



Seed size underlies the uncoupling in species composition between canopy and recruitment layers in European forests



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ABSTRACT

Increasing evidence supports that canopy richness favors multifunctionality in European forests. Given that recruitment represents one of the main demographic bottlenecks in plant communities, the provision of similar levels of forest functioning in the future will depend on successful natural regeneration in the present. Here, we evaluated whether canopy diversity enhances recruitment (abundance and richness) by providing a more diverse seed supply and a more heterogeneous environmental context; or, alternatively, if post-dispersal environmental filters outweigh these expected positive effects. For this purpose, we used a large-scale European platform comprising 173 forest plots that follow a canopy species richness gradient (from monoculture to mixed plots up to 5 tree species) in five forest types from Mediterranean to boreal forests. Despite that canopy diversity promoted a more diverse seed supply and a more heterogeneous light environment, this did not translate into a richer or more abundant community of recruits. In fact, we found an important uncoupling in species composition between recruitment and canopy layers. Our results suggest that strong post-dispersal filters, mediated by an interaction between seed size and latitude, drive this mismatch. Large-seeded species were over-represented in the recruitment at both extremes of the European gradient (Mediterranean and boreal forests), while the opposite trend occurred at intermediate latitudes. Altogether, our work shows that preserving a more diverse canopy may not ensure successful recruitment, and advocates future studies analyzing the role of post-dispersal filters on the assembly of European forests.

1. Introduction

Several forest ecology studies at the European scale have evidenced that high species richness is required to maintain ecosystem multifunctionality (Gamfeldt et al., 2013; van der Plas et al., 2016). This, together with an increasing demand for natural landscapes and the high cost of plantations has shifted back managers' attention towards natural regeneration (Johann, 2006). Natural regeneration is the process by which forest renewal is maintained by itself, being a critical stage in the life cycle of plants as it represents one of the main demographic bottlenecks (Leck et al., 2008). The way tree species establish, survive and grow, can have far-reaching impacts on the structure and dynamics of forest communities in the future (Harper, 1977; Nathan and Muller-Landau, 2000). Consequently, the future provision of functions and services by forests will considerably depend on current recruitment patterns. However, despite of the abundant and fruitful literature on plant community assembly (Götzenberger et al., 2012; Kraft et al.,

2015), there is no sound understanding of the role that canopy layer has on structuring the early regeneration community (but see Carnevale and Montagnini, 2002; Granda et al., 2012; Pérez-Ramos and Marañón, 2012). Filling this knowledge gap will improve our ability to predict better future stand dynamics in the face of global change and to design sustainable management practices.

At local scales, recruitment overcomes two consecutive ecological 'filters': seed arrival and post-dispersal survival (Clark et al., 2007a), and both can be influenced direct or indirectly by canopy attributes. Canopy composition through species' identities directly affects the local seed pool, which in turn determines seed rain patterns. For instance, the number of species in the canopy layer may favor seed rain richness, whereas the number of seeds may be determined by species' reproduction strategy (i.e. seed production). Overall, a richer and denser canopy layer is expected to promote a more diverse and abundant seed rain (Carnevale and Montagnini, 2002). However, though recruitment cannot occur without seed arrival, the presence of seeds does not

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guarantee establishment (Nathan and Muller-Landau, 2000). After primary dispersal, successful establishment depends on post-dispersal filters such as the suitability of local environmental conditions (Schupp et al., 2010), survival to seed predation (Kraft et al., 2015) and community-level processes like density-dependent mortality (Comita et al., 2014).

A richer canopy layer can also induce environmental heterogeneity through a mosaic of distinct environmental conditions relying on the combination of different species (Ampoorter et al., 2016). In fact, environmental conditions critical for seedling survival, such as light availability (Benavides et al., 2016; Nicotra et al., 1999), largely depend on specific attributes of trees in the canopy (e.g. leaf width and specific leaf area). Given that species have different regeneration niches (*sensu* Grubb, 1977), the probability that a higher number of species within the seed rain finds suitable recruitment sites is expected to increase with environmental heterogeneity, and hence, with canopy diversity. In addition, a richer seed supply is expected to relax competition via resource use partitioning among species (Johnson et al., 2017; MacArthur and Levins, 1967; Silvertown, 2004), leading to an increased probability of species coexistence and translated into a higher carrying capacity of seedlings. Thus, canopy diversity can *a priori* favor richness and abundance of recruits directly by providing a more diverse seed supply and, indirectly, by promoting a heterogeneous environmental context (hereafter “canopy-recruitment match scenario”).

