Microgeographic local adaptation and species distributions: the role of selective processes on early life history traits in the Symphonia syngameon.

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Abstract

1. Trees are characterised by the large number of seeds they produce. Although most of those seeds will never germinate, plenty will. Of those which germinate, many die young, and eventually only a minute fraction will grow to adult stage and reproduce. Is this just a random process? Do variations in germination and survival at very young stages rely on variations in adaptations to microgeographic heterogeneity? and do these processes matter at all in determining tree species distribution and abundance? 2. We have studied these questions with the Neotropical Symphonia syngameon. In the Guiana shield, Symphonia are represented by at least two sympatric taxa or ecotypes, Symphonia globulifera found almost exclusively in bottomlands, and a yet undescribed more generalist taxon/ecotype, Symphonia sp1. A reciprocal transplantation experiment (510 seeds, 16 conditions) was set-up and followed over the course of 6 years to evaluate the survival and performance of individuals from different ecotypes and provenances. 3. Germination, survival, growth, and herbivory showed signs of local adaptation, with some combinations of ecotypes and provenances growing faster and surviving better in their own habitat or provenance region. S. globulifera was strongly penalised when planted outside its home habitat but showed the fastest growth rates when planted in its home habitat, suggesting it's a specialist of a high-risk high-gain strategy. Conversely, S. sp1 behaved as a generalist, performing well in a variety of environments. 4. Synthesis: The differential performance of seeds and seedlings in the different habitats matches the known distribution of both ecotypes, indicating that environmental filtering at the very early stages can be a key determinant of tree species distributions, even at the microgeographic level and among very closely related taxa. Furthermore, such differential performance also contributes to explain, in part, the maintenance of the different ecotypes in the Symphonia syngameon living in intimate sympatry despite occasional gene flow.

Introduction

Trees may produce millions of seeds over their lifespan (Moles*et al.* 2004), yet the vast majority of those seeds will never become adults. Most of them will disappear in early life stages, when mortality is high (Valen 1975; Petit & Hampe 2006), through herbivory, disease, lack of resources like water (Slot & Poorter 2007), and maladaptation to their environment (Donohue*et al.* 2010). Such high mortality rates should provide ample opportunity for the action of natural selection (Petit & Hampe 2006; Donohue *et al.* 2010). Even though one must expect that any given seedling has much higher chances to die than to survive, identifying signals of adaptation to local micro-environmental conditions in young seedlings is paramount to understand species and phenotype distribution patterns. However, the causal links between environmental heterogeneity, spatial distribution of species and phenotypes, and local adaptation remain elusive in trees, mainly due to the lack of long-term studies, low statistical power, and insufficient understanding of the environmental factors determining local adaptation.

The study of seedling survival and growth is a straightforward way to make inferences on performance differences among tree species and populations (Baraloto*et al.* 2005). The analysis of common gardens, with or without the experimental application of environmental stresses meant to assess genetically driven phenotypic response variations in populations, is common practice. They make possible to compare the performance of individuals from different habitats (Valladares & Sánchez-Gómez 2006; Brousseau *et al.* 2013; Barton *et al.* 2020), populations (Ramírez-Valiente *et al.* 2009; Carsjens *et al.* 2014; Barton *et al.* 2020), or species (Lopez & Kursar 2003; Poorter & Markesteijn 2008; Queenborough *et al.* 2009) to test for local adaptation signals in traits of interest (de Villemereuil *et al.* 2016 for a review). In several cases however, adaptation is not proven (Lopez & Kursar 2003; López*et al.* 2009; Queenborough *et al.* 2009) or give counter-intuitive (Poorter & Markesteijn 2008; Pineda-García *et al.* 2011). Common gardens and experimental stresses may nevertheless not exactly replicate conditions experienced by seedlings in the wild, leading to possible biases in the conclusions drawn about divergence and trait/survival response to stress.

Reciprocal Transplant Experiments (RTE), whereby seeds or seedlings are translocated between sites in the field and grow in the same conditions as natural regeneration, may be a better option to observe adaptive processes as they occur in wild conditions, albeit sometimes with higher implementation costs and larger variance in the estimation of parameters as experimental conditions are less strictly controlled. RTEs are an elegant way to test the hypothesis of a link between habitat variation and species or phenotype distribution, because they allow observing performance variance directly across an array of environmental factors (Morris *et al.* 2007). These differences in performance components (i.e. survival, growth, and/or reproduction) between populations in different environments can be interpreted directly in terms of adaptation, based on straightforward theoretical expectations: local adaptation is found when local populations perform better than transplanted ones (the 'local *vs.*foreigner' condition) and any given population performs better in its own provenance than elsewhere (the 'home *vs.* away' condition) (Kawecki & Ebert 2004). Local adaptation can be further nuanced depending on the generality of patterns across the system: if 'local' individuals always outperform 'foreign' individuals for all populations and conditions, then genetic trade-offs are orchestrating the patterns of local adaptation; if, however, some populations perform better at 'home', but are not penalised elsewhere, then conditional neutrality may underpin the local adaptation (Anderson 2013). The two processes are not mutually exclusive and may coexist for different traits within a given system (Wadgymar*et al.* 2017).

In trees, conclusions from RTEs on local adaptation, mostly tested in seedlings due to the long lifecycle, are diverse: evidence of local adaptation to particular environmental parameters has been identified for a wide range of tree species (Fine *et al.* 2006; Wright 2007; Pizano *et al.* 2011; Pluess & Weber 2012; Smith *et al.* 2012; Baltzer & Davies 2012; Nagamitsu *et al.* 2015; Pluess*et al.* 2016; Mathiasen & Premoli 2016; Rellstab *et al.*2016; Barton *et al.* 2020); while the expected signals of local adaptation to, at least some environmental conditions, were not observed in other studies (Boshier & Stewart 2005; Eichhorn *et al.* 2006; Vizcaíno-Palomar *et al.* 2014; Latreille & Pichot 2017); In addition, RTEs have also shown that stark morphological differences between tree ecotypes may be due to purely phenotypic plasticity with no evidence of genetic influence (Fang*et al.* 2006). These results show the complexity of the relationship between environmental conditions and phenotypic traits through plasticity and local adaptation processes. The main constraint in interpreting the results obtained from RTEs is that one can only observe differential adaptation to a bundle of ecological factors that differ between habitats. By designing RTEs that cross more than one factor (*e.g.* differences in climate, soil properties, competition, and predators) one may be able to tease apart at least subsets of covarying ecological factors (Wadgymar*et al.* 2017). Such type of approach is thus extremely useful for understanding the mechanisms for spatial heterogeneity, which in turn is essential for the construction of predictive models of spatial distribution of species/phenotypes.

Lowland Neotropical forest, such as those in French Guiana, show a highly variable and complex mosaic of microhabitats linked to variations in topography and soil characteristics. Differences in water drainage has been long identified as a main ecological factor driving the tree community composition on the Guiana shield (Barthes 1991; ter Steege *et al.* 1993; Sabatier *et al.* 1997), allowing to position the species along a gradient of tolerance to prolonged water saturation of soil porosity and a gradient of tolerance to temporary water saturation (Pélissier *et al.* 2002). All these studies show that the most striking variations in tree species distribution at local scale result from the widespread gradient between seasonally flooded (SF) habitats along streams and all other surrounding habitats on slopes and hilltops (HT). These studies also showed that congeneric species often display opposite niche preferences across such gradients, as was pointed out by Allié *et al.* (2015). A typical example is provided by the genus *Symphonia* of African origin, with the species *S. globulifera,* widespread across the Neotropics, and a morpho-taxon of yet undetermined status, currently identified as*S. sp1* , which is known to occur in the Guiana shield. Adults of the two taxa, referred hereafter as 'ecotypes', are found in sympatry, often with intermingled crowns, but are environmentally segregated, with*S. globulifera* being strongly linked to SF habitats, while*S. sp1* is found on both HT and SF (Allié*et al.* 2015; Schmitt *et al. a. in review* ;), The two ecotypes are differentiated by the size of their leaves, flowers, and fruits, the texture of their bark, the presence of pneumatophores or prop roots (; Baraloto *et al.* 2007 Schmitt *et al. b. in review*), as well as differences in maximum diameter at breast height and growth rates (Hérault*et al.* 2011). Whether these morphological differences are the product of environmentally driven phenotypic plasticity or genetically determined is not yet known. The system constitutes an extreme case of microgeographic differentiation, and potentially, adaptation (Richardson *et al.* 2014), as trees of the two ecotypes are distributed in mosaic patches smaller than the pollen dispersal potential (20-50m) (Degen *et al.* 2004). The two ecotypes are genetically differentiated based on nuclear microsatellites (F_{ST} =0.086), although less so than African and South American population of *S. globulifera*(F_{ST} =0.31) (Torroba-Balmori *et al.*2017), or even than Neotropical population of *S. globulifera*(F_{ST} =0.138) (Dick & Heuertz 2008)The two ecotypes follow thus different evolutionary paths and may show genetic variants associated with adaptations to different habitats, but, genetically intermediate individuals (F1, F2, etc.) have been observed (N. Tysklind – unpublished data) suggesting that some mixing of the two ecotypes occurs in the field, leading us to believe that*Symphonia* operates as a syngameon in French Guiana. Syngameons were defined by botanists during the XXth century (Lotsy 1917; Grant 1971) to describe closely related plant species that are interfertile despite the presence of morphologically distinct groups classified as different species. This term covers today the most inclusive interbreeding evolutionary unit (Suarez-Gonzalez *et al.*2018), of which oak is one of the best representatives (Cannon & Petit 2019). The genetic differentiation between *Symphonia* ecotypes is smaller than among members of the oak syngameon (F_{ST} (SNPs)=0.13 (Lang *et al.* 2018).

