Freie Universität Bozen
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unibz

PhD in Mountain Environment and Agriculture
(xxxiii cycle)

PhD Dissertation

Meta-analyses upon the intraspecific plant trait variability within the environmental and geographic space

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Year 2020

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1 Summary

Summary

Quantifying plant intraspecific trait variation and fitness across species distribution ranges is key to understand population dynamics and local extinctions in the face of global environmental change. Despite the large amount of primary data available in the ecological literature and publicly available data repositories, quantitative syntheses addressing generalities and dissimilarities of such patterns across different species worldwide are still lacking.

In this PhD dissertation, I report three studies using meta-analytical approaches to quantify cross-species patterns of plant intraspecific trait variation within environmental and geographic space. A meta-analysis describing the intraspecific response of morpho-physiological leaf traits along elevational gradients is presented in Chapter I. Afterwards, I report a meta-analysis upon survival and intraspecific trait variation following reciprocal transplants within the elevational range of different plant species in Chapter II. Finally, in Chapter III we test whether the probability of occurrence modeled trough species distribution models (SDMs) is coupled with intraspecific trait variability in North American tree species so that individuals have higher fitness at the centre of their species environmental niche than at the edges, which we here define as 'fitness-centre' hypothesis.

The meta-analysis reported in Chapter I reveals that leaf mass per area (LMA), leaf nitrogen per unit of area (N$area$), leaf nitrogen per unit of mass (N$mass$) and leaf carbon isotope composition (δ^{13}C) significantly increase with increasing elevation worldwide. Conversely, leaf area (LA) and leaf phosphorous per unit of mass (P$mass$) shows no significant pattern with elevation. We also detect paired cross-species trends of covariation between leaf traits along elevation. By summarizing results of reciprocal transplant experiments in Chapter II, we found that individuals transplanted downward show larger biomass and height compared to their site of origin but failed to reach equal these traits and survival to that of local individuals. Individuals transplanted upward adjust their traits by decreasing plant growth and number of reproductive units to that of local individuals but nevertheless show lower survival. Importantly, we found that such patterns are moderated by temperature and precipitation difference between transplant sites at different elevations. Finally, in Chapter III we show that the 'fitness-centre' hypothesis does not hold true in none of the 66 North American tree species analyzed and that the lack of the relationship between individual fitness and the SDM-modeled probability of occurrence is pervasive across species differing in dispersal ability and climatic niche breadth.

Because plant functional traits and individual fitness play a crucial role in plant shift and local persistence following altered environmental conditions, studies reported here have relevant implications for biological conservation and contribute to characterize abiotic constraints within geographic distribution ranges. These results overall highlight the importance of meta-analytical approaches to assess cross-species patterns of intraspecific trait variability.

Zusammenfassung

Die Quantifizierung der intraspezifischen Merkmalsvariation und Fitness von Pflanzen über die Verbreitungsgebiete der Arten hinweg ist der Schlüssel zum Verständnis der

Populationsdynamik und des lokalen Aussterbens angesichts globaler Umweltveränderungen. Trotz der großen Menge an Primärdaten, die in der ökologischen Literatur und in öffentlich zugänglichen Datenspeichern verfügbar sind, fehlt es immer noch an quantitativen Synthesen, die sich mit den Allgemeinheiten und Unähnlichkeiten solcher Muster über verschiedene Arten weltweit beschäftigen.

In dieser Dissertation berichte ich über drei Studien, die meta-analytische Ansätze verwenden, um artenübergreifende Muster der intraspezifischen Merkmalsvariation von Pflanzen im ökologischen und geographischen Raum zu quantifizieren. Eine Meta-Analyse, die die intraspezifische Reaktion von morpho-physiologischen Blatteigenschaften entlang von Höhengradienten beschreibt, wird in Kapitel I vorgestellt. Anschließend wird in Kapitel II eine Meta-Analyse zum Überleben und zur intraspezifischen Merkmalsvariation nach wechselseitigen Transplantationen innerhalb des Höhenbereichs verschiedener Pflanzenarten vorgestellt. Schließlich testen wir in Kapitel III, ob die durch Artenverteilungsmodelle (SDMs) modellierte Vorkommenswahrscheinlichkeit mit der intraspezifischen Merkmalsvariabilität bei nordamerikanischen Baumarten gekoppelt ist, so dass Individuen im Zentrum der ökologischen Nische ihrer Art eine höhere Fitness haben als an den Rändern, was wir hier als "Fitness-Zentrum"-Hypothese definieren.

Die in Kapitel I berichtete Meta-Analyse zeigt, dass die Blattmasse pro Fläche (LMA), der Blattstickstoff pro Flächeneinheit (N_{area}), der Blattstickstoff pro Masseneinheit (N_{mass}) und die Blattkohlenstoff-Isotopenzusammensetzung ($\delta^{13}C$) mit zunehmender Höhe weltweit signifikant ansteigen, während die Blattfläche (LA) und der Blattphosphor pro Masseneinheit (P_{mass}) kein signifikantes Muster mit der Höhe zeigen. Wir entdecken auch gepaarte artenübergreifende Trends der Kovariation zwischen Blatteigenschaften entlang der Höhenlage. Indem wir die Ergebnisse der wechselseitigen Transplantationsexperimente in Kapitel II zusammenfassen, fanden wir heraus, dass Individuen, die nach unten verpflanzt wurden, eine größere Biomasse und Höhe im Vergleich zu ihrem Herkunftsort aufweisen, aber diese Eigenschaften und das Überleben nicht an die der lokalen Individuen angleichen konnten. Individuen, die nach oben verpflanzt wurden, passen ihre Eigenschaften durch ein geringeres Pflanzenwachstum und eine geringere Anzahl an reproduktiven Einheiten an die der lokalen Individuen an, zeigen aber dennoch ein geringeres Überleben. Wichtig ist, dass wir herausgefunden haben, dass solche Muster durch Temperatur- und Niederschlagsunterschiede zwischen Transplantationsstandorten in verschiedenen Höhenlagen gemildert werden. Schließlich zeigen wir in Kapitel III, dass die "Fitness-Zentrum"-Hypothese bei keiner der 66 untersuchten nordamerikanischen Baumarten zutrifft und dass das Fehlen der Beziehung zwischen individueller Fitness und der SDM-modellierten Wahrscheinlichkeit des Auftretens bei Arten, die sich in ihrer Ausbreitungsfähigkeit und klimatischen Nischenbreite unterscheiden, durchgängig ist.

Da die funktionellen Eigenschaften von Pflanzen und die individuelle Fitness eine entscheidende Rolle bei der Verschiebung von Pflanzen und der lokalen Persistenz nach veränderten Umweltbedingungen spielen, haben die hier berichteten Studien relevante Auswirkungen auf den biologischen Naturschutz und tragen dazu bei, abiotische Beschränkungen innerhalb geographischer Verbreitungsgebiete zu charakterisieren. Diese Ergebnisse unterstreichen insgesamt die Bedeutung meta-analytischer Ansätze zur Bewertung von artenübergreifenden Mustern der intraspezifischen Merkmalsvariabilität.

Riassunto

Misurare la variazione intraspecifica dei tratti funzionali e la fitness individuale delle piante all'interno dei loro areali di distribuzione è fondamentale per comprendere le dinamiche di popolazione e le estinzioni locali in risposta ai cambiamenti ambientali che avvengono a livello globale. Nonostante la grande quantità di dati primari disponibili nella letteratura ecologica e nei database pubblicamente disponibili, sono ancora carenti le analisi volte a riassumere quantitativamente generalità e differenze di variazione intraspecifica dei tratti funzionali tra diverse specie su larga scala.

In questa tesi di dottorato vengono riportati tre studi che utilizzano approcci meta-analitici volti a riassumere quantitativamente gli andamenti di variazione dei tratti intraspecifici di diverse specie di piante all'interno del loro areale di distribuzione geografico e ambientale. Nel Capitolo I viene riportata una meta-analisi che descrive la risposta intraspecifica dei tratti morfofisiologici delle foglie lungo i gradienti altitudinali. Successivamente, nel Capitolo II viene riportata una meta-analisi sulla variazione intraspecifica del tasso di sopravvivenza e dei tratti funzionali delle piante a seguito di trapianti reciproci lungo l'intervallo altitudinale di diverse specie. Infine, nel Capitolo III abbiamo testato in esemplari di specie arboree nordamericane qualora esista una correlazione tra la probabilità di occorrenza stimata tramite modelli di distribuzione (SDMs) e la fitness individuale, poichè una maggiore fitness dovrebbe essere presente al centro della nicchia ambiantale rispetto ai suoi margini, che qui definiamo come ipotesi di 'fitness-centre'.

La meta-analisi riportata nel Capitolo I mostra come la massa fogliare per area (LMA), l'azoto fogliare per unità di area (N$area$), l'azoto fogliare per unità di massa (N$mass$) e la composizione isotopica del carbonio fogliare (δ^{13}C) aumentino in modo significativo con l'aumento di altitudine a livello globale. Al contrario, l'area fogliare (LA) e il fosforo fogliare per unità di massa (P$mass$) non mostrano un andamento significativo in relazione all'altitudine. Qui riveliamo inoltre tendenze comuni tra diverse specie in termini di co-variazione tra i tratti fogliari lungo l'altitudine. Analizzando nel Capitolo II i risultati degli esperimenti di trapianto reciproco, viene mostrato come gli individui trapiantati ad altitudine più in bassa rispetto il loro luogo di origine abbiano una biomassa e un'altezza maggiori ma non riescano comunque ad adeguare questi tratti e il tasso di sopravvivenza a quello degli individui locali. Gli individui trapiantati verso l'alto tendono invece ad adattare i loro tratti riducendo la crescita e il numero di unità riproduttive rispetto a quelli degli individui locali, mostrando comunque un ridotto tasso di sopravvivenza. Di grande importanza è il risultato che mostra come le differenze di temperatura e precipitazione tra i siti di trapianto a diverse altitudini regolino tali andamenti. Infine, nel Capitolo III, viene dimostrato come l'ipotesi di 'fitness-centre' non sia valida in quasi nessuna delle 66 specie arboree nordamericane analizzate, e che la mancanza di correlazione tra fintess individuale e la probabilità di occorrenza della specie ottenuta tramite SDMs sia diffusa anche tra specie che differiscono per capacità di dispersione e per ampiezza di nicchia climatica.

Poiché i tratti funzionali e la fitness individuale giocano un ruolo cruciale nello spostamento delle piante e nella loro capacità di persistere in un luogo in risposta a condizioni ambientali alterate, gli studi qui riportati hanno importanti conseguenze per la conservazione biologica e contribuiscono a determinare quali vincoli abiotici determinino la distribuzione dei tratti all'interno degli areali delle specie. Questi risultati evidenziano in generale l'importanza degli approcci meta-analitici nel valutare la variabilità dei tratti intraspecifici tra diverse specie.

2 Introduction

Spatial distribution in a changing world

Species are spatially arranged depending on the interplay of two distinct dimensions of 'space', specifically the geographic space and the environmental space. The geographic space corresponds to those physical parts of the ecosystems where species interact with one another and with the abiotic environment (Huggett, 2004). The geographic range (or distribution) of a species represents therefore the areas of the geographic space occupied by the species. Differently, the environmental space refers to the set of abiotic and biotic conditions taking place in the geographic space. Such conditions can be conceptualized as a multidimensional hypervolume determining population growth rate (either positive or negative) of species (Soberon & Nakamura, 2009). The subset of the environmental space where positive population growth rates occur is represented by the 'niche' concept or, more precisely, to what was termed as 'fundamental niche' by Hutchinson (1957). Additionally, the niche concept include a subset of the fundamental niche, named 'realized niche' (Hutchinson, 1957) [or 'ecological potential' *sensu* Ellenberg (1953)], including the subspace of the niche constrained by dispersal limitation and biotic interactions with other species (e.g. competition or predation) (Guisan *et al.*, 2017).

Niche concepts and theory upon their relation with species distribution have become central in biogeographical and macroecological research (Guisan & Thuiller, 2005; Soberon & Nakamura, 2009). Understanding species distribution in the environmental and geographic space is important to quantify and predict species and communities response to global environmental changes at different temporal scales (Wiens *et al.*, 2009).

Starting from the last few decades, anthropogenic land-use and climate change are challenging scientists to understand how the altered status of the ecosystem is affecting the life on Earth. Humans now represent the major driver of patterns in global biodiversity and biogeochemistry change, as they profoundly modified half the land cover, consumed substantial amount of Earth's primary productivity and strongly increased CO_2 and reactive nitrogen concentrations in the atmosphere. As ever-growing anthropogenic impacts continue to rise, it is widely acknowledged that related variation in climatic conditions and land use are expected to impact the distribution of plant species and their interactions with other organisms, with concomitant consequences on the biosphere (IPCC, 2018).

Among most evidence-rich impacts of climate change are species distribution shifts for which a substantial body of research has shown that global warming and other anthropogenic factors shape migration and local extinction rates of plants and other organisms (Root *et al.*, 2003; VanDerWal *et al.*, 2012; Parmesan & Hanley, 2015). Because plant species distribution is highly dependent upon abiotic conditions, global environmental changes are predicted to increase the unbalance between current abiotic conditions and those which species adapted to live. Such changes in climatic conditions cause mainly upward migration trends towards higher elevation and global poleward range expansions as species track their optimal temperature range (Lenoir *et al.*, 2008; Chen *et al.*, 2011; VanDerWal *et al.*, 2012). Nevertheless, several studies have also reported species with the opposite trend along latitude and elevation (Lenoir *et al.*, 2010; Crimmins *et al.*, 2011; Rapacciuolo *et al.*, 2014). Such trends are likely attributable to anthropogenic impacts other than global warming, such as alteration in water avail-

ability (Crimmins *et al.*, 2011), land-use change (Bhatta *et al.*, 2018; Guo *et al.*, 2018) or competitive release at the lower margin of the species distribution following biotic invasions (Lenoir *et al.*, 2010).

To better understand the ability of populations to cope with environmental changes, there is a growing attention to the role of individual fitness and how this affects eco-evolutionary processes following range expansions and contractions (Anderson, 2016; Nadeau & Urban, 2019). Indeed, alternatively to shift their distribution, species can respond to altered environmental conditions by adjusting their morphophisological features trough local adaptation and phenotipic plasticity - some key mechanisms that are particularly relevant in sessile organisms, such as plants (Nicotra *et al.*, 2010; Valladares *et al.*, 2014). Furthermore, individuals can persist in isolated pockets hiding from the changing environment (so-called "microrefugia"), with eco-evolutionary consequences following genetic isolation (Rull, 2009).

Individual fitness and intraspecific trait variation in space

Understanding the link between space and the variation of individual fitness is a long-standing goal in ecology and biogeography (Reichstein *et al.*, 2014; Ricklefs & Jenkins, 2011; Violle *et al.*, 2014), with relevant implications in other fields such as conservation biology (Mimura *et al.*, 2016; Stockwell *et al.*, 2003) and agriculture (Escribano-Rocafort *et al.*, 2017; Martin *et al.*, 2016). There is a growing body of evidence showing that intraspecific trait variability has a non-negligible effect on species properties and ecosystem function, moderating plant responses to global environmental changes and contributing to trait variation across plant community assemblages (Albert *et al.*, 2010; Guisan *et al.*, 2019; Kichenin *et al.*, 2013; Messier *et al.*, 2010; Siefert *et al.*, 2015). Research upon morpho-physiological variation within species distribution ranges is also essential to identify populations of economic interest (Oleksyn *et al.*, 1992; Rehfeldt, 1989) and to predict how these could be affected by contemporary environmental changes (Aspinwall *et al.*, 2014).

In trait-based ecology, the fitness of organisms - independently whether this is considered at the individual, population or community level - can be either quantified as the direct outcome of one or more of its three components (i.e. growth, survival and reproduction), or by contextualizing the morpho-physiological features of individuals (i.e., functional traits) in a given set of biotic and abiotic conditions (Violle *et al.*, 2007). For example, fitness of individual plants can be measured as growth rate, probability to survive and amount of fertile seeds produced, because such features are positively coupled with fitness; at the same time, morpho-physiological functional traits such as specific leaf area (SLA), seed mass, vegetative height, biomass and leaf nutrient content correlates with individual fitness either positively or negatively depending on the environment where individuals grow (Figure 1a).

The environment acts as a filter on plants by selecting those sets of traits which are suitable for a given range of the key factors determining plant life such as temperature, soil moisture, nutrient availability and disturbance (Violle *et al.*, 2007). Since plant individuals and communities occur along gradients of these environmental factors, traits are expected to vary in space accordingly (McGill *et al.*, 2006). Consequently, patterns of individual fitness are expected to be not distributed at random in the environmental and geographic space. Instead, individual fitness distribution depends, in theory, upon I) the set of abiotic and biotic local conditions matching the species' niche (Pulliam, 2000); and II) the complex interplay between phenotypic plasticity,

local adaptation and historical factors (i.e. dispersal, gene flow, population density) (Crispo, 2008), which ultimately determine the probability of an individual to persist, grow and reproduce.
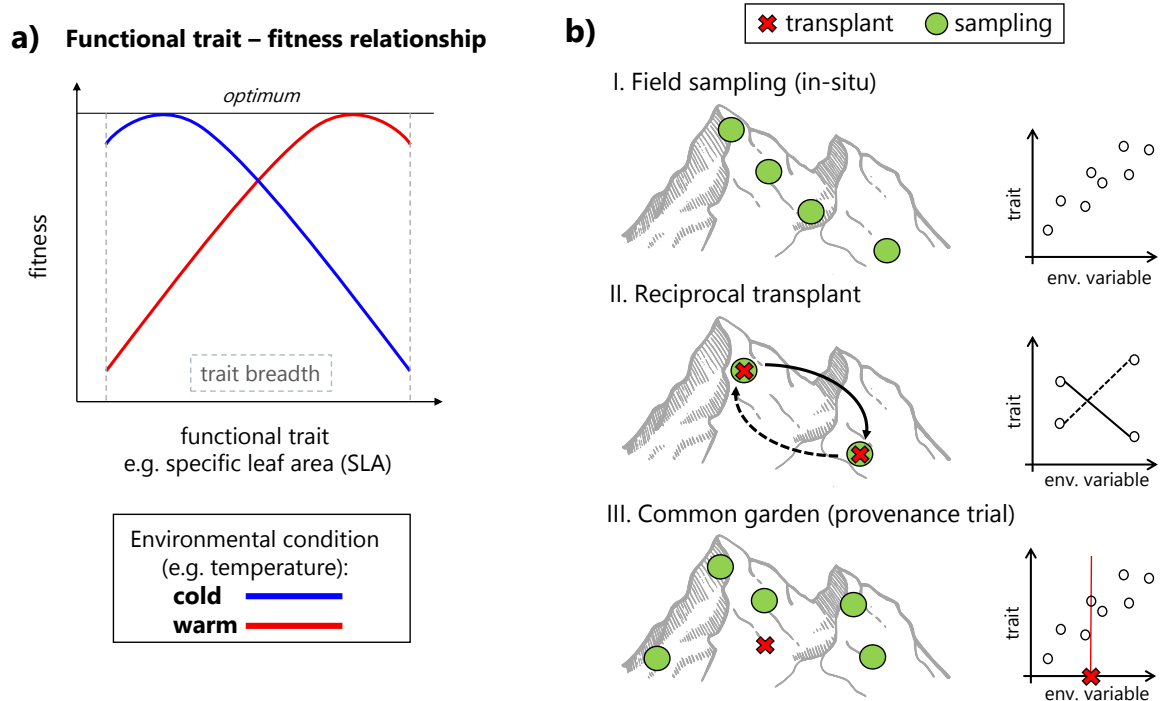

Figure 1: *Graphical representation of a) the relationship between individual fitness and functional traits; and b) the integrated quantification of individual fitness / functional trait variation across various experimental settings along environmental gradients, such us elevational gradients. Panel a) illustrates that plant functional trait association to individual fitness is often context-dependent. For example, a positive coupling between fitness and specific leaf area (SLA) is expected in individuals growing in warm/temperate environments (red curve) where larger leaves represent an advantage for competition; conversely, a negative association is often expected in colder environments (blue curve) where smaller and thicker leaves are necessary to survive cold temperatures. Hat-shaped fitness curves declines closed to trait breadth' boundaries (vertical dotted lines). Panel b) differentiate between hypothetical sampling design (left) and dose-response curve (right) obtained from each of the three experimental designs. In reciprocal transplants, individuals are transplanted in both sites and their performance compared to test for local adaptation. In common garden studies (or provenance trials) dose-response curves are based on the difference in environmental conditions between sites of origin and transplant site.*

Main experimental approaches to study individual fitness and intraspecific trait variation in the environment include I) sampling over environmental gradients; II) reciprocal transplants between sites of origin; and III) common garden experiments, where genotypes from contrasting environments and origins are grown in common gardens (Figure 1b). Such approaches allows to characterize trait variation with 'dose-response' curves assessing the relation between environmental and trait variation, either by in-situ sampling of individuals [see e.g. Friend *et al.* (1989)] or by using common garden experiments [see e.g. Mahony *et al.* (2019)] comparing how environmental conditions of the site of origin affect trait variation (de Villemereuil *et al.*, 2015). In addition, reciprocal transplant experiments are normally established to identify the

adaptive basis of trait variability by comparing performance of transplanted individuals to local individuals and to the individuals growing at their site of origin (Kawecki & Ebert, 2004).

Studies aiming at comparing plant populations located at different latitudes, elevations, or - more in general - environmental conditions, are important to understand how individual fitness is distributed in space. Specifically, elevational gradients are widely used to explore the relationship between temperature and plant traits, since increasing elevation result in a steep decrease in temperature (-1°C for an increase of ∼167 m in elevation) (Jump *et al.*, 2009). For this reason, mountain ecosystems represent unique locations to explore how temperature shapes patterns of traits distribution (Graae *et al.*, 2012; Jump *et al.*, 2009; Körner, 2007). In addition to temperature changes, increasing elevation in mountain environment usually implies changes in precipitation, soil conditions, nutrients availability and disturbances by land-uses (Fontana *et al.*, 2017; Stöcklin *et al.*, 2009; Wellstein & Kuss, 2010). Thus, elevational gradients can be generally applied to improve the understanding on the role of multiple drivers in shaping plant trait and fitness distribution.

Achieving quantitative synthesis in the face of climate change

Climate change has profoundly impacted ecological research (Pettorelli, 2012). Over the last few decades, a raising number of ecologists have started to investigate how different components of climate change influence the structure, composition and function of natural and semi-natural ecosystems worldwide (Haunschild *et al.*, 2016). Addressing these topics allow ecologists to inform policy and decision makers upon the most suitable strategies to achieve key environmental targets in the face of global environmental change. Global challenges include the preservation of viable ecosystem services through the conservation of biodiversity and the correct management of the ecosystem to guarantee sustainable use of resources (Brook & Fordham, 2015; Butchart *et al.*, 2010).

Many environmental problems including biodiversity conservation are global and transboundary (Lim, 2015), calling for the coordination of collaborative experimental research on a large geographic extent (Fraser *et al.*, 2013). Consequently, in order to achieve sound global evidence-based actions there is the urgent need to summarize the results obtained from multiple ecological experiments worldwide. Approaches such as long-term experimental platforms coordinated at national and international levels represent one of the most effective ways to synthesize evidences from multiple experimental units in response to climate change (Borer *et al.*, 2013; Fraser *et al.*, 2013). Examples of such networks are the International Tundra Experiment (ITEX) (Bjorkman *et al.*, 2018), evaluating responses of tundra plants to rising temperature; the Nutrient Network (Firn *et al.*, 2019), simulating the alteration of nutrient cycles; the TreeDivNet experiment (Verheyen *et al.*, 2015), assessing the long-term effects of multiple stress on tree diversity; and the Free-Air CO_2 Enrichment experiment (Medlyn *et al.*, 2015), quantifying ecosystem response to the increase of atmospheric CO_2.

While such experimental networks allow to better generalize findings compared to individual studies thanks to coordinated experimental settings, they are often demanding in terms of resources and they only address specific types of ecosystem and environmental factors based on the network's protocol. Conversely, fast-moving ecological research produces an ever-growing amount of primary data on various emerging topics with different experimental designs for which coordinated networks are difficult to

establish and maintain. Alternatively, qualitative approaches to achieve research synthesis, such as systematic reviews and vote counting, are often the main solution in case primary literature is scarce or too generic around a given phenomenon, but their results are often biased and lack of a quantitative estimate of the studied phenomenon (Gurevitch *et al.*, 2018). Quantitative research synthesis in ecology remains therefore an open challenge.

Meta-analysis, namely the quantitative scientific synthesis of research results (Borenstein *et al.*, 2009), represents an effective solution to overcome the above-mentioned limitations of ecological research synthesis (Gurevitch *et al.*, 2001; Harrison, 2010). Meta-analysis has more than forty years of rooted tradition in clinical research and has become a revolutionary method over multiple research fields by helping to establish evidence-based procedures and to address results of contradictory research outcomes (Gurevitch *et al.*, 2018). Such approach anticipates 'big data' and 'open science' movements encouraging different scientists to share their data to achieve stronger conclusions or generate new questions.

In meta-analysis, one or more outcomes extracted from primary studies are transformed in effect sizes, in a way that the outcomes of different studies are standardized on the same scale and thus comparable in a statistical analysis (Borenstein *et al.*, 2009). Such effect sizes are used as dependent variables of a model assessing the overall effects (i.e. the 'mean pooled estimate') and the heterogeneity of the outcomes. Such meta-analytical models are weighted by the inverse of the sampling variance, which makes larger studies more influential over the mean pooled estimate.
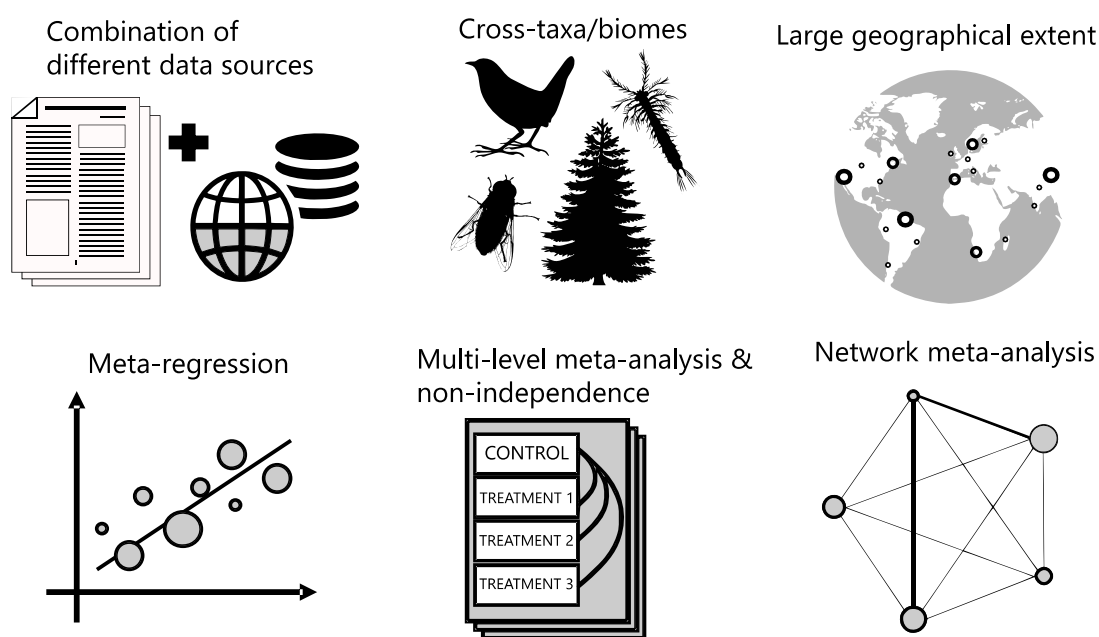
Figure 2: *Main features and potentials of ecological and biological meta-analyses. Typical features include I) the use of different data sources such as peer-reviewed literature or pre-compiled datasets; II) hypothesis tested across different systems (species and biomes); III) geographic coverage on a large extent. Relevant potentials include IV) meta-regression analysis exploring the impact of moderators on the effect size variation; V) multilevel meta-analytical models to deal with non-independent effect sizes; VI) network meta-analyses allowing to combine direct and indirect comparisons of multiple treatments over a single control group.*

Meta-analyses in ecology can benefit of a combination of different data sources, including open database (Culina *et al.*, 2018), and are often carried out on a large geographic extent involving potentially different kind of organisms. Other advantages of meta-analyses in ecology rely on the ability of recent meta-analytical advances to deal with heterogeneous and complex designs, a common characteristic of primary ecological research. Recent examples are I) meta-regression techniques, allowing to explore gradients of explanatory variables that cannot be assessed by a single study [see e.g. Limpens *et al.* (2011); Midolo *et al.* (2019a)]; II) mixed-effect multilevel meta-analytical models to deal with non-independent effect sizes and nested data structure (Lajeunesse, 2011; den Noortgate *et al.*, 2012); and III) network meta-analyses (Salanti *et al.*, 2007), allowing to combine direct and indirect comparisons of multiple treatments (e.g. different environmental stressors) over a single control group. Other specific advances in ecological meta-analyses analyze the variance of the mean estimates as response variable (Nakagawa *et al.*, 2014) and address phylogenetic dependence in meta-analytical models (Lajeunesse, 2009).

Meta-analyses are becoming more and more popular in ecology and evolution, especially in climate change and conservation research - yet with some frequent misuses and methodological limitations (Koricheva & Gurevitch, 2014; Nakagawa *et al.*, 2017). Particularly, meta-regression approaches allow to build cross-studies dose-response relationships with relevant implications in climate change. Such meta-analyses can be integrated into modelling frameworks aiming to describe the response of biodiversity to anthropogenic pressures, such as GLOBIO (Schipper *et al.*, 2019) and PREDICTS (Newbold *et al.*, 2015).

Objectives and hypotheses

In this PhD dissertation, I report three studies using meta-analytical approaches quantifying cross-species patterns of plant intraspecific trait variation within environmental and geographic ranges. A meta-analysis describing the intraspecific response of morpho-physiological leaf traits along elevational gradients is reported in Chapter I. Here, we hypothesized that plants follow common patterns of leaf morpho-physiological variation and trait-trait covariation along elevation across different species and mountain ranges. To test this hypothesis, we quantified with meta-regression the intraspecific response of different traits to elevation (i.e. the vertical distance between two sites sampled along a gradient) across multiple gradients. We also asked whether average environmental conditions of each gradient have an effect on trait variation, and whether traits of different plant functional types (herbaceous vs. woody) differs in the response to elevation.

Afterwards, I report a meta-analysis upon survival and intraspecific trait response following reciprocal transplant within the species elevational range in Chapter II. Using reciprocal transplant studies allowed us here to disentangle trait plasticity from local adaptation and to simulate cross-species responses to non-local conditions following plant elevational shift. Thus, we hypothesized intraspecific performance and trait variation across multiple transplant experiments is moderated by temperature and precipitation differences between sampling sites. We tested such hypothesis comparing pairs of transplanted individuals to those growing at their site of origin ('away vs. home') and to the local individuals found at the site of transplant ('foreign vs. local').

Finally, in Chapter III, we quantified how intraspecific growth rate and survival

of 66 North American tree species vary within the species modelled environmental niche by testing whether probability of species occurrence projected with species distribution models (SDMs) is coupled with individual fitness (which we here define as 'fitness-centre' hypothesis). We combined field data of individuals' growth rate (height and diameter standardized by age) available from the United States Forest Inventory Analysis plots with common garden data collected from 23 studies reporting individual growth rate, survival, height and diameter of individuals originated from different provenances in United States and Canada. We generally expected habitat suitability to be coupled with individual fitness based on ecological theory (Guisan & Thuiller, 2005; Pulliam, 2000) and species with higher dispersal ability and larger climatic breadth to exhibit higher 'fitness-suitability' associations, because of higher demographic synchrony and wider climatic variability promoting trait variability, respectively. Contrary to our expectations, we show the 'fitness-centre' hypothesis does not hold true in nearly any of the species analyzed. We further discuss theoretical aspects affecting the reliability of such hypothesis and discuss general implications of our findings.

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3 Chapter I – Global patterns of intraspecific leaf trait responses to elevation

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Abstract

Elevational gradients are often used to quantify how traits of plant species respond to abiotic and biotic environmental variations. Yet, such analyses are frequently restricted spatially and applied along single slopes or mountain ranges. Since we know little on the response of intraspecific leaf traits to elevation across the globe, we here perform a global meta-analysis of leaf traits in 109 plant species located in 4 continents and reported in 71 studies published between 1983 and 2018. We quantified the intraspecific change in seven morpho-ecophysiological leaf traits along global elevational gradients: specific leaf area (SLA), leaf mass per area (LMA), leaf area (LA), nitrogen concentration per unit of area (N*area*), nitrogen concentration per unit mass (N*mass*), phosphorous concentration per unit mass (P*mass*) and carbon isotope composition (δ^{13}C). We found LMA, N*area*, N*mass* and δ^{13}C to significantly increase and SLA to decrease with increasing elevation. Conversely, LA and P*mass* showed no significant pattern with elevation worldwide. We found significantly larger increase in N*area*, N*mass*, P*mass* and δ^{13}C with elevation in warmer regions. Larger responses to increasing elevation were apparent for SLA of herbaceous compared to woody species, but not for the other traits. Finally, we also detected evidences of covariation across morphological and physiological traits within the same elevational gradient. In sum, we demonstrate that there are common cross-species patterns of intraspecific leaf trait variation across elevational gradients worldwide. Irrespective of whether such variation is genetically determined via local adaptation or attributed to phenotypic plasticity, the leaf trait patterns quantified here suggest that plant species are adapted to live on a range of temperature conditions. Since the distribution of mountain biota is predominantly shifting upslope in response to changes in environmental conditions, our results are important to further our understanding of how plants species of mountain ecosystems adapt to global environmental change.

KEYWORDS: altitude, carbon isotope ratio, environmental gradient, intraspecific variability, leaf nutrient content, meta-analysis, phenotypic variability, plant functional traits

Introduction

Mountain ecosystems are characterized by a rapid change in climatic conditions along elevational gradients (Jump *et al.*, 2009; Körner, 2007). Spatial heterogeneity in site conditions is further increased by small-scale variation in topography, inclination, exposition and substrate. Steep climate gradients along short horizontal distances and pronounced small-scale heterogeneity in site conditions make mountain environments unparalleled natural laboratories to study how plants respond to changes in environmental conditions (Graae *et al.*, 2012; Jump *et al.*, 2009; Sides *et al.*, 2013). The environment selects for the optimal phenotype adapted to a given range of resources and conditions, for instance, temperature, soil moisture, nutrient availability and disturbance in each population (Keddy, 1992; Violle *et al.*, 2007; Wellstein & Kuss, 2010). Thus, various abiotic and biotic environmental conditions occurring across elevations tend to select different ecological strategies among individuals of the same species. Such strategies are reflected in species-specific patterns of changes in physiological and morphological leaf traits along elevation (Sides *et al.*, 2013), which in turn are expected to greatly affect higher levels of organization, such as populations, communities and ecosystems (Violle *et al.*, 2007). In this regard, leaf traits such as specific leaf area (SLA) and nutrient concentration at the community level are important for various ecosystem services, such as soil fertility (Ordoñez *et al.*, 2009), litter decomposition (Cornwell *et al.*, 2008) and carbon sequestration (Deyn *et al.*, 2008).

