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Title: '**Tree demographic performance of European tree species at their hot and cold edges.**'

Running title: 'Demographic performance at climatic edges.'

Georges Kunstler[1], Arnaud Guyennon[1], Sophia Ratcliffe[2,3], Nadja Rüger[4,5], Paloma Ruiz-Benito[6,7], Dylan Z. Childs[8], Jonas Dahlgren[9], Aleksi Lehtonen[10], Wilfried Thuiller[11], Christian Wirth[2,4,12], Miguel A. Zavala[7], Roberto Salguero-Gomez[13].

[1]Univ. Grenoble Alpes, Irstea, UR LESSEM, 38000 Grenoble, France.; [2]Department of Systematic Botany and Functional Biodiversity, University of Leipzig, Johannisallee 21-23, 04103 Leipzig, Germany.; [3]NBN Trust, 14-18 St. Mary's Gate, Lace Market, Nottingham NG1 1PF, UK.; [4]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany.; [5]Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancón, Panama.; [6]Departamento de Biologia y Geologia, Fisica y Quimica Inorganica, Escuela Superior de Ciencias Experimentales y Tecnologia, Universidad Rey Juan Carlos, Tulipan, 28933, Mostoles (Madrid), Spain.; [7]Grupo de Ecologia y Restauracion Forestal, Departamento de Ciencias de la Vida, Universidad de Alcala, Edificio de Ciencias, Campus Universitario, 28805 Alcala de Henares, Madrid, Spain.; [8]Department of Animal & Plant Sciences, The University of Sheffield, Sheffield, UK.; [9]Swedish University of Agricultural Sciences, Umea, 90183 Sweden.; [10]Natural Resources Institute Finland (Luke), Latokartanonkaari 9 FI-00790 Helsinki Finland.; [11]Univ. Grenoble Alpes, CNRS, Univ. Savoie Mont Blanc, CNRS, LECA, Laboratoire d'Ecologie Alpine, F-38000 Grenoble, France.; [12]Max-Planck-Institute for Biogeochemistry, Hans-Knöllstr. 10, 07745 Jena, Germany.[13]Department of Zoology, University of Oxford, 11a Mansfield Rd OX1 3SZ, Oxford, UK.

Species range limits are thought to result from a decline in demographic performance because of unsuitable climate at the edges. However, recent studies reporting contradictory patterns in tree species demographic performance at their edges cast doubt on our ability to predict climate change impacts on species ranges. Here we parameterised integral projection models with climate and competition effects for 27 tree species using forest inventory data from over 90,000 plots across

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Europe. Then, we predicted growth, survival, lifespan, and passage time – the time to grow to a large size – at the hot and cold edges and compared them to the range centre. We found that while growth and passage time of European tree species are constrained at their cold edge, survival and lifespan are constrained at their hot edge. Our study shows a more complicated picture than previously thought with demographic responses that differ between hot and cold edges.

Keywords: "demography, IPM, passage time, vitale rate, range edge"

Introduction

Increasing concerns have emerged regarding potential major redistributions of plant species ranges in the coming decades due to climate change (Zimmermann *et al.* 2013). Indeed, some studies have confirmed that these range shifts are already underway (Chen *et al.* 2011). Range shifts are directly related to changes in demographic rates and population dynamics. Demographic theories propose that if populations are at equilibrium, mean population growth rate (λ) will drop at the species' range edge ($\lambda < 1$) due to alterations in one or more vital rates contributing to λ (Case *et al.* 2005; Holt & Keitt 2005). This prediction is grounded in a long-standing hypothesis in biogeography, known as the 'abundance-centre hypothesis' (hereafter ACH, Brown 1984), which proposes that demographic performance decline at the range edge results in a decrease in abundance. This decline in demographic performance can arise directly because of abiotic constraints (*e.g.* frost) or indirectly because of changes in biotic constraints (*e.g.* competition) (Hargreaves *et al.* 2014; Pironon *et al.* 2017).

The number of studies that have directly tested the ACH with field data on population growth rates, and the vital rates that contribute to them, at the centre and the edge of species range is surprisingly limited. Nonetheless, these studies showed only weak or contradictory support for the ACH. Transplant experiments have shown that population growth rate or some vital rates tend to decline beyond the edge but not necessarily right at the edge (Hargreaves *et al.* 2014; Lee-Yaw *et al.* 2016). For long-lived organisms such as trees, their generation time rules out transplant experiments that would cover their full life cycle. Rather, researchers have to rely on models based

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on natural population monitoring data (see Purves 2009). Only a few studies have used this approach over the full species range and they found no clear evidence of a decrease in demographic performance at the edge (Purves 2009; Thuiller *et al.* 2014; Csergo *et al.* 2017). Some studies also tested the role of biotic interactions and found only weak evidence for the idea that biotic interactions constrain the demographic performance at the edge and that this effect is stronger for edges in productive environments than in unproductive environments (Cahill *et al.* 2014; Hargreaves *et al.* 2014; Louthan *et al.* 2015).

Our limited understanding of the demographic underpinnings of species ranges in long-lived organisms represents a major handicap to forecast climate change impacts on trees. Yet, trees play a crucial role in the biosphere by sheltering a significant proportion of biodiversity and carbon stocks and contributing to the livelihoods of local populations (van der Plas *et al.* 2018). Existing studies cover only a limited number of species and rather restricted areas of the species ranges, making it difficult to explain what drives the large variability in the demographic performance observed between edges and species. Several characteristics of the edges and species are likely to explain this variability. Firstly, the decline in demographic performance is likely to vary depending on the type of biophysical constraints at the edge (Gaston 2009). For instance, demographic constraints could differ between drought- and cold-limited edges because tolerance to different abiotic stress requires different adaptative strategies (Niinemets & Valladares 2006). Secondly, the decline in demographic performance is likely to vary depending on the vital rate considered (Gaston 2009; Hargreaves *et al.* 2014). Finally, the constraints on the demographic performance at the edge are likely to vary with species' physiological strategy (Anderegg *et al.* 2019). These physiological differences can be captured by species' climatic optimum and by functional traits related to species physiological climate response, such as wood (Chave *et al.* 2009) or leaf characteristics (Wright *et al.* 2017).

