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Climate and species stress resistance modulate the higher survival of large seedlings in forest restorations worldwide

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Abstract. Seedling planting plays a key role in active forest restoration and regeneration of managed stands. Plant attributes at outplanting can determine tree seedling survival and consequently early success of forest plantations. Although many studies show that large seedlings of the same age within a species have higher survival than small ones, others report the opposite. This may be due to differences in environmental conditions at the planting site and in the inherent functional characteristics of species. Here, we conducted a global-scale meta-analysis to evaluate the effect of seedling size on early outplanting survival. Our meta-analysis covered 86 tree species and 142 planting locations distributed worldwide. We also assessed whether planting site aridity and key plant functional traits related to abiotic and biotic stress resistance and growth capacity, namely specific leaf area and wood density, modulate this effect. Planting large seedlings within a species consistently increases survival in forest plantations worldwide. Species' functional traits modulate the magnitude of the positive seedling size–outplanting survival relationship, showing contrasting effects due to aridity and between angiosperms and gymnosperms. For angiosperms planted in arid/semiarid sites and gymnosperms in subhumid/humid sites the magnitude of the positive effect of seedling size on survival was maximized in species with low specific leaf area and high wood density, characteristics linked to high stress resistance and slow growth. By contrast, high specific leaf area and low wood density maximized the positive effect of seedling size on survival for angiosperms planted in subhumid/humid sites. Results have key implications for implementing forest plantations globally, especially for adjusting nursery cultivation to species' functional characteristics and planting site aridity. Nursery cultivation should promote large seedlings, especially for stress sensitive angiosperms planted in humid sites and for stress-resistant species planted in dry sites.

Key words: afforestation; forest plantations; forest restoration; outplanting performance; reforestation; seedling quality; specific leaf area; wood density.

Introduction

Forest restoration is a global priority for reverting forest loss and land degradation as well as for climate change mitigation (Verdone and Seidl 2017, Holl and Brancalion 2020). Additionally, large forested areas are managed worldwide for timber and nonwood products, playing an important role in local and global economies (Millennium Ecosystem Assessment [MEA] 2005). Seedling planting is often the main active method for forest restoration and the regeneration of managed stands (Stanturf et al. 2014). Thus, understanding the factors that promote successful seedling planting is key for effective restoration of forest ecosystem functions (Ostertag et al. 2015).

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For decades, the attributes that affect seedling outplanting performance have intrigued forest researchers and practitioners (Wakeley 1954). Attributes of seedlings grown in forest nurseries, such as seedling size, can be modified by the environment and the cultivation technique to which plants are exposed in the nursery (van den Driessche 1991, Grossnickle and El-Kassaby 2016). Understanding the interplay of cultivation techniques, plant attributes, and environmental conditions at planting sites is crucial for enhancing seedling survival in afforestation and reforestation (hereafter plantations) (Villar-Salvador et al. 2004). In this regard, shoot height and stem diameter are morphological attributes routinely used in nurseries to remove plants with poor survival potential because these attributes are easy to measure (Mexal and Landis 1990, Puttonen 1997, Grossnickle 2012). Yet, no consensus on the relationship between seedling size at planting and outplanting survival exists. For plants of the same age, many studies show that large seedlings, that is, plants that have high mass, stem volume or diameter, or height, have higher outplanting survival than small seedlings (Mason et al. 1996, South et al. 2005, Cuesta et al. 2010*b*, Pinto et al. 2012, Villar-Salvador et al. 2012). Other studies, however, reported lower outplanting performance of large seedlings than small ones, especially in dry sites (Tuttle et al. 1988, Rose et al. 1993, Trubat et al. 2011). The net effect of seedling size on outplanting survival can result from opposite ecophysiological processes mediated by plant size. On one hand, an increase in size can enhance survival through higher growth and resource mobilization (Villar-Salvador et al. 2012), which are key processes for seedling establishment, competition, and drought stress avoidance (Grossnickle 2005). On the other hand, size increase can reduce seedling survival because of higher transpiration, which can increase vulnerability to drought stress (Grossnickle 2012, Oliet et al. 2019).

