**Title**

Effects of planted tree species on biodiversity of conifer plantations in Japan: a systematic review and meta-analysis

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**Abstract** (250/250 words)

Natural forests were increasingly replaced by plantations globally. While plantations support less biodiversity compared to natural forests, they can serve as an important habitat for forest-dependent species. Understanding the key drivers of the habitat function of plantations is necessary to reconcile both forestry and biodiversity. Planted tree species is one of the important factors determining biodiversity of plantations. Here, we systematically collected studies comparing the biodiversity between conifer plantations and natural forests, and conducted meta-analyses to quantify the effects of planted tree family/species (cypress family: Japanese cedar *Cryptomeria japonica*, Hinoki cypress *Chamaecyparis obtuse*; pine family: Japanese larch *Larix kaempferi*, Japanese red pine *Pinus densiflora*, Todo fir *Abies sachalinensis*) on abundance and species richness of a wide range of taxa (all taxa, vertebrates, birds, invertebrates, terrestrial arthropods, plants, and understorey plants) in plantations in Japan. Abundance and species richness in plantations relative to natural forests differed among planted tree family/species. In plantations of pine family (mainly larch), abundance or richness did not significantly differ from those in natural forests for many taxa, suggesting the important role as habitats. By contrast, in cypress family (mainly cedar), abundance or richness was significantly lower than in natural forests for all analysis groups except understorey abundance. These results indicate that the habitat function of plantations and its management should be considered for each planted tree species, separately. Nevertheless, since our literature review identifies some research gaps, e.g., studies on vertebrates in western Japan were scarce, more comprehensive research efforts should be made in the future.

**Keywords (5/5)**: Pine family, Cypress family, Vertebrate, Invertebrate, Plant

**Main text**

**Introduction**

Natural forests have been lost, and plantations have been expanding globally (FAO 2020). Plantations now account for 7% of the world’s forests (FAO 2020), many of which have replaced natural forests (Puyravaud et al. 2010; Hua et al. 2018). Plantations are generally considered of lower biodiversity value than natural forests (Chaudhary et al. 2016), giving rise to the moniker of “green deserts” (Koh and Gardner 2010). However, several studies have shown that plantations can, in some contexts, support natural forest communities of a range of taxa (Estades and Temple 1999; Faria et al. 2007; Irwin et al. 2014; Spake et al. 2016). In landscapes already or increasingly dominated by plantations, conservation in plantations can be an effective and important means to promote biodiversity (Yamaura et al. 2012; Demarais et al. 2017; McFadden and Dirzo 2018), particularly in East Asia where one-third of the world’s plantations occur [China ranks first (4,792 million ha) and Japan ranks seventh (1,018 million ha) in the world; Payn et al. 2015; FAO 2020]. Identifying the factors that determine whether plantation or managed forests can sustain the biodiversity of natural forests is therefore necessary to reconcile both forestry and biodiversity (Brockerhoff et al. 2008; Demarais et al. 2017; Castaño‑Villa et al. 2019).

Quantitative syntheses of studies on biodiversity in plantation or managed forests have demonstrated that their biodiversity depends on a range of factors, including plantation age (Castaño‑Villa et al. 2019; Spake et al. 2019), plantation size (Castaño‑Villa et al. 2019), logging intensity (Burivalova et al. 2014), time since thinning (Spake et al. 2019), and landscape context (Mori et al. 2017; Castaño‑Villa et al. 2019). The planted tree species or ‘what is planted’ is likely of critical importance (Brockerhoff et al. 2008; Castaño‑Villa et al. 2019). Previous syntheses of empirical research comparing the biodiversity of plantations with different tree species have made high-level comparisons. For example, comparisons of plantations planted with native and exotic species, or mixed-species stands with monocultures have demonstrated that native, mixed stands generally support higher biodiversity than exotic monocultures (Castaño‑Villa et al. 2019; but see Vehviläinen et al. 2008). However, comparisons of the biodiversity in forests planted with specific tree species are needed to inform regional planning. This is because the species that is planted can exert strong influences on resource availability (light, water, and soil nutrients; Barbier et al. 2008; Petersson et al. 2019). This likely has consequences for the establishment of native plant communities (Fimbel and Fimbel 1996; Petersson et al. 2019; Yamaura et al. 2019), leading to differences in biodiversity among plantations with different planted tree species (i.e. ‘the tree species matters’; Felton et al. 2020).

