Multifaceted ecosystem services provided by tree communities: an approach from phylogenetic and functional signals in beneficial attributes of tree species

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博 士 論 文

Multifaceted ecosystem services provided by tree communities: an approach from phylogenetic and functional signals in beneficial attributes of tree species
（樹木群集による多面的生態系サービス供給：
樹種の有用性にみられる系統的・機能的シグナルに基づくアプローチ）

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Table of Contents

Abstract

Organisms and the communities play essential roles for ecosystem functions and services (i.e., human benefits from ecosystems). Effects of organisms and the communities on ecosystem functions/services are mediated by functional traits of organisms. Functional traits, which determines organisms' responses to the surrounding environment, are possibly important also for understanding impacts of environmental changes on ecosystem functions/services. Therefore, a trait-based approach is important for mechanistic understanding of the provision of ecosystem services and applied studies for sustainable uses of ecosystem services.

However, previous studies on the relationships between functional traits and ecosystem services have been considerably biased to some regulating services such as those related to carbon/nutrient cycling. Relationships between functional traits and many other ecosystem services that are largely influenced by sociocultural factors have been rarely investigated. Yet species responsible for those services are expected to be functionally non-random. In this study, by identifying functional traits responsible for such ecosystem services that sociocultural contexts are important, I tried to link the knowledge of community ecology to ecosystem service studies. I ultimately aimed to understand how spatiotemporal heterogeneity of community composition and biodiversity influence the provision of various ecosystem services by a trait-based approach. Then, through literature mining, I compiled 15 benefits linked to a wide variety of ecosystem services for 171 tree species common in Japan, including benefits specific to Japanese culture. Because functional traits often phylogenetically constrained, I firstly examined the potential associations between beneficial attributes and functional traits by phylogenetic analysis. I mainly investigated that (1) whether and how beneficial attributes are associated with phylogeny and functional traits, (2) how beneficial attributes are different among species, and that (3) how these associations influence the patterns of multiple ecosystem service provision.

First, in the chapter 2, I examined phylogenetic clustering in 15 beneficial attributes of tree species to see if beneficial attributes can be associated with functional traits. I evaluated the phylogenetic signal in each beneficial attribute and tested the bias of beneficial species among phylogenetic clades. Significant phylogenetic signals were detected in all 15 beneficial attributes. Distribution of beneficial species were also significantly uneven among phylogenetic clades in 10 benefits. These results suggest that phylogenetically constrained functional traits may somewhat influence the benefits. Next, I quantified the extent to which beneficial species differ for 105 possible combinations of benefits. Beneficial species overlapped significantly more than random expectation for 25 combinations of the benefits, whereas they differed significantly for 8 combinations of the benefits. Cluster analysis classified the species into five groups by similarity of their beneficial attributes. Distribution of these groups among phylogenetic clades was significantly uneven, indicating phylogenetically distant species tended to have different

bundles of beneficial attributes. There were both species which are highly versatile and have no benefits. Those suggest that multifunctionality, the number of benefits provided by a community, may increase with biodiversity via two alternative processes: increasing probability that a community include at least one versatile species or complementarity in benefits among species

Phylogenetic clustering in the beneficial attributes of tree species, which was shown in the chapter 2, suggests that the functional traits are responsible for the benefits of tree species. Then in chapter 3, I investigated whether and how the beneficial attributes were associated with functional traits. By using a gradient boosting machine (GBM), three models, i.e., the models that only traits, only phylogeny, and both traits and phylogeny were used as explanatory variables, were built for each benefit. As functional traits, I selected 22 traits of leaf, wood, root, seed, flower and fruit. All benefits were significantly associated with functional traits. Although available traits at present lacked some traits that are expected to be important for the benefits, prediction performances of trait models have comparable to those of phylogeny. The relative contribution of phylogeny to prediction were also negligible in traits and phylogeny models for most benefits. These results indicate that trait-based analysis is effective approach to even ecosystem services for which sociocultural background is very important.

In the previous chapters, I demonstrated non-random linkages between tree species and ecosystem services as follows: both positive and negative associations among beneficial attributes, the large variation among tree species in the number of benefits, and significant associations between the benefits and functional traits. Based on these findings, in chapter 4, I examined the two hypotheses about the provisioning of ecosystem services by communities: (1) associations among ecosystem services at a community level depends on those at a species level, and (2) multifunctionality of a community increases with biodiversity. I used the data on presence/absence of species at 1,086 sites across Japan. Ecosystem services and the diversity (multifunctionality) potentially provided by tree communities were estimated by relating the species composition with beneficial attributes of each species. For the first hypothesis, I quantified coappearance frequencies for the 105 possible combinations of the services among communities and compared with those among species. The coappearances at a community level was positively correlated with those at a species level but significant deviation from random expectation was also observed. This indicates that both associations among benefits at a species level and non-random community assembly processes are important for associations of ecosystem services at a community level. For the second hypothesis, I examined the associations among multifunctionality and three biodiversity indices, i.e., species richness, functional diversity, and phylogenetic diversity. Multifunctionality increased with any biodiversity indices. Among the indices, functional diversity was most important for prediction of multifunctionality.

In this study, I established a basis for trait-based analyses of ecosystem services of tree communities in Japan by identifying phylogenetic and functional signals in beneficial attributes of tree species. Then I demonstrated that both species identity and community assembly processes are important for associations of ecosystem services at a community level. I also showed positive associations between functional diversity and multifunctionality among tree communities. My achievements open the possibility of further studies to link community compositions and dynamics with ecosystem services, e.g., assessment of impacts of various environmental changes such as climate and land-use change on ecosystem services and analysis of the relationship between heterogeneity in tree communities at a landscape level and multifunctionality of ecosystem services. Such studies that associate spatiotemporal heterogeneity of community composition and dynamics with ecosystem services would greatly improve the understanding of ecosystem service provision and thereby contribute to management of ecosystem services in a sustainable manner.

Chapter 1: General introduction

Plants form communities of various structures partly as a result of interactions with the surrounding environment and the community compositions have various effects on ecosystem functions such as carbon and nutrient cycling. Among ecosystem functions, those beneficial for humans are called ecosystem services (Millennium Ecosystem Assessment, 2005). Ecosystem services can be classified into three groups based on the types of benefits (CICES, 2013): provisioning, regulating/maintenance, and cultural services. Provisioning services are nutritional, material and energetic outputs from ecosystems such as foods, timber, fiber, medicine, and genetic resources. Regulating and maintenance services are mediation or moderation of the ambient environment such as soil formation, carbon sequestration, water retention, coastal protection, and crop pollination. Cultural services are the non-material outputs from ecosystems that affect physical and mental states of people, including spiritual, aesthetic, educational, and recreational values of species and landscapes. Ongoing environmental problems such as global warming and land-use changes can have serious impacts on compositions and diversity of plant communities which are potentially important for ecosystem services (Cardinale et al., 2012; Newbold et al., 2015; Thom et al., 2017). Therefore, understanding how such human impacts spread to ecosystem services are essential to enjoy benefits of ecosystem services in a sustainable manner.

Identification of effect traits (functional traits responsible for effects to the surrounding environment and ecosystem functions/services) is key to assess provisioning of various ecosystem services (Lavorel and Garnier, 2002; Suding et al., 2008). For plants, numerous studies have demonstrated important roles of functional traits in some ecosystem functions/services (e.g., carbon assimilation and nutrient cycling are causally linked with leaf mass per unit area [LMA] and leaf lignin content, respectively) (de Bello et al., 2010; Hevia et al., 2017). Functional traits are important not only as a determinant of ecosystem services but also as a determinant of organisms' responses to spatiotemporal heterogeneity in environment (response traits) such as climatic gradient (Fortunel et al., 2014; Laughlin et al., 2011) and land-use change (Allan et al., 2015; Carreno-Rocabado et al., 2012; Chillo et al., 2018). Therefore, as long as response traits and effect traits are not independent, environmental heterogeneity would nonrandomly affect ecosystem services (Lavorel and Garnier, 2002; Suding et al., 2008).

Influences of functional composition and functional diversity of plant communities on ecosystem functions/services have been assessed by numerous studies (Cardinale et al., 2012; Diaz et al., 2007; Garnier et al., 2004; Tilman et al., 2014). Community weighted mean (CWM, the mean of trait values in a community which is weighted by the relative abundance of each species, representing the dominant trait value in a community) of key traits (e.g. leaf mass per area for productivity and leaf dry matter content for litter decomposition rate) are essential

determinants of some ecosystem functions/services (Fortunel et al., 2009; Garnier et al., 2004; Quested et al., 2007). Functional diversity promotes ecosystem functions/services such as productivity, litter decomposition, and aesthetic value (Duffy et al., 2017; Graves et al., 2017; Paquette and Messier, 2011; Tilman et al., 2014). The number of ecosystem functions provided by a single community, i.e. multifunctionality, also increases with increasing species richness (Gamfeldt et al., 2013; Hector and Bagchi, 2007; Isbell et al., 2011; Maestre et al., 2012; Zavaleta et al., 2010) and functional diversity (Finney and Kaye, 2017; Gross et al., 2017; Mouillot et al., 2011) possibly because functionally different species contribute to different ecosystem functions.

However, effect traits and influences of community composition have not been identified for many ecosystem services, especially services whose values depend on cultural contexts (de Bello et al., 2010; Hevia et al., 2017). Such studies have been considerably biased to a handful of services whose benefits have been considered universal irrespective of sociocultural backgrounds, such as carbon sequestration and nutrient cycling (de Bello et al., 2010; Hevia et al., 2017) and whose associations with functional traits are relatively clear. In contrast, for many other ecosystem services, value of a species may be specific to a certain sociocultural context and functional traits responsible for the service are often unclear. For example, plant species preferred as a wild edible plant are different depending on cultural and economic backgrounds of the consumers (Ghirardini et al., 2007; Koide and Kadoya, 2019). Similarly, it is obvious that a species sacred for a religion is beneficial only for believers of the religion. It has been unclear whether strong associations with species attributes such as functional traits and phylogeny can be expected for such kinds of ecosystem services.

Nevertheless, it is still reasonable to expect that species responsible for these services (i.e., dependent on cultural contexts) are also functionally non-random. Even when actual benefits depend on cultural and social contexts, potential for a benefit may be determined by functional traits. For example, edible plant species may be characterized by common traits (e.g., low fiber content and nontoxicity), although actually preferred species may differ among cultures (Ghirardini et al., 2007; Koide and Kadoya, 2019).

Despite the importance, a quest for associations between functional traits and such ecosystem services may be a little bit venturous because it is quite uncertain whether such relationships exist and the analysis requires enormous effort to consider numerous potentially important traits for various ecosystem services encompassing provisioning, regulating and cultural services. Phylogenetic approach can be an effective solution for this situation (Srivastava et al., 2012). Closely related species often share similar traits while distant relatives do not (phylogenetic signal [Diaz et al., 2013; Liu et al., 2015; Srivastava et al., 2012]). Therefore, phylogenetic information can be used as a surrogate for functional similarity and existence of a non-random phylogenetic pattern in an ecosystem service

suggests that the service is somehow affected by functional traits. Actually, a few previous studies has detected phylogenetic patterns in ecosystem services whose relationships with functional traits are unclear, e.g. provisioning of foods and medicine (Alrashedy and Molina, 2016; Ferrier et al., 2015; Forest et al., 2007; Saslis-Lagoudakis et al., 2012; Savo et al., 2015; but see Cámara-Leret et al., 2017).

In this study, to mechanistically understand the process of multiple ecosystem service provision by plants, I investigated how characteristics of species and communities influence provision of diverse ecosystem services using trait-based and phylogenetic approach. I focused on 15 kinds of beneficial attributes for 171 tree species common in Japan. The 15 benefits were selected to cover a wide range of ecosystem services whose provision from wild trees is important in modern-day Japanese society, including wood for furniture, edible plant as a mountain vegetable, a honey source, tolerance to salt wind, adding to the beauty of autumn color, and importance as a motif in traditional poetry. Identification of associations between these benefits and functional traits provides an essential basis for trait-based analyses of ecosystem services.

In chapter 2, I sought phylogenetic patterns in beneficial attributes of tree species and quantified the extent to which beneficial species differ among benefits. In chapter 3, the associations of various functional traits and the benefits were examined to identify effect traits which are responsible for the phylogenetic patterns of beneficial attributes. In chapter 4, I investigated how the associations among species and benefits found in chapter 2 and 3 influences the provision of ecosystem services by tree communities. Finally, I summarized the results in all chapters and discussed the significance of this study in ecosystem service studies.

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Chapter 2: Phylogenetic clustering in beneficial attributes of tree species directly linked to provisioning, regulating and cultural ecosystem services

Introduction

Understanding how biodiversity influences ecosystem services is essential for sustaining human livelihoods (Duncan et al., 2015; Kremen, 2005; Luck et al., 2009). Many studies that examined relationships between biodiversity and multifunctionality of plant communities have shown that higher biodiversity provides for more ecosystem functions or services (Finney and Kaye, 2017; Gross et al., 2017; Hector and Bagchi, 2007; Isbell et al., 2011; Maestre et al., 2012; Mouillot et al., 2011; van der Plas et al., 2016; Zavaleta et al., 2010). For example, in dryland plant communities around the world, Maestre et al. (2012) demonstrated that the multifunctionality of 14 ecosystem functions related to the cycling and storage of carbon, nitrogen, and phosphorus is positively related to species richness, and that this contribution to multifunctionality was more important than that from climatic factors. The positive effect of species richness on multifunctionality is at least partly because different species contribute to different ecosystem services (Hector and Bagchi, 2007; Isbell et al., 2011).

The differences in influence on ecosystem services among species can be explained by their functional traits (de Bello et al., 2010; Hevia et al., 2017). There are strong linkages between functional traits and ecosystem services at least for some ecosystem services (e.g., leaf mass per area for productivity [Wright et al., 2004] and leaf lignin content for decomposition [Cornwell et al., 2008]). Therefore, interspecific variations in traits can result in a trade-off in the supply of ecosystem services among species (Lavorel and Grigulis, 2012). Indeed, recent studies have shown that ecosystem multifunctionality is possibly underpinned by functional diversity rather than by species richness *per se* (Finney and Kaye, 2017; Gross et al., 2017; Mouillot et al., 2011). Because closely related species often have traits that are more similar than those shared between distant relatives (phylogenetic signal [Diaz et al., 2013; Liu et al., 2015; Srivastava et al., 2012]), phylogenetic diversity might be a predictor of ecosystem multifunctionality (Cadotte et al., 2017; MacIvor et al., 2016; Srivastava et al., 2012; Veron et al., 2017).

It remains unclear, however, whether such a biodiversity effect on multifunctionality is consistent across a range of ecosystem services. Most studies have focused on ecosystem functions or services whose relationship with functional traits and/or phylogeny is relatively apparent, straightforward, and well-documented; for example, productivity and nutrient cycling (de Bello et al., 2010; Hevia et al., 2017). However, for many other ecosystem services, particularly for provisioning and cultural services, relationships between traits and phylogeny are unclear and have been rarely examined. This is possibly because these services can often depend considerably on cultural and

social contexts. For example, the demand for wild edible plants as a provisioning service depends on the economic and cultural backgrounds of consumers (Schulp et al., 2014), and different species are preferred in different contexts even when similar species are available (Ghirardini et al., 2007). Similarly, aesthetic and religious (spiritual) values are generally specific to cultural background and these may show weaker phylogenetic signals (Cámara-Leret et al., 2017).

Nevertheless, it is still reasonable to expect that species responsible for these services (i.e., dependent on cultural contexts) are also functionally and phylogenetically non-random. Even when actual benefits depend on cultural and social contexts, functional traits may underlie the determination of benefits of individual species. Although preferred edible plant species may differ among cultures, these species may have similar traits (e.g., low fiber content and nontoxicity). Indeed, Cámara-Leret et al. (2017) showed the linkage among plant uses, functional traits and phylogeny in tropical American palms with a cross-cultural approach. Although functional traits may be key determinants of benefits of tree species, the number of potentially important traits for ecosystem services can be very large when considering various benefits encompassing provisioning, regulating and cultural services. Therefore, the quantification of phylogenetic clustering in the species influential to ecosystem services, which can potentially reflect the relationships between functional traits and ecosystem services (Saslis-Lagoudakis et al., 2012; Srivastava et al., 2012), would be a reasonable and effective first step.

In addition to the detection of a phylogenetic signal, the distributions of multiple benefits among species should be identified to resolve two consequences of ecosystem service provision: multifunctionality and trade-offs among ecosystem services. When phylogenetic signals are pervasive in ecosystem services, a positive relationship between biodiversity and multifunctionality can be achieved by two contrasting mechanisms. If a clade is characterized by highly versatile species (i.e., important for most ecosystem services), then higher biodiversity, but not phylogenetic diversity, will increase multifunctionality. On the other hand, if different phylogenetic groups are important for different ecosystem services, multifunctionality will be maintained by higher phylogenetic diversity. In addition, such differentiation of benefits among phylogenetic groups could result in some benefits not provided together (trade-off) at regional or landscape levels. For example, benefits less likely to be provided by a single species would be less likely to be provided by a single community, especially one with low biodiversity.

In this chapter I analyzed the phylogenetic patterns of 15 kinds of beneficial attributes for 171 tree species common in Japan to assess the generality of non-random linkages between ecosystem services and phylogeny. I specifically aimed (1) to quantify phylogenetic signals in these beneficial attributes, and (2) to explore the associations of the beneficial attributes among species. I hypothesized that phylogenetic clustering is general over the wide variety

of benefits and that different phylogenetic groups provide different bundles of benefits.

Materials and Methods

Studied species

In Japan, 67% of the land is covered by forests. Typical primary vegetation is evergreen broadleaved forests in the southwest and deciduous broadleaved forests in the north. Remote southern islands and some parts of the northernmost main island, Hokkaido, are characterized by subtropical evergreen forests and boreal coniferous forests, respectively (Fukushima, 2017). A large proportion of the forests is secondary forest that became established after past human disturbances.

I focused on 171 native tree species (woody seed plants except monocotyledons) in 48 families and 94 genera that are relatively common in canopy and subcanopy layers of natural temperate forests; 29 of the species are endemic to Japan (Table S.1). Each of the target species was recorded in at least 50 of the 10,715 census points of the vegetation survey of the sixth and seventh National Survey on the Natural Environment from the Biodiversity Center of Japan（http://gis.biodic.go.jp/webgis/sc-006.html). Target species were chosen purely on the basis of their occurrence frequency, irrespective of their utility. Rare species, which may not be recognized by citizens, were excluded from the analysis because information about their benefits could be lacking because of their rarity. Although the 171 common species account for only 37% of the tree species recorded in the vegetation survey, they account for 96% of the 10,698 occurrence records (Fig. S.1), indicating that they are an appropriate representation of vegetation in this region. Census points in the survey recorded as subtropical or boreal forests were excluded from analysis because the flora and local culture are considerably different in these regions as compared to the rest of Japan (Yoshinari, 2007). Although we also excluded survey data from plantations, the species selected include major plantation species in Japan because they were also frequent in natural forests.