Previous shadehouse common garden experiments (Baraloto*et al.* 2007) could not pinpoint differential physiological responses to drought and flooding between the two ecotypes, and thus the heterogeneous spatial distribution of *Symphonia* is not explained by these alone, at least as far as experiments in artificial conditions can tell. Nevertheless, mortality was higher in *S . sp1*after six weeks of controlled flooding, and wild *S. globulifera*seedlings tended to survive better in SF areas in the wild (Baraloto *et al.* 2007). To dissect the causes of the observed association of the two ecotypes with habitats, we established an RTE, considering both habitat and provenance region, in the field under the natural canopy. We hypothesise that germination, growth, herbivory defence, and survival, or a combination of these factors, are better for each ecotype and provenance in its habitat of origin than in other habitats; we argue that such differences contribute to explain the niche distribution patterns observed in the wild.

Materials and Methods

Experimental design and data collection:

The experimental design aimed to collect seeds from mother trees from two contrasting habitats and the associated ecotypes: SF-*S. globulifera* and HT-*S. sp1;* and from two broad regions with markedly different rainfall patterns: 'east', with the highest rainfall in French Guiana, and 'west', the driest part of French Guiana (Fig. 1). Seeds were transplanted onto experimental gardens installed on HT and SF habitats at two field sites in the 'east' and 'west' regions, respectively, which were not among the sampled sites for the seeds.

Seeds were collected between September 2008 and April 2009, due to largely unequal flowering times, from nine mother trees belonging to both ecotypes in the 'western' region and from five mother trees in the 'eastern' region, composing the variables "Provenance region" and "Ecotype" (Table 1). From each mother tree, 35-39 seeds were collected and sown in polypropylene germination plates with soil in a common shadehouse at the Kourou Agronomic Campus prior to transplantation into field sites between May and July 2009. This meant that seeds spent between 27 and 315 days in the shadehouse, depending on the seed collection and transplant dates. This introduced substantial differences among groups in the number of days spent in the shadehouse (Fig. 2a), the proportion of seeds that had germinated (*i.e.* at least cotyledons emerged from ground), as well as in the developmental stage reached by the germinated seedlings, at transplantation time. Although such differences among groups are likely to originate from ecological differences in flowering time, they can be viewed as biases in analyses. First of all, comparisons of germination trends among groups must be interpreted according to this bias; secondly, germination rates themselves must be included as an important cofactor, in its turn carrying information about amount of time spent in shadehouse, in the life history and growth-associated traits analyses. See below for how biases in seed collection were incorporated into the analysis of germination rates, and for how differences in germination status were considered in the analyses of other traits. Whether seeds had germinated at the moment of transplant or not was stored in the variable "transplant status". The moment at which individual seeds were first recorded as seedlings (*e.g.* moment of transplant, year 1, year 2, year 3, etc.) was stored as "germination timing". To avoid confusion, we hereafter refer to "seed" when discussing aspects regarding the phase prior to germination, "seedling" for those aspects regarding the phase after germination, and "individual" for those aspects regarding both seed and seedling phases.

Individuals (*i.e.* seed or seedling) were transplanted to gardens established at each field site (*i.e.* east *vs.* west) and habitat: three in SF and three in HT conditions in each site, totalling 12 gardens. Field site plantation and habitat compose the variables "Plantation region" and "Habitat", respectively (Table 2; Fig. 1). Each garden was fenced from large herbivores with chicken wire. Prior to transplanting, all understory vegetation (i.e. up to 5 cm D.B.H.) was removed; the canopy was left undisturbed. Regeneration other than the transplanted seedlings was removed yearly by hand. Individuals were distributed over the twelve gardens as follows: each garden was arranged in 44 ten-seedling slots. In each garden, six slots were randomly attributed to *Symphonia* (the remaining slots were used for other experiments), and then three individuals per mother plant were assigned to random positions within those slots in each garden. Individuals were allocated to different gardens depending on their provenance, ecotype, plantation region, and habitat without differentiating between those that had germinated in the shadehouse and transplanted as germinated seedlings or those transplanted as ungerminated seed (Table 2). Data for each individual (*i.e.* germination status at transplantation, germination year, survival, growth-associated traits, and herbivory) were collected at transplant date and then yearly in September from 2009 until 2014, except for 2012 (Suppl. Table 1). Individual survival was recorded as follows: 1 for seedlings found alive and 0 for ungerminated seeds transplanted to field sites and yet to germinate, and for seedlings previously living but found dead. Seedling height was measured in centimetres between the apical bud and the collar. Stem diameter was measured in millimetres at the collar in two orthogonal directions and estimated as the mean of the two measures. As an architectural trait, we selected "total number of leaves", an indicator of seedling leafiness. Herbivory was determined as follows: each leaf was assigned one of five classes of percentage of damaged area (0-20%; 20-40%; 40-60%; 60-80%; 80-100%) and then seedling herbivory attack level was estimated as the average of the percentage of damaged area of all its leaves (Suppl. Table 1).

Data analyses:

Two complementary analytical strategies were applied to the data to extract the biological significance of individual germination, survival, and performance depending on the studied predictor variables: a) random forest methods were used to explore variable importance, untangle and understand the structure of interactions among the covariates, and graphically visualise their effects on the dependent variables; and b) Linear model and Generalized linear model (GLM) were used to find general effects of predictor variables on the dependent variables. More specifically, we introduce a test based on the least-squares means, also named adjusted means (Searle*et al.* 1980), which allows us to compare the effect of growing in their 'home' habitat *vs.* 'away' habitat and of being 'local'*vs.* 'foreigner' in a given habitat, while averaging for other potential effects to make such comparisons meaningful and reduce the confusion of effects.

Random forest analyses:

Random forest methods and classification trees were applied to evaluate relative variable importance in explaining germination, survival, growth, leafiness, and herbivory on individuals at the end of the experiment (year 6) and the average yearly relative growth rate (RGR), untangle interactions among the predictor variables, and graphically visualise their effects on each of the responses. *Random forest* methods (Breiman 2001) are particularly suited for data where nonlinear relationships and complex interactions among variables are expected (Cutler*et al.* 2007). Classification trees visualize predictive models of responses significantly dependent on predictor variables. This is achieved by recursive binary classification of the data, where independence of the response (i.e. here germination, survival, growth, leafiness, and herbivory) and the covariates (i.e. here provenance region, ecotype, plantation region, habitat, and transplant status) is tested; then, if a significant dependence is found, the best split value for the predictor variable with the strongest effect is retained and used to divide the response in two groups. The process is then repeated with each of the groups, recursively, until no significant dependence between covariates and response can be found (Hothorn*et al.* 2006). In a *random forest,* the above classification tree is performed on a bootstrap subset of the data and a reduced number of predictor variables to obtain response predictions based on a majority vote of the whole forest. Such methodology allows assessing relative variable importance, by identifying those covariates which, when removed, ensue a significant drop of prediction power (Strobl*et al.* 2007). In our case, it allows us to identify if certain combinations of variables (e.g. *S. globulifera* in SF) lead to significant improvement of performance of 'home' or 'local' individuals.

We repeated the analyses including all the predictor variables as explanatory variables and removing transplant status (*i.e.* seed or seedling) to check if transplant status confounded the analysis of the impact of the covariates of interest (*i.e.* provenance region, ecotype, plantation region, and habitat). Furthermore, we evaluated the effects of provenance region and ecotype on shadehouse germination rates, and of all predictor variables on the germination rates of individuals planted as seeds in the field (Supplementary material 1).