Here, we explore these questions at the continental scale for 27 European tree species using forest inventory data documenting survival and growth of more than 1 million adult trees. First, we fitted survival and growth models to capture climate and competition impacts on these vital rates. Second, we built size-structured population models using integral projection models (IPM) (Ellner *et al.* 2016) to evaluate demographic performance based on four metrics: two vital rates - growth and survival, and two life trajectory metrics - mean lifespan and passage time (time to grow from

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small to large size). We then used these models to compare demographic performance at the hot or cold edges with the performance at the range centre for each species. Using these metrics we tested the following hypotheses: (1) demographic performance is reduced at the edge compared to the centre for one or more metric; (2) the decline in demographic performance is stronger with competition than without because competition restricts the demographic performance at the edge; (3) different metrics are reduced at the hot and the cold edge due to different biophysical constraints operating at these edges; demographic performance at the edges depends on (4) species climatic optimum and (5) functional traits related to species' climatic response (wood density, leaf economic spectrum traits, leaf size, and xylem vulnerability to embolism).

Materials and Methods

Forest inventory

We used the European forest inventory (NFI) data compiled in the FunDivEUROPE project (Baeten *et al.* 2013; Ratcliffe *et al.* 2015). The data covers 91,528 plots and more than 1 million trees in Spain, France, Germany, Sweden and Finland. NFIs record information on individual trees in each plot, including species identity, diameter at breast height (dbh), and status (alive, dead, harvested or recruited). Plot design varies between countries but generally plots are circular with variable radii depending on tree size (see Supplementary Materials). The minimum dbh of trees included in the dataset was 10 cm. Plots were remeasured over time allowing estimations of individual growth and survival. Only the French NFI is based on a single measurement but includes measurement of radial growth with cores and estimation of time since death allowing to estimate these vital rates. We selected species with > 2,000 individuals and > 500 plots, to ensure a good coverage of their range, growth, and survival. We excluded exotic species for which the distribution is mainly controlled by plantation operations. For the demographic analyses, we also excluded all plots with records of harvesting operations or disturbances between the two surveys, which would otherwise influence our estimation of local competition.

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Climate variables

We used two bioclimatic variables known to control tree demography (Kunstler *et al.* 2011): (1) the sum of degree days above 5.5 °C (*sgdd*), and (2) the water availability index (*wai*). *sgdd* is the cumulative day-by-day sum of the number of degrees > 5.5 °C and is related to the mean annual temperature and the length of the growing season. It was extracted from E-OBS, a high resolution (1 km^2) downscaled climate data-set (Moreno & Hasenauer 2016) for the years between the two surveys plus two years before the first survey. *wai* was computed using precipitation (P, extracted from E-OBS) and potential evapotranspiration (PET) from the Climatic Research Unit (Harris *et al.* 2014) data-set, as $(P - PET)/PET$ and is related to the water availability.

Integral projection models

An IPM predicts the size distribution, $n(z', t+1)$, of a population at time $t+1$ from its size distribution at t, $n(z,t)$ (with z the size at t and z' the size at $t+1$), based on the following equation (Easterling *et al.* 2000; Ellner *et al.* 2016):

$$n(z', t+1) = \int_L^U K(z', z) n(z, t) dz \tag{1}$$

The kernel $K(z', z)$ can be split into the survival and growth kernel ($P(z', z)$) and the fecundity kernel ($F(z', z)$), as follow $K(z', z) = P(z', z) + F(z', z)$. $P(z', z)$ is defined as $P(z', z) = s(z)G(z', z)$ and represents the probability that an individual of size z survives between t and $t+1$ and reaches the size z'. The size of the individuals z can range between L and U. NFI data do not provide direct information on tree fecundity, thus our models describe the fate of a cohort (a cohort IPM for individuals with dbh $>= 10$ cm) by focusing only on $P(z', z)$ (in Supplementary Materials, we provide a sensitivity analysis of tree population growth to fecundity)

For each of the 27 species, we fitted growth and survival functions depending on tree size, the two climatic variables (*sggd* and *wai*) and local competition estimated as the sum of basal area of competitors (following Kunstler *et al.* 2011). The shape of the response curve for these variables and the type of interaction between climate and size and climate and competition can have a large impact on vital rates predictions. To account for such uncertainties, we re-sampled 100 times 70% of the data to fit the model and select the best type of response curve and interactions based on

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the Akaike information criteria (*i.e.*, lowest AIC) (Burnham & Anderson 2002). Because there were fewer plots in extreme climatic conditions, we resampled the data with a higher probability of sampling plots in extreme climatic conditions for the given species. Then we used the remaining 30% of the data to evaluate the goodness of fit of the growth and survival models. Goodness of fit and response curves of growth and survival models are presented in the Supplementary Materials (Figures 4 to 13).

Growth model

After preliminary exploration, we selected two alternative shapes of the climatic response curves: asymptotic or quadratic polynomial corresponding to the equations 2 and 3. These choices correspond to two alternative biological models: (i) either all species have their optimum at high water availability and sum of degree days; or (ii) species have bell-shaped climate response curves with different optima along the climatic variables:

$$\begin{aligned} log(G_{i,p}) =& a_0 + a_{0,p} + a_1\, D_i + a_2\, log(D_i) + \\ & a_3\, BA_i + a_4\, \frac{1}{sgdd_p} + a_5\, \frac{1}{wai_p} + \varepsilon_i \end{aligned} \tag{2}$$

$$\begin{aligned} log(G_{i,p}) =& a_{0,c} + a_{0,p} + a_1\, D_i + a_2\, log(D_i) + a_3\, BAi + \\ & a_4\, sgdd_p + a_5\, sgdd_p^2 + a_6\, wai_p + a_7\, wai_p^2 + \varepsilon_i \end{aligned} \tag{3}$$

Where $G_{i,p}$ is the annual diameter growth of tree i in plot p, D_i is the dbh of tree i, BA_i is the sum of basal area of competitors of tree i per ha, $sgdd_p$ is the sum of growing degree days, wai_p is the water aridity index, a_0 to a_7 are estimated parameters, and $a_{0,p}$ is a normal random plot effect accounting for unexplained variation at the plot level. The intercept $a_{0,c}$ is country specific to account for differences in protocol between NFIs and ε_i is the unexplained tree level variability following a normal distribution. We fitted the models in R-cran separately for each species (R Core Team 2019) using the 'lmer' function ("lme4" package, Bates *et al.* 2015). We also tested models with interactions between the climatic variables - $1/sgdd_p$ and $1/wai_p$ for model (2) and $sgdd_p$ and

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wai_p for model (3)) - and size (D_i and $log(D_i)$ and the climatic variables and competition.