Beneficial attributes of tree species

I selected 15 benefits that span a wide variety of ecosystem services (Table 1). Of these, seven are provisioning services, three are regulating services, and five are cultural services. These 15 benefits are in relatively high demand in modern-day Japanese society and the demand is at least partly satisfied by natural forests, and not only by plantations and imported products. For example, I focused on timber for furniture rather than for construction because timber produced in domestic natural forests currently is rarely used for construction in Japan (Ki no Kenkyukai, 2012).

14

As noted above, I excluded from the analysis tree species that are common only in the subtropical or boreal forests. This is because traditional cultures in these areas are distinctively different from that in central Japan because of historical background (Yoshinari, 2007), and information about tree usage in these cultures is presumably not as thorough as that for central Japan. However, I did not exclude examples of usage in the subtropical or boreal cultures when judging whether a species is beneficial for a usage (see below for details) because it is not always clear from the literature whether a usage is specific to these cultures. Plant usage is not necessarily homogeneous even in the temperate area. However, delimiting the boundary where a species is considered as beneficial for a usage is difficult, especially in modern society where both immigration and culture diffusion are common. Therefore, in this study, I considered a species as beneficial if it is used for a purpose anywhere in Japan.

Some benefits important in Japan are possibly not recognized internationally. The shiitake mushroom (*Lentinula edodes* [Berk.] Pegler), which is essential for Japanese cuisine, requires a volume of bed logs of about 315,000 m³ for their annual production of about 8000 t (Ministry of Agriculture, Forestry and Fisheries, 2016). Salt tolerant species are important as a component of coastal windbreaks and also as a barrier against tsunamis. These species potentially provide their ecosystem service by either protecting their own habitats or providing seeds for landscape engineering in other locations (Fukuda, 2009). Chabana (literally "tea flower") is the plant used for the traditional flower arrangement for a tea ceremony. Flowers are sometimes collected from the wild and are one of the essential elements of the ceremony, bringing a sense of season and elegance.

Haiku (traditional Japanese short poetry) is a popular art form even now. Although there are no official statistics on the number of haiku lovers, the haiku contest hosted by ITO EN, Ltd (ITO EN Oi Ocha New Haiku Contest) has had over 1.6 million entries from the general public every year for the past decade (Ito en, 2017). For evaluating this benefit, I focused on seasonal words, "kigo". Kigo are associated with a particular season and include various plants (occupying about one third of kigo), animals, and events, along with other seasonal references. Kigo are conventionally used in haiku and listed in a book known as a "saijiki" (literally "year time chronicle").

For religious uses, there are various ceremonies and festivals with long traditions still performed by the public where specific plants play an important role. *Illicium anisatum* Gaertn. in Buddhism and *Cleyera japonica* Thunb. in Shinto are representative of religiously important plants, and their branches are essential as an ornament of shrines, temples, graves, and household altars. Annual yields (including harvest from plantations) of *I. anisatum* and *C. japonica* in 2015 were around 1900 t and 1000 t, respectively (Ministry of Agriculture, Forestry and Fisheries, 2017). Detailed descriptions of other benefits and their importance are summarized in Table 1.

Existing literature was mined to judge whether each of the 171 tree species could provide any of these 15

benefits. Given that literature for these benefits has been mostly published in Japanese, the literature was searched using CiNii books (https://ci.nii.ac.jp/books/), wherein books of all university libraries and many national institutes in Japan are registered. Ordinary internet searches (https://www.google.co.jp/) were also used as supplemental searches. Searches were performed using multiple terms associated with each benefit. The citation lists in the literature found by the searches were also consulted. Candidate publications were compared in terms of the number of species referenced, and the best literature was used for the analysis (Table 1). Information from multiple publications was combined when comparably informative books were available. Although the information in this literature might not be complete, it is reasonable to believe, after such an extensive search, that any lack of information indicates that the use of a species for that purpose is unusual, and thus the species is not very beneficial for that purpose, at least in Japan.

All benefits were treated as binary data (beneficial or not) and species without records were considered as not beneficial. For some benefits that were recorded as rank data in the literature, I set quality thresholds (Table 1). For the benefits of seasonal words for haiku, child's play and religious uses, a vernacular name often indicates multiple species with similar characteristics; correspondences between vernacular and scientific names were intrinsically indistinct. I therefore associated these vernacular names with a genus or section, and all species within the genus or section were considered as beneficial. Although this is a reasonable assumption in most cases, it might not work well in others. For example, although the vernacular name "kaede" ("maple" in English) is commonly known as the generic term for species of the genus *Acer*, some species (e.g., species with compound leaves) might not fit the general image for kaede. In this case, phylogenetic clustering in these benefits could be overestimated if all species of *Acer* were regarded equally beneficial as kaede. Thus, for testing the phylogenetic signal (described below), I also performed the analysis at a vernacular-name level, where all species corresponding to a vernacular name were treated as a single species. Note that this vernacular-name-level analysis definitely underestimates phylogenetic signals.

Phylogeny

I used the online software Phylomatic version 3 (Webb and Donoghue, 2005); http://phylodiversity.net/phylomatic/) to construct a phylogenetic tree of all species at the genus level (Fig. S.2), using megatrees R20120829 for gymnosperms and R20160415 for angiosperms (available at https://github.com/camwebb/tree-of-trees/blob/master/megatrees) which are based on APG IV (Byng et al., 2016). This phylogeny was subsequently dated by using the branch-length adjustment algorithm (BLADJ function) in Phylocom software version 4.2 (Webb et al., 2008), using taxon age estimates published by Wikstrom et al. (2001).

Of the 171 species, 14 were Coniferae, 1 was a basal angiosperm, 14 were Magnoliids, 4 were basal eudicots, 25 were Malvids, 68 were Fabids, 5 were Saxifragales, and 40 were Asterids.

Statistical analysis

Phylogenetic signals in each beneficial attribute were quantified on the basis of the *D* statistic of Fritz and Purvis (2010). A *D* value of 0 indicates that a variable is as phylogenetically clustered as would be expected under a Brownian evolution model, whereas a value of 1 indicates that a variable is randomly distributed across the tips of the phylogenetic tree. $D < 0$ and $D > 1$ indicate extreme phylogenetic clustering and phylogenetic over-dispersion, respectively. The deviation of an observed *D* value from 1 ($P_{D<1}$) and 0 ($P_{D>0}$) was examined via comparison with *D* values obtained from 1000 simulations of random and Brownian models, respectively. Additionally, I examined for non-random distribution of beneficial species among large phylogenetic clades, which are often characterized by different functional traits (Judd et al., 2015), by applying Fisher's exact test with 2000 replicates.

To examine the extent to which species vary among benefits, I evaluated the overlap of beneficial species for each of the 105 pairs of 15 benefits using the Sørensen index and Cohen's Kappa (κ). The Sørensen index is defined as $2|X \cap Y|/(|X| + |Y|)$, where |X| and |Y| are the number of beneficial species for each of the two benefits being compared. A Sørensen index of 0 indicates that there is no overlap of species between the two benefits, whereas an index of 1 indicates that the species are the same for both benefits. The κ statistic measures the agreement between two raters, taking into account the possibility of agreement by chance. $κ < 0$ indicates that beneficial species differ significantly between the two benefits more than expected by chance, whereas $κ = 1$ indicates that beneficial species are identical.

I next examined the association between phylogeny and bundles of benefits. To identify the patterns of bundles of benefits among species, I detected groups of species that are associated with similar benefits by hierarchical cluster analysis using a Jaccard similarity matrix and Ward's method (Murtagh and Legendre, 2014). The appropriate number of groups for cluster analysis was evaluated by 26 alternative indices and the optimal value was determined by majority voting of the 26 indices (Charrad et al., 2014). Non-random distribution of those groups among phylogenetic clades was examined by using Fisher's exact test as above.

All statistical analyses were performed using the R software package version 3.3.2 (R Core Team, 2017), with the *Caper* package (Orme et al., 2013) for analysis of phylogenetic signals, the *psych* package (Revelle, 2016) for calculation of Cohen's Kappa, and the *NbClust* package (Charrad et al., 2014) for determining the number of clusters.

Results

Phylogenetic clustering of beneficial species

Statistically significant phylogenetic clustering was detected in all 15 beneficial attributes (Table 2). The phylogenetic signals on the genus-level tree were significant even in analyses at the vernacular-name level (see Methods) for child's play and religious uses, although they were no longer significant for seasonal words for haiku. For some provisioning and cultural services (pulpwood, bed logs for mushrooms, honey source, autumn color, and child's play), the phylogenetic signal was strong (i.e., D values not significantly different from 0, which is expected under the Brownian model). For some benefits, the signals became stronger when the benefits were divided into subcategories (Table S.2), e.g., yellow dye ($D = 0.390$; $P_{D<1} < 0.001$, $P_{D>0} = 0.118$), strong tolerance to infertile soil ($D = 0.456$; $P_{D<1} = 0.001$, $P_{D>0} = 0.163$) and strong tolerance to smog ($D = 0.431$; $P_{D<1} < 0.001$, $P_{D>0} = 0.151$).

The distributions of beneficial species among phylogenetic clades were significantly non-random in more than half of the benefits (Fisher's exact text; Table 2). Pulpwood species, bed logs for mushrooms and honey sources were absent in five of the eight clades; species beneficial as a honey source in particular were exclusively distributed in clades of core eudicots (Asterids, Fabids and Malvids). In contrast, the distributions of species beneficial as medicine, dyes, and tolerance to infertility, salt wind and smog were not significantly uneven among phylogenetic clades, although they showed significant phylogenetic signals (Table 2).

Differences in beneficial attributes among phylogenetic groups

Among the 105 possible pairs of the 15 benefits, there was a significant overlap of beneficial species (i.e., a positive Sørensen index and κ significantly larger than 0) for 25 pairs (Table S.3). The trend was strongest between tolerance to smog and tolerance to salt wind (Sørensen index, 0.822; κ = 0.742 ± 0.109 [mean ± 95% CI]), followed by seasonal words for haiku and child's play (Sørensen index, 0.627; κ = 0.470 ± 0.144), and the other pairs of regulating services (tolerance to infertile soil and smog, and to infertile soil and salt wind; Table S.3). Beneficial species differed more than expected by chance (i.e., κ significantly less than 0) in eight pairs. Pulpwood species and honey sources were completely different (Sørensen index, 0.000; κ = –0.150 ± 0.056). Autumn color was the benefit most infrequently provided along with other benefits; species with bright autumn color were less frequently beneficial in terms of tolerance to infertile soil, salt wind and smog, pulpwood, and religious uses. Ornamental species for the tea ceremony (chabana) were not likely to be pulpwood or bed logs for mushrooms. For the remaining 72 pairs of benefits, the agreement between beneficial species was moderate and often no different than expected by chance.

Phylogenetic clustering of beneficial species and non-random associations among beneficial attributes often

resulted in species from different clades providing different bundles of benefits. Individual species provided from 0 to 12 of the benefits (4.32 ± 2.58, mean $\pm$ SD); no single species of the 171 combined all of the 15 beneficial attributes. Cluster analysis classified the species into five groups on the basis of their beneficial attributes (Fig. 1, Fig. S.3). The distribution of these groups among phylogenetic clades was significantly uneven (Fisher's exact test, $P < 0.001$; Fig. 2).

Group 1 comprised species combining regulating and cultural benefits. This group included a relatively high proportion of Saxifragales and Asterids, and did not include any Coniferae, basal angiosperms, basal eudicots or Malvids. Group 2 was characterized by relatively versatile species combining a variety of beneficial attributes, and accounted for more of the Fabids than did any of the other groups. Species in group 3 mainly had provisioning-type beneficial attributes, and also included species with no benefits. This group accounted for higher proportions of Coniferae, basal eudicots and Asterids than the other clades. Group 4 mainly consisted of species with culturally beneficial attributes such as autumn color, seasonal words for haiku and child's play. This group included a high proportion of Malvids. The many trees in group 5 were beneficial for autumn color or as ornaments in the tea ceremony and rarely beneficial in provisioning of materials. This group accounted for relatively high proportions of the Magnoliids, Fabids and Asterids, and did not include Coniferae or basal angiosperms.

Discussion

Phylogenetic clustering was detected in all of the 15 studied beneficial attributes, which include a variety of ecosystem services (Table 2). To my knowledge, phylogenetic patterns in beneficial attributes of plants have been examined for only a few kinds of benefits, such as providing food or medicine (Alrashedy and Molina, 2016; Ferrier et al., 2015; Forest et al., 2007; Saslis-Lagoudakis et al., 2012; Savo et al., 2015; but see Cámara-Leret et al., 2017). This chapter shows that phylogenetically clustered patterns are widespread even in provisioning and cultural benefits, whose values are often subjective and depend on the cultural and/or economic background of a beneficiary (Ghirardini et al., 2007; Schulp et al., 2014).

The phylogenetic clustering in beneficial attributes must be explained by some functional characteristics shared by related species because phylogenetic identity itself cannot have functions nor be recognized by humans. For example, conifer wood is preferred for pulpwood because its xylem tracheids are longer than the xylem vessels of hardwoods (Simpson and Conner-Ogorzaly, 2014). As for sources of honey, although the preference of honey bees is unclear, nectar secretion is associated with core eudicot evolution (Lin et al., 2014). Medicinal benefits of plants are based on plant bioactivity, which is probably correlated with phylogeny (Garnatje et al., 2017; Ronsted et al., 2012),

19

and traditional medicinal plants are also phylogenetically clustered in some countries other than Japan (Cámara-Leret et al., 2017; Ferrier et al., 2015; Forest et al., 2007; Saslis-Lagoudakis et al., 2012; Savo et al., 2015).

Phylogenetic clustering was also detected for seasonal words for haiku, child's play, and religious uses, although these benefits are specific to Japanese culture and the relationships with functional traits are not apparent. This can be partly explained by the fact that, for these benefits, people often do not distinguish closely related species and consider them under a single vernacular name. However, such a loose grouping under a common vernacular name itself strongly suggests that the related species are similar in beneficial attributes and possibly also in the characteristics that serve as keys for identification (Simpson and Conner-Ogorzaly, 2014). For example, the acorns from any *Quercus* species can be used as material for a toy by children (e.g., a spinning top or a balancing-acorn toy) and identification of the species is often difficult for them. The identification of the functional traits responsible for this phylogenetic clustering were addressed in chapter 3.

The analysis of species overlaps between pairs of benefits indicates that some beneficial attributes are either more-likely or less-likely combined in a single species than random expectations (Table S.3). There are two possible reasons why some beneficial attributes were often combined in a single species. One is that both benefits depend on the same traits. For example, the high overlap in medicinal and dye plants can be at least partly explained by chemical compounds that are expected to be important for both benefits, for example, phenolics and alkaloids. The other reason is that the different traits associated with each of the benefits are correlated through ecological or evolutionary background. For instance, *Quercus serrata* combines thick bark (Clarke et al., 2013; Rosell, 2016) and large seeds (Yi and Liu, 2014) to achieve a life history adapted to disturbances (Masaki et al., 1992). This combination of traits would make this species suitable for both mushroom growing, for which thick bark would probably be preferred (Maeda et al., 2016), and child's play, where the large seeds are used as a toy. Conversely, for rarely combined beneficial attributes, the associated traits might correlate through trade-off relationships. Future studies should verify these hypotheses on the basis of functional traits.

The bundles of benefits provided by a species were significantly different among phylogenetic clades (Fig. 2). Species of Coniferae were characterized by distinctive bundles of provisioning benefits (groups 2 and 3) whereas there were no conifers in cluster group 1, whose members provide benefits other than provisioning services. The characteristic trait combinations of Coniferae, such as the production of resin beneficial as a medicine and softer wood that is preferred for woodworking, as well as its suitability for pulpwood, would explain these results. The Coniferae were also absent from group 5, which includes species with the benefits of beautiful autumn colors and chabana, because of their evergreen leaves and indistinctive flowers. Conversely, Asterids occupied relatively large proportions

20

of groups 1 and 5. Their conspicuous flowers adapted for animal pollination (Judd et al., 2015) would be beneficial as ornaments, whereas they are rarely beneficial as timber, possibly because of their relatively small size (cf. Aiba et al., 2016). Fabids were characterized by a high proportion of relatively versatile species with many beneficial attributes (group 2). This can be explained by their functional characteristics; for example their edible fruit types such as nuts and drupes, high tannin content in their wood, which is probably related to dye and medicinal use, and nitrogen-fixing nodules on their roots (Judd et al., 2015), which might confer tolerance to abiotic stresses (Ngom et al., 2016). Alternatively, the versatility of some species might be explained by the abundance of the species in the study area (the "apparency hypothesis" [de Albuquerque and de Lucena, 2005; Goncalves et al., 2016]). It seems possible that a relatively rare species might not be considered beneficial even when the species has suitable functional characteristics for a purpose (but note that we excluded very rare species from this analysis). These results, as a whole, indicate that phylogenetically distant species often have different bundles of beneficial attributes, possibly based on differences in their functional traits. Whether these relationships among species are responsible for the synergies and trade-offs in ecosystem services at a landscape level were examined in chapter 4.

The relationships between phylogeny and benefits detected in this chapter suggest that higher community biodiversity can increase ecosystem multifunctionality via two different mechanisms as follows. First, phylogenetic diversity promotes multifunctionality of a tree community via the complementarity in beneficial attributes among phylogenetically and thus functionally distant species. For the simplest example from this study, because no single species provided both a source of honey and pulpwood (Table S.3), and these beneficial attributes are phylogenetically clustered (Table 2), co-occurrence of species belonging to different phylogenetic groups is essential to providing these two benefits. Second, species diversity also promotes community multifunctionality because a more diverse community has a higher probability of including at least one beneficially versatile species (i.e., the sampling effect). Although many studies have shown that higher plant biodiversity promotes ecosystem multifunctionality (Finney and Kaye, 2017; Gross et al., 2017; Hector and Bagchi, 2007; Isbell et al., 2011; Maestre et al., 2012; Mouillot et al., 2011; van der Plas et al., 2016; Zavaleta et al., 2010), these studies rarely identified the underlying mechanisms of the biodiversity effects. To understand the ecological processes underpinning ecosystem multifunctionality, future studies should examine the relative importance of these alternative mechanisms.