For the *random forest* analyses of growth performance and herbivory, only individuals germinated in 2009, whether in the shade-house or in the field and having a final measure in 2014 were analysed. Therefore, each individual has a unique discrete value for each trait in 2014, that is at age 5 (i.e. year 6). The average yearly relative growth rate (RGR) in height, diameter, and leafiness as well as the average herbivory were also summarised over the life of the individual, giving each individual a single value over the course of the experiment.

All analyses were run in the R statistical environment (R Core Team 2020) with the package 'party' (Hothorn*et al.* 2006; Strobl *et al.* 2009). Conditional inference trees were also grown in party with an $\alpha = 0.05$ and a minimum of 2 observations in each branch.

Linear models and general linear model analyses:

Linear model (LM) and generalized linear model (GLM) were additionally used to test the potential effects of different predictor variables on traits (*i.e.* germination, survival, growth, architecture, and herbivory), and most importantly to define an ad-hoc procedure to test local adaptation by subsuming in a single test both the 'home *vs.* away', and the 'local *vs.*foreigner' tests of Kawecki and Ebert (2004), while averaging over all possible other effects to disentangle the effect of the unbalanced final design. Our approach, as described below, aims at synthetically observing the effect of having been planted in the environment of provenance or in a different environment, in itself, on traits taken as proxies for individual performance. This contrasts with previous strategies for the detection of local adaptation, which rest on the separate analysis of the "home *vs.* away" and "local*vs.* foreigner" effects and deduce the presence of the effect from slope comparisons (*i.e.* , they test for population x environment interactions). In the wording of Kawecki and Ebert (2004), our method is tantamount to comparing the means of "'sympatric' and 'allopatric' deme-habitat combinations". While confounding the effects of "true" local adaptation and of global superiority of one population relative to all others (Kawecki & Ebert 2004), our LM/GLM approach has the comparative advantage of better coping with unbalanced design and, possibly, having greater power.

We denote e the ecotype ($e = 1$ for *S. globulifera*and $e = 2$ for *S. sp1*), h the habitat ($h = 1$ for SF, and $h = 2$ for HT, so that individuals growing at 'home' are specified by 11 or 22), o for provenance region ($o = 1$ for east and $o = 2$ for west), r for the plantation region ($r = 1$ for east and $r = 2$ for west), s for the transplantation status ($s = 1$ if transplanted as a seed or$s = 2$ for transplanted as a seedling), and finally, a for the age of the considered individual ($a = 1, \ldots, 5$). The full model for growth-associated traits (*i.e.* seedling height, stem diameter, leafiness, and herbivory) might be expressed as a normal response $\mathit{\Psi}_{\epsilon\eta o\rho\sigma\alpha}$ ˜ $N(\mu_{\epsilon\eta o\rho\sigma\alpha}$, $\sigma^2)$, while binary responses like the life history traits, germination and survival, are expressed as a Bernoulli distribution with probability of successp_{ehorsa}. In the following text, we show the development of formulas for the ecotype/habitat case, with subscripts$e$ for ecotype and h for habitat, as described above; formulas for the provenance region / plantation region case are identical, except that they bear subscripts o for provenance region and r for plantation region, as described above, and will not be further described here.

Germination success in the shadehouse and overall germination (G):

In the evaluation of the difference in germination success (G) in the shadehouse, individuals have not yet been transplanted, therefore, the only effects to account for were genetic effects: ecotype and provenance region. However, the time spent in the shadehouse depends on the collection and should be accounted for. The logit of the probability of germination (G) of the k^{th} seed is given by:

$$\text{logit}\left(p_{\text{eok}}^{G}\right) = u^{G} + \alpha_{e}^{G} + \delta_{o}^{G} + \varepsilon_{\text{eo}}^{G} +$$

Where t stands for the time spent in the shadehouse.

To correct the effects of unbalanced design and difference in time in the shadehouse, the effect of ecotype (e) on the difference in germination success (G) in the shadehouse, has been studied by a comparison of the classical least square means of ecotype:

$$\text{logit}\left(p||adj, G||e\right) = u^{G} + \alpha^{G}{}_{e} + \left(\beta\middle||G + \gamma^{G}{}_{e}\right)\acute{t} + \frac{1}{2}\sum_{o}\delta^{G}{}_{o} + \xi^{G}{}_{\text{eo}} + \eta^{G}{}_{o}\acute{t}, (2)$$

where ($\acute{t}$) is the average time spent in the shadehouse.

The same approach using least square means is used to study the overall germination except that we don't account for the time in the shadehouse. In case of germination success, a GLM approach is used to study the time of germination. The response is modelled through a geometric distribution and the log link function. Least Square Means are used to compare the expected time of germination.

Survival (S):

To evaluate differences in survival (S) among 'home' and 'away' groups, we developed the following approach: assuming the survival probability is constant over a year, the observed maximal age might be modelled as a geometric distribution whose probability of success,$p^S{}_{ehors}$, depends on ecotype *(e)* , habitat (h), provenance region (o), plantation region (r), and the transplantation status (s). The least-squares means for the log odd ratio of such probability is given by:

$$\text{logit}\left(p||adj, S||\text{eh}\right) = u^S + \alpha^S{}_{\text{eh}} + \frac{1}{8}\sum_{o,r,s} \delta^S{}_{\text{ots}} + \zeta^S{}_{\text{ehors}}, (3)$$

where $a^{\Sigma}{}_{\epsilon\eta}$ stands for the joint effect of ecotype and habitat,$\delta^{\Sigma}{}_{o\rho\varsigma}$ stands for all other effects like the provenance region, plantation region, and the transplantation status, and $\zeta^S{}_{\text{ehors}}$the interaction between those different effects on the survival probability.

Growth-associated traits:

As the aim of the analysis of growth-associated traits is identifying the potential effect of the growing 'home' *vs.* 'away', the mean$\mu_{\epsilon\eta o\rho\sigma\alpha}$ has to reveal the joint effect of ecotype and habitat; the joint effect of provenance region, plantation region, and transplantation status; and the age effect as well as all interactions between any two of these variables. Therefore, for any growth-associated trait (Y), $\mu_{\epsilon\eta o\rho\sigma\alpha}$ might be expressed as:

$u^Y{}_{\text{ehorsa}} = u^Y + \alpha^Y{}_{\text{eh}} + \delta^Y{}_{\text{ors}} + \left(\beta||Y + \gamma^Y{}_{\text{eh}} + \theta^Y{}_{\text{ors}}\right) a(4)$

where

- $\alpha^Y{}_{\text{eh}}$ stands for the joint effect of ecotype and habitat, with a total of 4 possible different combination of ecotype x habitat

- $\delta^Y{}_{\text{ors}}$stands for all other controlled effect like the provenance region, the plantation region, and transplantation status for a total of 8 possible different levels,

- β^Y is the effect of age,

- $\gamma^Y{}_{\text{eh}}$ is the differential effect of age according to the ecotype/habitat level,

- $\theta^Y{}_{\text{ors}}$ is the differential effect of age according to the provenance/plantation region/transplantation status levels.

Interaction between main effects of interest (*i.e*ecotype/habitat) and other controlled effects have not been incorporated as not all combinations have been observed.

To detect signals of local adaptation in growth-associated traits, we compared the effects of growing at the ecotype's (or provenance's) 'home' habitat *vs.* growing in the 'away' habitat. Such comparison was achieved by defining least-squares means at age a$\mu_{\epsilon\eta}{}^{a\delta\vartheta}$*(a)* (Russell V. Lenth, 2016) to account for the unbalanced design:

$$u^{adj,Y}{}_{\text{eh}}\left(a\right) = u^Y + \alpha^Y{}_{\text{eh}} + \left(\beta||Y + \gamma^Y{}_{\text{eh}}\right) a + \frac{1}{8}\sum_{o,t,s}\left(\delta^Y{}_{\text{ors}} + \theta^Y{}_{\text{ors}} a\right) (5)$$

The comparison between 'home' and 'away' habitat-ecotype pairs is performed age by age by forming the following contrast:

$C_a = \left(u_{11}^{adj,Y}\left(a\right) + u_{22}^{adj,Y}\left(a\right)\right) - \left(u_{12}^{adj,Y}\left(a\right) + u_{21}^{adj,Y}\left(a\right)\right)(6)$

which quantifies the difference of an average individual growing at 'home' (combination 11 or 22) and an average individual growing 'away' (combination 12 or 21).

