




Geographic patterns of seed dormancy strategies along latitudinal and climatic gradients, Japanese East Asian islands

Akinori Fuji^{1,5}  · Buntarou Kusumoto^{1,2,4} · Takayuki Shiono¹ · Yasuhiro Kubota¹ · Werner Ulrich³ · John B. Dickie⁵ · Si-Chong Chen^{5,6}

Received: 10 February 2023 / Revised: 30 July 2023 / Accepted: 31 July 2023 /
Published online: 21 August 2023

© The Author(s) under exclusive licence to Japanese Federation of Statistical Science Associations 2023

Abstract

Aim Seed traits and climatic covariates are hypothesised to be potential drivers determining the large-scale patterns of plant diversity; seed dormancy strategies function to escape unfavourable seasons. The associations of dormancy with seed mass and dispersal mode might facilitate for better understanding of plant biogeography in relation to trait-based community assembly. Here, we explore the geographical patterns of dormancy/non-dormancy strategies to infer seed trait-dependent filtering/sorting processes associated with climate factors.

Location Japan.

Taxon Woody plants.

Methods We compiled data on seed mass, dispersal and dormancy for 696, 1196 and 662 species respectively. We quantified the relationships between dormancy, seed mass and dispersal mode, and their geographical patterns related to minimum temperature of the coldest month and the length of the unfavourable period for plant growth.

Results Seed masses of plants with anemochorous, zoochorous and hydrochorous dispersal decreased towards higher latitudes, but those of barochorous seeds increased. The proportions of physiologically dormant species were comparatively high at higher latitudes with increasing climate harshness, whereas non-dormant, large-seeded species occurred at both climatically milder, lower latitudes, and harsher, higher latitudes. These geographic patterns demonstrate that plant regeneration responses are the outcome of multi-dimensional interactions between seed dormancy, seed mass and dispersal mode .

Main conclusions Seed trait assembly patterns were shaped by correlative relationships between seed mass, dispersal modes and dormancy types in response to the minimum temperature and the unfavourable period. Physiologically dormant species with smaller seeds are predominant in higher latitudes with colder unfavourable seasons, suggesting a risk spreading strategy to delay germination timing until the optimal seasons for growth. The high proportion of non-dormant species with larger seeds at higher latitudes indicates a stress tolerance strategy for seedling survival after germination. Seed dormancy is a critical factor adapted to abiotic/biotic niche filtering, and consequently contributes to shaping biogeographical patterns along climatic gradients.

Keywords Seed dormancy · Latitudinal diversity gradient · Seed trait-dependent filtering · Seed mass · Seed dispersal · Species diversity

1 Introduction

Climatic gradients are major factors that shape plant species diversity across terrestrial biomes (Kubota et al., 2018; Vázquez-Rivera & Currie, 2015). Macroecological climatic covariates of various functional traits, which determine habitat suitability for individual species, underpin the geographical patterns of plant species richness and functional diversity at the assemblage level (Shiono et al., 2015). In the case of woody plants, hierarchical trait-driven assembly processes have been well investigated in terms of species-specific life history strategies (Adler et al., 2014) and large-scale environmental and climatic filters (Kichenin et al., 2013; Swenson et al., 2012). However, much less is known about seed traits that play a key role in plant colonisation and establishment success (Huijser & Schmid, 2011; Saatkamp et al., 2019). Seed morphology and physiology are hypothesised to act as filtering factors causing species sorting and packing in particular areas (Sandra et al., 1998; Pérez-Harguindeguy et al., 2013). Therefore, climate-dependent seed strategies (as environmental adaptations) should influence the geographical patterns of plant diversity. A better knowledge of the seed trait filter processes related to abiotic factors might allow prediction of the future impacts of climate change on plant species assembly (Chen et al., 2019, 2020; Kichenin et al., 2013).

Seed mass, dispersal mode and dormancy are key traits in relation to germination response to environmental cues or variability. They determine the species-specific regeneration niche at the local scale (e.g., disturbance; Grubb, 1977; McIntyre et al., 1999) and probably shape large-scale patterns of community composition along with environmental factors (Correa et al., 2022; Wang et al., 2021; Wisnoski et al., 2019). Globally, large-seeded species dominate at lower latitudes, whereas small-seeded species become dominant at higher latitudes (Moles et al., 2007). More importantly, seed dormancy is highly adaptive and/or phylogenetically conserved trait, depending on the type of dormancy, that determines survival through the timing of germination (Willis et al., 2014). In general, seeds remain dormant under unfavourable conditions such as drought or low temperatures to prevent seedling mortality (Baskin & Baskin, 2004; Finch-Savage & Leubner-Metzger, 2006; Willis et al., 2014). Especially in

woody plants, the occurrence or frequency of dormant species is known to exhibit large-scale geographical patterns and to be linked to climate regimes. For example, non-dormant woody plant seeds are ubiquitous in tropical and subtropical vegetation, but they are less common in temperate and boreal regions with lower precipitation and temperature (Baskin & Baskin, 2014; Zhang et al., 2022). Casas et al. (2017) reported that seed dormancy is associated with the length of the growing season and seed size: non-dormancy dominates in species with large seed mass occurring in regions with long growing seasons. These patterns of seed dormancy coupled with seed mass and dispersal mode could be associated with plant growth form and vegetation type. Nevertheless, previous studies have mostly been limited to particular plant taxa and focused on seed trait adaptations to severe environments, e.g., drought conditions (Escobar et al., 2018, 2021). Biogeographical analyses of seed traits assembly associated with environmental drivers have been scarce, especially in relation to a wide range of climatic gradients (Butler et al., 2007; Poschlod et al., 2013). Notably, we lack knowledge of the geography of seed dormancy types and how they covary with seed mass and mode of dispersal. As seed traits are closely associated with plant size, lifespan and growth form, they might be extremely important for plant community assembly, as currently acknowledged (Venable & Brown, 1988; Greene & Johnson, 1993; Thomson et al., 2011; Chen et al., 2019).

Here, we focus on the woody plant assemblages of the Japanese East Asian islands spanning subtropical evergreen, temperate deciduous and hemi-boreal habitats. Large-scale patterns of species richness and community composition are determined by filtering processes of leaf and woody traits in relation to climatic harshness and seasonality, especially for temperature rather than precipitation (Shiono et al., 2015). In this regard, seed traits, which have been overlooked in the context of community assembly studies (Saatkamp et al., 2019), are worthy of further attention, by investigating diversification and adaptations in relation to climatic factors along the latitudinal gradient. We start from the assumption that species assembly with different seed traits involving dormancy associated with seed mass and dispersal mode is mainly driven by the minimum winter temperature and the length of the unfavourable period for plant growth. We then test which types of dormancy particularly show latitudinal and climatic gradients and how these trends covary with seed dispersal mode and seed mass. Finally, we discuss how the community-wide diversity of dormancy patterns might be related to survival strategies.