Survival model

Survival models were fitted with a generalised linear model with a binomial error. The predictors and interactions explored were the same as in the growth model. To account for variable survey times between plots we used the complementary log-log link with an offset representing the number of years between the two surveys (y_p) (Morris *et al.* 2013). We fitted the model in R-cran using the 'glm' function. We did not include a random plot intercept because in most plots no individuals died between the surveys, making the estimation of the random plot effect challenging.

Tree harvesting

Although we excluded plots with evidence of harvesting between the two surveys to fit the survival functions, most European forests are subject to management, which has a strong impact on population dynamics (Schelhaas *et al.* 2018). Harvesting of dying or damaged trees is probably resulting in an underestimation of the natural mortality rate. To make sensible predictions with our IPMs it was thus necessary to incorporate a harvesting rate to prevent an overestimate of tree lifespan. We set a mean harvesting rate, estimated across all species and inventories, as 0.5 % per year. We did not model size and climate dependence of the harvesting rate, as we focused on climatic and not anthropogenic constraints on tree demography.

Prediction of demographic metrics at the edges and centre of species range

Species distribution

To identify the edge of a species range, a simple representation of its distribution is necessary. Across Europe, there is a strong correlation between *sgdd* and *wai*, and so we described species ranges along a single climatic axis corresponding to the first axis (PC1) of the PCA of *sgdd* and *wai* (Supplementary Materials, Figure 3). Species showed a clear segregation along this climatic axis in Europe (Figure 1). Based on the coordinates on PC1 of the plots where the species was present, we identified the centre of the range as their median value, the hot and dry edge (hereafter hot edge) and the cold and wet edge (hereafter cold edge), respectively, as their 5% and 95% quantiles.

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To evaluate which species' edges corresponded to an actual limit in the species distribution and not just to limits in the coverage of the data, we fitted species distribution models with BIOMOD2 (Thuiller *et al.* 2009). To do so we used presence/absence data covering all Europe (Mauri *et al.* 2017) (see Supplementary Materials). For comparison of the demographic performance at the edge *vs.* the centre of the distribution, we retained only the edges with a at least 10% drop in the probability of presence of the species predicted by the SDM (Figure 1).

Demographic metrics

To evaluate how individual performance varied between the range centre and the edges, we derived four metrics representing key dimensions of population performance. The first two metrics were related to individual vital rates, and were defined by the growth and survival of 15 cm dbh individuals (focusing on small individual because of their strong effect on population dynamics, Grubb 1977). The last two metrics were related to individual lifetime performance integrating the vital rates in the IPM, and were defined by the mean lifespan of a 10 cm dbh individual and the passage time of a 10 cm dbh individual to 60 cm. The details of the numerical methods used to compute lifespan and passage time from the IPM are provided in the Supplementary Materials. Model diagnostics showed that our numerical approach was not sensitive to the number of size bins retained for the IPM (*i.e.* # bins > 800 , see Figure 14 in Supplementary Materials).

We predicted the four demographic metrics at the centre and the hot and cold edges of the species range using their positions on the climatic axis (each position on PC1 is associated with a unique combination of *sggd* and *wai*). We integrated uncertainty into our estimate by deriving a prediction for each of the 100 re-sampled growth and survival models (see above). Because competitive interactions may also be important in controlling species demography at the edge of the range (Louthan *et al.* 2015), we made these predictions either without competition (by setting BA to 0) or with a high level of competition (by setting BA to $30m^2ha^{-1}$, corresponding to a closed forest).

Analysis of the relative demographic performance at the edges

For each demographic metric (m) we computed the relative difference in the metric at the edge (hot or cold) *vs.* the centre as: $\Omega^m_{edge} = (m_{edge} - m_{centre})/m_{centre}$. Firstly, for each metric, we tested

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whether species demographic performance declines at the edge compared to the centre (hypothesis 1) by fitting a mixed model to m as function of the range position type (edge *vs.* centre) and a random species effect (with the function *lmer* in *lme4*). Secondly, we tested whether the effects were different without or with competition (hypothesis 2). We ran this analysis separately for hot and cold edges to see how demographic responses differ between them (hypothesis 3). Thirdly, we explored whether Ω^{m}_{edge} was dependent on the climatic optimum of the species (the median position on PC1) (hypothesis 4) by fitting Phylogenetic generalised least squares (PGLS) regression using a phylogeny extracted from Zanne *et al.* (2014). We accounted for the uncertainty in the demographic response by including a weight proportional to the inverse of the variance of Ω^{m}_{edge}. The PGLS regression with maximum likelihood estimation of Pagel's lambda (a measure of the phylogenetic signal ranging between 0 and 1) did not always converged. In those cases we fitted a PGLS model with a Brownian model (Pagel's lambda set at 1). We retained only the regressions that were both significant (after a Bonferroni correction to account for multiple comparisons) and had a non-negligible magnitude of the effect (Camp *et al.* 2008). The magnitude of the effect was considered negligible when the confidence interval of the effect size intercepted the interval -0.10 and 0.10 (Camp *et al.* 2008). Effect sizes were computed as the standardised slope (Schielzeth 2010).

Finally, we explored the effect of four functional traits (see below) that are known to influence tree response to climate (hypothesis 5), by testing the link between each trait individually and Ω^{m}_{edge} with the same PGLS regression approach. We selected: (i) wood density, which is related to drought and temperature response (Chave *et al.* 2009; Stahl *et al.* 2014); (ii) the leaf economic spectrum (LES) because species at the conservative end of the spectrum are thought to be more tolerant to extreme climate (Reich 2014); (iii) leaf size, which is related to plant response to water stress and frost (Wright *et al.* 2017); and (iv) xylem vulnerability to embolism measured by the water potential leading to 50% loss of xylem conductivity, Ψ_{50}, a strong predictor of drought-induced mortality (Anderegg *et al.* 2016). LES is based on the covariance of specific leaf area, leaf lifespan, and leaf nitrogen per mass (Wright *et al.* 2004). We used leaf nitrogen per mass (N_{mass}), as it was the LES trait with the best coverage across our species. Trait data were sourced from open databases (Wright *et al.* 2004, 2017; Chave *et al.* 2009; Choat *et al.* 2012; Maire *et al.* 2015).

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Results

Demographic responses differ between edge types and metrics

Across the 27 species we found evidence of a significant decrease in growth and increase in passage time (longer time needed to grow from 10 to 60 cm) at the cold edge in comparison with the centre of the distribution but no effect at the hot edge (Figure 2). In contrast, at the hot edge, we found evidence of a significant decrease in both tree survival and lifespan (Figure 2). This is consistent with the hypothesis that at least one metric will decline in performance at the edge, and that different metrics are affected depending on the edge type. In contrast, we found that lifespan was significantly longer at the cold edge than at the centre of the distribution (Figure 2). Generally, these patterns were unaffected by local competition (Figure 3), however, it is important to note that the increase in lifespan at the cold edge became non-significant at high levels of competition, which may show that competition constrains performance at the edge for some species.