Many plant species are used in forest plantations, encompassing a wide functional diversity (Hua et al. 2016). Plant functional traits, such as organ structure and nutrient concentration, or biomass allocation pattern, affect plant resource economy, growth capacity, and stress resistance (Violle et al. 2007, Reich 2014), which in turn can influence seedling survival in forest plantations (Martínez-Garza et al. 2013, Charles et al. 2018, Werden et al. 2018). Traits that confer stress resistance are usually associated with low plant growth and resource acquisition capacity (Reich 2014), indicating a trade-off between growth rate and survival (Martínez-Vilalta et al. 2010). For instance, plant species with high specific leaf area (SLA; leaf area per leaf mass ratio) grow quickly and have a high photosynthesis rate (Reich 2014), but are more vulnerable to herbivory (Hanley et al. 2007) and less resistant to drought stress (Bartlett et al. 2012, Greenwood et al. 2017, Zhu et al. 2018, Harrison and LaForgia 2019). Similarly, wood density (WD; the wood mass per volume) reflects organ construction effort and determines plant water transport capacity and vulnerability to embolism (Hacke et al. 2001, Liang et al. 2020). High WD species show inherent low relative growth rate, but usually have high drought, herbivore, and disease resistance (Chave et al. 2009, Anderegg et al. 2016, Greenwood et al. 2017). Accordingly, plant species that live in poor resource habitats and under adverse conditions tend to have low SLA and high tissue density (Poorter and De Jong 1999, Wright et al. 2001, Chave et al. 2009). Thus, SLA and WD can be used as a functional and ecological framework to classify plant species according to their stress resistance and growth capacity.

We argue that the contradictory results on the relationship between seedling size at planting and outplanting survival may be due to inherent differences in species' functional characteristics, which could modulate the effect of seedling size on outplanting survival (Gardiner et al. 2019), and this effect could be contingent upon environmental conditions at planting sites (Charles et al. 2018). Increasing seedling size may positively affect outplanting survival in stress-resistant species because they may more effectively offset the negative ecophysiological effects linked to large size, whereas the opposite may occur in less stress-resistant plants. For example, we can expect that increased water stress linked to seedling size may hinder less plant functioning in species with inherent low vulnerability to drought-induced embolisms. Knowledge of how seedling size, plant functional strategy, and environmental conditions interact to determine seedling survival can provide guidelines for designing cultivation methods to match forest restoration objectives for a wide range of conditions and species.

The present study evaluated on a global scale the direction (i.e., positive, negative, or neutral) and the magnitude of the effect of seedling size at outplanting on seedling survival. Moreover, we assessed whether aridity at the planting site and key functional traits related to plant stress resistance, namely, SLA and WD, modulate this relationship. We hypothesized that (1) for seedlings of the same age, an increase in size enhances outplanting survival (H1), (2) the positive effect of size on survival is reduced in dry sites (H2), but (3) increased in species having stress-resistant traits (H3). To test these hypotheses, we conducted a global meta-analysis on the literature evaluating the effect of seedling size on outplanting performance. We also compiled data on SLA and wood density from scientific literature and published databases as indicators of species growth and stress-resistance capacity.

Materials and Methods

Literature search

During November 2015, we systematically searched the literature (Côté et al. 2013) in the following databases: Web of Science, Scopus, Sociedad Española de Ciencias Forestales (SECF), SciELO, and the

Reforestation, Nurseries, and Genetic Resources (U.S. Department of Agriculture Forest Service; RGNR). We used the following terms: ["survival" OR "field performance" OR "establishment" OR "outplanting"] AND ["seedling quality" OR "seedling size" OR "plant quality" OR "plant size" OR "nursery"]. Additionally, we collected studies from nonindexed journals from Asia, Eastern Europe, and South America. From this body of literature (>12,000 articles), we retained 4,366 articles from the agriculture, ecology, environmental sciences, and forestry categories that were further screened to 602 articles based on titles and abstracts (Appendix S1: Fig. S1). These screened articles were then selected if (1) they included data on plant size at planting and outplanting survival; (2) outplanting performance was evaluated under field conditions (experiments where survival was evaluated in containers were excluded); and (3) seedling size differences were not due to different provenances, seedling age, stock type (container vs. bareroot), and/or mycorrhization, because these can affect outplanting performance and have confounding effects with seedling size (Grossnickle and El-Kassaby 2016, Grossnickle and MacDonald 2018).

The final 142 selected articles (Appendix S2) provided 324 case studies encompassing 86 species (Appendix S1: Table S1) and 142 locations distributed worldwide (Fig. 1). An article provided different case studies if (1) more than one species were planted, (2) two or more nursery cultivation techniques (e.g., fertilization and irrigation) were tested, (3) different stock types or seedling ages were planted, or (4) if seedlings were planted in different locations or on different dates (one case study per species, cultivation technique, stock type, age, location, and planting date, respectively). By doing so, we avoided mixing data from seedlings of different age or that were cultivated using distinct techniques or that were planted at different sites or on different dates.