Alternatively, post-dispersal processes may cancel out the direct link between the adult and recruitment communities. In particular, seed predation dictates which species actually emerge and their relative abundances (Larios et al., 2017). Usually, animals do not forage opportunistically but preferentially feed on certain species (Lichti et al., 2017). Thus, under strong post-dispersal predation pressures, the composition of the community of seedlings can strongly differ from the initial seed supply (Germain et al., 2013; Maron et al., 2012). Moreover, after emergence, the density of adults in the canopy may impose intrinsic limitations on seedling densities, *via* negative density-dependent mortality (NDD) (Connell, 1971; Janzen, 1970). Namely, increasing abundance of host-specific natural enemies such as seed predators, herbivores and pathogens in the surrounding areas of adult trees may reduce recruitment near conspecific adults. Such negative distance-dependent effects have been well-documented in tropical and temperate forests (Comita et al., 2014). This limitation on dominant competitors’ recruitment releases optimal microsites to be used by less competitive species, favoring the species replacement of dominant species in the canopy layer. This process, coined as ‘community compensatory trend’, provides recruitment advantages to rare species (Fricke and Wright, 2017; Terborgh, 2012), and may trigger a decoupling between the composition of the canopy layer and the community of recruits (Houle, 1998; Pérez-Ramos and Marañón, 2012). Therefore, if strong post-dispersal filters operate non-randomly on plant species establishment, the relationship between canopy and recruitment may not be straightforward (hereafter “canopy-recruitment mismatch scenario”).

These two scenarios, that tightly link the canopy and recruitment layers, are non-mutually exclusive. Depending on which one prevails, a diverse canopy layer may ensure natural regeneration and similar species composition in forests or not. This is a key question when designing management strategies aimed at preserving these habitats and their services in the future (EASAC, 2017). The overarching goal of this study was to evaluate if canopy diversity promotes natural regeneration. In particular, we asked if (1) canopy diversity enhances recruitment through a more diverse seed supply and increased environmental heterogeneity; or alternatively (2) if non-random post-dispersal survival cancels out the effects of the canopy layer. Finally, given the context-dependent nature of the processes involved in plant community assembly (Inman-Narahari et al., 2016); we evaluated whether recruitment patterns (canopy-recruitment match vs mismatch scenarios) are maintained across a latitudinal gradient. For this purpose, we used a comprehensive database of tree canopy composition and recruitment

patterns in 173 permanent European forest plots located at contrasting latitudes (from Mediterranean to boreal forest), and following a richness gradient (from monoculture to mixed plots up to 5 tree species).

2. Material and methods

2.1. Study sites

The study was conducted within the framework of the European project FunDivEUROPE (<http://www.fundiveurope.eu/>), which includes a network of permanent forest plots distributed in five mature European forests. As mature forests, we refer to forest systems with complex age distributions and stand structure. These systems better reflect plant community assembly than experimental plantations because their composition is the result of environmental filters operating for several decades (Leuschner et al., 2009). In addition, these forests are some of the most representative European forest types, covering a large European bioclimatic gradient (Figure A1): from the southernmost continental Mediterranean forest located in Spain (40.7°N, -1.9°E), through a sub-continental temperate forest in Romania (47.6°N, 25.3°E) and a temperate forest in Germany (51.5°N, 10.2°E), to the northernmost forests as a hemiboreal forest in Poland (52.7°N, 23.9°E) and a boreal one located in Finland (62.6°N, 29.9°E). In each forest type, between 28 and 43 plots of 30 × 30 m size were set. Plots followed a species richness gradient of local dominant tree species in the canopy (focal species in this study), from monospecific to mixed plots with three species in the boreal forest, four species in Spain, Romania and Germany and five species in the case of the hemiboreal forest in Poland. The focal species considered in the five forests encompassed conifers, deciduous broadleaved species and one evergreen broadleaved species (Table A1). Most species were only present in a unique forest type, except for *Pinus sylvestris*, *Picea abies* and *Acer pseudoplatanus* (Table A1). Plots within forests were chosen following three main criteria: (i) similar relative abundance of the focal tree species within mixed plots (i.e. high evenness), minimizing the presence of non-dominant species within the plot (i.e. preferably the summed basal area of these species was below 5% of the total basal area, with a maximum of ca. 10%); (ii) minimal signals of recent management, and (iii), similar environmental characteristics in terms of topography, slope and soil properties. Further information about experimental design can be found in Baeten et al., (2013). In summary, we used five forest types, 173 plots and 13 focal tree species to test the relationship between recruitment and canopy richness (see Table A1 for more details about the study sites).

2.2. Data collection

2.2.1. Regeneration sampling

Regeneration surveys were carried out in 2012, from April to late August, ensuring that all tree species had fully expanded leaves by the sampling date. Samplings were performed in a subplot of 16 m² (4 × 4 m) located on the center of the plot of 30 × 30 m. In each subplot, we quantified recruitment abundance and richness through identifying all saplings of the focal tree species and counting them. Focusing on focal species may have result in an underestimation in the number of individuals and species represented in the recruitment layer. However, it is good approximation to assess recruitment dynamics in the context of ecosystem services, since these are mostly delivered by common species rather than rare ones (Winfree et al., 2015). Saplings were considered those individuals attending to the following criteria: (i) those older than one year old, avoiding newly emerged seedlings, i.e. with no internode in the main stem or still with cotyledons. Thus, we measured survivors to the first extreme abiotic conditions such as drought, considered a main bottleneck for recruitment in Mediterranean areas (Matías et al., 2011). (ii) Individuals with a height up to 1.50 m tall (Benavides et al., 2016) and (iii) individuals naturally

regenerated from seeds. For those species with tendency to sprout, e.g. *Quercus* sp. or *B. pendula*, we correctly identified samplings from vegetative offsprings (not considered in this study) following Espelta et al., (1995).