All GLM analyses were run in the R statistical environment with the packages ‘car’ (Fox & Weisberg 2010), ‘multcomp’ (Hothorn*et al.* 2008), ‘emmeans’ (Lenth 2016, 2018), and visualized using ‘ggplot2’ (Wickham 2009).

Results

Description of the data:

A total of 510 individual *Symphonia* were followed over the course of 6 years. Of these, 36.1% had germinated at the time of transplant and were transplanted as seedlings. The remainder were transplanted as seeds. Overall germination reached 61.2% by the end of the experiment (Table 1). At the end of the experiment 37% of seedlings were alive, and survival was lowest in western SF gardens (Table 2). Summary statistics of growth-associated traits (i.e. height, diameter, total number of leaves) and average herbivory over the course of the 6 years for those individuals germinated in 2009 and still alive at the end of the experiment are reported in Table 3.

Impact of the transplant status on survival: seeds vs. seedlings.

The classification tree analysis of the success of germination (Supplementary material 1) indicated strong effects of the provenance region independently of the transplant status: seeds having germinated in the shadehouse or seeds having germinated in the field. The same result was observed using GLM when considering the global success of germination (*i.e.* whatever the transplant status, all the seeds that have germinated at some point, during the 6 years of the experiment). Since the main effect tested was observed in both the seeds that have germinated in shadehouse and the seeds that have germinated in the field, the two transplant statuses were merged together for the rest of the analyses.

Effects of covariates on germination and survival of Symphonia seedlings

To overcome the bias in duration of time at the shadehouse among the different ecotype x provenance groups (Fig. 2a), we compared the probability of germination success in the shadehouse of the two ecotypes depending on the region of provenance after the average time in the shade house (*i.e.* 89 days). A significantly lower probability of germination success in the shadehouse was identified for western*S. sp1* compared to all other groups (Fig. 2b), even when accounting for the difference in time in the shadehouse. However, the analysis of overall germination (*i.e.* shadehouse and field combined) indicated that provenance and plantation habitat, rather than ecotype, were the main drivers of the variance in germination success (Fig. 2c and Fig. 3). The analysis of the delay on germination showcases that provenance also had a strong impact on the timing of germination (Fig. 2d), where seeds from the west germinate significantly later than those from the east (west: 13 months *vs.* east: 3 months).

In terms of overall germination and survival, classification trees identified that provenance region, plantation region, habitat, and ecotype as significant variables explaining overall germination and survival of individuals at the 5% threshold, exposing the complexity of the interactions among predictor variables (Fig. 3). Provenance had the strongest impact, where most individuals from the east (Fig. 3, nodes 9, 10, 11) had germinated, while those from the west systematically suffered from lower germination rates (Fig. 3, nodes 2, 3, 4, 5, 6, 7 and 8). Eastern provenance individuals planted in the east plantations survived significantly better than when planted in the west (Fig. 3, node 9). Western provenance individuals survived better in the east than in the west (Fig. 3, node 2). Germination and survival were lowest for western provenance individuals, planted in the west in SF habitats, regardless of ecotype (Fig. 3, node 4). Finally, for western provenance individuals, planted in the west, in HT habitats, there is a significant ecotype effect, where *S. sp1* (i.e. ‘local’) germinates and survives significantly better (Fig. 3, node 6) than *S. globulifera* (i.e. ‘foreign’) (Fig.3, node 7).

Effects of predictor variables on growth-associated traits of Symphonia seedlings

According to the classification trees, ecotype had the strongest significant effect on 5 out of 7 growth-associated traits and herbivory: average RGR height, diameter, total number of leaves, and average RGR in number of leaves, and average relative herbivory, separating *S. globulifera* from *S. sp1* (Fig. 4). *S. sp1* grew faster (Fig. 4b, 5a,b), was thinner (Fig. 4c, 5e,f) but leafier (Fig. 4e, 5i,j), and suffered less herbivory than *S. globulifera* (Fig. 4g, 5n). Habitat also had significant effects on four growth-associated traits, revealing that: individuals were taller on average in SF than in HT (Fig. 4a), that *S. globulifera* grew faster and was leafier in SF than in HT (Fig. 4b node 3, 4e node 3), and that *S. sp1*suffered the least herbivory when planted in SF habitats (Fig. 4g, 5n). Finally, plantation region had an impact on the height of individuals planted in HT (Fig. 4a node 3) and on the RGR in diameter (Fig. 4d), with individuals planted in the west being taller and thicker than those in the east.

The Linear Model analyses, where LS Means were used to correct for unbalanced design, of the growth-associated traits comparing 'home'*vs.* 'away' (*i.e.* ecotype x habitat and provenance x plantation combinations) corroborated the RF results but focused on a yearly comparison to provide a contrasting view. Figure 5 illustrates the significantly better growth performances (*e.g.* height, diameter, and TNL, as well as their relative growth compared to reference measures at age 0) of individuals grown in their 'home' ecotype x habitat combination compared to those in 'away' ecotype x habitats combination, and that the differences increase with age (Fig. 5a,b,e,f,i,j).

The provenance x plantation analyses showed significant, or near significant, effects in the early ages for height, diameter, and total number of leaves, where 'home' individuals outperformed 'away' individuals, but the significance disappeared in later years (Fig. 5c,g,k). Individuals grown in their 'home' provenance x plantation combination, had significantly larger diameters at ages 3-5 relative to their diameter at age 0 compared to individuals in 'away' provenances x plantation combination (Fig. 5h).

Discussion

Local genetic differentiation and its adaptive significance are widely recognised in plants and evidence of microgeographic adaptive processes is accumulating for trees (Wright 2007; Ramírez-Valiente*et al.* 2009; Brousseau *et al.* 2013, 2015, 2018; Carsjens*et al.* 2014; Pluess *et al.* 2016; Rellstab *et al.*2016; Barton *et al.* 2020). Differences in seedling performances along ecological gradients are typically interpreted as underlying observed interspecific differences in the distribution of mature trees; in a way, our two ecotypes in the *Symphonia* syngameon behave in a species-like way relative to habitat preferences, given that they can grow in mixed or neighbouring stands, where morphological and genetic hybrids are occasionally found, and yet they retain their respective ecological properties.

Superior performances of 'home' and 'local' individuals in life-history and growth-associated traits suggest that *Symphonia* trees have locally adapted to different environmental conditions across French Guiana. We find both 'home' *vs.* 'away', and 'local' *vs.*'foreigner' examples of local adaptation (*sensu*Kawecki & Ebert 2004)). The patterns are, however, complex; revealing that the measured traits are not exclusively caused by genetic trade-offs in the underlying genes coding for the patterns of local adaptation.

Patterns of germination:

The classification trees and the estimated shadehouse and overall probability of germination (Fig. 2 and Suppl. Fig. 3, 4, 5) exposed some unexpected patterns: Western *S. sp1* seeds have a significantly lower probability of germination under the controlled conditions of the shadehouse after 89 days than all other groups (Fig. 2b). However, overall germination at the end of the experiment of western *S. sp1* planted in HT in the west was relatively high (~70%, Fig. 2c), indicating that germination for western *S. sp1* in western HT recovered while in the field. The germination of western *S. sp1* in other habitat-region combinations remained very low till the end of the experiment (Fig. 2c). In stark contrast, all four eastern provenance combinations of ecotype and habitat planted in the east had nearly 100% overall germination success. Western seeds germinated significantly later than eastern seeds (Fig. 2d: 1 year later on average). Such differential success rate and timing of germination among ecotype-provenance combinations could be due to differences in local adaptation to germination timing and cues. Matching germination with the best possible conditions for seedling growth is paramount for seedling survival, and the timing and environmental cues underpinning such favourable conditions may vary across a species range. Variation in seed dormancy duration, and the genetic basis for such variation, has been reported as evidence for local adaptation among populations of*Arabidopsis thaliana*(Donohue 2009; Postma *et al.* 2015, 2016). Similarly, the regional differences in germination success over the course of our study may indicate evolutionary advantages for delayed germination of*Symphonia* in the west or rapid germination of *Symphonia* in the east (Fig. 2d). A higher seed quiescence or dormancy level, or tighter environmental requirements for germination, may have emerged as a local adaptation in western *Symphonia* , especially in *S. sp1*¸ as a means to cope with a drier environment (Dalling*et al.* 2011), and spreading seedling mortality risk across several years (Gremer & Venable 2014). Supporting such hypothesis, we observe reduced survival of eastern provenance-individuals in the west (Fig. 3) indicating that the western plantations are in a harsher environment overall. Conversely, a quicker germination time may be a local adaptation in response to differences in seed mortality rate (*e.g.* herbivory, disease, or ageing) between regions or ecotypes (Dalling*et al.* 2011; Postma *et al.* 2015)

