

The relationship between seed mass and mean time to germination for 1037 tree species across five tropical forests

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Summary

1. Theoretical models predict that large-seeded species should germinate more rapidly than small-seeded species, since large seeds are more likely to have higher post-dispersal seed predation than small seeds. A prompt germination strategy would therefore enable large seeds to reduce risks of mortality.

2. To assess this predicted relationship between seed mass and mean time to germination (MTG), we used a meta-analysis of published data sources. Our data base contained information for these two traits for 1037 tree species from five tropical areas worldwide (Brazil, India, Ivory Coast, Malaysia and Panama). Both cross-species analyses and phylogenetically independent contrasts (PIC) were conducted on the log-transformed values of seed mass and MTG.

3. Log-seed mass was a significantly phylogenetically conserved trait in all five data sets. Log-MTG was significantly phylogenetically conserved in all sites except for Malaysia and India.

4. Log-MTG and log-seed mass were significantly positively correlated in all sites except for Malaysia. PIC analyses showed a significantly positive relationship in Brazil, India and Ivory Coast but not in Malaysia and Panama. When all sites were combined, PIC analyses indicated a significant positive relationship between these two traits.

5. Our findings do not support the hypothesis that large seeds germinate faster than small seeds, but rather that small seeds germinate faster. We interpret our results in light of phylogenetic and biophysical constraints. We propose four alternative mechanisms that could account for the observed pattern, including developmental constraints, water absorption and investment to physical defences.

Key-words: mean time to germination, phylogenetically independent contrasts, seed mass, trait conservatism, tropical trees

Introduction

Plants face the highest risks of mortality during early life stages. In natural environments, unfavourable conditions for germination and seedling establishment may occur unpredictably both in time (Cohen 1966) and space (Comins, Hamilton & May 1980). Seeds have therefore developed fine-tuned germination strategies to offset these fluctuations in habitat suitability (Fenner & Thompson 2005). Theoretical

models predict that intermediate times to germination should be optimal, since both extremes in the gradient of time to germination are likely to be disadvantageous for successful establishment (Cohen 1966; Rees 1994). For example, fast germinating species expose the entire seedling cohort to more unpredictable environments (Daws *et al.* 2007a), while very slowly germinating species accumulate risks of seed predation, or may miss the opportunity to fill the free suitable micro-sites for establishment. However, considerable among-species variation in time to germination (Vazquez-Yanez & Orozco-Segovia 1993; Baskin & Baskin 1998) suggests that it is selectively advantageous to maintain high variability in this trait (Nikolaeva 1999; Donohue 2002; Forbis, Floyd & de Queiroz 2002; Donohue *et al.* 2005).

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Time to germination is a classic example of bet hedging (Cohen 1966; Claus & Venable 2000; Venable 2007) since it is a strategy to improve long-term reproductive success by spreading risk over time (Venable 2007). Consequently, it might be expected that this trait has coevolved with other plant traits that are directly involved in regeneration success. One of the most studied regeneration traits is seed mass, which varies over more than 10 orders of magnitude, illustrating the manifold evolutionary forces acting upon this trait (Leishman *et al.* 2000; Moles *et al.* 2005a,b). The relationship between seed size and germination strategy has motivated much interest, mostly in temperate environments. Theoretical models predict that small seeds are more likely to show delayed germination than large seeds (Venable & Brown 1988; Rees 1994). Large-seeded species are expected to have higher post-dispersal predation than small-seeded species (Janzen 1971; Louda 1989; Bate, Peart & Leighton 1998), and should therefore show prompt germination to avoid risks of mortality. Conversely, small-seeded species may be more persistent in the soil seed bank (Venable & Brown 1988; Rees 1994), and are thus expected to show delayed germination. Empirical data support this hypothesis in grasslands (Grime *et al.* 1981), but no conclusive evidence has been found in other temperate environments (Jurado & Westoby 1992; Leishman & Westoby 1994). The generality of this prediction is thus tentative, and remains to be tested more widely.