2 Materials and methods

2.1 Study area

The Japanese East Asian islands, including the Ryukyu archipelago and the Izu-Bonin islands, form a long chain of islands located off the eastern coast of the Asian continent. They are mostly continental islands, but also include some oceanic islands that have never been connected to the continent or main archipelagos. The mean annual temperature ranges from -5.3 to 24.2 °C, indicating that the study area covers a

wide range of temperature with seasonality in the temperate zone. The annual precipitation is 650–4538 mm, which is among the highest in the world. The precipitation exhibits pronounced seasonality; indeed, the precipitation in the driest months often exceeds 100 mm in many places. Therefore, there are no wet or dry seasons as seen in other regions (Fig. S1 in Appendix S2). This warm and wet monsoon climate contributes to the development of diverse biomes (subtropical, temperate and hemi-boreal vegetation) that shape a biodiversity hotspot in East Asia (Kubota et al., 2014, 2015).

2.2 Species distribution data

Distribution data for woody plant species were derived from a database of the Japan Biodiversity Mapping Project (J-BMP) including all vascular plants (<https://biodiversity-map.thinknature-japan.com/en/>). These data have a spatial resolution of 10×10 km² resolution and contain 4698 grid cells with terrestrial areas. Species occurrence information was collected by searching the botanical literature on the flora of Japan. Most of the references were species checklists and phytosociological tables (see Kubota et al., 2015 for a compilation of species occurrence and distribution range data). Species names followed those in the Japanese Scientific Names Index (Yonekura & Kajita, 2003). In this study, planted and non-native species (introduced after the modernisation; ca. 150 years ago) were excluded from the dataset.

2.3 Environmental data

We focused on latitude and climate factors that reflect harshness and seasonality. Air temperature data at the 1-km grid cell level were extracted from the Chelsa ver.2.1 database (Karger et al., 2017). We focused on bio6 (minimum temperature in the coldest month) as the index of temperature harshness and on monthly mean temperature between 1981 and 2010 to calculate the length of the unfavourable period for plant growth (months below 5 degrees; Kikuzawa et al., 2013). Note that the Japanese East Asian islands are entirely under humid climate with high rainfall (see Fig. S1 in Appendix S2); thus, precipitation and its seasonality play only a small role in shaping plant diversity pattern (Shiono et al., 2015). The definition of the unfavourable growth period is based on Baskin and Baskin (2014): they defined 0–10 °C as the effective cold temperature and 5 °C as the optimal temperature to break dormancy for many species. To collate with the plant distribution maps, we averaged the climatic data at the 1-km grid cells and aggregated into the same 4698 grid cells of 10 km \times 10 km as the species distribution data.

2.4 Seed trait data

We collected information on seed traits including mass, dispersal mode and dormancy by a literature census (see Appendix S1 for references). We compiled data on seed mass for 696 species, seed dispersal for 1196 species and seed dormancy for 662 species, accounting for 58.1%, 99.9% and 55.3% of Japanese woody plant species

(1197 species except for bamboos), respectively. Most seed mass data were compiled from the Royal Botanic Gardens Kew Seed Information Database (<https://data.kew.org/sid/>). Additionally, we used data of the Global Tree Seed Bank Project Japan (Millennium Seed Bank Partnership).

Seed dormancy type and dispersal mode were based on Baskin and Baskin (2014), Japanese literature, and the Data Warehouse of the Millennium Seed Bank Partnership (<http://brahmsonline.kew.org/msbp/SeedData/DW>). Dispersal modes were classified into five categories (anemochory, barochory, zoochory, hydrochory and autochory). According to the literature (e.g., Baskin & Baskin, 2014), seed dormancy can be classified into five types: morphological dormancy (MD); physiological dormancy (PD); morpho-physiological dormancy (MPD); physical dormancy (PY) and physical plus physiological dormancy (PYPD). However, we were unable to collect sufficient embryo size data, which is a critical factor to distinguish MD and MPD from ND and PD, respectively (Baskin & Baskin, 2014). Therefore, in this study, we used a combined classification in the geographical pattern analyses: non-dormancy including morphological dormancy (ND_MD); physiological dormancy including morpho-physiological dormancy (PD_MPD); physical dormancy (PY); and physical plus physiological dormancy (PYPD) (Table 1). We confirmed that MD and MPD species are rare in the study region (Table S1 in Appendix S3) and their presence/absence did not significantly change the geographical patterns (Fig. S1 in Appendix S4). When a species can produce both dormant and non-dormant seeds, we treated the species as a physical/physiological dormancy species (i.e. PD_MPD, PY, or PYPD).

Table 1 Seed dormancy types of Japanese woody plants

Class of dormancy		*Germinate within 1 mo, 4 w, 30d (+) or not (–)	*Need cold/warm stratification (+) or not (–)	Embryo size full (+), small (–)	Seed coat permeable (+) impermeable (–)
Modified definition in this study	Baskin & Baskin classification				
ND_MD	ND	+	–	+	+
	MD	+	–	–	+
PD_MPD	PD	–	+	+	+
	MPD	–	+	–	+
PY	PY	–	–	+	–
PYPD	PYPD	–	+	+	–

Seed dormancy was classified into five types following Baskin and Baskin (2014): morphological dormancy (MD); physiological dormancy (PD); morphophysiological dormancy (MPD); physical dormancy (PY) and physical plus physiological dormancy (PYPD). In this study, we could not collect sufficient data on embryo size, and thus omitted embryos as a factor in classifying dormancy types. We finally combined non-dormancy (ND) and MD into ND_MD, and PD and MPD into PD_MPD

*Germination after next spring

2.5 Statistical analysis

To quantify phylogenetic signals in seed dormancy types and dispersal modes, we constructed a phylogeny for 1197 Japanese woody plant species based on molecular data from GenBank and the Open Tree of Life project (Smith & Brown, 2018). We used two types of phylogenetic signal measure: the D statistic (Fritz & Purvis, 2010) and Blomberg's K (Blomberg et al., 2003). The D statistic ranges from $-\infty$ to ∞ , where smaller and larger values mean phylogenetic clustering and over-dispersion, respectively; $D = 1$ indicates that the observed binary variable is randomly distributed on the phylogeny, and $D = 0$ corresponds to the expectation from a Brownian motion model. Blomberg's K varies from 0 to ∞ , where $K = 1$ corresponds to the expectation from a Brownian motion model; $K < 1$ and $K > 1$ indicate that the relatives are less or more similar than expected, respectively. The statistical significance of the phylogenetic signals was tested from 1000 permutations. We also tested the phylogenetic signals in the presence/absence of dormancy information, to check for phylogenetic bias in our data.