There is a growing body of evidence showing that intraspecific trait variation (ITV) — due to phenotypic plasticity or local adaptation — has a significant and non-negligible effect on species properties and ecosystem function. For instance, accounting for ITV helps to better understand phenotypic plasticity, plant assembly and ecosystem processes in community ecology (Albert *et al.*, 2010b,?; Helsen *et al.*, 2017; Kichenin *et al.*, 2013; Messier *et al.*, 2010).

Studies comparing plant species individuals located at different elevations (i.e. along elevational gradients or transects) on single slopes or mountain ranges provide relevant insights on the patterns of the adaptation of the leaf in response to biotic and abiotic variations in the environment (Birmann & Körner, 2009; Seguí *et al.*, 2017; Woodward, 1983)). Changes in leaf traits have been widely adopted as a global indicator of plants' trade-offs between growth rate and resource conservation among species (Reich *et al.*, 1997; Wright *et al.*, 2004), although leaf trait coordination (e.g. in the leaf economic spectrum) may not hold at the local scale (Messier *et al.*, 2017, 2016, 2010), nor at the intraspecific level [Wright & Sutton-Grier (2012); but see Albert *et al.* (2010)].

The variation in leaf morphophysiology observed along elevation depends on a set of abiotic and biotic environmental factors that typically change with elevation (Körner, 2007; Read *et al.*, 2014).As elevation increases, temperature and atmospheric pressure tend to decrease, and solar radiation under clear-sky conditions tend to increase(Körner *et al.*, 1988). Especially, air temperature has been described as a key factor that strongly covaries with elevation worldwide and determines vegetation distribution in mountain environments (Jump *et al.*, 2009; Körner, 2007; Körner & Paulsen, 2004). Among other factors affecting plant growth, increased elevation usually implies changes in precipitation, solar radiation, wind velocity, soil fertility and disturbances by land use (Fisher *et al.*, 2012; Lembrechts *et al.*, 2016; Macek *et al.*, 2009), but the direction and strength of the relationship between elevation and these factors may vary strongly across the globe (Körner, 2007).

In general, species composition and turnover are strongly affected by elevation

in mountains (Körner, 2003). Although there is no clear elevation–climate relationship in mountain environments worldwide, lower elevation conditions tend to favour resource-acquisitive strategies that help individuals to face higher competition due to higher temperature and resource availability (Callaway *et al.*, 2002; Read *et al.*, 2014). Conversely, higher elevations tend to be characterized by lower temperature and lower competition, pushing individuals to invest more energy in the conservation of resources (Callaway *et al.*, 2002; Callis-Duehl *et al.*, 2016; Pfennigwerth *et al.*, 2017). In general, individuals of the same species growing at higher elevation are expected to show lower leaf area (LA) and higher SLA due to increased density of leaf tissues as morphological adaptation to colder conditions (Körner, 2003; Poorter *et al.*, 2009). Decreasing temperature with elevation can also be accompanied by decreasing herbivory pressure (Rasmann *et al.*, 2013), allowing plants to produce morphologically different leaves at higher elevations [i.e. with lower phenolic content, richer in N content and lacking spines; Callis-Duehl *et al.* (2016)]. Furthermore, despite the covariation among leaf traits (Albert *et al.*, 2010b,?; Poorter & Bongers, 2006), it remains unclear to what extent single trait's variation is linked to other trait response to elevation. For example, physiological leaf traits such as N and P concentrations in the leaf and the C isotope composition (δ^{13}C) often covary with morphological leaf traits (e.g. LA and dry mass) across elevations (Birmann & Körner, 2009; Gerdol *et al.*, 2018; Hultine & Marshall, 2000; Zhu *et al.*, 2010). In general, intraspecific trait–trait relationships have been attributed to physiological and structural trade-offs of the leaf in response to changes in environmental conditions (Ghimire *et al.*, 2017; Onoda *et al.*, 2017).

Several studies addressed the response of intraspecific leaf trait variation along elevational transects on single slopes or mountain ranges. However, the direction of such changes is expected to vary considerably among studies observed [see e.g. different SLA responses in Macek *et al.* (2009); Seguí *et al.* (2017); Woodward (1983)], as the sources of heterogeneity in trait response to elevation are manifold. First, studies often report data for only one or few species that largely differ in their ecology and life form. For example, tree species perceive different microclimatic conditions compared to shorter herbs (Frey *et al.*, 2016; Körner, 2007). Furthermore, woody species are expected to show larger heterogeneity in trait variation due to broader ontogenetic plasticity (Borges, 2009; Siefert *et al.*, 2015). Another source of heterogeneity is the divergent response of precipitation to elevation worldwide (Körner, 2007) because precipitation determines moisture supply and might affect the trait–elevation relationship (Martin & Asner, 2009). Moreover, it has been shown that intraspecific leaf trait response to aridity can differ between functional groups and between biogeographic species pools, emphasizing the relevance of the evolutionary differences in species strategies (Wellstein *et al.*, 2017). However, applying meta-analytical approaches based on multilevel mixed-effect models allows us to compare results from different contexts by controlling for species-specific responses and for the climatic conditions of each gradient [see e.g. Benítez-López *et al.* (2017); Midolo *et al.* (2019a)]. To our knowledge, only Read et al. (2014) applied a meta-analysis to summarize patterns of trait variation along global elevational gradients reported in 36 studies focusing either on intra- or interspecific variation. However, their analyses quantified the overall correlation between trait and elevation but did not focus on the effect of elevational change on trait variation within single gradients, and was limited only to the traits of the leaf economic spectrum [i.e. leaf mass per area (LMA), N content per area (N*area*), N content (N*mass*)], without considering other key traits such as SLA (the inverse of LMA), leaf phosphorous content (P*mass*) and δ^{13}C.

Here, we tested the overarching hypothesis that intraspecific leaf trait adjustment appears in the same direction showing a common trait–elevation relationship across different plant species worldwide. Therefore, we conduct a meta-analysis of the intraspecific leaf trait variation along 92 elevational gradients worldwide reported in 71 studies in total in order to (a) reveal the overall effects of elevation on leaf trait variation, (b) test whether average environmental conditions of each gradient (mean temperature of the growing season, mean annual radiation, aridity and mean absolute elevation of the lowest site) have an effect on trait variation, and (c) examine if traits of different plant functional types (herbaceous vs. woody) differs in the response to elevation. Finally, we (d) explore whether variation of single leaf traits along elevation follow consistent patterns with other traits reported in the same study.

Materials & Methods

Trait selection

We analysed intraspecific variation of seven leaf functional traits in our analysis: SLA, LMA, LA, N$mass$, N$area$, P$mass$ and δ^{13}C. We focused our analysis on leaf traits given their influence on plant growth, development and ecological performance (Poorter & Bongers, 2006; Wright *et al.*, 2004). Our choice was also based on data availability; since the chosen leaf traits are relatively easy to measure, for instance compared to many belowground root traits (Pérez-Harguindeguy *et al.*, 2013), they are consequently more frequently reported in the literature.

The SLA is the inverse of LMA and both indicate the ratio between leaf size and leaf dry weight. Since elevational gradient studies normally report either the mean SLA or the mean LMA, and very rarely the values for every leaf sampled in a given site, it was not possible to convert SLA in LMA, or vice versa. Thus, to maximize the information in the meta-analysis, we included both SLA and LMA and analysed the traits in two separate datasets. In rare cases where original publications reported data of leaf dry weight and LA for every sample or both the SLA and LMA means, we included mean SLA and LMA in both datasets for those studies (10.5% of the studies).

Study selection

We searched for studies on Web of Science combining keywords related to elevational gradients and reflecting different dimensions of leaf traits, for example: ("altitude*" OR "elevation*") AND ("SLA" OR "leaf traits" OR "leaf nutrients") (see Appendix I.1 for complete search string). This resulted in a sample of 659 studies published up to March 2018, of which we scanned the titles and abstracts and then selected 71 studies that fit to our criteria. Studies eligible for inclusion reported means of traits of individuals of the same species sampled across at least two different elevations within a single slope or mountain range. We only included studies explicitly quantifying trait response along elevational gradients in their experimental design. We excluded studies that investigated trait variation across a large geographical range such as latitudinal gradient studies without clear focus on the effect of elevation only.

Studies selected in the meta-analysis reported 92 elevational gradients published between 1983 and 2018 across the globe (Figure 1) and focused on intraspecific leaf trait variation of 109 seed plant species from 38 families in total (see summary list in Table I.2.1; Appendix I.2). These studies reported traits sampled between 1981 and

2015. Each study reported data for one or more of the leaf traits selected for the meta-analysis.
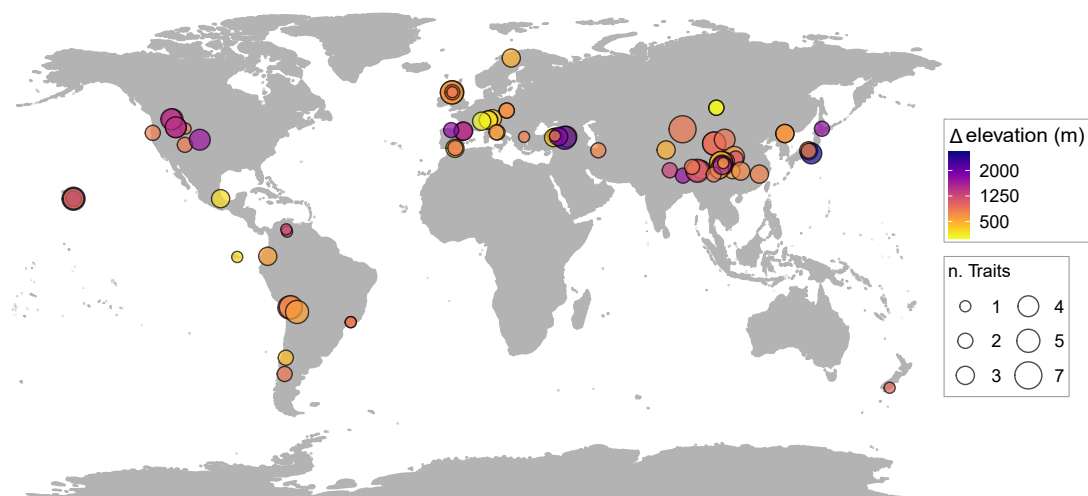

Figure 1: *Geographical distribution of the 92 elevational gradients included in the meta-analysis. For each gradient, point size depict the number of leaf traits available and the colours depict the larger value of difference in elevation (i.e. the vertical distance between the highest site sampled along the gradient and the lowest site sampled)*

Data collection

We extracted the mean, standard error and sample size of each trait reported in each site sampled along the elevational gradient and the absolute elevation (m a.s.l.) of the sites sampled. We used WebPlotDigitizer (Rohatgi, 2020) to extract the data if available only in graphs or retrieved data directly from tables or the main text. In addition, we extracted the name of each species analysed and the geographical coordinates of the location where the study was performed. Species names were checked across the datasets to standardize species synonyms.

We calculated difference in elevation (m) [sensu McVicar & Körner (2012)] as the vertical distance between sites sampled along the gradient and the lowest site sampled (see the graphical framework in Figure I.3.1; Appendix I.3). Following our main hypothesis, we used difference in elevation as the main predictor in our analyses expecting higher trait variation when comparing individuals growing at larger vertical distance due to potentially larger differences in abiotic and biotic conditions between sampled sites. In addition, we collected six other predictors for each single elevational gradient that we expected to moderate trait response to difference in elevation: (a) absolute elevation of the lowest point sampled (m a.s.l.); (b) mean growing season temperature (MGST, °C); (c) aridity index (the ratio between mean annual precipitation and mean annual potential evapotranspiration); (d) mean annual solar radiation (W/m^2); (e) average latitude of site sampled along the gradient; and (f) plant functional type (herbaceous or woody).

Climatic data (temperature, aridity and solar radiation) were estimated using the mean coordinates of all sites of the gradient, or by using the generic coordinates for the study area in case geographical coordinates of sites sampled within each gradient were not provided. We estimated the MGST as the mean temperature of warmest quarter of the year (i.e. the warmest contiguous 3 month period) from the WorldClim database

('BIO10') [version 2.0; www.worldclim.org, Fick & Hijmans (2017)]. Similarly, we also calculated the average solar radiation from the CliMond database (Kriticos *et al.*, 2011). The aridity index was calculated as the ratio of annual precipitation (estimated by WorldClim database) to the potential evapotranspiration extracted from the CGIAR-CSI GeoPortal (Trabucco & Zomer, 2010), meaning that higher aridity index values indicate lower aridity. Climatic data were extracted with the 'raster' function of the R package *raster* (Hijmans, 2017) with 30 s ($0.93 \times 0.93 = 0.86$ km^2 resolution at the equator). We were not able to collect data on how different environmental conditions vary between elevations either because most of the studies did not report such data or because geographical coordinates of sites sampled showed incompatible accuracy with the available climatic databases (e.g. in many cases, sites at different elevations along the same transect were located within the same 0.86 km^2 raster pixel).

Data analysis

We calculated log-response ratios (lnRR) for each species' trait along elevational gradients and used those as the effect size in our meta-analysis (Hedges *et al.*, 1999). Response ratios were calculated as follows (Equation 1):

$$lnRR_i = \ln(\bar{T}_{Ai}) - \ln(\bar{T}_B) \tag{1}$$

where T_A is the mean value of a trait measured at the higher elevational level *i* compared to the mean of the same trait measured on the same species at a lowest elevation present along the gradient (T_B) (see the graphical framework in Figure I.3.1; Appendix I.3). For non-negative trait values (i.e. all traits considered except for δ^{13}C), a positive value of lnRR indicates that the mean of a certain trait for a given species increases relatively to the mean sampled at the lowest elevational level. Thus, for δ^{13}C, a negative value of lnRR means that leaf δ^{13}C is increasing with elevation, and vice versa.

Since the selected studies normally reported data for multiple elevational levels i along the gradient, we calculated lnRR for each elevation compared with the lowest. Because this violates the assumptions of independence of the effect sizes [Gleser & Olkin (1994); i.e. multiple T_{Ai} values compared to T_B], we accounted for the correlation among effect sizes by computing the variance–covariance (VCV) matrix proposed by Lajeunesse (2011) for each dataset. The VCV matrix models the dependencies that arise when using the same control group and estimating multiple effect sizes (Lajeunesse, 2015). The inverse of the sampling variance of the VCV matrix was used to weight the precision of the effect size when modelling the data Lajeunesse (2011). To compute the VCV matrix, we calculated the sampling variance of each pairwise comparison based on Hedges *et al.* (1999), as follows (Equation 2):

$$\hat{\sigma}^2(lnRR_i) = \frac{(SD_B)^2}{N_B \bar{T}_B^2} + \frac{(SD_{Ai})^2}{N_{Ai} \bar{T}_{Ai}^2} \tag{2}$$

where *SD* is the standard deviation of the mean and *N* is the number of replicates (i.e. number of plant individuals sampled) extracted from the papers (see Equation for the description of other symbols). We imputed missing *SD* values using the coefficient of variation from all complete cases using the 'impute_SD' function of the R package *metagear* (Lajeunesse, 2015). An example of how the VCV matrix was computed and used to weight the models is available in the R code from the repository (Midolo *et al.*, 2019b).

We analysed the data with multilevel linear mixed-effect models using the 'rma.mv' function of the R package *metafor* (Viechtbauer, 2010). Models were fitted with crossed, nested and non-nested random effect terms as follows: $(1 \mid gradient/ID) + (1 \mid species)$. Such structure includes both the identity of each elevational gradient (*gradient*) and the species (*species*) as non-nested random components (Benítez-López *et al.*, 2017; Midolo *et al.*, 2019a). Following Konstantopoulos (2011), we nested each observation *ID* within the *gradient* grouping level in the random structure of the models to account for the possibility that the underlying true effects within each elevational gradient are not homogeneous. To address question (a) presented in the introduction, we first fitted single meta-regression models using difference in elevation only as moderator. Secondly, to answer questions (b) and (c), we performed a multimodel inference analysis quantifying the importance of climatic variables and plant functional types to moderate trait variation starting from the full model including each predictor. For each response variable (i.e. each leaf trait), we ranked a set of models according to the small-sample-size corrected Akaike information criterion AIC_c) using the 'glmulti' function of the R package *glmulti* (Calcagno, 2013). The relative importance of each predictor was evaluated with the AIC_c weight ($AIC_c W$), calculated as the sum of the weights for the models in which the predictor appeared (Burnham & Anderson, 2010). For each response variable, we used a confidence set of models by selecting the smallest subset of models that have a cumulative sum of $AIC_c W \geq 0.95$ (Johnson & Omland, 2004). We calculated the unconditional estimates of the predictors over the confidence set of models averaged. The relative importance of each predictor in the confidence set was calculated as the sum of the Akaike weights over all the models in which the predictor appeared. We also explored potential interactions between the elevation difference and other predictors, but the interactions were excluded from the multimodel inference approach presented here because of the reasons explained in Appendix I.4. Continuous variables were log-transformed (when showing a positive skewness) and then scaled prior to modelling. We checked for collinearity among continuous predictors prior to modelling and found no correlation among predictors ($\rho < 0.7$).

We checked for potential overparameterization for each of the lowest AIC_c models selected by plotting the profile of the (restricted) log-likelihood over all the variance and the correlation components of the models (Viechtbauer, 2010). We analysed publication bias by using the 'funnel' function of the R package *metafor* (Viechtbauer, 2010) and used the modification of the Egger's test proposed by Nakagawa & Santos (2012) to assess funnel plots' asymmetry of the null-models' residuals. We found no evidence for funnel plot asymmetry for all traits analysed except for P*mass*. The funnel plot of P*mass* was found to be asymmetric due to the large heterogeneity of the true effect, which was not reduced significantly by the inclusion of any predictor in the model. However, the asymmetry of the residuals did not support evidence of publication bias for P*mass* when analysed in a contour-enhanced funnel plot[Nakagawa & Santos (2012); see Appendix I.5].

Finally, to answer question (d), we calculated pairwise Pearson's correlation coefficients of log-response ratios to quantify the degree of association between trait variations along elevational gradients (see Figure I.6.1, Appendix I.6). The correlation coefficients were estimated on a subset of data retaining only the studies reporting both traits. When correlations were significant ($\rho < 0.01$), the trait–trait relationships were quantified with standardized major axis (SMA) slopes [see e.g. Onoda *et al.* (2017); Wright *et al.* (2004)] estimated using the 'sma' function of the *smatr* R package (Warton *et al.*, 2011). The SMA was fitted using robust Huber's M estimation to han-

dle outliers (Taskinen & Warton, 2013). Since this method does not account for the sampling variance nor for the non-independence of the effect sizes, we also estimated the relationship between traits by fitting meta-analytical models (as described above) with the lnRR of the first trait as the response and the second trait as the predictor (Vanneste *et al.*, 2019). We applied these asymmetric regressions with the aim to check whether trait–trait relationships were affected by non-independence and the weight of the observations. The relationships found with asymmetric regression were virtually non-distinguishable from the results using the SMA and the correlation analyses (Figure I.6.2, Appendix I.6). We did not apply multivariate meta-analytic models to estimate the relationship among our response variables along elevation, as the correlation among leaf traits reported by the individual studies were not available and they were necessary to compute a VCV matrix in meta-analyses with multiple correlated outcomes (Berkey *et al.*, 1998; Lajeunesse, 2011).

All the analyses were performed in R version 3.4.4 (R Core Team, 2018).

Results

Despite large variation in the magnitude of trait response, we found clear evidence that intraspecific leaf traits of plants follow consistent patterns of change in response to increasing elevation worldwide. Both sets of models analysing the effect of elevation alone (Figure 2) and the multimodel analysis (Figure 3), indicated that SLA and δ^{13}C response ratios (lnRRs) linearly decreased with increasing difference in elevation, while LMA, N*area* and N*mass* lnRRs increased with elevation. Elevation difference showed the highest relative importance (AIC$_c$W) across candidate models (Figure 3) for SLA, LMA, N*area*, N*mass* and δ^{13}C. Conversely, we found no significant evidence of a consistent trend in LA and P*mass*. LA had a regression slope estimate close to zero, while P*mass* overall increased with elevation, but with a large confidence interval of the slope estimate (Figure 2).

Among relevant predictors moderating overall trait–elevation relationship, the multimodel analysis indicated that only N*mass* was significantly influenced by MGST (Figure 3). However, the lowest AIC$_c$ models of N*area*, N*mass*, P*mass* and δ^{13}C retained MGST as a significant predictor, indicating that overall larger positive trait variation occurred along elevational gradients with relatively warmer growing seasons (Figure 4). The meta-regression analysis also indicated that both herbaceous and woody species tended to have leaf traits changing with the same direction along elevation. However, we found response ratios of SLA to decrease more strongly in herbaceous species than woody species (Figure 3), although the same pattern was not observed in the dataset of LMA. We found no significant evidence for the absolute elevation at the lowest site, mean annual solar radiation, latitude and aridity index to significantly affect the trait variation in any of the leaf functional traits analysed.

The comparisons of response ratios of different traits reported in the same study and species revealed that certain leaf traits tend to covary along elevational gradients (Figure 5). We found the relative change in δ^{13}C to linearly decrease with increasing LA ($R^2 = 0.40$) and SLA ($R^2 = 0.24$), and with decreasing LMA ($R^2 = 0.61$) and N*area* ($R^2 = 0.38$). Conversely, N*mass* and P*mass* variations were not correlated with δ^{13}C variation. Furthermore, P*mass* did not change consistently with any of the other investigated traits except N*mass* ($R^2 = 0.34$) indicating that two traits positively covary along elevation.
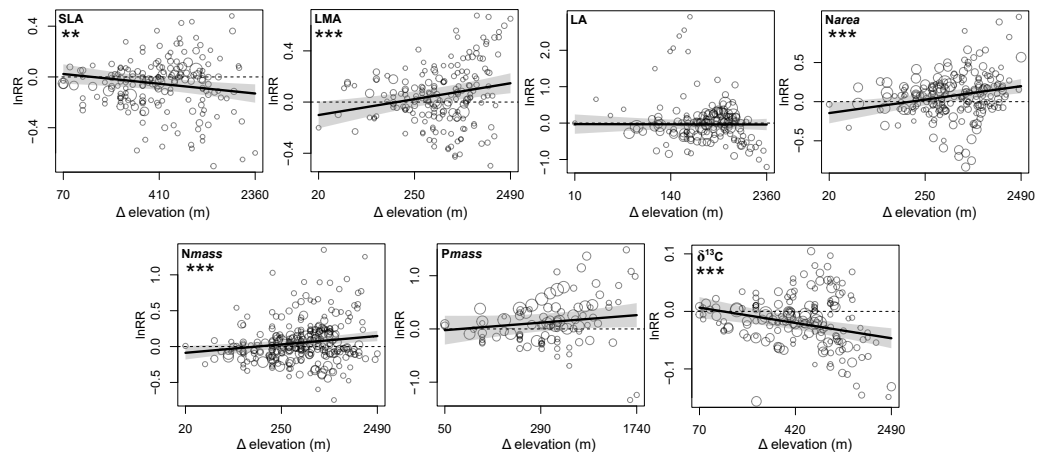
Figure 2: *Intraspecific leaf trait variation (lnRRs) in response to difference in elevation (i.e. the vertical distance between two sites sampled along a gradient) across gradients included in the meta-analysis. Solid lines represent the slope estimate of the model (and 95% confidence intervals) with difference in elevation as a predictor only. Significance levels (**$\rho < 0.01$; ***$\rho < 0.001$) are provided for the slope estimates. A positive value of lnRR indicates that the mean of a certain trait for a given species increases relatively to the mean sampled at the lowest elevational level, except for carbon isotope composition ($\delta^{13}C$) (see 'Materials & Methods'). The dashed lines indicate no change compared to the site sampled at the lowest elevation. Point size depicts the observation weight (weighted by 1/SE). The values on the x-axes are back-transformed from the log-scale in each dataset separately for graphical representation purposes*

Discussion

Leaf traits response to elevation

Our results corroborate that changes in intraspecific leaf traits follow general patterns in response to elevation and that such patterns occur across different plant species and mountain ranges worldwide. This agrees with previous meta-analyses which found consistent patterns of trait variation across multiple elevational (Read *et al.*, 2014) and latitudinal (De Frenne *et al.*, 2013) gradient studies. Despite large variation, we found that elevation significantly affected all leaf traits analysed (SLA/LMA, N*area*, N*mass* and $\delta^{13}C$) except LA and P*mass*. Overall, we showed that with increasing difference in elevation, plants of the same species produce leaves adapted to abiotic stress (low temperature). At the same time, leaves exhibit lowered competitive abilities (e.g. lower SLA) and decreasing herbivore pressure (i.e. higher N*area* and N*mass*) with increasing elevation (Callis-Duehl *et al.*, 2016). It remains uncertain whether trait variation across elevations is genetically fixed via local adaptation or can be attributed to phenotypic plasticity (Bresson *et al.*, 2011; Morecroft & Woodward, 1996; Pfennigwerth *et al.*, 2017).
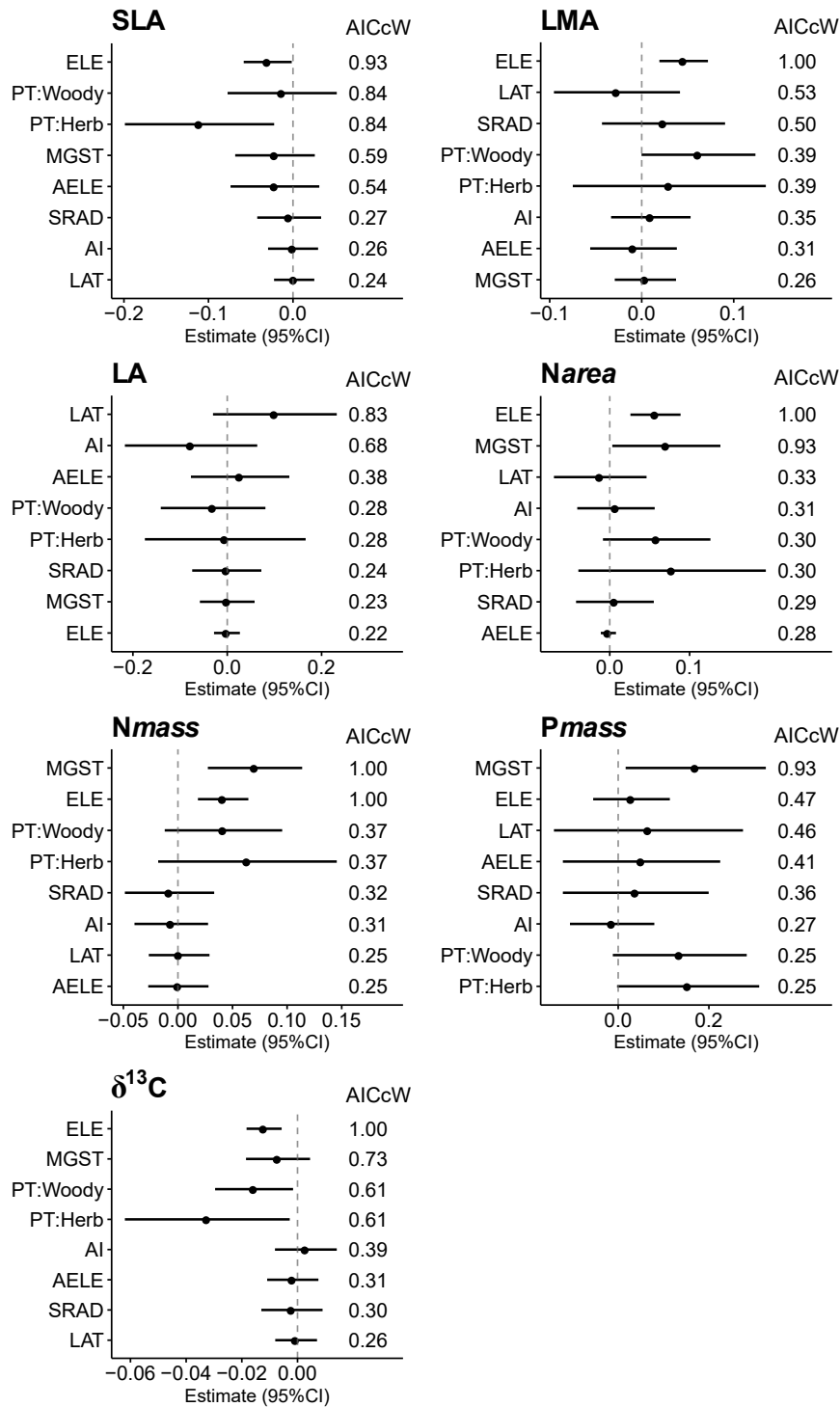
Figure 3: *Averaged estimates and 95% confidence intervals (CI) for fixed effects included in the confidence set of models explaining response ratios (lnRR) of intraspecific leaf trait variation observed across elevational gradients. Continuous predictors are scaled to standardize the magnitudes of the estimates. The relative importance (AIC$_c$W) is the sum of AIC$_c$ weights of models in which a given predictor is retained. AELE, absolute elevation of the lowest site sampled in a gradient; AI, aridity index; ELE, difference in elevation; LAT, latitude; MGST, mean growing season temperature; PT, plant functional types mean pooled effect size (woody or herbaceous); SRAD, mean annual solar radiation*

Figure 4: *Intraspecific leaf trait variation (lnRRs) along elevational gradients of Narea, Nmass, Pmass and $\delta^{13}C$ in response to the average mean growing season temperature (MGST) (°C, three warmest months) of each elevational gradient. Solid lines represent the slope estim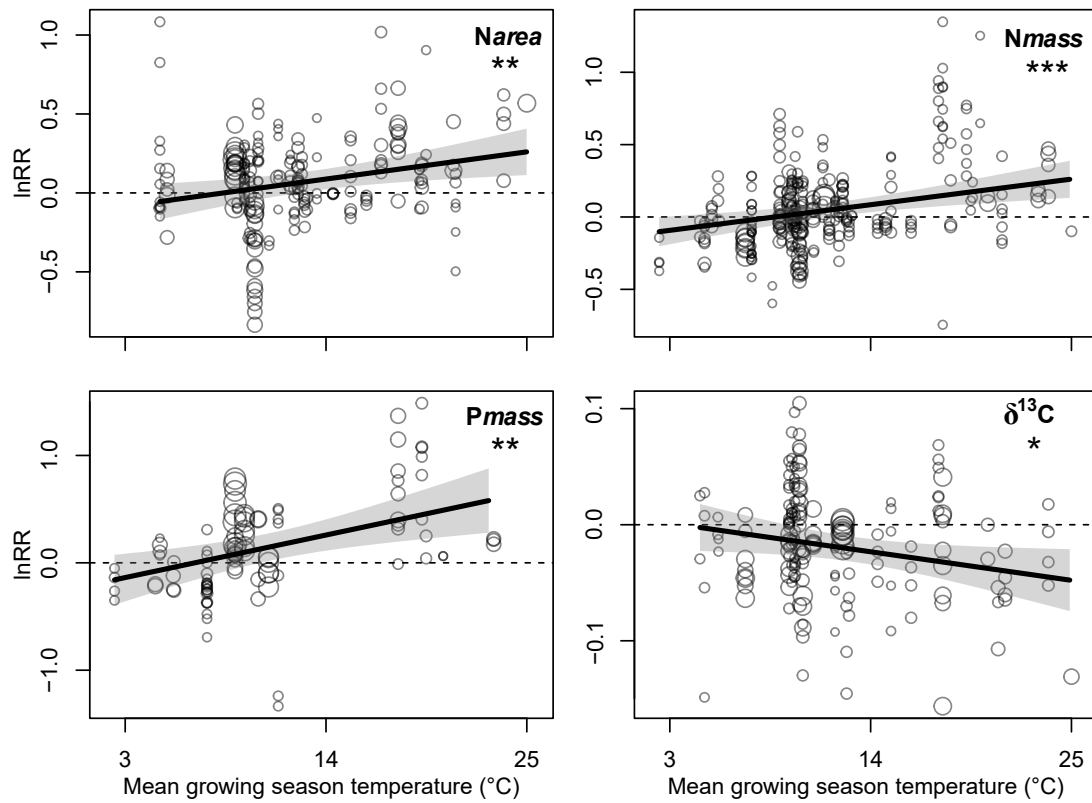ate (and 95% confidence intervals) obtained from the lowest AIC_c model in which MGST was retained as moderator. Significance levels (*$\rho < 0.05$; **$\rho < 0.01$; ***$\rho < 0.001$) are provided for the slope estimate. A positive value of lnRR indicates that the mean of a certain trait for a given species increases relatively to the mean sampled at the lowest elevational level, except for carbon isotope composition ($\delta^{13}C$) (see 'Materials & Methods'). The dashed lines indicate no change compared to the site sampled at the lowest elevation. Point size depicts the observation weight (weighted by 1/SE)*

With a review of common garden experiments, Read *et al.* (2014) found that genetic differentiation often explains a significant amount of intraspecific variation in LMA, N*mass* and N*area* among populations at different elevations and latitudes. However, few common garden experiments have recently highlighted the role of phenotypic plasticity to strongly mediate intraspecific plant traits' variation along elevation (Anderson & Gezon, 2014; Henn *et al.*, 2018; Lajoie & Vellend, 2018).
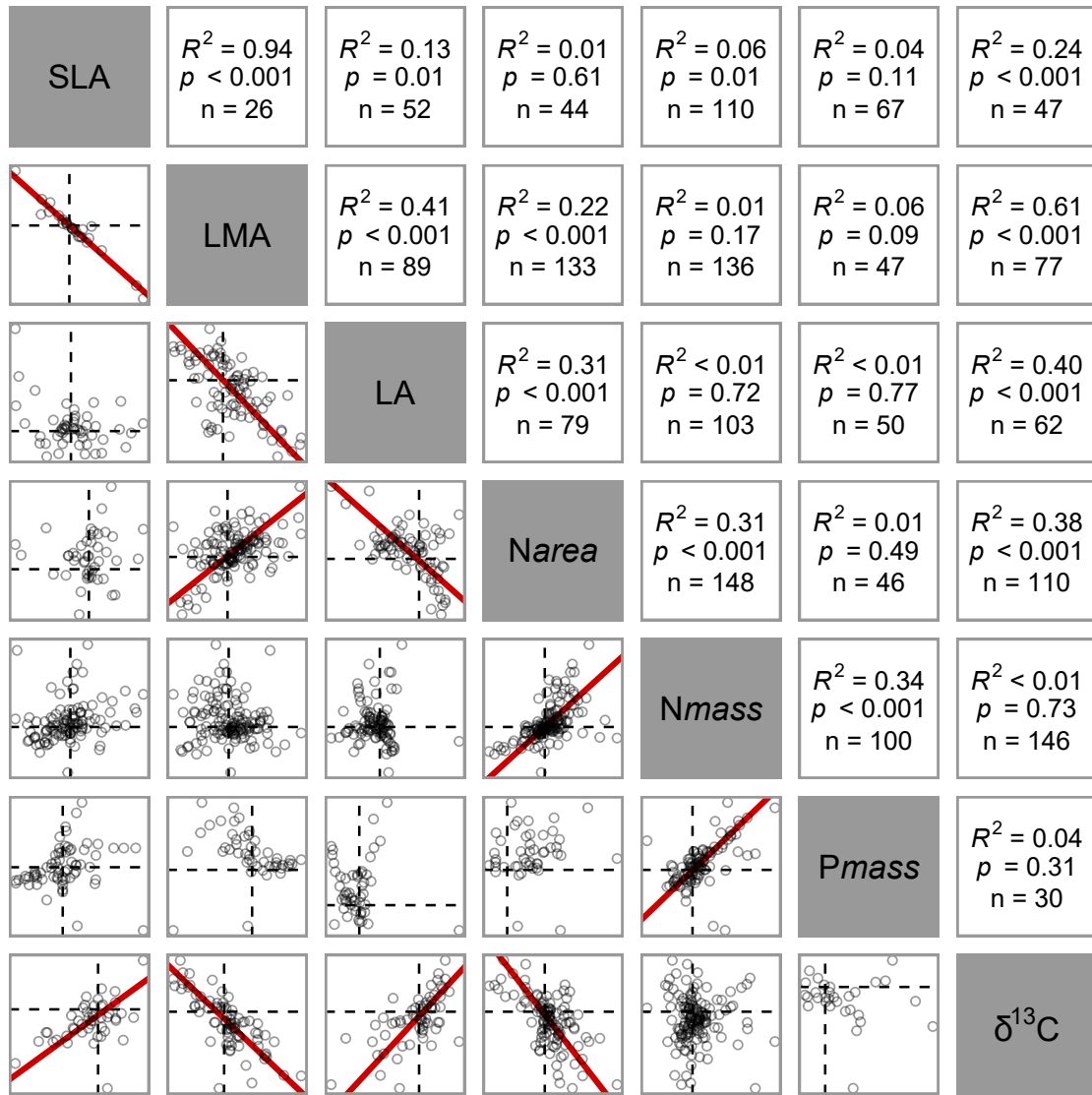
Figure 5: *Standardized major axis (SMA) results analysing the relationship among response ratios (lnRR) of leaf traits across elevations. Each SMA is obtained from a subset of studies reporting data for both traits used in the SMA. The bottom-left part of the figure shows scatterplots of the lnRRs of each combination (with dashed lines indicating lnRR = 0) and the SMA slope [in red, only showed when the p-value of the correlation coefficient was smaller than 0.01; see (Onoda* et al.*, 2017)]; the to-right part of the figure report for each SMA the squared correlation coefficient (R^2), p-value of the test of correlation coefficient (ρ) and the number of observations available for each subset (n). A negative correlation with leaf carbon isotope composition response ratios ($\delta^{13}C$) indicate that $\delta^{13}C$ is positively correlated with a given trait (see 'Materials & Methods')*

The detected changes in SLA and LMA along elevational gradients indicate that the leaves tend to be thicker and the tissues denser in response to decreasing temperature and increasing irradiance (Poorter *et al.*, 2009). Although plants species growing at high elevations worldwide tend to produce small leaves (Wright *et al.*, 2017), our results indicated that intraspecific LA variation is not affected by increasing difference in elevation. Our findings suggest that individuals may need to maintain large LA to capture light while compensating the lower photosynthetic efficiency driven by the increased leaf tissue density as expressed in SLA and LMA (Poorter *et al.*, 2009).