Although, our sampling unit is much smaller than the scale of forest stand (i.e. plot size), previous studies have detected significant relationships between canopy and recruitment patterns using the same subplot area (4 m × 4 m) (Benavides et al., 2016, 2015; Rabasa et al., 2013). However, to take into account potential sampling biases, we extended our regeneration richness surveys to the main plot of 30 × 30 m in three out of five forests (boreal, sub-continental temperate and continental Mediterranean forests).

2.2.2. Tree canopy and seed supply characterization

In each 30 × 30 m plot, we identified and measured the basal area of each adult tree. Then, we calculated the effective number of species (ECR, effective canopy richness) as the exponential of the Shannon index (Jost, 2006). This index accounts for the number of different tree species (species richness in the plot) and their evenness (i.e. proportional basal area for each specific species within plot).

To assess local seed supply, for each individual tree we estimated seed production following Greene and Johnson (1994) equation:

$$Q_{S_{ij}} = 0.0107ms_j^{-0.58} \times S_i^{1.08} \quad (1)$$

Seed production of the *i*-th tree from the *j*-th species ($Q_{S_{ij}}$), is inversely correlated to mean seed mass of the *j*-th species (ms_j) and directly proportional to the individual tree size (S_i). See Eq (2) for calculations of this component). Green and Johnson equation is suitable to use in our study since they were obtained for the same species or, at least belonged to the same genera. Moreover, Greene and Johnson (1994) found that the relationship between seed production and basal area had a monotonic increasing response (Eq (1)) when basal areas are less than ~ 0.4 m², which represents the range of at least > 95% of trees in our study sites. Mean seed mass of species (ms_j) was obtained averaging seed mass from different databases —Seed Information database-SID (“Royal Botanic Gardens Kew,” 2018) and LEDA traitbase (Kleyer et al., 2008) — and tree size S_i was calculated from the basal area of each *i*-th individual (BA_i) following the empirical equation of Whittaker and Marks, (1975):

$$S_i = 113000 \times BA_i^{0.855} \quad (2)$$

To infer the quantity of seeds arriving to the *h*-th regeneration subplot (Q_{S_h}), we weighted seed production of each individual tree ($Q_{S_{ij}}$) by its distance to the center of the *h*-th subplot ($dist_{hi}$). This way, we took into account that seed arrival exponentially declines with distance (Gómez-Aparicio et al., 2011; Ribbens et al., 1994). To estimate total seed supply, we summed contributions of each individual tree following eq. (3).

$$Q_{S_h} = \sum_{i=1}^n Q_{S_{ij}} * e^{-dist_{hi}} \quad (3)$$

Finally, we summed seed supply for each species and calculated the effective number of species (ESS, effective seed supply richness) to estimate the diversity of the local seed supply. Our estimates of seed arrival assume similar dispersal kernels for all species. To evaluate the effects of such assumption, we simulated seed dispersal in our study plots. For this, adult trees produced seeds according to Eqs. (1)–(2) and dispersed them following a negative exponential kernel (Nathan et al., 2012), that reflected species-specific values observed in literature. The model tracked the number and identity of seeds that fell in the regeneration subplot (see Appendix B for model details). Then, we compared “real” values of Q_{S_h} and ESS with those obtained with Eqs. (1)–(3). We found a strong correlation between “real” and estimated values (Pearson correlation 0.70, $p < 0.01$ and 0.71, $p < 0.01$, Q_{S_h} and ESS respectively). Therefore, our simulations confirmed that our estimations were able to reflect differences among plots in local seed

supply.

2.2.3. Environmental data

We measured different key environmental factors for regeneration to characterize the local environmental heterogeneity at plot (30 × 30 m) and regeneration subplot level (4 × 4 m). At the plot level, we subdivided each plot in a grid-cell of quadrats of 10 × 10 m and we established a sampling point of 1 m² at every quadrat corner and in the plot center (17 points in total) (Figure A1). In each point, we took a hemispherical photograph using a horizontally-levelled digital camera (CoolPix 995, Nikon, Tokio, Japan), mounted on a tripod and aimed at the zenith, using a fish-eye lens of 360° field of view (FCE8, Nikon) (Valladares and Guzmán 2006). Photographs were taken in the center of each sampling point (1 m²) at 0.5–0.7 m above the ground (e.g Benavides et al., 2016). Then, photographs were analyzed with Hemi-view v.2.1 software (Delta-T Devices Ltd, Burwell, UK) to obtain total light availability through the global site factor (GSF) and the diffuse light using the indirect site factor (ISF). Additionally, in three out of five forest types with contrasting bioclimatic conditions (boreal, sub-continental temperate and continental Mediterranean forests), we recorded the soil depth with a soil auger by drilling to a depth of 60 cm (depth enough to ensure a normal root growth of saplings) and visually estimated the percent of stoniness, shrubs and herbs over 17 points of the grid-cell. As a measure of heterogeneity, we estimated the coefficient of variation (CV) for each environmental variable in each plot (e.g. Quilchano et al., 2008; Wiens, 2000). Besides, in the three forest types where additional variables were measured, we estimated overall environmental heterogeneity in each plot as the average of the coefficient of variation of all environmental variables.