We calculated species richness (SR) and mean log-scaled seed mass (SM) for each dormancy type and dispersal mode at the 10 km \times 10 km grid cell level (4698 cells in total). We standardised the relative dominance of species (proportion of species with each dormancy type and dispersal mode to total number of species) and mean seed mass using a null model, where species labels were randomly shuffled on the species \times seed trait matrix and respective SR and SM were re-calculated. This procedure was repeated 1000 times to obtain the null distribution. In the null model, we included all Japanese woody plant species (1197 species, including those without seed information) to account for a potential representation bias in our seed dataset. Then, we calculated the standardised effect size (SES) for SR and SM as: $(X_{\text{obs}} - \text{mean of } X_{\text{null}}) / \text{standard deviation of } X_{\text{null}}$, where X_{obs} is an observed value and X_{null} is the null value. We confirmed that the null values showed small skewness (average = 0.1, min = -0.4 , and max = 3.1 for species dominance; average = -0.1 , min = -2.5 , max = 1.0 for log-scaled seed mass), suggesting no serious bias in SES calculation (Botta-Dukát, 2018).

We analysed the relationships between the SES of SR and SM and environmental/geographical factors using bivariate regression models. We set the SES value as the response variable. As explanatory variables, we set latitude (degrees), minimum temperature in the coldest month ($^{\circ}\text{C}$) and length of the unfavourable growth period (months; mean temperature $< 5^{\circ}\text{C}$), which was based on 5°C as the optimal temperature to break dormancy for many species (Baskin & Baskin, 2014). Because of strong intercorrelations between the environmental/geographical variables (Pearson's correlation coefficient $r \approx 0.9$), we analysed each explanatory variable separately. The relative importance of the environmental/geographical variables was evaluated by the coefficient of determination (R^2) of the models. To check the nonlinearity of the relationships, we also fitted regression models with and without a quadratic term and compared their R^2 values.

We also tested using unfavourable growth lengths based $< 0^{\circ}\text{C}$ and $< 10^{\circ}\text{C}$ to define the unfavourable growth period. We confirmed the choice of temperature thresholds

had only marginal effects on the regression coefficients, especially for the linear terms; the only exception was hydrochorous species, whose distribution range was limited to low latitudinal (warm) regions; the explanatory powers of regression models were also comparable between the differences in threshold temperature with a few exceptions. Therefore, we only showed the results of $< 5\text{ }^{\circ}\text{C}$ in the main text (see Figs. S6–S9, S12, and S13 in Appendix S4 for the results of $< 0\text{ }^{\circ}\text{C}$ and $< 10\text{ }^{\circ}\text{C}$).

All analyses were performed and graphics produced with R version 4.0.4 (R Development Core Team, 2021) using the ‘data.table’ (Dowle & Srinivasan, 2021), ‘V.PhyloMaker’ (Jin & Qian, 2019) to construct phylogeny, ‘picante’ (Kembel et al., 2010) and ‘caper’ (Orme et al., 2012) package to analyse phylogenetic signals.

3 Results

3.1 Seed trait patterns

Seed dispersal modes and dormancy types mostly showed significant phylogenetic signal across all woody plant species studied (Table S2 in Appendix S3). The strength of the phylogenetic signal was relatively high for anemochory ($D = -0.338$ and $K = 0.618$) and low for ND ($D = 0.842$ and $K = 0.005$): in fact, anemochorous species are distributed in particular order/family clades (e.g. Salicaceae in Malpighiales), whereas ND species are widely scattered across the phylogenetic tree (see Table S1 in Appendix S3).

The number of species examined in all models was consistently highest in the central areas of Japan (Fig. S5 in Appendix S4), reflecting the broad geographical pattern of species richness of woody plants in Japan. Species abundance and seed mass showed clear geographical patterns for each dispersal mode and each dormancy type (Fig. 1 and Appendix S4). For anemochory, hydrochory and zoochory, seed mass decreased with increasing latitude (Fig. 1), whereas there were inflection points (geographical gaps) in the latitudinal trend of seed mass between the subtropics (ca. 30°) and temperate zone (ca. 40°). In contrast, barochorous seed mass increased with latitude. PD_MPD seed mass decreased with increasing latitude, whereas ND_MD seed mass showed a U-shaped latitudinal pattern with the bottom at around 35° to 40° N (Fig. 1 and Appendix S4). There was no significant difference in seed mass between the ND_MD and PD_MPD dormancy types (Fig. S2 in Appendix S4).

The standardised effect size of number of species richness of anemochorous taxa increased with increasing latitude, whereas zoochorous and hydrochorous richness decreased (Fig. 1). Barochorous species were relatively diverse across the islands and showed no latitudinal gradient (Fig. 1). These geographical patterns of dispersal modes were also associated with dormancy types. The diversity of PD_MPD species with anemochory and barochory was greater in higher latitudes (Fig. 2, Figs. S3, S6, S8, S10 and S12 in Appendix S4 and Table S1 in Appendix S5), although PD_MPD zoochorous and hydrochorous species were relatively rich in lower latitudes. PY species were more diverse at lower latitudes, although there was no clear latitudinal pattern in seed mass (Fig. S5 in Appendix S4). For ND_MD anemochory, species richness increased with increasing latitude, whereas for ND_MD zoochory, hydrochory and barochory,