The N*area*, N*mass* and P*mass* are traits representing the amount of proteins and nucleic acids stored in the leaf that can be invested for photosynthesis and growth (Ghimire *et al.*, 2017; Onoda *et al.*, 2017). In concordance with the previous meta-analysis of Read *et al.* (2014), we showed N*area* to follow a positive trend across elevational gradients worldwide. Conversely, Read *et al.* (2014) found no relationship between elevation and N*mass* with a mean correlation close to zero, possibly because of the strong interdependence of N*mass* with soil fertility, which does not necessarily covary with elevation (Körner, 2007). Thus, the positive trend we found for N*mass* along elevation was in contrast with the hypothesis that leaf traits shows resource-conservative strategies with increasing elevation difference (Pfennigwerth *et al.*, 2017; Read *et al.*, 2014). In addition, increasing LMA is expected to lower the fraction of leaf N invested in the synthesis of photosynthetic proteins (resulting in lower N*mass*) and to increase the internal resistance to CO_2 diffusion to the sites of carboxylation (Ghimire *et al.*, 2017; Onoda *et al.*, 2004, 2017). However, the changes in leaf nutrient content we observed were consistent with Körner (1989) and with the increase in leaf N and P concentration towards the poles as average temperature decreases (Reich & Oleksyn, 2004). Furthermore, the increasing Nmass at lower temperatures might reflect the acclimation of optimal N use efficiency and decreased N dilution due to the reduced aboveground biomass growth rate (Weih & Karlsson, 1999, 2001). Our findings on the intraspecific leaf trait covariation along elevational gradients (Figure 5) were partially in concordance with the leaf economic spectrum so far conceived at the interspecific level (Wright *et al.*, 2004): variation in N*mass* was found to be positively correlated with LMA and N*mass*, but we found no relationship of LMA (and SLA) with N*mass* and P*mass* variations. However, it is noteworthy that the regional- and global-scale patterns reported in literature on the leaf economic spectrum are primarily interspecific effects, typically based on a single estimate per species for each trait and ignoring within-species variation (Bolnick *et al.*, 2011; Wright & Sutton-Grier, 2012). It remains unclear whether these patterns should be reflected at the intraspecific level across environmental gradients at smaller spatial and ecological scales (Albert *et al.*, 2010; Wright & Sutton-Grier, 2012).

The δ^{13}C increase with elevation suggests that the difference between CO_2 partial pressure inside the leaf to that in the atmosphere increases with elevation. Changes in δ^{13}C are generally attributed to the shifts between CO_2 demand of leaf mesophyll and the diffusion of CO_2 from the atmosphere through the stomata (Hultine & Marshall, 2000; Körner *et al.*, 1988). The δ^{13}C is then linked to photosynthetic water-use efficiency (WUE), quantified as the ratio of amount of photosynthetic carbon gain to water loss via transpiration (Hultine & Marshall, 2000). The increasing δ^{13}C with elevation we found is consistent with the conclusion that plants at higher elevation show higher leaf δ^{13}C worldwide (Körner *et al.*, 1988; Wang *et al.*, 2013). Environmental factors influencing the positive trend of δ^{13}C along elevational gradients are not fully clear in the literature (Körner *et al.*, 1991; Morecroft *et al.*, 1992), but evidence suggest that such trend is linked to both decreasing temperature and atmospheric pressure (Cernusak *et al.*, 2013). Lower oxygen partial pressure increases the carboxylation efficiency of the Rubisco enzyme (Farquhar & Wong, 1984) and the decreasing temperature slows down the transport of water in the plant, resulting in reduced leaf CO_2 diffusion rates (Cernusak *et al.*, 2013). Additionally, the leaf δ^{13}C response may not depend on environmental factors directly but on the morphophysiological adjustment of the leaf to elevation (Gerdol *et al.*, 2018; Hultine & Marshall, 2000; Vitousek *et al.*, 1990; Zhu *et al.*, 2010). Indeed, our results indicate that δ^{13}C increase when LA is re-

duced (Figure 5), possibly because the plant adapts the level of WUE to transpiration rate and light interception, which both depend on the LA (Wright *et al.*, 2017). Finally, similar to what we suggested for leaf N, the covariation we found for δ^{13}C with SLA and LMA (Figure 5) in both datasets might reflect leaf physiological compensation to decreasing carboxylation efficiency induced by increasing leaf tissue density (Vitousek *et al.*, 1990).

Climatic factors influencing the response of leaf traits to elevation

Our analysis revealed that the directions of trait–elevation relationships generally do not differ across different climates mountain ranges worldwide. However, our multi-model inference analysis revealed that the magnitude of the intraspecific leaf trait variation along elevational gradients is affected by the mean temperature of the growing season. The overall responses of N*area*, N*mass*, P*mass* and δ^{13}C to increasing elevation tended to be stronger along elevational gradients located in warmer macroclimates (Figure 4). However, a significant interaction between the elevation difference and mean temperature of the gradient appeared only for N*mass* such that N*mass* increases with elevation difference more strongly in warmer compared to colder gradients (see Appendix I.4). These findings show that plants growing on warmer mountain ranges tend to store larger amounts of N per unit of mass in response to increasing elevation compared to plant species located in mountain ranges where the growing season is characterized by lower temperatures. This is probably linked to the overall higher N concentration in the leaf of plants in cold climates (Körner, 1989), which smoothens the effect of increasing N content with decreasing temperatures along elevational gradients compared to generally warmer climatic conditions. From an ecological point of view, this also suggests that species growing on warmer mountains tends to become potentially more competitive and resource-acquisitive with elevation compared to species located in colder mountain areas. In addition, the current climate warming trends enhance species richness and abundance along elevational gradients and might thus favour plant species that are adapted to live in N-rich conditions, because these species are expected to show higher nutrient content and resource investment in response to increasing competition (Rumpf *et al.*, 2018a).

We found that the response to increasing difference in elevation does not depend on the elevation of the lowest site sampled, indicating that leaf traits of plants growing both at higher and lower elevation respond with the same magnitude of change to increasing elevational range. This suggests that although plants growing at higher absolute elevation levels show, for example, higher LMA and nutrient concentration (Körner, 1989, 2003), their relative change to increasing elevational range is expected to be proportionally equal to the one of species with lower LMA and nutrient concentration at lower elevation, possibly because absolute elevation alone does not significantly impact plant growth on a large geographical extent (Körner, 2007).

Finally, we acknowledge the importance of including potential interactions between the elevation difference and other climatic moderators when modelling plant trait variation across elevational gradients (see Appendix I.4). However, models including interactions become more difficult to be analysed [e.g. with multimodel inference; see Grueber *et al.* (2011)] and call for a restricted selection of a priori hypotheses to limit the number of ecologically meaningful interactions (Burnham & Anderson, 2010; Dochtermann & Jenkins, 2011).

Plant functional types responses

We found significant differences in magnitude of variation in SLA across woody and herbaceous species. Our results indicated a larger negative response in herbaceous species in intraspecific SLA with increasing elevation compared to woody species. These findings support the general hypothesis that fast-growing herbaceous plants are better able to express phenotypic plasticity in response to changes in environmental conditions (Maire *et al.*, 2013), compared to woody species (Siefert *et al.*, 2015). However, differences in the magnitude of traits response across functional groups found in SLA were not reflected in the LMA dataset nor in any of the other traits analysed here, possibly because herbaceous and woody functional types overlap substantially in their leaf trait characteristics (Wright *et al.*, 2004). In addition, the overall low differences between plant functional types response to elevation reflected the results of Siefert *et al.* (2015) who compared the relative extent of ITV in plant communities and found no significant difference in the magnitude of variation between woody and herbaceous species. Furthermore, elevation might not be a relevant driver in such context, but aridity gradients have been showed to affect intraspecific trait response across functional groups (Wellstein *et al.*, 2017). In general, larger attention should be paid to the role of different functional groups when analysing within-species trait variability along environmental gradients, as different groups might exhibit contrasting magnitudes of intraspecific variation [see e.g. Albert *et al.* (2010)].

From elevation to temperature changes

The relationships between elevation difference and leaf traits we explored here showed strong similarity with the trait syndrome characterizing plants adapting to colder environments along spatial temperature gradients (Reich & Oleksyn, 2004; Tian *et al.*, 2016). Indeed, temperature is the main factor affecting plant growth that covaries consistently with elevation in different mountains worldwide (Jump *et al.*, 2009; Körner, 2007). Similar to latitudinal gradients (De Frenne *et al.*, 2013), elevational gradients offer a promising tool to infer plant responses to temperature change. Combining information obtained from elevational and latitudinal gradients holds the potential to advance our knowledge on plant trait responses to global warming (Fukami & Wardle, 2005; Read *et al.*, 2014). However, space-for-time substitution approaches may still inaccurately represent short-term ecosystem change in trait-based ecology [see e.g. Bjorkman *et al.* (2018)]. In addition, predicting the potential effects of temperature change based on multiple elevational and latitudinal gradients suffers from various weaknesses. Besides the heterogeneity caused by different experimental designs, study aims and biogeographical contexts, which can be accounted by using meta-analytical approaches [see e.g. Midolo *et al.* (2019a)], studies analysed often do not report data on temperature change along each gradient (Graae *et al.*, 2012) as well as other relevant factors such as humidity, soil fertility and land use. As a result, both elevational and latitudinal gradients are still currently underused to study climate change on a large geographical extent (De Frenne *et al.*, 2013).

In addition, it is noteworthy that our findings suggest a common pattern of intraspecific SLA (and LMA) variation across multiple elevational gradients worldwide. Conversely, the response of SLA to drought, for instance, depend on the functional group and geographical location (Wellstein *et al.*, 2017). According to our findings, traits of species located in different biomes of the world are similarly adapted to an in-

crease in elevation, while plants can show contrasting strategies to deal with drought at smaller geographical scales (Wellstein *et al.*, 2017). This means that direction of plant functional responses to temperature changes could be predicted more easily while plant functional response to changes in water availability has to be tested against the evolutionary background of the species. Moreover, in line with De Frenne *et al.* (2013), Read *et al.* (2014) and Wellstein *et al.* (2017), our findings further reinforce the importance of intraspecific variation as important driver of functional plant response to climate changes.

Concluding remarks

We here combined results of multiple elevational gradients studies focusing on leaf trait variation with a meta-analysis to reveal patterns of intraspecific morphophysiological traits adjustment to high-elevation conditions worldwide. Summarizing evidence from a variety of elevational gradients helps us to understand the potential implications of climate change on individual species in the coming years when focusing on temperature changes taking into account other changes across elevations (Körner, 2007). Irrespective of the mechanisms behind traits variation along elevational transects, we clearly showed that populations located along elevational gradients exhibit individuals adapted to different abiotic conditions. Since the distribution of mountain biota is shifting upslope in response to climate change (Lenoir *et al.*, 2008; Rumpf *et al.*, 2018a,b; Steinbauer *et al.*, 2018), our results are particularly important to understand how plants adapt to such elevation shift in a warming planet. Within the considered temperature range, our findings indicate that future upward migrating species most likely will lower their SLA and increase their nitrogen content and 13C. However, our analysis was restricted within the elevational range of the species. Trait variation outside the realized elevational range has rarely been tested so far [Violle & Jiang (2009), but see e.g. Cui *et al.* (2018)]. In this context, experimental research would establish new knowledge on the hidden part of plant variability. For example, experimental networks conducted on a large geographical extent represent a promising opportunity to simulate niche expansion under global environmental change, such as the International Tundra Experiment evaluating plant responses to accelerated rising temperature (Bjorkman *et al.*, 2018; Elmendorf & Moore, 2008); the Nutrient Network simulating atmospheric N deposition (Firn *et al.*, 2019); and the Free-AirCO $_2$ Enrichment experiments investigating ecosystems response to elevated atmospheric CO_2 concentration (Medlyn *et al.*, 2015).

Finally, the magnitude of ITV we observed is expected to scale up to higher levels of biological organization (Violle *et al.*, 2007). Thus, when analysing functional trait response to elevation at the community level, intraspecific variability is expected to significantly contribute to the variation observed among plant assemblages at different elevation levels.

Finally, we extend our gratitude to all the authors of the primary studies included in the meta-analysis who indirectly contributed to this work.

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4 Chapter II – Plant performance and survival across transplant experiments depend upon temperature and precipitation change along elevation

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Abstract

1. Understanding how plant individuals perform in non-local sites is key in the context of contemporary range shifts along elevation. Transplant experiments conducted in mountain ecosystems are rising as key tools to measure the intraspecific response of individuals transplanted across contrasting elevations. However, a synthesis quantifying patterns of plant performance in response to changes in abiotic factors across different species and mountain ranges is still lacking.

2. We conducted a meta-analysis to quantitatively summarize patterns of plant species' performance variation in response to changes in temperature and precipitation within their elevation range across multiple transplant experiment studies. We compiled a dataset obtained from 38 studies and 49 vascular plant species in total addressing intraspecific performance variation in terms of survival, germination, biomass, height, number of vegetative organs, number of reproductive units, SLA and leaf size. We both compared pairs of transplanted individuals to those growing at their site of origin ('away vs. home') and to the local individuals found at the site of transplant ('foreign vs. local').

3. Overall, individuals transplanted downward showed larger biomass and height compared to their site of origin but failed to adjust these traits and survival to that of local individuals. Individuals transplanted upward adjusted their traits by decreasing plant growth and number of reproductive units to that of local individuals but showed lower survival. Importantly, changes in survival, biomass, height, leaf size, number of vegetative organs and reproductive units increased linearly with the difference in mean annual temperature between site of transplant and site of origin in the 'away vs. home' comparison. Conversely, changes in biomass, leaf size, number of vegetative organs and reproductive units increased with mean annual precipitation difference between sites in the 'foreign vs. local' comparison.

4. *Synthesis*. We detected common trends in survival and intraspecific trait variation across different species and transplant experiments conducted along elevational gradients. Because plasticity and adaptation play a crucial role in plant shifts, establishment and persistence under non-local environmental conditions, our meta-analysis contributes to better understand how rapid plant shifts are constrained by climatic conditions within species' elevational range.

Introduction

Plant species distribution is highly influenced by changes in climatic conditions (Kelly & Goulden, 2008; Lenoir *et al.*, 2008; Rumpf *et al.*, 2018a). Global environmental changes are predicted to increase the disequilibria between current environmental conditions and those to which individuals have locally adapted. Such disequilibria might cause changes in elevational and latitudinal optima of species distribution ranges, with possible consequences in biotic homogenization and changes in biodiversity (Bertrand *et al.*, 2011; De Frenne *et al.*, 2013; Pulido *et al.*, 2019; Rumpf *et al.*, 2018b; Svenning & Sandel, 2013).

In response to altered environmental conditions, plants can adapt (Nicotra *et al.*, 2010; Valladares *et al.*, 2014) and shift over short (Scherrer & Körner, 2010) and large geographic distances (Jump & Penuelas, 2005; Peñuelas *et al.*, 2013). Generally, changes of the environmental conditions in situ or differences of the environmental conditions encountered in newly conquered habitats can have eco-evolutionary effects on a species. For example, at warmer trailing edges, populations might shrink and survive with changes in the genetic pool of the population (Nadeau & Urban, 2019). At leading edges, during the process of spread, bottleneck effects might affect the genetic diversity of the species (Gilbert *et al.*, 2018). Despite the strong evidence of most species moving toward higher elevation in response to global warming (Chen *et al.*, 2011; Parolo & Rossi, 2008; Rumpf *et al.*, 2018b), various studies have also reported species with downward optimum elevation shifts (Crimmins *et al.*, 2011; Dobrowski *et al.*, 2013; Rapacciuolo *et al.*, 2014). Such opposite trend is either attributable to competitive release at the lower margin of the distribution niche (Lenoir *et al.*, 2010), to land-use change (Bhatta *et al.*, 2018; Guo *et al.*, 2018), or caused by other climate change-impacted variables than temperature (Dobrowski *et al.*, 2013; Rapacciuolo *et al.*, 2014), such as water availability (Crimmins *et al.*, 2011). It is therefore important to understand how the performance and survival of specimens originated from different elevations respond to altered conditions following both upward and downward shifts. Because many plant species are not able to shift fast enough along elevation to keep up with ongoing climatic changes (Rumpf *et al.*, 2018b), both local adaptation and plasticity of functional traits play a relevant role when predicting species range shifts under climate change (Jump & Penuelas, 2005; Valladares *et al.*, 2014). In general, local adaptation arises from genetic selective pressures promoting trait expressions adapted to the local environment (Kawecki & Ebert, 2004), while phenotypic plasticity represents the ability of a genotype to adjust its phenotype when exposed to different abiotic and biotic conditions without genetic variation (Ghalambor *et al.*, 2007; Sultan, 2000). In the short term, plasticity may be beneficial in the establishment and persistence of plants in new environments, and it is therefore a key mechanism for individuals colonizing range margins in response to global environmental changes (Matesanz *et al.*, 2010; Nicotra *et al.*, 2010). However, both adaptation and plasticity can also interact, leading for example to populations differing in the degree of locally adaptive plasticity (Schmitt & Dudley, 1996). In fact, a recent modelling study confirmed that natural patterns of environmental variation favour the evolution of adaptive transgenerational plasticity (Colicchio & Herman, 2020). Furthermore, plasticity can even delay adaptation by shifting the phenotypes in the population towards their ecological optimum and preserving genes from natural selection (Fox *et al.*, 2019).

Complementary to latitudinal gradients, elevation gradients are overall rising as key ecological tools to understand plant responses to changes in environmental condi-

tions occurring over geographic distances (Graae *et al.*, 2012; Jump *et al.*, 2009; Körner, 2007). Plant species experience different environmental conditions along their elevation range of distribution which is expected to determine intraspecific patterns of trait variation (Midolo *et al.*, 2019; Read *et al.*, 2014), together with genetic differentiation (de Villemereuil *et al.*, 2018; Gonzalo-Turpin & Hazard, 2009). Beside steep temperature variation, elevational change often encompasses changes in precipitation and humidity, but such variation does not necessarily correlate with elevation across mountains worldwide (Körner, 2007). Thus, geographical temperature and precipitation variation represent relevant predictors to be accounted when comparing elevation or latitudinal gradient studies originated from different experimental and environmental contexts (De Frenne *et al.*, 2013; Körner, 2007).

Transplant experiments represent a powerful approach to empirically ascertain adaptation and plasticity along environmental gradients (Kawecki & Ebert, 2004) with important implications on plant species distribution under climate change (Lee-Yaw *et al.*, 2016). In general, transplant experiments are becoming increasingly relevant in applied ecology, for instance to simulate trait response to climate change along environmental gradients (De Frenne *et al.*, 2014), to understand the elevational shift of invasive non-native species (?Kollmann & Bañuelos, 2004) and to identify potential niche limits with transplants beyond species' distribution ranges (Hargreaves *et al.*, 2014; Lee-Yaw *et al.*, 2016). When such experiments are conducted along elevation gradients, individuals of different population origin are transplanted at different elevations to identify the basis of adaptive intraspecific trait variation. Specifically, in reciprocal transplants, individuals of different populations are reciprocally transplanted between elevations of origin, simultaneously assessing how specimens respond to upward and downward shifts within the species range (Cui *et al.*, 2018; Gonzalo-Turpin & Hazard, 2009; Lajoie & Vellend, 2018). Reciprocal transplant experiments thereby allow to test for local adaptation, which is expected to occur when individuals show larger mean performance growing in their site of origin ('home') compared to 'away' sites, and when 'local' individuals have on average higher performance than transplanted 'foreign' individuals (Blanquart *et al.*, 2013; Kawecki & Ebert, 2004). At the same time, reciprocal transplant experiments hold the potential to quantify phenotypic plasticity, simulating plant species distribution shifts in response to environmental change (Cui *et al.*, 2018; Henn *et al.*, 2018).

Despite recent syntheses involving transplant and common-garden experiments to elucidate patterns of plant performance and adaptation change along environmental gradients (Halbritter *et al.*, 2018; Leimu & Fischer, 2008; Pulido *et al.*, 2019), little efforts have been payed to summarize recent literature on the intraspecific responses along elevation across multiple reciprocal transplant experiments. Only Halbritter *et al.* (2018) to our knowledge, reported a systematic review including transplant experiments across elevations showing significant evidence of higher biomass and survival in local individuals compared with foreign ones. However, their analysis on reciprocal transplants did not disentangle climatic variation (in temperature and precipitation) along elevation across transplant sites and focused on 22 species and 14 reciprocal transplant experiment studies available up to 2015. Here, we report novel results of a meta-analysis of 38 transplant experiments studies focusing on the response of 49 plant species in total to both upward and downward transplants within the species' elevational range across different mountain ranges of the globe. We focused on eight response traits capturing the three major dimensions of plant individual performance [i.e. survival, growth and fecundity; Violle *et al.* (2007)], namely survival of individu-

als at the end of transplant, germination percentage, above-ground biomass, vegetative height, number of vegetative organs, number of reproductive units, SLA and leaf size. Specifically, we aimed (a) to quantify how plant survival and different traits are overall affected by upward and downward transplants when transplanted individuals of the same species are compared both to those growing at their site of origin ('away vs. home') and to individuals of the local population ('foreign vs. local'); and (b) to test whether temperature and precipitation difference between transplant and origin sites, as well as absolute temperature and precipitation of the transplant site, plant functional group and horizontal geographic distance between sites, explain intraspecific survival and trait variation patterns in response to experimental transplantation.

Materials & Methods

Study selection and inclusion criteria

We searched for primary studies in Scopus and Web of Science with the use of advanced search strings containing terms related to transplant experiments, plant individual performance (e.g. 'survival', 'growth', 'reproduction') and elevation (see Appendix II.1 for advanced search strings and flow chart of primary study selection [Figure II.1.1]). After excluding duplicates, we identified 488 candidate primary studies published up to December 2019. We only included studies conducted at the intraspecific level along single elevation transects or gradients, where individuals are reciprocally grown within in-situ transplant sites excluding interactions with individuals of other species. Thus, we excluded studies and observations that investigated trait variation between different plant species and assemblages or at large geographical scales (namely, transplants conducted along latitudinal gradients or without clear focus on the effect of elevation change). Our meta-analysis was restricted to transplant experiments reporting data originated from measurements on individuals planted and growing within transplant sites only. Furthermore, we only selected studies with transplant sites occurring within the elevational range of the species. In case a study reported transplants beyond the species' elevational range, we did not include such data. We included studies on nonnative species as long as the species had its current distribution within the elevational range analysed (i.e. two studies on *Ageratina adenophora* in Western Himalaya and Southwest China [see Appendix II.2, Table II.2.1]).

For the aim of our meta-analysis, we were mainly looking for reciprocal transplant experiments studies including both upward and downward transplants within the elevational range of the species. However, we also included transplant experiment studies with no fully reciprocal transplant design, namely only comparing transplanted individuals either to local individuals [e.g. (de Villemereuil *et al.*, 2018)] or to those transplanted within their site of origin only [e.g. (Flegrová & Krahulec, 1999)]; see Appendix II, Table II.2.1]. We scanned the abstract and the content of the papers and identified 38 studies eligible for inclusion published between 1990 and 2019 (Figure II.2.1). Our dataset encompassed 19 families with 49 vascular plant species in total: forbs (22), graminoids (17) and trees (10) (see Appendix II.2 for summary list of study and species included). The list of primary studies used in the meta-analysis is provided in the 'Data sources' section. Transplant experiment studies were located in Europe (18), America (13), East Asia (5) and Australia (2) (Figure II.2.2).

Trait selection and data collection

We focused our analysis on survival and seven of the most frequently reported traits across studies selected: germination percentage, above-ground biomass, vegetative height, number of vegetative organs, number of reproductive units, SLA and leaf size. Studies selected for meta-analysis reported one or more of the response traits mentioned above (see Figure 1 and Appendix II.2 for number of studies and observations available for each response variable, study and species assessed).

Survival and the intraspecific variation in such traits are expected to capture different components of plant performance at the individual level (Violle *et al.*, 2007) in response to changes in environmental conditions following transplant. Survival and germination are positively related to fitness, as they reflect the ability of individuals to establish in the environment. Conversely, other functional traits considered here tend to be positively related to fitness in certain environments and negatively in others. Specifically, in mountain ecosystems, plants adapted to high elevations normally show resource-conservative strategies resulting in lower SLA, growth and reproductive output to cope with larger abiotic stress compared to individuals found at lower elevation (Midolo *et al.*, 2019; Milla, 2009). Oppositely, lower elevation conditions tend to select for individuals with higher resource-acquisitive strategies in response to higher competition due to higher temperature and resource availability (Read *et al.*, 2014). Thus, plant performance in relation to adaptive trait variation in transplant experiments depend on the trait considered and on the direction of the transplant along elevation.

We collected survival and trait data reported by papers at the end of the experiment, which coincided with end of the growing season after transplant or after multiple years for perennial species. Survival was reported as the percentage of individuals surviving to the transplant, while germination as the percentage of seeds germinating after transplants. Biomass data collected were reported as above-ground biomass of individuals. Number of vegetative organs was reported in studies as the mean number of leaves or vegetative shoots present in single individuals or tillers (in graminoids). We categorized the 'number of reproductive units' either as the number of flowers, inflorescences, fruits or dispersal units per individual. We acknowledge that these metrics vary largely depending on the individuals, species and study under consideration; however, these metrics were all measured as indicators of plant reproductive output along elevations [see e.g. Halbritter *et al.* (2018)]. We only included leaf size values when it was reported as the area of the leaf (m^2), excluding leaf diameter, length or width.

We extracted the mean and standard error (or standard deviation and sample size) of each trait available reported in each transplant site. We obtained these data from graphs and figures using WebPlotDigitizer (Rohatgi, 2020), or retrieved those directly from tables, main texts or supporting information of the papers. We also extracted the elevation of each transplant site, the geographical coordinates. We contacted the authors of the primary studies to obtain data on missing standard deviation, sample size, elevation or geographical coordinates in case these were not reported in the papers directly. We also asked for data on plant traits and climatic variable that were potentially measured in the study, but not reported in the main results.

Within each dataset, we categorized each transplant in two types: 'downward' (when seeds or seedlings are transplanted to a lower elevation compared to their origin) or 'upward' (when seeds or seedlings are transplanted to a higher elevation compared to their origin). We used in total six bioclimatic predictors we expected to moderate

trait variation along elevation following transplants: (a) the difference in mean annual temperature between transplant site and site of origin (ΔMAT); (b) the difference in mean annual precipitation between transplant site and site of origin (ΔMAP); (c) the absolute mean annual temperature at the transplant site (MAT); (d) the absolute mean annual precipitation at the transplant site (MAP); (e) the geographical distance between site of transplant and site of origin of the plant population; and (f) the functional group of the species (classified as forbs, graminoids or trees). We calculated ΔMAT as the absolute MAT difference between transplant sites, while ΔMAP was expressed proportionally to the MAP baseline as the log-transformed ratio of MAP change between transplants.

In order to estimate MAT and MAP of each site, we combined geographic coordinates and elevation of transplant sites reported in the studies. For transplant sites located in Europe, North America and South America, we obtained MAT and MAP with the following software packages: 'ClimateEU' (v4.63), 'ClimateNA' (v5.21), 'ClimateSA' (v1.12) available at `https://sites.ualberta.ca/~ahamann/data.html`, based on the methodology described by Wang *et al.* (2016). For sites located in Asia Pacific we used the 'ClimateAP' (v2.20) software package available at `http://climateap.net` (Wang *et al.*, 2017). These softwares downscale the baseline climatic data (1961-1990; 2.5 arc min resolution) to scale-free point data through dynamic local elevation adjustments. The software packages mentioned above covered all site locations, except for three sites located in Hawaii. We obtained MAT and MAP at these sites from 234 m × 250 m resolution data available at the website of Evapotranspiration and Rainfall Atlas of Hawaii [available at `http://evapotranspiration.geography.hawaii.edu` and `http://rainfall.geography.hawaii.edu` respectively; Giambelluca *et al.* (2013, 2014)].

Across all sites, the ΔMAT values showed overall high correlation with the absolute difference in elevation between sites (= 0.98) reflecting the strong negative relationship between elevation and air temperature (Appendix II.3, Figure II.3.1). Conversely, elevation difference showed no correlation with ΔMAP (= 0.24; Appendix II.3, Figure II.3.1). Finally, we calculated the shortest horizontal geographic distance between transplant site and site of origin with the 'distGeo' function from the R package *geosphere* (Hijmans, 2017). We included geographic distance to account for different study design and potential effects of gene flow (isolation by distance) on trait expression between transplanted population (Anderson *et al.*, 2015; Sexton *et al.*, 2014). The geographic distance (km) was log-transformed prior to modelling due to positive skewness of its distribution.

Data analysis

We both compared transplanted individuals to those transplanted at their site of origin ('away vs. home') and to the local individuals growing at the transplant site ('foreign vs. local'). Such comparisons represent the inverse approach described by Kawecki & Ebert (2004) (named 'home vs. away' and 'local vs. foreign', respectively), proposing that local adaptation is supported when (a) populations growing away their site of origin show lower fitness; and (b) populations growing at their own site show higher fitness than populations originated from a foreign site. Thus, in the context of our study, our approach quantifies individual' plastic response to transplantation with respect to home site ('away vs. home') and the adaptation gap of transplanted non-local individuals with respect to local ones ('foreign vs. local').

For each type of comparison, response variable and transplant, we calculated the

log-transformed response ratio (Hedges *et al.*, 1999), as follows (Equation 1):

$$lnRR_i = \ln(\bar{X}_T) - \ln(\bar{X}_O) \tag{1}$$

where $\bar{X}_T$ is the mean of a trait measured at the transplanted sites and $\bar{X}_O$ is either the mean of the same trait sampled on individuals of the same species growing at the site of origin ('away vs. home') or local individuals growing at the transplant site ('foreign vs. local'). Thus, the value of lnRR indicates the proportional intraspecific variation of the mean of a certain trait following transplant with respect to the mean sampled at the site of origin ('away vs. home') or local plants ('foreign vs. local'). We used the inverse of the sampling variance to weight observations in meta-analysis (Borenstein *et al.*, 2009). We calculated the sampling variance of each lnRR following Hedges *et al.* (1999), as follows (Equation 2):

$$\hat{\sigma}^2(lnRR_i) = \frac{(SE_T)^2}{\bar{X}_T^2} + \frac{(SE_O)^2}{\bar{X}_O^2} \tag{2}$$

where *SE* is the standard error of the mean extracted from the papers. When studies did not report standard error or other data to compute it, we used the 'imputeSD' function of the *metagear* R package (Lajeunesse, 2011) to estimate standard deviation using the coefficient of variation (the $SD/\bar{X}$) from all complete cases. We imputed *SD* for 15% of the total amount of observations (see Table II.2.2 for the fraction of observations *SD* imputed in each response dataset). For studies reporting more than two reciprocally transplanted population origins, effect sizes were non-independent, as multiple $\bar{X}_T$ were compared to the same control group ($\bar{X}_O$) (Noble *et al.*, 2017). Thus, we modelled the nonindependence among effect sizes by calculating the variance-covariance matrix of the sampling variance for each dataset following Lajeunesse (2011). The matrices obtained were then used to weight the precision of the effect sizes in the models.