Forest covers approximately 25 million hectares in Japan, constituting two-thirds of the total land area (FAO 2020). Plantations account for more than 40% of this area, principally as monocultures of conifer species [Cupressaceae (hereafter cypress family): Japanese cedar *Cryptomeria japonica*, Hinoki cypress *Chamaecyparis obtuse*; Pinaceae (hereafter pine family): Japanese larch *Larix kaempferi*, Japanese red pine *Pinus densiflora*, Todo fir *Abies sachalinensis*, and Sakhalin spruce *Picea glehnii*] (Yamaura et al. 2012). All of these tree species are native to Japan (Hayashi 1960), although species have been planted beyond their naturally occurring range (Yamaura et al. 2012). Species of cypress family have been planted nationwide, mainly in warm regions; Japanese cedar plantations cover 44,376 km2 (~43% of plantations in Japan) and Hinoki cypress covers 25,951 km2 (~25% of plantations in Japan) (Appendix S4.3). In cool regions, Japanese larch has been planted widely (9,766 km2, ~10% of plantations in Japan; Appendix S4.3). In Hokkaido, northernmost part of Japan, Todo fir is the major planted species (7,764 km2, ~8% of plantations in Japan; Table S5). *Pinus* (e.g., Japanese red pine) plantations are widely distributed throughout the Honshu, Shikoku and Kyusyu Islands (8,177 km2, ~8% of plantations in Japan; Table S5).

Climate and topography restrict the area where each tree species is planted; not many tree species are used for plantations in a specific area (Mitsuda et al. 2007; Nothdurft et al. 2012). Thus, local studies examining biodiversity of plantations have tended to focus on only one planted tree species. In a recent meta-analysis, Spake et al. (2019) synthesized studies measuring biodiversity responses to plantation management in Japan, but did not consider planted tree species, so the relative biodiversity value of plantations of different tree species is unclear. The invasion by broad-leaved tree species is more prevalent in pine than cypress family plantations (Yamaura et al. 2019), likely leading to greater biodiversity (Yoshida et al. 2005; Ohsawa 2007; Yoshii et al. 2015; Lindbladh et al. 2017). A synthesis of planted tree species effects on plantation biodiversity is urgently needed in Japan, to inform management plans that aim to enhance biodiversity and ecosystem services in plantations. Indeed, clearcutting of mature plantations is increasing across Japan in effort to increase domestic wood supply (Forestry Agency 2018; Kakizawa et al. 2018), and guidance on how to manage each species plantations, or which species to replant in some regions where multiple tree species can be planted, is needed.

Here we evaluate the relative biodiversity value of planted tree species in Japan. We systematically collected studies comparing biodiversity between conifer plantations and natural forest controls, and conducted meta-analyses to quantify the effects of planted tree family/species on abundance and species richness of various taxa (vertebrates, invertebrates, plants) in plantations in Japan. Specifically, we examined whether the species richness and abundance in plantations relative to natural forests differed among planted tree family or species. We expected greater biodiversity in plantations of pine than cypress families. Furthermore, for vertebrates, we also examined differences in plantation biodiversity among seasons. This is important because biodiversity in temperate forests is season-dependent (Kawamura et al. 2019); in deciduous broad-leaved forests that cover the northern half of Japan, the abundance of food resources for vertebrates drastically change among seasons (Herrera 1978; Huston and Wolverton 2009). Many animal populations consequently alter their range, habitat use, behavior patterns, or food habits (Marchand 2014), suggesting that the habitat function and consequent biodiversity values of plantations may vary with season.

**Materials and Methods**

**Biodiversity comparisons**

We set out to measure plantation biodiversity as relative to local ‘natural’ forests with likely high conservation value, in order to calibrate plantation biodiversity against regional differences in species richness and abundance. We therefore sought studies that compared biodiversity between replicate plantations and natural forests, to enable the calculation of an effect size – representing the difference in biodiversity between natural and planted forests. This makes it possible to make broad biodiversity comparisons between plantation species across Japan, while accounting for regional variation in richness or abundance of natural communities, which vary greatly across Japan due to broad bioclimatic gradients (Kira 1991). Following FAO (2020), we consider ‘natural forests’ as those forests that are regenerating naturally, regardless of previous disturbance. In temperate regions including Japan, few primary or old-growth forests remain in most areas, especially in productive areas (de Gouvenain and Silander 2017; Yamaura et al. 2020). Although some previous studies compared plantation biodiversity to that in old-growth forests (including selectively logged stands), most studies compared to that in secondary forests (e.g., Nagaike 2002; Irwin et al. 2014). Thus, we used natural forests, including old-growth and secondary ones, as a reference for comparison to plantations.