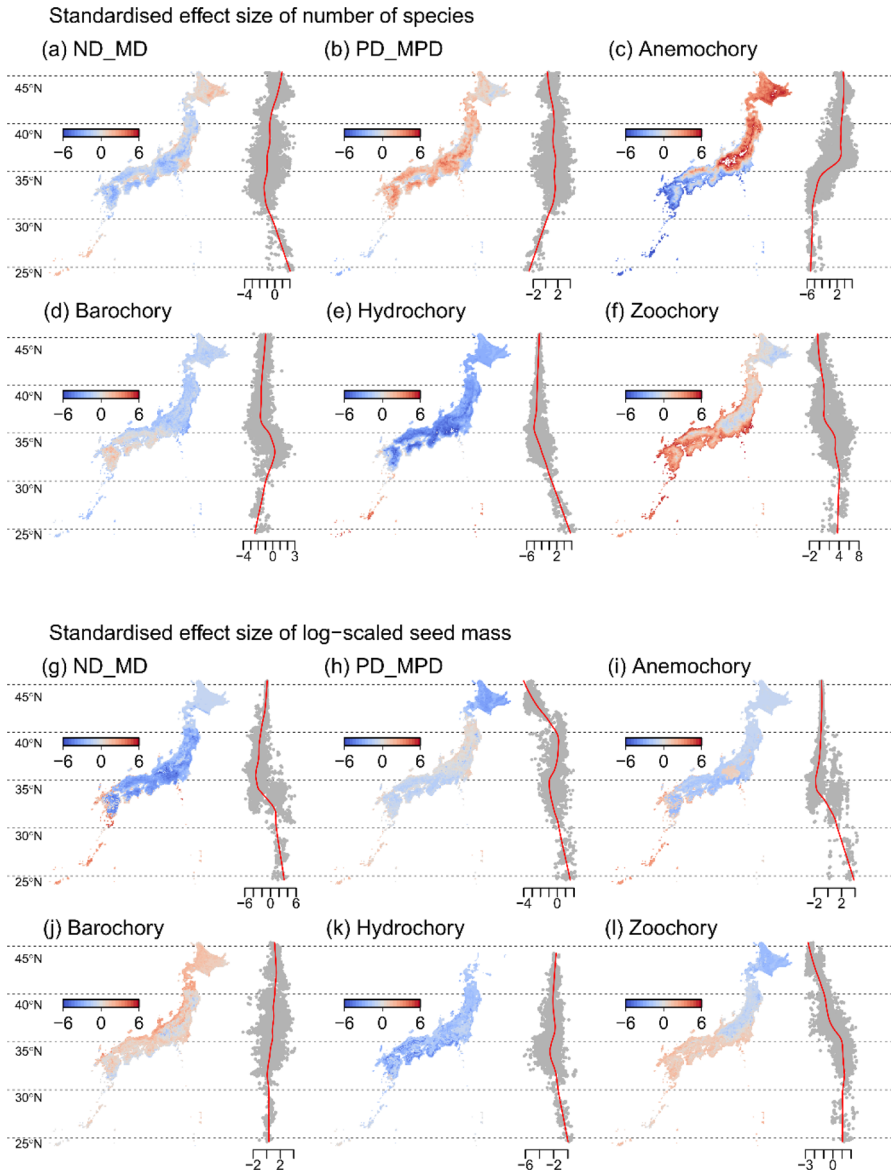


Fig. 1 Geographical patterns of standardised effect size (SES) of number of species and log-scaled seed mass for each dormancy type and dispersal mode. Scatter diagrams at the right side of each panel indicate the latitudinal pattern of the variable with Lowess curve (smoothing parameter = 0.3): individual gray symbols show values at the 10 km × 10 km grid cell level. The dormancy types are non-dormancy and morphological dormancy species (ND_MD; **a, g**), and physiological and morphophysiological dormancy species (PD_MPD; **b, h**). The dispersal types are anemochory (**c, i**), barochory (**d, j**), hydrochory (**e, k**) and zoochory (**f, l**)

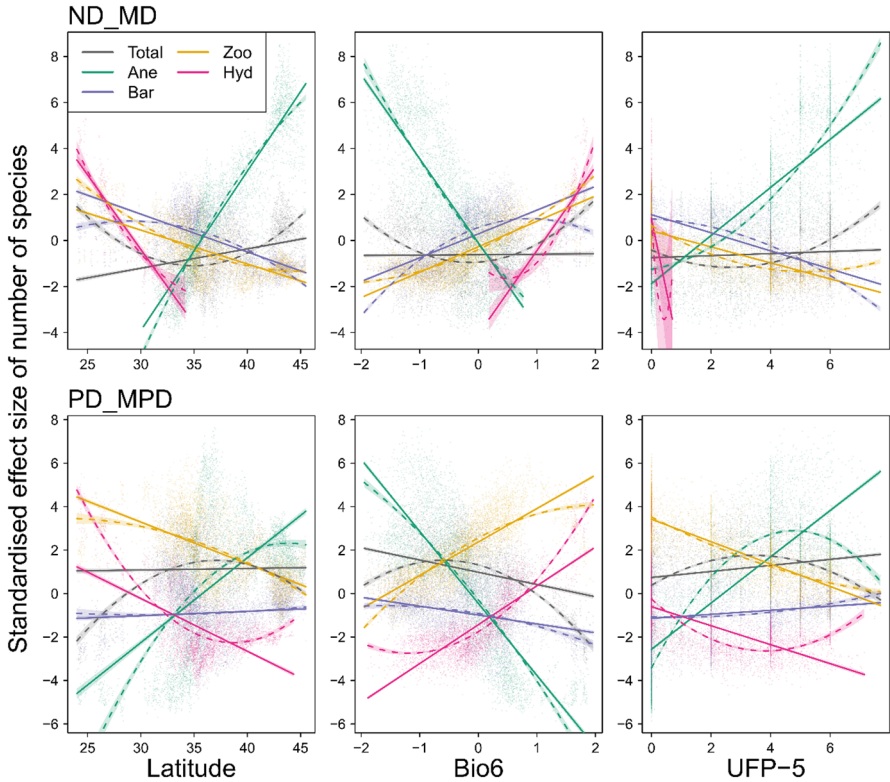


Fig. 2 Relationships between standardised effect size (SES) of number of species per dormancy type and dispersal mode and three environmental variables: latitude, minimum temperature of the coldest month (bio6) and unfavourable growth period defined as months below 5 °C (UFP-5). Solid and broken lines represent the prediction from the linear and quadratic regression models, respectively. The dormancy types are non-dormancy and morphological dormancy species (ND_MD), and physiological and morphophysiological dormancy species (PD_MPD). The dispersal modes are anemochory (ane), barochory (bar), hydrochory (hyd) and zoochory (zoo)

richness decreased with latitude (Fig. 2, Fig. S3, S6, S8, S10 and S12 in Appendix S4 and Table S1 in Appendix S5).

3.2 Environmental drivers of seed trait patterns

The diversity of PD_MPD species with anemochorous and barochorous seeds was negatively associated with minimum temperature and positively associated with the length of the unfavourable period, whereas that of PD_MPD species with hydrochory and zoochory showed the opposite trends with these climatic variables (Fig. 2, Figs. S3, S6, S8, S10 and S12 in Appendix S4 and Table S1 in Appendix S5). PD_MPD seed mass was positively associated with minimum temperature and negatively associated with the length of the unfavourable period (Fig. 3, Figs. S4, S7, S9, S11 and S13 in Appendix S4 and Table S1 in Appendix S5).