Data analysis was performed in R version 3.6.0 (R Core Team, 2019). The R script used in the analysis is available at the data repository (Midolo, 2020). We modelled the data using three-level mixed-effect meta-analytic models (Konstantopoulos, 2011) with the 'rma.mv' function of the R package *metafor* (Viechtbauer, 2010). Models were run separately for each response variable to estimate how single traits responded to various moderators and because they were capturing different plant fitness components. We accounted for the correlation in the true effects using a nested random-effect structure, with the observation '*ID*' (i.e. the variable uniquely identifying each effect size within the dataset) nested within the grouping-level variable '*study*' in the random structure of the model (1 | *study/ID*). The random structure accounts for underlying true effect of each observation within the study to be not homogeneous (Konstantopoulos, 2011; Midolo *et al.*, 2019).

To address our first question, we fitted single meta-regression models using transplant type along elevation (downward vs. upward) as moderator only, excluding the intercept term. These models estimate the overall mean of the pooled effect and significance of the intraspecific variation of each trait to downward and upward transplant for both 'away vs. home' and 'local vs. foreign' datasets. Furthermore, to address our second question, we analysed the response of the effect sizes to the mean annual temperature (ΔMAT) and precipitation (ΔMAP) change between sites of transplant and site of origin. We estimated marginal pseudo-R^2 of each model as the proportional reduction in the total variance of the null model. We also fitted multiple meta-regression

models by including other covariates (MAT of the transplant site, MAP of the transplant site, geographical distance and functional group) and used a multimodel inference analysis to estimate the relative importance and conditional estimate of each predictor starting from the full model including all predictors. For the response variable of each trait, we ranked the models based on the sample-size corrected Akaike information criterion (AIC_c) using the R package *MuMIn* (Barton, 2019). We estimated the relative importance of each predictor by calculating the AIC_c weights ($AIC_c W$) of the models in which the predictor was included (Burnham & Anderson, 2010). We obtained the conditional estimate (and 95% CI) of each predictor, by averaging the estimates over a confidence set of models selected as the smallest subset reaching a cumulative sum of $AIC_c W \geq 0.95$ (Johnson & Omland, 2004). We did not include all potential interactions nor quadratic terms to the full model to avoid the so-called 'problem of too many models' (Dochtermann & Jenkins, 2011), which would have resulted in a large candidate models per dataset and potentially leading to spurious results (Grueber *et al.*, 2011). Instead, we focused on single terms only to include biologically sound and interpretable models (Dochtermann & Jenkins, 2011).

Following Nakagawa & Santos (2012), we tested funnel plots' asymmetry by computing the p-value of the intercept of linear models fitting the residuals of null models to the weight of the observations (the inverse of the standard error), namely the Egger's test (Egger *et al.*, 1997). None of the metrics showed evidence of funnel plots' asymmetry (Egger' $\rho \geq 0.05$). Funnel plots are shown in Appendix II.4 (Figures II.4.1-II.4.2).

Results

We found common trends in survival and intraspecific trait variation across multiple species and transplant experiments analysed. Without accounting for climatic variation along elevation, responses varied, in general, depending on the trait considered, on the type of transplant along elevation (downward and upward) and on the type of comparison analysed ('away vs. home' and 'foreign vs. local'; Figure 1). In the 'away vs. home' comparison, individuals transplanted upward showed overall significantly lower survival, biomass, height, number of reproductive units and leaf size compared to those growing at their lower elevation of origin, while those transplanted downward showed significantly higher biomass and height compared to individuals growing at higher elevation of origin. On the other hand, in the 'foreign vs. local' comparison, we found significantly lower survival, biomass, height, number of reproductive units, leaf size and higher SLA in individuals transplanted downward and compared to local low-elevation individuals; conversely, no significant differences in trait means were detected in individuals transplanted upward compared to local high-elevation individuals, suggesting overall trait adjustment following transplant. Nevertheless, survival was lower compared to that of local individuals (Figure 1). Germination percentage and number of vegetative organs showed large variation in response suggesting that these traits were overall poorly affected by the direction of transplant.
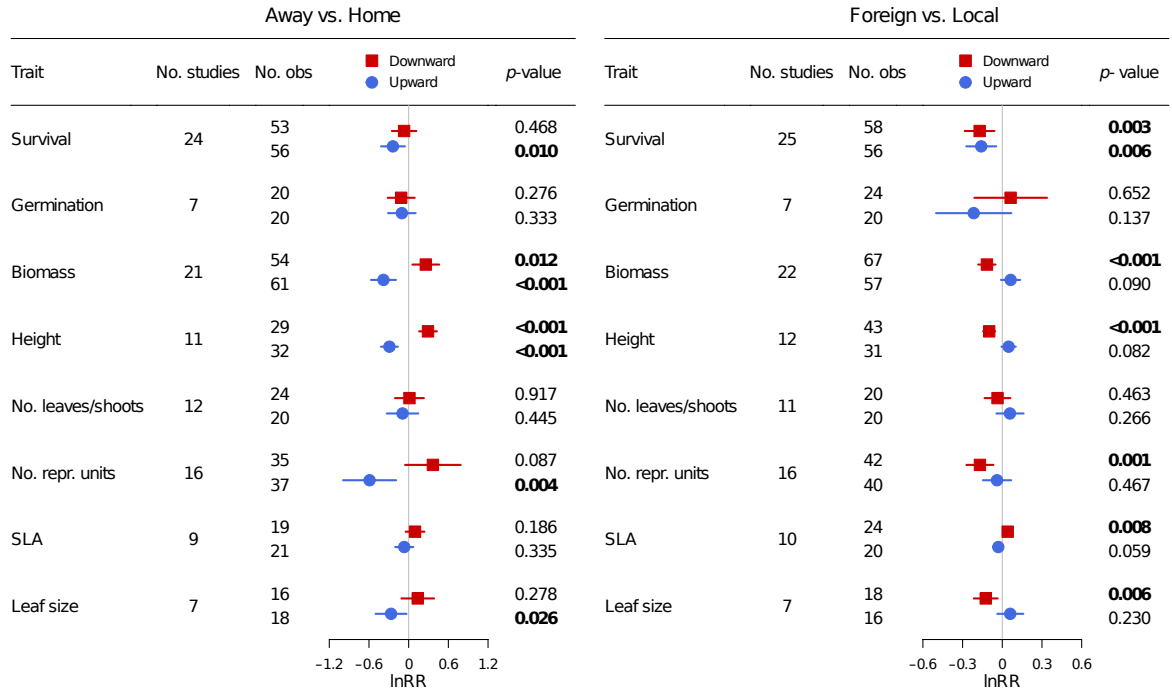
Away vs. Home

Trait	No. studies	No. obs	Downward / Upward	p-value
Survival	24	53 / 56		0.468 / **0.010**
Germination	7	20 / 20		0.276 / 0.333
Biomass	21	54 / 61		**0.012** / **<0.001**
Height	11	29 / 32		**<0.001** / **<0.001**
No. leaves/shoots	12	24 / 20		0.917 / 0.445
No. repr. units	16	35 / 37		0.087 / **0.004**
SLA	9	19 / 21		0.186 / 0.335
Leaf size	7	16 / 18		0.278 / **0.026**

x-axis: lnRR (−1.2, −0.6, 0, 0.6, 1.2)

Foreign vs. Local

Trait	No. studies	No. obs	Downward / Upward	p-value
Survival	25	58 / 56		**0.003** / **0.006**
Germination	7	24 / 20		0.652 / 0.137
Biomass	22	67 / 57		**<0.001** / 0.090
Height	12	43 / 31		**<0.001** / 0.082
No. leaves/shoots	11	20 / 20		0.463 / 0.266
No. repr. units	16	42 / 40		**0.001** / 0.467
SLA	10	24 / 20		**0.008** / 0.059
Leaf size	7	18 / 16		**0.006** / 0.230

x-axis: lnRR (−0.6, −0.3, 0, 0.3, 0.6)

Figure 1: *Mean pooled effect sizes and 95% CI of intraspecific variation (lnRR) in response to upward and downward transplants along elevation across the experiments included in the meta-analysis. The lnRR represents the mean response ratio for both individuals growing at the transplant site to those growing at their site of origin ('away vs. home'), and individuals originated from different elevations to the local individuals growing at the transplant site ('foreign vs. local'). Number of studies and effect sizes ('no. obs') are reported for each trait and response. Models are fitted by using transplant type along the elevation gradient (downward or upward) as moderator only without the intercept term to estimate the mean pooled effect and significance of each level (in bold when $\rho < 0.05$)*

Several trait variation patterns were significantly moderated by the difference in mean annual temperature (ΔMAT) and precipitation (ΔMAP) between site of transplant and site of origin (Figures 2 and 3). In the 'away vs. home' comparison, we found that the magnitude of survival, biomass, height, number of vegetative organs, number of reproductive units and leaf size is significantly related to ΔMAT (Figure 2), being the moderator with the highest $AIC_c W$ in the multimodel inference analysis for these traits. In addition, changes in survival, biomass and number of vegetative organs were also shown to be positively related to ΔMAP in the 'away vs. home comparison' (Figure 3). Conversely, in the 'foreign vs. local' comparison, biomass, height, number of vegetative organs, number of reproductive units and leaf size were positively related to ΔMAP, while germination and SLA showed a negative relationship with ΔMAP (Figure 2). Changes in biomass, height and number of reproductive units were also negatively related to ΔMAT under the 'foreign vs. local' comparison (Figure 3). We detected low evidence of other variables assessed to affect the trait variation observed here. However, we found that responses in germination compared to local individuals were overall larger in sites with higher MAT of the transplant site, and that the number of reproductive units compared to local individuals was slightly negatively related to increasing horizontal geographic distance (Figure 3).
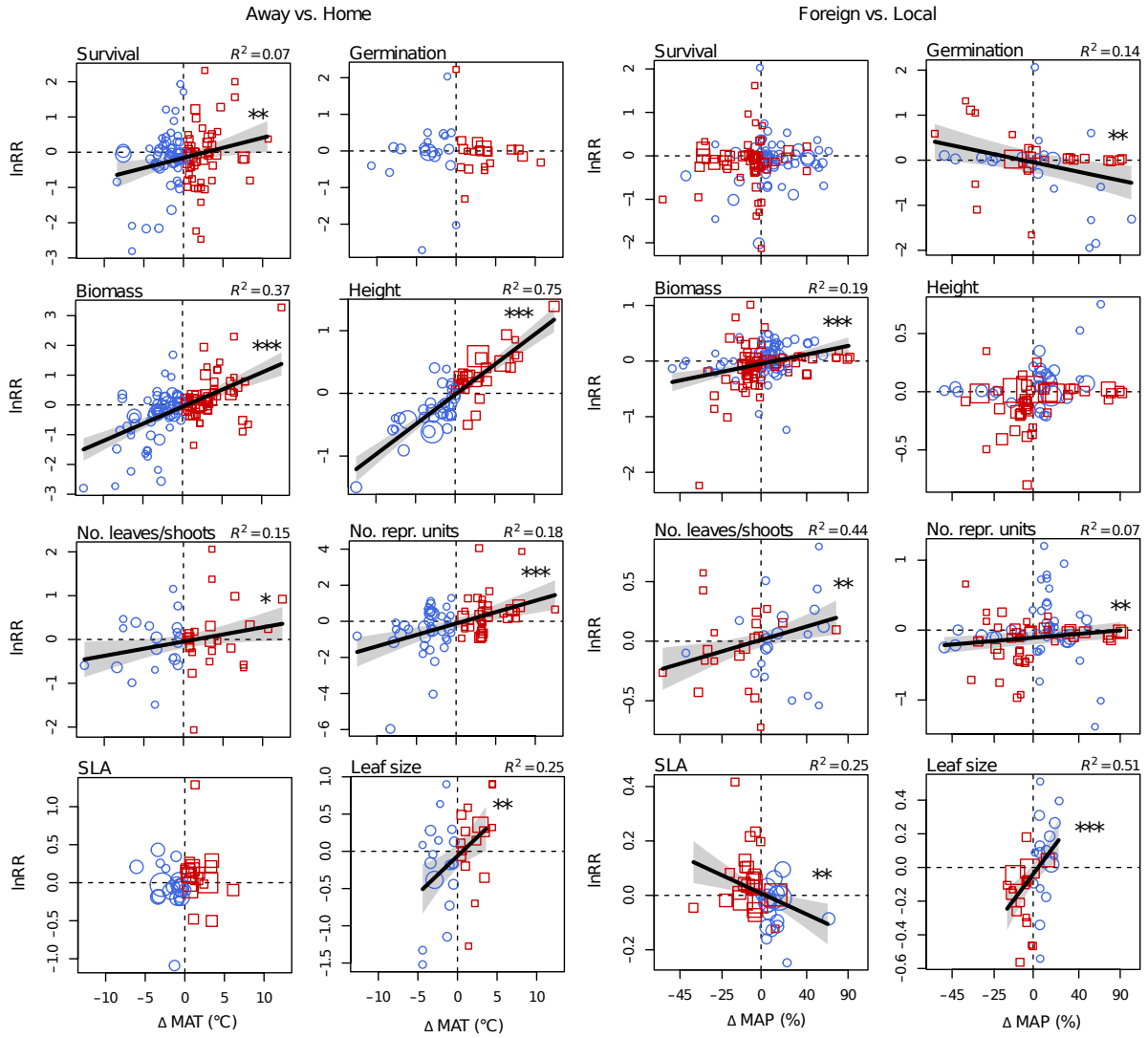
Figure 2: *Survival and intraspecific trait variation (lnRR) in response to the difference in mean annual temperature (ΔMAT) and precipitation (ΔMAP) between the site of transplant and site of origin, following downward (□) and upward (○) transplant along elevation for 'away vs. home' and 'foreign vs. local' comparisons respectively (see also Figure 1). ΔMAP is expressed as the log-transformed ratio of precipitation change between transplant site (back-transformed as percentage values on the x-axis text). Horizontal dashed lines indicate no change compared to the individuals growing at the site of origin ('away vs. home') and to local individuals ('foreign vs. local'). Vertical dashed lines indicate no change in ΔMAT or ΔMAP between transplant sites. Solid lines represent the slope estimate of the model (and 95% confidence intervals) with ΔMAT or ΔMAP as a predictor only (only showed when ρ < 0.5). Significance levels (*ρ < 0.05; **ρ < 0.01; ***ρ < 0.001) are provided for each slope estimate. Point size depicts the observation weight (weighted by 1/SE)*

Discussion

Our meta-analysis identified general patterns of survival and intraspecific trait response to experimental transplantation along elevation across different species and mountain ranges. By comparing responses of transplanted individuals to those living at their site of origin and to local individuals, we showed that survival and plant functional traits follow common cross-species trends of variation in response to exper-

imental transplants within populations located at different elevations. Similarly, previous studies detected convergent trends of intraspecific trait variation across elevations world-wide, but only focused on local populations occurring along the gradients (Midolo *et al.*, 2019; Read *et al.*, 2014), which cannot assess survival response to elevation change nor distinguish between adaptation and plasticity. Overall, our results indicate that chances of survival and plant trait adjustment under different environmental conditions largely depend on the direction of the transplant along elevation (downward or upward). Still, the performance of transplanted individuals is unlikely to surpass that of locally adapted individuals ('foreign vs. local'), although plasticity of foreign populations was overall sufficient to adjust trait phenotypic expression to that of local genotypes in upward transplants.
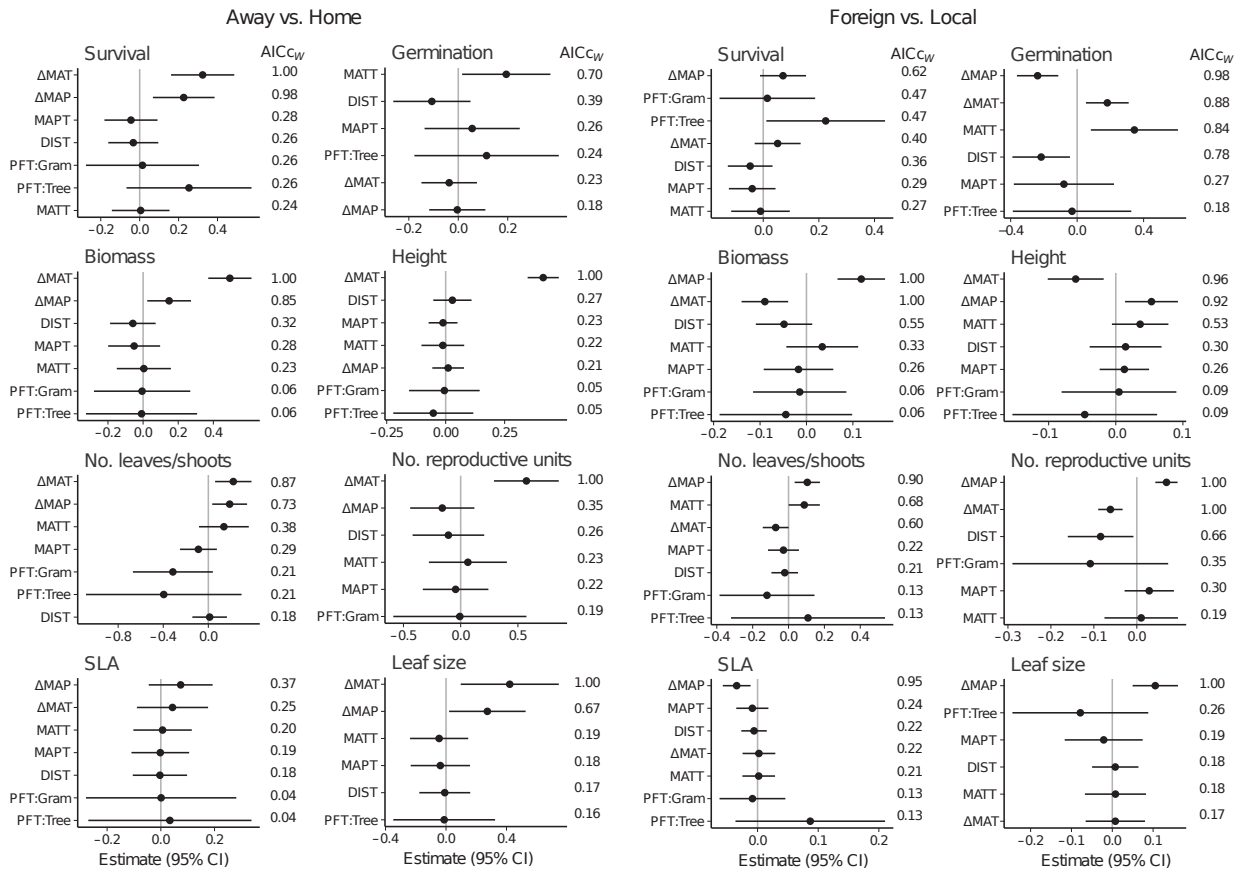

Figure 3: *Conditional averaged estimates and 95% confidence intervals (CI) for fixed effects included in the confidence set of models explaining survival and intraspecific trait variation across transplant experiments for 'away vs. home' and 'foreign vs. local' comparisons (see also Figure 1). The relative importance (AIC_cW) is calculated as the sum of AIC_c weights of models where the predictor is retained. Continuous predictors are scaled to standardize magnitudes of the estimates. ΔMAT = difference in mean annual temperature between transplant site and site of origin; ΔMAP = difference in mean annual precipitation between transplant site and site of origin; MATT = mean annual temperature of transplant site; MAPT = mean annual precipitation of transplant site; DIST = the geographical distance between site of transplant and site of origin; PFT = plant functional types mean pooled effect size for trees and graminoids, compared to forbs (intercept term)*

Furthermore, differently from previous meta-analyses conducted on elevational gradients (Midolo *et al.*, 2019; Read *et al.*, 2014), we accounted for temperature and

precipitation variation between site of transplant and site of origin to translate the elevational change into some of its main direct abiotic components. While a previous synthesis on common-garden experiments conducted by Halbritter *et al.* (2018) found limited evidence of environmental conditions to affect variation in survival and plant phenotypic expression in reciprocal transplants along elevation, our results showed instead clear evidence that such variation depends on mean annual temperature and precipitation difference. Such discrepancies might reflect the significantly larger amount of data used in our analysis. Indeed, our meta-analysis represented, to our knowledge, the most updated and larger quantitative review on reciprocal transplant experiments conducted in mountain ecosystems so far. Nevertheless, we acknowledge that primary data on intraspecific transplant experiments are still relatively rare in the literature compared to other approaches (Midolo *et al.*, 2019; Read *et al.*, 2014), for example for leaf traits like SLA and leaf size, which were reported by a fairly small number of studies analysed here (see Figure 1).

Mean effect of downward and upward transplants

Downward transplants overall significantly increased plant growth traits (biomass and height) compared to their site of origin while survival was not affected ('away vs. home'). However, our results indicate that such individuals have higher biomass, height, leaf size, number of reproductive units and show overall lower survival compared to that of local individuals. Conversely, individuals transplanted upward responded with reduced growth—possibly due to environmental constraints on growth found at higher elevations (i.e. reduced biomass, height and leaf size). Nonetheless, they were significantly less able to survive compared to both home and local individuals.

In light of our findings, we suggest that non-local abiotic conditions found at higher elevations might represent a strong limitation for successful plant establishment and persistence under upward plant shifts. However, we underline that (a) rather than being an abrupt movement to sites with different climatic conditions, plant range shifts observed across elevations [e.g. Chen *et al.* (2011); Rumpf *et al.* (2018b)] are relatively slow and continuous processes where the population can possibly adjust plant fitness while shifting in sites matching their environmental niche; and (b) in the transplant experiments analysed here, plants are grown in sites excluding interactions with individuals of other species, and thereby they do not account for relevant changes in biotic pressures along the elevation gradient. Because competition is generally higher in warmer sites at low elevations while facilitation tends to increase with elevation (Callaway *et al.*, 2002), we suggest that lower biotic stress at higher elevations could favour plant establishment and persistence during upward plant shifts occurring across non-artificially transplanted populations [but see Lenoir *et al.* (2010) for downward range shifts when competitive release occurs at lower elevations instead].

Differences in climatic conditions moderating plant individual performance

Survival and trait variation we observed in transplanted individuals in 'away vs. home' was linearly dependent on the temperature change between sites (Figure 2). In general, higher temperature at lower elevations is expected to promote phenotypes with higher acquisitiveness traits and thereby higher competitive ability (e.g. higher leaf size and plant height); conversely, lower temperature at high elevations selects for phenotypes

with more resource-conservative traits to cope with harsher abiotic pressures (Körner, 2003; Read *et al.*, 2014). In addition, individuals that originated from lower elevations often include genotypes that are maladapted to cold environments and have low frost resistance (Körner, 2007), explaining the negative response to upward experiments found in the 'away vs. home' comparison.

Biomass and height are key traits of the competitive and dispersal ability of individuals in plant communities (Gaudet & Keddy, 1988; Thomson *et al.*, 2017). Their intraspecific increase in 'away vs. home' with temperature change is consistent with transplant experiments conducted along latitudinal gradients showing that plant individuals adjust their performance when transplanted in sites with higher temperatures by increasing growth compared to the individuals growing at their site of origin (De Frenne *et al.*, 2011, 2014). Adaptive plasticity in biomass and height in individuals originated from colder sites may reflect their ability to rapidly increase their growth when the short 'windows of opportunity' take place in cold alpine environments (Münzbergová *et al.*, 2017). Moreover, we observed the same positive trend for the number of reproductive units and survival in 'away vs. home' comparisons, highlighting increased reproductive effort and persistence under warmer conditions respectively. Because plant reproduction at high elevation largely depends on fine-tuning of their phenology with growing season (Vitasse *et al.*, 2014), once cold-adapted plants are exposed to warmer temperature they are no longer constrained by season length, potentially improving their reproductive fitness. Conversely, low-elevation genotypes are less suited to complete their seasonal life cycle within the narrower time frame set by phenology at high elevations and their seedlings are less capable to survive freezing (Körner, 2016; Körner *et al.*, 2016). In addition, the negative response of biomass, height and number of reproductive units to ΔMAT in the 'foreign vs. local' comparison (Figure 3) corroborates that individuals at low elevations are locally adapted to warmer conditions and show higher growth and reproductive performance than foreign individuals with increasing temperature difference.

Although previous experimental and observational studies have shown relevant effect of water availability on intraspecific trait variability (Aspinwall *et al.*, 2017; Souza *et al.*, 2018), changes in precipitation and humidity along elevation are still often neglected in elevational gradient studies as it is often difficult to collect and integrate rainfall data (and snow precipitation) in studies conducted in complex mountain areas (Graae *et al.*, 2012; Körner, 2007). While survival and germination responses were not affected positively by precipitation change (the latter, even showed a slightly negative relationship with MAP change), growth and reproductive outputs increased with positive MAP change under the 'foreign vs. local' comparison, with transplanted plants improving their performance compared to local individuals only when introduced in sites with higher precipitation compared to their site of origin, irrespective of the direction of transplant along elevation. The responsiveness to MAP change described above might explain the fewer differences in trait variation between downward and upward elevation changes in the 'foreign vs. local' comparison (Figure 1), as MAP change was not correlated with elevation in our data. In general, plant performance often declines with increasing drought frequency and reduced water availability (Peñuelas *et al.*, 2004; Pratt & Mooney, 2013). Finally, the high variation found for germination possibly reflects that this trait is highly dependent on conditions at the time of germination, while the other traits integrate over the whole growing season or over years.

While previous studies detected a strong dependence of intraspecific SLA variation along environmental gradients (Midolo *et al.*, 2019), we found no evidence of intraspe-

cific SLA variation across transplants to depend on changes in temperature conditions. Surprisingly, we revealed that SLA tends to decrease with increasing ΔMAP in the 'foreign vs. local' comparison, while SLA is generally expected to decrease in dryer environments (Poorter *et al.*, 2009). A possible explanation is that SLA is reduced at the intraspecific level mainly in case of extreme drought events (Wellstein *et al.*, 2017) or with experimentally reduced water inputs (Navas & Garnier, 2002), while the direction of SLA variation along continuous precipitation gradients is often species-dependent (Dwyer *et al.*, 2014).

Leaf size varied with temperature change similarly to the other traits under the 'away vs. home' comparison. Decreasing leaf size at the intraspecific level with increasing elevation in natural population is attributed to reduced contact area with the environment, increasing tolerance to lower temperatures (Bresson *et al.*, 2011). Our result is consistent with leaf size' positive relationship with temperature across species worldwide (Wright *et al.*, 2017) and highlight the enhanced plastic competitive ability of plants at lower elevations (Lajoie & Vellend, 2018; Pfennigwerth *et al.*, 2017).

Conclusions

We here reported results that provide general insight into the intraspecific response of mountain plants to elevational shifts in relation to non-local climatic conditions. Thus, our results are particularly important to understand how mountain biota respond to elevational shifts caused by global environmental changes.

Altogether, our finding corroborates that plant individuals shifting downward along elevation profit from stress release by increasing their performance in the new environment, but their probability of survival and their ability to adjust traits to that of local individual is poor. Thus, local adaptation requires longer time, as downward-directed short-term establishment is a commonly successful process, while, on the contrary, their long-term persistence will possibly depend upon the subsequent process of local adaptation where success is not taken for granted. Conversely, plant species transplanted upward suffer from stress increase and their response could reflect phenotypic plastic adjustment to cope with this stress or a direct environmental constraint on their fitness. However, local adaptation is a longer-term process that likely determine the success of species while shifting its elevation range. In addition, it is key to consider that if a species can successfully track changes in environmental condition (induced, for example, by climate change) it would not necessarily need to adapt while shifting in response to these. Therefore, dynamics of non-local plant populations in mountain ecosystems should be monitored in the future to better understand their long-term fate.

Importantly, our results also indicate that predicting optimum elevation change within populations located at different elevations needs to account for variation in precipitation, as this was the strongest predictor modulating the differences in individual performance between transplanted and local individuals. Finally, because there is growing evidence on the importance of intraspecific trait variation on population and community dynamic (Albert *et al.*, 2010; Violle *et al.*, 2012), we stress that intraspecific variation over a wide environmental gradient should be accounted to improve spatial predictions on range shifts of plant species and their local adaptation (Benito-Garzón *et al.*, 2019; Guisan *et al.*, 2019).

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AUTHORS' CONTRIBUTIONS
G.M. design the study, collected the data, performed the meta-analysis and wrote the draft of the manuscript; C.W. helped to interpret results and contributed substantially to revisions.

DATA AVAILABILITY STATEMENT
We report at the end of this manuscript the reference of the primary studies used in the meta-analysis to give proper citation credit to the authors (the 'Data sources' section). The raw data and an R script containing codes used in the meta-analysis are available from the Figshare Data Repository: `https://doi.org/10.6084/m9.figshare.11962590.v1` (Midolo, 2020).

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5 Chapter III – Individual fitness is decoupled from coarse-scale probability of occurrence in North American trees

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Abstract

Habitat suitability estimated with probability of occurrence in species distribution models (SDMs) is used in conservation to identify geographic areas that are most likely to harbor individuals of interest. In theory, probability of occurrence is coupled with individual fitness so that individuals have higher fitness at the centre of their species environmental niche than at the edges, which we here define as 'fitness-centre' hypothesis. However, such relationship is uncertain and has been rarely tested across multiple species. Here, we quantified the relationship between coarse-scale probability of occurrence projected with SDMs and individual fitness in 66 tree species native of North America. We used I) field data of individuals' growth rate (height and diameter standardized by age) available from the United States Forest Inventory Analysis plots; and II) common garden data collected from 23 studies reporting individual growth rate, survival, height, and diameter of individuals originated from different provenances in United States and Canada. We show 'fitness-centre' relationships are rare, with only 12% and 11% of cases showing a significant positive correlation for field and common garden data, respectively. Furthermore, we found the 'fitness-centre' relationship is not affected by the precision of the SDMs and it does not depend upon dispersal ability and climatic breath of the species. Thus, although the 'fitness-centre' relationship is supported by theory, it does not hold true in nearly any species. Because individual fitness plays a relevant role in buffering local extinction and range contraction following climatic changes and biotic invasions, our results encourage conservationists not to assume the 'fitness-centre' relationship when modelling species distribution.

KEYWORDS: centre-periphery, ecological niche model, individual performance, intraspecific variability, meta-analysis, transplant experiment

Introduction

Probability of occurrence estimated with species distribution models (SDMs) is widely used in large-scale conservation assessments to predict range shifts and local extinction rates in response to global environmental changes (Peterson *et al.*, 2002; Thuiller *et al.*, 2005; Pacifici *et al.*, 2015). To improve reliability of SDMs' projections, recent advances integrate and combine various processes such as eco-evolutionary dynamics (Cotto *et al.*, 2017), dispersal limitation (Engler *et al.*, 2012) and local adaptation (Benito-Garzón *et al.*, 2019; Peterson *et al.*, 2019). However, it is still debated to what

extent coarse-scale probability of occurrence reflects underlying ecological and demographic processes related to the concept of environmental niche (Thuiller *et al.*, 2014; Wittmann *et al.*, 2016; Pironon *et al.*, 2018).

In theory, probability of occurrence (sometimes referred as 'habitat suitability' in SDMs) is expected to reflect the set of abiotic conditions that maximize the physiological optimum of a species (Guisan *et al.*, 2017). Although SDMs are not designed to model individual fitness or local abundance, areas with higher probability of occurrence in geographic space indicate, in principle, the locations where a species can better establish and maintain populations. Nevertheless, such assumption in SDMs relies on a hypothetical absence of biotic interactions, dispersal limitation and evolutionary change (Pearson & Dawson, 2003). In addition, micro-habitat variation unrelated to the coarse scale climate modeled by SDMs could greatly affect species distribution and fitness (Potter *et al.*, 2013).

Understanding relationships between species occurrence and ecological processes is key to evaluate conservation strategies based upon SDMs under present-day and future climate change scenarios (Franklin, 2010). To this aim, the reliability of species occurrence obtained from SDMs and other niche modeling approaches can be evaluated testing the 'centre-periphery' hypothesis, which states that demographic performance and genetic variaiton is highest at the centre of the preferred environmental niche and decreases toward the edges (Pironon *et al.*, 2018).

While previous studies focusing on the 'centre-periphery' hypothesis are focusing on local abundance (i.e. the 'abundant-centre' hypothesis; see Box 1) (Dallas *et al.*, 2017; Santini *et al.*, 2019; Osorio-Olvera *et al.*, 2020), a less frequently tested assumption in the niche modeling literature is that individuals have higher fitness at the centre of their species environmental niche than at the edges within their native range, which hereafter we refer to as the 'fitness-centre' hypothesis (Box 1). Because such hypothesis reflects the fundamental ecological theory surrounding the concept of ecological niche (Pulliam, 2000), some has proposed that positive coupling can be expected between individual fitness and modeled probability of occurrence in SDMs (Thuiller *et al.*, 2010; Wittmann *et al.*, 2016; Mammola *et al.*, 2019). Indeed, probability of occurrence is commonly used as an ecological niche indicator approximating Grinnellian niche (namely the niche component defined by non-interactive abiotic environmental variables) alongside other metrics of niche-centroid distance (Santini *et al.*, 2019; Osorio-Olvera *et al.*, 2020). Nevertheless, there are multiple reasons to expect weak support of 'fitness-centre' hypothesis in SDMs, both biological and methodological.

First, the 'fitness-centre' hypothesis assumes that specimens have the highest fitness under the environmental conditions where they occur more frequently, and that their maximum fitness is reached where these conditions are met. However, due to dispersal limitation and historical factors, species may not be in equilibrium with current environmental conditions, that is, species distribution may be still responding to last glacial period (c. 115 – 12 ka) and anthropogenic land-use changes and fragmentation (Svenning & Skov, 2004; Svenning & Sandel, 2013; Wagner *et al.*, 2015). In addition, there is mounting evidence that individuals of a population might not be locally adapted nor express higher individual fitness in local rather than non-local conditions(Svenning & Sandel, 2013; De Frenne *et al.*, 2014; Midolo & Wellstein, 2020). Such factors do not just disregard the assumption behind the 'fitness-centre' hypothesis, but also bias the estimation of the environmental niche in SDMs (Pearson & Dawson, 2003). Second, individual fitness, like local abundance (Pironon *et al.*, 2015; Santini *et al.*, 2019), may not linearly increase from the centre to the edge of the environmental niche. Instead,

performance curves can have abrupt declines above or below certain thresholds within the climatic envelope of the species. For instance, rapid changes in performance (e.g. photosynthetic rate and frost tolerance) in response to temperature affects plant distribution and elevational zonation (Körner, 2003).