Data extraction

Because we aimed to assess the association between two continuous variables (seedling size and survival), for each case study we recorded the Pearson's correlation coefficient (*r*) (Rosenberg et al. 2013) between these variables. Seedling size parameters were plant mass, shoot mass, stem volume, stem diameter, or shoot height. This correlation coefficient resulted from the mean survival and seedling size parameters of groups (i.e., mainly treatments or blocks in experiments) of plants of different size. When *r* was not reported but at least four groups of seedlings were compared, we calculated *r* from data reported in the text, tables, or figures. If survival was evaluated multiple times, we used the closest measurement to the first year after outplanting, because this

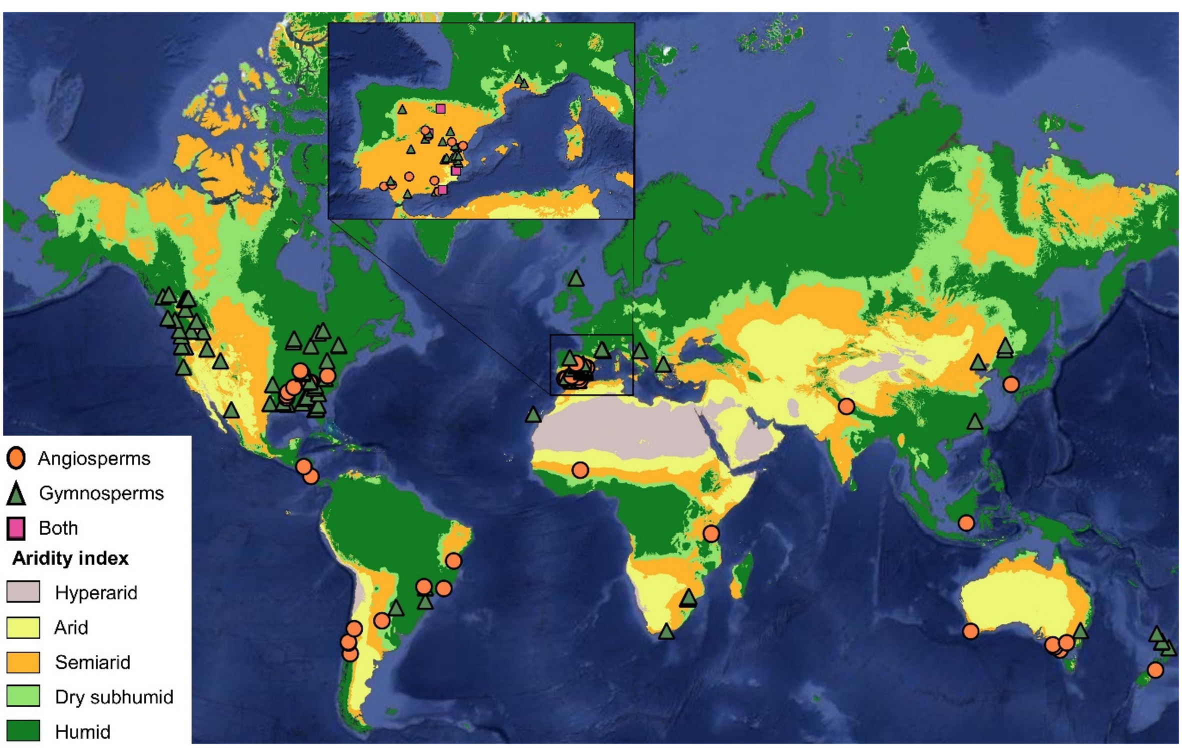

Fig. 1. Distribution of planting locations ($n = 142$) from studies used in the meta-analysis with indication if planted species are angiosperms or gymnosperms. Different colors on the map indicate regions with the same climatic classification according to the global aridity index.

period is usually the most critical for plant survival and the largest effect of seedling size is expected (Grossnickle 2005, Oliet et al. 2009). If multiple seedling size parameters were reported, we prioritized the parameter that better reflects plant size in the following order: plant mass > shoot mass > stem volume > stem diameter > shoot height. Additionally, the number of independent samples (i.e., groups of plants) for each case study was recorded. We used ImageJ (Schneider et al. 2012) to extract values when reported in figures.

Angiosperms represented 57% of the studied species (Appendix S1: Table S1). All gymnosperms were conifers and were involved in 65% of case studies. Plantation location coordinates were either recorded from the articles or approximated using Google Earth from cited location. Site drought stress condition was classified according to climate types defined by the aridity index (AI) (United Nations Environment Programme [UNEP] 1997):

$$\mathrm{AI} = \frac{\mathrm{AP}}{\mathrm{PET}},$$

where AP and PET are the mean annual precipitation and potential evapotranspiration, respectively. AI for each location was extracted from the Global Aridity Index Geospatial Database (Trabucco and Zomer 2018), which is calculated from the WorldClim 2.0 data set (Fick and Hijmans 2017) for years 1970–2000 at a resolution of 30 arc-sec. Climate of locations were classified according to UNEP (1997) as: arid ($0.03 < \mathrm{AI} < 0.2$), semiarid ($0.2 < \mathrm{AI} < 0.5$), dry subhumid ($0.5 < \mathrm{AI} < 0.65$), and humid ($\mathrm{AI} > 0.65$). No location was classified as hyperarid ($\mathrm{AI} < 0.03$) (Fig. 1).