Behind the overall demographic response at the edge, there were large variations between species. For each metric and edge type we found species showing a decrease and species showing an increase in performance (Supplementary Materials; Figures 16 to 23).

Demographic responses vary with species climatic optimum

Growth response at the hot and cold edges was related to the climatic optimum of the species; species with climatic optimum in hot climates were more constrained at their hot edge while species with climatic optimum in cold climates were more constrained at their cold edge. This result is depicted in Figure 4 by a positive relationship between Ω^{m}_{edge} for growth at the hot edge and the median climate of the species and a negative relationship Ω^{m}_{edge} for the growth at the cold edge. The same pattern is visible for passage time, but in the opposite direction, because passage time is longer when growth is slower (Figure 4). The responses of Ω^{m}_{edge} for survival and lifespan were much weaker or null. We found a negative relationship for survival at the hot edge, which was largely related to a few extreme species, and no effect for lifespan (Figure 4).

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Weak links between demographic response and species traits

N_{mass} had the strongest relationship with Ω^{m}_{edge} of all the traits we tested. At the hot edge, species with high N_{mass} experienced a stronger decrease in their survival and lifespan than species with a low N_{mass} (Figure 5). In contrast, at the cold edge, species with low N_{mass} experienced a stronger decrease in their survival and lifespan than species with high N_{mass} (Figure 5). In addition, species with high N_{mass} had less limitation of their growth at the hot edge than species with low N_{mass} (Figure 5).

Relationships between Ω^{m}_{edge} and wood density, leaf size and xylem vulnerability to embolism were generally weak (Supplementary Materials, Figures 25 to 27). Species with small leaf area had better survival, growth, and passage time at the cold edge than large leafed species (Supplementary Materials, Figure 27) and species with high Ψ_{50} experienced a stronger decrease in their growth at the hot edge than species with low Ψ_{50}. However, the pattern was driven by a few species (Supplementary Materials, Figure 26).

Discussion

Our analysis based on pan-European forest inventory data and integral projection models of 27 species, found weak support for the ACH prediction that demographic performance is lower at the edge than at the centre of the species range. Instead, decline in demographic performance was strikingly different between the cold and the hot edges. At cold and wet edges, growth and passage time were constrained, whereas at hot and dry edges, survival and lifespan were constrained. Beyond these general patterns, we found important variability between species in their demographic performance at the edge, which was partially explained by species' climatic optimum and traits.

Different demographic responses at the hot and the cold edge

We found mixed support for the ACH, not all the demographic metrics were limited at the edges and patterns were variable between species. This is consistent with observational studies that found limited evidence of a relationship between species demography and their distribution. For instance, both Thuiller *et al.* (2014) and Csergo *et al.* (2017) found limited correlation between

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plants demographic performance and probability of presence. In addition, Purves (2009) reported mixed evidence of a decrease in demographic performance at the south and north edges of North American tree species.

Growth and passage time were constrained at the cold edge in comparison with the centre of the species distribution. This is consistent with studies on North American tree species, that found a decrease in growth at the cold edge in adult trees (Purves 2009) and juveniles (Ettinger & HilleRisLambers 2017; Putnam & Reich 2017). In contrast with the ACH, we found a tendency for a slightly faster growth at the hot edge than at the centre, which has also been reported in North American trees (Purves 2009; Ettinger & HilleRisLambers 2017; Putnam & Reich 2017).

At the hot and dry edge, tree survival and lifespan were lower than at the centre of the range. In contrast, Purves (2009) found no such decrease in survival at the hot edge of eastern North American species. This difference could be explained by the fact that the hot edge of most European species corresponds to both a hot and a dry climate, whereas in eastern America the hot edge is less constrained by drought (Zhu *et al.* 2014). We found that lifespan was longer at the cold edge than at the centre of the distribution. This is in contradiction with the classical view that survival is constrained in cold climates and the results of Purves (2009). Given that tree growth rate is constrained at the cold edge, this longer lifespan could be explained by a tradeoff between tree growth rate and tree longevity (both inter- and intra-specific, see Black *et al.* 2008; Di Filippo *et al.* 2015) and the observation that survival rate correlates negatively with site productivity (Stephenson *et al.* 2011).

Lack of competition effect

Numerous studies have proposed that competitive interactions could be crucial in setting demographic limits, particularly at the productive edge (see Hargreaves *et al.* 2014; HilleRisLambers *et al.* 2013; Louthan *et al.* 2015; Alexander *et al.* 2016; Ettinger & HilleRisLambers 2017; Jump *et al.* 2017). In our analyses, we explored the effect of competition by comparing the demographic metrics estimated without competition or with a high level of competition. Despite the strong effects of competition on both growth and survival and interactions between competition and climate, competition did not influence the demographic response at the edges. The only evidence of competition contraints at the edge that we found was that without competition; lifespan increased at

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the cold edge only in the absence of competition.

Three main reasons could explain the lack of competitive effect on the demographic response at the edge in our study. Firstly, we did not differentiate between intra- and inter-specific competition, whereas inter-specific competition might have the strongest impact at the edge (Alexander *et al.* 2016). Secondly, we did not analyse competitive effect on population growth rate, it was thus not possible to evaluate whether competitive exclusion could be at play at the edges (Chesson 2018). Thirdly, properly estimating competitive effect with observational data is notoriously difficult (Tuck *et al.* 2018).

Strong effect of species median climate on growth response at the edge

We found that the hotter the centre of the species range the greater was the constraints on growth and passage time at its hot edge. The same pattern was found with the cold edge and the species climate optimum proximity to cold extreme. This is in agreement with the general pattern of vegetation productivity in Europe, which is at its maximum in temperate climates where both drought and cold stress are limited (Jung *et al.* 2007).