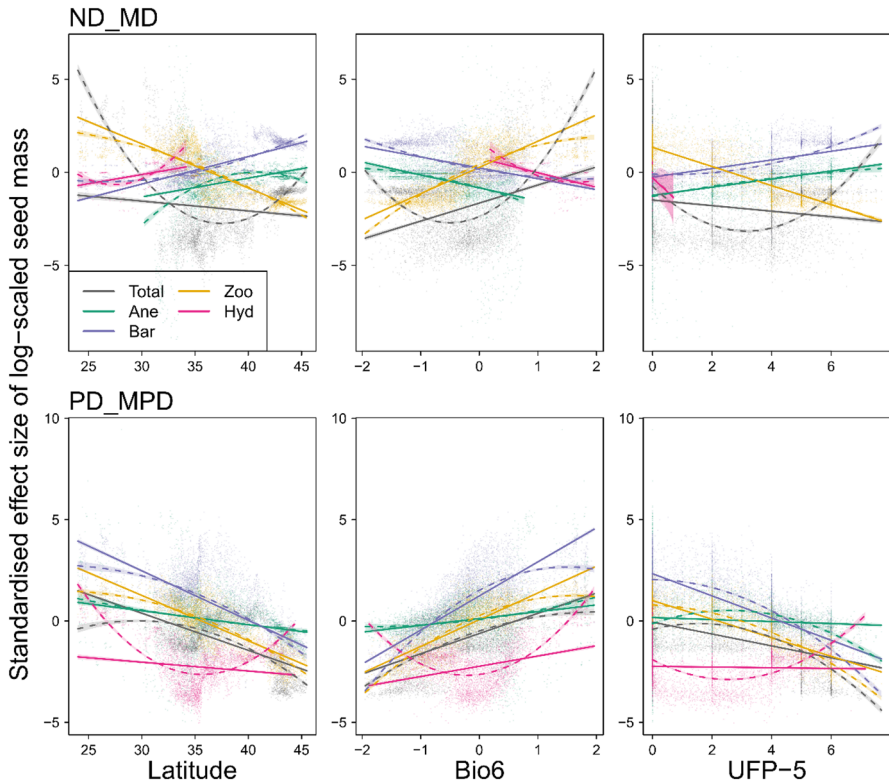


Fig. 3 Relationships between standardised effect size (SES) of log-scaled seed mass for different dormancy types and dispersal modes and three environmental variables: latitude; minimum temperature of the coldest month (bio6); and unfavourable growth period, defined as months below 5 °C (UFP-5). Solid and broken lines represent the prediction from the linear and quadratic regression models, respectively. The dormancy types are non-dormancy and morphological dormancy species (ND_MD), and physiological and morpho-physiological dormancy species (PD_MPD). The dispersal modes are anemochory (ane), barochory (bar), hydrochory (hyd) and zoochory (zoo)

Total ND_MD species richness was not associated with environmental factors, and the correlation patterns showed a contrast between dispersal modes. ND_MD anemochorous species richness was negatively correlated with minimum temperature and positively correlated with the length of the unfavourable period, whereas ND_MD barochorous, hydrochorous and zoochorous species richness were positively correlated with minimum temperature and negatively correlated with the length of the unfavourable period (Fig. 2, Figs. S3, S6, S8, S10 and S12 in Appendix S4 and Table S1 in Appendix S5).

For ND_MD anemochory and barochory, seed mass was associated negatively with minimum temperature and positively with the length of the unfavourable period (Fig. 3, Figs. S4, S7, S9, S11 and S13 in Appendix S4 and Table S1 in Appendix S5). In contrast, for ND_MD zoochory, seed mass was associated positively with minimum temperature and negatively with the length of the unfavourable period.

ND_MD hydrochory showed no distribution in the region where the unsuitable growth period ($< 5\text{ }^{\circ}\text{C}$) was greater than one month, and their seed mass showed negative correlations with minimum temperature and the length of the unfavourable period (Fig. 3, Figs. S4, S7, S9, S11 and S13 in Appendix S4 and Table S1 in Appendix S5).

4 Discussion

This study documents the geographical patterns of seed traits across subtropical, temperate and hemi-boreal regions. The correlative patterns between seed mass, dispersal modes and dormancy demonstrate diversification of seed trait strategies in relation to their trade-offs and environmental factors. Our findings are in partial agreement with those reported in previous studies, but differ in other respects because of region-specific species assembly processes on the East Asian islands, as discussed below.

Latitudinal gradients of seed mass, i.e., smaller seeds toward higher latitudes, have been documented globally (Moles & Westoby, 2003; Moles et al., 2007) and regionally (Lord et al., 1997). A factor in shaping latitudinal seed mass gradients is the geographical shift of plant growth forms from woody plants in low latitudes to herbaceous plants in mid and high latitudes. However, our study based on a single growth form (i.e., woody plants) also confirmed a latitudinal seed mass gradient, suggesting the existence of other macroecological mechanisms of seed mass geography, in addition to a growth form shift (Fig. 1 and Appendix S3). In fact, dispersal modes and dormancy types (ND_MD versus PD_MPD) affected the latitudinal gradient in seed mass. Specifically, barochory showed an increasing trend of seed mass with latitude, and ND_MD large-seeded species were predominant in both lower and higher latitudes (Figs. 1 and 3 and Appendix S3). Moreover, we found geographical gaps in the latitudinal seed mass gradient. The seed mass gap between subtropical and temperate regions reflects the distribution of hydrochorous species such as Malpighiales, including mangroves that are limited to the subtropical islands (Fig. 1). Their large seeds are likely to be recalcitrant/viviparous and are notable for their buoyancy, meaning they can be dispersed by ocean currents (Bardou et al., 2020; Clarke et al., 2001). Meanwhile, another gap between temperate and hemi-boreal regions was resulted from the filtering out of large-sized barochorous species (e.g., Fagales, Ericales or Rosales) in hemi-boreal regions (Wyse & Dickie, 2017) and the corresponding dominance of anemochorous species with small seeds such as Salicaceae (Karrenberg et al., 2003; Nishiyama et al., 1990). These findings indicate that the mechanisms shaping latitudinal seed mass patterns across the East Asian islands are highly complex and interact with dispersal modes and dormancy types (including non-dormancy), which are potentially linked with life history strategies (Moles et al., 2005).

Importantly, the geographical patterns of seed traits could be explained by the minimum temperature and length of the period unsuitable for plant growth (Fig. 2 and Appendix S2); this finding provides general support for the prediction that physiological or morphophysiological dormancy becomes predominant with increasing climate harshness (Baskin & Baskin, 2014; Dayrell et al., 2016). Notably, seed mass patterns were mainly related to dispersal modes (anemochory, zoochory or hydrochory) rather than dormancy types (Fig. 1 and Appendix S3). A previous study on the Fabaceae

reported that the seed mass of non-dormant species was greater than that of dormant species (Casas et al., 2017). Our findings may have resulted from expanding the target species from a specific family (Fabaceae) to all woody plant species, and the relationship between seed mass, seed dispersal mode and seed dormancy type may differ among the taxa.

The standardised effect size of species richness of each dispersal mode and dormancy type differed geographically, especially for particular orders/families because seed traits showed significant phylogenetic signals (Appendix S3). Non-dormant anemochory was diversified at high latitudes, whereas non-dormant barochory or zoochory and non-dormant hydrochory species were diversified at low to mid latitudes. These patterns suggest that seed trait-dependent filtering plays an important role in shaping large-scale patterns of plant diversity (Thomson et al., 2011; Gioria et al., 2020; Wang et al., 2021). We note that non-dormant species, which were relatively diversified across a variety of clades (Appendix S3), were also substantially distributed in climatically harsh areas (Figs. 1 and 2), which is inconsistent with the report by Casas et al. (2017) that non-dormant species of Fabaceae are abundant under climatically mild and stable conditions. This difference reflects a U-shaped relationship of seed mass with minimum temperature (Fig. 3), i.e., small- and large-sized seed species without dormancy were abundant in both climatically stable and harsh areas. This result suggests non-linearity of environmental filtering effects on trait assembly (Rolhauser et al., 2021), working at opposite ends (cold and warm) of the temperature gradient. Such adaptations to contrasting environmental conditions may have resulted in the similar phenotypic trait. Increasing seed mass at lower latitudes with a warm climate may be explained by metabolic cost (Murray et al., 2004). Additionally, large-sized seeds were found in areas with cold temperatures: although they cannot avoid unfavourable timing by dormancy, such seeds have an advantage in the survival and establishment success of seedlings under climatically harsh conditions (Westoby et al., 1996; Leishman et al., 2000; Moles & Westoby, 2006).