This study provides a basis for future studies to link ecosystem services with various ecological processes related to phylogeny. Recent studies have shown that various processes in plant communities—for example community assembly processes (Kraft and Ackerly, 2010; Vamosi et al., 2009) and extinction due to climate change (Eiserhardt et al., 2015; Willis et al., 2008) or human disturbances (Knapp et al., 2008) —are phylogenetically non-

random. The findings in this chapter facilitate studies that associate ecosystem services and multifunctionality with these ecological processes to understand the spatiotemporal patterns in, and human impacts on, ecosystem services.

Conclusions

In this chapter I demonstrated that phylogenetic clustering is general in 15 beneficial attributes of tree species that are essential for a wide range of ecosystem services in Japan. As a result, phylogenetically distant species tended to have different bundles of beneficial attributes. These findings suggest that phylogenetic diversity promotes multifunctionality in tree communities through complementary service provisioning among phylogenetically distant species. The findings in this chapter are also important as a basis for understanding associations between community assembly processes and ecosystem services. The role of functional traits in determining the beneficial attributes and their phylogenetic clustering were investigated in next chapter.

Table 1. Detailed descriptions of the 15 studied benefits.

Benefit	Indicator of importance	Ecosystem service classification	References
Wood for furniture	60,000 m³ (Annual domestic supply)	Provisioning *Fibres and other materials from plants, algae and animals for direct use or processing*	Hatusima (1976) Hashizume et al. (1997) Hirai (1996) Hotta et al. (1989) Kishima et al. (1977)
Pulpwood	5.2 million m³ (Annual domestic supply. About 30% harvested from natural forests)	Provisioning *Fibres and other materials from plants, algae and animals for direct use or processing*	Hatusima (1976) Hashizume et al. (1997) Hirai (1996) Hotta et al. (1989) Kishima et al. (1977)
Bed logs for mushroom cultivation	315,000 m³ (Annual domestic supply)	Provisioning *Materials from plants, algae and animals for agricultural use*	Hatusima (1976) Hashizume et al. (1997) Hirai (1996) Hotta et al. (1989) Kishima et al. (1977)
Edible wild plants	2600 t (Annual domestic supply from forests)	Provisioning *Wild plants, algae and their outputs*	Hashimoto (2001) Hashimoto (2003) Hashimoto (2007) Suga (2015)
Medicinal uses	2600 t	Provisioning	Izawa (1998)

	(Annual domestic supply)	*Fibres and other materials from plants, algae and animals for direct use or processing*	Kimura and Kimura (1981) Minoru et al. (2002)
Dye	No data	Provisioning	Yamazaki (2012)
Materials for Kusaki-zome, the Japanese art of natural dyeing. Only typical dye plants that have been traditionally used were considered as beneficial.		*Fibres and other materials from plants, algae and animals for direct use or processing*	
Honey source	2865 t	Provisioning	Sasaki (2010)
Produces good nectar for honey. The "excellent" and "good" nectar sources in Sasaki (2010) were considered as beneficial.	(Annual domestic supply of honey)	*Reared animals and their outputs*	
Tolerance to infertile soil	58,945 ha	Regulating and maintenance	Obata et al. (1993)
Important as a seed source for afforestation of degraded areas. The "strong" and "somewhat strong" classes in Obata et al. (1993) were considered as beneficial.	(Area of national forest reserves for prevention of landslides)	*Mass stabilization and control of erosion rates / Decomposition and fixing processes*	
Tolerance to salt wind	84,425 ha	Regulating and maintenance	Obata et al. (1993)
Important as a seed source for windbreak forests. Threshold is same as tolerance to infertile soil.	(Area of national forest reserves as a shelter against wind, sand or tides)	*Micro and regional climate regulation*	

Tolerance to smog
    Important as a seed source for greening plants for industrial areas.
    Threshold is same as tolerance to infertile soil.
	No data	Regulating and maintenance
		Micro and regional climate regulation
			Obata et al. (1993)

Bright autumn color
    Plants whose leaves turn red, orange, yellow, or purple in autumn.
    Species whose leaves eventually turn brown before falling were not considered as beneficial.
	No data	Cultural
		Aesthetic
			Hayashi (2008)
			Kameda (2015)

Chabana Materials for traditional flower arrangement essential for tea ceremony.	1,761,000 persons (Number of citizens that joined in a traditional tea ceremony in the previous year)	Cultural *Aesthetic*	Tsukamoto (2014)

Seasonal words for haiku
    Use in traditional short Japanese poetry as a seasonal word ("kigo").
    Rarely used species (five or fewer examples in a reference book) were not considered as beneficial.
	1.6 million entries *per* year to a haiku contest	Cultural
		Aesthetic / Symbolic
			Ida et al. (2008)

Child's play Materials for child's play in nature, not including wooden toys.	No data	Cultural *Entertainment*	Fuzimoto (1989) Kawahara (2013)
Religious uses Use in rituals as an offering, an ornament, a symbol for a deity, or for other purposes.	2900 t (Annual domestic supply of *Cleyera japonica* and *Illicium anisatum*)	Cultural *Sacred and/or religious*	Kimura (1996) Nagasawa (2012)

For religious uses, *C. japonica* and *I. anisatum* are the most important species. Annual domestic supply data are from domestic production statistics of the Ministry of Agriculture, Forestry and Fisheries in 2015 (Ministry of Agriculture, Forestry and Fisheries, 2016, 2017), except for medicinal data, which are from the Japan Kampo Medicines Manufacturers Association in 2014 (Japan Kampo Medicines Manufacturers Association, 2016). The area of national forest reserves is from the Forestry Agency (2015). The indicator for chabana is from the Survey on Time Use and Leisure Activities in 2016 (Statistics Bureau, 2017). Ecosystem service classification is according to the Common International Classification of Ecosystem Services (CICES, 2013). Italic text in the ecosystem service classification indicates class-level categories in CICES. References in this table are those consulted to judge the beneficial attributes of species.

Table 2. Summary of phylogenetic signals and results of Fisher's exact test examining distributions among clades for 171 beneficial tree species.

Benefit	Phylogenetic signal		Fisher's exact test
	N	*D*	*P*
Pulpwood	16	**−0.117****	**0.001**
Child's play	54	**−0.055****	**0.001**
	(28/145	**0.490***	0.446)
Bed logs for mushrooms	30	**0.005****	**<0.001**
Autumn color	69	**0.165****	**<0.001**
Seasonal words for haiku	48	**0.262****	**<0.001**
	(25/148	0.824	0.352)
Honey source	37	**0.276****	**0.012**
Wood for furniture	62	**0.484***	**<0.001**
Edible	64	**0.484***	**0.03**
Religious uses	36	**0.618***	**0.009**
	(30/165	**0.713***	**0.006**)
Chabana	60	**0.650***	**0.004**
Tolerance to salt wind	53	**0.672***	0.327
Tolerance to smog	54	**0.675***	0.058
Dye	36	**0.701***	0.278
Medicine	70	**0.767***	0.85
Tolerance to infertile soil	50	**0.831***	0.129

Benefits are listed in order of strength of the phylogenetic signal. *N* is the number of tree species providing each benefit. Values in parentheses are the results of vernacular-name-level analyses. For these results, the denominator represents the total number of species at the vernacular-name level, which is less than 171. *Significant deviation of the *D* value from 1 ($P_{D<1} < 0.05$), which indicates a phylogenetically non-random pattern; **no significant deviation of the *D* value from 0 ($P_{D>0} > 0.05$), indicating a strong signal that is as phylogenetically clustered as would be expected under a Brownian evolution model.

Figures
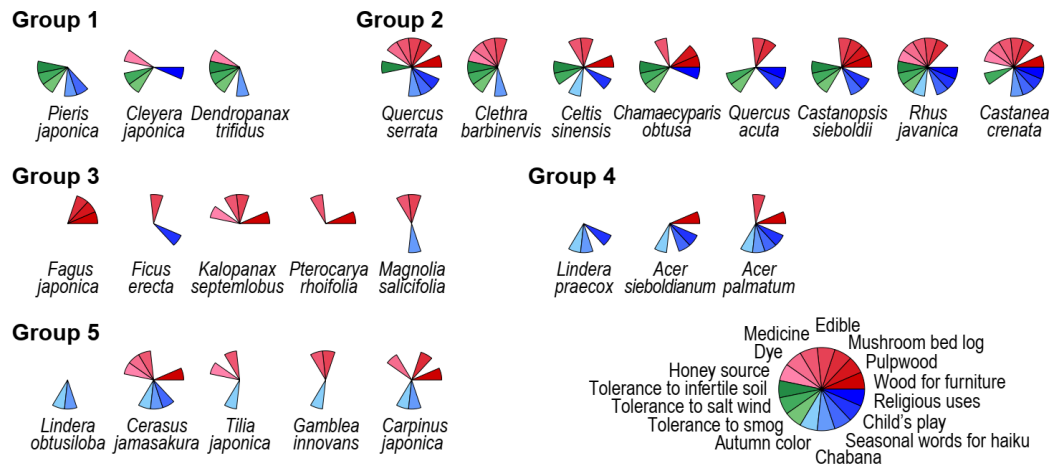
Fig. 1. Examples of bundles of beneficial attributes for individual species in the five groups obtained from cluster analysis. The filled segments indicate the benefits that species can provide. Segment colors indicate the category of ecosystem services: reds are provisioning services, greens are regulating and maintenance services, and blues are cultural services. See Fig. S.3 for the full results for the 171 species. Species are ordered according to the cluster dendrogram.
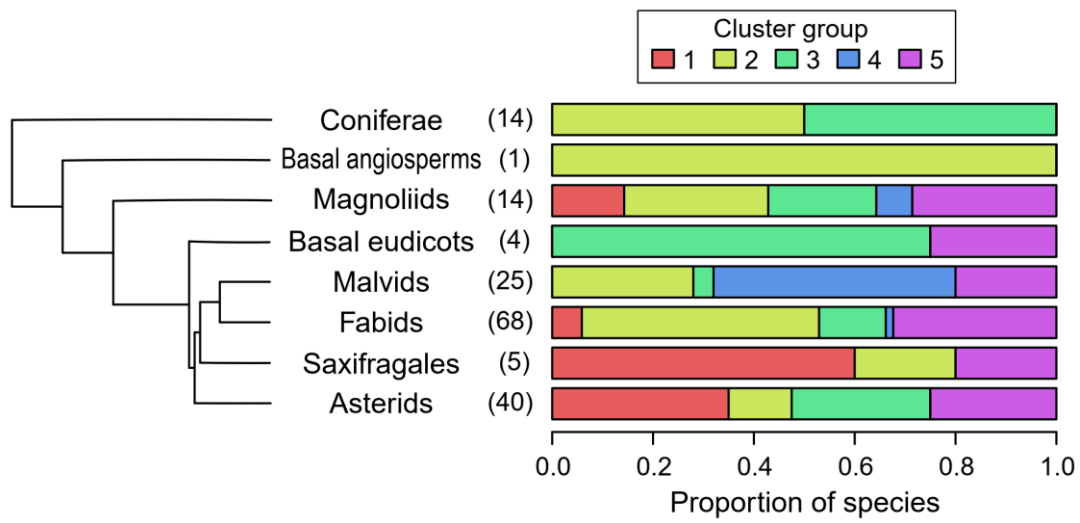
Fig. 2. Phylogenetic distribution of the five groups of species obtained in the cluster analysis of beneficial attributes. The colored segments of each bar show the proportion of the total number of species in that clade classified into each cluster group. The numbers in parentheses are the number of species in the clade.

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Chapter 3: Linking functional traits to ecosystem services: quantification of important traits for provisioning, regulating, and cultural benefits of tree species

Introduction

Trait-based analysis is one of the effective measures to assess ecosystem services and their responses to spatiotemporal heterogeneity in environment (de Bello et al., 2010; Lavorel and Grigulis, 2012; Lavorel et al., 2011). Functional traits of organisms are at least partly responsible for provisioning of various ecosystem services. For plants, numerous studies have demonstrated causal links between some ecosystem functions/services (e.g., carbon assimilation and nutrient cycling) and functional traits (e.g., leaf mass per unit area [LMA] and leaf lignin content) (de Bello et al., 2010; Hevia et al., 2017). Functional traits are also important as a determinant of organisms' responses to spatiotemporal heterogeneity in environment such as climatic gradient (Fortunel et al., 2014; Laughlin et al., 2011) and land-use change (Aiba et al., 2016; Allan et al., 2015; Carreno-Rocabado et al., 2012; Chillo et al., 2018). As a result, as long as functional traits responsible for influences from environment (response traits) and those responsible for effects to the surrounding environment (effect traits) are not independent of each other, environmental heterogeneity would nonrandomly affect ecosystem services (Lavorel and Garnier, 2002; Suding et al., 2008). Therefore, identification of effect traits for various ecosystem services is essentially important to understand contributions of functional composition of communities to ecosystem service provisioning (Lavorel et al., 2011), to investigate effects of functional diversity to ecosystem multifunctionality (Finney and Kaye, 2017; Gross et al., 2017; Lavorel et al., 2011; Mouillot et al., 2011) and to predict responses of ecosystem service supply to environmental changes (Allan et al., 2015; Chillo et al., 2018; Madani et al., 2018).

However, effect traits have not been identified for many ecosystem services, especially services whose values depend on cultural contexts (de Bello et al., 2010; Hevia et al., 2017). Demands for ecosystem functions/services whose relationships with functional traits have been actively studied, e.g. carbon assimilation and nutrient cycling, are relatively independent of cultural and social backgrounds of beneficiaries. In contrast, for example, most preferred wild edible plants, plant species that are important as a motif of traditional art, and plant species that are religiously important are manifestly dependent on cultural and social backgrounds of beneficiaries. Actually, Cámara-Leret et al. (2017), who performed one of the few empirical assessments of associations between functional traits and cultural services, showed that associations with traits are weaker in services that dependent on cultural backgrounds in South American palms.

In the chapter 2, I demonstrated that phylogenetic clustering is widespread in various ecosystem services

including those largely influenced by culture in Japanese tree species. Significant phylogenetic clustering was detected even for benefits as religious importance, materials for child's play, and motif for traditional Japanese poem. Because phylogeny itself cannot have any function, this result suggests that effect traits for these beneficial attributes are phylogenetically clustered in these tree species. Therefore, identification of functional traits responsible for these benefits is an important next step to understand the process for provisioning of ecosystem services.

Although ecosystem services may be eventually somehow explained by functional traits, whether a trait-based analysis is a more effective tool for application studies than a phylogeny-based analysis is a separate problem. Our life depends on numerous ecosystem services and the number of functional traits that are responsible for these services also will be very large. Due to enormous time and effort required for measurement of the traits, key traits for an ecosystem service are not always available. For the meantime, a phylogeny-based analysis may outperform a trait-based analysis where some essential traits are not available. Therefore, from a perspective of application studies, a comparison of the performances of phylogeny and currently available traits as predictors of ecosystem services is relevant as a guide for future practices.

In this chapter, I examined associations between 22 functional traits including leaf, wood, fruit, flower and root traits and the 15 beneficial attributes for which significant phylogenetic signals were detected in the chapter 2. Then the strengths of associations were compared with those of phylogeny. A machinelearning technique, gradient boosting, which enables consideration of non-linear responses to and high-order interactions among numerous variables was used for modeling of the associations. Specific questions are (1) Are functional traits better predictors of beneficial attributes of tree species than phylogeny? and (2) how are the functional traits associated with the beneficial attributes?

Materials and methods

Studied species and benefits

Of the 171 species focused in the previous chapter, some functional traits (see below) were not available for two species (*Betula schmidtii* and *Quercus aliena)*. As the result, 169 native tree species in 48 families and 94 genera were analyzed in this chapter. Analyzed benefits are identical with those in the previous chapter.

Functional traits

A total of 22 traits were collected by the field measurement or from literatures. Leaf traits (LMA [g m^{-2}], leaf area [cm^2], leaf strength [kN m^{-1}], nitrogen content [%], tannin content [%], phenol content [%], lignin content

[%], neutral detergent fiber [NDF] content [%]) and wood density (g cm^{-3}) were measured by collecting leaf and wood samples from 23 natural forests and an arboretum across Japan from 2011 to 2016. Three individuals of each species were typically sampled at each of 1–12 sites. Leaves were collected from a sunlit crown of mature individual using a telescopic 15-m carbon-fibre pole. A wood sample about 5 cm long was also collected from the same individuals using an increment borer (diameter, 5.15 mm) at a height of about 1.2 m.

Several healthy, typical mature leaves were scanned on a flatbed scanner (GT-S630, Epson), with the maximum allowable number for the available space on the scanner stage. Dry masses of the leaves were measured after oven-drying at 60 °C to a constant weight. The scanned images were analyzed by using version 1.45 of the ImageJ image analysis software (National Institutes of Health, Bethesda, MD, USA) to obtain leaf area. Then the dry weight divided by the leaf area to calculate leaf mass per unit area for the whole leaf, including the petioles and the rachis of a compound leaf (Cornelissen et al., 2003). The length of each wood sample was measured using calipers after trimming into a cylinder shape (Muller-Landau, 2004). Then these samples were oven-dried at 60 °C to a constant weight. Wood density was calculated as the dry weight divided by the fresh volume. Leaf strength was measured as the maximum force required to penetrate a leaf lamina by a metal rod of 2mm diameter. The maximum force per the circumference of the rod (6.28mm) was defined as leaf strength. Leaf nitrogen content was determined by a NC analyzer (SUMIGRAPH NC-900; Sumitomo Chemical, Osaka, Japan). Leaf tannin content was evaluated based on proanthocyanidin activity (Julkunen-Titto 1985). Leaf phenol content was quantified by the Folin-Ciocalteu method (Waterman and Mole 1994). Leaf lignin content was determined by an improved acetyl bromide procedure (Iiyama and Wallis, 1990), and the concentration of lignin was calculated to fit the equation derived from (Fukushima and Hatfield, 2001). Leaf NDF content was analyzed by Van Soest method (Van Soest, 1994).

Functional type, adult height (m), seed mass (g), flower and fruit traits were taken from the literatures listed in Supplement. Species were categorized into three functional types: conifers, evergreen broad-leaved, deciduous broad-leaved. Four flower traits and four fruit traits were used: flower size (mm; the larger one of corolla length or diameter), inflorescence size (mm; inflorescence length or, if flowers are not clustered, flower size), flower color (white, pink, red, yellow, and green), flower season (the first month of the flowering season), fruit size (mm; the larger one of fruit length or diameter), fruit color (black, gray, red, brown, yellow, green, and blue), fruit type (cone, achene, samara, nut, legume, follicle, capsule, drupe, berry, pome, sorosis, and syconium), fruit season (the first month of the fruiting period). Flower sizes and inflorescence sizes of conifers were regarded as 0 and flower color was none, because conifers does not have obvious flowers.