Finally, in niche modeling approaches, probability of occurrence is nearly always estimated at coarse-scale resolution using macroclimatic data, while species occurrence and individual fitness may strongly depend on micro-habitat (Suggitt *et al.*, 2010; Greiser *et al.*, 2020). Consequently, low probability of occurrence predicted in a geographical unit may indicate that a smaller fraction of it is suitable rather than the whole unit is less suitable for the species. Such micro-habitat dependency would then confound 'fitness-centre' relationships obtained in SDMs, for instance, in species whose occurrences and fitness are associated with micro-topography (Scherrer & Körner, 2011) or slope exposure depending on the latitude (Holland & Steyn, 1975).

Previous studies using SDMs to address the 'fitness-centre' hypothesis used various functional traits as surrogates of individual fitness in both animals (Larson *et al.*, 2010; Pellissier *et al.*, 2013; Wittmann *et al.*, 2016; Mammola *et al.*, 2019; Barela *et al.*, 2020) and plants (Elmendorf & Moore, 2008; Thuiller *et al.*, 2010; Sangüesa-Barreda *et al.*, 2018; Chardon *et al.*, 2020) and overall reported heterogeneous results. These studies generally tested the hypothesis on single species [but see (Thuiller *et al.*, 2010)] or normally used few observations of trait data collected in the field [but see Chardon *et al.* (2020)], possibly due to the rarity of the species under consideration [e.g. Mammola *et al.* (2019)] or because sampling functional traits at the intraspecific level over large areas is time-consuming and expensive.

Due to data availability restrictions, it is still difficult to draw conclusion on the validity of the 'fitness-centre' hypothesis. However, both forest inventories and common garden experiments represent data sources on plant species occurrences and intraspecific functional traits in SDM-related approaches (Benito-Garzón *et al.*, 2019), but have not been applied to test the 'fitness-centre' hypothesis. Specifically, field-observed traits reflect the fitness experienced by the individuals at their local site. In contrast, common gardens remove bias due to differing growing conditions at the site of origin to the ones of the common garden site, allowing for the quantification of adaptive trait variation while filtering out variation caused by site-specific conditions observed at the site of origin, which could confound 'fitness-centre' associations. From this point of view, fitness data obtained from common gardens could show stronger 'fitness-centre' relations than field-collected data.

Here, we tested whether individual fitness traits correlate with probability of occurrence projected with SDMs across 66 tree species native of North America within their native range (Figure 1). We first compiled two datasets on individual growth rate in forest inventory plots of Western United States (hereafter, 'field' data), and growth and survival data reported in 23 common garden studies conducted in the United States and Canada (hereafter, 'common garden' data). Secondly, we trained and tested SDMs at 10 km resolution using soil and climatic predictors and presence-absence data from United States and Canada's Forest National Inventories. Finally, we applied a meta-analytical approach to estimate the mean correlation between individual fitness and coarse probability of occurrence estimated at the sampling location (in 'field' data) or at the site of origin of the individuals (in the 'common garden' data) across multiple species, and accounted for potential modifying factors like dispersal ability and the climatic niche' breadth of the species.

We show that associations between individual fitness and coarse-scale probability

of occurrence are rare and not affected by species-specific traits or by the precision of the SDMs. We conclude that hypothesized 'fitness-centre' relationships represent an exception rather than the rule when modeling environmental niches in the geographic space. More broadly, our findings reject the universality of 'centre-periphery' hypothesis and pose important constraints in conservation projects based upon such assumption.

Box 1. List of hypotheses mentioned in this study

Centre-periphery hypothesis (CPH): biogeographical paradigm stating that genetic variation and demographic performance of species decrease from the centre to the edge of its geographic and environmental range. The CPH is based on the principle that populations and individuals are more isolated near the range limit of the species, resulting in lower demographic (population-level) and fitness (individual-level) performances. Thus, we here consider the CPH as the overarching hypothesis of the 'abundant-centre' and 'fitness-centre' hypotheses mentioned in the present study. We recommend Pironon *et al.* (2017) for a detailed overview on the CPH.

Abundant-centre hypothesis: subhypothesis of CPH referring to the species' demographic performance, and specifically to the abundance of individuals. The 'abundant-centre' hypothesis states that species abundance is higher at the centre of the species range and it decline toward range edges (Sagarin *et al.*, 2006). Such hypothesis has been traditionally proposed as a general macroecological rule, but it is still currently under debate. Recent studies are focusing on abundance variation within the environmental range of the species, using ecological niche indicators to estimate the species environmental range [see e.g. Dallas *et al.* (2017); Santini *et al.* (2019); Osorio-Olvera *et al.* (2020)]. The 'abundant-centre' hypothesis is not addressed in this study.

Fitness-centre hypothesis: subhypothesis of CPH referring to the fitness of individuals quantified by functional traits or survivorship. The 'fitness-centre' hypothesis defined here states that individual fitness is expected to be higher at the centre of the species range and it decline toward range edges. Like the recent literature on the 'abundant-centre' hypothesis, we link the 'fitness-centre' hypothesis to the environmental range of the species, using probability of occurrence as an ecological niche indicator. Thus, under the 'fitness-centre' hypothesis, a positive coupling is expected between individual fitness and probability of occurrence.

Materials & Methods

We tested the 'fitness-centre' hypothesis across 66 species by calculating the correlation between individual fitness traits sampled within the species distribution range and the coarse probability of occurrence estimated at sampling locations obtained from SDMs. The analysis was performed in three main steps, as summarized in Figure 1: I) collection of intraspecific individual fitness data; II) estimation of probability of occurrence

using SDMs for each species; III) meta-analysis combining the 'fitness-centre' relationships across multiple species and exploration of potential modifying factors.
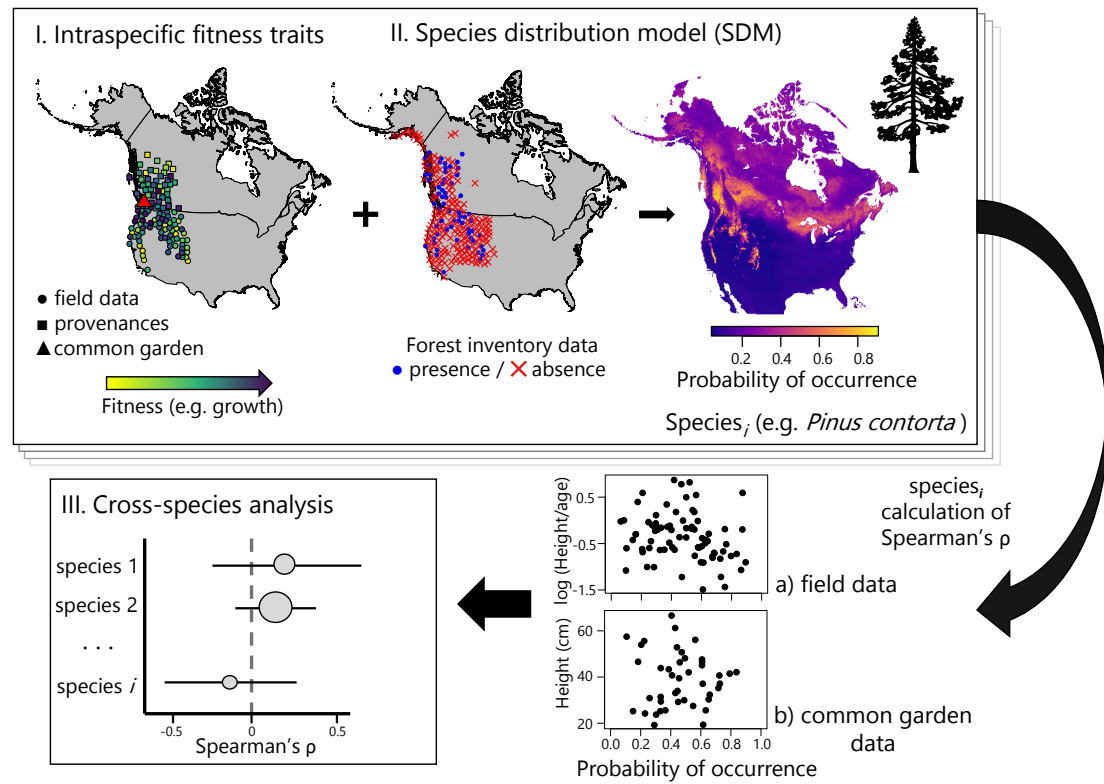

Figure 1: *Schematic representation of the methodological steps applied in this study (each step reflects subsections of the 'Material and Methods' section): I) for multiple species (in the example, lodgepole pine Pinus contorta), we estimated individual fitness from field data (Forest Inventory Analysis of US Forest Service) and/or common garden experiments available from the literature (in the example, data from Mahony et al. 2020, see 'Data Sources' section); II) we obtained probability of occurrence from species distribution model (SDM) using presence-absence data retrieved from United States and Canada's National Forest Inventories. After we calculated the correlation between individual fitness at site location and probability of occurrence for multiple species and individual fitness traits, we III) applied a meta-analytical approach to estimate the mean correlation coefficient across multiple species. Geographic points in the figure are spatially thinned for plotting purposes*

Individual fitness estimation

We used two datasets on tree species individual fitness containing I) field data collected in contiguous Western United States including the Rocky Mountains, the Great Basin and the pacific coast states (i.e. in Arizona, California, Colorado, Idaho, Montana, Nevada, New Mexico, Oregon, Utah, Washington, Wyoming), and II) common garden data collected from provenance trial experiments located in United States and Canada. We analyzed 66 tree species in total (44 found in the field dataset only, 13 in the common garden dataset only, and nine in both datasets). The list of species and details on the number of observations available is reported in Appendix III.1.

Species selection criteria. We restricted the analysis to tree species native to United States and Canada (hereafter, Northern America) to reduce variation originating from

input data and regions with different biogeographic conditions. Because our presence-absence data used in SDMs were limited to Northern America, we did not consider species with substantial parts of the geographic range located in Mexico to avoid missing occurrences from the warmest area when estimating the environmental niche (Soberón *et al.*, 2018). Nevertheless, we retained species with the southernmost distribution range located in Mexico in case their occurrence is confined to high-elevation areas where we expected similar climatic conditions of low-elevation areas found at higher latitudes of Northern America [e.g. ponderosa pine (*Pinus ponderosa*), black cottonwood (*Populus trichocarpa*), Douglas-fir (*Pseudotsuga menziesii*)]. Indeed, occurrences of these species showed a linear negative relation between latitude and elevation, at least within Northern America (Appendix III.2; Figure III.2.1). Information on species' ranges distribution were obtained from the "Atlas of United States Trees" (US Geological Survey, 1999) and "Plants of the World Online" (POWO, 2020).

Trait data collection. For the field data, we used the United States Forest Inventory Analysis database (FIA) to obtain data on individual growth as a proxy of individual fitness (retrieved from FIA's datamart: `https://apps.fs.usda.gov/fia/datamart`). To quantify yearly average growth of individuals, we only retained observations where either height or diameter at breast height (DBH) were reported in combination with the age of the individual. Observations reporting age in combination with height or DBH were only available in plots located in continental Western United States. Depending on the species and sampling procedure, age was either reported as tree rings from an increment core sample extracted at the root collar (TOTAGE = 'total age') or at the breast height (1.37 m above ground) (BHAGE = 'breast height age'). Thus, to eliminate the effect of stand density and tree age on the size-growth relations (Pretzsch & Dieler, 2011), we calculated the median of the ratio between height and/or DBH to TOTAGE and/or BHAGE for each plot and species. We used the median to avoid effects of outliers. Individual height and diameter were standardized by the age to capture vertical and radial tree growth rate, a trait which inherently captures individual fitness (Violle *et al.*, 2007). Thus, our metric assigns higher fitness to shorter-lived trees with greater height or DBH compared to older trees who reached maximum growth rate. In general, individual growth rate is a key component of individual fitness of an organism (Violle *et al.*, 2007). Specifically, growth rate of trees enhances individual competitive ability in natural forest ecosystems (Morgenstern, 1996) and can positively influence reproductive success of individuals (Avanzi *et al.*, 2020). In addition, individual growth rate has been previously shown having a positive coupling with SDM-modelled probability of occurrence in Grass Carp *Ctenopharyngodon idella* (Wittmann *et al.*, 2016). We only retained species with at least 30 plots with calculable individual height or DBH to age ratios. Number of presences (and corresponding absences) per single trait and species selected ranged from 31 to 17956 (median = 301, sd = 2920) (see Appendix III.1).

For the common garden data, we collected individual fitness from the literature on provenance trial experiments. These studies report data on specimens originating from different locations (i.e. provenances) and simultaneously grown in one or more common garden located within the species range. Data reported are sampled over individuals of the same age sampled at the end of the experiment or throughout it. In February 2020 we searched in Web of Knowledge for primary studies reporting data from common garden experiments conducted in Northern America (see Appendix III.3 for the search string). Our initial search string yielded 476 results from Web of Knowledge. We also searched for common garden data at the United States Forest Service

Research Data Archive. We selected additional sources from studies cited by the articles retained in the search string that were eligible for inclusion. After screening results from the main search string and the Forest Service Research Data Archive, we selected 19 primary studies and four data papers eligible for inclusion (see 'Data Source' section). On average, experiments reported trait data after 13 (sd = 11) growing seasons (range of the year of experiments' start = 1961-2014, and experiments' end = 1979-2016). Each source selected reported at least one of the following mean responses for each provenance and species: height, diameter, survival or growth rate. Height, diameter and survival were reported as the data collected after a certain period or at end of the experiment Since common gardens were relatively short-running and conducted on coetaneous-transplanted individuals, height and diameter reported at the end of the common garden trials represent growth rate over the period of the common garden trial. Thus, we assumed height and diameter in 'common garden' data to be directly proxies of individuals' growth rates. In addition, we used final height and diameter in the 'common garden' data as proxies of individuals' growth rate as these are commonly used as growth indicators in provenance trials experiments [for example, see Taïbi et al. (2014); and Warwell & Shaw (2017) in 'Data Sources']. Conversely, growth rate was reported by studies as the mean yearly increment of height, biomass or volume of each provenance during the experiment. We collected the geographical coordinates and mean value of the response measures for each study, provenance and common garden' site. Data were retrieved from tables, figures and supporting information of the study, or provided directly by the authors. Provenances assessed per studies and species ranged in total from six to 281 (median = 42, sd = 51.2).

Probability of occurrence estimation

Presence-absence data. We obtained presence-absence data from the USDA Forest Inventory Analysis (FIA) (Burrill *et al.*, 2018) and ground plots of Canada's National Forest Inventory (https://nfi.nfis.org). These datasets contain geographical coordinates of standardized plots and can be therefore used to train and test SDMs. By relying on forest inventory plots, we used true absence data to fit SDMs rather than randomly generated pseudo-absences.

The United States FIA dataset contained ground plot inventories sampled from 1968 to 2019, each made by four subplots of 168 m^2 area located within 1-acre sample area [see Burrill *et al.* (2018) for detailed description of sampling design]. From these plots we only selected those located in continental United States and excluded those located in artificial forest stands. In addition, we excluded plots located in 'Private' or 'Native American' land, to reduce the effects of cultural management and because these plots' coordinates are swapped with other plots within the same county for legal reasons. Our selection resulted in 103786 plot locations in total available from the United States. The Canada NFI dataset contained ground plots sampled from 1992 to 2007 with 400 m^2 and 50 m^2 area for surveys of large (DBH ≥ 9 cm) and small (DBH < 9 cm) trees, respectively. In total, 985 plot locations were used as background for presence-absence data in Canada.

For each of the 66 species selected for the analysis, we randomly sampled n absence locations 30 times among all the sampled plots, where n was the number of presences available from that species across ground plots data. Given the computationally intensive calculations of SDMs, we used 30 replicates per algorithm applied and species [see e.g. Davis *et al.* (2018) for another use of the same number of replicates for compu-

tationally heavy analyses]. To sample corresponding absences more uniformly in the study area and to overcome potential different sampling efforts across Northern American states, we selected absences within each state up to the equal number of presences available for that state. Such approach allows not to randomly select absences within areas where the species is absent due to historical factors (Guisan *et al.*, 2017). Finally, for each of the 30 replicates, we thinned observations to a minimum distance of 10 km to reduce spatial autocorrelation using the 'ecospat.occ.desaggregation' function of the R package *ecospat* (Cola *et al.*, 2017). This distance reflected the resolution of the environmental predictors used in SDMs and it was selected to account for maximum distance uncertainty of presence-absence data in Canada's ground plots (10 km) and to reduce overly close-sampled areas in US.

Coordinates of presence-absence data (i.e. the plot location) used in our analysis had 1.6 km and 10 km uncertainty for United States FIA and Canada NFI data, respectively (except for 433 plots located in British Columbia, Quebec and New Brunswick, of which exact coordinates were available). For this reason, we explored how coordinate imprecision potentially affected results and conclusion of our analysis due to inaccurate estimate of environmental conditions at locations where the species occurs. We report methodological details and results of this sensitivity analysis in the Appendix III.4. The sensitivity analysis was performed on the subset of species and presence / absence data did not affect our conclusions.

Species distribution models. We modeled and projected current species' probability of occurrence in North America (decimal degrees' longitude: -179 to -52; and latitude: 24 to 83) using the *sdm* R package (Naimi & Araújo, 2016). We applied bioclimatic and soil data at a resolution of 10 km at the equator as predictors. We used 19 climatic variables from WorldClim database [version 2.0; www.worldclim.org, Fick & Hijmans (2017)] and the aridity index, measured as the ratio of mean annual precipitation (estimated by WorldClim database) to the potential evapotranspiration extracted from the CGIAR-CSI GeoPortal (Trabucco & Zomer, 2010). In addition, we used six soil variables (i.e. depth to bedrock, bulk density, organic carbon content, soil pH in H_2O, cation exchange capacity and weight percentage of sand particles) obtained from Soil-Grids database (Hengl *et al.*, 2017). Soil variables were obtained by averaging estimated parameters within the top 30 cm layer (except for depth to bedrock). To avoid collinearity among predictors, we automatically selected a subset of predictors for each species by iteratively excluding variables with the variance inflation factor (VIF) greater than 10 using the 'vifstep' function of the *usdm* R package (Naimi *et al.*, 2014) and only retained selected variables occurring across all the 30 replicates.

We ran SDMs models using six different algorithms for each of the 30 replicates per species. We used subsampling partitioning using 30% of randomly sampled observations in each run to test the model (Guisan *et al.*, 2017). The algorithms used in modeling were the following: Generalized Linear Model (GLM), Generalized Additive Model (GAM), Boosted Regression Tree (BRT), Random Forest (RF), Multivariate Adaptive Regression Splines (MARS) and Support-Vector Machine (SVM). We used model ensemble to project probability of occurrence by weighting each model by the True Skill Statistic ('TSS') using the maximum sum of model sensitivity and specificity as cutoff optimization threshold.

Meta-analysis

Effect size calculation. After we obtained the spatial projections of probability of occurrence, we extracted for each species the probability of occurrence at the locations where traits were sampled in ground plots ('field' data), and locations where the provenances tested at the common garden site originated ('common garden' data). Then, because our goal was to assess the coupling between SDM-modeled probability of occurrence and individual fitness, we used Spearman's correlation coefficient between each trait and the probability of occurrence of the species as the effect-size to quantify the direction and magnitude of the 'fitness-centre' relationship [see e.g. Santini *et al.* (2019); Osorio-Olvera *et al.* (2020)]. For the 'field' data, we used the 'weightedCorr' function of the *wCorr* R package (Bailey, 2017) to weight correlation coefficients by the number of individuals sampled in each plot. In the case of the 'common garden' data, we computed unweighted correlation coefficients for each common garden site and species assessed by single study, as the number of individuals sampled per provenance was the same within each trial unit.

Nearby sample sites may not be independent and therefore, for each pairwise correlation, we checked for spatial autocorrelation of the residuals obtained from a linear model with trait value as the dependent variable, and probability of occurrence and its quadratic term as the predictors. Before fitting the linear model, we log-transformed growth traits in the 'field' data as these were in most cases positively skewed. Then, we used the 'spline.correlog' function of the *ncf* R package (Bjornstad, 2020) over the residuals of the linear model to obtain Moran's *I* correlograms. From these, we identified the minimum geographic distance to which spatial autocorrelation was estimated to be not significant. To remove the effect of spatial autocorrelation, we then calculated 999 times the correlation coefficient between probability of occurrence and trait measurements by randomly thinning each time the sampling locations to the minimum distance threshold estimated for each species and trait. Random thinning was performed using the 'thin' function of the *spThin* R package (Aiello-Lammens *et al.*, 2015). We then took the median of both sample size and correlation coefficients to be used in meta-analysis. Our procedure means that the end-results are influenced by all sample sites available but distant and more independent sample sites are given a higher importance than sample sites showing substantial spatial autocorrelation to nearby sample sites.

We estimated the significance of each correlation coefficient by back-transforming 95% confidence intervals obtained by the Fisher's z-transformation, which allow to estimate associated sampling variance of correlation coefficients [i.e. $1/(N\text{-}3)$; where N is the sample size] (Borenstein *et al.*, 2009).

Linear mixed-effect models. Using linear mixed effect-models we applied an approach similar to a meta-analysis to estimate the mean effect of 'fitness-centre' relationship across the species and traits analyzed, and to investigate how such relationship is affected by potential modifying factors. We used the 'lmer' function of the *lme4* R package (Bates *et al.*, 2015) for each dataset separately (i.e. 'field' and 'common garden' data). We used Spearman's correlation coefficients as the dependent variable of the fixed component of the model, and the species and the study (namely, the identifier of the common garden study) as crossed random effects in the 'common garden' data [i.e. (1| *species*) + (1| *study*)]. For the 'field' data, only the species was used as random effect. We weighted each correlation coefficient by multiplying the sample size of the

correlation coefficient by the maximum True Skill Statistic (TSS) of the SDM obtained from that species. In other words, observations with many sampled locations and with probability of occurrence obtained from more accurate models contributed more to the overall mean estimate.

We checked whether SDMs' TSS and sample size (namely, the weight assigned to each correlation coefficient used in the mixed-effect models) affected the correlation observed between probability of occurrence and individual fitness. Such approach is comparable to the analysis of publication bias in meta-analysis (Borenstein *et al.*, 2009). Thus, we estimated the significance of the intercept of a linear regression model using the residuals of the null mixed-effect model as dependent variable, and the observation's weight (= sample size * maximum TSS) as predictor (Nakagawa & Santos, 2012). The weight term used in linear mixed effect models had no influence on the variation of correlation coefficients (see Appendix III.5; Figures III.5.1-III.5.2).

We first estimated the mean weighted correlation between fitness and probability of occurrence using null models for each dataset. Secondly, we used five predictors we expected to moderate the effect sizes: the different metrics of individual's fitness traits, the main taxonomic group (angiosperm and gymnosperm), species dispersal ability, and species temperature and precipitation breadth (i.e. the climatic range of the species). We used different metrics of individual's fitness traits as moderator to identify whether different dimension of fitness have intrinsically different relationship with probability of occurrence, or if they overall respond in a similar way. In addition, in the 'common garden' data, we also used the probability of occurrence of the location of the common garden site as predictor.

Dispersal ability affects population isolation and gene flow shaping functional trait variability and local adaptation within the species' range (Sexton *et al.*, 2014; Pironon *et al.*, 2017). Species' seed weight was used as a proxy of species dispersal ability and obtained from the Seed Information Database (SID) of the Royal Botanic Gardens Kew (2020). Two species of poplar [black cottonwood (*Populus trichocarpa*) and narrowleaf cottonwood (*Populus angustifolia*)], lacked data on seed weight and for these we used the median of the genus. Similarly, larger climatic variability within the species' range is expected to facilitate intraspecific functional trait variability (Kuppler et al. 2020), thus potentially affecting the probability of detecting such variation within a gradient of probability of occurrence. Temperature and precipitation breadth were estimated as the difference between the 90% and 10% quantile values estimated at the location of the species' occurrences. We used temperature and precipitation average of the warmest year quarter ('BIO10' and 'BIO18' in WorldClim, respectively) at 10 km resolution. We log-transformed seed weight and precipitation breadth tre to strong positively skewedness.

We scaled and centered all continuous variables to a mean of 0 and standard deviation of 1 using the 'scale' function of R (R Core Team, 2020), and checked for collinearity prior to modeling. Starting from a full model including all the predictors mentioned above, we performed a stepwise backward selection via likelihood ratio tests.

Results

We found poor support for the 'fitness-centre' hypothesis in North American tree species. Pairwise correlation coefficients between individual fitness and probability of occurrence ranged from -0.50 to 0.49 ('field' data) and -0.64 to 0.56 ('common garden' data), with mean-weighted-correlation close to zero (Figure 2). Importantly, only the 12%

78

and 11% of the correlation coefficients were positively significant for the 'field' and the 'common garden' data, respectively. In addition, and contrary to what is expected by the 'fitness-centre' hypothesis, we found few correlations with a negative significant trend (corresponding to the 10% and 2% of observations, for the 'field' and the 'common garden' data, respectively). Thus, in the 'field' data, significant positive associations were detected consistently across all response traits in only six out of 53 species analyzed: Rocky Mountain maple (*Acer glabrum*), bigtooth maple (*Acer grandidentatum*), red alder (*Alnus rubra*), giant chinquapin (*Chrysolepis chrysophylla*), foothill pine (*Pinus sabiniana*) and coast redwood (*Sequoia sempervirens*). In the 'common garden' data, Douglas-fir (*Pseudotsuga menziesii*) was the species showing the highest fraction (38%) of positively significant pairwise correlations across common garden sites and traits examined, while others showed 17% or less.
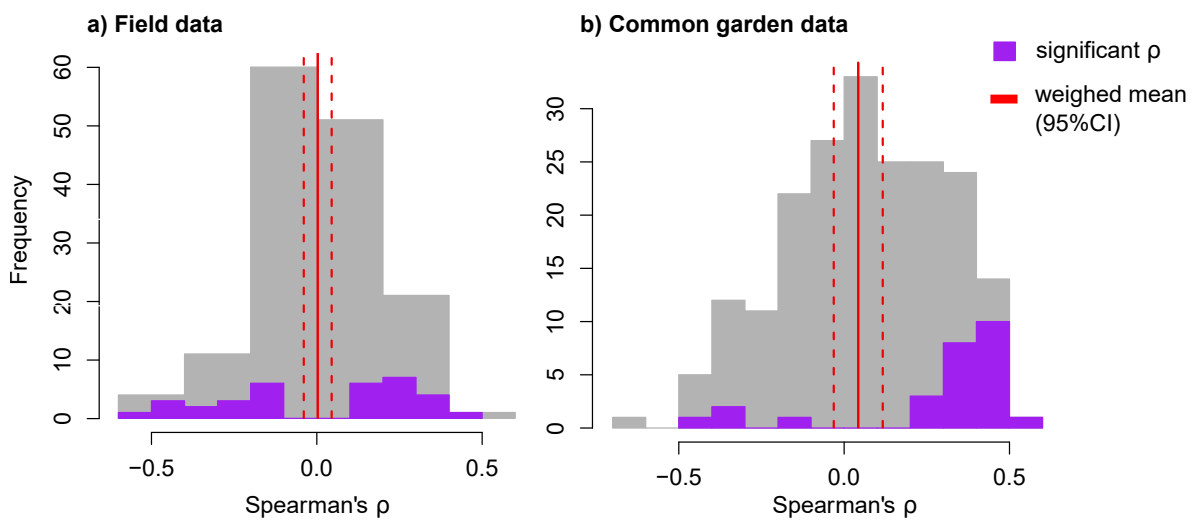

Figure 2: *Overall distribution of the Spearman's correlation coefficients (ρ) between species' probability of occurrence and individual fitness sampled in a) field data (from Forest Inventory Analysis of US Forest Service, FIA) and b) common garden experiments' data. Purple-shaded bars represent the distribution of significant coefficients (p-val < 0.05). Red vertical lines indicate the mean pooled estimate (solid line) and its 95% CI (dashed lines) obtained from null mixed effect models using species (and study as well, for common garden data) in the random component of the model. Observations in the model are weighted by multiplying the sample size of the correlation coefficient by the maximum 'True Skill Statistic' (TSS) of the SDM obtained from that species.*

Overall, mean correlations were not significantly different across the trait measurement types analyzed, suggesting similar responses between survival and various dimensions of individual growth (Figure 3). Furthermore, none of the species' trait predictors considered in multiple regression (i.e. seed weight, temperature breadth and precipitation breadth) had a significant effect on the variation of the correlation coefficients. In the 'field' data, the mean correlation of angiosperms (estimate = 0.08; SE = 0.03) was significant differently to that of gymnosperms, which was equal to zero. The mean correlation in angiosperms was however too low to indicate a positive 'fitness-centre' association and no such differences were detected in the 'common garden' data (Appendix III.5; Figure III.5.3).
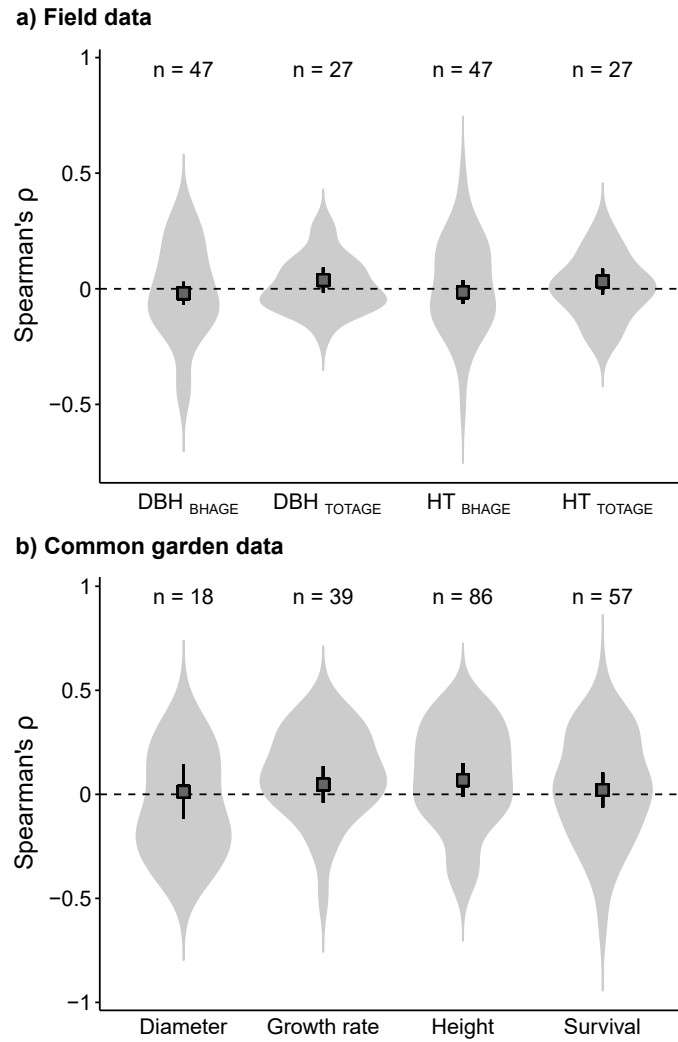
Figure 3: *Distribution of Spearman's correlation coefficients (ρ) between species' probability of occurrence and individual fitness across different response traits analyzed (violin plot) for a) field data (from Forest Inventory Analysis of US Forest Service, FIA) and b) common garden experiments' data. No significant difference was detected across different response traits analyzed in both datasets. Grey squared points indicate mean pooled effect (and 95% CI) obtained from mixed-effect models using response trait type as predictor (n = number of pairwise correlations). Horizontal dashed line indicates Spearman's correlation equal to zero. Response traits in field data are diameter at breast height (DBH) and tree height (HT) standardized to age estimated at the root collar (TOTAGE) or at the breast height (BHAGE).*

Discussion

By combining individual fitness data from forest inventories and common gardens in North America, we showed that individual fitness indicators (growth and survival) are poorly associated with coarse-scale probability of occurrence projected with SDMs. Furthermore, we found the lack of 'fitness-centre' relationships are pervasive across species with different potential dispersal ability and climatic breadth. Finally, we detected no influence of the precision of SDMs [expressed with maximum True Skill Statistic (TSS) of models used to ensemble the models] on the magnitude and direction of the 'fitness-centre' correlations. Thus, our results reject the 'fitness-centre' hy-

pothesis stating that individual fitness is higher in locations with higher SDM-modeled probability of occurrence.

Why the 'fitness-centre' hypothesis may not hold

The 'fitness-centre' hypothesis has been detected for certain species in previous studies (Nagaraju *et al.*, 2013; Wittmann *et al.*, 2016; Sangüesa-Barreda *et al.*, 2018; Mammola *et al.*, 2019) but not in others (Larson *et al.*, 2010; Barela *et al.*, 2020; Chardon *et al.*, 2020). However, these studies show three main methodological limitations (which we will discuss in detail below). Such limitations concern the restricted number of species analyzed, the amount of observation available to quantify 'fitness-centre' relationships, and the type of trait data used to address the hypothesis.

First, previous studies tested the hypothesis on one or few species. Because our results suggest that 'fitness-centre' correlations across multiple species are normally distributed around the zero, restricting the analysis to only few species makes the hypothesis more likely to be supported by chance alone (Santini *et al.*, 2019). Thus, while positive 'fitness-centre' associations are clear for certain species, these may simply not hold true in other species (Thuiller *et al.*, 2010; Pellissier *et al.*, 2013) or even show a negative relationship (Barela *et al.*, 2020). Indeed, our analysis did not detect an effect of species-specific traits (dispersal ability and climatic breadth) on the 'fitness-centre' relationship, suggesting that correlations are randomly distributed across ecologically different species.

Second, due to sampling limitations, previous studies often used few individual fitness records, which are likely a poor representation of the full geographic range [but see Chardon *et al.* (2020)]. Conversely, our datasets allowed us to address the hypothesis over a significantly larger amount of observations over the entire species range. In addition, we used presence-absence data to train and test SDMs, which is generally a preferable approach than 'presence-only' SDMs (Guisan *et al.*, 2017). Appropriate sampling across the species range allows for better estimation of the covariation between traits and the environmental optimum of the species (Soberón *et al.*, 2018). Indeed, consistent with our findings, Chardon *et al.* (2020) used a comprehensive set of geographic records of the cushion plant *Silene acaulis* and showed no relationship between individual fitness (plant individual size) and probability of occurrence, even within the same genetic and geographic groups.