Here, we readdress this issue in tropical forest environments. Despite low variation in climatic conditions year round, tropical forest plants display a wide array of germination strategies; ranging from seeds that are disseminated already germinated, to those that can spend several years in the soil seed bank (Garwood 1983; Vazquez-Yanes & Orozco-Segovia 1993). This substantial variation in time to germination has been mostly related to successional status and seed size (Foster & Janson 1985; Vazquez-Yanes & Orozco-Segovia 1993). Pioneer species tend to produce large crops of small seeds, and are typically associated with a delayed germination strategy. This strategy maximizes the chances to colonize gaps or to be incorporated in the soil seed bank, until optimal high light conditions enable seed germination (Salisbury 1974; Vazquez-Yanes & Orozco-Segovia 1993). In contrast, shade-tolerant species are more likely to produce smaller crops of large seeds and are expected to germinate fast to reduce predation risks (Foster & Janson 1985). While the field studies mentioned above support the general theoretical model, more recent, quantitative studies assessing the relationship between seed size and germination delay in tropical environments find either a negative (Murali 1997) or a non-significant (Jurado & Flores 2005) relationship between seed size and time to germination.

A key problem with this theory is that germination is a complex phenomenon involving both specific features of the seed and environmental factors (Baskin & Baskin 1998). Several mechanisms may prevent germination, including physiological factors inside the embryo, developmental constraints and mechanical barriers in the fruit or seed coat. These mechanisms are generally referred to as dormancy

(Baskin & Baskin 1998), which slows or stops the germination of a viable seed under favourable conditions (Vleeshouwers, Bouwmeester & Karssen 1995; Finch-Savage & Leubner-Metzger 2006). Seed dormancy is difficult to assess since it is usually gauged by the lack of germination, yet the absence of germination does not imply dormancy (Vleeshouwers *et al.* 1995). Secondly, many studies assessing the relationship between seed size and time to germination have not accounted for possible phylogenetic constraints. When evaluating relationships between traits, species cannot be treated as independent because they may share a common evolutionary history. Phylogenetic studies using compiled information on seed mass revealed the importance of considering evolutionary histories and niche conservatism in explaining the variability of this trait (Lord, Westoby & Leishman 1995; Moles *et al.* 2005a).

Here, we reassess the relationship between seed mass and mean time to germination (MTG) for 1037 tree species across five tropical forests by taking into account the evolutionary history of these species. In line with the abovementioned theories, we hypothesize that large-seeded species should germinate faster than small-seeded species to avoid risks of predation related mortality. Specifically, we address the following questions: (i) Is there a phylogenetic conservatism in both MTG and seed mass? (ii) What is the relationship between MTG and seed mass?

Methods

DATA SET

We assembled a data base containing information on MTG and seed mass for 1037 tree species across five tropical countries. Taxonomic information at the family level was updated using the recent classification of the Angiosperm Phylogeny Group (APG II 2003).

(1) In Brazil, our data set was extracted from a large botanical project carried out by Lorenzi (2002) and his collaborators. Information on MTG and seed mass is available for species occurring naturally throughout Brazil, but we retained only the species known to occur in Amazonian forests to focus on wet tropical species only. This represents a total of 319 tree species in 54 families.

(2) In India, our data set relies on a study carried out by the Karnataka Forest Institute and reported in the peer-reviewed literature (Murali 1997). Karnataka's evergreen forests experience a monsoonal climate. This data set includes data on MTG and on seed mass for 98 tree species. However, we excluded eight species that received seed pre-treatments (such as scarification or heat) to release dormancy before germination trials, resulting in a total of 90 tree species in 34 families.

(3) In Ivory Coast, the data originate from a forestry project carried out in the 1960s by the 'French Centre Technique Forestier Tropical'. It includes a large number of germination trials in controlled conditions for the western African wet forest tree species (de la Mensbruge 1966). This data set includes data on MTG and seed mass for 277 tree species in 49 families.

(4) In Malaysia, the data set was assembled by Ng (1978) at the Forest Research Institute of Malaysia. Data on MTG were reported for hundreds of wet forest tree species but data on seed mass was not directly available. We thus compiled seed mass data for 114 tree

species in 42 families among those reported by Ng (1978) from the Seed Information Database (SID) of the Royal Botanic Gardens, Kew (Flynn, Turner & Stuppy 2006).

(5) Finally, in Panama we used an unpublished data set, assembled as part of a community-wide study on the ecology of plant germination in Barro Colorado Island, a semi-deciduous forest experiencing a pronounced annual dry season (Daws, Garwood & Pritchard 2005, 2006). MTG and seed mass were reported for 237 tree species in 55 families.