Fine root branching intensity (low, intermediate, high) and fine root diameter (thin; root tip diameter ≤

0.2mm, intermediate; 0.2–0.5mm, thick; ≥ 0.5mm) were taken from Karizumi (2010).

Analysis

Associations between beneficial attributes and functional traits or phylogeny were examined using a gradient boosting machine (GBM). This method is an ensemble learning that combines numerous weak decision trees that are developed to complement the existing model. The method is effective in the case that underlying processes are unknown, numerous explanatory variables are involved, and the relationships among variables are anticipated to be nonlinear and complex (Elith et al., 2008; Willcock et al., 2018) and have higher ability to distinguish correlated variables (Friedman, 2001).

Three models, i.e. trait model, phylogeny model, and trait and phylogeny model, were constructed for each benefit. Response variable was binary data whether the species are beneficial for the use or not. Categorical explanatory variables were coded as integers as follows. Colors of flowers and fruits were coded in the order of hue circle. For fruit types, dry fruit (indehiscent fruit: cone, achene, samara and nut; dehiscent fruit: legume, follicle and capsule), sap fruit (drupe, berry and pome), and collective fruit (sorosis and syconium) were coded as 1 to 12. Families and genera were respectively coded in the manner that lower values were assigned to more ancestral taxa based on Christenhusz et al. (2011) for gymnosperms and Byng et al. (2016) (APG IV) for angiosperms. To avoid overfitting, optimal values for total number of trees, maximum depth of variable interactions, minimum number of observations in the tree terminal nodes, and subsampling rate were determined by leave-one-out cross-validation (LOOCV). Shrinkage parameter was set at 0.001. The models predict a probability that each species is beneficial for a usage. Then the probability was converted to binary prediction to maximize Cohen's kappa index, which was used as an index of model performance. Relative influences of explanatory variables were evaluated in each model as the reduction in predictive performance when each explanatory variable was randomly permuted.

All analyses were performed using the R software package version 3.4.3 (R Core Team, 2017) with the *gbm* package (Ridgeway, 2007) to fit generalized boosted regression models, the *cv.models* package (https://github.com/Marchen/cv.models) to search best fitting model and to perform cross validation.

Results

Prediction performances of GBM models for which both 22 functional traits and family were used as explanatory variables were significantly higher than random expectations for all the 15 benefits (Fig. 1). Benefits as bed log for mushroom ($\kappa = 0.64 \pm 0.16$ [mean $\pm$ 95% CI]), autumn color ($\kappa = 0.64 \pm 0.12$), child's play ($\kappa = 0.63 \pm$

0.14) and honey sources ($\kappa = 0.60 \pm 0.14$) were well-predicted while prediction performance was relatively low for benefit as medicine ($\kappa = 0.28 \pm 0.15$).

Prediction performances of the three alternative models, i.e. trait model, family model, and trait and family model, were generally similar (Fig. 1). However, once traits are included in the model, relative contributions of family were generally low for beneficial attributes excluding pulpwood (Fig 2). The result was similar even when genus instead of family was used as phylogeny (Fig. S.4 and S.5) although functional characteristics are often more similar within genus than in family. The benefit as pulpwood was strongly associated with conifers (Fig. S.6a) rather than with any functional trait in my model, indicating some conifer-specific traits that were not included in the model are important for pulpwood.

Multiple functional traits were important for most benefits. Many of the detected associations between functional traits and benefits seem reasonable. Probability to be wood for furniture and that to be pulpwood both increased with adult height (Fig. 3a, b). Species tended to be more beneficial as wild edible plants (including nuts) with increasing seed mass (Fig. 3d). Dye plants were characterized by higher leaf phenol content (Fig. 3f). Honey sources were typically species with a large flower and/or inflorescence (Fig. S.6b) that broom in spring and summer (Fig. 3g). Strong tolerance to infertile soil was related to sparsely branched root system (Fig. 3h). Tolerance to salt and religious uses were positively associated with leaf strength (Fig. 3i, o) while bright autumn color was negatively associated with the trait (Fig. 3k). For ornament in tea ceremony, larger flowers were preferred (Fig. 3l). Benefits as motif of haiku poem and materials of child's play were associated with larger fruits (Fig. 3m, n).

Discussion

I revealed that, for 15 benefits of tree species for which significant phylogenetic clustering was detected in the chapter 2, prediction models based on functional traits are comparable with models based on phylogeny in terms of prediction performance (Fig. 1 and S.4). Furthermore, when both functional traits and phylogeny were included in a single model, relative contributions of phylogeny to prediction were almost negligible in most benefits (Fig. 2 and S.5). These results suggest that functional traits consistently play important roles as determinants of ecosystem services even when sociocultural backgrounds are important for the service.

Some associations between functional traits and benefits detected in this study are quite reasonable and possibly causal relationships. For example, the positive association between physical strength of leaves and religious uses (Fig. 3o) seems reasonable because, in Japan, evergreen (usually has stronger leaves than deciduous species) has religious meanings as an emblem of the vital force and persistence of life (Shinto Education Institute of the Association

of Shinto Shrines, 2004). Additionally, even in evergreen species, stronger leaves that are resistant to wilt may be preferred for ritual uses of cut branches (e.g. as a sacred ornament of shrines). Seed size was important for edible plants (Fig. 3d) because the proportion of species used as nuts was higher than other usages in our analysis (45 of the 67 edible plants were used as nuts) and larger seeds is obviously required for nuts. Larger flower and fruits which was required for use as display in tea ceremony and motif for haiku poem (Fig. 3l, m) seem important for ornamental value (Goodness et al., 2016). Positive association between use as dye and leaf phenol content (Fig. 3f) is not surprising because many natural dyes, e.g., fustin of *Toxicodendron succedaneum* and tannic acid of *Castanea crenata*, are phenolics (Mitsuo, 1997). It seems also natural that larger stature is required for use as timber for furniture (Fig. 3a).

In contrast, some associations should not be interpreted as a causal relationship. For some benefits, traits essential for the provisioning were clearly not included in the model due to lack of trait data at this moment, e.g. amount of nectar for honey source and physiological adaptations for salt tolerance. In these benefits, it appears that some functional traits which are expected to correlate strongly with a truly important trait were detected as an important trait. For example, it is unlikely that size of flower or inflorescence itself is important for honey source. However, the size would be a good indicator of amount of nectar because both traits are important for attraction of pollinators (Orban and Plowright, 2014). For another example, although physiological adaptation to salt was not available for our species, this influence may be alleviated by a correlation between physiological adaptation and physical one such as leaf strength because both types of adaptation are important for salt tolerance (Acosta-Motos et al., 2017). It should be noted that some associations, e.g. a negative association between flower size and use as bed log for mushroom (Fig. 3c), are possibly not explained reasonably by correlations among traits.

The fact that prediction performances were similar among the three models, i.e., trait model, phylogeny mode, and trait and phylogeny model (Fig. 1), may indicate that functional traits and phylogeny are not complementary to each other as explanatory variables for the beneficial attributes. Such a situation can occur only when all traits responsible for the benefits are strictly clumped in some taxa. An alternative, more likely interpretation of the result is that prediction performances of trait models remained similar extents to those of phylogeny models due to lack of some essential traits. The 22 traits used in my model are far from complete and some causally important traits were not included for most benefits. For example, although the positive association between adult height and benefit as wood for furniture seems a causal relationship as described above, some other traits that were not included in our model such as color, grain, and the length of fiber, would also be influential for the benefit. If such traits have information complementary to the 22 traits and phylogeny, prediction performances of trait models will outperform those of phylogeny model with further accumulation of trait data. In either case, the results in this chapter suggest that

a trait-based analysis of ecosystem services is as effective as a phylogeny-based analysis even at present.

As a whole, the analysis in this chapter indicates that diverse traits of various organs are required to predict the 15 benefits (Fig. 4). Functional traits whose roles as response traits against various environment and as effect traits for many ecosystem functions (e.g., adult height and leaf strength) were important also for these benefits. In addition, less-frequently investigated traits such as flower size, fruit size, and root branching intensity were also important. Three of the five cultural services were associated with reproductive traits although these traits have been rarely considered in past studies that often put their focuses on associations between vegetative traits and carbon/nutrient cycling (Goodness et al., 2016; Hevia et al., 2017).

Associations between functional traits and beneficial attributes may be important as a basis of synergies and trade-offs among ecosystem services. Some coappearances of benefits among the species that detected in the chapter 2 can be explained by relationships between functional traits and benefits. For example, benefits as motif of haiku poem and material of child's play were often provided together by a single species because both benefits are positively associated with fruit size (Fig. 3m, n). Likewise, the trend that a species combines salt tolerance and religious value can be explained by their positive associations with leaf strength (Fig. 3i, o). Meanwhile, such species rarely beneficial in terms of autumn color, which is negatively associated with leaf strength. (Fig. 3k). Whether these coappearances of benefits at a species level are responsible for synergies/trade-offs and bundles of services at a landscape level is an important theme for future studies, which was partly addressed in the chapter 4.

The identification of effect traits on benefits of tree species, which is achieved in this chapter, will help us understand how tree communities contribute to provisioning of ecosystem services. Because functional traits play an essential role also as a determinant of responses of tree species to spatiotemporal heterogeneity in environment, a trait-based analysis enables to understand impacts of environmental changes on ecosystem services. Numerous studies have reported changes in functional compositions with climatic gradients (Fortunel et al., 2014; Laughlin et al., 2011), succession (Aiba et al., 2016; Ruiz-Benito et al., 2017; Weiher et al., 2011), and land use intensity (Allan et al., 2015; Carreno-Rocabado et al., 2012; Chillo et al., 2018). For example, in Japanese forests, community weighted mean of adult height, LMA and seed mass increases with the secondary succession after land use change (Aiba et al., 2016). As a result, potential value of forests in terms of provisioning of wood for furniture, pulp, and seed source of salt tolerant species may increase with succession. 4

Conclusions

In this chapter, I identified potential effect traits of 15 benefits of tree species which have been rarely

investigated and whose values as a service often depend on sociocultural backgrounds. Performances of functional traits as explanatory variables of the benefits were comparable to those of phylogeny although some important traits were unavailable. Many essential traits that govern plant's responses to environment were often important also for the benefits, suggesting that these traits mediate impacts of human disturbance such as climate change and land-use change on various ecosystem services. These findings that significant associations between functional traits and benefits are widespread facilitate a comprehensive trait-based analysis on roles of community assembly processes in provisioning of ecosystem services.
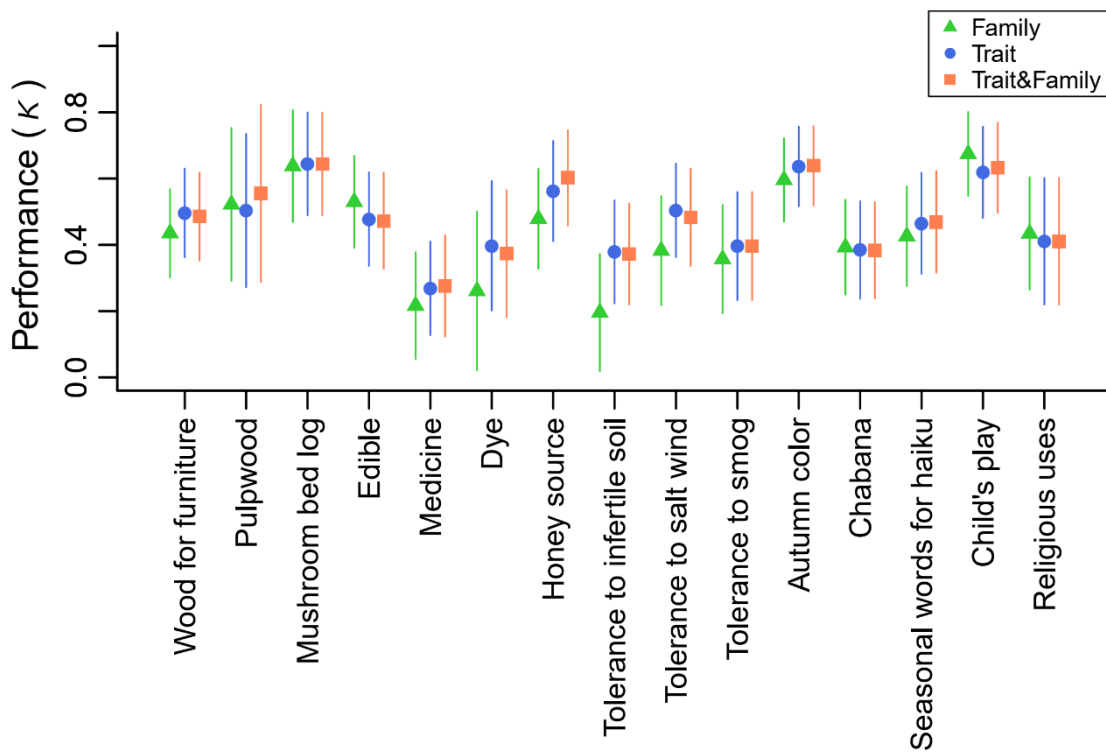
Fig. 1. Prediction performances of GBM models evaluated by Cohen's kappa coefficients. Results for three different models, i.e. family only model, trait only model, and family and trait model.
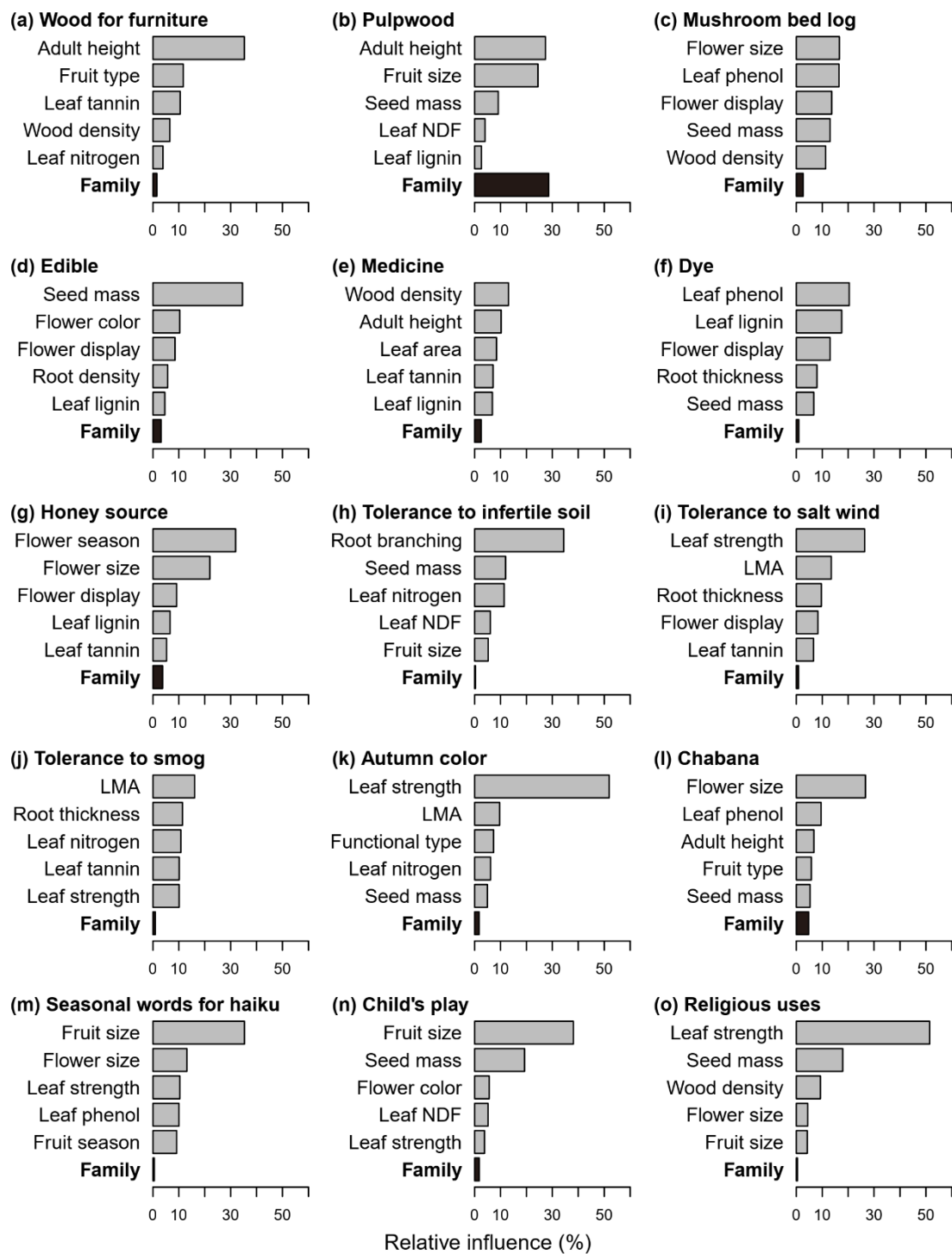
Fig. 2. Relative influences of the 5 most influential traits and family for each benefit. Family was indicated in bold labels and black bars.
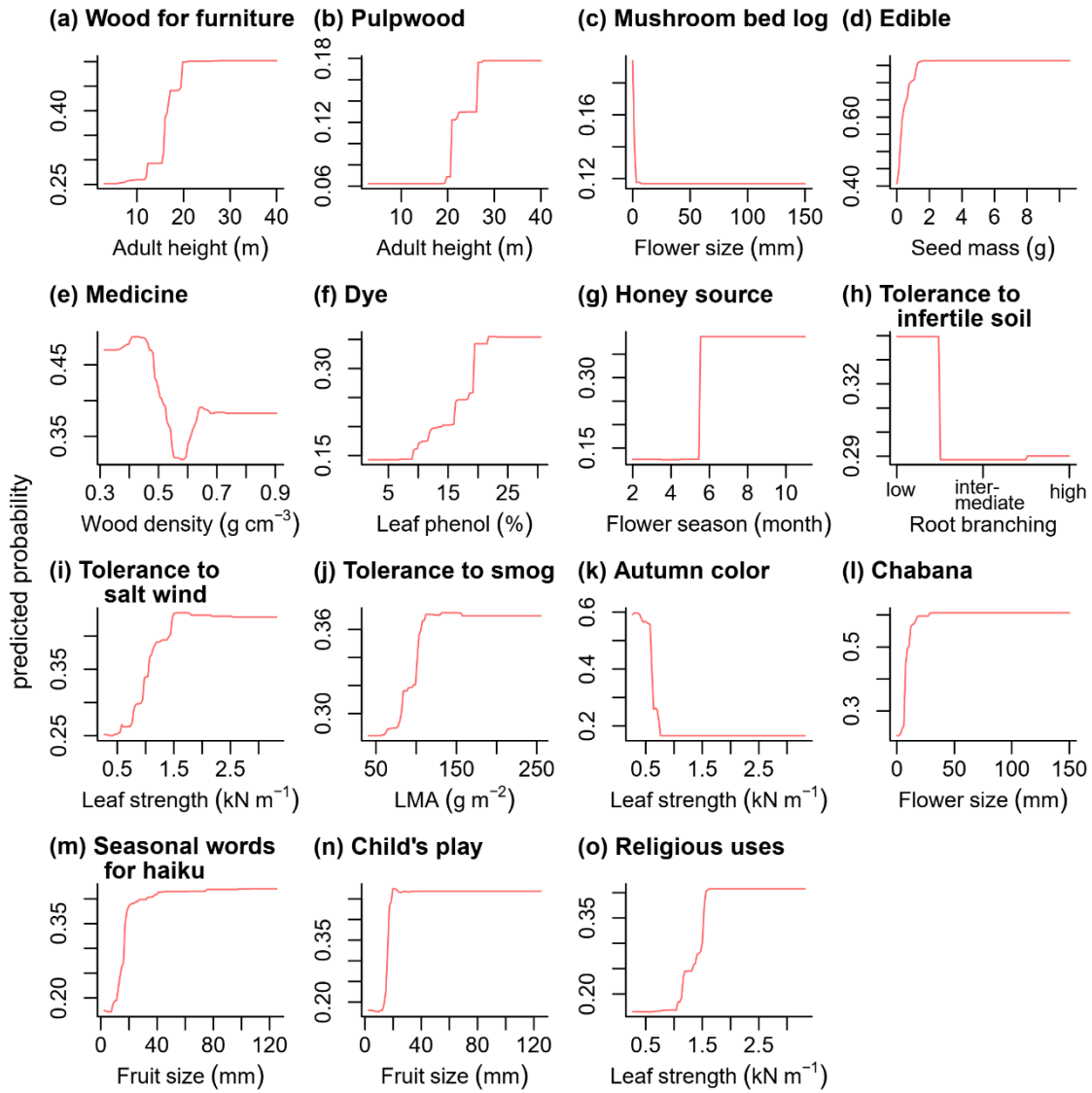
Fig. 3. Partial dependence plots of beneficial attributes for the most influential traits in the traits and family model.
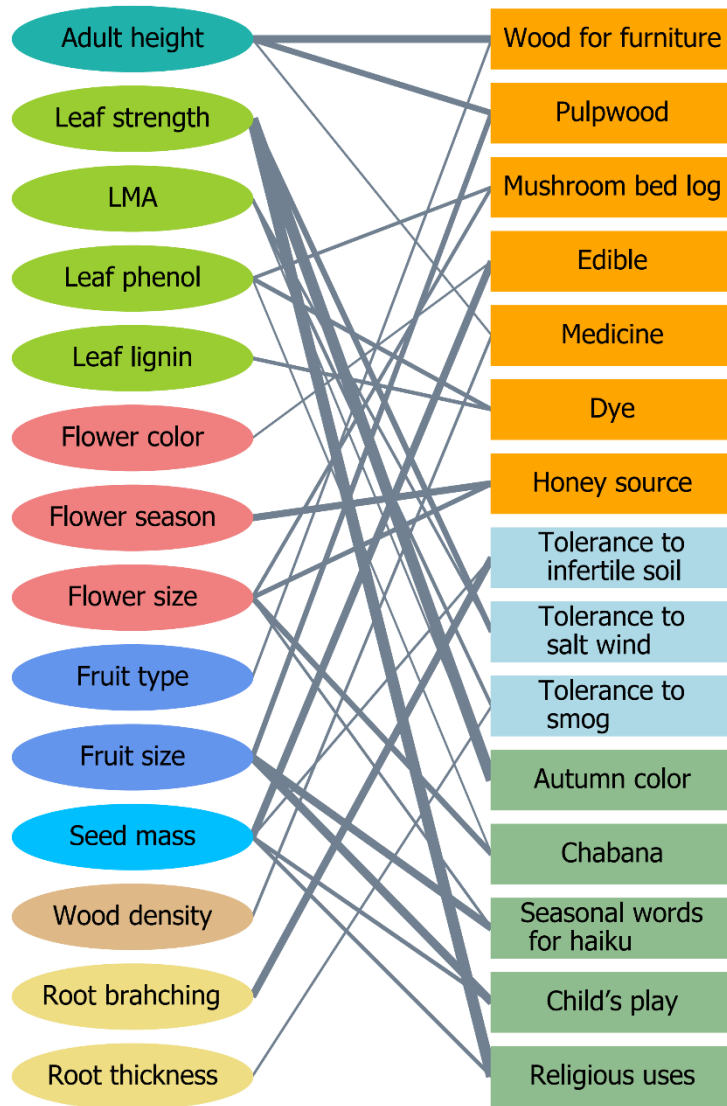
Fig. 4. Summary of the most and the second most influential functional traits for the 15 benefits. Width of the lines are proportional to the relative influence.

