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

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ABSTRACT

Phylogenetic diversity is expected to be an important predictor of ecosystem multifunctionality because distant relatives are often more functionally different than close relatives. However, the general extent of non-random linkages between phylogeny and ecosystem services remains unclear. In this study, we examined phylogenetic clustering and associations of beneficial attributes of tree species that are essential for various aspects of ecosystem services to assess the generality of the phylogenetic bias in ecosystem service provision. Through literature mining, we compiled 15 benefits linked to a wide variety of ecosystem services for 171 tree species common in Japan to examine phylogenetic clustering in the beneficial attributes. In addition, we examined whether taxonomically different species provide different bundles, or suites, of benefits. Significant phylogenetic signals were detected in all 15 beneficial attributes even though some benefits are specific to Japanese culture. Beneficial species overlapped significantly more than random expectation for 25 of the 105 possible combinations of the benefits, whereas they differed significantly for eight 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 that phylogenetically distant species tended to have different bundles of beneficial attributes. Fabids tended to provide more kinds of benefits than species in other clades. Overall our analysis suggests that, at least in tree communities of Japan, phylogenetic diversity can potentially increase ecosystem multifunctionality via complementarity of beneficial attributes among phylogenetically distant species. Future analyses of actual relationships between phylogenetic diversity and multifunctionality of tree communities will provide further insights into the ecological processes sustaining ecosystem multifunctionality.

1. 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).

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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 study, we 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. 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 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. We specifically aimed (1) to quantify phylogenetic signals in these beneficial attributes, and (2) to explore the associations of the beneficial attributes among species. We hypothesized that phylogenetic clustering is general over the wide variety of benefits and that different phylogenetic groups provide different bundles of benefits.

2. Materials and methods

2.1. 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.

We 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 A.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 our 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. A.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.

2.2. Beneficial attributes of tree species

We 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, we 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).

As noted above, we excluded from our analysis tree species that are