To account for environmental conditions at the subplot level (4 × 4 m), where recruitment was measured, we divided our subplots into 16 quadrats of 1 m² each. In each quadrat, we quantified cover of stones, shrubs and herbs and calculated the coefficient of variation of these values (Figure A1B, yellow triangles). In addition, we estimated light and soil depth heterogeneity, as the coefficient of variation of the measurements taken in the four closer points of the grid-cell of the main plot (30 × 30 m) plus the point located on the plot center (Figure A1B, blue circles). In sum, at the subplot-level, cover heterogeneity was obtained from the 16 values of the 16 quadrats within the subplot; while light and soil heterogeneity were calculated from one measure recorded in the center of the plot and four points of the main grill-cell around the plot center.

2.3. Statistical analyses

2.3.1. Effects of canopy diversity on local seed supply and environmental heterogeneity

We used Gaussian linear mixed models (GLMM, Breslow and Clayton, 1993) to test whether a more diverse canopy layer promoted environmental heterogeneity at the plot level (30 × 30 m). We run a model for the overall environmental heterogeneity and for each environmental factor independently (GSF, ISF, soil depth and biotic and abiotic covers). In all cases, forest type was included as a random factor. Then, we assessed the effects of canopy diversity on seed rain diversity by means of Gaussian linear mixed models with forest type as a random factor. Marginal and conditional-R² were calculated in all cases following the method outlined by Nakagawa and Schielzeth (2013).

2.3.2. Effects of canopy diversity and environmental heterogeneity on recruitment patterns

We modeled regeneration abundance as a negative binomial process, and when the sample size had a great number of zeros (absence of regeneration) we used hurdle models. Hurdle models evaluate consecutively the occurrence of recruitment (the presence or not of saplings) using a binomial distribution and, the regeneration abundance, conditional of the binomial part (positive presence), using a negative

binomial distribution (Dalrymple et al., 2003). Our response variable was the number of saplings within the regeneration subplots and our explanatory variables were seed quantity (Q_{s_i}), seed supply diversity (ESS), and the heterogeneity in light, soil depth, stoniness, shrubs and herbs at the regeneration subplot level. Recruitment abundance was analyzed combining datasets from the five regions including forest type as a random factor and for each forest type independently. We used package glmmTMB (Brooks et al., 2017) for this purpose.

Similarly, recruitment richness was analyzed using a generalized linear mixed model (GLMM) with a Poisson distribution and forest type as a random factor. The explanatory variables were the same as for recruitment abundance model, except for seed quantity that was not included. We also ran similar models for each forest type independently. To evaluate any bias associated to regeneration subplot size, we applied richness models to data at the plot level (30 × 30 m) in the three forests types for which we had this information available (boreal, sub-continental temperate and continental Mediterranean forests).

2.3.3. Effects of post-dispersal filters on recruitment

To assess a potential mismatch in species composition between canopy and recruitment layers, we plotted species composition in the adult community against their composition in the community of recruits. Subsequently, we evaluated the strength of post-dispersal filters. Firstly, we regressed recruitment richness against seed supply diversity using Gaussian regression models. Non-significant effects would depict the presence of strong post-dispersal filters. Given that seed size (measured as seed mass) is a key trait modulating post-dispersal survival (i.e. predation, Larios et al., 2017) and NDD (Lebrija-Trejos et al., 2016), we evaluated if the potential mismatch between the canopy and recruitment would respond to seed size effects. For this purpose, we calculated changes in relative abundances of species from the adult to the recruitment community for each plot following the next equation: $\Delta A_j = (A_{rj} - A_{c_j})/A_{c_j}$; being A_{rj} the relative abundance of the j -th species in the community of recruits and A_{c_j} its relative abundance in the canopy layer. Positive values occur when the j -th species is over-represented in the community of recruits and negative values when it is under-represented. Values close to 0 imply that species abundances do not change. For each forest type we regressed ΔA_j against seed size by means of Gaussian regression models.

3. Results

We found large differences in the number of saplings among forests (Fig. 1). The highest values of regeneration abundance were found in forests located at intermediate latitudes in Europe, with an average abundance value of ~ 3.8 and ~ 7 saplings per m^2 in sub-continental

temperate forest in Romania and in the temperate forest in Germany, respectively. In contrast, the forests located on the boundaries of the European gradient presented the lowest values of recruitment abundance with ~ 0.2 and ~ 0.5 saplings per m^2 in boreal and continental Mediterranean forests, respectively. A similar trend was also found for recruitment richness (Fig. 1).