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Chapter 4: Importance of species identity and community composition for ecosystem services of tree communities

Introduction

Species identity and the diversity within communities have various effects on the functions of communities (Cardinale et al., 2012; Diaz et al., 2007; Garnier et al., 2004; Tilman et al., 2014). Important roles of both community weighted mean values of traits (CWM, the mean of trait values in a community which is weighted by the relative abundance of each species, representing the dominant trait value in a community) and species diversity within communities as a determinant of ecosystem functions of plant communities have been demonstrated in numerous studies. For example, CWM of leaf dry matter content negatively correlates with decomposition rate (Fortunel et al., 2009; Garnier et al., 2004; Quested et al., 2007), and species or functional diversity is a key property for over-yielding (Duffy et al., 2017; Paquette and Messier, 2011; Tilman et al., 2014). The number of functions provided by a single community, i.e. multifunctionality, also increases with increasing species richness (Gamfeldt et al., 2013; Hector and Bagchi, 2007; Isbell et al., 2011; Maestre et al., 2012; Zavaleta et al., 2010) and functional diversity (Finney and Kaye, 2017; Gross et al., 2017; Mouillot et al., 2011).

Species composition would be also important for ecosystem services provided by a plant community. However, many ecosystem services are different from ecosystem functions in that value of a species is specific to a certain sociocultural context and associations with species attributes are often unclear. For example, plant species preferred as a wild edible plant are different depending on cultural and economic backgrounds of the consumers (Ghirardini et al., 2007; Koide and Kadoya, 2019). Similarly, it is obvious that a species sacred for a religion is beneficial only for believers of the religion. It has been unclear whether strong associations with species attributes can be expected for such kinds of ecosystem services. As a result, studies on relationships between community composition and ecosystem services have been considerably biased to a handful of services whose benefits have been considered universal irrespective of sociocultural backgrounds, such as carbon sequestration and nutrient cycling (de Bello et al., 2010; Hevia et al., 2017).

In the chapter 2 and 3, I demonstrated remarkably non-random relationships between tree species and a wide range of ecosystem services including those deeply associated with cultural backgrounds in Japan. The main findings in these chapters were following: (1) Tree species which contribute to each ecosystem services are either more or less overlapped depending on the combination of ecosystem services, (2) the number of ecosystem services provided by a single tree species is considerably different among species, (3) all the 15 benefits studied are

significantly predictable by unique suites of functional traits of tree species. Those results suggest that, under random community assembly process, (1) coappearance frequencies of ecosystem services in communities are at least partly explained by those in species and (2) ecosystem multifunctionality increase with species richness and/or functional diversity due to complementarity in benefits among species and/or increasing probability of including at least one relatively multipurpose species.

However, whether such patterns can be observed in actual tree communities is unclear because actual community assembly processes are more or less non-random (Cornwell and Ackerly, 2009; Fortunel et al., 2014; Kraft et al., 2008; Weiher et al., 2011) and occurrence frequencies are considerably different among species (Boulangeat et al., 2012; Gotzenberger et al., 2012; Weiher et al., 2011). For example, although two ecosystem services associated with light and heavy wood respectively will be provided by different species, it is uncertain whether these two services are provided together at a community level. This is because a local community may be functionally divergent, i.e., includes both light-wooded and heavy-wooded species more frequently than random expectation, due to assembly processes such as local niche partitioning. In such a case, the two services may be frequently provided together by a single community although they are rarely provided together by a single species. For another instance, if a highly versatile species occurs very frequently, communities would be homogeneously multifunctional and thereby any other patterns in ecosystem services would be obscured.

In this chapter, I focused on the 15 benefits of 159 trees species in 1,086 temperate tree communities to investigate patterns in the multifunctionality. Ecosystem services potentially provided by tree communities were estimated by relating vegetation survey data with beneficial attributes of each species. I first evaluated tendency of coappearance for the 105 possible pairs of the services among the communities and compared the frequencies with those at a species level. Then associations of total number of services in each community, i.e. multifunctionality, with three biodiversity indices, that is, species richness, functional diversity, and phylogenetic diversity, were examined. I aimed to answer the following questions: (1) Are associations among ecosystem services at a community level consistent with those at a species level? (2) Does multifunctionality of tree communities increase with the biodiversity?

Materials and methods

Vegetation data

I used tree community data of primary and secondary temperate forests collected in the sixth and seventh National Survey on the Natural Environment from the Biodiversity Center of Japan (http://gis.biodic.go.jp/webgis/sc-006.html). This vegetation survey data was recorded all present species in each site. Of the 171 species selected in the

chapter 2, 159 species in 48 families and 91 genera for which required trait data (see below) were available were used in this chapter (Table S.1). Of the 10,715 census points in natural temperate forests, 1,086 points that are 225 m^2 in area and whose canopy and subcanopy layers were constituted only by the 159 target species were analyzed (Fig. 1).

Ecosystem services and multifunctionality

I focused on the 15 benefits that are identical with those in the chapter 2 (chapter 2. Table 1). A tree community including at least one species that is beneficial for a usage was considered to have potential to provide the service. Then the number of services provided by a single community was considered as the multifunctionality.

Biodiversity

Three indices of biodiversity that represent the different aspects, i.e. species richness, phylogenetic diversity, and functional diversity, were considered. Functional diversity was calculated as the sum of branch length of a dendrogram based on trait dissimilarity for species present in a community (Petchey and Gaston, 2006). The trait dendrogram was constructed based on 6 traits: leaf mass per unit area (LMA, g m^{-2}), adult height (m), wood density (g cm^{-3}), seed mass (g), flower size (mm), fruit size (mm). The details for measurements of these traits were described in the chapter 3. Similarly, phylogenetic diversity (Faith, 1992) was calculated as the sum of the branch length of the phylogenetic tree constructed in the chapter 2 (Fig. S.2).

Analysis

Coappearances for the 105 possible pairs of the services at a community level and at a species level were evaluated by Cohen's Kappa coefficients (κ). This coefficient indicates extent of coappearance for a pair of services as a relative value to the frequency of coappearance expected by chance. κ ＝−1, 0, and 1 indicate that two services never coappear, frequency of coappearance is identical with that expected by chance, and two services always coappear. The association between coappearances at a species level and those at a community level among the 105 possible pairs of services was examined by using a Pearson's correlation coefficient (*r*).

To evaluate importance of non-random assembly processes on the coappearance pattern, the observed κ values were compared with those of 200 randomly assembled communities generated by trial-swap method (Miklos and Podani, 2004). Trial-swap method is a method to randomize a community matrix by maintaining both occurrence frequency of each species and species richness in each site. In addition, whether number of pairs significantly higher or lower than the random expectation is significantly large (i.e. larger than the expectation from *p* = 0.025) or not was

examined by binomial test.

Associations between multifunctionality and tree diversity were examined using a gradient boosting machine (GBM, see the chapter 3 for the details). Multifunctionality of communities were modeled as a function of three diversity indices (species richness, functional diversity, and phylogenetic diversity), 3 geographical information (latitude, longitude and elevation) and vegetation type (4 categories: combinations of primary or secondary and cool temperate or warm temperate forest). Poisson distribution was assumed for the regression. To avoid overfitting, 10-hold cross-validation was performed and optimal values of following meta-parameters were determined: total number of trees, maximum depth of variable interactions, minimum number of observations in the tree terminal nodes, and subsampling rate. Shrinkage parameter was set at 0.001. Relative influences of explanatory variables were evaluated as the reduction in predictive performance when each explanatory variable was randomly permuted.

All analyses were performed using the R software package version 3.4.3 (R Core Team, 2017) with the *vegan* package (Oksanen et al., 2017) for calculation of functional diversity, the *picante* package (Kembel et al., 2010) for phylogenetic diversity, the *gbm* package (Ridgeway, 2007) to fit generalized boosted regression models, and the *cv.models* package (https://github.com/Marchen/cv.models) for parameter tuning and cross validation.

Results

Coappearances of ecosystem services in tree communities

Tendencies of coappearance for the 105 possible pairs of the ecosystem services at a community level were significantly positively correlated with those at a species level ($r = 0.49$, $p < 0.01$). However, the correlation was weaker than the expected correlations for randomly assembled communities ($r = 0.78 \pm 0.03$ [mean $\pm$ SD]). At a community level, 18 pairs of services were more often coappeared and 43 pairs were less often coappeared than the expectation from randomly assembled communities (P values for these trends are both < 0.01; Fig. 2), indicating that also non-random assembly processes are important for coappearances of services in tree communities.

Relationships between multifunctionality and biodiversity

Multifunctionality of tree communities significantly positively correlated with all the three indices of biodiversity. The correlation was strongest for functional diversity ($\rho = 0.71$) although the difference with species richness ($\rho = 0.67$) and phylogenetic diversity ($\rho = 0.68$) were not significant.

A GBM analysis in which vegetation type, elevation, latitude, and longitude were accounted revealed that variability in multifunctionality among sites was mostly explained (77.3% of the total explained variability) by

functional diversity. Multifunctionality virtually monotonically increased and then saturated with increasing functional diversity (Fig. 4). Contributions of species richness (1.7%) and phylogenetic diversity (5.5%) were limited. These results were robust even when only angiosperms or deciduous species were analyzed or when analyses were performed for each vegetation type separately.

Discussion

Forty-nine percent of the variation in coappearance frequencies for the 105 possible pairs of the services were explained by the coappearance frequencies at a species level. In other words, pairs of ecosystem services less-likely provided by a single species, e.g. chabana (ornamental flower in tea ceremony) vs pulpwood and dye vs pulpwood (Fig. 2), were less-often provided by a single community. In contrast, pairs of services frequently provided by a single species, e.g. seasonal words for haiku poem and material for child's play, were often provided together by a single community. Although interrelationships among ecosystem services at a regional scale or spatial heterogeneity in bundles of services have been investigated by numerous studies (Crouzat et al., 2015; Lin et al., 2018; Raudsepp-Hearne et al., 2010; Turner et al., 2014), few studies have focused on influences of species identity for the patterns. This study is, to my knowledge, the first to demonstrate characteristics of species, i.e., a bundle of services provided by a species, which is possibly determined by the functional traits as discussed in the chapter 3, are responsible for relationships among ecosystem services at a regional scale.

In addition to the coappearance pattern at a species level, nonrandom community assembly processes seem also important for the coappearance pattern at a community level. Both number of pairs of services more frequently coappeared at a community level and those less frequently coappeared at a community level were significantly larger than random expectation. This is possibly because a single trait or a suite of correlated traits plays important role for both community assembly and provisioning of a service. For tree communities, numerous studies have reported that a trait distribution pattern in a local community can be either convergent (Cornwell and Ackerly, 2009; Fortunel et al., 2014) or divergent (Cornwell and Ackerly, 2009; Stubbs and Bastow Wilson, 2004) as a result of assembly processes such as environmental filtering and biotic interactions. Because most of the 15 services are significantly associated with various functional traits, any nonrandom trait distribution in a community lead to either frequent or less-frequent coappearance of a pair of services. For example, a community constituted by many dense-wooded species as a result of environmental filtering would more frequently provide multiple services positively associated with wood density.

Multifunctionality of a community increased with biodiversity. Although similar positive associations have been reported by some previous studies (Finney and Kaye, 2017; Gross et al., 2017; Mouillot et al., 2011), the finding

in this chapter is meaningful as it shows biodiversity positively associates with multifunctionality even when many services affected by sociocultural backgrounds are included. Many services focused in this study, e.g. provisioning of food and medicine and importance for traditional culture and religion, have been rarely considered in ecological studies of ecosystem services despite their importance in society. The results in this chapter, along with the previous chapters on phylogenetic and functional signals in the beneficial attributes, demonstrate that promotion of multifunctionality by biodiversity is not specific to well-studied services such as carbon and nutrient cycling but can be generally expected for various ecosystem services whose phylogenetic and functional backgrounds have been rarely investigated.

When three indices of biodiversity, i.e., species richness, phylogenetic diversity, and functional diversity, were together included in a GBM model, heterogeneity in multifunctionality among communities was mostly explained by functional diversity. This fact indicates that, in these communities, species richness and phylogenetic diversity not accompanied by functional diversity do not contribute to the multifunctionality. This is reasonable because any benefits of organisms should arise from functional traits rather than taxonomic and phylogenetic identity *per se*. In addition, the positive association between functional diversity and multifunctionality remained significant even within a functional group (e.g., deciduous species) and a forest type (e.g., cool temperate forests), indicating that not only distinct functional differences (e.g., leaf habit) but also more subtle functional differences are important for multifunctionality.

As a whole, the analyses in this chapter indicate importance of community composition and the assembly processes for provisioning of ecosystem services at a regional scale. Understanding spatial heterogeneity, interrelationships, and multifunctionality in ecosystem services cannot be achieved without knowledge of associations between functional traits and ecosystem services, species compositions of communities, and community assembly processes. Spatiotemporal patterns in functional composition of plant communities and the responsible processes for the patterns have been reported by numerous studies, e.g., turn-over in functional compositions along environmental gradients (Cornwell and Ackerly, 2009; Fortunel et al., 2014; Laughlin et al., 2011), functional responses to recent climate change (Fauset et al., 2012; Ruiz-Benito et al., 2017; Zhang et al., 2018), and impacts of land-use change on functional composition (Aiba et al., 2016; Allan et al., 2015; Carreno-Rocabado et al., 2012; Chillo et al., 2018). The results suggest that all these patterns in functional compositions in communities would be at least partly responsible for spatiotemporal patterns in ecosystem services.