In all of these studies, plants were grown in nurseries under constant conditions of light and watering. The number of seeds sown per species was variable and was not reported in the literature sources. To our knowledge, seed pre-treatments were not applied in any study, except for the Indian one. Since it is difficult to assess when these pre-treatments are necessary, and whether they are effective (Baskin & Baskin 2003), the relevant species were excluded from the analyses. For Brazil, Ivory Coast and Malaysia, the range of times to germination was presented, and we report the mean between these extreme values. For India and Panama, MTG was reported as time to 50% germination. For most of the species included in the data sets, we compared our information on seed mass to the large SID of Kew Botanic Gardens (Flynn *et al.* 2006).

STATISTICAL ANALYSES

Trait conservatism

We tested for phylogenetic conservatism in both traits across the Angiosperm phylogeny. For seed mass, phylogenetic conservatism is expected at a global scale based on Moles *et al.* (2005a), but it is not obvious in local floras. To our knowledge, the phylogenetic conservatism of germination delay has never been tested before. We assembled a local phylogenetic hypothesis for each of the five data sets, based on the APG II consensus subtending tree onto which more refined family-level phylogenies were grafted (henceforth referred to as a 'mega-tree'). Pruning of the mega-tree for each of our five sites was conducted using the Phylomatic software (Webb & Donoghue 2005). Phylomatic starts with the family-level tree of Angiosperms and considers genera as polytomies within families and species as polytomies within genera.

To quantify the amount of trait conservatism, we computed D_i , the root mean square deviation of trait values at daughter nodes:

$$D_i = \sqrt{\sum_{j=1}^{N_i} (T_j - T_i)^2 / N_i}$$
, where T_j is the value of the trait at node j , and N_i is the total number of daughter nodes descended from parent node i . We calculated the D statistic for the log-transformed values of both MTG and seed mass. Tests of significance on these metrics were performed by reshuffling the traits across the tip nodes a thousand times. If trait evolution is conserved, then D should be small relative to the null hypothesis of no phylogenetic signal. If however, closely

related species are highly divergent, then there will be many large contrasts near the tips of the tree, with fairly small contrasts towards the root due to a similar spread in trait values across major clades.

Trait conservatism was carried out using the Phylocom software (version 3.41, routine Analysis of Traits, AOT; Webb, Ackerly & Kembel 2007). Phylocom reports the number of random draws for which D values are lower (P_L) or higher (P_H) to the observed values of D . For instance, if P_H is close to the total number of randomizations, then most of the random draws show a higher spread in trait values than the observed one, and we infer that the corresponding trait is conserved.

Correlation between seed mass and time to germination

We correlated the log-transformed values of MTG and seed mass across species, without accounting for phylogenetic relatedness. We also used phylogenetically independent contrasts (PIC; Felsenstein 1985) to account for the evolutionary history of the species. PIC were calculated as the difference between mean trait values between the two nodes (or two species) descending from the same node. Following Pagel & Harvey (1992), phylogenetic branch lengths were set to 1, and polytomies were resolved at random to provide one contrast. For polytomies, daughter nodes were ranked by trait value and split at the median in two groups (high and low). For pairs of continuous traits, the Phylocom software calculates standardized independent contrasts and it returns a Pearson correlation coefficient R across these contrasts. The significance of these coefficients is not easy to assess in PIC analyses, as pointed out by Webb *et al.* (2007). Thus, we performed linear regressions predicting the contrasts in the log-transformed values of MTG against the log-transformed values of seed mass for each site (Garland, Harvey & Ives 1992). Since a given contrast is calculated as the difference between the trait values of two nodes, the sign of each data point is arbitrary. Because of this property of the data points, regressions must pass through the origin (Garland *et al.* 1992; Moles *et al.* 2005a). Cross-species correlations and linear regressions were performed using the R statistical package (R Development Core Team 2007, version 2.6.1).