Plant functional traits

We selected SLA and WD to assess if plant functional traits modulate the seedling size–survival relationship. These two variables can be easily measured, are widely available in scientific literature and published databases, and are consistently related to key plant functions within and across major biomes. We used published papers and databases to obtain species SLA and WD values (Appendix S1: Table S1). Most data came from adult plants, but species ranking according to functional traits changes little along ontogeny (Cornelissen et al. 2003).

Effect-size calculation and statistical analyses

For each case study, we calculated the *r* between seedling size at planting and outplanting survival as the estimate of the effect size in our meta-analysis. The distribution of the *r* becomes skewed as it approaches ±1. Thus, we transformed *r* into a metric (*z*) with desirable statistical properties using the Fisher's *z*-transformation:

$$z = \frac{1}{2}\log_e \frac{1+r}{1-r},$$

which has a variance estimate of

$$v_z = \frac{1}{n-3},$$

where *n* is the number of independent samples used to estimate *r*.

To analyze the effect of seedling size on outplanting survival, we used mixed models adjusted for a meta-analysis (Borenstein et al. 2009), which allows incorporating fixed (moderators), and true random effects and nesting factors. We evaluated the overall effect size by fitting a null mixed effect meta-analysis model assuming that each case study was a random sample of a larger overall population, and considering the article identity as a nesting factor to avoid violating the assumption that effect sizes are independent from each other. We considered that the seedling size–survival relationship was either positive or negative if the 95% confidence interval (CI) of the estimated overall effect size did not overlap zero. We evaluated the extent of heterogeneity by using the statistic I^2 (Higgins and Thompson 2002), which estimates the percentage of variability due to heterogeneity rather than the sampling error. The model was fitted using all case studies ($n = 324$).

We also explored whether climate aridity and plant taxonomic group (angiosperm and gymnosperm) explained part of the heterogeneity in the true effect. For this, we incorporated these factors into the null mixed effect meta-analysis model. We could not establish the location of eight case studies, and they were removed before fitting the models ($n = 316$; 111 angiosperm and 205 gymnosperm case studies). Because only eight case studies were in arid locations, we merged the arid and semiarid categories. To evaluate significant differences between factor levels, we conducted an omnibus test based on a chi-square distribution with the number of coefficients tested as degrees of freedom, following default settings in the *metafor* package (Viechtbauer 2010) of Rv3.5.3.

To evaluate the effect of species' functional traits on the magnitude and direction of the effect size, we incorporated SLA and WD as moderators into the null mixed-effect meta-analysis model. Because of fundamental differences in leaf and xylem structure and ecophysiology between angiosperms and gymnosperms (Niinemets and Valladares 2006, Choat et al. 2012, O'Brien et al. 2017), separate models for each taxonomic group were fitted. Specifically, in our study angiosperms had higher SLA and WD than gymnosperms (Appendix 1: Fig. S2). In addition, SLA decreased with aridity, and WD increased in angiosperms. In contrast to angiosperms, aridity did not affect plant functional traits in gymnosperms. Finally, as aridity strongly influences species' functional traits, we also considered models for arid/semiarid and subhumid/humid locations, separately.

Phylogenetic signal in effect size, publication bias, and sensitivity analyses

To assess whether evolutionary relationships may explain variability in the effect size (z), we used the R function *phylosig* as implemented in the *phytools* R package (Revell 2012) along with a species-level time-calibrated molecular phylogeny of DNA obtained using the software V.PhyloMaker (Jin and Qian 2019). Briefly, we pruned the mega-phylogeny provided by Jin and Qian (2019) to our species list. Then, to account for phylogenetic uncertainty (missing species), we generated a distribution of $n = 500$ possible phylogenetic hypotheses where the missing species ($n = 12$) were inserted at random at the crown node of their corresponding genera (Jin and Qian 2019), and results of all subsequent phylogenetic analyses were averaged across all the trees (Rangel et al. 2015). Phylogenetic signal was estimated by fitting the lambda model of evolution (Pagel 1999) to the effect-size values on each phylogenetic hypothesis, and statistical significance was assessed using likelihood-ratio tests. The lambda statistic has a natural scale between zero (lack of correlated evolution) and one (correlation between species equal to Brownian expectation), and it overcomes other phylogenetic signal statistics (Molina-Venegas and Rodríguez 2017). Phylogenetic signal was estimated for the complete phylogeny and for angiosperms and gymnosperms, respectively.

We assessed publication bias visually with funnel plots and statistically with Egger's regression test (Egger et al. 1997), which considers sample size as a predictor in the meta-analysis model (Rothstein et al. 2005). We also calculated the Rosenberg's fail-safe number (Rosenberg 2005) to evaluate the number of studies needed to overturn the results. The hat value and standardized model residuals were computed to identify potential influential outliers (Winter et al. 2018), which were effect-size values that were two times greater than the average hat values and/or standardized residual values exceeding 3.0 (Viechtbauer and Cheung 2010). Then, we fitted the mixed model adjusted for meta-analysis used to evaluate the seedling size–survival relationship but without including the potential outliers. To evaluate whether the magnitude of the effect size changed over time, we used publication year as a moderator in the meta-analysis (Gibert et al. 2016).