Higher canopy diversity promoted both, higher global (GSF) and indirect (ISF) light heterogeneity. Nonetheless, it did not affect other dimensions of environmental heterogeneity (Table A2; i.e. stoniness and biotic cover, soil depth). In addition, canopy diversity enhanced the effective number of species in the local seed supply (estimate 0.20 ± 0.04 , $p < 0.01$, $Rm^2 = 0.22$, $Rc^2 = 0.26$).

Regarding regeneration abundance, we did not observe clear patterns. At low and intermediate latitudes, seed quantity and heterogeneity of different biotic variables (shrub and herb covers) had a positive effect on recruitment abundance. In contrast, in boreal forests, seed quantity and light heterogeneity had a negative and marginally significant effect on the number and the occurrence of recruits, respectively. In the overall abundance model, we found that seed diversity negatively affected the occurrence of recruits and environmental heterogeneity tended to have a non-significant or negative effect (Table 1, regeneration abundance). In the case of recruitment richness, it was poorly explained by our explanatory variables (Table 1, regeneration richness); and similar results were found for recruitment richness data on 30 × 30 m plots from continental Mediterranean, sub-continental temperate and boreal forests (Table A3).

We found that species composition in the sapling community was largely different to the canopy layer in the five studied forests (Fig. 2). For instance, we observed absence of recruitment for some species dominating the canopy layer (e.g. *B. pendula* in boreal and hemiboreal forests, *P. sylvestris* in hemiboreal forest or *P. abies* in the temperate forest) while others, non-dominant tree species were common in the community of recruits (*P. abies* in boreal forests, *C. betulus* in the hemiboreal forest, *A. alba* and *F. sylvatica* in the sub-continental temperate forest, *F. excelsior* and *A. pseudoplatanus* in the temperate forest and *Q. ilex* and *Q. faginea* in the continental Mediterranean forest) (Fig. 2). In addition, our analyses revealed that the diversity of seeds arriving to the regeneration plots did not enhance recruitment richness (values around 0, Fig. 3A), suggesting the presence of important post-dispersal filters. These post-dispersal filters were modulated by the interplay between forest latitude and seed size. Saplings from species with larger seeds were over-represented in the recruitment community at the boundaries of the European gradient (boreal and continental Mediterranean forest) whereas the opposite trend was observed at intermediate latitudes (Fig. 3B).

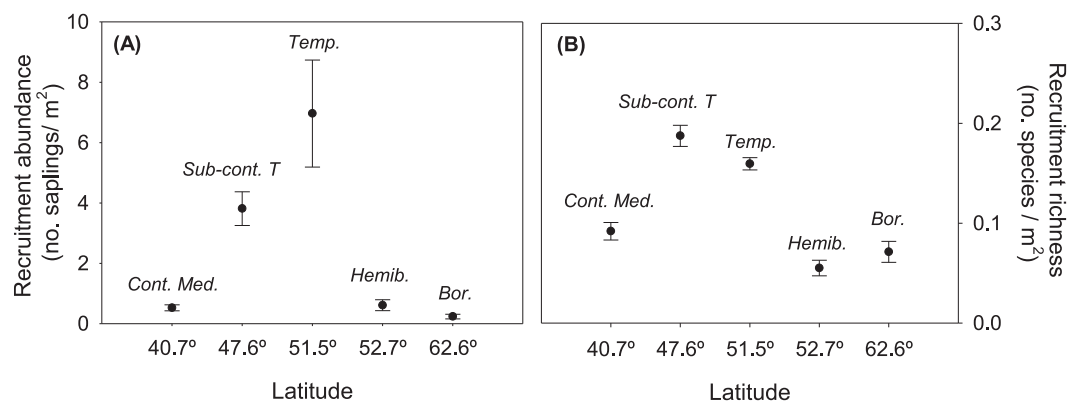


Fig. 1. Mean and standard error (SE) of regeneration abundance and richness for the dominant tree species in the five studied forests in Europe sorted by latitude. Forest code: continental Mediterranean forest in Spain (Cont. Med); sub-continental temperate forest in Romania (Sub-cont. T); Temperate forest in Germany (Temp.); hemiboreal forest in Poland (Hemib.) and boreal forest in Finland (Bor.).

Table 1

Results from zero-inflated models and Gaussian linear mixed models testing the effect of seed supply diversity (ESS), seed quantity (Q_{sh}) and environmental heterogeneity in soil depth, cover of shrubs, herbs and rocks on recruitment abundance and richness. Shaded cells indicate that the overall model, using forest type as a random factor. † $P < 0.10$; * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Soil depth was not measured in the forests marked with the symbol (-), therefore, it was not included in the model.