Patterns of growth-associated traits:

The LSMeans analyses exposed how individuals in their home habitat significantly outperformed individuals in away habitats in terms of growth-associated traits, and the classification trees pinpointed how that signal was dominated by significant decreases in growth-associated traits for *S. globulifera* when planted in HT, indicating a reduction in competitive growth performance of individual *S. globulifera* in HT. Conversely, we did not detect any significant effect of habitat for *S. sp1* , suggesting a capacity to perform well regardless of habitat. Individual tree vigour, as in the difference between observed and expected growth, has been shown to have a pervasive effect on Neotropical tree survival, where variance in individual vigour along the tree's life was the most important variable predicting survival, well above ontogenetic status or species membership (Aubry-Kientz*et al.* 2015). Variance in growth performance, such as seen in*S. globulifera,* can be interpreted as variance in vigour, which could be one of the mechanisms explaining the variance in survival patterns we observed among *Symphonia* seedlings. The observed variance in growth is indeed in accordance with the rarity of adult*S. globulifera* in HT habitats, and the more generalist distribution of *S. sp1* across habitats (Allié*et al.* 2015; S. Schmitt, unpublished data).

Patterns of survival and contributions towards understanding the patterns of species distribution:

The classification trees of combined germination and survival reveal complex interactions among the predictor variables, not only explaining the patterns of survival of*Symphonia* individuals in our experiment, but also potentially explaining patterns of species distribution in French Guiana and the maintenance of ecological differences between ecotypes within the*Symphonia* syngameon.

The groups with the highest survival (>50% after 6 years) were western-provenance *S. sp1*planted in western HT, and eastern-provenance individuals planted in the east regardless of ecotype and habitat (Fig. 3). These two high survival groups also had high germination rates (Fig. 2c). The first group is suggestive of very specific local adaptation. It is the only group planted in the west with a relatively high survival (*i.e.*>50% survival at age 5, compared to <25% for the rest of groups transplanted in the west). *S. sp1* is common in hilltops throughout French Guiana and may therefore be able to cope better in the drier west. Furthermore, it is only western *S. sp1*which significantly separate from all others in terms of survival, perhaps indicative not only of an ecotype adaption to drier HT, but also a regional effect where eastern *S. sp1* are particularly drought tolerant. This case constitutes a double example of a 'local *vs.*foreign' evidence of local adaptation across two variables (both habitat and regional), stressing the efficacy of the selection pressures in eastern HT habitats. Variations in survival and germination in *S. sp1* are furthermore accompanied with an overall lower performance of*S. globulifera* seedlings when planted in HT; both probably contributing to contrasted distributions between the two ecotypes. We did not detect an adaptive cost for *S. sp1* in the form of lower survival in either eastern gardens nor in SF habitats, suggesting that either 1) conditional neutrality (i.e. whereby an adaptation conveys a performance advantage in one environment without costs in alternative environments) is at play in the genetic basis underlying its improved performance in dryer conditions (Anderson 2013; Wadgymar *et al.* 2017), or that 2) our experimental design did not capture the selective pressures penalising *S. sp1* in wetter conditions, such as those found in SF habitats or eastern gardens. The latter could be related to environmental variables we did not account for in the experiment or related to stages we missed across the trees' life history (Miglia*et al.* 2005).

The second group with comparatively high survival confirms a better performance of eastern individuals in eastern field sites compared to western field sites, indicative of either local adaptation at the regional level to heavier rainfalls, or alternatively, poor drought tolerance, as the survival of eastern-provenance individuals, regardless of ecotype, planted in the west drops significantly. This constitutes an example of 'home *vs.* away' pattern of local adaptation, but not 'local *vs.* foreign' as western-provenance individuals have a high survival in the east once germinated. Given the general high survival of individuals in east plantation gardens, and the non-appearance of other factors significantly affecting survival in these gardens, we infer a less stressful environment in the eastern field site for*Symphonia* in general. We did not capture evidence of differences in survival between ecotypes or habitats in the east, which exemplifies the potential confusion between divergent selection and differences in habitat quality.

Overall, we find evidence that *S. sp1* has better survival in the driest conditions, suffers less herbivory, and has no penalisation on other environments, which suggests a habitat generalist behaviour, and matches the extant species distribution. Conversely, *S. globulifera* is triple penalised out of SF (*i.e.* lower TNL, lower RGR in height, and higher herbivory), suggesting that it is a habitat specialist limited to SF habitats. The apparent limitation in habitat availability for *S. globulifera* could be compensated by the faster adult growth rate and a potentially higher reproductive output because of the larger maximum sizes in *S. globulifera* than*S. sp1* allowing the coexistence of both ecotypes. The variance in juvenile performance in the two habitats also helps explain the maintenance of the ecological differences between ecotypes, which could contribute to the preservation of the genetic integrity of each ecotype even when occasional hybridisation occurs between them.

Selective pressures behind the signals of local adaptation:

The experimental setup was designed to detect adaptation patterns to the combined effects of the contrasted habitats, with a focus on soil factors influencing hydric regime. Our results show a pattern consistent with an adaptive advantage of western*S. sp1* to the driest conditions included in the experiment (i.e. western HT), potentially mediated through improved water use efficiency (Baltzer*et al.* 2005).

Beyond the sharp variations in water regime, many other variables covary across the microhabitats presented here (*i.e.* east *vs.*west, SF *vs.* HT): access to resources such as light and soil nutrients, the risk of death, the floristic and soil microbiota community, and presence of herbivores vary significantly between HT and SF.

SF habitats have a higher fertility and access to light than HT habitats, however, trees living in SF habitats double their risk of death through tree fall (Ferry*et al.* 2010), creating a high-risk high-gain environment. Species specializing in SF habitats must therefore adapt their resource allocations accordingly. *S. globulifera* seedlings in SF were the tallest (Fig. 5a) and had the largest diameters after 6 years (Fig. 5e), potentially indicative of an ecotype adaptation towards a strategy maximising growth in a risky environment.

Arthropod assemblages in French Guiana SF and HT habitats are significantly different, where leaf feeders in particular are more abundant in HT than in SF (Lamarre*et al.* 2016). Herbivory was highest for *S. globulifera*regardless of all other covariates, and lowest for *S. sp1* in SF habitats, suggesting different predator avoidance strategies between ecotypes. Our herbivory analyses are in agreement with those of previous studies, where similar patterns are observed in RTEs between species specializing in high and low herbivory pressure environments: species which are normally exposed to a higher herbivory environment (*i.e.* similar to *S. sp1*), experienced reduced herbivory in low herbivory environments (*i.e.*similar to SF) compared to their 'home' environment and species from low-herbivory environments (Fine*et al.* 2004, 2006; Baltzer & Davies 2012). *S. globulifera*tissues are rich in secondary metabolites of the *b* is-xanthone family, known to have insecticidal properties in other organisms (Ondeyka *et al.* 2006; Wezeman*et al.* 2015); the leaves are particularly rich in globulixanthone E (Cottet*et al.* 2014), which has strong anti-microbial activity (Nkengfack*et al.* 2002). *S. globulifera* populations from Cameroon and French Guiana differ for their content in anti-microbial and anti-parasitic compounds (Cottet*et al.* 2017), suggesting that chemical differences may also occur between *S. globulifera* and *S. sp1.* Under this hypothesis,*S. sp1* may have adapted to a higher herbivory environment (HT) by increasing the production of unpalatable and toxic compounds to compensate for a potential limitation in resources in HT habitats (Bryant*et al.* 1985; Fine *et al.* 2004, 2006). Such scenario would also explain the lower herbivory rate of *S. sp1* in SF habitats compared to HT habitats.

Limitations of the study:

The power of our tests and the meaning of their results may suffer from multiple biases. Differences in germination successes lead to unbalances. While the analytical method we developed is meant to compensate them, they may still affect the results. Maternal effects (*e.g.* maternal provision to seeds) may still influence seedling growth and resources, because seedling mass is probably still in the same order of magnitude as seed mass. Epigenetic inheritance may also contribute to differences in seedling reactions to environmental cues. In the absence of precise information about genetic divergence and gene expression / regulation differences between ecotypes, it is hard to tell which mechanism is at play in the*Symphonia* system. Finally, as stressed by Miglia *et al.*(2005), to gain a comprehensive understanding of the ecological factors driving survival and performance of related taxa across environmental variables, multi-life-stage comparisons including germination, som

atic growth, and reproduction should be included.