Results

The five sites showed similar patterns in the frequency distribution of the traits studied (Table 1). Across all sites, seed mass varied from 3.5×10^{-5} to 1.5×10^3 g, with most seeds varying between 0.1 and 0.5 g. MTG ranged from 4 to 810 days, with most species germinating between 10 and 40 days. Average seed mass differed significantly among sites ($K = 117.61$, $P < 0.0001$, Fig. 1), ranging from 0.64 g for Panama to 7.76 g for Brazil. MTG was also significantly different across sites

Table 1. Average and standard deviation (SD) of seed mass (g) and mean time to germination (MTG) (d), and ranges for each site

Sites	Number of species	Seed mass		MTG	
		Mean (SD)	Range	Mean (SD)	Range
Brazil	319	7.8 (84.7)	1.5×10^{-4} –1500	35.6 (42.6)	4–450
India	90	1.4 (3.3)	2.1×10^{-3} –20	17.1 (6.4)	8–45
Ivory Coast	277	4.8 (13.2)	2.1×10^{-3} –100	47.6 (110.2)	7–810
Malaysia	114	2.9 (10.2)	2.0×10^{-4} –83	72.5 (102.0)	9–669
Panama	237	0.6 (2.2)	3.5×10^{-5} –20.7	55.1 (65.4)	5.50–404.25

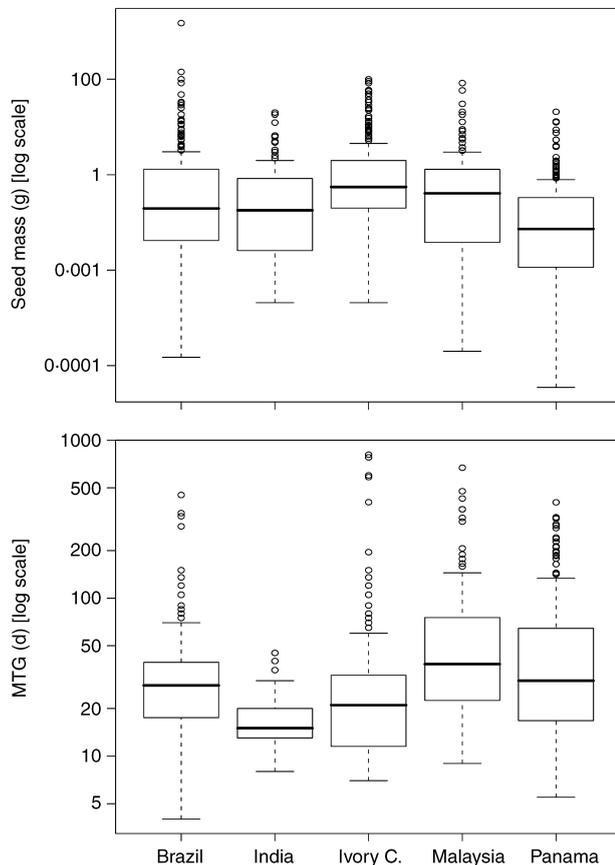


Fig. 1. Box plot illustrating variation in (a) \log_{10} seed mass and (b) \log_{10} mean time to germination (MTG) within each of the five study sites.

Table 2. D statistics (root mean square deviation of trait values at daughter nodes) for seed mass and mean time to germination (MTG) for each site. Also reported P_L , the number of randomizations for which D was lower than or equal to the observed data. The P -values are calculated for one-tailed test as P_L divided by the number of randomizations. Significant values are indicated in bold

Site	Seed mass			MTG		
	D	P_L	P -value	D	P_L	P -value
Brazil	0.54	1	10^{-3}	0.14	1	10^{-3}
India	0.59	28	0.03	0.09	682	0.68
Ivory Coast	0.40	1	10^{-3}	0.14	1	10^{-3}
Malaysia	0.65	1	10^{-3}	0.27	288	0.3
Panama	0.56	1	10^{-3}	0.25	1	10^{-3}

($K = 111.9$, $P < 0.0001$, Fig. 1) ranging from 17.2 days for India to 72.5 days for Malaysia.

Log-transformed seed mass was a significantly conserved trait in all sites (Table 2). Log-transformed MTG was significantly conserved in all sites except for Malaysia and India. In India, it was actually over-dispersed, but not significantly (Table 2).

A few families accounted for a significant portion of the species sampled. Fabaceae dominated in Brazil, India, Ivory Coast and Panama (22.9%, 28.1%, 22.7% and 11.6%

Table 3. Cross-species correlation between the log-transformed values of seed mass and of mean time to germination (MTG) for each site. We report the estimates, the P -values and the R^2 . Significant values are indicated in bold

Site	Estimate	P -value	R^2
Brazil	+0.07	< 0.001	0.06
India	+0.04	< 0.01	0.08
Ivory Coast	+0.24	< 0.001	0.27
Malaysia	+0.01	0.7	10^{-2}
Panama	+0.06	< 0.01	0.03

respectively). In Malaysia, the most abundant families were the Dipterocarpaceae and the Fabaceae (14.9% and 12.3%, respectively). The over-representation of a few families and the phylogenetic conservatism of both traits justify controlling for phylogenetic constraints in cross-species correlation analyses.