Third, while previous studies addressing the 'fitness-centre' hypothesis solely rely on fitness data collected in-situ, common garden data reported here were used to quantify survival and to test directly for the association between adaptive trait variation and modeled probability of occurrence. Common garden experiments where individuals are grown in controlled conditions removes in-situ individual variation originated from other causes than probability of occurrence. In our case, growth rate of an individual trees can be affected by local biotic interactions with surrounding trees (e.g. light competition), presence of herbivores, parasites and sylvicultural management (Smith *et al.*, 1997). Our approach showed nevertheless that adaptive trait variation and survival observed at common garden sites are unrelated to the coarse scale predictions of species occurrence.

Our findings agree with recent literature addressing the 'centre-periphery' hypothesis over multiple plant and animal species and revealing no consistent trend [Thuiller *et al.* (2014); Dallas *et al.* (2017); Pironon *et al.* (2017); Santini *et al.* (2019); but see Osorio-Olvera *et al.* (2020)]. Overall, recent simulations on artificial landscapes have

showed support to the 'centre-periphery' relationships only when certain conditions are met (i.e. deterministic population growth, high dispersal, low competition), which rarely occur in the reality of natural systems (Dallas & Santini, 2020). Particularly, Dallas *et al.* (2017) showed that abundance of tree species (as well as birds, fishes and mammals) in the United States does not correlate with distance to the environmental centroid reporting mean 'abundance-distance' correlation coefficients close to zero. Similarly, Thuiller *et al.* (2014) found uncertain relationship between probability of occurrence and tree populations' dynamics (population growth rate, carrying capacity and population density) in Northern America and Europe. Like our study, Thuiller *et al.* (2014) included data from forest inventory plots located in Western United States; yet, their analysis focused on population-level traits (i.e. basal area) related to local abundance rather than individual tree growth.

Pironon *et al.* (2017) and Santini *et al.* (2019) report various arguments for which 'centre-periphery' hypothesis might not hold true that are transferable to our hypothesis tested here: I) individual fitness can show abrupt rather than linear declines from the centre to the edge of the environmental niche; II) fitness might depend on biotic interactions, which are not accounted for in SDMs; III) occurrences of specimens and their individual performance might not be in equilibrium with the environment.

In addition, we also highlight that coarse-scale modeling approaches cannot capture microhabitat properties where individuals live. Since important factors affecting plant growth depend upon micro-habitat (Suggitt *et al.*, 2010) and topography (e.g. slope aspect) (Cantlon, 1953; Holland & Steyn, 1975), the lack of support for the 'fitness-centre' hypothesis found here and elsewhere needs to be circumscribed to the coarse-scale level only. Under this point of view, more advanced niche modeling approaches accounting for micro-habitat conditions (Lembrechts *et al.*, 2019) and biotic interactions through joint distribution models (Clark *et al.*, 2017) would be more likely to detect a consistent trend between individual fitness and probability of occurrence. In general, additional uncertainties other than coarse-scale resolution to detect such trends could be present when SDMs fail to properly model species distribution under certain circumstances, such as missing relevant environmental variables for certain species or wrong model structures.

We acknowledge that tree fitness in the 'field' data were potentially affected by noise caused by temporal variation in sampling growth rate of different individuals at different times that do not match environmental conditions of bioclimatic predictors used to obtain SDMs. We further note that unaccounted temporal fluctuation of individual fitness in space (e.g. caused by pests' outbreaks and forest utilization) could produce additional noise to 'field' data retrieved from forest inventory data [see e.g. (Thuiller *et al.*, 2014)]. Yet, we also underline that climatic data used in our SDMs represented the historical averaging climatic conditions (1970-2000) matching the time period in which individuals were sampled in the 'field' data and that such cross-individuals temporal fluctuation is virtually absent in 'common garden' data, where individuals are simultaneously grown and sampled.

Finally, we here mainly focused on growth rate data (except for survival assessed in the 'common garden' data). Yet, a combination of indicators other than growth rates, like fecundity and seedling survival, could potentially be more closely correlated to probability of occurrence modeled by SDMs than individual growth rate, as these are key determinant of plant persistence in space.

General implications

Addressing the validity of the 'fitness-centre' hypothesis has important implications for conservation and applied biodiversity management. Indeed, several conservation studies are based upon estimations of coarse modeled habitat suitability based on occurrence records to predict areas where species will most likely harbors individuals of that species [see e.g. Peterson *et al.* (2002); Fitzpatrick *et al.* (2008); Zhang *et al.* (2020)]. However, a lack of the underlying 'fitness-centre' relationship alters our interpretation of how modeled probability of occurrence is linked to the ability of specimens to survive and grow in a given location, affecting decisions on where to prioritize conservation efforts. Based on our results, areas with lower probability of occurrence might be occupied by individuals with higher fitness compared to those located in areas estimated with higher probability of occurrence. In such cases, the fitness of individuals located in areas with lower probability of occurrence are likely to be either positively affected by certain biotic and micro-habitat conditions neglected by SDMs, or locally adjusting through adaptation and plasticity, for instance, in response to climate change (Nicotra *et al.*, 2010). In addition, eco-evolutionary processes in response to range shifts occurring in areas with lower probability of occurrence could help maintaining high genetic variation enhancing individual fitness, as long as climate change or other factors do not enhance isolation and restrain gene flow from populations nearby (Pironon *et al.*, 2017; Nadeau & Urban, 2019).

We suggest that using data on intraspecific variability of fitness-related traits in concert with SDMs could improve conservation planning. Indeed, mapping functional traits in space can be used as a tool to evaluate the output of SDMs and its biological meaning. For instance, identifying populations with greater longevity and dispersal ability located in areas with high probability of occurrence could help to trace most suitable biological corridors facilitating range shifts. Conserving high-fitness individuals occurring in most environmentally suitable areas could also produce more economically effective conservation plans when resources are limited.

Concluding remarks

Here, we determine that spatial variation in individual fitness within the species range is not explained by the output of SDMs, contrary to what showed by some previous analyses. Although our results were limited to a single system (i.e. tree species in North America) our results clearly highlight that a strong pattern cannot safely be assumed to work in any system unless there is specific evidence of a 'fitness-centre' coupling for a certain system. In that regard, we highlight that we could not find any evidence of dispersal capacity and climatic breath to influence the overall results. Thus, the main takeaway from our study is that while the 'fitness-centre' is supported by theory surrounding the concept of environmental niche (Pulliam, 2000; Guisan & Thuiller, 2005), it does not hold true in nearly any species. Because individual fitness plays a relevant role in buffering local extinction and range contraction following environmental changes and biotic invasions (Anderson, 2016), our results imply that conservation projects relying on the assumption of the 'fitness-centre' hypothesis should be revised. We thus recommend assessing how individual fitness vary within the current species range along modeled probability of occurrence before inferring conclusions on present and future range contractions based on SDMs.

AUTHORS' CONTRIBUTIONS

G.M. and S.F. conceived the project idea. G.M. collected and analyzed the data and wrote the manuscript. S.F and C.W. helped to interpret results and contributed substantially to revisions.

DATA AVAILABILITY STATEMENT

We report references of common-garden studies in the 'Data Source' section. Data on the correlation coefficients used in the 'meta-analysis' are available at the Figshare data repository*. Raw data on forest inventories are available online for United States (`https://apps.fs.usda.gov/fia/datamart`) and upon request to the Canadian Forest Service (`https://nfi.nfis.org/en/datarequest`).
* = data will be made publicly available once the manuscript is accepted for publication

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6   Concluding remarks

We here quantified cross-species trends of intraspecific trait variation within species geographic and environmental range. The studies presented here covered various plant traits and metrics of individual fitness (growth rate, reproduction and survival) using data from 132 peer-reviewed scientific articles in total, mainly located in the Northern Hemisphere (Northern America, Europe and Asia) and measuring intraspecific trait variability across elevational gradients in-situ (Chapter I), reciprocal transplants (Chapter II), forest inventory plots and common garden experiments (Chapter III). Overall, studies reported here highlight how such patterns are pervasive across different plant species, yet with some exception depending on trait analyzed and environmental context.

The findings presented in this thesis have relevant implications in trait-based macroecology, biogeography and climate change ecology. Because plants are shifting in response to global environmental changes, studies conducted on a large geographical extent and covering different species are key to understand future population dynamics and to improve conservation projects.

Specifically, Chapter I & II address potential implications of temperature change on plant trait expression and fitness. The main take-home message here is that, despite some clear variation across studies and species considered, intraspecific trait variation follows common trends in response to elevational change. Such variation in plant traits highlight that individuals fitness is coupled with abiotic variation in most of mountain ranges analysed, with relevant implications in predicting how the mountain biota is likely to respond to climatic changes. Yet, to ascertain the role of temperature and other abiotic factors on functional traits and biological processes in general, environmental gradients should be evaluated against temperature (and covarying abiotic variables, such as precipitation) instead of using elevation as direct surrogate. In addition, reciprocal transplant studies testing for local adaptation and phenotypic plasticity are required to characterize traits variation along such gradient.

Chapter III addressed how species distribution models (SDMs) capture the ecological theory surrounding the concept of ecological niche. In general, SDMs have interesting potential to model biological processes (including trait variability) in space. The lack of 'fitness-centre' hypothesis found here highlight that, although we can obtain sound predictions on the probability where a species might be located in a given area, we cannot safely assume higher fitness will occur among individuals located in that area. Such findings inform researchers working on ecological niche modeling with the aim to predict changes in habitat suitability for conservation purposes. Future advances in modeling species distribution could benefit in integrating functional traits and population dynamics to improve the accuracy and the applicability of these models in cost-effective conservation strategies. To this aim, future research calls for I) good representation of trait data of the modeled organisms; and II) a proper understanding of how such traits vary within the environmental and geographic space occupied by the species under consideration, with major attention to factors operating ad different scales and resolutions (for example, by accounting for both micro-habitat and macroclimate dependencies).

Because the findings of our analyses were mainly limited to trait and climatic data availability, major focus should be payed on less commonly studied plant traits in the future (e.g. reproductive and phenological traits) involving novel experimental designs to test the effects of different elevation-dependent variables other than temper-

ature change (e.g. precipitation, soil properties and anthropogenic disturbance) and including the effects of micro-habitat, a key component buffering the effect of climate change in plants living at high elevation. Furthermore, findings presented here represent trait variation occurring within the abiotic niche of the plant only, since our studies did not account for biotic interactions. Disentangling biotic components and environmental variation driving intraspecific trait variation in the experimental design is challenging for researchers, but necessary to test the relevance of our findings in future research. An additional challenge for future research concern the scale of intraspecific variability in space. The scale of our findings was limited within the species distribution range. Thus, understanding trait variation outside their range remains an urgent question in conservation to predict plant fitness following range expansions or biological invasions.

7 Acknowledgements

I first thank C. Wellstein for her contribution to the manuscripts presented here and, more importantly, for constantly supporting in my research ideas and projects during the last three years.

I also express my gratitude to P. De Frenne and N. Hölzel for providing external supervision to my PhD and for their help in the first manuscript published during my PhD reported in Chapter I.

Special thanks to S. Faurby and the Alex Antonelli's lab for hosting me in their group at Gothenburg Global Biodiversity Centre and for their essential support on the research presented in Chapter III.

I dedicate my PhD thesis to Primo Levi (1919-1987).

8 Appendices

Appendix I

I.1: Search string for primary studies collection

TS=(("SLA" OR "leaf size" OR "specific leaf area" OR "leaf dry matter" OR "leaf nitrogen" OR "leaf phosphorus" OR "leaf N" OR "leaves traits" OR "leaf trait" OR "leaf traits") AND (altitude* OR altitudinal OR elevation))

I.2: List of primary studies and species analysed in the meta-analysis

Table I.2.1: *Summary of primary studies included in the meta-analysis. Table reports the country in which the studies were located, species name, leaf traits considered, the elevation of the lowest site (LE; m a.s.l.) and the elevation of the highest site (HE; m a.s.l.).*

Study	Country	Species	Trait	LE	HE
Almeida et al. (2013)	Ecuador	*Lasiocephalus ovatus*	Nmass; Pmass; SLA	4200	4800
Bansal & Germino (2010)	USA	*Abies lasiocarpa; Pseudotsuga menziesii*	SLA	2200	3050
Bilgin & Guzel (2017)	Turkey	*Tilia rubra*	Narea; Nmass; Pmass; SLA	330	974
Bilgin et al. (2016)	Turkey	*Vaccinium Arctostaphylos; Vaccinium myrtillus*	LMA; Narea; Nmass; Pmass; SLA	60	2300
Birmann & Körner (2009)	Austria; Switzerland	*Picea abies; Pinus cembra*	LMA; Narea; Nmass	1720	2200
Bowman et al. (1999)	USA	*Frasera speciosa*	LMA; Narea; Nmass; Pmass	1800	3500
Bresson et al. (2011)	France	*Fagus sylvatica; Quercus petraea*	LA; LMA; Narea	150	1600
Casper et al. (2012)	Mongolia	*Festuca lenensis; Potentilla acaulis*	δ^{13}C; Nmass	1660	1800
Castillo et al. (2013)	Ecuador	*Croton scouleri*	LA	10	260
Castrillo (2006)	Venezuela	*Espeletia schultzii*	SLA	3100	4200
Chai et al. (2015)	China	*Quercus aliena; Quercus spinosa*	LA; Nmass; Pmass; SLA	1480	2200
Chen et al. (2015)	China	*Quercus aquifolioides*	δ^{13}C; LALMA; Narea; Nmass	2500	3800
Cordell et al. (1999)	USA	*Metrosideros polymorpha*	δ^{13}C; LA; Narea; Nmass	107	2469
Cranston et al. (2015)	New Zealand	*Donatia novae-zelandiae*	SLA	0	1000

De Lillis (2004)	Nepal	*Abies spectabilis; Betula utilis; Juniperus wallichiana; Quercus semecarpifolia; Rhododendron campanulatum*	δ^{13}C; Nmass	3000	3800
Dogan et al. (2015)	Turkey	*Hedera helix*	Narea; SLA	10	400
Du et al. (2017)	China	*Quercus variabilis*	LMA; Nmass; Pmass	546	1323
Ellison & Farnsworth (2005)	USA	*Darlingtonia californica*	LMA; Nmass	411	1241
Feng et al. (2013)	China	*Quercus aquifolioides*	δ^{13}C; Narea; SLA	2600	3500
Friend et al. (1989)	Scotland	*Nardus stricta; Vaccinium myrtillus*	δ^{13}C; Narea	200	1000
Geeske et al. (1994)	USA	*Metrosideros polymorpha*	LA; LMA	70	2350
Gratani et al. (2012)	Italy	*Crepis pygmaea; Isatis apennina*	LA; LMA	2250	2350
Gratani et al. (2014)	Italy	*Sesleria nitida*	LA; LMA	1100	1895
Hultine & Marshall (2000)	USA	*Abies lasiocarpa; Picea engelmannii; Pinus contorta; Pseudotsuga menziesii*	δ^{13}C; LMA; Narea; Nmass	808	2591
Idol et al. (2007)	USA	*Acacia koa*	LMA; Narea; Nmass; Pmass	1200	2050
Kilic et al. (2012)	Turkey	*Amelanchier rotundifolia; Rhamnus oleoides*	LMA; Narea; SLA	450	800
Kofidis & Bosabalidis (2008)	Greece	*Nepeta nuda*	LA	950	1760
Kogami et al. (2001)	Japan	*Reynoutria japonica*	δ^{13}C; LMA; Narea; Nmass	10	2500
Kong et al. (2012)	China	*Rhododenron aganniphum*	δ^{13}C; Nmass; SLA	4190	4450

Kudo (1996)	Japan	*Alnus maximowiczii; Betula ermanii; Betula platyphylla; Quercus mongolica*	Nmass; SLA	140	1700
Leverkus et al. (2015)	Spain	*Quercus ilex; Quercus pyrenaica*	δ^{13}C; Nmass; Pmass	1680	2045
Li et al. (2004)	China	*Picea asperata; Picea likiangensis*	δ^{13}C; SLA	3600	3900
Li et al. (2006)	China	*Quercus aquifolioides*	δ^{13}C; Narea; Nmass; SLA	2000	3600
Li et al. (2007)	China	*Hippophae rhamnoides*	δ^{13}C; Narea; Nmass; SLA	2000	3600
Li & Bao (2014)	China	*Campylotropis polyantha*	LA	1650	2000
Li et al. (2014)	China	*Chimonobambusa utilis*	LA; SLA	1500	2000
Li et al. (2017)	China	*Pinus hwangshanensis*	LA; LMA; SLA	1200	2000
Liu et al. (2016)	China	*Pinus tabuliformis*	δ^{13}C; Nmass	1000	2200
Luo et al. (2005)	China	*Abies fabri; Cyclobalanopsis oxyodon; Lithocarpus cleistocarpus; Phoebe chinensis*	Narea; Nmass; SLA	1900	3700
Ma et al. (2015)	China	*Potentilla saundersiana*	Nmass; SLA	4350	5200
Macek et al. (2009)	Argentina Bolivia Chile	*Polylepis rugulosa; Polylepis tarapacana; Polylepis tomentella*	δ^{13}C; LA; Nmass; Pmass; SLA	3180	5010
Martin & Anser (2009)	USA	*Metrosideros polymorpha*	Narea; SLA	107	2469
Milla et al. (2009)	Spain	*Saxifraga canaliculate; Saxifraga trifurcata*	Nmass; SLA	100	1872
Morecroft et al. (1992)	Scotland	*Alchemilla alpina*	δ^{13}C; LA; Nmass; Pmass; SLA	200	1100

Ozbucak et al. (2017)	Turkey	*Cyclamen coum*	LMA; Nmass; SLA	0	1850
Peng et al. (2012)	China	*Abies faxoniana*	δ^{13}C; LMA; Narea; Nmass	2579	3000
Rada et al. (1998)	Venezuela	*Espeletia schultzii*	Nmass	2950	4200
Rajsnerova et al. (2015)	Czech Republic	*Fagus sylvatica*	LMA; Narea	400	1100
Rosado et al. (2016)	Brazil	*Alchornea triplinervia*; *Hyeronima alchorneoides*; *Mollinedia schottiana*; *Rustia formosa*	SLA	100	1000
Schoeb et al. (2013)	Spain	*Arenaria tetraquetra*	LA; SLA	2315	3240
Seguì et al. (2018)	Chile	*Viola maculata*	LA; SLA	1900	2350
Shi et al. (2015)	China	*Quercus spinose*; *Rumex dentatus*; *Salix atopantha*	δ^{13}C; Narea; SLA	2400	3500
Sriladda et al. (2014)	USA	*Shepherdia rotundifolia*	LA; SLA	1642	2507
Steinke et al. (2008)	Argentina	*Nothofagus antarctica*	LA; Nmass	800	1700
Sundqvist et al. (2011)	Sweden	*Betula nana*; *Empetrum hermaphroditum*; *Trollius europaeus*; *Vaccinium vitis-idaea*; *Viola biflora*	Nmass; Pmass; SLA	500	1000
Takahashi & Matsuki (2016)	Japan	*Solidago virgaurea*	LMA; Nmass	1600	2400
Takahashi & Miyajima (2008)	Japan	*Abies mariesii*; *Abies veitchii*; *Betula ermanii*; *Sorbus commixta*	δ^{13}C; LMA; Nmass	1600	2500

Taneda et al. (2016)	Nepal	*Rhododenron anthopogon; Rhododenron arboretum; Rhododenron barbatum; Rhododenron campanulatum; Rhododenron thomsonii*	LA; Nmass	2750	4470
Turkis & Ozbucak (2010)	Turkey	*Cistus creticus*	Narea	30	880
Wang et al. (2017)	China	*Rhododendron agglutinatum*	LA; LMA; Narea; Nmass; Pmass	370	4150
Wieser er al. (2010)	Austria	*Pinus cembra*	SLA	1950	2180
Williams-Linera (2000)	Mexico	*Carpinus caroliniana; Clethra Mexicana; Hedyosmum mexicanum; Liquidambar styraciflua; Oreopanax xalapensis; Quercus xalapensis; Turpinia insignis*	LA; Nmass; SLA	1250	1470
Woodward (1983)	Scotland	*Agrostis tenuis; Carex bigelowii; Festuca ovina; Lolium perenne*	SLA	320	1150
Woodward (1986)	Scotland	*Vaccinium myrtillus*	LA; Narea; SLA	200	1100
Xu et al. (2014)	China	*Abies faxoniana*	δ^{13}C; LMA; Narea; Nmass	2550	3150
Yan et al. (2012)	China	*Pinus koraiensis*	δ^{13}C; Narea; Nmass	760	1420
Yosefzadeh et al. (2009)	Iran	*Buxus colchica*	LA; LMA	420	1200
Zhang et al. (2005)	China	*Quercus pannosa*	LMA; Narea	3240	4170
Zhang et al. (2016)	China	*Picea schrenkiana*	δ^{13}C; LA; LMA; Narea; Nmass; Pmass; SLA	1420	2300

| Zhao et al. (2008) | China | *Picea crassifolia* | δ^{13}C; LA; LMA; Narea; Nmass; Pmass | 2500 | 3500 |
| Zhu et al (2010) | China | *Calligonum roborovskii* | LMA; Nmass; SLA | 2100 | 2600 |

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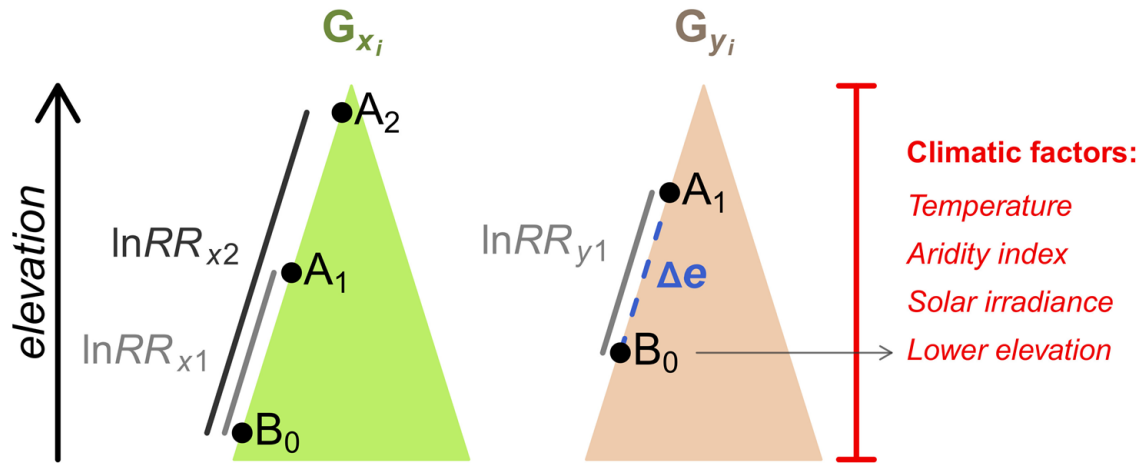## I.3: Details on the calculation of the effect size

Figure I.3.1: *Graphical representation of the calculation of the effect size ('lnRR'), elevation ('Δe'; in blue) and the other predictors adopted in the meta-regression (in red). Within each gradient G_i, multiple effect sizes were calculated for each site Ax sampled above the lowest B_0 [i.e. lnRR = ln(T_A) – ln(T_B); where T is the mean of a trait of a species sampled on the two sites]. The vertical distance between A_x and B_0 is what we defined as elevation (Δe) in the context of our study and used as the main predictor in our analysis. We also estimated the average climatic factor for each mountain range / slope assessed. Lower elevation (i.e. the elevation measured in m a.s.l. of B_0) was also used as moderator for each gradient.)*

I.4: Model selection including interactions

Alongside the analysis presented in the main text of the manuscript, we performed a model selection by fitting and comparing all possible candidate models ranked by the Bayesian Information Criterion (BIC) starting from a full model with the following formula of the fixed-effect part (Eq. 1):

$$y_i \sim ELE * (AELE + SRAD + LAT + MGST + AELE + PT) \tag{1}$$

where y_i = log-transformed response ratio of a given leaf trait; ELE = elevation difference, $AELE$ = absolute elevation of the lowest site sampled in a gradient, $MGST$ = mean growing season temperature, PT = plant functional types mean pooled effect size (woody or herbaceous), LAT = latitude, AI = aridity index, $SRAD$ = mean annual solar radiation. The model selection above address the hypothesis that responses to elevation difference (i.e. the distance between sites sampled) are modulated by climatic conditions and plant functional types across different elevational gradients. We carried out this analysis to explore whether statistically significant interactions are retained compared to the candidate set of models analyzed with multimodel inference presented in the main text where the interactions were not included. We present such analysis here in the Supporting Information as its scope is complementary to our work, but it was not implemented in our system framework nor it aims to address the hypotheses and expectations presented in this study (see questions i-iv in the introduction). In addition, we did not apply a multimodel inference to the full model in Eq. (1) because we wanted to avoid the so-called 'problem of too many models' (in our case, 793 models in total) (Burnham & Anderson, 2010; Dochtermann & Jenkins, 2011), producing potentially spurious results (Grueber *et al.*, 2011).

The models retained within +4 ΔBIC units from the lowest BIC model are indicated in Table S.4.1. SLA, P*mass* and δ^{13}C lowest BIC models showed no significant interactions, reflecting in general results reported in Figure 3 and Figure 4 in the main text. Lowest BIC models for LMA, LA, N*area* and N*mass* retained instead significant interactions (see Table S4.2). The lowest BIC models of N*area* and LMA indicated a significant interaction with absolute elevation of the lowest site (AELE) and mean annual solar radiation (SRAD), respectively. Contrary to what observed in our main results, the N*area* model indicated that N*area* decreases with increasing elevation in sites that are conducted in high mountains (interaction term estimate = -0.050; p-val < .001). The LMA model indicated that the increase in elevation is stronger in sites with higher mean annual solar radiation. Interestingly, The N*mass* model indicated that the positive response of N*mass* to elevation is stronger in warmer mountains. Several interactions within the LA model possibly reflect the presence of a particularly strong LA variation reported in a study conducted in the Galapagos conducted on a woody species in Galapagos (Castillo *et al.* (2013); see Appendix S2), since the removal of this study filtered out e.g. the interaction between elevation and mean growing season temperature in the lowest BIC model (not showed).

Table I.4.1: *Fixed effects of the models with the lowest BIC (Bayesian Information Criterion) [(within +4 ΔBIC units from the lowest BIC model (in bold)] for each response variable analyzed. ELE = elevation difference; AELE = absolute elevation of the lowest site sampled in a gradient; MGST = mean growing season temperature; PT = plant functional types mean pooled effect size (woody or herbaceous); LAT = latitude; AI = aridity index; SRAD = mean annual solar radiation. Models are ranked and compared by fitting the maximum-likelihood method ("ML").*

TRAIT	Fixed effect	BIC	ΔBIC
SLA	**~ ELE**	**-106.47**	**0.00**
	~ PT + ELE	-105.17	-1.31
	~ 1	-104.85	-1.63
	~ PT	-103.92	-2.56
	~ AI + PT + ELE	-103.11	-3.36
	~ MGST + ELE	-102.91	-3.56
	~ AELE + ELE	-102.64	-3.83
LMA	**~ ELE + SRAD + ELE:SRAD**	**-111.02**	**0.00**
	~ AELE + LAT + ELE + AELE:ELE + LAT:ELE	-109.34	-1.68
	~ AELE + LAT + PT + ELE + AELE:ELE + LAT:ELE + PT:ELE	-108.53	-2.50
	~ AELE + ELE + SRAD + AELE:ELE + ELE:SRAD	-107.71	-3.31
	~ AELE + LAT + PT + ELE + AELE:ELE + LAT:ELE	-107.53	-3.50
	~ AELE + PT + ELE + AELE:ELE + PT:ELE	-107.23	-3.80
	~ AELE + ELE + AELE:ELE	-107.10	-3.92
LA	**~ AI + LAT + MGST + PT + ELE + SRAD + AI:ELE + MGST:ELE + PT:ELE + ELE:SRAD**	**116.87**	**0.00**
	~ AELE + LAT + MGST + PT + ELE + SRAD + AELE:ELE + LAT:ELE + MGST:ELE + PT:ELE	117.91	-1.05
	~ AI + LAT + MGST + PT + ELE + SRAD + AI:ELE + LAT:ELE + MGST:ELE + PT:ELE + ELE:SRAD	118.45	-1.58
	~ AELE + LAT + MGST + PT + ELE + SRAD + AELE:ELE + MGST:ELE + PT:ELE	119.28	-2.41
	~ AI + MGST + PT + ELE + AI:ELE + MGST:ELE + PT:ELE	120.06	-3.20
	~ AI + LAT + MGST + PT + ELE + AI:ELE + MGST:ELE + PT:ELE	120.15	-3.28
	~ AI + MGST + PT + ELE + SRAD + AI:ELE + MGST:ELE + PT:ELE + ELE:SRAD	120.22	-3.35
N*area*	**~ AELE + MGST + ELE + AELE:ELE**	**-34.97**	**0.00**
	~ MGST + ELE	-34.83	-0.13
	~ AELE + LAT + MGST + ELE + AELE:ELE + LAT:ELE	-34.02	-0.95
	~ ELE	-33.29	-1.67
	~ AELE + ELE + AELE:ELE	-32.87	-2.10
	~ AI + MGST + ELE + SRAD + AI:ELE + MGST:ELE + ELE:SRAD	-31.39	-3.58
	~ AI + MGST + ELE + SRAD + AI:ELE + ELE:SRAD	-30.97	-4.00
N*mass*	**~ MGST + ELE + MGST:ELE**	**-88.97**	**0.00**

	~ MGST + ELE	-88.45	-0.52
P*mass*	**~ MGST**	**107.42**	**0.00**
	~ MGST + ELE	110.29	-2.87
	~ 1	110.35	-2.93
	~ MGST + ELE + MGST:ELE	110.41	-2.98
	~ AELE + MGST	111.31	-3.89
δ^{13}C	**~ ELE**	**-600.82**	**0.00**
	~ MGST + ELE	-600.06	-0.76
	~ AI + ELE	-598.94	-1.88
	~ AI + PT + ELE	-597.69	-3.13
	~ PT + ELE	-597.18	-3.64
	~ MGST + PT + ELE	-596.90	-3.92

Table I.4.2: *Results of models with the lowest BIC (Bayesian Information Criterion) for LMA, LA, Narea and Nmass. Interaction terms are marked with ":". ELE = elevation difference; AELE = absolute elevation of the lowest site sampled in a gradient; MGST = mean growing season temperature; PT = plant functional types mean pooled effect size (woody or herbaceous); LAT = latitude; AI = aridity index; SRAD = mean annual solar radiation.*

Trait	Predictor	Estimate	SE	Z-val	p-val	LCI	UCI
LMA	intrcpt	0.046	0.03	1.543	0.123	-0.012	0.104
	ELE	0.047	0.013	3.668	>.001	0.022	0.072
	SRAD	0.031	0.029	1.079	0.280	-0.026	0.088
	ELE:SRAD	0.051	0.014	3.505	>.0001	0.022	0.079
LA	intrcpt_herb	0.128	0.131	0.976	0.329	-0.129	0.385
	AI	0.022	0.090	0.239	0.811	-0.155	0.198
	LAT	0.162	0.059	2.76	0.006	0.047	0.278
	MGST	-0.077	0.058	-1.327	0.184	-0.19	0.037
	intrcpt_wood	-0.098	0.154	-0.634	0.526	-0.399	0.204
	ELE_herb	0.456	0.090	5.048	>.0001	0.279	0.634
	SRAD	0.221	0.095	2.331	0.02	0.035	0.407
	ELE:AI	-0.286	0.042	-6.738	>.0001	-0.369	-0.203
	ELE:MGST	0.120	0.033	3.69	>.0001	0.056	0.184
	ELE_wood	-0.571	0.103	-5.548	>.0001	-0.773	-0.369
	ELE:SRAD	-0.133	0.040	-3.323	0.001	-0.212	-0.055
N*area*	intrcpt	0.052	0.033	1.576	0.115	-0.013	0.116
	AELE	-0.012	0.035	-0.351	0.726	-0.082	0.057
	MGST	0.072	0.026	2.778	0.005	0.021	0.123
	ELE	0.065	0.016	4.082	>.001	0.034	0.096
	ELE:AELE	-0.050	0.015	-3.235	0.001	-0.08	-0.02
N*mass*	intrcpt	0.042	0.026	1.653	0.098	-0.008	0.093
	MGST	0.064	0.022	2.922	0.003	0.021	0.107
	ELE	0.039	0.012	3.360	0.001	0.016	0.062
	ELE:MGST	0.032	0.013	2.536	0.011	0.007	0.056

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Grueber CE, Nakagawa S, Laws RJ, Jamieson IG (2011) Multimodel inference in ecology and evolution: challenges and solutions. *Journal of Evolutionary Biology*, **24**, 699–711. doi:10.1111/j.1420-9101.2010.02210.x. URL https://doi.org/10.1111/j.1420-9101.2010.02210.x.

Nakagawa S, Santos ESA (2012) Methodological issues and advances in biological meta-analysis. *Evolutionary Ecology*, **26**, 1253–1274. doi:10.1007/s10682-012-9555-5. URL https://doi.org/10.1007/s10682-012-9555-5.

Sutton JT, Nakagawa S, Robertson BC, Jamieson IG (2011) Disentangling the roles of natural selection and genetic drift in shaping variation at MHC immunity genes. *Molecular Ecology*, **20**, 4408–4420. doi:10.1111/j.1365-294x.2011.05292.x. URL https://doi.org/10.1111/j.1365-294x.2011.05292.x.

I.5: Mean pooled effect sizes and funnel plots of the null-model residuals

Pooled effect sizes derived from the all-encompassing meta-analyses (null models result) showed LMA, N*area*, and N*mass* to overall increase, and SLA and δ^{13}C to decrease, in individuals of the same species measured at higher elevation and compared to those at lower elevations, independently from the inclusion of predictors to explain such responses (see Figure S5.1).