Regeneration abundance									
	N	ESS	Q_{sh}	CV Stoniness	CV Soil depth	CV Shrubs	CV Herbs	CV GSF	AIC
Overall ^{2I}	170	(-)** ¹			-	(-) ^{†2}			1381
Continental Mediterranean	35		(+) ^{***}				(+)*		215.49
Sub-continental temperate	27			(-)**			(+)*		273.93
Temperate	37		(+)*		-	(+)*			417.59
Hemiboreal ^{2I}	43				-				250.69
Boreal ^{2I}	27		(-) ^{†2}					(-) ^{†1}	131.75

^{2I} Zero inflated model: ¹recruitment occurrence; ²recruitment abundance

Regeneration richness									
	N	ESS	CV Stoniness	CV Soil depth	CV Shrubs	CV Herbs	CV GSF	AIC	
Overall	172			-				491.9	
Continental Mediterranean	36					(+) [†]		99.37	
Sub-continental temperate	27							89.01	
Temperate	38			-				114.64	
Hemiboreal	43			-				102.88	
Boreal	28							74.33	

4. Discussion

The future composition of forests can largely depend on current recruitment, which in turn may be strongly modulated by the attributes

of the trees in canopy layer (Carnevale and Montagnini, 2002). Nonetheless, little is known about this process in European forests, where natural regeneration is a conservation goal on current management policies (Rametsteiner and Simula, 2003). Overall, our work provides

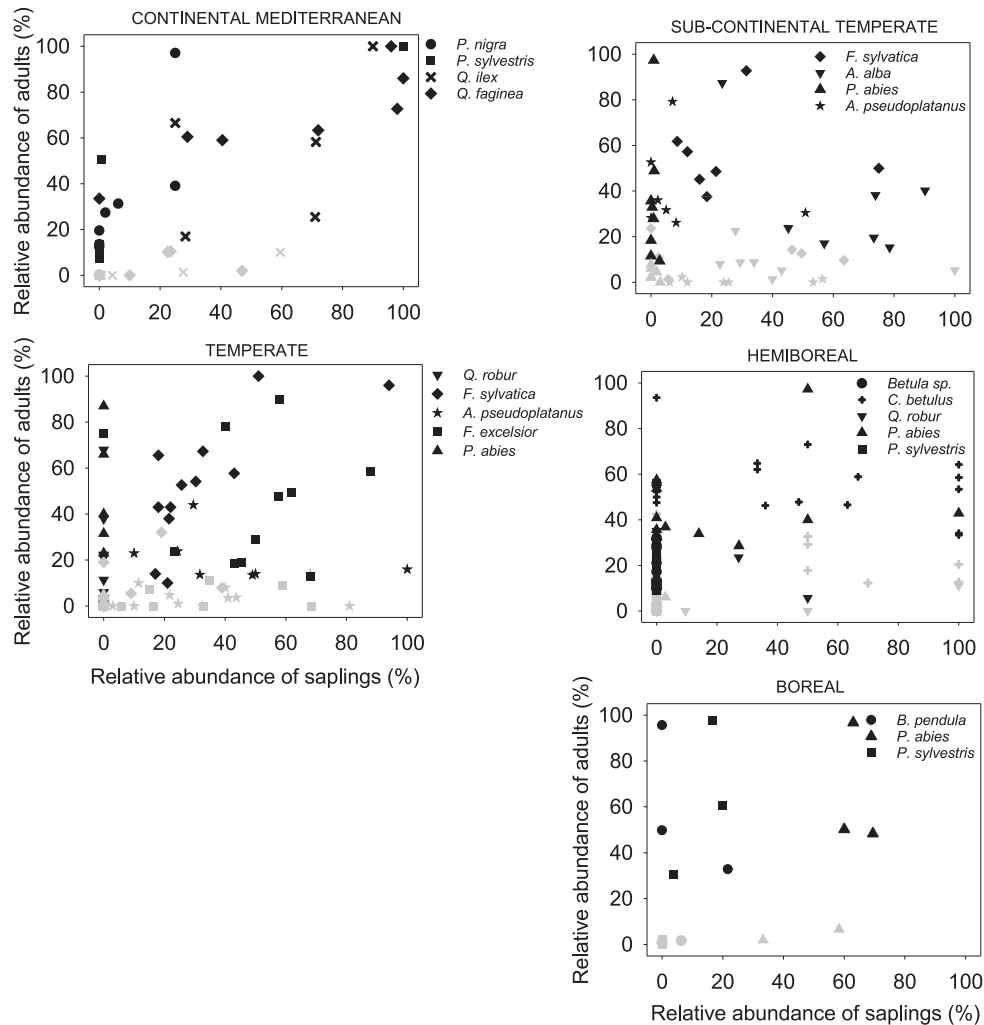


Fig. 2. Comparison between relative abundance of adults and saplings for the focal tree species in the five studied forests. Each point represents the average abundance of each species for each canopy combination. Points in ‘black’ and ‘grey’ depict tree species being dominant in the canopy or not, respectively.