Conclusion:

The critical importance of natural selection on genetic differences expressed during early life stages, when trees experience the highest mortality, has been recognised (Donohue*et al.* 2010; Postma & Ågren 2016). Our RTE experiment has given us insights into the ecological mechanisms governing differential germination and survival of cohorts of individuals in their own and foreign natural environments. We have revealed significant life-history and growth-associated trait differences between ecotypes and between provenances, that match with known environmental constraints (*i.e.* hydric regimes, nutrient availability, death risk, and herbivory risks), and may be the result of coevolution of germination phenology and seedling survival. *S. globulifera* seedlings were penalised in HT habitats with reduced growth and higher herbivory, however, in SF habitats they outgrew other such groups (ecotypes x habitat), a pattern also observed in adults *Symphonia* , suggesting that *S. globulifera* has a specialized competitive advantage in SF habitats, which may results in higher reproductive output if greater adult biomass is attained, and thus, allowing the coexistence for both ecotypes and the maintenance of the syngameon. Our results therefore suggest a link between differential growth and survival in seedlings, on the one hand, and adult tree distribution, on the other hand, and indicates that processes occurring at early life stages, far from being of an exclusively stochastic nature, contribute in a significant way to the selective processes and ecological filters that determine a species' pattern of distribution across habitats. Furthermore, our results suggest that even relatively small environmental differences, such as those between HT and SF, can lead to the evolutionary differentiation and maintenance of distinct taxa in sympatry with different life-history traits to suit such mosaic environmental heterogeneity despite occasional geneflow. Overall, the *Symphonia* model furthers our comprehension of the eco-evolutionary processes underpinning the diversity and the spatial structuring of Neotropical tree communities as well furthering our understating of the processes involved in the maintenance of syngameons in sympatry.

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Author contributions:

IS and CSS conceived the idea and designed the experiment. MC, VT and SOC established the RTE experiment. MC, AT, LB, VT and SOC coordinated the field measurement campaigns. BF contributed with soil and habitat characterisation. NT and MPE conducted the data analyses; NT, IS, CSS, and MPE wrote the manuscript. All authors contributed critically to previous drafts and gave their final approval for publication.

Data availability:

The data will be submitted to the TRY plant database upon acceptance of the manuscript.

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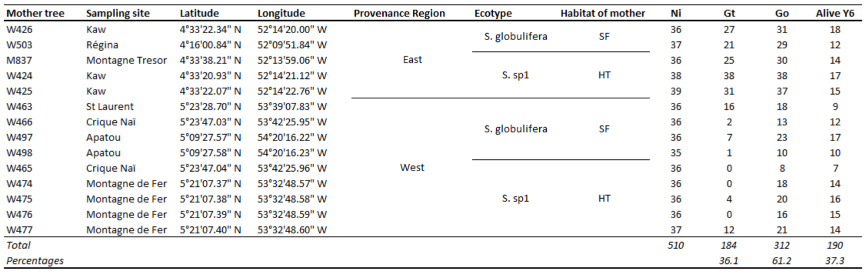
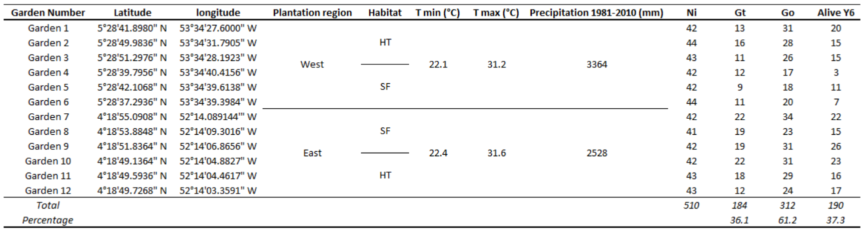
Tables:

Table 1 : *Symphonia* individual information: the**Mother tree** from which the seed was collected, the**sampling site** and **latitude** and **longitude**where the mother tree was found. Two general **provenance regions**are indicated (e.g. east and west), as well as the **ecotype** to which the mother belonged (*S. globulifera* or *S. sp1*) and the type of **habitat** the mother tree was found: seasonally flooded (**SF**) and hilltops (**HT**). The number of seeds collected (**Ni**), the number of seeds germinated at the time of transplant (**Gt**), and that had germinated overall at the end of the experiment (**Go**), and the number of seedlings alive at year 6 (**Alive Y6**) are also tabulated.



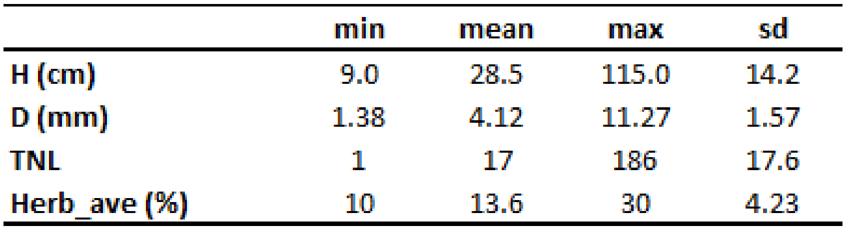
Mother tree	Sampling site	Latitude	Longitude	Provenance Region	Ecotype	Habitat of mother	Ni	Gt	Go	Alive Y6
W426	Kaw	4°33'22.34" N	52°14'20.00" W	East	S. globulifera	SF	36	27	31	18
W503	Régina	4°16'00.84" N	52°09'51.84" W				37	21	29	12
M837	Montagne Tresor	4°33'38.21" N	52°13'59.06" W		S. sp1	HT	36	25	30	14
W424	Kaw	4°33'20.93" N	52°14'21.12" W				38	38	38	17
W425	Kaw	4°33'22.07" N	52°14'22.76" W				39	31	37	15
W463	St Laurent	5°23'28.70" N	53°39'07.83" W	West	S. globulifera	SF	36	16	18	9
W466	Crique Naï	5°23'47.03" N	53°42'25.95" W				36	2	13	12
W497	Apatou	5°09'27.57" N	54°20'16.22" W				36	7	23	17
W498	Apatou	5°09'27.58" N	54°20'16.23" W				35	1	10	10
W465	Crique Naï	5°23'47.04" N	53°42'25.96" W		S. sp1	HT	36	0	8	7
W474	Montagne de Fer	5°21'07.37" N	53°32'48.57" W				36	0	18	14
W475	Montagne de Fer	5°21'07.38" N	53°32'48.58" W				36	4	20	16
W476	Montagne de Fer	5°21'07.39" N	53°32'48.59" W				36	0	16	15
W477	Montagne de Fer	5°21'07.40" N	53°32'48.60" W				37	12	21	14
Total							*510*	*184*	*312*	*190*
Percentages								*36.1*	*61.2*	*37.3*

Table 2 : Reciprocal transplantation experimental garden information: The **garden number** , the **latitude** and**longitude** , the **plantation region** , **habitat** are indicated. Climatic conditions minimum (**Tmin**) and maximum temperatures (**Tmax**) and average **precipitation** (mm) between 1981 and 2010 at nearby stations, Regina (**east**) and Iracoubo (**west**), are indicated (Meteo France). The habitat type of each garden is also indicated: seasonally flooded (**SF**) or hilltop (**HT**). The number of seeds planted in each garden (**Ni**), the number of seeds germinated at the time of transplant (**Gt**), and that had germinated overall at the end of the experiment (**Go**), and the number of seedlings alive at year 6 (**Alive Y6**) are also tabulated.