Weak traits effect on species demographic response at the edge

Part of the variation in the demographic response at the edge was related to N_{mass}, a key dimension of the leaf economic spectrum. An important difficulty in the interpretation of these results is that our understanding of the link between leaf economic traits and climate is limited. Multiple mechanisms, some of them contradictory, have been proposed to explain the link between leaf N and climate. For instance, it is generally considered that species with low N_{mass} have a more conservative strategy of resource use and perform better in stressful conditions than species with high N_{mass} (Reich 2014). In agreement with this finding, we found that species with low N_{mass} had a better survival and lifespan at the hot edge. In contrast, high leaf N has been linked with photosynthesis tolerance to drought and low temperature because of higher enzyme activities (Wright *et al.* 2003; Reich & Oleksyn 2004). Consistent with this mechanism, we found that species with high N_{mass} had a better survival and lifespan at the cold edge and a better growth at the hot edge.

We found limited relationships between leaf size or xylem vulnerability to embolism and de-

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mographic response, which was surprising as the mechanisms related to climate response are better understood for these traits. Smaller leaves were related to a longer lifespan at the hot edge and a better survival, growth and passage time at the cold edge. This in agreement with Wright *et al.* (2017) who proposed that large leaves are disadvantaged in hot and dry climates because their transpiration rate during the day is too high and are disadvantaged in cold climate because they have greater risks of reaching critical low temperatures during the night. Anderegg *et al.* (2019) also reported weak link between traits and drought related mortality at the edge, with only an effect for xylem vulnerability to embolism. The effect was, however, that drought adapted species experienced higher drought mortality at the edge.

On the challenge of connecting population dynamics and species ranges

Based on our results, it is difficult to conclude if there is a clear decrease in population growth rate at the edges. A key limitation is that our analysis did not include the regeneration phase, which is thought to be a bottleneck in tree population dynamics (Grubb 1977). In the Supplementary materials, we provide an evaluation of the importance of this phase for tree population growth rate with an elasticity analysis of matrix population models extracted from the COMPADRE Plant matrix database (Salguero-Gómez *et al.* 2015). The analysis shows that the regeneration and adult phases were equally important (see Figure 29 in Supplementary Materials). Our analysis thus captures an important part of a tree's life cycles. However, we can not rule out the possibility that the regeneration phase has a disproportional importance for the dynamics at the edge, as several studies have shown that this phase is extremely sensitive to climate [Clark *et al.* (2014);Defossez-2016]. Integrating regeneration in IPMs is challenging because we have much less data on this stage (Needham *et al.* 2018).

It is also important to keep in mind that species ranges are not necessarily related to the mean population growth rate but rather to its temporal variability and the population resilience because they control extinction risk (Holt *et al.* 2005). Another explanation is that suitable habitats where population growth rates are unaffected might exist up to the edge due to the presence of suitable microsites (Cavin & Jump 2017). In this case, the species ranges arise because the fraction of suitable habitats available to the metapopulation decrease (Holt & Keitt 2000). Finally, tree species distributions might not be in equilibrium with the current climate. This could be because species

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are either still in the process of recolonising from their ice age refugia (Svenning & Skov 2004) or already affected by climate change. Such disequilibrium should however be visible by better performance at the cold edge (Talluto *et al.* 2017) and we found no evidence of this in our results.

Synthesis

Our field study shows that trees' demographic responses at range edges are more complex than predicted by the ACH. Here, the patterns of demographic response of the 27 European tree species varied between their hot and cold edges. We only found strong evidence of demographic limits for edges occurring in extreme conditions (hot edges of hot-distributed species and cold edges of cold-distributed species). Our findings open an important perspective, as they show that one should not expect the same demographic response at the hot *vs.* the cold edge and that we need to refine predictions of climate change impacts in function of the species and edge characteristics.

Acknowledgments

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FIGURES

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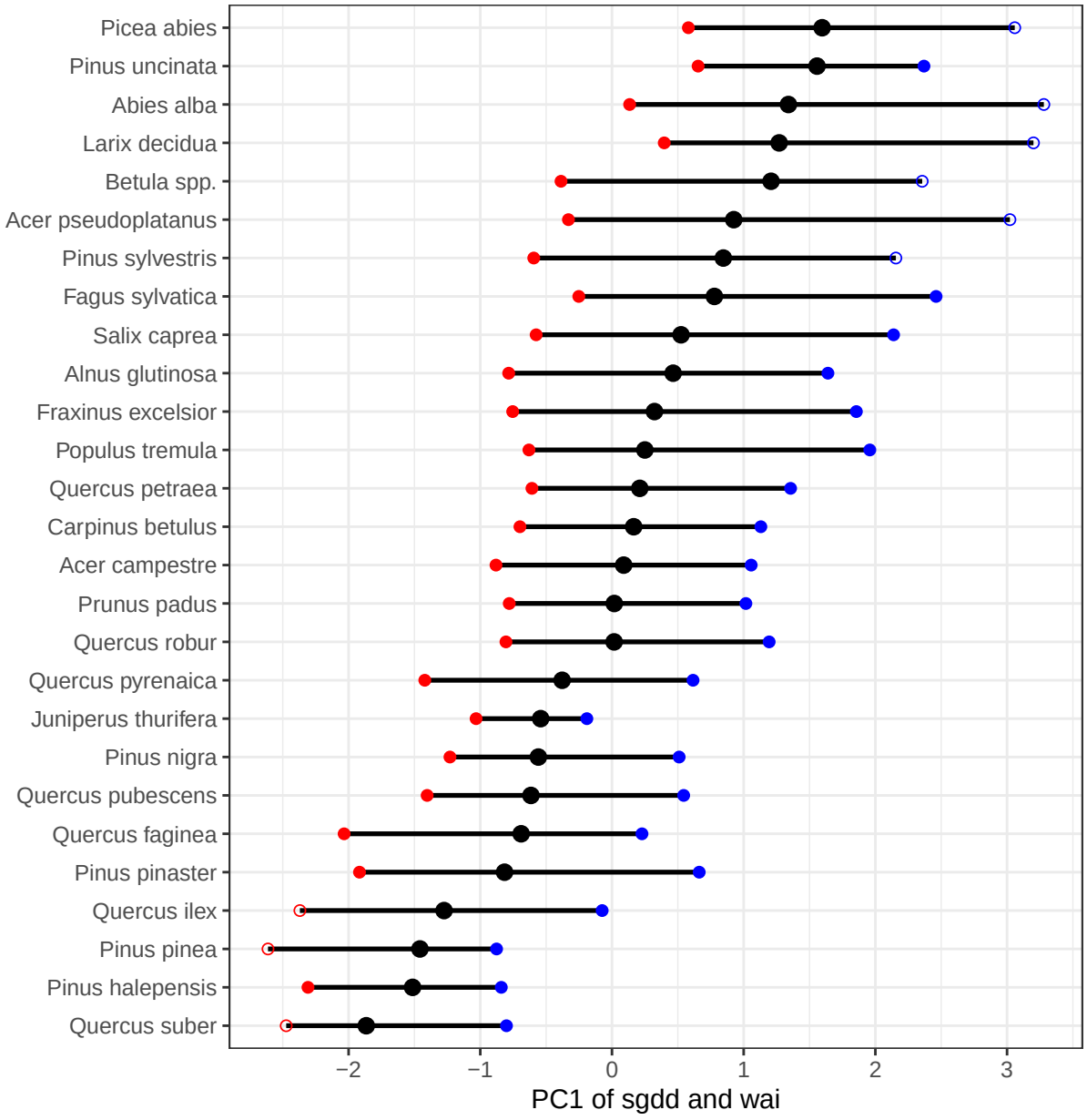