Conclusions

In this chapter, I showed a positive association between coappearance frequencies of ecosystems services at a species level and those at a community level for the first time. Additionally, the coappearance pattern at a community level was significantly deviated from the random expectation, suggesting that non-random assembly processes are also important for associations of services at a community level. Furthermore, I found a considerable positive association between functional diversity and multifunctionality of a tree community, which was rarely demonstrated for ecosystem services dependent on sociocultural factors. These results indicate that community composition and the assembly processes play essential roles in the provisioning of various ecosystem services. Further studies that associate community composition and dynamics with ecosystem services would greatly improve our understanding of ecosystem service provisioning.
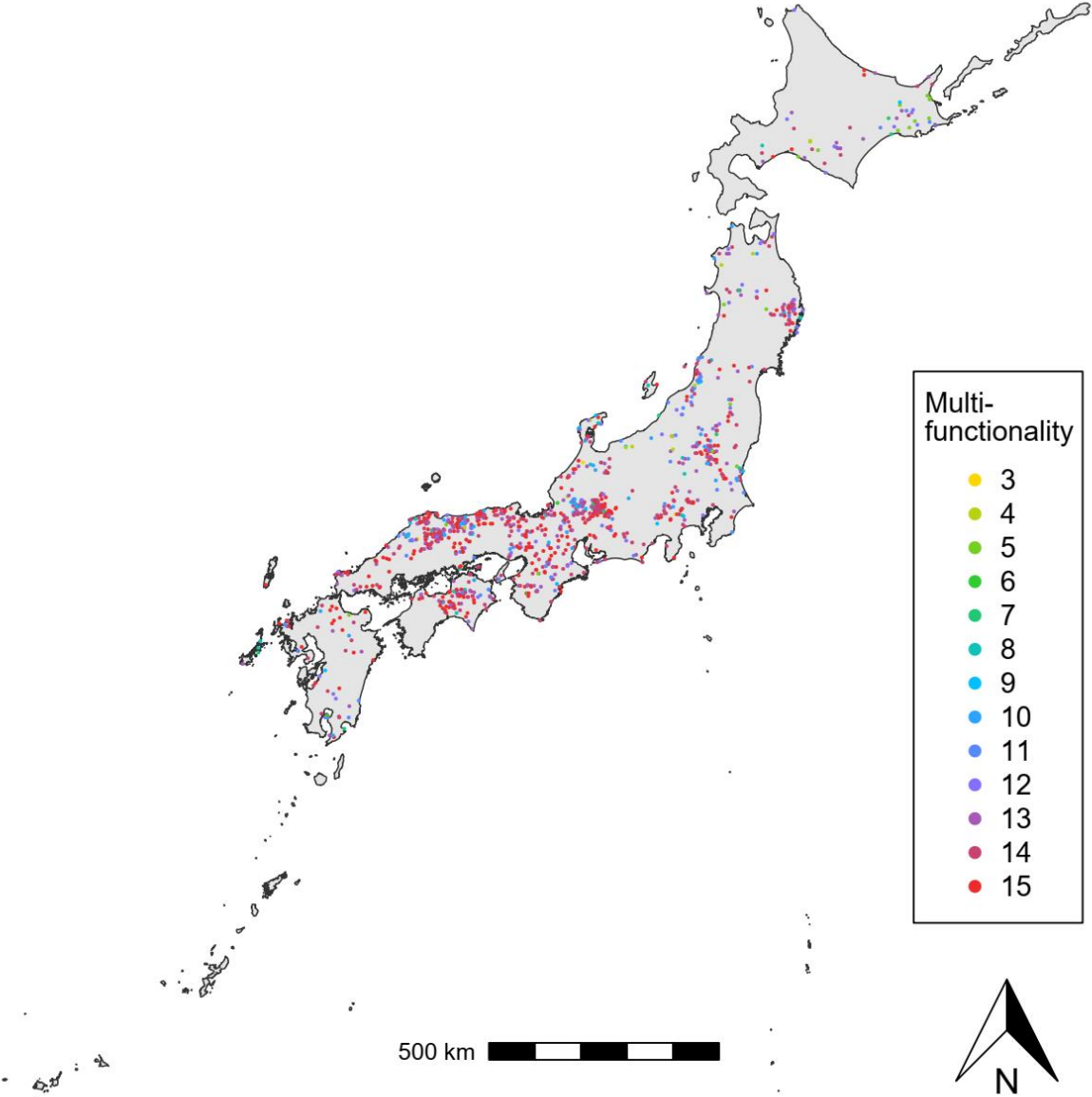
Fig. 1. Locations of 1,086 census points and the multifunctionality (the total number of services provided in each community).
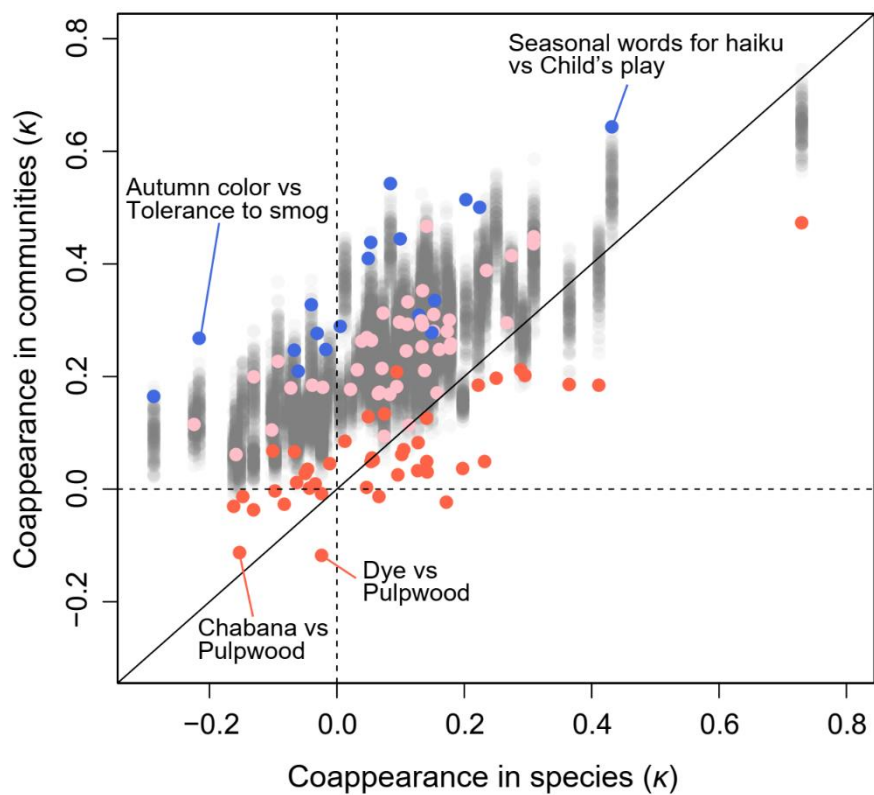
Fig. 2. Correlations between coappearance frequencies at a species level and those at a community level for the 105 possible pairs of the 15 services. Colored symbols indicate observed values. Gray symbols indicate coappearance frequencies in 200 randomly assembled communities generated by trial-swap method. Red (blue) symbols indicate values significantly lower (higher) than the random expectation.
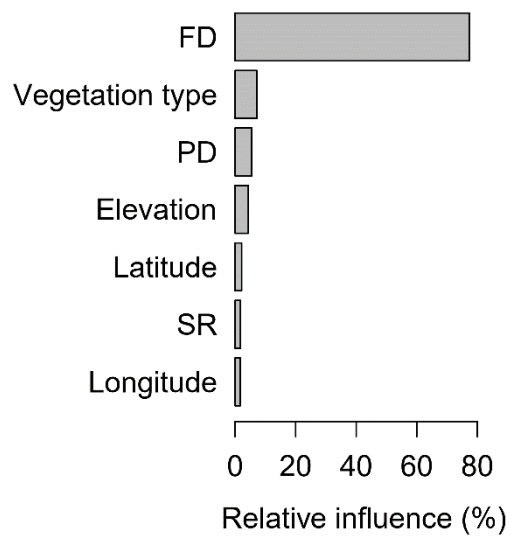
Fig. 3. Relative influences of each explanatory variables for multifunctionality of communities. Vegetation type was classified into 4 categories: primary or secondary forest in cool temperate or warm temperate regions.
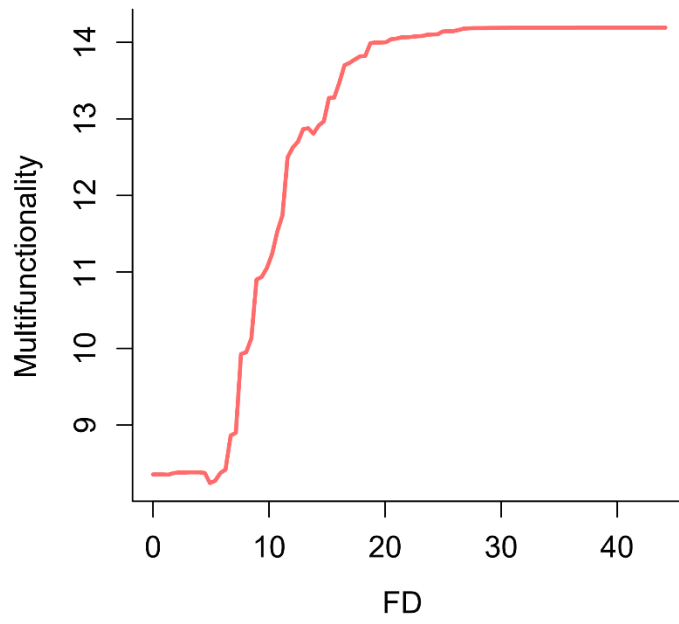
Fig. 4. Partial dependence of multifunctionality on functional diversity of a community

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Chapter 5: General discussion

In the chapter 2, I showed phylogenetic clustering in 15 beneficial attributes of tree species whose relationships with phylogeny and functional traits were unknown. This result suggests that these beneficial attributes have functional backgrounds although sociocultural factors are important for many of the 15 benefits. As a next step, in the chapter 3, I identified functional traits responsible for each of the 15 beneficial attributes, i.e. effect traits. These achievements suggest that most ecosystem services including those have been rarely focused in community ecology have a linkage with community composition and dynamics via phylogeny and functional traits. Therefore, investigations on such contributions of community composition and dynamics would greatly improve our understanding on processes of ecosystem service provisioning. As an example, in the chapter 4, I examined (1) How associations among benefits at a species level is important at a community level, and (2) Whether biodiversity of a community increase the multifunctionality. For associations among benefits at a community level, both associations at a species level and nonrandom community assembly processes were important. Multifunctionality of a community increased with the functional diversity. These findings demonstrate importance of considering community composition and the assembly processes for understanding spatiotemporal patterns in ecosystem services.

It is interesting future theme that whether our findings in tree species in Japan are general across cultural regions. Associations between functional traits and ecosystem services might be similar among cultures because physical, physiological, and psychological effects of a functional character should be at least partly shared by all human beings. For instance, medicinal plants that has been traditionally used in geographically separate and botanically disparate regions tend to belong to same phylogenetic clades (Saslis-Lagoudakis et al., 2012). This is because drug efficacy is common to humans and medicinal compounds often cluster in some phylogenetic clades (Garnatje et al., 2017; Saslis-Lagoudakis et al., 2012). For wild foods, volume of edible parts for the collecting effort and not so hard texture might be commonly important (Kosic et al., 2017; Schulp et al., 2014). People would generally feel that larger flower is beautiful (Lindemann-Matthies and Bose, 2007). Alternatively, it is also likely that trait-service associations are contrasting among cultures. For example, it is not uncommon that a spice with a characteristic taste that is highly preferred in a country is avoided by foreigners. Although evergreen plants often symbolize eternity and vitality in countries of higher altitudes, people in tropics may not think the trait as valuable. In such cases, associations of ecosystem services with phylogeny and functional traits would be specific to a cultural background. If trait-service associations are globally consistent even for services whose value depends on sociocultural backgrounds, functional traits can be used as a global indicator of services just like LMA for productivity. In contrast, if culture-specific associations are detected, services' responses to environment including human disturbances also

would differ among cultures even when functional responses of communities are similar.

In this thesis I established a basis for trait-based analyses of ecosystem services. Identification of effect traits for various ecosystem services allow us to link various achievements in functional analyses of communities with ecosystem services. For example, my achievements enable linking functional responses of tree communities to human disturbances with ecosystem services. Because species responses to environment are determined by their functional traits, functional compositions of communities are modified by human impacts such as climate change (Fauset et al., 2012; Ruiz-Benito et al., 2017; Zhang et al., 2018) and land-use changes (Aiba et al., 2016; Allan et al., 2015; Carreno-Rocabado et al., 2012; Chillo et al., 2018). In Japan, functional diversity decreases in secondary forests established after a land-use change at least in some conditions (Aiba et al., 2016). Combined with my finding in the chapter 4 that multifunctionality increased with functional diversity, a land-use change would negatively affect multifunctionality of a tree community in Japan. Studies on influences of community assembly processes on spatiotemporal patterns in ecosystem services also would be interesting. Assembly processes such as environmental filtering, where response traits mediate the survival or elimination of species in a certain environment (Lavorel and Garnier, 2002; Suding et al., 2008), often make trait distribution in a local community convergent (Weiher et al., 2011). Such processes would restrict kinds of ecosystem services provided by a local community, which may cause trade-offs of ecosystem services among local communities. As a result, heterogeneous vegetation, which can provide different bundles of ecosystem services, may be more important for multifunctionality at a landscape scale than random expectation. Such trait-based approaches for ecosystem services based on my achievements will improve mechanistic understanding of the provision of multiple ecosystem services by species and communities. The mechanistic understanding is essential for ecosystem management for sustainable use of ecosystem services in changing world.

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Supplementary information

Table S.1. Tree species studied and their benefits.

Id	Clade	Family	Scientific name	Number of benefits			Benefits														
				Mean for clade	Mean for family	species	WF	PW	BM	EW	MU	DY	HS	IN	SW	SM	AC	CH	SH	CP	RU
1	Coniferae	Pinaceae	*Abies firma* **Siebold et Zucc.**	4	4	3	1	1													1
2			*A. homolepis* **Siebold et Zucc.**			1		1													
3			*A. sachalinensis* **(F.Schmidt) Mast.**			1		1													
4			*Pinus densiflora* **Siebold et Zucc.**			8	1	1	1		1			1					1	1	1
5			*P. parviflora* **Siebold et Zucc.**			4	1												1	1	1
6			*P. thunbergii* **Parl.**			9	1	1			1			1	1	1			1	1	1
7			*Tsuga sieboldii* **Carrière**			1		1													
8		Cupressaceae	*Chamaecyparis obtusa* **(Siebold et Zucc.) Endl.**		5	7	1	1			1			1	1	1					1
9			*Cryptomeria japonica* **(Thunb. ex L.f.) D.Don**			6	1				1	1							1	1	1
10			*Juniperus rigida* **Siebold et Zucc.**			1					1										
11			*Thujopsis dolabrata* **(L.f.) Siebold et Zucc.**			4	1				1			1	1						
12		Taxaceae	*Cephalotaxus harringtonii* **(Knight ex Forbes) K.Koch**		3	1				1											
13			*Torreya nucifera* **(L.) Siebold et Zucc.**			4					1	1						1			1
14		Podocarpaceae	*Podocarpus macrophyllus* **(Thunb.) Sweet**		6	6	1				1	1			1			1		1	
15	Basal angiosperms	Schisandraceae	*Illicium anisatum* **Gaertn.**	1	1	1															1

No.	Group	Family	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14
16	Magnoliids	Lauraceae	*Cinnamomum camphora* (L.) J.Presl	4	3	6	1		1		1	1	1			1	
17			*C. tenuifolium* (Makino) Sugim. ex H.Hara			7	1		1	1	1	1	1				1
18			*Lindera erythrocarpa* Makino			1								1			
19			*L. obtusiloba* Blume			2								1	1		
20			*L. praecox* (Siebold et Zucc.) Blume			3								1	1	1	
21			*L. triloba* (Siebold et Zucc.) Blume			3				1				1	1		
22			*Litsea coreana* H.Lev.			1								1			
23			*Machilus japonica* Siebold et Zucc. ex Blume			2	1	1									
24			*M. thunbergii* Siebold et Zucc.			8	1	1	1	1	1	1	1			1	
25			*Neolitsea aciculata* (Blume) Koidz.			0											
26			*N. sericea* (Blume) Koidz.			2						1	1				
27		Magnoliaceae	*Magnolia kobus* DC.		5	7			1		1	1	1	1	1	1	
28			*M. obovata* Thunb.			6		1	1		1			1	1	1	
29			*M. salicifolia* (Siebld et Zucc.) Maxim.			3		1	1					1			
30	Basal eudicots	Trochodendraceae	*Trochodendron aralioides* Siebold et Zucc.	1	1	1			1								
31		Sabiaceae	*Meliosma myriantha* Siebold et Zucc.		1	1								1			
32			*M. rigida* Siebold et Zucc.			1											1
33		Eupteleaceae	*Euptelea polyandra* Siebold et Zucc.		2	2			1					1			
34	Malvids	Rutaceae	*Phellodendron amurense* Rupr.	5	5	7	1		1	1	1	1	1				
35			*Zanthoxylum ailanthoides* Siebold et Zucc.			2			1		1						

No.	Family	Species															
36	Simaroubaceae	*Picrasma quassioides* **(D.Don) Benn.**	1	1			1										
37	Sapindaceae	*Acer amoenum* **Carrière**	5	5	1								1		1	1	1
38		*A. carpinifolium* **Siebold et Zucc.**		4	1								1		1	1	
39		*A. cissifolium* **(Siebold et Zucc.) K.Koch**		3									1		1	1	
40		*A. crataegifolium* **Siebold et Zucc.**		5	1		1						1		1	1	
41		*A. distylum* **Siebold et Zucc.**		3									1		1	1	
42		*A. japonicum* **Thunb.**		5	1								1	1	1	1	
43		*A. maximowiczianum* Miq.		4				1					1		1	1	
44		*A. micranthum* **Siebold et Zucc.**		3									1		1	1	
45		*A. palmatum* **Thunb.**		6	1		1						1	1	1	1	
46		*A. pictum* **Thunb.**		8	1	1	1	1				1	1		1	1	
47		*A. rufinerve* **Siebold et Zucc.**		6	1		1						1	1	1	1	
48		*A. shirasawanum* **Koidz.**		4	1								1		1	1	
49		*A. sieboldianum* Miq.		4	1								1		1	1	
50		*A. tenuifolium* (Koidz.) Koidz.		3									1		1	1	
51		*Aesculus turbinata* **Blume**		11	1		1	1	1	1		1	1	1	1	1	
52	Anacardiaceae	*Rhus javanica* **L.**	7	12		1	1	1	1	1	1	1	1		1	1	1
53		*Toxicodendron succedaneum* **(L.) Kuntze**		7				1	1	1		1	1	1				1
54		*T. sylvestre* **(Siebold et Zucc.) Kuntze**		4			1	1	1				1				
55		*T. trichocarpum* **(Miq.) Kuntze**		5			1		1			1	1	1			