The log-transformed values of MTG and seed mass were significantly positively correlated in all sites except for Malaysia (Table 3). PIC analyses showed a significantly positive relationship in Brazil, India and Ivory Coast but not in Malaysia and Panama (Fig. 2). All sites combined, PIC analysis showed a significantly positive relationship between the two traits (Fig. 2).

Discussion

TRAIT CONSERVATISM IN SEED MASS AND MTG

Seed mass was a phylogenetically conserved trait at all sites, and MTG was phylogenetically conserved at all sites except for India and Malaysia. This suggests that, despite large inter-specific variation, the range of variation in these traits is limited by phylogenetic affiliation. Similarly, Moles *et al.* (2005a,b) used phylogenetic analyses to infer the evolution of seed size for *ca.* 13 000 plant species, and found that despite wide divergences in seed size, there was evidence of phylogenetic constraints on this trait. Thus, our findings are consistent with Moles *et al.* (2005a,b), and further show that germination delay is a phylogenetically conserved trait.

In the Indian and Malaysian data sets, we did not find significant trait conservatism in MTG. This may be explained by the fact that these data sets are small (Table 1), and that taxonomic groups of the local flora may not have been sufficiently well represented. Each of these two data sets include a high number of families with respect to the number of species, and thus have the lowest number of species per family among the five data sets (2.6 and 2.7 in India and Malaysia, respectively vs. 5.9, 5.7 and 4.3 in Brazil, Ivory Coast and Panama, respectively). The issue of sampling effort is of importance in phylogenetic inference methods, since the effect of taxon membership on a particular trait relies on the selected species. Thus, the findings obtained for the Indian and Malaysian flora are probably the result of the misrepresentation of some families in the data set.