Figure 1: Species distribution along the axis one of the PCA of the two climatic variables sgdd and wai. The centre of the species distribution along this axis is represented by a black circle and the hot and dry edge and the cold and wet edge by red and blue circle respectively. Filled circles represent edges with a clear drop of the probability of presence that were selected for the analysis.

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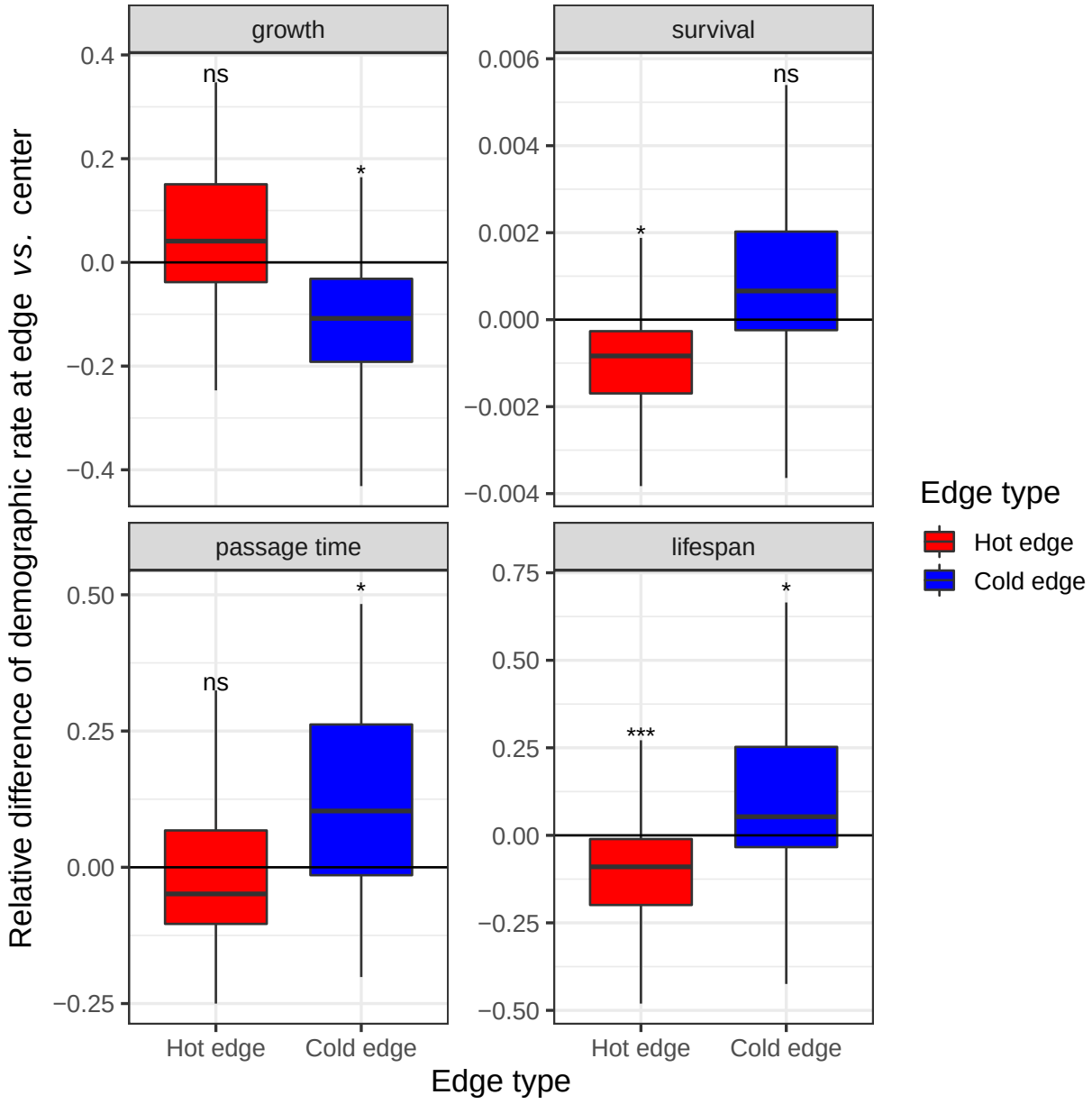

Figure 2: **Differences in the demographic metrics at edge *vs.* the centre of the distribution (/Users/kunstler/Dropbox/sAPROPOS/sAPROPOS_ForInv/figures/Demo_diff_resample_overall_sp_best2.pd**
The box-plot of the relative difference between the edge and the centre computed over the 100 data resampling and the 27 species is represented for the four demographic metrics (annual diameter growth and survival for an individual 15cm in diameter, passage time from 10cm in diameter to 60cm in diameter and lifespan of tree 15cm in diameter) and the two edge types (hot in red, cold in blue). The p value of the test for the difference in each demographic metric and edge typ is presented at the top of the box-plot (ns : non significant, * : p value < 0.05, ** : p value < 0.01, *** : p value < 0.001). The p value was computed with a mixed model with species as a random effect (see Methods for details).