Comparison of geographical patterns between dormant-seeded and non-dormant species suggest adaptive ecological/evolutionary strategies in response to the minimum temperature and the length of the unfavourable period for plant growth along latitude, as illustrated in Fig. 4. The predominance of physiologically dormant, small-sized seed species in harsh-climate areas suggests that seed dormancy (i.e., dispersal over time) functions as a risk-spreading/avoidance strategy to delay germination until the appearance of better conditions (Baskin & Baskin, 2004; Finch-Savage & Leubner-Metzger, 2006; Willis et al., 2014). In contrast, the predominance of non-dormant species in both warm and cool climates suggests a stress-tolerance strategy in relation to large seed size and dispersal modes (e.g., barochorous and anemochorous species in harsh climates) that enable survival and establishment success after germination (Rees, 1994). Our results show that seed dormancy contributes to macro-scale climate niche filtering, whereas seed mass and dispersal modes are associated with biotic filtering at a local scale. These findings imply a geographical variability of seed banks, which might serve as a proxy for region-specific compositional stability within ecological time frames (DeMalach et al., 2021).

In conclusion, seed traits of Japanese woody plants, including evergreen and deciduous broadleaved species and conifers, are linked to seed mass, dispersal modes and

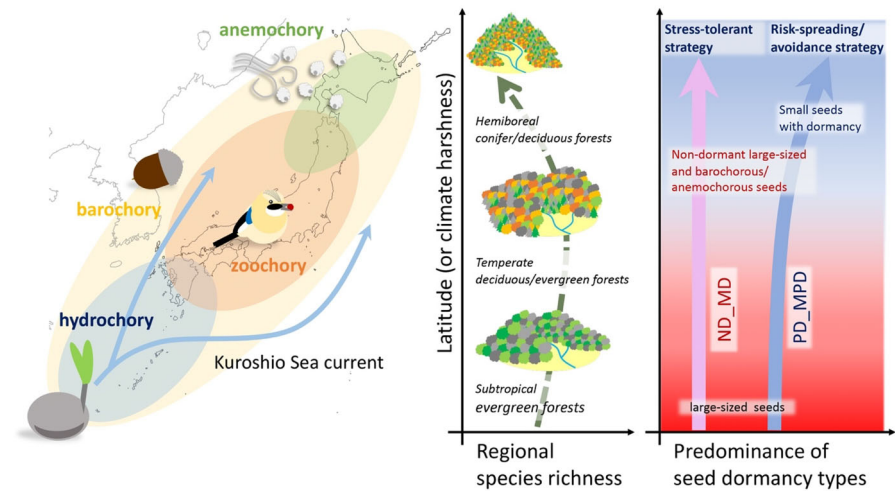


Fig. 4 Geographical patterns of seed traits of woody plants on East Asian islands in Japan. The regional species richness at the 10-km grid cell level was highest in the middle parts of Japan (Fig. S4 in Appendix S4). Woody plants with dormant or non-dormant seeds diversify their adaptive ecological/evolutionary strategies related to seed mass and dispersal modes along the latitudinal climate harshness gradient. The predominance of species with physiological dormancy and small seeds in harsh climate areas suggests that seed dormancy functions as a risk-spreading/avoidance strategy to escape unfavourable germination timing. The predominance of non-dormant barochorous and anemochorous species in a harsh climate and zoochorous and hydrochorous species in a warm climate suggest a stress-tolerance strategy related to large seeds that enables survival and establishment after germination. ND_MD, non-dormancy and morphological dormancy; PD_MPD, physiological and morphophysiological dormancy

dormancy types relative to climatic factors including minimum temperature and the unfavourable period for plant growth. The geographical patterns of dormant versus non-dormant seeds, which are also associated with seed mass and dispersal modes, revealed highly complex adaptations to different abiotic/biotic filtering processes (Laanisto & Niinemets, 2015; Liu et al., 2017). For species with small-sized seeds, physiological and morphophysiological dormancy, which are most frequent in temperate regions, play a major role in avoiding mortality or damages resulting from unfavourable weather conditions. Seed dormancy or non-dormancy, especially in cool hemi-boreal regions or hot/dry subtropical regions, can be regarded as a critical factor for community assembly involving dispersal, germination, and establishment at the beginning of plant life history and consequently contribute to shaping large-scale plant diversity patterns through seed trait-dependent filtering. There are still significant knowledge gaps on seed dormancy; for example, morphological dormancy appears to be dependent on embryo size development. Further explorations using more detailed seed dormancy data are required to develop seed trait functional biogeography of plant communities (Saatkamp et al., 2019).

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s42081-023-00215-0>.

Acknowledgements We thank members of the Kubota-lab, the University of the Ryukyus and Sharon Balding, Kate A Hardwick and Naomi Carvey of the Millennium Seed Bank of the Royal Botanic Gardens, Kew. Financial support was provided by the Japan Society for the Promotion of Science (Nos. 15H04424, 20H03328 and 21H04946) and the Environment Research and Technology Development fund of the Ministry of the Environment, Japan (4-1501 and 4-1802). This study was supported by the Program for Advancing Strategic International Networks to Accelerate the Circulation of Talented Researchers, the Japan Society for the Promotion of Science. BK was supported by the Japan Society for the Promotion of Science (No. 21K05687).

Data availability As we are currently writing a paper using this data, we will share the data upon request (depending on the purpose of its use).

Declarations

Conflict of interest On behalf of all the authors, the corresponding author states that there is no conflict of interest.