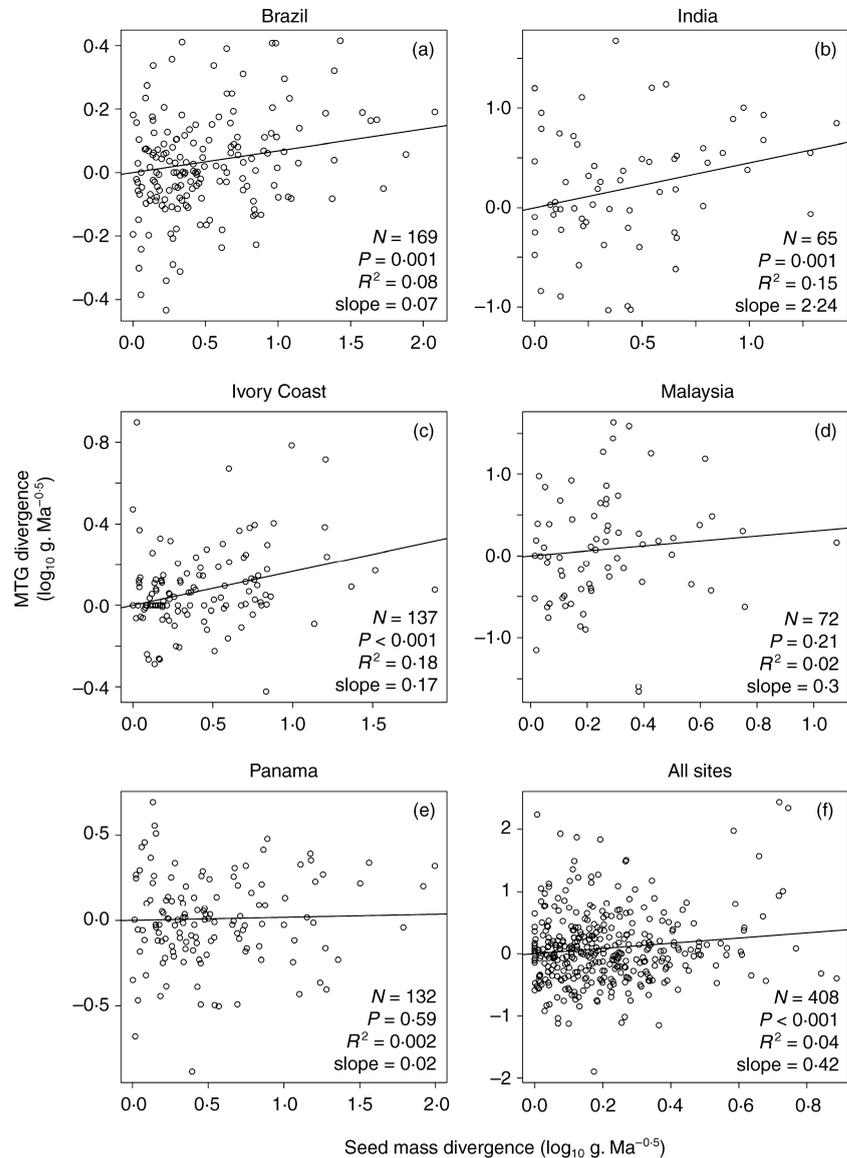


Fig. 2. Relationship between divergence in log₁₀ seed mass and divergence in log₁₀ mean time to germination (MTG) for each of the five study sites, and for all the sites combined. We report the number of contrasts, the estimates from the linear model predicting the contrast of the log-transformed values of MTG against the contrast of the log-transformed values of seed mass, the *P*-values, and the *R*².

RELATIONSHIP BETWEEN SEED MASS AND GERMINATION DELAY

The most significant finding of our study is that we found strong evidence for a positive relationship between MTG and seed mass. When accounting for phylogenetic relatedness, this relationship was significant in Brazil, India and Ivory Coast. This relationship was not significant in Malaysia and Panama, but nonetheless the trend between these two traits was positive. With all sites combined, PIC analyses also showed a significantly positive correlation between seed mass and MTG. Our finding thus holds across tropical forests over various geographical areas, differing in diversity, climate and biogeographical history.

A positive relationship between MTG and seed mass is not consistent with theoretical arguments based on a lower survivorship of large seeds due to a higher post-dispersal predation (Janzen 1971; Louda 1989). Indeed, a recent study gathering data for hundreds of species worldwide did not find

any evidence of a negative relationship between seed size and post-dispersal seed survivorship (Moles, Warton & Westoby 2003), and other seed predation studies in the tropics have shown similar trends (Osunkoya 1994; Blate *et al.* 1998). Thus, our results are consistent with these studies and suggest that predation may not be a major selective force acting on time to germination in large-seeded species. Large-seeded species might be attractive for their high-nutrient contents and greatest net reward (Charnov 1976), but they may also contain secondary compounds that make them unpalatable to generalist consumers (Kollmann, Coomes & White 1998; Finkelstein & Grubb 2002). Chemical toxicity may thus be a better determinant of feeding preferences among seed predators than seed size (Janzen 1969).

The inter-specific correlation between seed mass and MTG may indicate physical or developmental constraints that limit their independent variation and evolution (Wright *et al.* 2007). One explanation for the positive relation between these two regeneration traits is that seed mass must control, to a

certain extent, the germination ability of seeds in tropical tree species. Is the association of large seeds with delayed germination and of small seeds with prompt germination shaped by selection or by biophysical constraints? Selective forces may drive the observed patterns between seed mass and MTG if small-seeded species exhibit a rapid-germination strategy to pre-empt suitable micro-sites in advance of larger-seeded, more competitive species. In contrast, large-seeded species might be spreading germination in time to offset risks linked to environmental hazards. This would indicate that large-seeded species display a bet hedging strategy while small-seeded species do not. However, this is unlikely since both time to germination and seed size are considered as bet hedging traits, reducing variance in survivorship across varying environments (Venable & Brown 1988; Claus & Venable 2000). Future studies taking into account the variance as well as the mean in germination delay would enhance our understanding of time to germination as a bet hedging strategy and its relation to seed size (Venable & Brown 1998).

We suggest that the positive relationship between MTG and seed mass is the result of biophysical constraints. Here we propose four mechanisms that could account for this pattern. Firstly, if the seed embryo of a large seed requires more time to develop within the seed before seedling emergence, then one would expect MTG to be greater for large than small seeds. Many authors have hypothesized that underdeveloped embryos are a primitive feature among seed plants (Martin 1946; Nikolaeva 1999; Forbis *et al.* 2002; but see Baskin *et al.* 2006). Interestingly, some of the species showing the strongest patterns of extended times to germination in our data sets belong to basal clades (e.g., Annonaceae, Arecaceae and Magnoliaceae). Yet, many other families also exhibit considerable MTG, making it difficult to draw clear conclusions on this point. Several studies have reported a delay in germination due to embryo underdevelopment in large-seeded neotropical trees, such as *Minuartia guianensis* (Camargo & Ferraz 2004), and *Virola* species (Flores 1996; Piña Rodriguez & Figliolia 2005; Sautu *et al.* 2007), suggesting that this may be a widespread phenomenon in large-seeded tropical tree seeds.