The two most commonly measured biodiversity metrics were considered: abundance and species richness. Abundance measures per unit area included cover, biomass, or occurrence rates derived from multiple surveys in the same plots. Species richness, the number of species in a community is the 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 unit across treatments. We use the term species richness to avoid confusion with abundance, which is often measured as density (per unit area). Due to the limited availability of raw data, we cannot use other biodiversity metrics, such as estimated species richness (e.g. Chao-1; Chao 1984), or species composition or functional diversity metrics that can offer greater scope for interpretation when comparing different regions (McGill et al. 2006; Shipley 2007; Katayama et al. 2019).

**Systematic review and data extraction**

We performed the literature search, assessed eligibility, and extracted data following the PRISMA approach (Moher et al. 2009). To avoid language bias (Konno et al. 2020), we searched literature in both English and Japanese languages, using the Web of Science Core Collection (WoS on April 17th, 2019) and J-stage (the first time: on May 8th, 2019; the second time: on August 5th, 2019), respectively. For the WoS, we used the following search terms related to topics (TS): TS=(Japan) AND TS=(forest\* OR woodland\*) AND TS=(“species richness” OR richness OR abundance OR density OR cover) AND TS=(plantation\* OR planted OR planting). For the J-stage, due to the limited number of terms that can be used, the search was divided into searches as follows: [the first time: TS=(*Shu-su* species richness OR *Kotai-su* abundance) AND TS=( *Jinkou-rin* OR *Syokurin* plantation); the second time: TS=(*Mitsudo* density OR *Hido* cover) AND TS=( *Jinkou-rin* OR *Syokurin* plantation)]. 4,638 articles were retrieved in total: 638 from WoS and 4,000 from J-Stage. Most studies on biodiversity in plantations in Japan have examined species richness and/or abundance of focused taxa, and we confirmed that adding ‘diversity’ and ‘biodiversity’ had almost no effects for collecting papers in preliminary searches. Thus, we did not include these terms for searching.

Potentially relevant articles were initially screened according to their titles and abstracts, after which 229 full-articles were assessed for eligibility. To be included in our meta-analysis, a study had to (1) sample biodiversity in both plantation forests (treatment group) and ‘natural forests’ (control group) which we defined as including secondary forests, (2) measured species richness (including family and genus richness) or abundance at least three replicate stands for both control and treatment groups (sample size), (3) report mean, standard deviation (SD) and sample size of species richness or abundance both for the control and treatment groups (or provide data from which these statistics can be derived), and (4) describe the planted tree family/species of plantations. Additional literature was identified by “snowballing”: searching for references within retrieved articles. We also searched for other articles published by the first or corresponding authors of the included literature, by checking personal publication lists or the keyword search on Google Scholar using their name in English or Japanese (first 100 hits for each). These additional searches were conducted only for the studies that were deemed relevant after the initial abstract/title screen. For articles that satisfied conditions (1)-(2) but not (3) or (4), we attempted to contact authors for the required data.

A total of 115 articles satisfied the criteria for inclusion in the meta-analyses (PRISMA diagram in Appendix S1.1). From these studies, we extracted the following data: i) natural forest attributed (canopy tree species and stand age), and plantation attributes (planted tree family/species, and stand age), ii) surveyed taxa, iii) survey seasons, and iv) prefectures. For abundance and/or species richness in both natural forests and plantations, we extracted mean values, SD, and sample size (Appendix S1.2). When multiple articles contained the same data, the data from only one article was used for the analyses. Conversely, when an article contained multiple comparisons such as from multiple taxa, regions, states of natural forests, or states of plantations, we treated them as individual studies (see Appendix S2 for the classification of forests). For studies that surveyed biodiversity from multiple plots within plantations according to the distance from adjacent natural forests, we used only the plots most distant from natural forests, to avoid edge effects (deMaynadier and Hunter 1998).