No.		Family	Species															
56		Malvaceae	*Tilia japonica* (Miq.) Simonk.		3	3			1		1			1				
57			*T. maximowicziana* Shiras.			2					1			1				
58		Staphyleaceae	*Euscaphis japonica* (Thunb.) Kanitz		3	3			1					1	1			
59	Favids	Fabaceae	*Albizia julibrissin* Durazz.	5	8	11	1		1	1	1	1	1	1	1	1	1	1
60			*Maackia amurensis* Rupr. et Maxim.			4	1				1		1	1			
61		Rosaceae	*Aria alnifolia* (Siebold et Zucc.) Decne.		4	6	1		1			1	1	1	1			
62			*A. japonica* Decne.			2								1	1			
63			*Cerasus jamasakura* (Siebold ex Koidz.) H.Ohba			7	1			1	1	1		1	1	1		
64			*C. leveilleana* (Koehne) H.Ohba			4	1				1			1		1		
65			*C. maximowiczii* (Rupr.) Kom.			4	1				1			1		1		
66			*C. sargentii* (Rehder) H.Ohba			6	1			1		1		1	1	1		
67			*Laurocerasus spinulosa* (Siebold et Zucc.) C.K.Schneid.			0												
68			*Padus buergeriana* (Miq.) T.T.Yu et T.C.Ku			3	1		1					1				
69			*P. grayana* (Maxim.) C.K.Schneid.			7			1	1	1	1	1	1	1			
70			*Photinia glabra* (Thunb.) Maxim.			3							1	1		1		
71			*Pourthiaea villosa* (Thunb.) Decne.			4		1		1				1	1			
72			*Sorbus commixta* Hedl.			6			1	1			1	1	1	1		
73		Moraceae	*Ficus erecta* Thunb.		4	2			1							1	
74			*Morus australis* Poir.			5	1		1	1	1				1			
75		Cannabaceae	*Aphananthe aspera* (Thunb.) Planch.		5	5			1	1	1	1				1	

No.	Family	Species													
76		*Celtis jessoensis* **Koidz.**		4	1			1	1				1		
77		*C. sinensis* **Pers.**		7	1			1	1		1	1	1	1	
78	Ulmaceae	*Ulmus davidiana* **Planch.**	3	4		1			1		1	1			
79		*U. laciniata* (Trautv.) **Mayr**		2					1				1		
80		*Zelkova serrata* (Thunb.) **Makino**		3	1					1					1
81	Rhamnaceae	*Hovenia dulcis* **Thunb.**	4	5	1			1	1		1			1	
82		*H. trichocarpa* **Chun et Tsiang**		2	1			1							
83	Betulaceae	*Alnus firma* **Siebold et Zucc.**	4	5		1			1	1		1	1		
84		*A. hirsuta* (Spach) **Turcz. ex Rupr.**		5	1				1	1		1	1		
85		*A. japonica* (Thunb.) **Steud.**		5	1				1	1		1	1		
86		*Betula ermanii* **Cham.**		4	1	1						1	1		
87		*B. grossa* **Siebold et Zucc.**		2	1								1		
88		*B. maximowicziana* **Regel**		4	1	1						1	1		
89		*B. platyphylla* **Sukaczev**		7	1	1			1	1	1	1			1
90		*B. schmidtii* Regel		1									1		
91		*Carpinus cordata* **Blume**		2			1						1		
92		*C. japonica* **Blume**		5	1			1		1			1	1	
93		*C. laxiflora* (Siebold et Zucc.) **Blume**		3	1			1					1		
94		*C. tschonoskii* **Maxim.**		2			1						1		
95		*Ostrya japonica* **Sarg.**		2	1								1		
96	Juglandaceae	*Juglans mandshurica* **Maxim.**	4	8	1			1	1	1	1	1	1	1	1

No.	Family	Species															
97		*Platycarya strobilacea* **Siebold et Zucc.**		1			1										
98		*Pterocarya rhoifolia* **Siebold et Zucc.**		2	1			1									
99	Myricaceae	*Morella rubra* **Lour.**	6	6			1	1	1		1	1	1				
100	Fagaceae	*Castanea crenata* **Siebold et Zucc.**	7	11	1		1	1	1	1		1			1	1	1	1
101		*Castanopsis cuspidata* (Thunb.) Schottky		9	1		1	1		1		1	1			1	1	1
102		*C. sieboldii* **(Makino) Hatus. ex T.Yamaz. et Mashiba**		9	1	1	1	1				1	1	1		1	1	
103		*Fagus crenata* **Blume**		4	1	1	1	1										
104		*F. japonica* **Maxim.**		3	1	1	1											
105		*Lithocarpus edulis* **(Makino) Nakai**		7			1	1		1	1	1	1		1			
106		*L. glaber* **(Thunb.) Nakai**		2				1							1			
107		*Quercus acuta* **Thunb.**		6			1	1				1	1				1	1
108		*Q. acutissima* **Carruth.**		7			1	1	1	1		1					1	1
109		*Q. aliena* Blume		4										1	1	1	1
110		*Q. crispula* **Blume**		7	1		1	1		1		1					1	1
111		*Q. dentata* **Thunb.**		12	1		1	1	1	1	1	1	1	1	1	1	1	1
112		*Q. gilva* **Blume**		6			1	1				1	1				1	1
113		*Q. glauca* **Thunb.**		6			1		1			1	1				1	1
114		*Q. myrsinifolia* **Blume**		7			1	1	1			1	1				1	1
115		*Q. phillyreoides* **A.Gray**		6				1			1	1	1				1	1
116		*Q. salicina* **Blume**		8			1	1	1		1	1	1				1	1

No.	Order	Family	Species																	
117			*Q. serrata* **Murray**			9	1		1	1	1	1		1				1	1	1
118			*Q. sessilifolia* **Blume**			3		1											1	1
119			*Q. variabilis* **Blume**			8		1	1	1		1			1	1			1	1
120		Salicaceae	*Idesia polycarpa* **Maxim.**		4	2					1			1						
121			*Salix caprea* **L.**			5							1		1			1	1		1
122		Euphorbiaceae	*Mallotus japonicus* **(L.f.) Müll.Arg.**		6	9		1	1	1	1	1	1	1		1	1			
123			*Neoshirakia japonica* **(Siebold et Zucc.) Esser**			2		1							1				
124		Elaeocarpaceae	*Elaeocarpus japonicus* **Siebold et Zucc.**		4	2		1	1										
125			*E. zollingeri* **K.Koch**			5		1	1			1		1	1				
126		Celastraceae	*Euonymus sieboldianus* **Blume**		7	7	1		1	1			1	1	1	1			
127	Saxifragales	Hamamelidaceae	*Distylium racemosum* **Siebold et Zucc.**	5	5	4							1	1	1			1	
128			*Hamamelis japonica* **Siebold et Zucc.**			6				1			1		1	1	1	1	
129		Daphniphyllaceae	*Daphniphyllum macropodum* **Miq.**		6	7			1	1			1	1		1	1	1	
130			*D. teysmannii* **Zoll. ex Kurz**			4							1	1		1			1
131		Cercidiphyllaceae	*Cercidiphyllum japonicum* **Siebold et Zucc. ex Hoffm. et Schult.**	5	5	5	1					1				1	1		1
132	Asterids	Ericaceae	*Lyonia ovalifolia* **(Wall.) Drude**	4	3	2										1	1		
133			*Pieris japonica* **(Thunb.) D.Don ex G.Don**			5							1	1	1		1	1	
134			*Vaccinium bracteatum* **Thunb.**			1				1									
135		Clethraceae	*Clethra barbinervis* **Siebold et Zucc.**		8	8			1	1	1	1	1	1	1		1		
136		Theaceae	*Camellia japonica* **L.**		4	8			1	1		1		1	1		1		1	1

No.	Family	Species													
137		*Stewartia monadelpha* **Siebold et Zucc.**		1									1			
138		*S. pseudocamellia* **Maxim.**		4				1				1	1	1		
139	Styracaceae	*Pterostyrax hispidus* **Siebold et Zucc.**	4	2				1				1				
140		*Styrax japonicus* **Siebold et Zucc.**		6				1	1	1	1		1			1
141		*S. obassis* **Siebold et Zucc.**		3				1	1			1				
142	Symplocaceae	*Symplocos coreana* **(H.Lev.) Ohwi**	1	0												
143		*S. glauca* **(Thunb.) Koidz.**		0												
144		*S. kuroki* **Nagam.**		1		1										
145		*S. prunifolia* Siebold et Zucc.		1								1				
146	Primulaceae	*Myrsine seguinii* **H.Lev.**	3	3	1	1						1				
147	Ebenaceae	*Diospyros kaki* **Thunb.**	7	7		1	1		1			1	1	1	1	1
148	Pentaphylacaceae	*Cleyera japonica* **Thunb.**	4	4				1		1	1					1
149		*Eurya japonica* **Thunb.**		5				1	1	1	1					1
150		*Ternstroemia gymnanthera* **(Wight et Arn.) Bedd.**		4			1	1		1	1					
151	Oleaceae	*Fraxinus lanuginosa* **Koidz.**	3	2	1		1									
152		*F. mandshurica* **Rupr.**		1	1											
153		*F. sieboldiana* **Blume**		2	1							1				
154		*Ligustrum japonicum* **Thunb.**		6				1	1	1	1	1				
155	Lamiaceae	*Callicarpa japonica* **Thunb.**	3	6				1		1		1	1	1	1	
156		*Premna microphylla* **Turcz.**		0												

No.	Family	Species			WF	PW	BM	EW	MU	DY	HS	IN	SW	SM	AC	CH	SH	CP	RU
157	Adoxaceae	***Viburnum furcatum* Blume ex Maxim.**	5	5											1	1	1	1	1
158	Araliaceae	***Chengiopanax sciadophylloides* (Franch. et Sav.) C.B.Shang et J.Y.Huang**	4	4				1	1		1				1				
159		***Dendropanax trifidus* (Thunb.) Makino ex H.Hara**		5							1	1	1		1			1	
160		***Gamblea innovans* (Siebold et Zucc.) C.B.Shang, Lowry et Frodin**		3				1	1						1				
161		***Kalopanax septemlobus* (Thunb.) Koidz.**		4				1	1	1					1				
162	Pittosporaceae	***Pittosporum tobira* (Thunb.) W.T.Aiton**	6	6					1				1	1	1			1	1
163	Aquifoliaceae	***Ilex pedunculosa* Miq.**	3	5							1	1	1		1			1	
164		***I. rotunda* Thunb.**		3									1			1	1		
165		***I. chinensis* Sims**		2							1				1				
166		***I. crenata* Thunb.**		4									1		1	1			1
167		***I. integra* Thunb.**		4							1				1	1		1	
168		***I. macropoda* Miq.**		2					1						1				
169	Cornaceae	***Cornus controversa* Hemsl. ex Prain**	5	7			1			1			1		1	1		1	1
170		***C. kousa* F.Buerger ex Hance**		6				1	1	1	1						1	1	
171		***C. macrophylla* Wall.**		2					1				1						

The number "1" in a column means that the species provides that benefit. Abbreviations of benefits: WF, wood for furniture; PW, pulpwood; BM, bed logs for mushroom cultivation; EW, edible wild plants; MU, medicinal uses; DY, dye; HS, honey source; IN, tolerance to infertile soil; SW, tolerance to salt wind; SM, tolerance to smog; AC, bright autumn color; CH, chabana; SH, seasonal words for haiku; CP, child's play; RU, religious uses. Scientific name of species used in chapter 3 are shown in bold tests.

Table S.2. Phylogenetic signals in subdivisions of the studied beneficial attributes.

Beneficial attribute	Attribute details	Phylogenetic signal	
		N	*D*
Edible	Edible parts:		
	Leaf	19	**0.652***
	Fruit and seed	45	**0.092****
	Flower	3	1.058
Medicine	Efficacy:		
	Analeptic	7	1.008
	Antiphlogistic	12	0.941
	Childhood diseases	5	1.228
	Circulatory	7	0.922
	Digestive	24	0.907
	External	35	0.877
	Eyes and teeth	3	1.319
	Female diseases	1	0.591
	Insecticide	4	0.979
	Nervous	9	0.937
	Otolaryngology	9	**0.622***
	Pains	5	0.713
	Respiratory	12	0.935
	Urinary	10	0.844
Dye	Color:		
	Red	20	1.08
	Brown	35	**0.681***
	Yellow	25	**0.390****
	Green	10	0.867
	Blue	2	0.652

	Purple	21	0.831
	Gray	30	**0.745***
Honey source	Nectar quality:		
	Excellent	13	**0.691***
	Good	24	**0.393****
Tolerance to infertile soil	Tolerance level:		
	Strong	14	**0.456****
	Somewhat strong	36	0.851
Tolerance to salt wind	Tolerance level:		
	Strong	25	**0.770***
	Somewhat strong	28	0.832
Tolerance to smog	Tolerance level:		
	Strong	13	**0.431****
	Somewhat strong	41	**0.834***
Autumn color	Color:		
	Red	32	**0.230****
	Orange	34	**0.378****
	Yellow	62	**0.335****
	Purple	2	**−0.100****
Seasonal words for haiku	Examples of poems:		
	6–15	11	0.724
		(10/141	0.746)
	16–25	26	**−0.220****
		(8/141	0.783)
	More than 25	12	**−0.174****
		(7/141	0.652)

Child's play	Part used:		
	Leaf	16	0.813
		(11/145	0.773)
	Flower	2	0.957
		(2/145	1.010)
	Fruit and seed	45	**−0.388****
		(20/145	**0.160****)
Religious uses	Usage:		
	Offering	34	**0.634***
		(28/165	**0.744***)
	Implement	7	0.873
		(7/165	0.885)
	Burn	8	0.791
		(7/165	0.735)
	Exorcise	6	**0.567****
		(6/165	**0.557****)

N is the number of tree species providing each benefit. Values in parentheses are the results of analyses at a vernacular-name level. The total number of species at the vernacular-name level (<171) is shown as the denominator. "D" is the D statistic of Fritz and Purvis (2010). *Significant deviation of the D value from 1 ($P_{D<1} < 0.05$), which indicates a phylogenetically non-random pattern; **no significant deviation of the D value from 0 ($P_{D>0} > 0.05$), indicating a strong signal that is as phylogenetically clustered as would be expected under a Brownian evolution model.

Table S.3. Overlap of beneficial species for the 105 possible pair of combinations of beneficial attributes (Sørensen index).

Pulpwood	Mush-room bed log	Edible	Medicine	Dye	Honey source	Tolerance to infertile soil	Tolerance to salt wind	Tolerance to smog	Autumn color	Chabana	Seasonal words for haiku	Child's play	Religious uses	
0.308	0.261	0.429	0.424	0.347	0.242	0.357	0.296	0.259	0.412	0.295	**0.491**	**0.448**	0.327	Wood for furniture
	0.174	0.075	0.140	0.115	**0.000**	**0.273**	0.116	0.114	**0.047**	**0.026**	0.094	0.114	0.192	Pulpwood
		0.404	0.240	0.303	0.179	0.325	0.337	0.310	0.182	**0.133**	0.282	**0.405**	0.303	Mushroom bed log
			0.537	**0.400**	0.297	0.404	**0.444**	0.407	0.361	0.339	0.357	**0.525**	0.340	Edible
				0.491	0.355	**0.550**	**0.472**	0.452	0.345	0.462	0.407	0.387	0.340	Medicine
					0.301	**0.419**	0.337	0.356	0.286	0.354	0.310	0.289	0.333	Dye
						0.276	**0.444**	**0.396**	0.302	0.351	0.235	0.220	0.274	Honey source
							0.563	**0.596**	**0.235**	0.418	0.388	0.385	0.349	Tolerance to infertile soil
								0.822	**0.164**	0.372	0.277	**0.430**	**0.472**	Tolerance to salt wind
									0.211	0.386	0.392	0.407	**0.489**	Tolerance to smog
										0.434	**0.462**	0.358	**0.114**	Autumn color
											0.389	0.280	0.208	Chabana
												0.627	0.310	Seasonal words for haiku
													0.467	Child's play

Legend:
- κ ≥ 0.5
- 0 < κ < 0.5
- κ ~ 0 (No fill)
- κ < 0
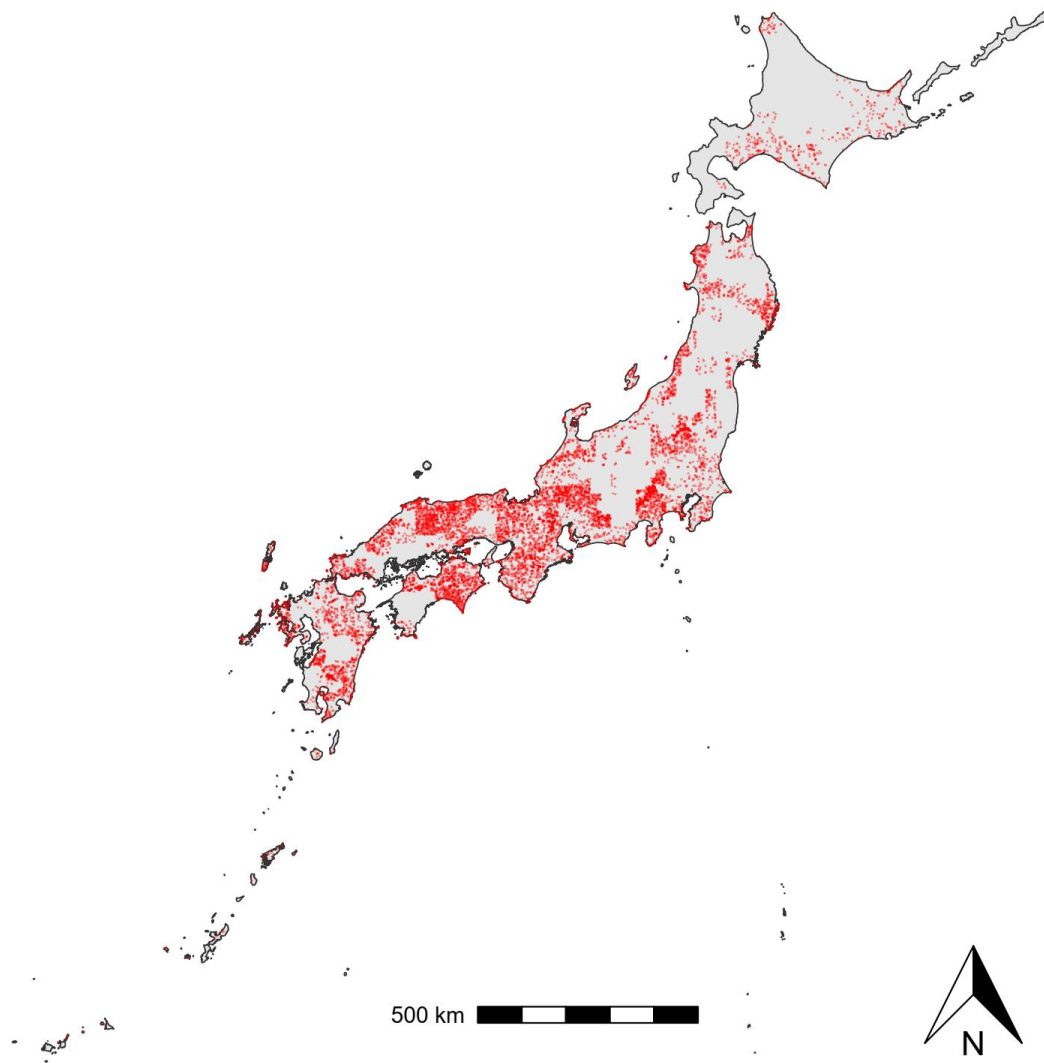
Cell shading reflects the estimated Kappa coefficient.