References

- Adler, P. B., Salguero-Gómez, R., Compagnoni, A., Hsu, J. S., Ray-Mukherjee, J., Mbeau-Ache, C., & Franco, M. (2014). Functional traits explain variation in plant life history strategies. *Proceedings of the National Academy of Sciences USA*, *111*, 740–745.
- Bardou, R., Parker, J. D., Feller, I. C., & Cavanaugh, K. C. (2020). Variability in the fundamental versus realized niches of North American mangroves. *Journal of Biogeography*, *48*, 160–175.
- Baskin, J. M., & Baskin, C. C. (2004). A classification system for seed dormancy. *Seed Science Research*, *14*, 1–16.
- Baskin, J. M., & Baskin, C. C. (2014). *Seeds: Ecology, biogeography, and evolution of dormancy and germination* (2nd ed.). Academic/Elsevier.
- Blomberg, S. P., Garland, T., Jr., & Ives, A. R. (2003). Testing for phylogenetic signal in comparative data: Behavioral traits are more labile. *Evolution*, *57*, 717–745.
- Botta-Dukát, Z. (2018). Cautionary note on calculating standardized effect size (SES) in randomization test. *Community Ecology*, *19*, 77–83.
- Butler, D. W., Green, R. J., Lamb, D., McDonald, W. J. F., & Forster, P. I. (2007). Biogeography of seed-dispersal syndromes, life-forms and seed sizes among woody rain-forest plants in Australia's subtropics. *Journal of Biogeography*, *34*, 1736–1750.
- Chen, S.-C., Poschold, P., Antonelli, A., Liu, U., & Dickie, J. B. (2020). Trade-off between seed dispersal in space and time. *Ecology Letters*, *23*, 1635–1642.
- Chen, S.-C., Tamme, R., Thomson, F. J., & Moles, A. T. (2019). Seeds tend to disperse further in the tropics. *Ecology Letters*, *22*, 954–961.
- Clarke, P. J., Kerrigan, R. A., & Westphal, C. J. (2001). Dispersal potential and early growth in 14 tropical mangroves: Do early life history traits correlate with patterns of adult distribution? *Journal of Ecology*, *89*, 648–659.
- Correa, D. F., Stevenson, P. R., Umaña, M. N., Coelho, L., de Lima Filho, D., de Salomão, R. P., Amaral, I. L., Wittmann, F., Matos, F. D., Castilho, C. V., et al. (2022). Geographic patterns of tree dispersal modes in Amazonia and their ecological correlates. *Global Ecology and Biogeography*, *32*, 49–69.
- Dayrell, R. L. C., Garcia, Q. S., Negreiros, D., Baskin, C. C., Baskin, J. M., & Silveira, F. A. O. (2016). Phylogeny strongly drives seed dormancy and quality in a climatically buffered hotspot for plant endemism. *Annals of Botany*, *119*, 267–277.
- de Casas, R. R., Willis, C. G., Pearse, W. D., Baskin, C. C., Baskin, J. B., & Cavender-Bares, J. (2017). Global biogeography of seed dormancy is determined by seasonality and seed size: A case study in the legumes. *New Phytologist*, *214*, 1527–1536.
- DeMalach, N., Kigel, J., & Sternberg, M. (2021). The soil seed bank can buffer long-term compositional changes in annual plant communities. *Journal of Ecology*, *109*, 1275–1283.
- Dowle, M., & Srinivasan, A. (2021). data.table: Extension of 'data.frame'. R package version 1.14.0. <https://CRAN.R-project.org/package=data.table> accessed 16 Apr 2021.

- Escobar, D. F. E., Rubio de Casas, R., & Morellato, L. P. C. (2021). Many roads to success: Different combinations of life-history traits provide accurate germination timing in seasonally dry environments. *Oikos*, *130*, 1865–1879.
- Escobar, D. F. E., Silveira, F. A. O., & Morellato, L. P. C. (2018). Timing of seed dispersal and seed dormancy in Brazilian savanna: two solutions to face seasonality. *Annals of Botany*, *121*, 1197–1209.
- Finch-Savage, W. E., & Leubner-Metzger, G. (2006). Seed dormancy and the control of germination. *New Phytologist*, *171*, 501–523.
- Fritz, S. A., & Purvis, A. (2010). Selectivity in mammalian extinction risk and threat types: A new measure of phylogenetic signal strength in binary traits. *Conservation Biology*, *24*, 1042–1051.
- Gioria, M., Pyšek, P., Baskin, C. C., & Carta, A. (2020). Phylogenetic relatedness mediates persistence and density of soil seed banks. *Journal of Ecology*, *108*, 2121–2131.
- Greene, D. F., & Johnson, E. A. (1993). Seed mass and dispersal capacity in wind-dispersed diaspores. *Oikos*, *67*, 69–74.
- Grubb, P. J. (1977). The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Reviews*, *52*, 107–145.
- Huijser, P., & Schmid, M. (2011). The control of developmental phase transitions in plants. *Development*, *138*, 4117–4129.
- Jin, Y., & Qian, H. (2019). V. PhyloMaker: An R package that can generate very large phylogenies for vascular plants. *Ecography*, *42*, 1353–1359.
- Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, H. P., & Kessler, M. (2017). Climatologies at high resolution for the earth's land surface areas. *Scientific Data*, *4*, 170122.
- Karrenberg, S., & Suter, M. (2003). Phenotypic trade-offs in the sexual reproduction of Salicaceae from flood plains. *American Journal of Botany*, *90*, 749–754.
- Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., & Webb, C. O. (2010). Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, *26*, 1463–1464.
- Kichenin, E., Wardle, D. A., Peltzer, D. A., Morse, C. W., & Freschet, G. T. (2013). Contrasting effects of plant inter- and intraspecific variation on community-level trait measures along an environmental gradient. *Functional Ecology*, *27*, 1254–1261.
- Kikuzawa, K., Onoda, Y., Wright, I. J., & Reich, P. B. (2013). Mechanisms underlying global temperature-related patterns in leaf longevity. *Global Ecology and Biogeography*, *22*, 982–993.
- Kubota, Y., Hirao, T., Fujii, S., Shiono, T., & Kusumoto, B. (2014). Beta diversity of woody plants in the Japanese archipelago: Roles of geohistorical and ecological processes. *Journal of Biogeography*, *41*, 1267–1276.
- Kubota, Y., Kusumoto, B., Shiono, T., & Ulrich, W. (2018). Environmental filters shaping angiosperm tree assembly along climatic and geographic gradients. *Journal of Vegetation Science*, *29*, 607–618.
- Kubota, Y., Shiono, T., & Kusumoto, B. (2015). Role of climate and geohistorical factors in driving plant richness patterns and endemism on the east Asian continental islands. *Ecography*, *38*, 639–648.
- Laanisto, L., & Niinemets, Ü. (2015). Polytolerance to abiotic stresses: How universal is the shade–drought tolerance trade-off in woody species? *Global Ecology and Biogeography*, *24*, 571–580.
- Leishman, M. R., Wright, I. J., Moles, A. T., & Westoby, M. (2000). The evolutionary ecology of seed size. *Seeds: The Ecology of Regeneration in Plant Communities* (2nd ed.). CABI publishing.
- Liu, Y., Barot, S., El-Kassaby, Y. A., & Loeuille, N. (2017). Impact of temperature shifts on the joint evolution of seed dormancy and size. *Ecology and Evolution*, *7*, 26–37.
- Lord, J., Egan, J., Clifford, T., Jurado, E., Leishman, M., Williams, D., & Westoby, M. (1997). Larger seeds in tropical floras: Consistent patterns independent of growth form and dispersal mode. *Journal of Biogeography*, *24*, 205–211.
- McIntyre, S., Lavorel, S., Landsberg, J., & Forbes, T. D. A. (1999). Disturbance response in vegetation: Towards a global perspective on functional traits. *Journal of Vegetation Science*, *10*, 621–630.
- Moles, A. T., Ackerly, D. D., Tweddle, J. C., Dickie, J. B., Smith, R., Leishman, M. R., Mayfield, M. M., Pitman, A., Wood, J. T., & Westoby, M. (2007). Global patterns in seed size. *Global Ecology and Biogeography*, *16*, 109–116.
- Moles, A. T., Ackerly, D. D., Webb, C. O., Tweddle, J. C., Dickie, J. B., Pitman, A. J., & Westoby, M. (2005). Factors that shape seed mass evolution. *Proceedings of the National Academy of Sciences USA*, *102*, 10540–10544.
- Moles, A. T., & Westoby, M. (2003). Latitude, seed predation and seed mass. *Journal of Biogeography*, *30*, 105–128.