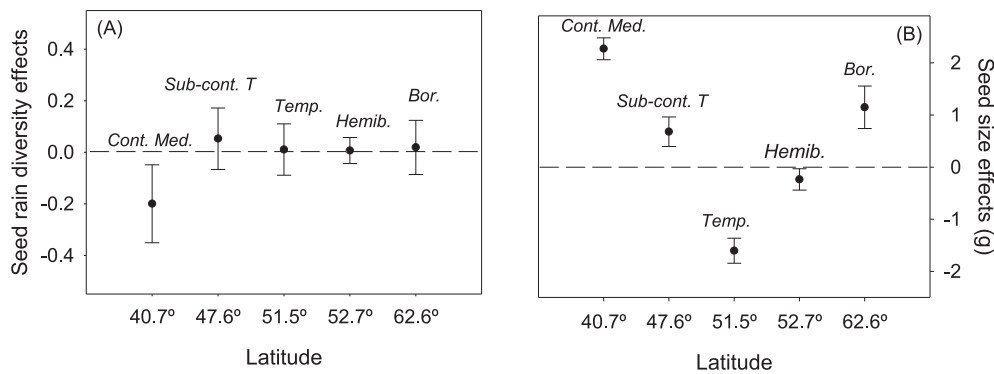


Fig. 3. (A) Effect size (\pm s.e.) of the seed supply diversity on the richness the community of recruits and (B) effects of seed size measured as seed mass in g (\pm s.e.) on changes in the relative abundance of species from the canopy to the recruitment layer. Forests are sorted by latitude. In figure A, effect size values within 0 depict the presence of strong post-dispersal filters. In figure B, positive values imply that large seeded species are over-represented in the recruitment community, the opposite for negative values. Forest code: continental Mediterranean forest in Spain; sub-continental temperate forest in Romania; Temperate forest in Germany; hemiboreal forest in Poland and, boreal forest in Finland.

compelling evidence of a mismatch between the composition of the community of adult and juvenile trees, likely mediated by seed size effects. The presence of strong post-dispersal filters strongly modified which species actually recruited, blurring the effects of the local seed supply. As a result, canopy diversity *per se* did not guarantee enhanced seedling establishment.

According to the “canopy-recruitment match scenario”, our study showed that canopy diversity improved conditions for recruitment. In particular, our results suggest that it provided a more diverse seed supply and promoted heterogeneous light environments. The former would release competition among seedlings via niche partitioning (Johnson et al., 2017; MacArthur and Levins, 1967; Silvertown, 2004). The latter would increase the opportunities of establishment and survival of multiple individuals with different light requirements (Ameztegui and Coll, 2011; Ligot et al., 2013). Strikingly, these apparently optimal conditions did not translate into a more abundant or richer community of recruits.

Regarding abundance, it depended on factors operating independently from canopy richness. In some communities, seed rain quantity and the heterogeneity of the vegetation cover affected the number of recruits. However, none of these factors depended on the diversity of the canopy layer. In continental Mediterranean and temperate forests, recruit abundance was positively affected by the number of seeds arriving. This is consistent with numerous experimental studies reporting increasing recruitment rates after seed addition in a wide range of plant communities (Clark et al., 2007a, 2007b; Dickson and Foster, 2008; Münzbergová, 2012). Regarding vegetation cover, patterns differed among forest types. In the temperate forest, shrub cover heterogeneity enhanced recruitment, probably thanks to shrub facilitation (nursery effects). In this forest type, the presence of shrubs was limited to very few plots, and when present, their representation was low (cover < 10%). However, a minimal shrub layer (i.e. more heterogeneous environments) was enough to trigger a positive effect on recruitment abundance. Shrub facilitation may have involved protection against herbivory, water stress or photoinhibition (Gómez-Aparicio et al., 2004; Padilla and Pugnaire, 2009). In contrast to the temperate forest, in continental Mediterranean and sub-continental forests, recruitment abundance was promoted by heterogeneity in the herb cover. Herbaceous species often use large amount of water, which can limit the establishment of certain woody species (Rey Benayas et al., 2005). Species with superficial root systems in the seedling stage strongly compete for water with herbs, while those with deep primary roots are expected to be less affected. Therefore, a high heterogeneity in the herb cover can facilitate the presence of species exploiting different soil layers resulting in a higher carrying capacity of seedlings. This may have been particularly true in the Mediterranean forest, where water scarcity during summer limits recruitment (Lloret et al., 2005) and species with contrasting root systems coexist (pines vs oaks). In fact, our

findings showed a positive effect of heterogeneity in the herb cover on both—recruitment diversity and abundance, marginally significant and significant respectively.

In the case of richness, patterns found here were even more unexpected. In almost all forest types, none of our variables explained the effective number of species present in the community of recruits. This lack of effects was also observed when the sampling unit was extended to the plot level (30 × 30 m), suggesting that our results were not biased by sampling scale (Kobe and Vriesendorp, 2009). These findings contradict previous studies showing that richer and denser canopy layer promotes a richer community of recruits (Carnevale and Montagnini, 2002; Olson and Wagner, 2011). Furthermore, this result refutes the hypothesis stating that environmental heterogeneity *per se* can bolster plant species diversity (Dufour et al., 2006; Lundholm, 2009) via niche partitioning (Bolker et al., 2003; Chesson, 2000; Costanza et al., 2011). In our study, the absence of relationship between seed supply diversity and the recruitment richness was translated into a mismatch in species composition between the canopy and recruitment layers (“canopy-recruitment mismatch scenario”). This suggests that post-dispersal filters are key in structuring European forests.