We found no evidence of funnel plot asymmetry across data analyzed, except for P*mass* dataset (Egger's p-val = 0.001) (see Figure S5.2). However, non-significant effect sizes were present in the funnel, so that missing effect sizes are unlikely to be due to publication bias, bur rather than lack of studies reporting P*mass* decreasing with elevation (Figure S5.2). As predictors did not reduced residuals asymmetry, we adopted the 'trim and fill' test applied to the null models' residuals, as a tool of sensitivity analysis (Nakagawa & Santos, 2012; Sutton *et al.*, 2011). The 'trim-and-fill' method identifies the number of observations missing from the meta-analysis that would be necessary to correct funnel plot asymmetry, and consequently estimates the effect that these studies might have had on the outcome (Duval & Tweedie, 2000; Sutton *et al.*, 2011). From a random-effects meta-analytic procedure applied to null-model residuals (Nakagawa & Santos, 2012), the trim-and-fill test added 24 data points to the original 100 residuals data points and provided the estimate of +0.16, which we used to adjust our original estimates (lnRR P*mass*=0.14; Figure S5.3). Importantly, adjusting our original mean estimates did not change the mean direction of change of lnRR P*mass*, which did not alter our main conclusions, i.e. leaf P concentration tend to overall increase along elevation (although large variation in such response is present, which makes the slope estimate not significantly different from zero).
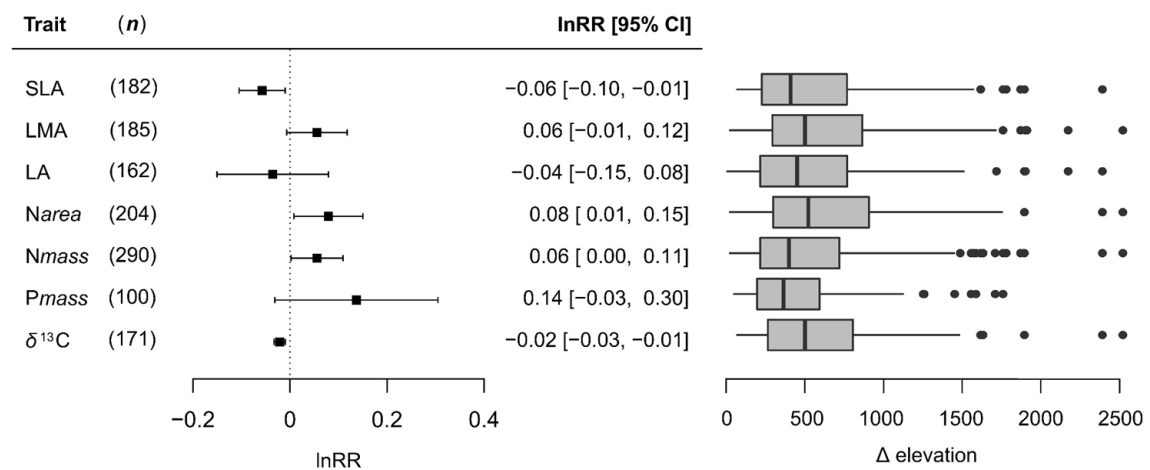

Figure I.5.1: *Results of the meta-analysis of log-response ratios (lnRR) for each leaf trait analyzed. Model outputs is obtained from models without any predictors (null models) and report the mean of the pooled effect size (and 95% CI) across all studies analyzed. The figure shows on the right the boxplots distribution of elevation of observations included in each dataset.*
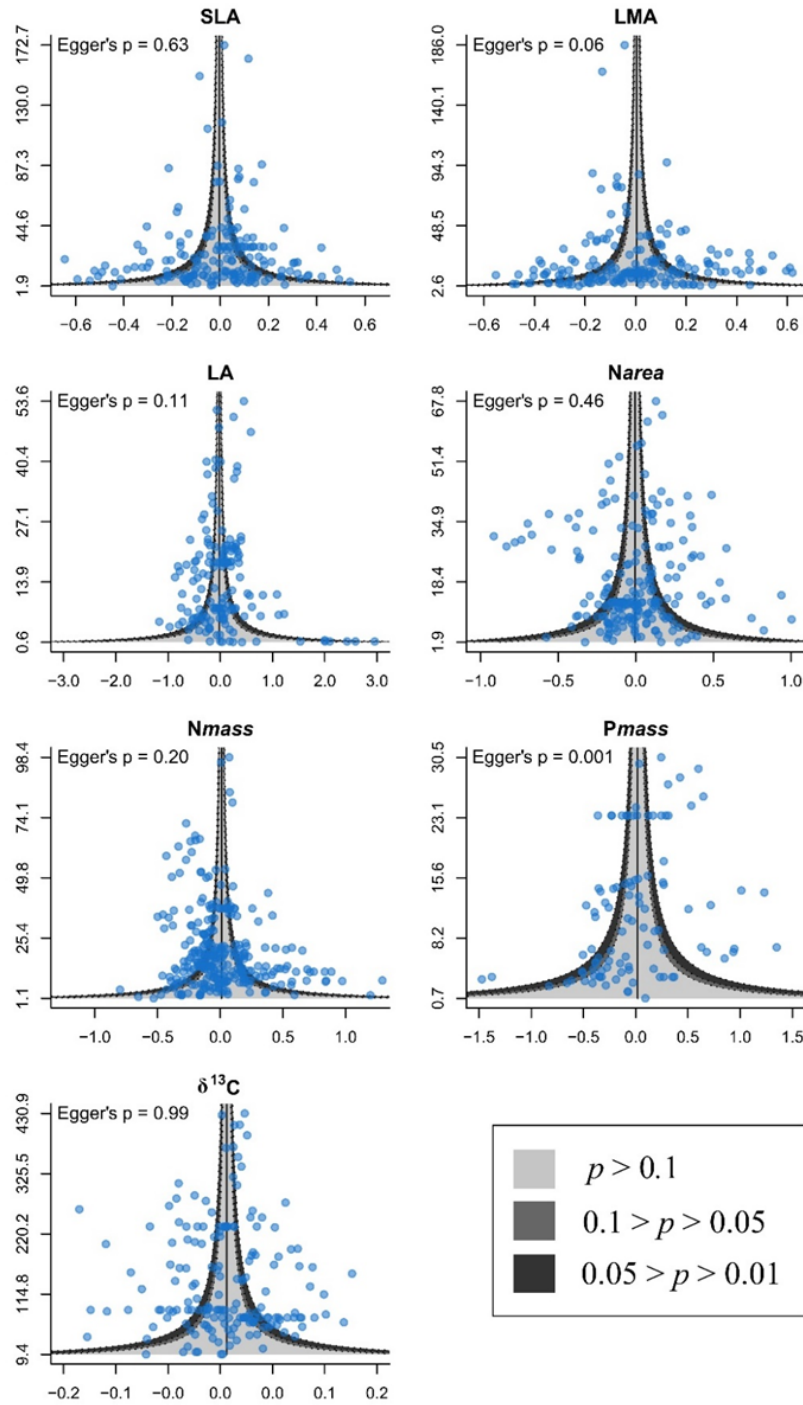
Figure I.5.2: *Contour-enhanced funnel plot for null-model residuals and p value of the Egger's test (see 'Methods' section). Shading colors of the plots represent the significance levels of the residuals estimates (white areas of the funnel correspond to estimates with ρ < 0.01). For Pmass, the presence of non-significant estimates at the left of the funnel suggest that funnel plot asymmetry detected by the Egger's test is not due to publication bias (see also Figure S5.3).*
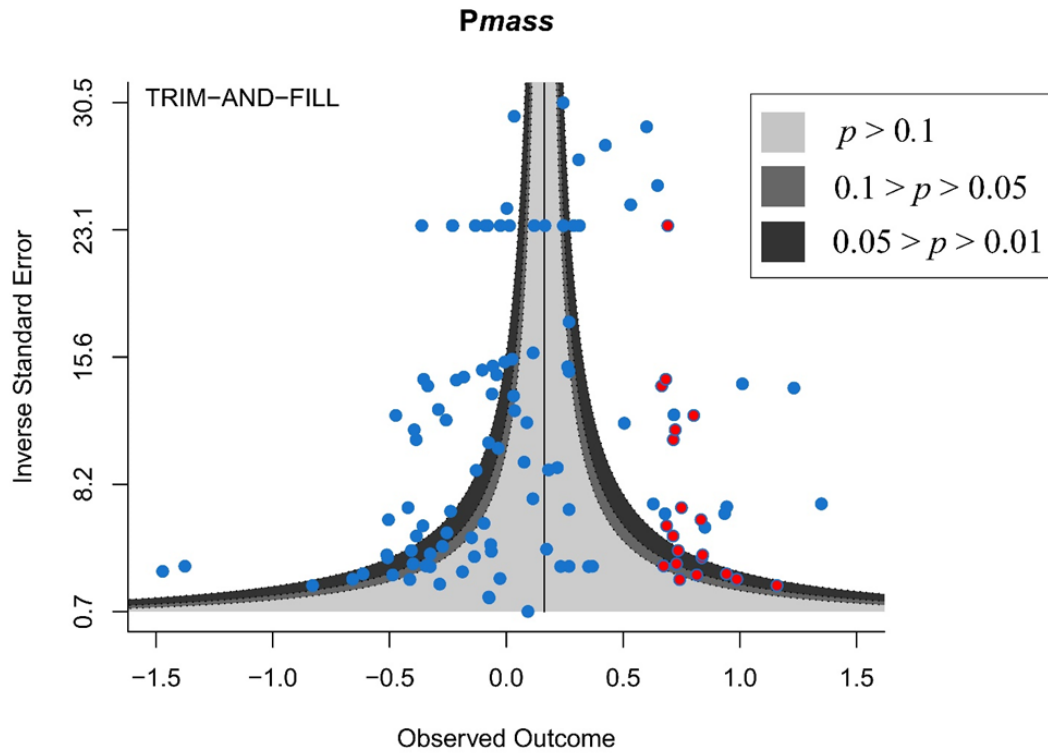
Figure I.5.3: *Contour-enhanced funnel plot for null-model residuals of Pmass with 24 'trim-and-fill' data points (in red) added by the test that correct for funnel plot asymmetry. The vertical line of the corrected funnel plot (= + 0.16) represent the adjusted value of the funnel with the trim-and-fill method. Shading colors of the plots represent the significance levels of the residuals estimates (white areas of the funnel correspond to estimates with $\rho < 0.01$).*

I.6: Trait-trait correlation coefficients and asymmetric regression analysis
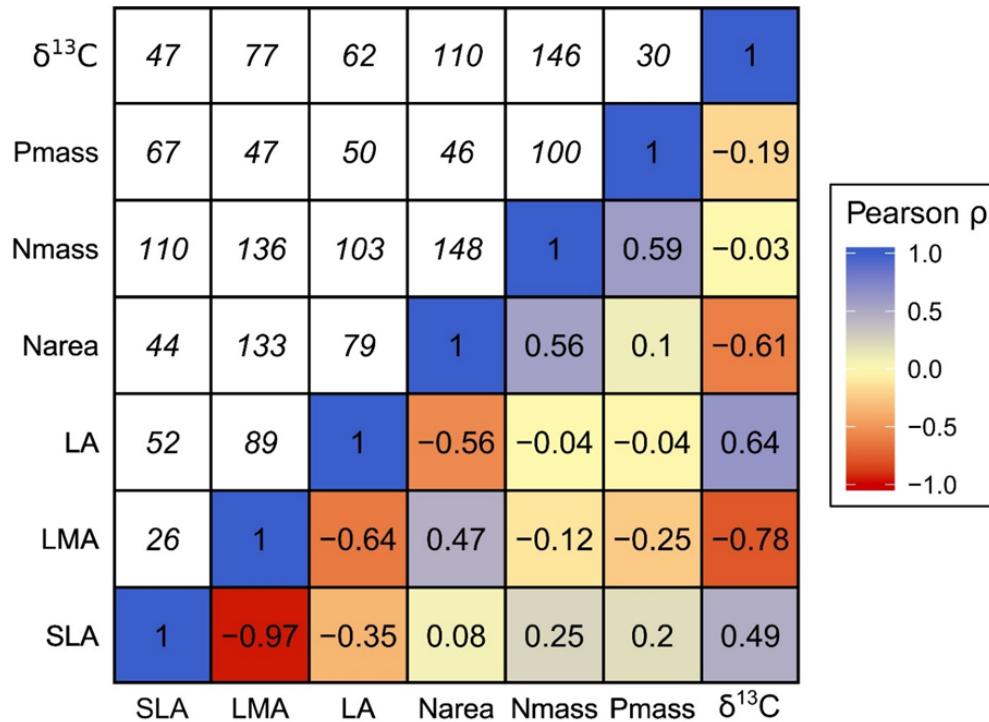

Figure I.6.1: *Heatmap of the Pearson's correlation coefficients between response ratios (lnRR) of the leaf traits included in the meta-analysis. The correlations are obtained from a subset of studies reporting data for both traits used in the regression. Bottom-right part of the figure indicate the strength and the direction of the correlation; the top-left part indicates the number of observations available for each subset (white cells, in italic). A negative correlation with leaf carbon isotope composition response ratio ($\delta^{13}C$) indicate that $\delta^{13}C$ is increasing positively correlated with a given trait (see 'Materials Methods').*
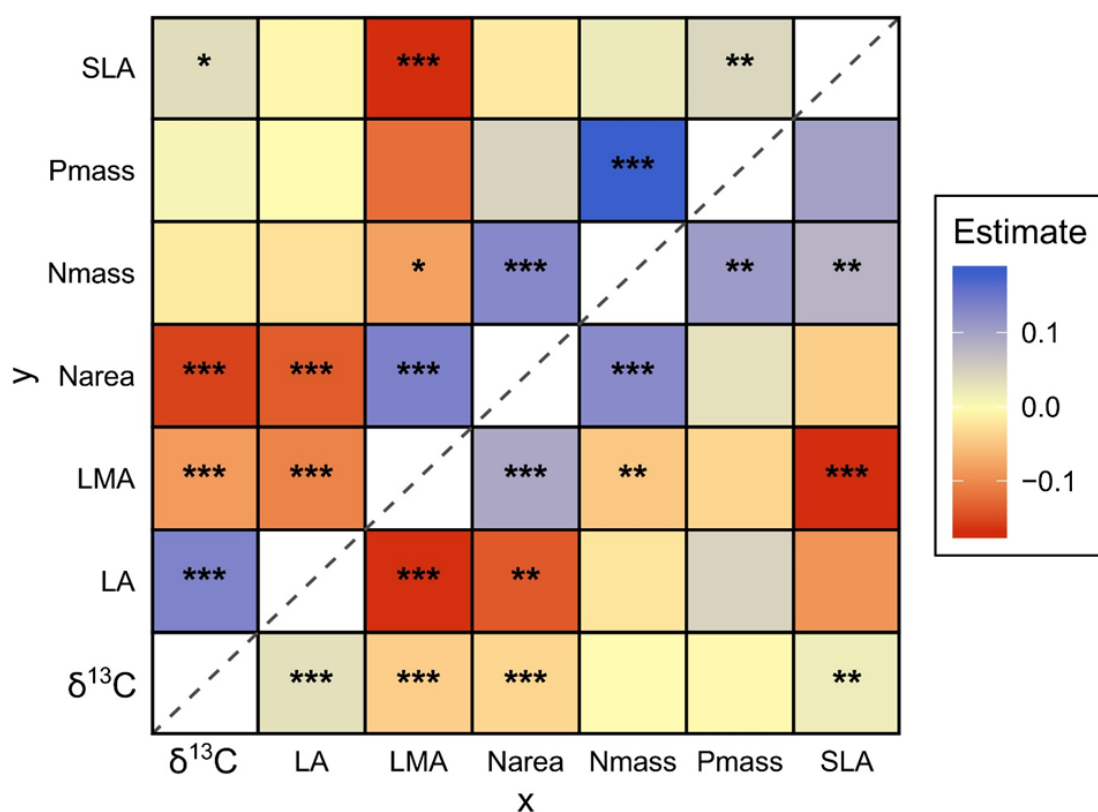
Figure I.6.2: *Heatmap of the slope estimates of models obtained from the regression between response ratios (lnRR) of the leaf traits included in the meta-analysis. Models are obtained from a subset of studies reporting data for both traits used in the regression. Values are slope estimates obtained by fitting a model with the lnRR of the first trait as response (y-axis) and the second trait as predictor (x-axis). Significance levels of slope estimates are given (*ρ < .05; **ρ < .01; ***ρ < .001) for each combination. A negative estimate of leaf carbon isotope composition response ratio ($\delta^{13}C$) indicate that $\delta^{13}C$ is increasing positively correlated with a given trait (see 'Materials Methods').*

Appendix II

II.1: Search strings and flow chart for the selection of primary studies

WebOfKnowledge: TS=((("transplant* experiment*" OR "common garden*" OR "reciprocal* transplant*") AND (fitness* OR germinat* OR "seed* emergenc*" OR "seed* product*" OR surviv* OR grow* OR reproduct*)) AND (elevation* OR altitud*))

Scopus: (TITLE-ABS-KEY ((("transplant* experiment*" OR "common garden*" OR "reciprocal* transplant*") AND (fitness* OR germinat* OR "seed* emergenc*" OR "seed* product*" OR surviv* OR grow* OR reproduct*)) AND (elevation* OR altitud*)))
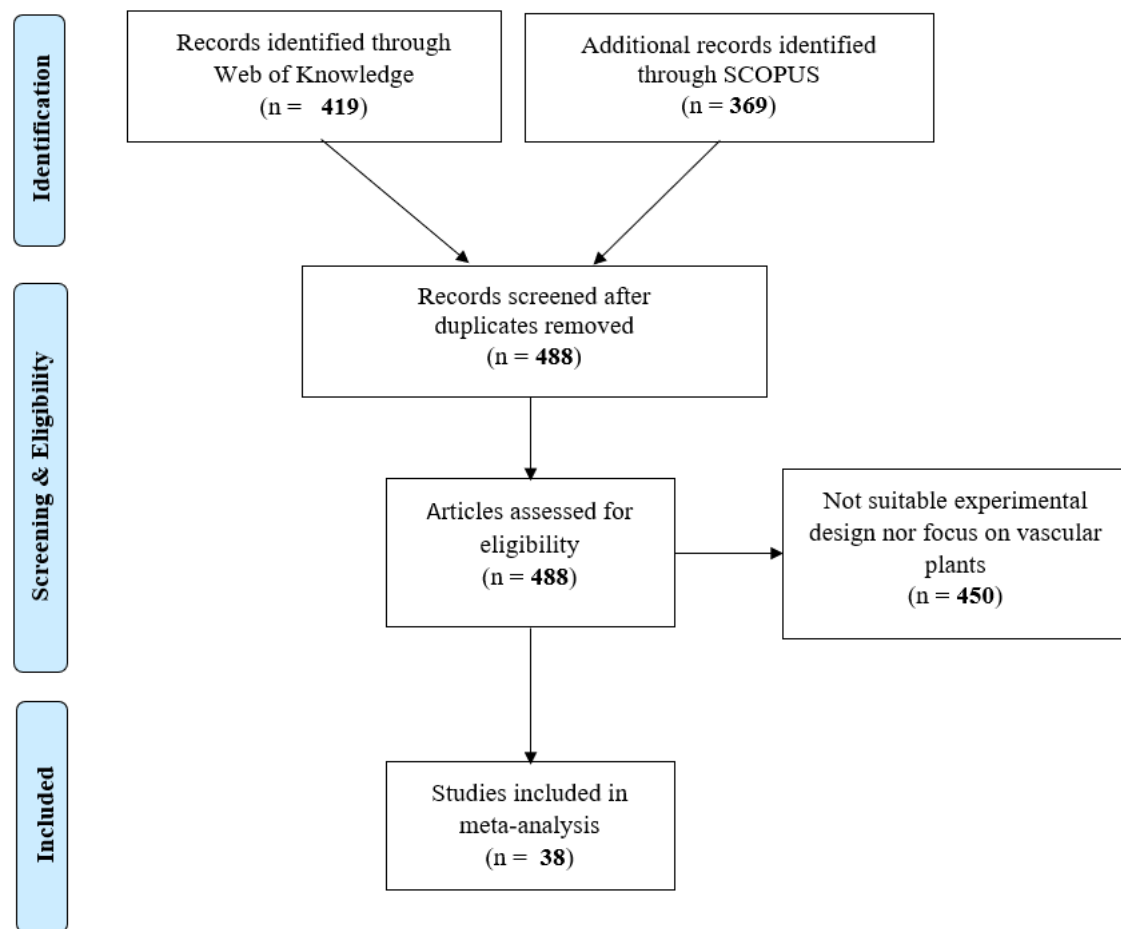

Figure II.1.1: *PRISMA flow chart showing the procedures (blue boxes) and steps (white boxes) to select the number of publications (in bold) for the meta-analysis eligibility procedure. Eligibility criteria are explained in 'Materials Methods' section of the manuscript.*

II.2: Summary of primary studies, species included and number of observations in the datasets

Table II.2.1: *Summary table of primary studies, country of the experiment and species (and family). Table reports for each species in a given study the following attributes: the maximum absolute elevation difference between transplant sites (ΔE); the response variable assessed (S=survival; G=germination; B=biomass, H=height, LN=number of vegetative organs; FN=number of flowers; SLA=specific leaf area; LA=leaf size); the amount of effect sizes calculated per each trait available in each dataset ('away vs. home' 'foreign vs local'); whether observations were calculable for both types of comparisons (ah='away vs. home'; fl='foreigin vs local') or only one of these.*

study*	country	species (family)	ΔE	Response	n.obs (min-max)**	data
Bakhtiari et al. (2019)	Switzerland	Cardamine pratensis (Brassicaceae)	1150	B	2	ah+fl
		Plantago major (Plantaginaceae)	1150	B - SLA	2	ah+fl
Bastida et al. (2015)	Spain	Aquilegia vulgaris nevadensis (Ranunculaceae)	400	S - G - B - LA	2	ah+fl
		Aquilegia vulgaris vulgaris (Ranunculaceae)	300	S - G - B - LA	2	ah+fl
Bemmels & Anderson (2019)	USA	Boechera stricta (Brassicaceae)	243	S - G - H - FN - SLA	3-6	ah+fl
Byars & Hoffmann (2009)	Australia	Craspedia lamicola (Asteraceae)	147	S - LN	6	ah+fl
Byars et al. (2007)	Australia	Poa hiemata (Poaceae)	147	S	6	ah+fl
Center et al. (2016)	Costa Rica	Quercus oleoides (Fagaceae)	630	S - G - LN	4	ah+fl
Chen et al. (2019)	China	Larix potaninii (Pinaceae)	101	S - B - H	1	ah
		Picea likiangensis (Pinaceae)	101	S - B - H	1	ah
Cui et al. (2018)	China	Viola biflora (Violaceae)	330	S - LN	4	ah+fl
Datta et al. (2017)	India	Ageratina adenophora (Asteraceae)	759	B - H - FN - SLA - LA	2	ah+fl

Reference	Country	Species (Family)				
Fetched et al. (2000)	Puerto Rico	Clibadium erosum (Asteraceae)	650	B - LA	2	ah+fl
		Prestoea acuminata (Arecaceae)	650	B	2	ah+fl
		Prestoea acuminata (Asteraceae)	650	LA	2	ah+fl
		Psychotria berteriana (Rubiaceae)	650	B - LA	2	ah+fl
Flegrová & Krahulec (1999)	Czech Republic	Anthoxanthum alpinum (Poaceae)	220	S - LN - FN	1	ah
		Anthoxanthum odoratum (Poaceae)	220	S - LN - FN	1	ah
Frei et al. (2014)	Switzerland	Briza media (Poaceae)	564	B - FN	4	ah+fl
		Ranunculus bulbosus (Ranunculaceae)	564	B - FN	4	ah+fl
		Trifolium montanum (Fabaceae)	564	B - FN	4	ah+fl
Galen et al. (1991)	USA	Polemonium viscosum (Polemoniaceae)	500	S	1	ah+fl
Gimenez-Benavides et al. (2007)	Spain	Silene ciliata (Caryophyllaceae)	320	S - G - LN	2-4	ah+fl
Gonzalo-Turpin & Hazard (2009)	France	Festuca eskia (Poaceae)	631	S - B - H - FN - SLA	6	ah+fl
Grassein et al. (2014)	France	Bromus erectus (Poaceae)	1350	S - B	2	ah+fl
		Carex sempervirens (Cyperaceae)	400	S - B	2	ah+fl
		Dactylis glomerata (Poaceae)	1350	S - B	2	ah+fl
		Festuca paniculata (Poaceae)	400	S - B	2	ah+fl
		Sesleria caerulea (Poaceae)	400	S - B	2	ah+fl

Reference	Country	Species (Family)				
Haggerty & Galloway (2011)	USA	Campanulastrum americanum (Campanulaceae)	692	S - FN	4	ah+fl
Halbritter et al. (2015)	Switzerland	Plantago lanceolata (Plantaginaceae)	1645	B - FN	2-4	ah+fl
		Plantago major (Plantaginaceae)	1645	B - FN	2	ah+fl
Hall et al. (1990)	Canada	Leymus cinereus (Poaceae)	554	B - H - FN	2	ah+fl
Hamala et al. (2018)	Norway	Arabidopsis lyrata (Brassicaceae)	800	S - FN	2	ah+fl
Hamann et al. (2016)	Switzerland	Poa alpina (Poaceae)	792	S - B - H - FN - SLA	4	fl
Hamann et al. (2017)	Switzerland	Geum reptans (Rosaceae)	110	B - LN - FN - SLA	2	ah+fl
Hautier et al. (2009)	Switzerland	Poa alpina (Poaceae)	641	LN - FN	3	ah+fl
Hsu et al. (2014)	Taiwan	Asplenium antiquum (Aspleniaceae)	1350	S - B	6	ah+fl
Kesselring et al. (2019)	Switzerland	Anthyllis vulneraria (Fabaceae)	330	S - B - FN	4-6	ah+fl
Kim & Donohue (2013)	USA	Erysimum capitatum (Brassicaceae)	1646	S - G - LN	5-6	ah+fl
Lajoie & Vellend (2018)	Canada	Oxalis montana (Oxalidaceae)	325	S - B - H - SLA - LA	12	ah+fl
Latreille & Pichot (2017)	France	Abies alba (Pinaceae)	591	S - B - H	8	ah+fl
Leger et al. (2009)	USA	Bromus tectorum (Poaceae)	440	S	2	ah+fl
Link et al. (2003)	USA	Poa secunda (Poaceae)	534	B	2	ah+fl
Mathiasen & Premoli (2016)	Argentina	Nothofagus pumilio (Fagaceae)	291	S - B - H - LN - SLA - LA	2	ah+fl

Reference	Country	Species	**		n.	*
Pluess et al. (2011)	Switzerland	Scabiosa columbaria (Caprifoliaceae)	635	LN - FN - SLA - LA	4	ah+fl
Reinhardt et al. (2011)	USA	Pinus flexilis (Pinaceae)	465	S - B - SLA - LA	4	ah+fl
Schmidt et al. (2018)	Switzerland	Carex flava (Cyperaceae)	1473	S - B - H - LN - FN	2	ah+fl
		Carex viridula (Cyperaceae)	1473	S - B - H - LN - FN	2	ah+fl
Tiscar et al. (2018)	Spain	Pinus nigra (Pinaceae)	600	S - G	2-4	ah+fl
Villemereuil et al. (2018)	France	Arabis alpina (Brassicaceae)	484	S - B - H	3-4	fl
Williams et al. (1995)	Hawaii	Pennisetum setaceum (Poaceae)	1975	S - B - H - LN - FN	6	ah+fl
Zhao et al. (2013)	China	Ageratina adenophora (Asteraceae)	1422	G - B - H - FN	12	ah+fl

* = see "Data sources" section of the main manuscript for full references list;

** = note "min-max" values, n. observations per type of comparison and/or response may vary depending on the study, elevational gradient and species under consideration. If number of observations differed in such a way, we here reported the range only

Table II.2.2: *Summary table indicating number of studies, species and observations (i.e. the number of response ratios) calculated for each response and comparison (AvsH='away vs. home'; FvsL='foreign vs. local') used in the meta-analysis. The table also report the mean value of percentage of observations for each dataset that were not reported by primary studies and were thereby imputed before conducting the meta-analysis (see Material Methods in the main manuscript).*

	n. of studies		n. of species		n. of observations		
Response	AvsH	FvsL	AvsH	FvsL	AvsH	FvsL	missing SD values (%)
Survival	24	25	32	31	109	114	56.0
Germination	7	7	8	8	40	44	0
Biomass	21	22	32	32	115	124	12.7
Height	11	12	12	12	61	74	25.4
N. leaves/shoots	12	11	14	12	44	40	0
N. repr. units	16	16	20	18	72	82	2.4
SLA	9	10	9	10	40	44	0
Leaf size	7	7	10	10	34	34	0
Total*	38		49		1071		15

* = Total numbers refer to unique values, namely different datasets shared multiple studies and species.
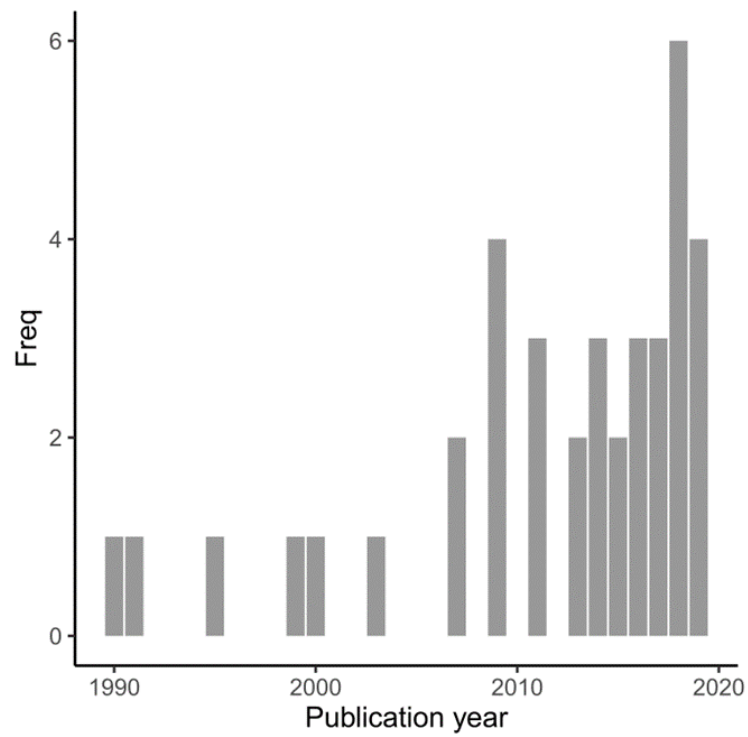
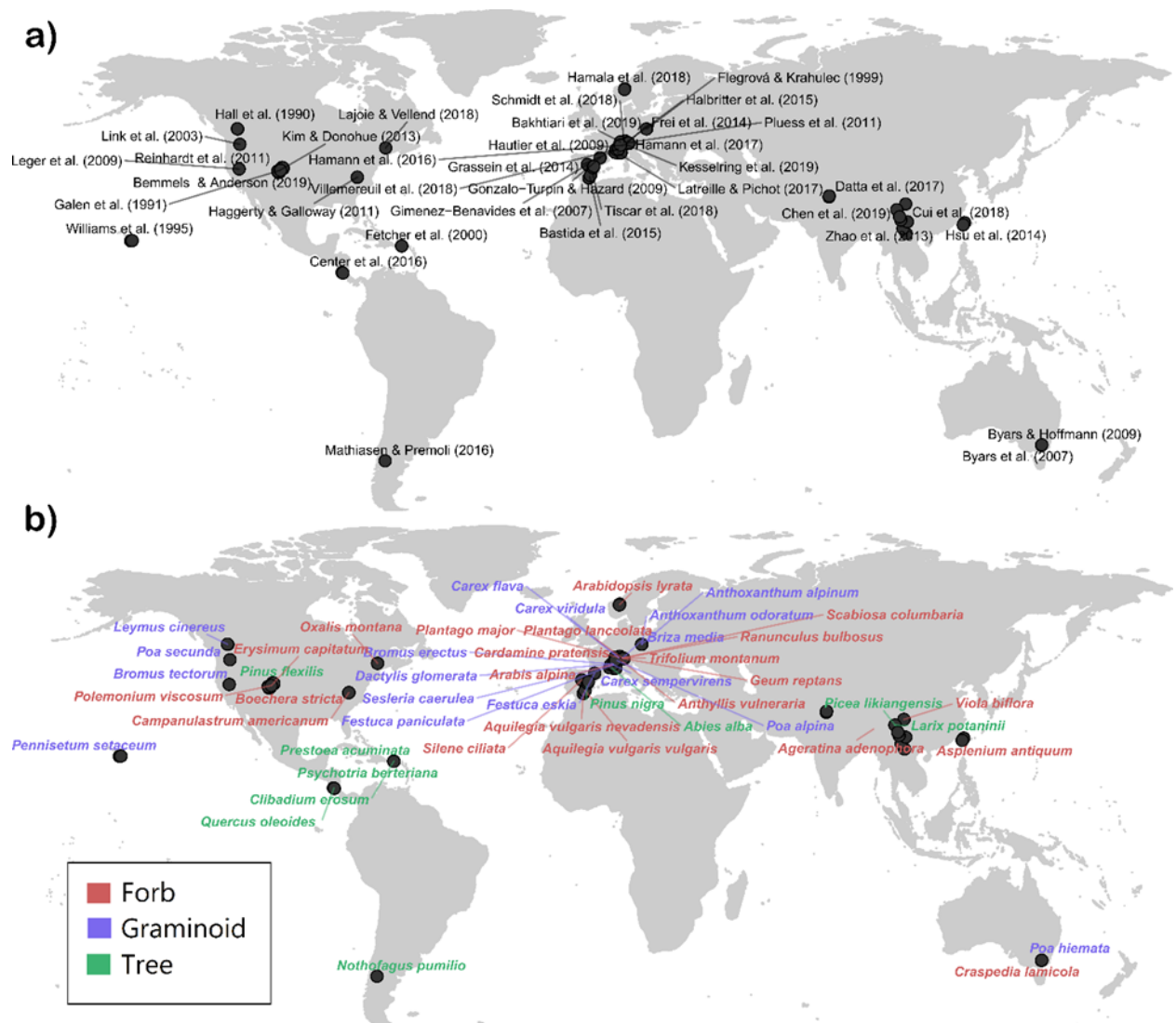**Figure II.2.1**: *Distribution of the publication year of primary studies selected in meta-analysis.*

Figure II.2.2: *Geographical distribution of the transplant sites in each study (a) and species (b) analyzed. See Table II.2.1 for additional information on studies included in meta-analysis.*