- Moles, A. T., & Westoby, M. (2006). Seed size and plant strategy across the whole life cycle. *Oikos*, *113*, 91–105.
- Murray, B. R., Brown, A. H. D., Dickman, C. R., & Crowther, M. S. (2004). Geographical gradients in seed mass in relation to climate. *Journal of Biogeography*, *31*, 379–388.
- Nishiyama, K. (1990). The role of seed dispersal and seedling traits in colonization and coexistence of *Salix* species in a seasonally flooded habitat. *Ecological Research*, *5*, 317–331.
- Orme, D., Freckleton, R., Thomas, G., Petzoldt, T., Fritz, S., Isaac, N., & Pearse, W. (2012). Caper: comparative analyses of phylogenetics and evolution in R. R package version 0.5, 2, 458.
- Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M. S., Cornwell, W. K., Craine, J. M., Gurvich, D. E., Urcelay, C., Veneklaas, E. J., Reich, P. B., Poorter, L., Wright, I. J., Ray, P., Enrico, L., Pausas, J. G., de Vos, A. C., ... Cornelissen, J. H. C. (2013). New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, *61*, 167–234.
- Poschold, P., Abedi, M., Bartelheimer, M., Drobnik, J., Rosbakh, S., & Saatkamp, A. (2013). Seed ecology and assembly rules in plant communities. In E. van der Maarel & J. Franklin (Eds.), *Vegetation Ecology* (2nd ed.). Wiley.
- R Development Core Team. (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>. Accessed 16 Apr 2021.
- Rees, M. (1994). Delayed germination of seeds: A look at the effects of adult longevity, the timing of reproduction, and population age/stage structure. *American Naturalist*, *139*, 484–508.
- Rolhauser, A. G., Waller, D. M., & Tucker, C. M. (2021). Complex trait-environment relationships underlie the structure of forest plant communities. *Journal of Ecology*, *109*, 3794–3806.
- Saatkamp, et al. (2019). A research agenda for seed-trait functional ecology. *New Phytologist*, *221*, 1764–1775.
- Sandra, D., Marcelo, C., & Fernando, C. (1998). Plant functional traits and environmental filters at a regional scale. *Journal of Vegetation Science*, *9*, 113–122.
- Shiono, T., Kusumoto, B., Maeshiro, R., Fujii, S., Götzenberger, L., de Bello, F., & Kubota, Y. (2015). Climatic drivers of trait assembly in woody plants in Japan. *Journal of Biogeography*, *42*, 1176–1186.
- Smith, S. A., & Brown, J. W. (2018). Constructing a broadly inclusive seed plant phylogeny. *American Journal of Botany*, *105*, 302–314.
- Swenson, N. G., Enquist, B. J., Pither, J., Kerkhoff, A. J., Boyle, B., Weiser, M. D., Elser, J. J., Fagan, W. F., Forero-Montaña, J., Fyllas, N., Kraft, N. J. B., Lake, J. K., Moles, A. T., Patiño, S., Phillips, O. L., Price, C. A., Reich, P. B., Quesada, C. A., Stegen, J. C., ... Nolting, K. M. (2012). The biogeography and filtering of woody plant functional diversity in North and South America. *Global Ecology and Biogeography*, *21*, 798–808.
- Thomson, F. J., Moles, A. T., Auld, T. D., & Kingsford, R. T. (2011). Seed dispersal distance is more strongly correlated with plant height than with seed mass. *Journal of Ecology*, *99*, 1299–1307.
- Vázquez-Rivera, H., & Currie, D. J. (2015). Contemporaneous climate directly controls broad-scale patterns of woody plant diversity: A test by a natural experiment over 14,000 years. *Global Ecology and Biogeography*, *24*, 97–106.
- Venable, D. L., & Brown, J. (1988). The selective interactions of dispersal, dormancy, and seed size as adaptations for reducing risk in variable environments. *The American Naturalist*, *131*, 360–384.
- Wang, X., Alvarez, M., Donohue, K., Ge, W., Cao, Y., Liu, K., Du, G., & Bu, H. (2021). Elevation filters seed traits and germination strategies in the eastern Tibetan Plateau. *Ecography*, *44*, 242–254.
- Westoby, M., Leishman, M., & Lord, J. (1996). Comparative ecology of seed size and dispersal. *The Royal Society*, *351*, 1309–1318.
- Willis, C. G., Baskin, C. C., Baskin, J. M., Auld, J. R., Venable, D. L., Cavender-Bares, J., Donohue, K., de Casas, R. R., The NESCent Germination Working Group. (2014). The evolution of seed dormancy: environmental cues, evolutionary hubs, and diversification of the seed plants. *New Phytologist*, *203*, 300–309.
- Wisnoski, N. I., Leibold, M. A., & Lennon, J. T. (2019). Dormancy in metacommunities. *The American Naturalist*, *194*, 135–151.
- Wyse, S. V., & Dickie, J. B. (2017). Predicting the global incidence of seed desiccation sensitivity. *Journal of Ecology*, *105*, 1082–1093.
- Yonekura, K., & Kajita, T. (2003). BG Plants: Japanese scientific names index (Ylist). Available at: http://bean.bio.chibau.jp/bgplants/ylist_main.html.

Zhang, Y., Liu, Y., Sun, L., Baskin, C. C., Baskin, J. M., Cao, M., & Yang, J. (2022). Seed dormancy in space and time: Global distribution, paleo-and present climatic drivers and evolutionary adaptations. *New Phytologist*. <https://doi.org/10.1111/nph.18099>

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.

Authors and Affiliations

Akinori Fuji^{1,5}  · Buntarou Kusumoto^{1,2,4} · Takayuki Shiono¹ · Yasuhiro Kubota¹ · Werner Ulrich³ · John B. Dickie⁵ · Si-Chong Chen^{5,6}

✉ Akinori Fuji
fuji.akinori@gmail.com

✉ Yasuhiro Kubota
kubota.yasuhiro@gmail.com

¹ Faculty of Science, University of the Ryukyus, 1 Senbaru, Nishihara, Okinawa 903-0213, Japan

² Present Address: Faculty of Agriculture, Kasuya Research Forest, Kyushu University, 394 Tsubakuro, Sasaguri, Fukuoka 811-2415, Japan

³ Department of Ecology and Biogeography, Nicolaus Copernicus University, Toruń, Poland

⁴ Royal Botanic Gardens, Kew, Richmond TW9 3AE, UK

⁵ Royal Botanic Gardens Kew, Wellcome Trust Millennium Building, Wakehurst Place, Ardingly RH17 6TN, West Sussex, UK

⁶ CAS Key Laboratory of Aquatic Botany and Watershed Ecology, Wuhan Botanic Garden, Chinese Academy of Sciences, Wuhan 430074, China