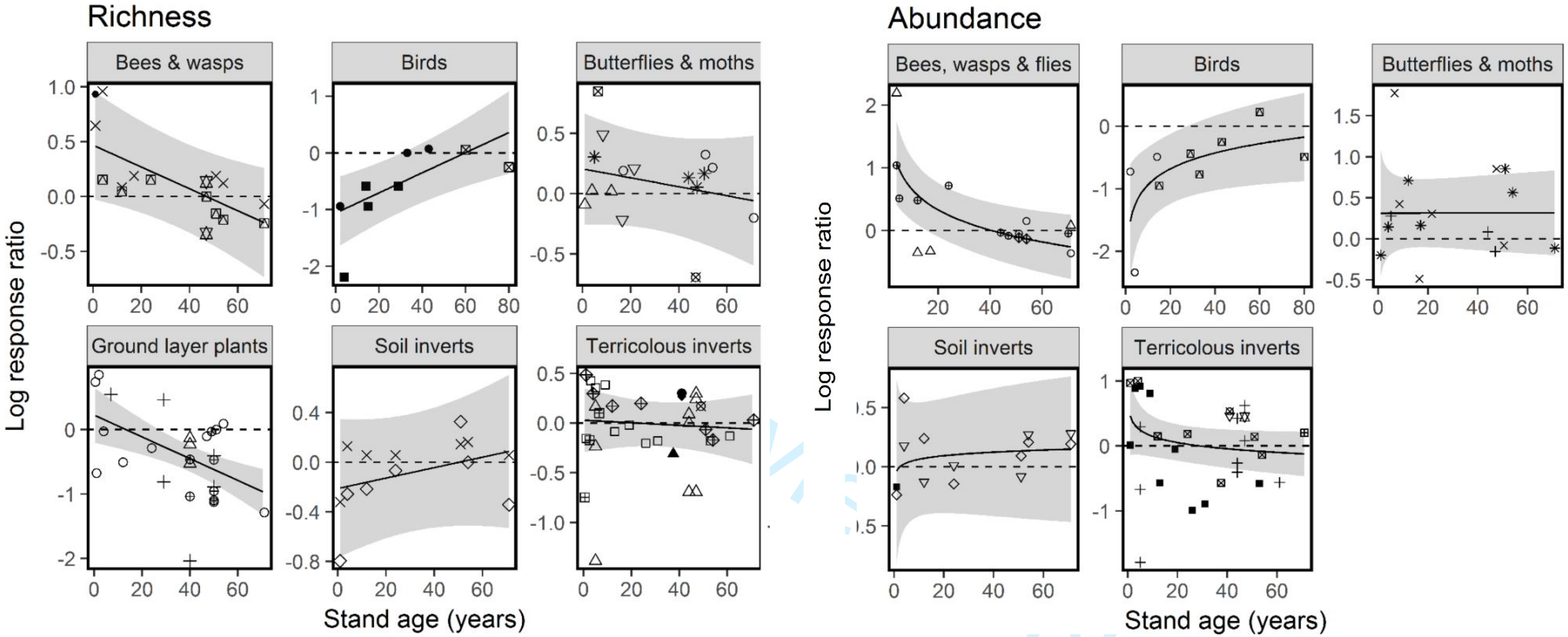

Figure 5. Influence of stand age on species richness effect sizes in younger secondary forest stands relative to older (>100-yr) abandoned forest stands. The horizontal dashed lines reference zero difference between extended rotation and younger treatment forest stands. Regressions used coefficients of the minimum adequate model. Grey shading shows 95% prediction intervals based on between-study uncertainty in fixed effects only. Different symbols correspond to different publications.