Results

Does seedling size affect outplanting survival?

Most relationships between seedling size and survival were positive (79% of the study cases). Consequently, the meta-analysis revealed a significant positive relationship between seedling size at outplanting and survival (estimated $z = 0.69 \pm 0.07$ (SE), $P < 0.0001$, which corresponds to an estimated $r = 0.60 \pm 0.07$). Phylogenetic signal lambda was close to zero and nonsignificant regardless of the focal clade and the phylogenetic hypothesis ($P = 1$ in all cases), suggesting that the positive relationship between seedling size and survival cannot be explained by evolutionary relationships. We observed high heterogeneity for the relationships between seedling size and survival ($I^2 = 91.1\%$, CI = 87.6–93.7%), indicating that most heterogeneity is not explained by sampling error. Although funnel plots (Appendix S1: Fig. S3) and regression tests (estimated intercept = 0.58 ± 0.08, $P < 0.001$) showed publication bias, the Rosenberg's fail-safe number (191,610) suggests that its impact was nonsignificant. Significant meta-analytic result is robust if the fail-safe N is greater than $5k + 10$, where k is the number of studies already in the meta-analysis. We detected 43 potential outliers (13% of case studies); when removed, we observed their influence on the cumulative effect size was negligible (estimated $z = 0.66 \pm 0.08$, $P < 0.0001$). We found no change in z with publication year (estimated slope = -0.003 ± 0.005, $P = 0.60$).

Do aridity, plant taxonomic group, and functional traits modulate the seedling size–survival relationship?

Aridity did not modulate the magnitude of the positive relationship between seedling size and survival. This relationship was significantly stronger in gymnosperms than in angiosperms, with greater differences in arid and semiarid locations (Fig. 2).

For angiosperms planted in arid and semiarid locations, reduction in SLA increased the positive effect of seedling size on survival (Fig. 3). By contrast, the positive effect of seedling size on angiosperm survival in subhumid and humid locations increased with increasing values of SLA and decreasing values of WD, respectively (Figs. 3, 4). In gymnosperms, plant functional traits affected the seedling size–survival relationship only in subhumid and humid locations. The positive effect of seedling size on survival was stronger as SLA decreased and WD increased (Figs. 3, 4). Despite SLA and WD modulating the positive effect size of the relation between seedling size and survival, the effect-size values never changed into negative values with variation of SLA or WD.

Discussion

Our meta-analysis shows that planting large seedlings within a species and of the same age increases outplanting survival in forest plantations worldwide, and the pattern is consistent for angiosperm and gymnosperm species across a wide range of aridity conditions (Fig. 2). Notably, species' functional traits modulate the seedling size–survival relation, but the effect depended on aridity and whether species were angiosperms or gymnosperms

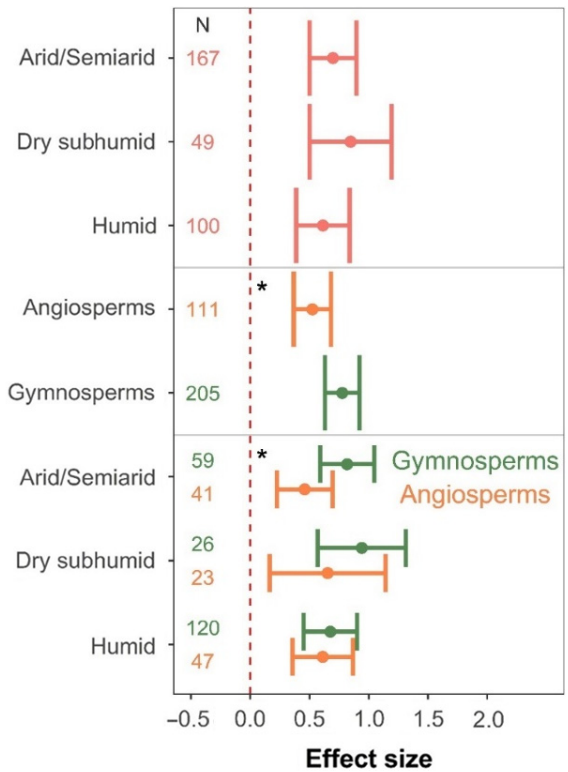

FIG. 2. Predicted effect size ($z \pm 95\%$ confidence interval) for the relationship between seedling size at planting and outplanting survival in relation to the aridity of the planting location, the plant taxonomic group (angiosperms vs. gymnosperms), and the combination of the two factors. The number of case studies for each combination is depicted on the left part of the figure. Asterisks show significant differences ($P < 0.05$) between angiosperms and gymnosperms.

(Figs. 3, 4). These results provide insights into how functional attributes determine seedling performance in forest plantations and have key implications for designing nursery cultivation protocols adjusted to species' functional characteristics and planting site conditions.