**Effect size estimation**

We performed the meta-analyses using “metafor” v. 2.1.0 (Viechtbauer 2010) in R v. 3.6.1 (R Core Team 2019). We used the standardized mean difference, Hedges’ *g* as the effect size metric (Borenstein et al. 2009) for examining the differences in abundance and species richness between natural forests and plantations:

$$g=\left(Mt-Mc\right)J/S$$

where *Mt* and *Mc* are the mean values of the abundance or species richness in the treatment (plantations) and control (natural forests) groups, respectively, *J* is a term that corrects bias due to small sample size, and *S* is the pooled SD of both groups. *J* and *S* are defined as follows:

$$J=1-3/(4df-1)$$

$$S=\sqrt{\left\{\left(nt-1\right)St^{2}+\left(nc-1\right)Sc^{2}\right\}/(nt+nc-2)}$$

where *df* is the degree of freedom, calculated by subtracting two from a total sample size of natural forests and plantations, *St* and *nt* are the SD and sample size of the treatment group, respectively, and *Sc* and *nc* are those of the control group. Hedges’ *g*, which standardizes the mean difference by the variance of each study, allows the comparison of studies that vary in measurement units. Positive values of Hedges’ *g* indicate that abundance or species richness is greater in plantations than in natural forests, while negative values correspond to lower abundance and richness.

**Meta-analysis**

We estimated summary effect sizes characterising differences between natural and plantation forests, using weighted random-effects models, which assume that studies with different methods and materials have different true effect sizes (Borenstein et al. 2009). This was done on subgroups of the richness and abundance effect sizes as follows: for each planted tree family (pine family and cypress family) and species (Japanese cedar, Hinoki cypress, Japanese larch, Todo fir, and Japanese red pine; hereafter cedar, cypress, larch, fir, and red pine, respectively).

To test whether summary effects (subgroup means) differed among planted tree family/species, we evaluated statistical differences among the subgroup means with Cochran’s *Q* test (significant when *p*<0.05; Borenstein et al. 2009). When its 95% confidence intervals did not overlap zero, we interpreted the difference between plantations and natural forests as significant. We followed Cohen’s classification to interpret effect sizes, as small, moderate, and large effects from values of *g* in the region of 0.2, 0.5, and 0.8 respectively (Cohen 1987). Heterogeneity between studies was estimated using the *Q* test and *I2* statistic, representing the percentage of variance between effect sizes that cannot be attributed to sampling error (Borenstein et al. 2009; Senior et al. 2016). Following Higgins et al. (2003), we interpret the heterogeneity, as small, moderate, and large heterogeneities from values of *I2* in the region of 25, 50, and 75%, respectively.

Meta-analyses were performed separately for abundance and species richness in each of seven taxonomic groups: i) all taxa, ii) vertebrates, iii) birds (a subset of vertebrates, excluding mammals and fishes), iv) invertebrates, v) terrestrial arthropods (a subset of invertebrates, excluding soil and aquatic animals, and molluscs), vi) plants, and vii) understorey plants (a subset of plants, excluding data only for trees above a certain height and thickness, hereafter “understorey”). For vertebrates and birds, we further tested whether the effect sizes differed among seasons (spring-summer and autumn-winter). Here, we estimated summary effects for both seasons, for all effect sizes representing differences between natural forests and plantations. We did not subgroup further by planted tree families/species, due to a low sample size of studies in autumn-winter. Summary effects were only estimated for subgroups with at least three effect sizes derived from different studies. Because of the limited number of studies, we could not use other taxonomic groups, e.g., fungi and bacteria (three individual studies only for cypress family plantations), mammals (four studies for cypress family plantations [one on the Japanese Macaque *Macaca fuscata*, three on the Japanese Hare *Lepus brachyurus*], three studies for pine family plantations [each study on bats, rodents, and the Sika Deer *Cervus nippon*, respectively]), soil animals (three studies for cypress family plantations, and three studies for pine family plantations), aquatic animals (three studies only for cypress family plantations). In addition, results of preliminary analyses suggested negligible differences among summary effects using different weighting methods, small effects of pseudo-replication, no serious bias derived from differences in plot size, and validity of using Hedges’ *g* (Appendix S1.2, S3; Lajeunesse 2015; Spake and Doncaster 2017; Hamman et al. 2018; Spake et al. 2020). Moreover, we also examined whether summary effects differed among natural forest types, stand age classes of plantations, and those of natural forests. For many analysis groups, there were no obvious effects (Appendix S2).