Secondly, longer MTG in large-seeded species could be related to water absorption. Before germination, the embryo needs to reach the full turgor required for cell elongation (Vazquez-Yanes & Orozco-Segovia 1993). It has been shown that small seeds have a faster water absorption capacity than large seeds, since they have a larger surface area to mass ratio (Kikuzawa & Koyama 1999). If seeds are released with low moisture content or if they undergo desiccation in the soil, small-seeded species will gain water more rapidly than large-seeded species, particularly if seeds are on the soil surface, as opposed to buried. However, while this might account for small differences in MTG, it is difficult to imagine that differences in the rate of water uptake alone account for the wide range of variation we observed.

Thirdly, it has been proposed that large-seeded species invest proportionately greater resources into physical defences, such as a thick endocarp or seed coat, in response to high

predation risks (Fenner 1983; Blate *et al.* 1998; Moles *et al.* 2003). The presence of a thick seed coat may delay germination by limiting oxygen exchange, or by acting as a physical constraint to embryo growth (i.e. germination). Indeed, Daws *et al.* (2005) found that among large-seeded neotropical tree species, those with a 'thinner' seed coat (as assessed by the proportion of the seed mass that was accounted for by the seed coat) had shorter times to germination than those with a 'thicker' seed coat. The relationship between seed predation and seed mass is not robustly established (Moles *et al.* 2003) and studies evaluating the relationship between seed mass and seed coat thickness/hardness are also scarce (Fenner 1983).

Fourthly, water-impermeable seed coats (physical dormancy) may also contribute to extended times to germination. In such species, imbibition (and hence germination) is only able to occur once the seed coat had been breached by, for example, large soil temperature fluctuations (e.g. *Apeiba membranacea*; Daws *et al.* 2006). Among the species in our data sets, physical dormancy is most likely to be prevalent among species in the Fabaceae (Baskin & Baskin 1998). However, in our data sets this family shows wide variation in MTG (range: 4–356 days; median = 16 days), suggesting that either most tropical forest Fabaceae have seeds without physical dormancy or that conditions in the nursery trials were sufficient for rapid loss of physical dormancy. Clearly, further studies on tropical tree seeds are required to test the different ideas proposed.

Two of our sites, Malaysia and Panama, did not show a significant relationship between MTG and seed mass in the PIC analyses (although Panama was significant in the cross-species analysis). The trend of the relationship was however consistent with our general conclusion in both sites. In the other sites, seed mass explained on average only 15% of the variation in MTG. Although this is a comparatively low amount of variation explained, Moles *et al.* (2005a) also found low values of R^2 (0.10 and lower) in PIC analyses investigating the effects of climatic variables on seed mass across species. Our findings suggest that other biotic or abiotic factors act upon MTG, with the unexplained variation in MTG potentially attributable to the interplay of germination timing with other seed traits. Time to germination is indeed known to correlate with others seed traits such as desiccation sensitivity (Daws *et al.* 2005), seed coat thickness, (Daws *et al.* 2005, 2007b), timing of dispersal (Garwood 1983; Daws *et al.* 2005), and dispersal syndrome (Bu *et al.* 2008).

Conclusions

Once dispersed, seeds face predation risks, parasite attacks, and environmental hazards due to drought, leaf litter, soil burial and low light availability. All of these factors make seed germination one of the most critical phases during plant ontogeny. Because seed mass is an important correlate of regeneration strategy, we expected this trait to be associated with germination delay. The data presented here show evidence of a positive association between seed mass and MTG, independent of taxon membership. A significant proportion of variance in MTG remained unexplained in all the studied

sites, suggesting that other factors are responsible for the wide inter-specific variation in germination timing displayed by tropical plants. Comprehensive studies combining community-level as well as multivariate approaches are needed to improve our understanding of the evolutionary and ecological forces shaping germination timing.

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