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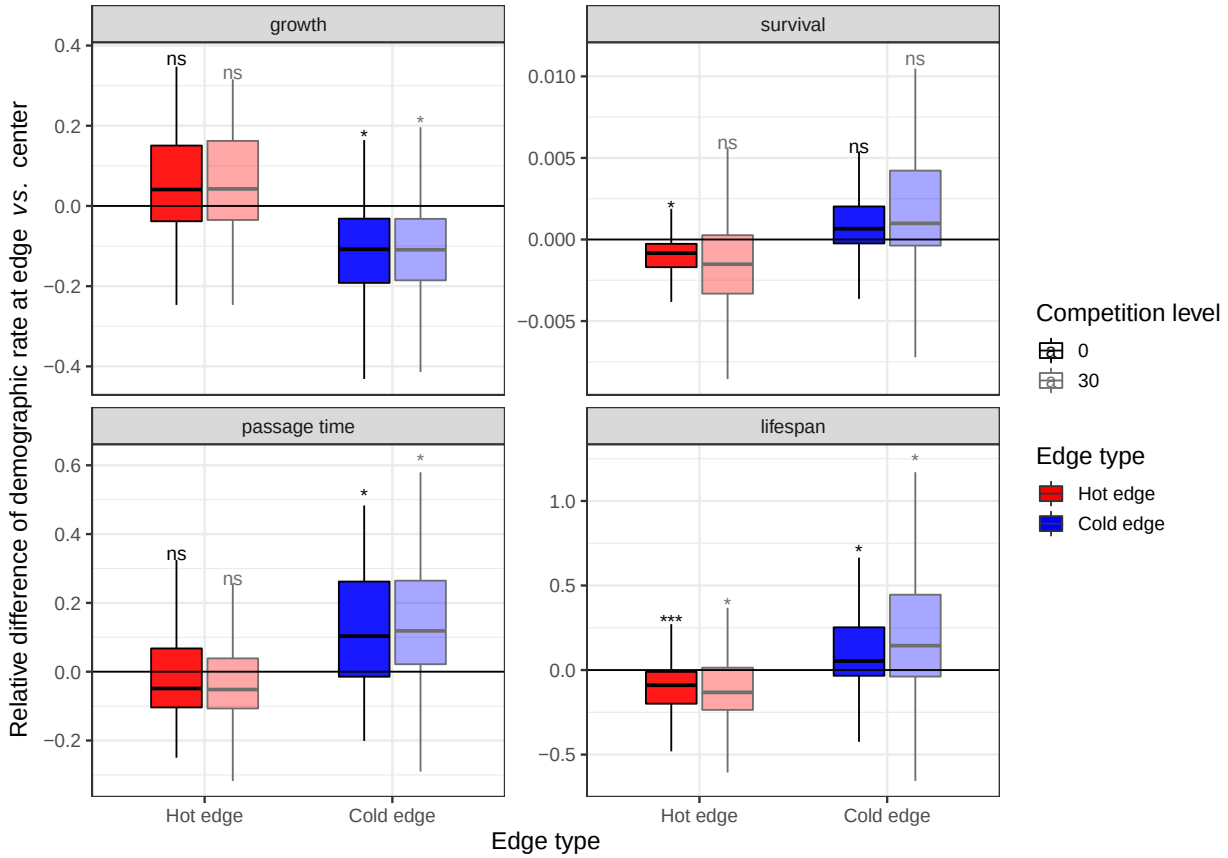

Figure 3: **Differences in the demographic metrics at edge *vs.* the centre of the distribution (/Users/kunstler/Dropbox/sAPROPOS/sAPROPOS_ForInv/figures/Demo_diff_resample_overall_sp_BATOTc without and with a high level of competition.** The box-plot of the relative difference between the edge and the centre computed over the 100 data resampling and the 27 species is represented for the four demographic metrics (annual diameter growth and survival for an individual 15cm in diameter, passage time from 10cm in diameter to 60cm in diameter and lifespan of tree 15cm in diameter), the two edge types (hot in red, cold in blue), and the two levels of competition (without competition: basal area of competitors, $BA = 0$, no transparency, with a high level of competition: basal area of competitors, $BA = 30m^2\,ha^{-1}$ color transparency). The p value of the test for the difference in each demographic metric and edge type is presented at the top of the box-plot (ns : non significant, * : p-value < 0.05, ** : p-value < 0.01, *** : p-value < 0.001). The p-value was computed with a mixed model with species as a random effect (see Methods for details)

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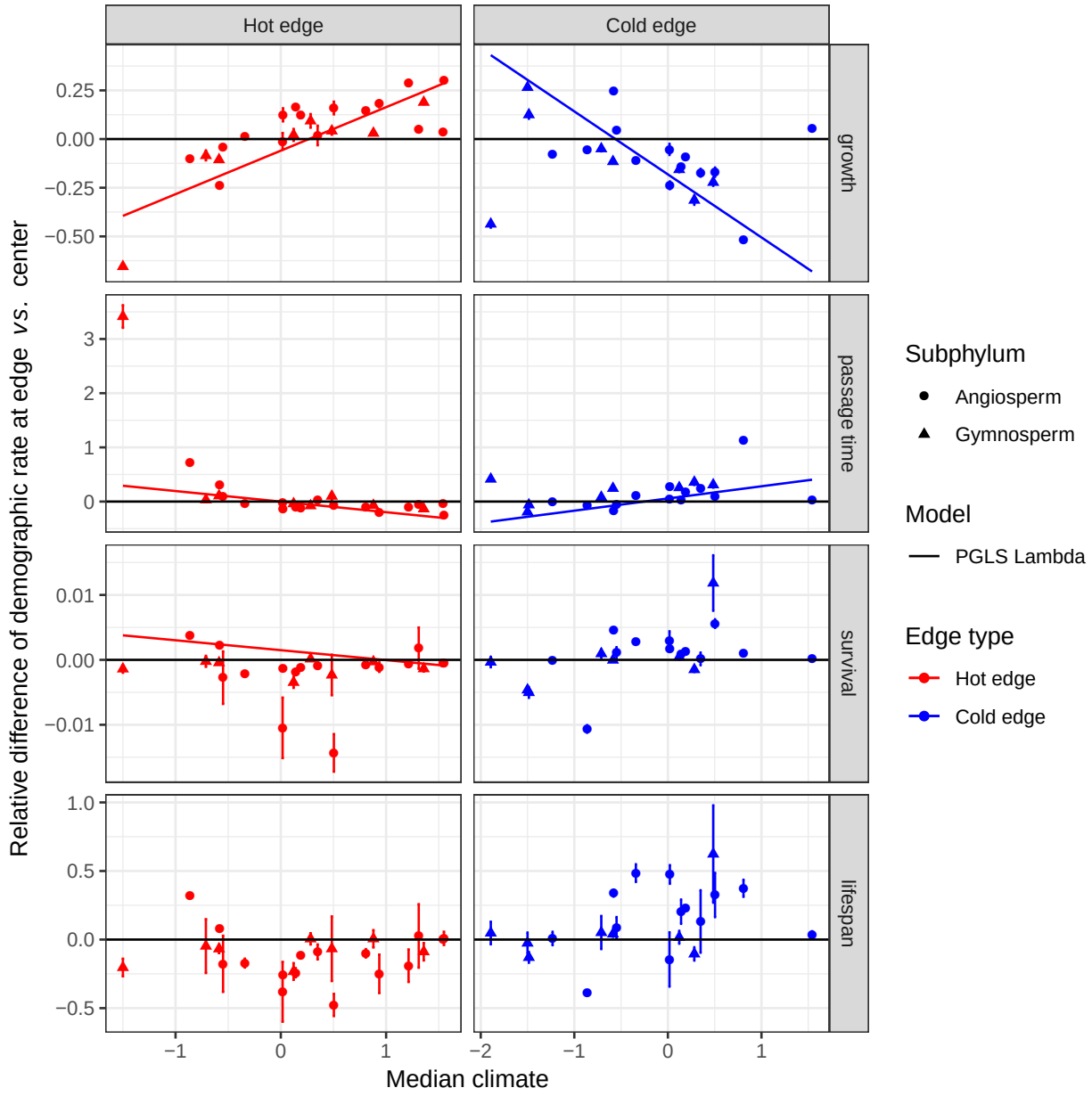