**Publication bias**

We tested for the possibility of publication bias, wherein the publication of results is more likely for statistically significant and expected findings (Borenstein et al. 2009). We did this for the analyses of each planted tree family (pine and cypress family) for abundance and species richness of all taxa. First, we produced a funnel plot, in which the inverse standard error (sample size relative to variance) is plotted against the effect sizes. Asymmetry in this plot, indicative of publication bias, was tested using Egger’s test (Egger et al. 1997). Using a trim-and-fill analysis with R0 estimator, we estimated the number of “unpublished comparisons” in our dataset, its effect size, and the averaged Hedges’ *g* with corrected publication bias, for each planted tree family (Duval and Tweedie 2000a, 2000b; Peters et al. 2007).

**Results**

**Data description**

115 published articles yielded 667 individual effect sizes representing differences between planted and natural forests. Studies on plants (mainly understorey) and invertebrates (mainly terrestrial arthropods) were conducted widely across Japan, although few studies were from some parts of western Japan (few studies on both taxa were in the Chugoku and Kinki regions, and no studies on plants were in the Shikoku region; Table S3 in Appendix S4.1, Appendix S4.2a-b). By contrast, for vertebrates (mainly birds), most studies were conducted in eastern Japan (the Kanto, Tohoku and Hokkaido regions), and few studies were in western Japan where the proportion of plantations to natural forests is high (three studies in the Chubu and Chugoku regions on birds, one in the Shikoku region on fishes, and one in the Kyushu region on the Japanese Macaque *Macaca fuscata*; Table S3 in Appendix S4.1, Appendix S4.2c, 4.3). In terms of planted tree species, the number of studies on larch relative to its planting area was high compared to the other species of pine family, and there were fewer studies on cypress than those on cedar (Table S4 in Appendix S4.1, Appendix S4.3).

**Effects of planted tree family**

In cypress family plantations, both abundance and species richness were significantly lower than natural forests for all biological groups except understorey abundance (*g* took values between −0.75 for bird abundance and −0.22 for invertebrate abundance; Fig. 1). By contrast, in pine family plantations, the value was significantly lower than that in natural forests only for species richness of all taxa (*g*=−0.28, upper *CI*=−0.002; Fig. 1h) and abundance of vertebrates and birds (vertebrates: *g*=−0.14, upper *CI*=−0.02, birds: *g*=−0.18, upper *CI*=−0.05; Fig. 1b‑c), and rather, tended to be higher for abundance of invertebrates and terrestrial arthropods (invertebrates: *g*=0.17, lower *CI*=−0.10; terrestrial arthropods: *g*=0.26, lower *CI*=−0.02; Fig. 1d‑e). Effect sizes that were generally negative for both biodiversity metrics tended to be more strongly negative for abundance and richness in cypress than pine family plantations (Fig. 1, Appendix S4.4). Differences between subgroup mean effect sizes for pine and cypress families were significant for seven of 14 biological groups (abundance: all taxa, vertebrates, birds, invertebrates, and terrestrial arthropods; species richness: all taxa and terrestrial arthropods; Fig. 1a‑e, h, k‑l, Appendix S4.4). For all subgroups except abundance and species richness of birds in cypress family plantations, we found significant between-study heterogeneity of effect sizes (Appendix S4.4). Subgroup heterogeneities were large for both abundance and richness of plants and understory in both plantations (*I2* took values between 78.18% for understorey abundance in cypress family plantation and 93.57% for understorey richness in pine family plantations), and for richness of other taxonomic groups in pine family plantations (*I2* took values between 72.86% for invertebrates and 93.53% for vertebrates), and confidence intervals for abundance and species richness of understorey in pine family plantations were also extremely wide (Fig. 1g, n, Appendix S4.4).