We found that seed size (measured as seed mass) determined species establishment in the community of recruits and that this effect was context-dependent. Seed size is a key plant trait tightly linked to important post-dispersal processes, such as seed predation, competition or negative density-dependent mortality (Fenner and Thompson, 2005; Larios et al., 2017; Moles and Westoby, 2004). In particular, we found that large-seeded species were overrepresented at the boundaries of the European gradient (boreal and continental Mediterranean forests) whereas the opposite trend was found at intermediate latitudes (i.e. temperate forests). This is in line with the idea that less fecund but large-seeded species can benefit from stressful conditions; but that these advantages may not hold in benign environments (Muller-Landau, 2010). Large seeds have a higher amount of stored resources in comparison to small-seeded species. This can provide them a higher probability to germinate since they are more likely to be cached by effective dispersers (Pesendorfer et al., 2016), and a better capacity to cope with adverse environmental conditions and competition at the seedling stage (Fenner and Thompson, 2005; Lebríja-Trejos et al., 2016). Nonetheless, a higher seed size usually implies lower fecundity (Henery and Westoby, 2001) and higher post-dispersal predation due to their higher nutritional value (Jansen et al., 2004). Thus, under milder environmental conditions, the benefits of producing large seeds may not outweigh those of increased fecundity (i.e. smaller-seeded species). The fact that we found higher number of saplings in temperate forests (i.e. middle conditions for recruitment) and an overrepresentation of small-seeded species in the recruitment layer supports this view.

Nevertheless, other factors beyond the seed size-fecundity trade off may be operating in our study. For instance, in Mediterranean forests,

the negative effect of seed size was driven by poor regeneration of pine species (*P. sylvestris* and *P. nigra*). In Mediterranean areas, pine recruitment is becoming seriously affected by more frequent drought stress (Castro et al., 2004; Galiano et al., 2013) and forest fires (Carnicer et al., 2014), together with a low capacity of response to environmental changes at the seedling stage in comparison to oaks (Bastias et al., 2018). In boreal and hemiboreal forests, recruitment limitation of *B. pendula*, was probably associated with a strong competition with the herbaceous vegetation (Hynynen et al., 2010), abundant in these two forests (> 30% of cover). Finally, the lack of regeneration of *P. sylvestris* in the hemiboreal forest may respond to a dense canopy layer that intercepts direct sunlight (mean GSF 0.11), which is critical for the recruitment of this shade-intolerant species (Gaudio et al., 2011). Irrespectively of the mechanism involved (size-fecundity trade-offs vs species-specific recruitment bottlenecks), our results agree with previous works documenting that post-dispersal filters can dramatically change the diversity and composition of European forests (Granda et al., 2012; Moser et al., 2010; Pérez-Ramos and Marañón, 2012).

Our study represents a first attempt to understand at a regional scale the role of canopy diversity on forest regeneration in European forests. However, there are important limitations that need to be acknowledged. Firstly, our regeneration sampling was limited to dominant (focal) tree species. Therefore, we did not include all individuals and species present in the recruitment layer. Still, our conclusions are robust to such simplification, as non-focal species represented less than 5% of the basal area in the canopy layer and their abundance was even lower in the community of recruits (CCB pers. obs.). Even more, if saplings of non-focal species would be actually common, the mismatch between the canopy and recruitment layer would have been even stronger. Our second main limitation is that local seed supply was indirectly estimated rather than directly quantified. Nevertheless, some of our focal species are dispersed by scatter-hoarders (i.e. oaks, beech, Wall and Beck, 2012), and a direct assessment with seed traps would have not detected buried seeds, thus, biasing our estimates of seed rain diversity (ESS) and not amending our limitations. Therefore, we believe that our approach reflect general patterns of seed supply since they acknowledge the three main processes involved in its generation, i.e. trade-offs between seed size and fecundity (Henerly and Westoby, 2001), the local abundance of adult trees (Whittaker and Marks, 1975) and distance effects on seed arrival (Nathan et al., 2012).

5. Conclusion

We found a strong mismatch in species composition between the canopy and the recruitment layers in five different European forests that covered a wide bioclimatic gradient from boreal to Mediterranean. Moreover, our results suggest that this mismatch is driven by the presence of strong post-dispersal filters mediated by seed size, which blur the optimal conditions for recruitment initially provided by canopy diversity (i.e. a richer seed supply and a more heterogeneous environment). However, the identity and strength of these post-dispersal filters remains unsolved. In European latitudes, several studies have assessed the role of negative density-dependent mortality on plant community assembly (Comita et al., 2014; Granda et al., 2012). In contrast, the role of post-dispersal seed predation has been largely overlooked (Larios et al., 2017). We hope our work stimulates future studies aimed at identifying the ecological mechanisms driving post-dispersal filters and at quantifying their role in forest recruitment. This will improve our understanding of recruitment, providing valuable information to design optimal and sustainable management practices. The information provided by this study enabled us to gain insight into the effect of canopy diversity on recruitment patterns and helps to predict future shifts in species composition in European forests and further, in the functions and services that they provide us.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2019.117471>.

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