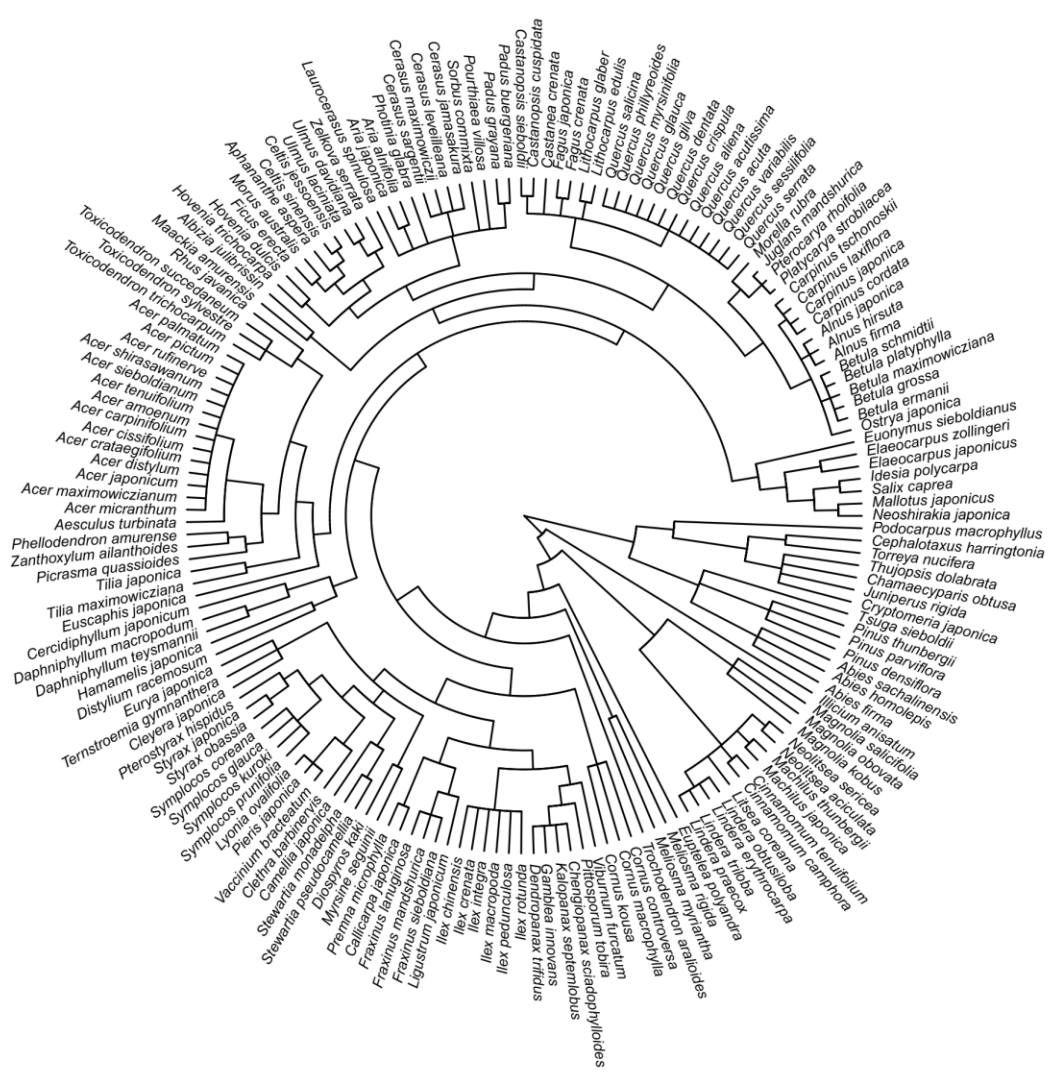**Fig. S.1.** Census points for vegetation survey data where the studied species occurred. The census data are from the Biodiversity Center of Japan (http://gis.biodic.go.jp/webgis/sc-006.html).

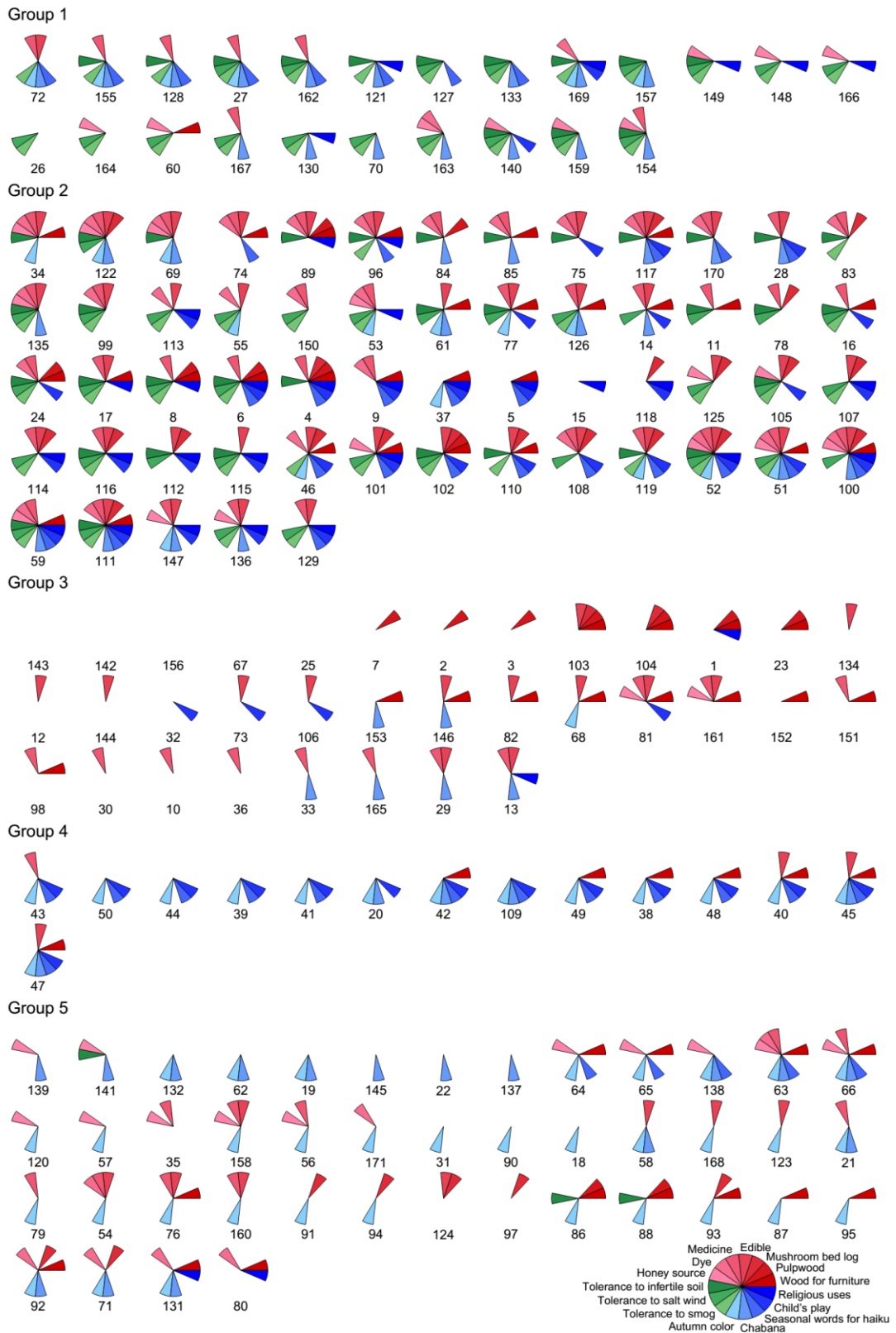**Fig. S.2.** Phylogenetic tree of the 171 studied species.

Fig. S.3. Bundles of beneficial attributes for the 171 tree species studied, grouped according to the results of cluster

analysis. Filled segments indicate the benefits that species can provide. Segment colors vary according to the category of ecosystem services: reds are provisioning services, greens are regulating and maintenance services, and blues are cultural services. Numbers under each plot correspond to the species identification numbers in Table A.1. Species are ordered according to the cluster dendrogram.
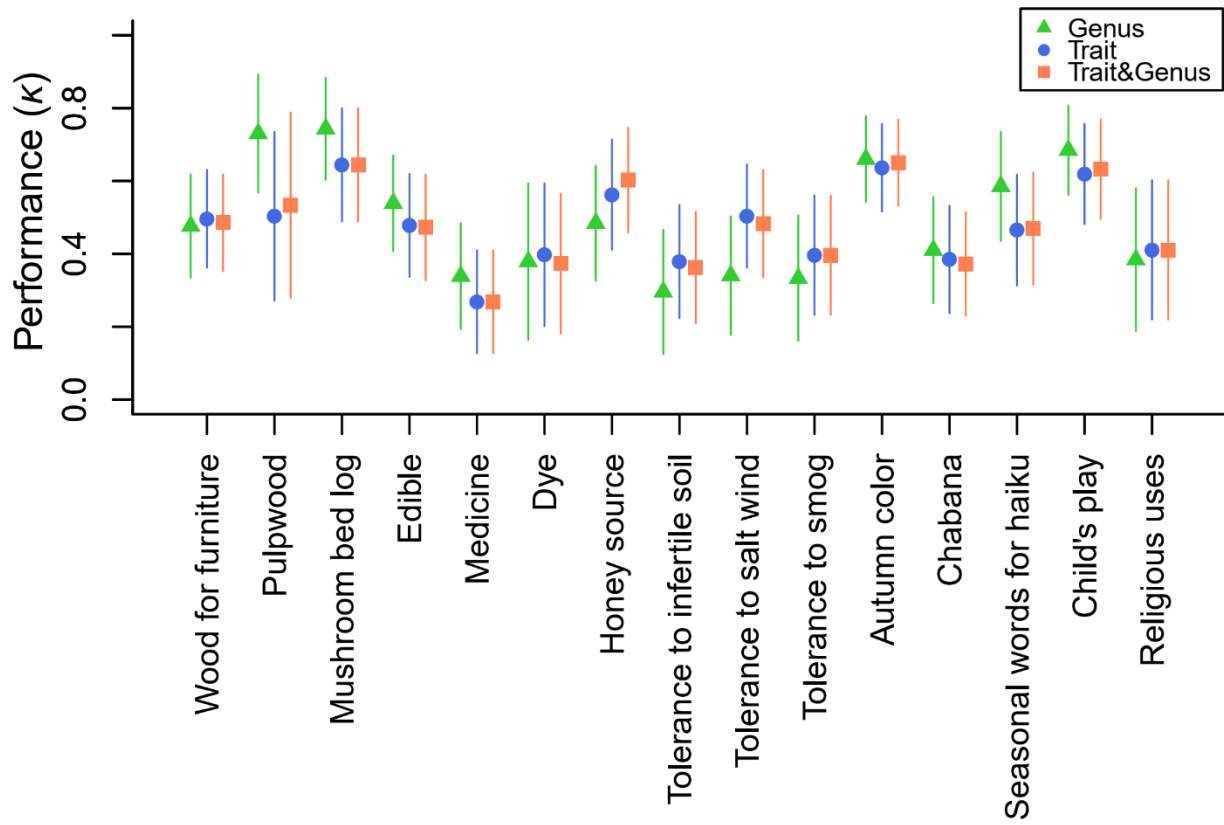
Fig. S.4. Prediction performances of GBM models evaluated by Cohen's kappa coefficients. Results for three different models, i.e. genus only model, trait only model, and genus and trait model.
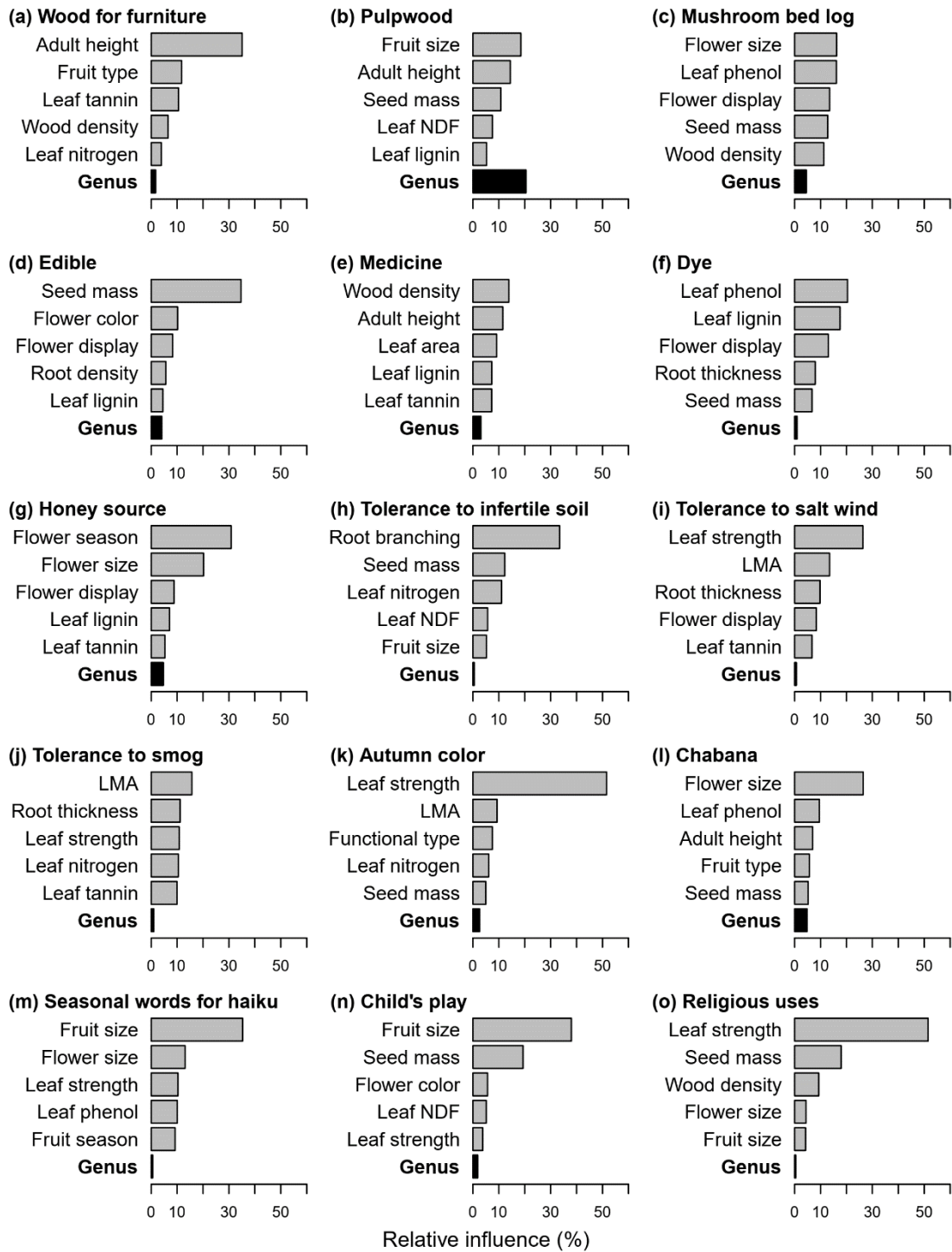
Fig. S.5. Relative influences of the 5 most influential traits and genus for each benefit. Genus was indicated in bold labels and black bars.
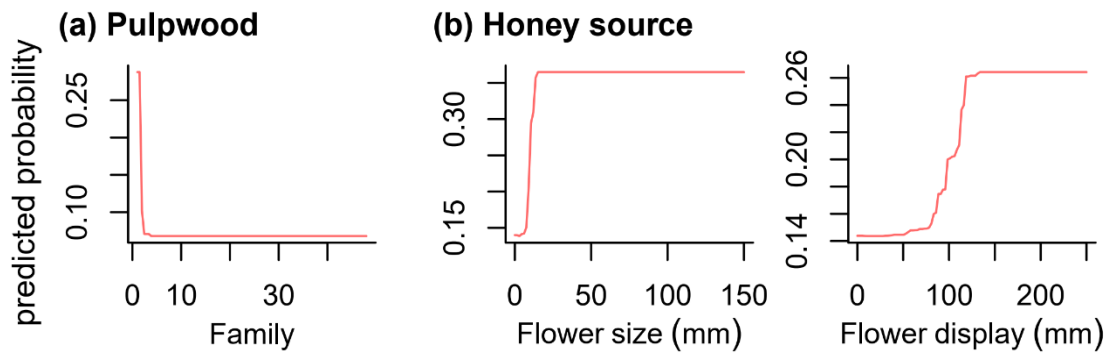
Fig. S.6. Partial dependence plots of (a) pulpwood species for numbered family, (b) honey sources for sizes of a flower and its display in the traits and family model.

References of functional type, adult height, seed mass, flower and fruit traits.

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