**Effects of planted tree species**

For all biological groups with available data, with the exception of plant and understorey abundance, cedar plantations were the most strongly negative, indicating lower abundance and species richness in cedar plantations than natural forests (Fig. 2a‑b, d‑e, Fig. S5a, d‑g in Appendix S3.2, Appendix S4.4). Studies on larch plantations generally showed only weakly negative effect sizes (Fig. 2, Fig. S5, Appendix S4.4), and rather positive for abundance of invertebrates and terrestrial arthropods (invertebrates: *g*=0.21, lower *CI*=−0.08; terrestrial arthropods: *g*=0.20, lower *CI*=−0.10), and understorey species richness (*g*=1.24, lower *CI*=−0.56) (Fig. 2d‑e, Fig. S5g in Appendix S3.2, Appendix S4.4). These suggest larch plantations supported similar biodiversity levels to natural forests, and are superior to cedar plantations. Data were limited for comparing biodiversity of other tree species. For all taxa and birds, abundance in red pine plantations and species richness in fir plantations were comparable to those in natural forests (Fig. 2a, c, Fig. S5a, c in Appendix S3.2,). For plants including understorey, abundance in fir plantations was significantly lower than that in natural forests, by contrast, abundance and species richness in cypress plantations did not significantly differ from those of natural forests (Fig. 2f‑g, Fig. S5f‑g in Appendix S3.2,). For most subgroups, we detected significant between-study heterogeneity of effect sizes (Appendix S4.4). In larch plantations, moderate or large heterogeneities were detected for all subgroups, and in cedar plantations, heterogeneity was large for plants and understorey biodiversity and richness of invertebrates and terrestrial arthropods (Appendix S4.4).

**Effects of seasons**

Effect sizes representing biodiversity differences among plantations and natural forests varied according to season (Fig. 3, Appendix S4.4). For bird and vertebrate abundance and bird richness, effect sizes were more strongly negative when surveying in spring-summer than in autumn-winter (Fig. 3). This demonstrates that the animal abundance and richness in plantations were lower than those of natural forests in the spring-summer (Fig. 3). By contrast, in autumn-winter, abundance and species richness in plantations were comparable to, or significantly higher than those in natural forests (vertebrate abundance: *g*=0.11, lower *CI*=0.03; Fig. 3). For only spring-summer, we detected moderate to large between-study effect size heterogeneity, although we note number of studies in autumn-winter was low (Appendix S4.4).

**Publication bias**

For studies on abundance of all taxa, the presence of publication bias for cypress family plantations was indicated by Egger’s test (cypress family: *t*=−3.19, *d.f.*=247, *p*<0.01; pine family: *t*=−1.77, *d.f.*=166, *p*=0.08), however, trim and fill analysis estimated the existence of zero unpublished studies (i.e., correcting the publication bias was not necessary). For the effect size of species richness of all taxa, the presence of publication bias for both cypress and pine family plantations was suspected by Egger’s test (cypress family: *t*=−4.34, *d.f.*=144, *p*<0.01; pine family: *t*=−2.01, *d.f.*=112, *p*=0.05). The trim-and-fill analysis estimated that there were 11 unpublished comparisons with higher effect sizes for cypress family plantations, although correcting the publication bias was not necessary for pine family plantations (Fig. S10 in Appendix S4.5). After adding false data of unpublished comparisons, species richness in cypress family plantations still remain to be significantly lower than that in natural forests, and the value of averaged Hedges’ *g* for cypress family plantations was lower than that for pine family ones, however, the difference among planted tree family became not significant (Fig. S11 in Appendix S4.5).

**Discussion**

To our knowledge, this is the first meta-analysis to examine whether the biodiversity value of plantations, relative to natural forests, varies according to planted tree family/species. While abundance and richness were consistently lower in plantations than in natural forests for a range of taxa, the difference was less strongly negative for pine family plantations (mainly larch) than cypress family plantations (mainly cedar) (Fig. 1‑2, Fig. S5 in Appendix S3.2). These results are important for biodiversity conservation in plantation landscapes because it demonstrates that forests collectively treated as “plantations”, will differ in their ability to support biodiversity according to planted tree species.