Garden Number	Latitude	longitude	Plantation region	Habitat	T min (°C)	T max (°C)	Precipitation 1981-2010 (mm)	Ni	Gt	Go	Alive Y6
Garden 1	5°28'41.8980" N	53°34'27.6000" W	West	HT	22.1	31.2	3364	42	13	31	20
Garden 2	5°28'49.9836" N	53°34'31.7905" W						44	16	28	15
Garden 3	5°28'51.2976" N	53°34'28.1923" W						43	11	26	15
Garden 4	5°28'39.7956" N	53°34'40.4156" W		SF				42	12	17	3
Garden 5	5°28'42.1068" N	53°34'39.6138" W						42	9	18	11
Garden 6	5°28'37.2936" N	53°34'39.3984" W						44	11	20	7
Garden 7	4°18'55.0908" N	52°14.089144"' W	East	SF	22.4	31.6	2528	42	22	34	22
Garden 8	4°18'53.8848" N	52°14'09.3016" W						41	19	23	15
Garden 9	4°18'51.8364" N	52°14'06.8656" W						42	19	31	26
Garden 10	4°18'49.1364" N	52°14'04.8827" W		HT				42	22	31	23
Garden 11	4°18'49.5936" N	52°14'04.4617" W						43	18	29	16
Garden 12	4°18'49.7268" N	52°14'03.3591" W						43	12	24	17
Total								*510*	*184*	*312*	*190*
Percentage									*36.1*	*61.2*	*37.3*

Table 3 : Summary statistics (**min** imum, **mean** ,**max** imum, and standard deviation (**sd**)) of growth traits and herbivory of seedlings germinated in 2009 and still alive in 2014. Height (**H**), Diameter (**D**), the total number of leaves (**TNL**), and average herbivory (yearly average of percentage of damaged area of all its leaves) over the course of the 6 years (**Herb_ave**).



	min	mean	max	sd
H (cm)	9.0	28.5	115.0	14.2
D (mm)	1.38	4.12	11.27	1.57
TNL	1	17	186	17.6
Herb_ave (%)	10	13.6	30	4.23

Figures:

Figure 1: Geographical location, pluviometry, and design of reciprocal transplantation experimental sites. a) Location of French Guiana along the north of South America; b) Greyscale map of pluviometry across French Guiana and location of the two plantation sites (Laussat and Régina). Average rainfall: Laussat (2500mm/year), Régina (3500mm/year) (reproduced from Brousseau *et al* ., 2015 with permission). c) Design of the reciprocal transplantation experiment. The black sigmoid curves represent the edaphic difference between HT and SF; The details on cartoon trees represent the different morphologies found in *Symphonia* associated with the HT and SF (*i.e. S. sp1* in HT and *S. globulifera* in SF); solid lines represent juveniles planted in the same habitats and region as their provenance. Dashed lines represent transplants between habitat within regions. Dotted lines represent transplants between regions within habitats. Dotdashed lines represent transplants across regions and habitats.

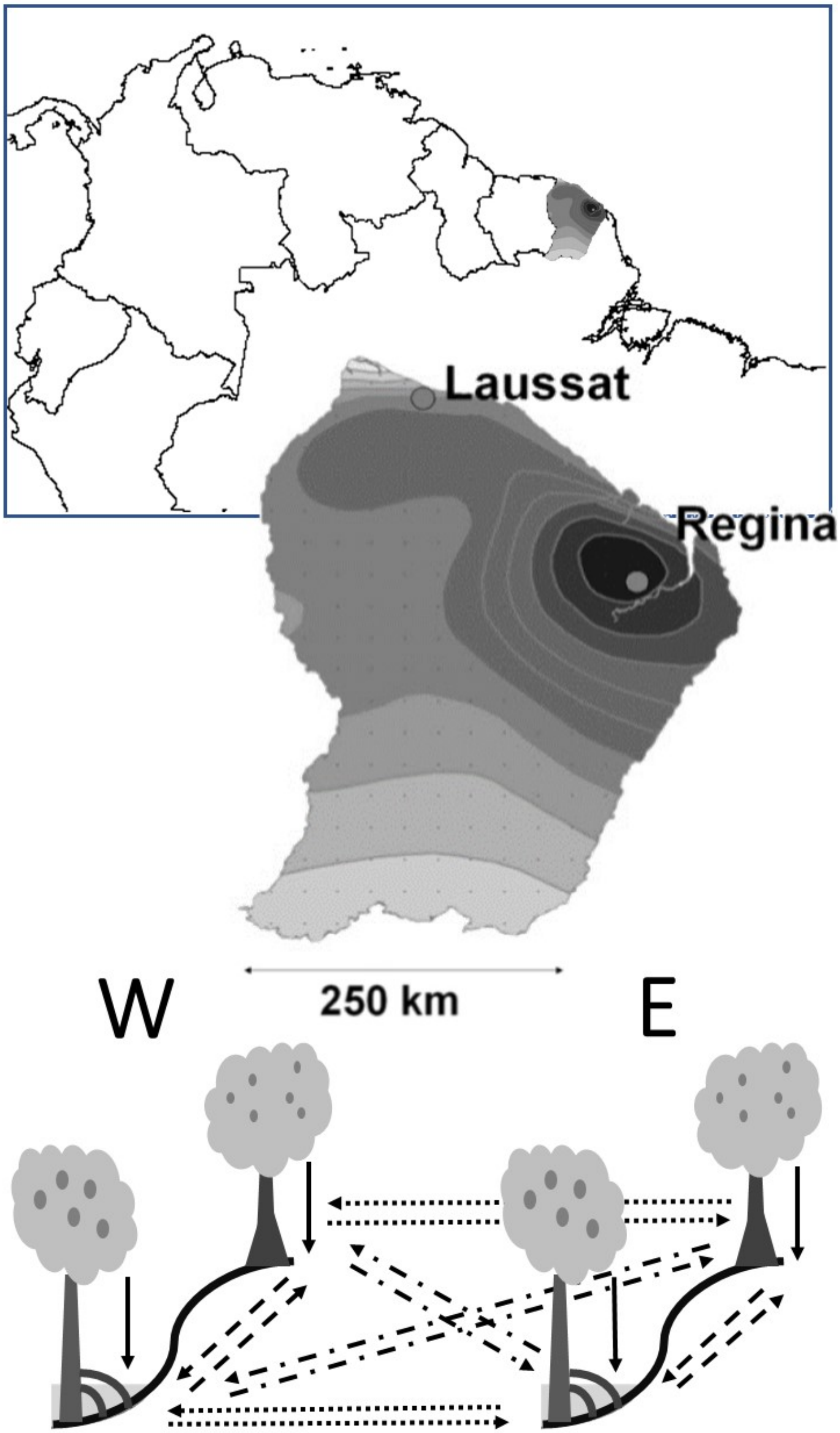


Figure 2: Analysis of germination success of *Symphonia*seeds. a) time spent in the shadehouse before

transplantation to the gardens by **ecotype** and **provenance** . b) Probability of germination in the shade house before transplantation by**ecotype** and **provenance** . c) Overall probability of germination success by ecotype, provenance, habitat, and plantation. Ecotypes can refer to either *S.globulifera* (**glo**) or*S.sp1* (**sp1**); habitat can be either Hilltop (**HT**) or Seasonally flooded (**SF**); Region of provenance (**Prov** .) and plantation can be either east (**E**) or west (**W**).