Global pattern and the effect of aridity

Larger seedlings within a species showed higher outplanting survival, supporting our hypothesis H1. Large seedlings usually have higher root and shoot growth capacity than small seedlings (Villar-Salvador et al. 2004, Cuesta et al. 2010*b*), which is critical for seedling establishment, especially under harsh conditions (Grossnickle 2005, Grossnickle 2012). Current photosynthesis and remobilization of stored carbohydrates and nutrients fuel seedling growth during establishment (Millard and Grelet 2010, Uscola et al. 2015, Villar-Salvador et al. 2015). Both processes are intimately and directly related to seedling size (Dyckmans and Flessa 2001, Millard and Grelet 2010, Villar-Salvador et al. 2012). When challenged by abiotic or biotic stressors, high root and shoot growth of large seedlings may allow greater resource capture than small ones. For instance, in sites where light is limited by competition, large seedlings can more effectively outcompete other vegetation than small seedlings (Grossnickle 2000). Similarly, large and deep rooting after outplanting is important for accessing soil water during drought, which for many plants is key to survive in dry climates (Padilla and Pugnaire 2007, Luis et al. 2009).

Contrary to H2, the positive effect of seedling size on outplanting survival was not reduced in arid/semiarid sites (Fig. 2). This suggests that, during establishment, the putative negative effects of higher water stress because of greater transpiration in larger seedlings usually do not cancel out the benefits due to higher growth (i.e., increased competitive capacity and stress avoidance because of larger root systems). Increased transpiration with seedling size can be compensated by a deep and extensive root system capable of meeting plant transpirational demand (Cuesta et al. 2010*b*, Grossnickle 2012, Villar-Salvador et al. 2012). Additionally, plantations are usually established during the wet season. This reduces the negative effects of large size while facilitating extensive and deep root growth during the wet season, which is critical for drought avoidance during the dry season (Grossnickle 2005, Padilla and Pugnaire 2007, Villar-Salvador et al. 2012). Finally, most species outplanted in dry locations show traits that confer high drought resistance (see angiosperms in Appendix S1: Fig. S2), which might also explain the positive effect of seedling size on survival in dry planting sites according to our H3.

Despite the clear positive effect of seedling size on survival in semiarid/arid sites, we cannot ignore that several studies showed poor performance of large seedlings compared to small seedlings, especially in dry locations (Tuttle et al. 1988, Rose et al. 1993, Trubat et al. 2011). It may be that sometimes the positive effect of seedling size on survival is overruled by particularly dry sites, unusually dry years, outplanting outside the optimum planting window (Palacios et al. 2009, Trubat et al. 2011), or if species and provenances did not match the planting site conditions (Dumroese et al. 2016).

Species' functional traits modulate the positive effect of seedling size on survival

We found evidence that the magnitude of the positive relationship between seedling size and survival increased in species having stress-resistant traits (Figs. 3, 4). However, this effect depended on the aridity of planting locations and differed between angiosperms and gymnosperms, partly supporting our H3. Two results support H3. First, the positive effect of seedling size on survival was stronger for gymnosperms than for angiosperms, especially in arid/semiarid locations (Fig. 2). Compared to angiosperms, gymnosperms have lower hydraulic conductance and, consequently, lower