**Effects of planted tree family or species**

We found that plantations of pine family (mainly larch) had a less negative effect on biodiversity, relative to natural forests, than plantations of cypress family (mainly cedar). There are several potential explanations for this finding. First, pine family plantations generally have sparser canopies and allow more light to reach the forest floor, supporting more abundant understorey than those of cypress family plantations (general light availability: cedar/cypress/fir < larch < red pine; Maebashi Forestry Office 1997; Yamaura et al. 2008; Takahata et al. 2017; Forestry Agency 2019). Secondly, the relative abundance of canopy broad-leaved tree species is also generally higher within plantations of pine family, including fir and Sakhalin spruce *Picea glehnii* that have darker forest floor (Yamaura et al. 2019). This is likely due to the generally lower stocking density of pine family plantations, permitting the establishment of broad-leaved species (Yamaura et al. 2019). Third, red pine and larch trees support more insect larvae (e.g. moths and butterflies) than cedar trees (up to 4.5 times more), comparable to that supported by deciduous broad-leaved trees (Yui and Ishii 1994). Therefore, pine family plantations with abundant broad-leaved trees and understorey provide various and abundant food and habitat resources for invertebrates including terrestrial arthropods (e.g., dead woods, flowers, and leaves; Ohsawa 2004; Taki et al. 2010). In turn, these forests would provide important prey resources for birds and other vertebrates, as well as suitable structures for nesting or shelter from predators (e.g., cavity trees and dense bush) (Yui and Ishii 1994; Newton 1998; Kikuchi et al. 2013; Simonetti et al. 2013).

Contrary to previous studies suggesting that pine family plantations support more abundance of understorey or canopy tree species than cypress family ones, we did not detect an effect of planted tree family on abundance and species richness for plants (Fig. 1f-g, m-n). Abundance and species richness of understorey in cypress plantations tended to be similar to natural forests (Fig. 2g, Fig. S5g in Appendix S3.2). We note here that five of six comparisons for this analysis came from a single article, but were considered independent because surveys were conducted in five distinct regions (see Methods). In this article, the plantations surveyed in each region exceeded typical rotation ages (oldest stand age in each region: 67‑287). Older cypress family plantations would also likely support richer understorey because of both artificial and natural (self) thinning (Igarashi and Kiyono 2008). We detected large between-study heterogeneity for plants and understorey in both plantations, and wide confidence intervals for understorey effect sizes for pine family plantations. These results suggest that habitat function of plantations for supporting plant communities can vary strongly, in relation to e.g. subtaxon or management practice. However, the number of studies on plants may be not enough to measure the effects of planted tree family/species. More studies on plants in plantations are therefore needed to clarify the effective situation for conserving plant communities in plantations of each planted tree species.

**Effects of season**

For vertebrates (mainly birds), the function of plantations to support natural forest biodiversity differed among seasons. In spring-summer, both abundance and species richness were lower in plantations than natural forests. In autumn-winter however, plantation richness and abundance levels were comparable to natural forests. From spring to summer, breeding vertebrates rely on prey (e.g., insects for birds) and suitable structures for nesting or hiding (e.g., cavities and shrubs) that are more abundant in natural forests (Yui and Ishii 1994; Kikuchi et al. 2013). By contrast, in autumn to winter, the amount of prey resources is drastically reduced and the difference between plantations and natural forests would diminish. Therefore, plantations in this season may be comparable habitats to natural forests. Moreover, plantations with high densities of trees, especially those with evergreen conifer species, may provide superior shelter against harsh climate and predators in winter conditions than natural deciduous broad-leaved forests (Petit 1989; Minamino et al. 2007; Minamino and Akashi 2008). Furthermore, conifer plantations in lowlands are preferred as wintering habitats by some migratory bird species breeding conifer forests in highlands or cool regions (Yamaura et al. 2009; Yabuhara et al. 2019). For vertebrate conservation and management, we should consider the possibility that abundant conifer plantations existing across Japan play important roles as wintering habitats.

**Limitations and future research directions**

For species richness of all taxa, differences in effect sizes between pine and cypress families became non-significant after accounting for publication bias using trim-and-fill methodology (Appendix S4.5). This suggests that our analyses overestimated the magnitude of negative effect size. Even in cypress family plantations, there are cases with abundant broad-leaved trees (treated as unsuccessful plantations), and such stands would support rich biota (Masaki et al. 2004). Thus, when the function of plantations as habitats are evaluated to be high, it is important to publish the results as valuable knowledge, even in small sample situations. Not only the amount of broad-leaved trees, but also stand age would be important for many taxa (Appendix S2.1; Spake et al. 2019). Managing these stand variables is needed to utilize the potential of plantation as habitats for both cypress and pine family.