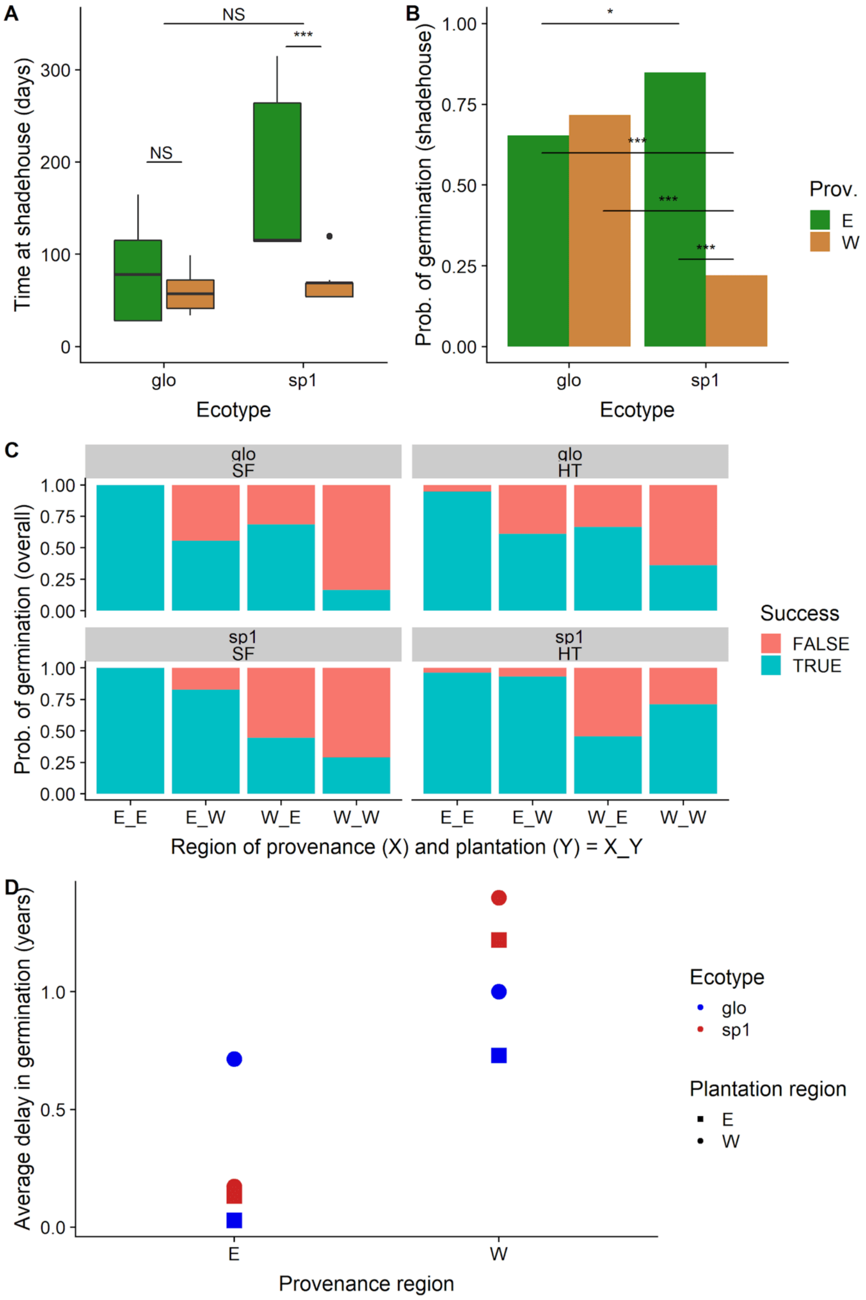


Figure 3: Classification tree of germination and survival of*Symphonia* seeds and juveniles after 5 years according to the variables studied covariates of interest: **Prov_Region**=provenance region (**E** =East; **W** =West),**Plant_Region** = planting region (**E** =East;**W** =West), **Habitat** = planting habitat (**SF** =Season-

nally flooded; **HT** =hilltops),**Ecotype** = ecotype of the mother tree (**globu** =*S.globulifera* ; **sp1** =*S.sp1*). Individual responses (germination, survival, and mortality) were categorised as: **U** , ungerminated at the end of the experiment,**D1-D5** , dead at year 1 to year 5 respectively, **A** , alive at the end of the experiment.

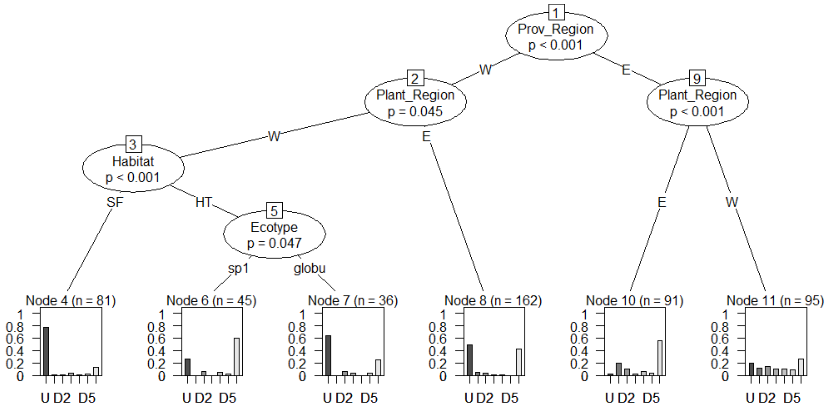


figure 4: Classification tree analyses of juvenile phenotypic traits according to the studied covariates of interest.**Prov_Region** =provenance region (**E** =East;**W** =West), **Plant_Region** = planting region (**E** =East; **W** =West), **Habitat** = planting habitat (**SF** =Seasonnally flooded; **HT** =hilltops),**Ecotype** = ecotype of the mother tree (**glo** =*S.globulifera* ; **sp1** =*S.sp1*). Measured phenotypic traits: **H=** Height at age 5, **RGR_H** =relative growth rate in H; **D=** diametre at age 5 , **RGR_D** = relative growth rate in D; **TNL** =total number of leaves,**RGR_TNL** =relative growth rate in TNL;**HERB_AVE** =average herbivory over the course of the experiment. Only individuals germinated in 2009 (shadowhouse or field) were included. Only individuals alive in 2014 were included for measures at age 5. Only individuals with at least two annual measures were included for RGR analyses.

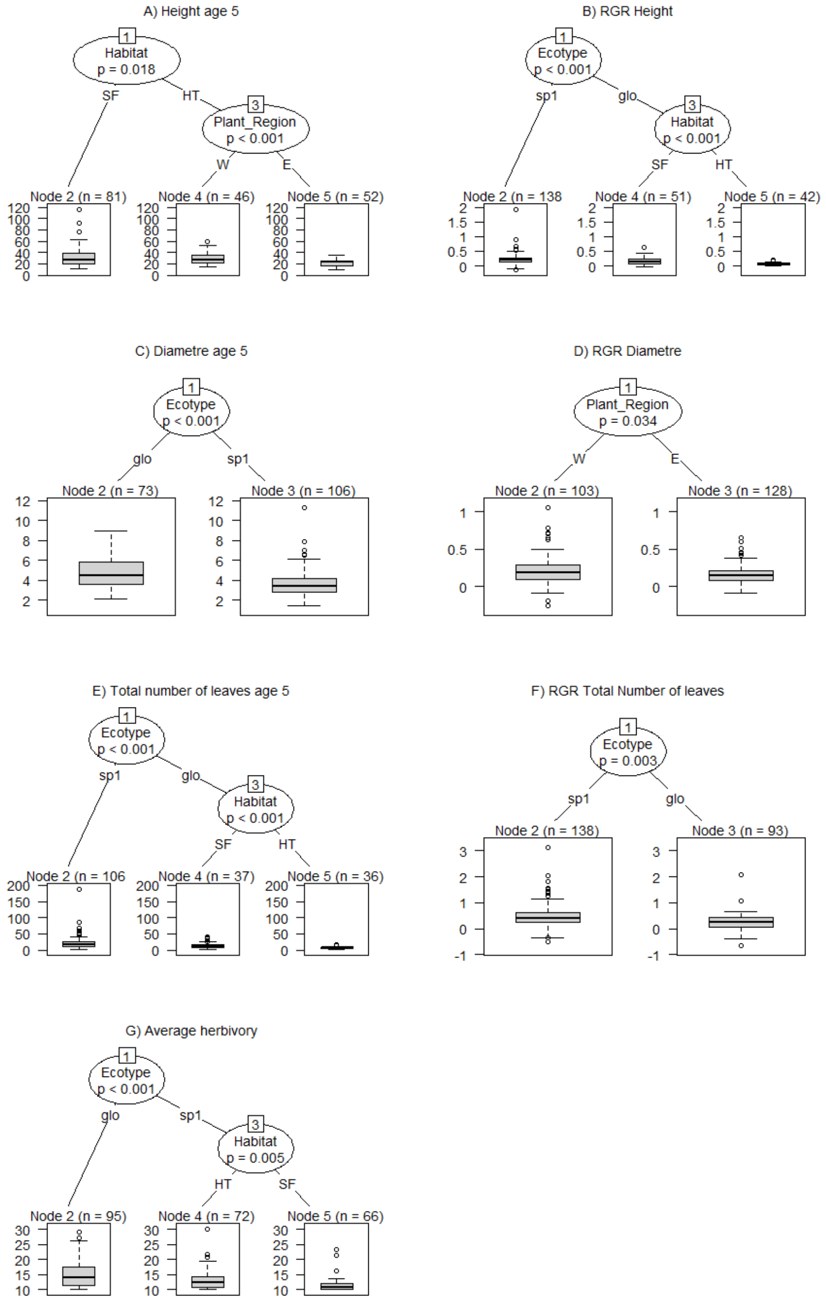


Figure 5: Least square means yearly analysis of growth traits (Height (**H**), Diameter (**D**), Total number of leaves (**TNL**)), and herbivory (**Herb**) of *Symphonia*seedlings. **Age** in years in on the X axes. Log of growth traits and herbivory, and log of growth traits and herbivory at age compared to that at age 0 are on the Y axes. Two comparisons are shown:**Ecotype x Habitat** (a,b,e,f,i,j,m,n) and **Provenance x Plantation** (c,d,g,h,k,l,o,p). Ecotypes: *S. globulifera*(**glo**) and *S. sp1* (**sp1**). Habitats: hilltops (**HT**) and seasonally flooded (**SF**). Provenance: east (**E**) and west (**W**). Plantation: east (**E**) and west (**W**). Groups growing in their 'home' environment relative to the comparison are denoted by a triangle. Groups growing

in 'away' environments relative to the comparison are denoted by circles. Significance: non-significant (**NS**), 0.05 (*), 0.01 (**), 0.001 (***).