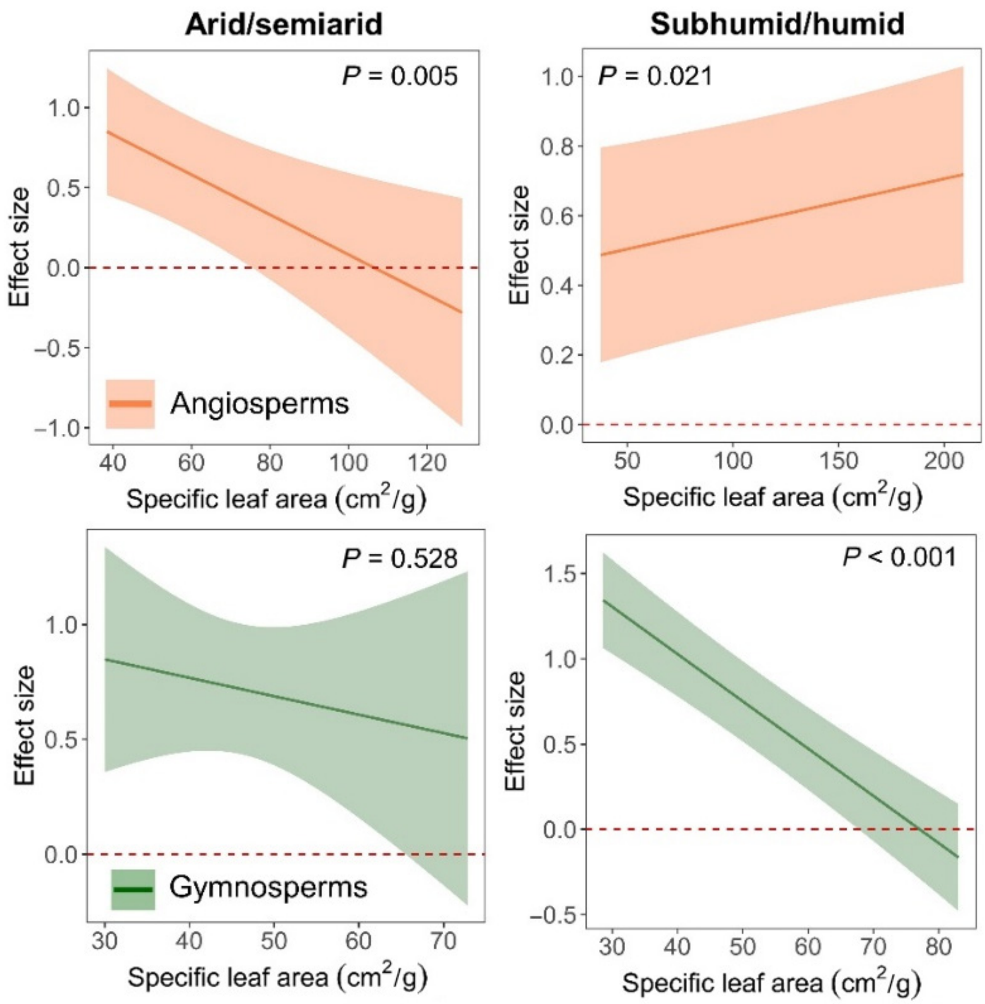

FIG. 3. Predicted effect size ($z \pm 95\%$ CI) for the relationship between seedling size at planting and the outplanting survival of angiosperms (above) and gymnosperms (below) in relation to specific leaf area in arid/semiarid and subhumid/humid locations. The dashed line at zero indicates no significant effect between seedling size and outplanting survival.

transpiration rate for individuals of equivalent size (Niinemets and Valladares 2006, Choat et al. 2012, O'Brien et al. 2017). Additionally, gymnosperms had lower SLA than angiosperms in our study (Appendix S1: Fig. S2) and low SLA plants usually have higher resistance to abiotic stress and herbivory than high SLA plants (Anderegg et al. 2016, Greenwood et al. 2017). Thus, relative to large angiosperm seedlings, functional differences can reduce the stress experienced by large gymnosperm seedlings during establishment. Second, the positive effect of seedling size on angiosperm survival was maximized in low-SLA species in arid/semiarid locations. Having low SLA can mitigate the vulnerability of large seedlings to water stress and allow for higher water supply due to higher root growth (Villar-Salvador et al. 2012).

Interestingly, the magnitude of the positive effect of seedling size on angiosperms' survival in wet sites was maximized by the traits that minimized it in dry climates, that is, high SLA and low WD. This syndrome is usually associated with fast growth and high resource acquisition capacity, but low stress resistance. In humid sites, competition for light with natural vegetation is usually the main limiting factor of seedling performance after outplanting (Grossnickle 2000, 2012). In this context, the advantage of large seedlings is more apparent with fast-growing, low stress-resistance species that more rapidly outcompete smaller seedlings and site vegetation by capturing resources more effectively (Jobidon et al. 2003).

In contrast to angiosperms, plant functional traits did not influence the magnitude of the positive effect of seedling size on gymnosperm survival in arid/semiarid sites. Gymnosperms planted in dry locations are inherently more drought-stress resistant than gymnosperms from humid locations (Salazar-Tortosa et al. 2018),