Figure 4: **Changes in demographic responses at the edge (/Users/kunstler/Dropbox/sAPROPOS/sAPROPOS_ForInv/figures/Demo_diff_resample_PC1_lm_overall_sp_ in function of species climatic optimum.** Species demographic response at the edge - measured as the relative differences of the demographic metrics at edge *vs.* the centre of the distribution - in function of the median position of the species on the first axis of the climate PCA. For each species the mean (point) and the 95% quantiles (error bar) of the demographic response over the 100 data resampling is represented for both the hot (red) and the cold (blue) edges. Phylogenetic generalised least squares (PGLS Lambda) regressions are represented only for significant relationship with a non negligible magnitude of the effect. Gymnosperm and angiosperm species are represented with different symbols.

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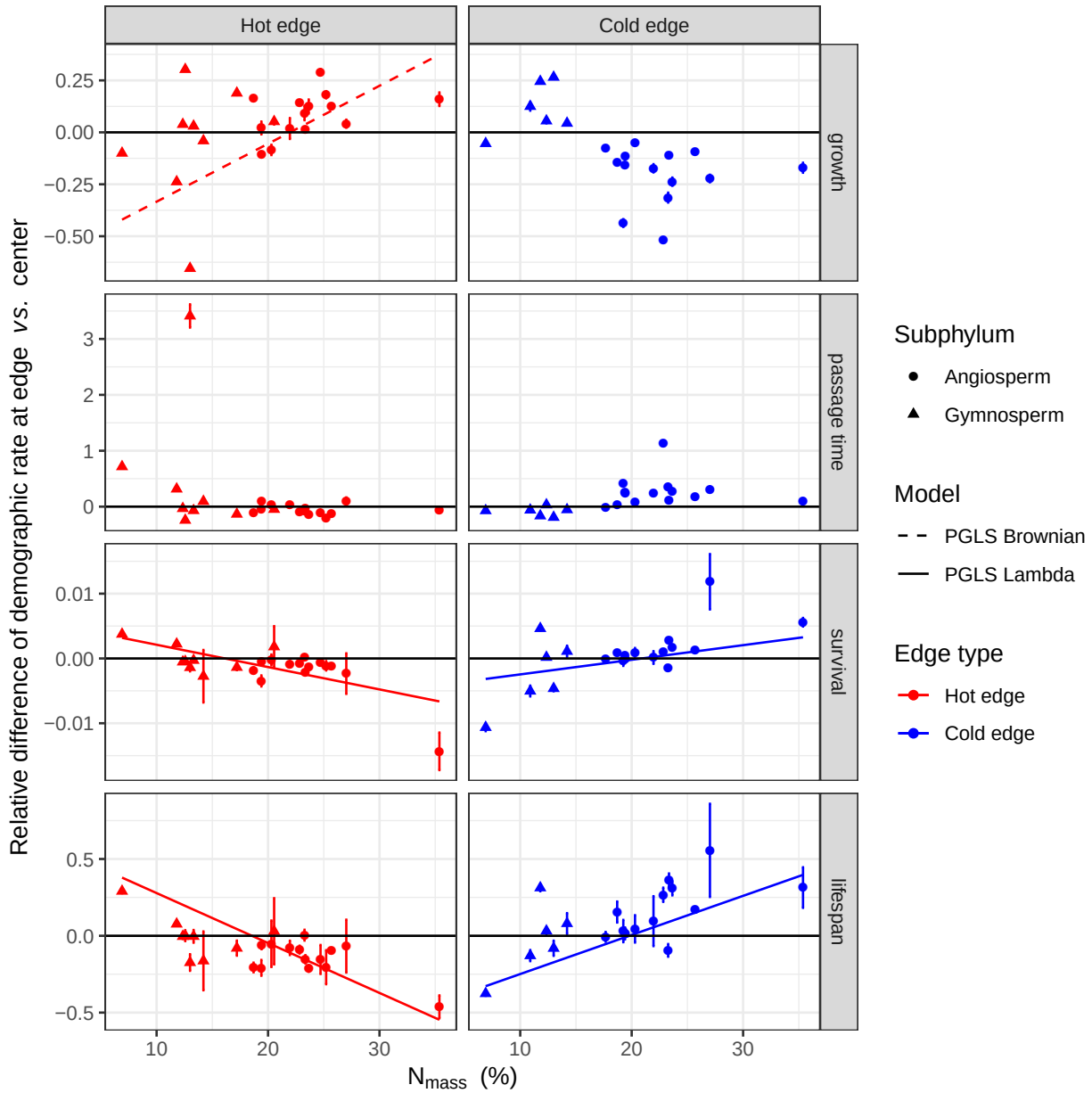

Figure 5: **Changes in demographic responses at the edge (/Users/kunstler/Dropbox/sAPROPOS/sAPROPOS_ForInv/figures/Demo_diff_resample_Nmass_lm_overall_ in function of species leaf N per mass.** Species demographic response at the edge - measured as the relative differences in the demographic metric at edge *vs.* the centre of the distribution - as a function of species leaf nitrogen per mass. For each species the mean (point) and 95% quantiles (error bar) of the demographic response over the 100 data resampling is represented for both the hot (red) and the cold (blue) edges. Phylogenetic generalised least squares (PGLS) regressions are represented only for significant relationship with a non negligible magnitude of the effect (see details in caption of Figure 4).

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