 Studies on pine family plantations were predominantly on larch, especially for taxa other than birds, and there were fewer studies on plantations of cypress than those of cedar (Table S4 in Appendix S4.1; Fig. 2). Thus, we could examine the habitat function of plantations of less-studied tree species (i.e., Todo fir, Japanese red pine, and Hinoki cypress) for only some taxonomic groups. Furthermore, few studies on vertebrates were conducted in western Japan, where the proportion of plantations to forests is high and cypress family is mainly used (Table S3 in Appendix S4.1, Appendix S4.3). Results of this meta-analysis indicated that the function as habitats compared with natural forests was generally low in cypress family plantations, and the function of plantations for vertebrates increased in autumn-winter. However, the roles of cypress family plantations in each season remain unknown, especially in western Japan, which is an important region for wintering forest birds including migratory species (Kawamura et al. 2019). Therefore, to understand the role of plantations as habitats in each season, studies are required on cypress family plantations in western Japan, especially in the wintering season.

**Implications for conservation and forest management**

Pine family plantations such as larch have important roles as biodiversity resources in Japan. This means that it is possible to manage these plantations as alternative habitats to natural forests. It provides an important implication for conservation in an era when plantations are expanding worldwide; timber production and biodiversity conservation can be achieved simultaneously depending on the planted tree species (‘matrix management’; Lindenmayer and Franklin 2002). By contrast, cypress family plantations, which account for 68% of plantations in Japan (Appendix S4.3), had generally low functions to conserve biodiversity. Whereas, results among comparisons varied, and many of them exhibited positive effect sizes: abundance or species richness was higher in plantations than in natural forests (for abundance: 101 of 249 comparisons; for species richness: 45 of 146 comparisons). It suggests that we have room for improving the function of cypress family plantations. Indeed, thinning cypress family plantations can promote the recruitment of broad-leaved trees (Utsugi et al. 2006), and the amount of broad-leaved trees increases when stand age of cypress family plantations exceeds 100 years (Igarashi and Kiyono 2008; Yamaura et al. 2019). It has been suggested that retaining mixed broad-leaved trees when thinning or harvesting is important to enhance plantation biodiversity, and management for transforming some conifer plantations to mixed forests has been proposed and addressed for many parts of Japan (Forestry Agency 2018; Yamaura et al. 2019). Especially within cypress family plantations, it would be important to retain and raise broad-leaved trees, even if they are small trees.

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**Declaration of interest statement**

None declared.

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**Figures**



Fig. 1. Effects of planted tree family [Cupressaceae (cypress family): Japanese cedar, Hinoki cypress, *Thujopsis dolabrata var. hondae*; Pinaceae (pine family): Japanese larch, Todo fir, Japanese red pine, and Sakhalin spruce, etc.] on the averaged Hedges’ *g* for abundance (a-g) and species richness (h-n) of each analysis group. Hedges’ *g* indicates the difference in abundance or species richness between plantations and natural forests, and negative values mean that abundance or species richness is lower in plantations than in natural forests. Filled dots and solid bars indicate the estimated means and its 95% confidence intervals, respectively [for understorey species richness in pine family plantations (n), the upper 95% *CI* (=1.11) is not shown]. Cochran’s *Q* test was conducted for each analysis to examine the difference in estimates among subgroups, and the significance was indicated by asterisk on the right side of each block (\*\*\*: *p*<0.01, \*\*: *p*<0.05, \*: *p*<0.1). *n* and *k* left outside the frame represent the number of comparisons and that of independent comparisons, respectively.



Fig. 2. Effects of planted tree species (cypress family: Japanese cedar, Hinoki cypress; pine family: Japanese larch, Todo fir, Japanese red pine) on the averaged Hedges’ *g* for abundance of each analysis group [all taxa (a), vertebrates (b), birds (c), invertebrates (d), terrestrial arthropods (e), plants (f), and understorey (g)]. See details in Fig. 1.



Fig. 3. Effects of survey seasons (SP/SU: spring-summer, AU/WI: autumn-winter) on the averaged Hedges’ *g* for abundance and species richness of vertebrates and birds. We dealt with only the differences between natural forests and plantations, not with those among planted tree species, due to the scarcity of studies in autumn-winter. See details in Fig. 1.