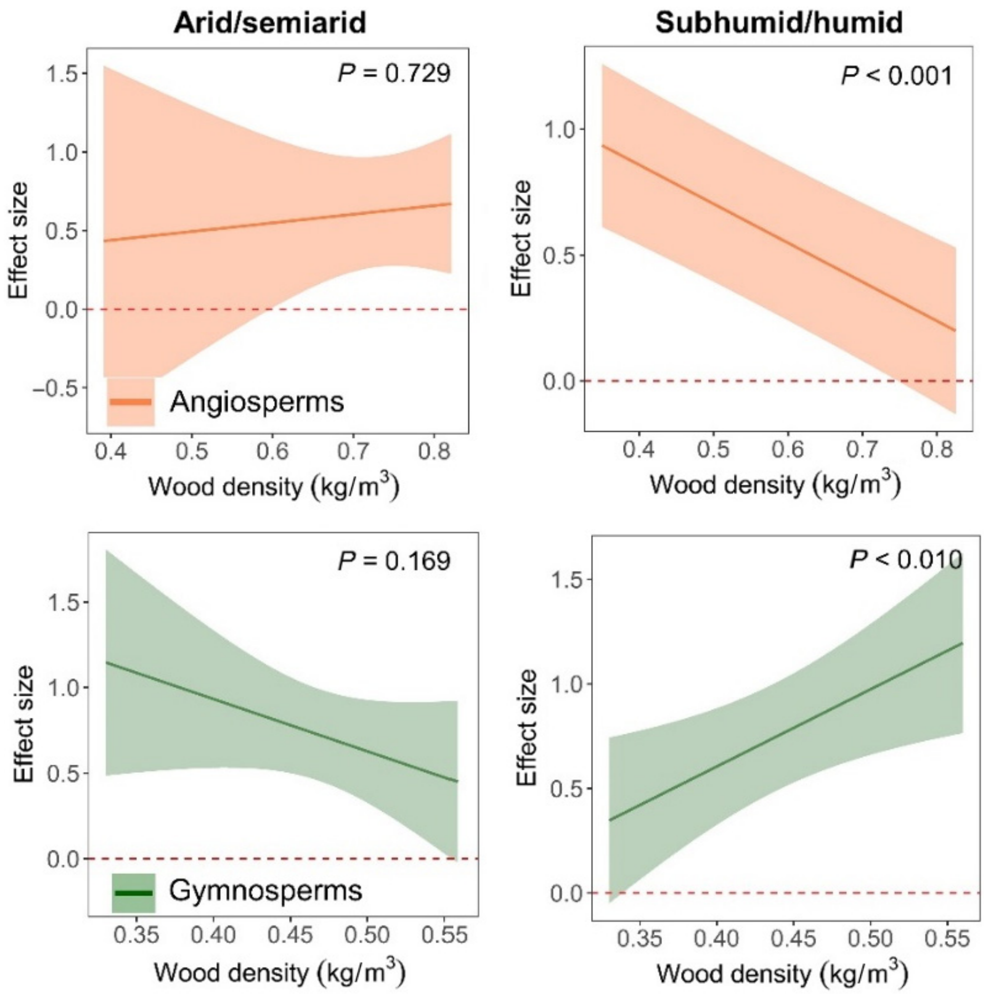

FIG. 4. Predicted effect size ($z \pm 95\%$ CI) for the relationship between seedling size at planting and the outplanting survival of angiosperms (above) and gymnosperms (below) in relation to wood density in arid/semiarid and subhumid/humid locations. The dashed line at zero indicates no significant effect between seedling size and outplanting survival.

which likely explains the lack of any plant functional traits effect on the seedling size–survival relationship in arid/semiarid sites. However, in wet sites the positive effect of seedling size on survival was unexpectedly maximized in gymnosperms with low SLA and high WD. It is possible that gymnosperms planted in more mesic climates are often used in frost-prone locations or in sites with shallow, poor soils (e.g., mountain pines in southern Europe and *Pinus ponderosa* on southerly aspects in the northern Rocky Mountainsof the United States) or high herbivory, where seedlings can be exposed to moderate harsh conditions and consequently traits that confer stress resistance for establishment such as low SLA can be an advantage.

Implication for forest plantations

The consistent positive relationship between seedling size and outplanting survival calls for revaluating nursery cultivation protocols. Cultivation should be directed to promote seedling size. Plant or shoot mass, stem volume, or stem diameter have been recommended to characterize seedling size rather than using only shoot height, because height can overestimate seedling size (Thompson 1985). Maximizing seedling growth can be achieved by increasing fertilization rate especially of nitrogen, using larger containers, reducing cultivation density, or seeding earlier to lengthen the growing season (van den Driessche 1991, Villar-Salvador et al. 2004, South et al. 2005, Cuesta et al. 2010*a*).

Several studies emphasized the importance of species selection based on functional traits for forest restoration success (Martínez-Garza et al. 2013, Charles et al. 2018, Werden et al. 2018). Our study expands on this knowledge, as it provides insights into how to cultivate target seedlings of different species, based on species' functional attributes and aridity conditions at planting sites. Implementation of cultivation methods to maximize seedling size for species selected for dry sites should be favored in angiosperms with low SLA and high WD, a syndrome related with slow growth but high stress resistance. In contrast, for wet sites where competition is the main establishment limitation, maximizing seedling size would mainly benefit angiosperms with high SLA and low WD, a combination of traits that confer fast growth capacity (Reich 2014).

This study focused on species' functional characteristics and aridity as modulators of the magnitude and direction of the relationship between seedling size and survival. Other factors related to nursery cultivation and management of planting sites can, however, also drive early survival and shift the magnitude of the seedling size–survival relationship (Grossnickle and El-Kassaby 2016, Andivia et al. 2019). Future studies should assess how this relationship is affected by stock type (bare-root and container seedlings), plantation date, soil type and soil preparation technique, and postplanting management (e.g., weeding or tree shelters). Understanding these aspects is important for effective establishment of forest plantations worldwide.

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Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.2394/full

Open Research

Data (Andivia et al. 2021) are available on Figshare: https://doi.org/10.6084/m9.figshare.14160449