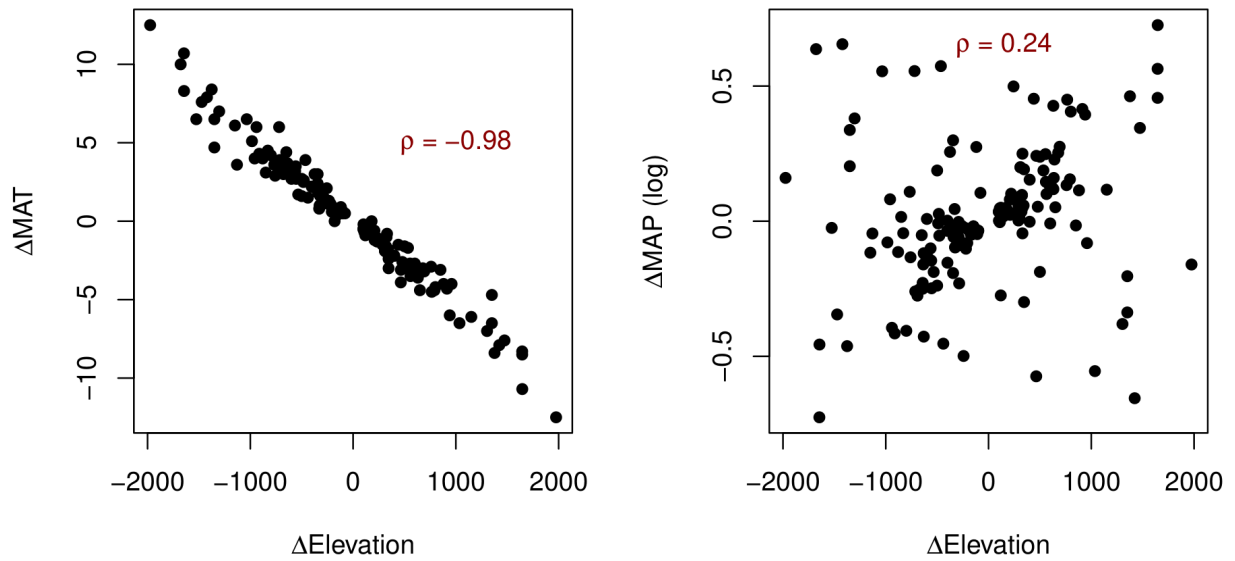**II.3: Correlations between elevation and climatic variables**

Figure II.3.1: *Relation between elevation difference and MAT (left) and MAP (log-transformed; right) difference. Such differences are calculated between the transplant sites and the sites of origin across all studies included in meta-analysis.*
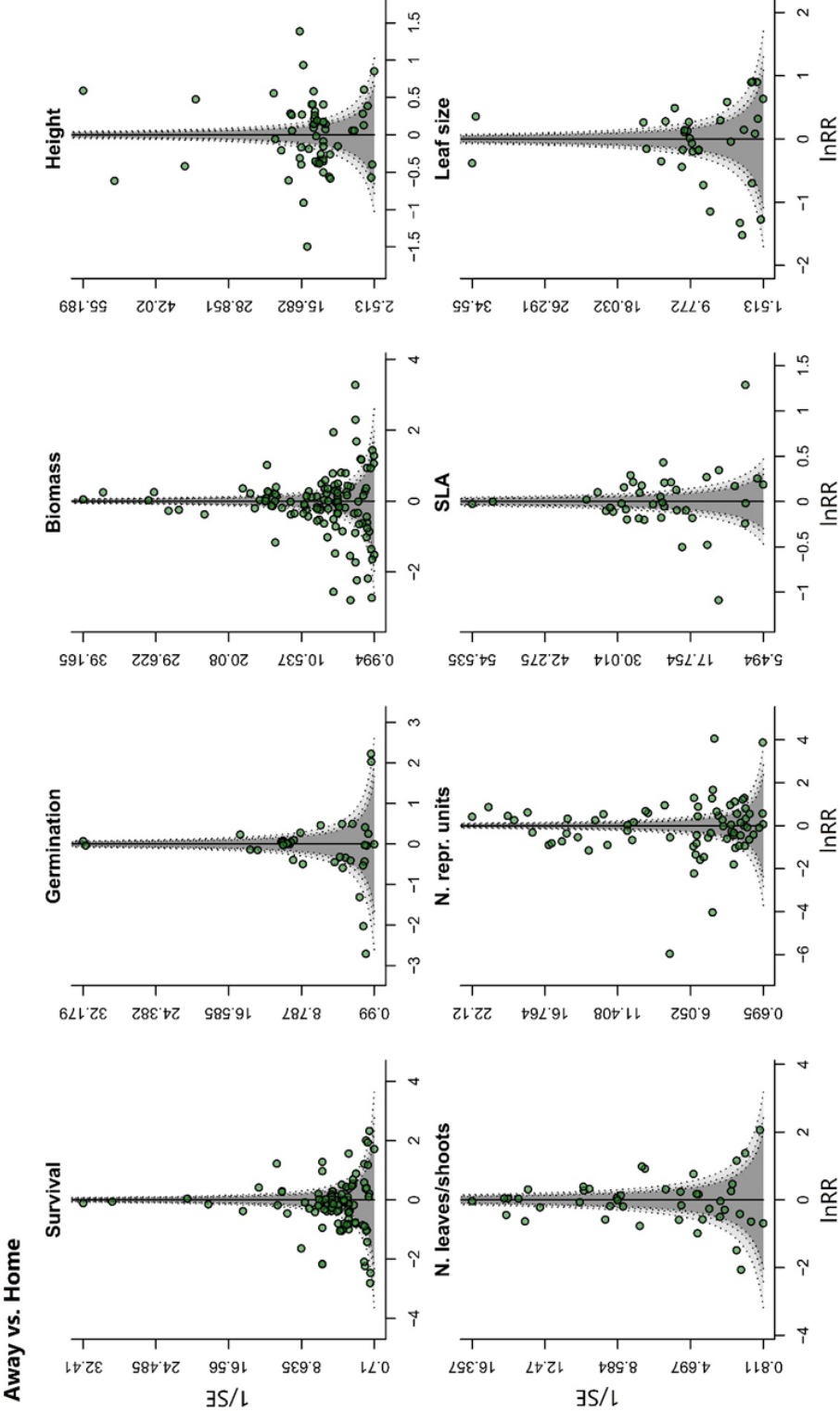
II.4: Contour-enhanced funnel plots

Figure II.4.1: *Contour-enhanced funnel plot of null-model residuals for each trait analyzed in 'Home vs. Away' datasets. Effect sizes are plotted vs. their weight (1/SE). Shaded areas depict significance of the effect sizes (dark grey: ρ ≥ 0.1; medium grey: ρ ≥ 0.05; light grey: ρ ≥ 0.01; white: ρ < 0.01).*
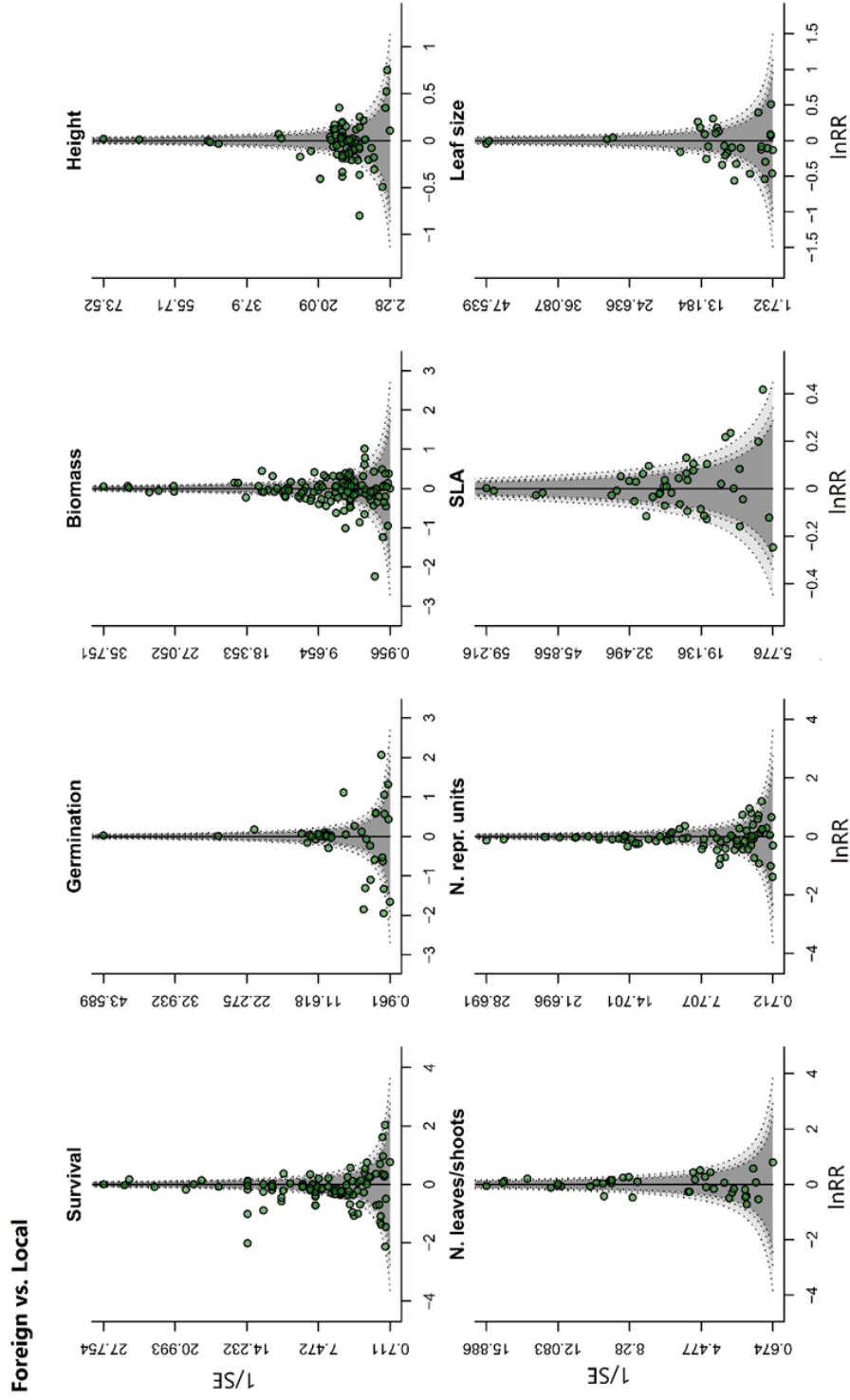
Figure II.4.2: *Contour-enhanced funnel plot of null-model residuals for each trait analyzed in 'Foreign vs. Local' datasets. Effect sizes are plotted vs. their weight (1/SE). Shaded areas depict significance of the effect sizes (dark grey: ρ ≥ 0.1; medium grey: ρ ≥ 0.05; light grey: ρ ≥ 0.01; white: ρ < 0.01).*

Appendix III

III.1: List of species included in the analysis

Table III.1.1: *List of 53 native tree species of Western North America included in the 'field' dataset [source: United States Forest Inventory Analysis database (FIA)]. Green highlight indicates the nine species assessed in the 'common garden' data as well (see Table S1.2). The table reports the number (or minimum – maximum number, depending on trait considered) of observations used to calculate 'fitness-centre' correlations. The 'initial n obs.' column refers to the number of total records available before thinning the data to remove spatial autocorrelation (see 'Material and Methods' section of the main article for details); "-" indicates no thinning was necessary to compute the correlation coefficient (i.e. no spatial autocorrelation detected for those observations). The 'presence' column refers to the number of presences used to fit SDMs (the number of absences was equal to the number of presences) and obtained from Canada and United States' forest inventory plots.*

Species	Family	n obs.	initial n obs.	presences
Abies amabilis	Pinaceae	32-43	1620	1770
Abies concolor	Pinaceae	12-308	-	3555
Abies grandis	Pinaceae	20-277	698-3918	4336
Abies lasiocarpa	Pinaceae	43-70	3231-8949	10376
Abies magnifica	Pinaceae	89-430	-	479
Abies procera	Pinaceae	75-85	470	521
Abies shastensis	Pinaceae	301	-	331
Acer glabrum	Sapindaceae	276	-	692
Acer grandidentatum	Sapindaceae	170	-	258
Acer macrophyllum	Sapindaceae	39-161	-	836
Alnus rubra	Betulaceae	854	-	1073
Arbutus menziesii	Ericaceae	88	-	806
Betula papyrifera	Betulaceae	38-167	-	11976
Calocedrus decurrens	Cupressaceae	82-92	1190-1190	1344
Cercocarpus ledifolius	Rosaceae	48-167	-	1827
Chamaecyparis lawsoniana	Cupressaceae	95	-	108
Chamaecyparis nootkatensis	Cupressaceae	196	-	996
Chrysolepis chrysophylla	Fagaceae	74	-	673
Juniperus occidentalis	Cupressaceae	56-114	-	1428
Juniperus osteosperma	Cupressaceae	34-132	4939	7495
Juniperus scopulorum	Cupressaceae	39-84	1691	2398
Larix lyallii	Pinaceae	81	-	98
Larix occidentalis	Pinaceae	19-133	-	3356
Lithocarpus densiflorus	Fagaceae	66	-	678
Picea engelmannii	Pinaceae	12-84	1761-7791	8692
Picea pungens	Pinaceae	56-70	-	270
Picea sitchensis	Pinaceae	188	-	1676
Pinus albicaulis	Pinaceae	147-463	-	2875
Pinus aristata	Pinaceae	138	-	158

Pinus attenuata	Pinaceae	108	-	144
Pinus contorta	Pinaceae	6-299	1737-9588	11173
Pinus edulis	Pinaceae	6-18	4919	5787
Pinus flexilis	Pinaceae	58-239	-	1734
Pinus jeffreyi	Pinaceae	58-144	699	755
Pinus lambertiana	Pinaceae	55-77	1023	1200
Pinus longaeva	Pinaceae	31	-	40
Pinus monophylla	Pinaceae	36-118	-	3705
Pinus monticola	Pinaceae	5-93	-	1702
Pinus ponderosa	Pinaceae	16-100	862-9988	11272
Pinus sabiniana	Pinaceae	127-127	-	147
Populus angustifolia	Salicaceae	54-54	-	74
Populus tremuloides	Salicaceae	95-1101	-	17525
Populus trichocarpa	Salicaceae	131-131	-	414
Pseudotsuga menziesii	Pinaceae	32-90	1978-17956	19297
Quercus chrysolepis	Fagaceae	88-88	-	1066
Quercus gambelii	Fagaceae	48-114	2049	2828
Quercus kelloggii	Fagaceae	71-71	-	756
Quercus macrocarpa	Fagaceae	25-25	33	1920
Sequoia sempervirens	Cupressaceae	66-66	-	66
Taxus brevifolia	Taxaceae	58-215	-	631
Thuja plicata	Cupressaceae	40-288	-	3026
Tsuga heterophylla	Pinaceae	20-161	-	4899
Tsuga mertensiana	Pinaceae	25-98	-	2596

Table III.1.2: *List of native tree species of North America (22 in total) and data sources (23 in total) included in the 'common garden' dataset.* Green *highlight indicates the nine species assessed in the 'field' data as well (see Table S1.1). The table reports the number (or minimum – maximum number, depending on trait considered) of observations (= provenances) used to calculate 'fitness-centre' correlations. Numbers in brackets refers to the number of total records available before thinning the data to remove spatial autocorrelation (see 'Material and Methods' section of the main article for details); no brackets indicates no thinning was necessary to compute the correlation coefficient (i.e. no spatial autocorrelation detected for those observations). The 'n trial sites' column indicates the number of trial sites with data source (study) and species. The 'presence' column refers to the number of presences used to fit SDMs (the number of absences was equal to the number of presences) and obtained from Canada and United States' forest inventory plots. See the main article for complete references of data sources.*

Species	Family	n obs. (initial)	Source	n trial sites	presences
Abies balsamea	Pinaceae	12	Akalusi & Bourque (2018)	1	10977
Alnus rubra	Betulaceae	64	Xie et al. (1996)	1	1073
Chamaecyparis thyoides	Cupressaceae	6-30	Mylecraine et al. (2005)	3	169
Fraxinus americana	Oleaceae	20 (46)	Marchin et al. (2008)	1	5758
Fraxinus pennsylvanica	Oleaceae	18	Bresnan et al. (1996)	1	4755
Fraxinus pennsylvanica	Oleaceae	13-47	Steinere et al. (1988)	10	4755
Juglans nigra	Juglandaceae	13-25	Bresnan et al. (1994)	7	1212
Juniperus scopulorum	Cupressaceae	19	van Haverbeke & King (2006)	6	2398
Juniperus virginiana	Cupressaceae	7-65	van Haverbeke & King (2006)	6	2292
Picea glauca	Pinaceae	13-28	Sebastian-Azcona et al. (2018)	1	4909
Picea pungens	Pinaceae	43	van Haverbeke (2006)	1	270
Pinus albicaulis	Pinaceae	6	McLane & Aitken (2012)	9	2875
Pinus albicaulis	Pinaceae	10-41	Warwell & Shaw (2017)	2	2875
Pinus banksiana	Pinaceae	21	Savva et al. (2007)	1	3074
Pinus contorta	Pinaceae	44-47 (281)	Mahony et al. (2020)	1	11173
Pinus ponderosa	Pinaceae	7-138	Rehfeldt (2011)	2	11272
Pinus ponderosa	Pinaceae	15-75	van Haverbeke (2005)	14	11272

Pinus rigida	Pinaceae	27-32	Ledig et al. (2003)	5	1280
Populus balsamifera	Salicaceae	21	Soolanayakanahally et al. (2009)	1	3125
Populus deltoides	Salicaceae	13	Friedman et al. (2011)	1	569
Populus fremontii	Salicaceae	16	Cooper et al. (2019)	3	31
Populus tremuloides	Salicaceae	13-43	Ding et al. (2017)	5	17525
Populus trichocarpa	Salicaceae	6-7 (137)	McKown et al. (2014)	1	414
Pseudotsuga menziesii	Pinaceae	14-77	Rehfeldt (2011)	3	19297
Quercus alba	Fagaceae	13-14	Huang et al. (2015)	3	10056

III.2: Latitude-elevation relations of occurrences data in twelve tree species with southernmost distribution range located in Northern Mexico
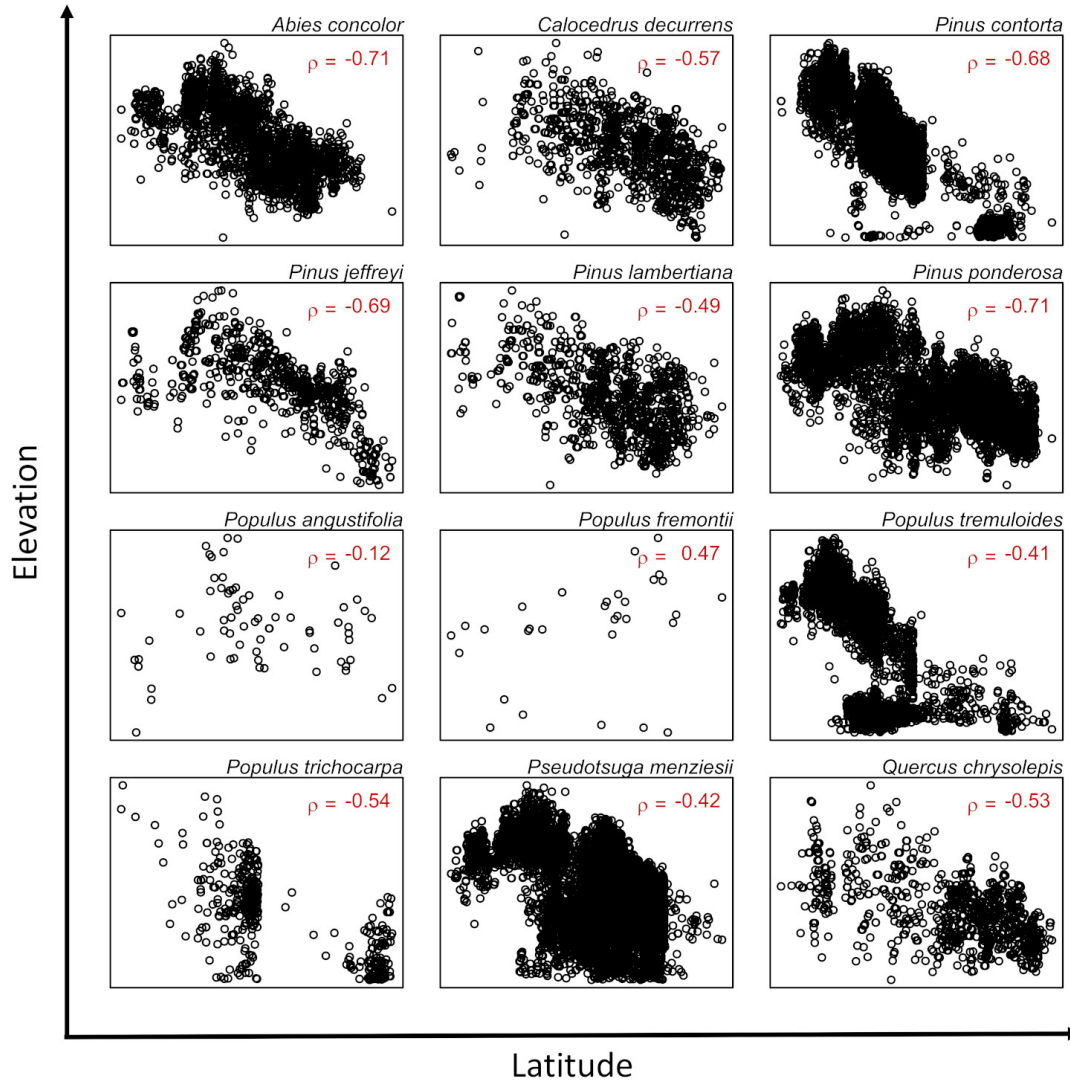
Figure III.2.2: *Scatterplots of latitude (x-axis) versus elevation (y-axis) of presence data used to fit species distribution models (SDMs) of twelve tree species with southernmost distribution range located in Northern Mexico. Occurrences of these species shows a general negative relation [Spearman' correlation coefficient (ρ)] between latitude and elevation within our data in Northern America (United States and Canada) - except for narrowleaf cottonwood (Populus angustifolia) and Frémont's cottonwood (Populus fremontii), for which fewer occurrence records were available. We thus expected the fewer occurrences located in Mexico to be confined to high-elevation areas, with similar climatic conditions of low-elevation areas at higher latitudes in Northern America. Consequently, we properly represented the range of climatic conditions experienced by the species within their current distribution.*

III.3: Search string for common-garden trials search in Web of Knowledge

TS=((provenance* OR (origin* AND transplant*)) **AND** (reproduct* OR "height" OR surviv* OR "diameter" OR "dbh" OR growth* OR fitness) **AND** (plant* OR tree* OR conifer* OR gymnosperm* OR angiosperm* OR seedling*) **AND** ("North* America" OR "USA" OR "United States" OR "Canada" OR "Alabama" OR "Alaska" OR "Arizona" OR "Arkansas" OR "California" OR "Colorado" OR "Connecticut" OR "Delaware" OR "Florida" OR "Georgia" OR "Idaho" OR "Illinois" OR "Indiana" OR "Iowa" OR "Kansas" OR "Kentucky" OR "Louisiana" OR "Maine" OR "Maryland" OR "Massachusetts" OR "Michigan" OR "Minnesota" OR "Mississippi" OR "Missouri" OR "Montana" OR "Nebraska" OR "Nevada" OR "New Hampshire" OR "New Jersey" OR "New Mexico" OR "New York" OR "Carolina" OR "Dakota" OR "Ohio" OR "Oklahoma" OR "Oregon" OR "Pennsylvania" OR "Rhode Island" OR "Tennessee" OR "Texas" OR "Utah" OR "Vermont" OR "Virginia" OR "Washington" OR "Wisconsin" OR "Alberta" OR "British Columbia" OR "Manitoba" OR "New Brunswick" OR "Newfoundland" OR "Labrador" OR "Northwest Territories" OR "Nova Scotia" OR "Nunavut" OR "Ontario" OR "Prince Edward" OR "Quebec" OR "Saskatchewan" OR "Yukon"))

III.4: Sensitivity analysis

Coordinates of presence-absence data (i.e. the plot location) used in our analysis had 1.6 km and 10 km uncertainty for United States FIA and Canada NFI data, respectively (except for 433 plots located in British Columbia, Quebec and New Brunswick, of which exact coordinates were available). For this reason, we explored how coordinates imprecision potentially affected results and conclusion of our analysis due to inaccurate estimate of environmental conditions at locations where the species occurs.

To this aim, we first calculated elevational variation (EV) as the range of elevation standardized by the mean (at 250m-resolution) around an area of 1.6 km and 10 km radius around each plot location in United States and Canada, respectively (except for the plots located in British Columbia, Quebec and New Brunswick). Thus, elevational variation (EV) was estimated as follow:

$$EV = [max(E)\text{–}min(E)]/mean(E) \tag{1}$$

elevation (E) at 250 m resolution around the plot was obtained from the MERIT Digital Elevation Model (Yamazaki *et al.*, 2017).

Because environmental variation within a coarse scale is unlikely to be large unless there is high elevational variation (at least for climatic predictors), we used EV around the plot as a proxy of uncertainty of the environmental conditions predicted at plot's location.

We found that certain bioclimatic conditions used in species distribution modeling were non-independent from EV across plots analyzed (Figure S4.1). This occurred for example in certain mountain areas having extreme climatic variables and high elevational variation around the plot. This mean that removal of these plots might influence the modeled niche of certain species present or absent in that points.

Nevertheless, subsetted plots with elevational variation $EV \geq 0.25$. Such threshold value was selected arbitrarily to remove half of the presence-absence data available. We repeated the whole analysis explained in the 'Methods' section of the main article by computing new SDMs over this subset of presence-absence data. This analysis was restricted to 54 species (42 in the 'field' data; 21 in the 'common garden' data; 9 species shared) only as 12 species no longer had enough presence locations to compute SDMs.

We here show that excluding these points did not influenced our overall results and main conclusion (Figures S4.2-S4.3). Nevertheless, we acknowledge that the exclusion of these data points might have excluded relevant part of the climatic gradients occupied by some species. Thus, SDMs obtained this way might be potentially less reliable to what presented in our main article.

References

Yamazaki D, Ikeshima D, Tawatari R, *et al.* (2017) A high-accuracy map of global terrain elevations. *Geophysical Research Letters*, **44**, 5844–5853. doi:10.1002/2017gl072874. URL https://doi.org/10.1002/2017gl072874.
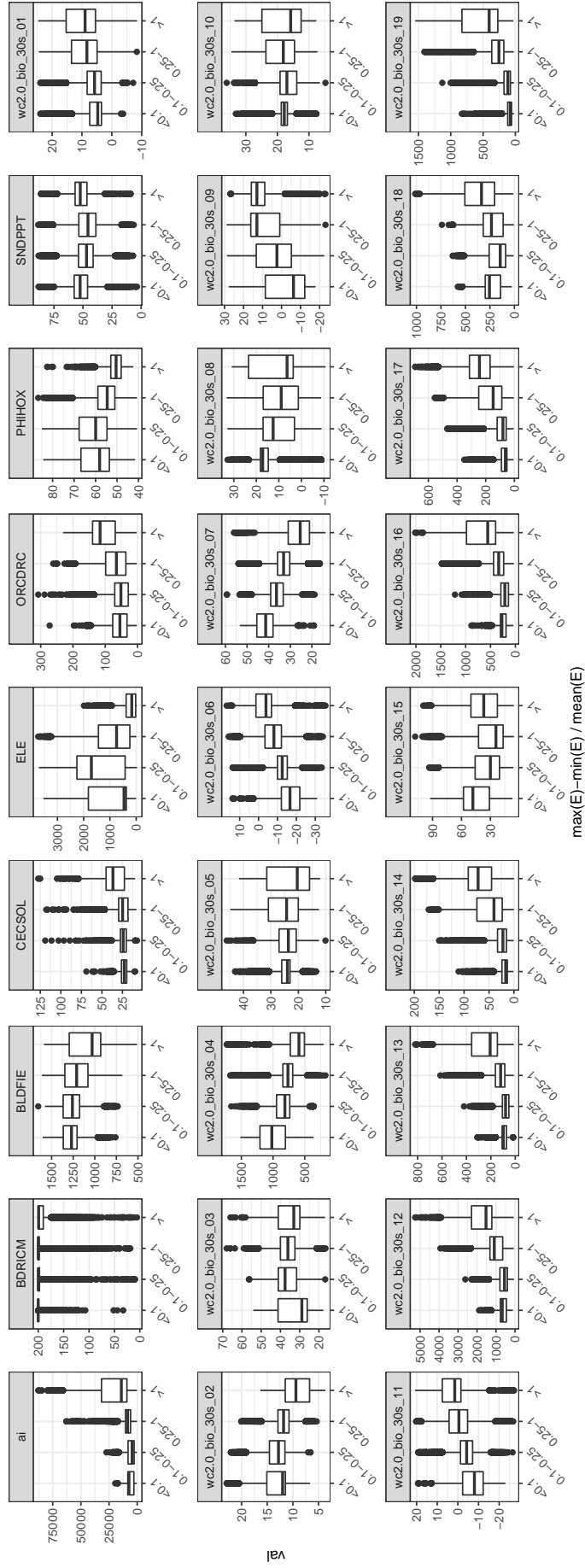
Figure III.4.1: *Relationship between environmental predictors used in species distribution models and elevation (E) variation around the plot location (on the x-axis; transformed into class values for representation purposes). AI = aridity index; BDRICM = depth to bedrock; BLDFIE = bulk density, CECSOL = soil cation exchange capacity; ELE = elevation; ORCDRC = organic carbon content; PHIHOX = soil pH in H_2O; SNDPPT = weight percentage of sand particles; BIO.01-19 = WolrdClim2.0 climatic predictors. Bioclimatic predictors used in SDMs (except for elevation, which was not included as predictors) are at10 km resolution estimate.*
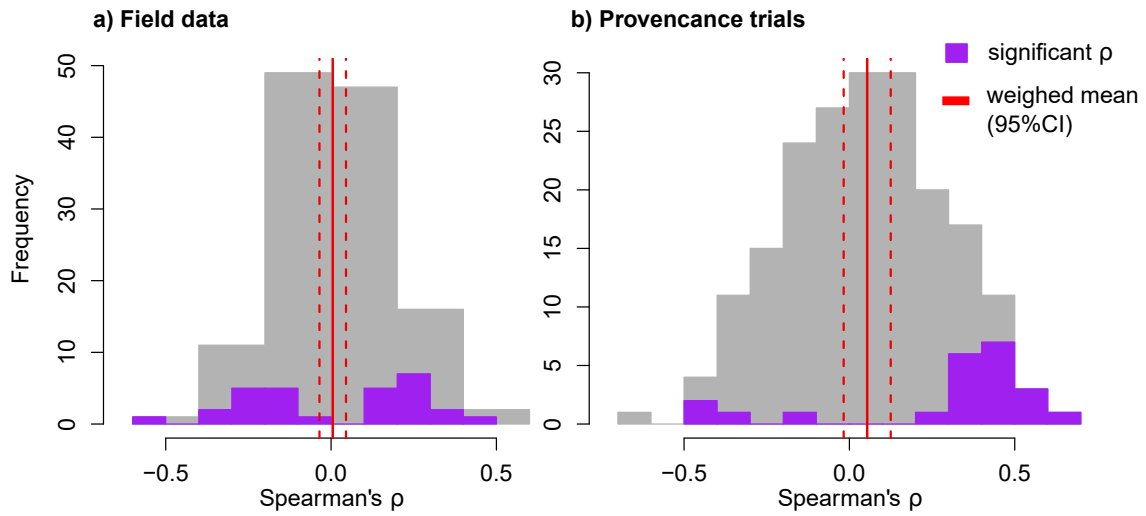
Figure III.4.2: *Overall distribution of the Spearman's correlation coefficients (ρ) between species' probability of occurrence and individual fitness sampled in a) field data and b) common garden experiments data using data obtained from SDMs fitted with a restricted set of presence-absence data (i.e. sensitivity analysis). Purple-shaded bars represent the distribution of significant coefficients (p-val < 0.05). Red vertical lines indicate the mean pooled estimate (solid line) and its 95% CI (dashed lines) obtained from null mixed effect models using* species *(as well as* study *for 'common garden' data) in the random component of the model. Observations in the model are weighted by multiplying the sample size of the correlation coefficient by the maximum 'True Skill Statistic' (TSS) of the SDM obtained from that species.*
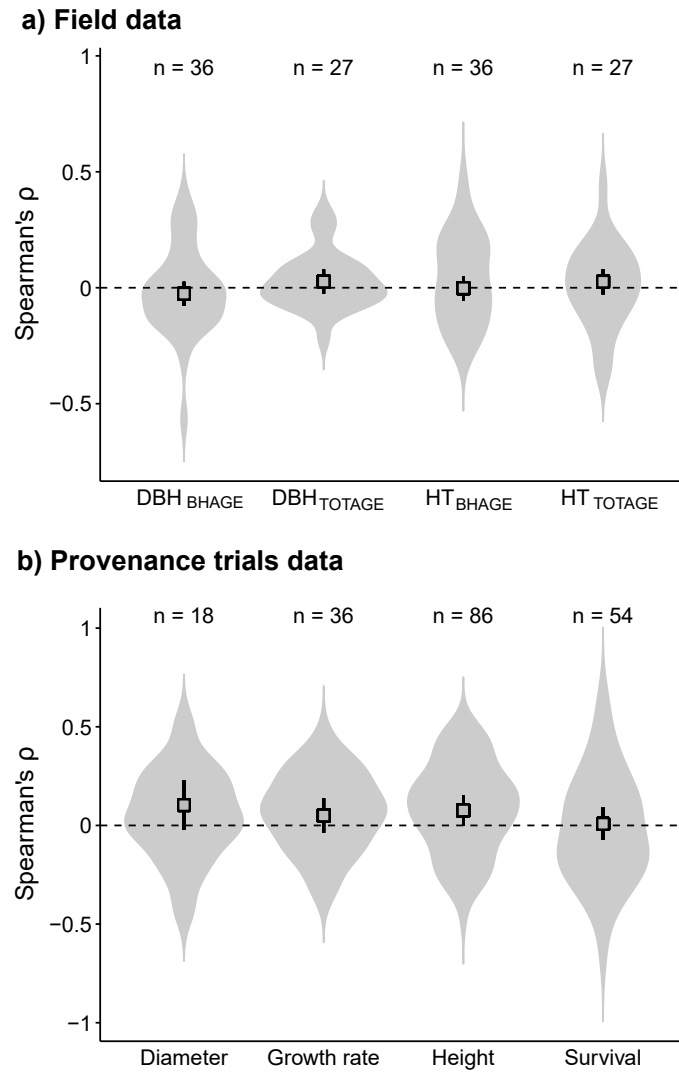
a) Field data

b) Provenance trials data

Figure III.4.3: *Distribution of Spearman's correlation coefficients (ρ) between species' probability of occurrence and individual fitness across different response traits analyzed (violin plot) for a) field data and b) common garden experiments data using data obtained from SDMs fitted with a restricted set of presence-absence data (i.e. sensitivity analysis). No significant difference was detected across different response traits analyzed in both datasets. Grey squared points indicate mean pooled effect (and 95% CI) obtained from mixed-effect models using response trait type as predictor (n = number of pairwise correlations). Horizontal dashed line indicates Spearman's correlation equal to zero. Response traits in field data are diameter at breast height (DBH) and tree height (HT) standardized to age estimated at the root collar (TOTAGE) or at the breast height (BHAGE).*

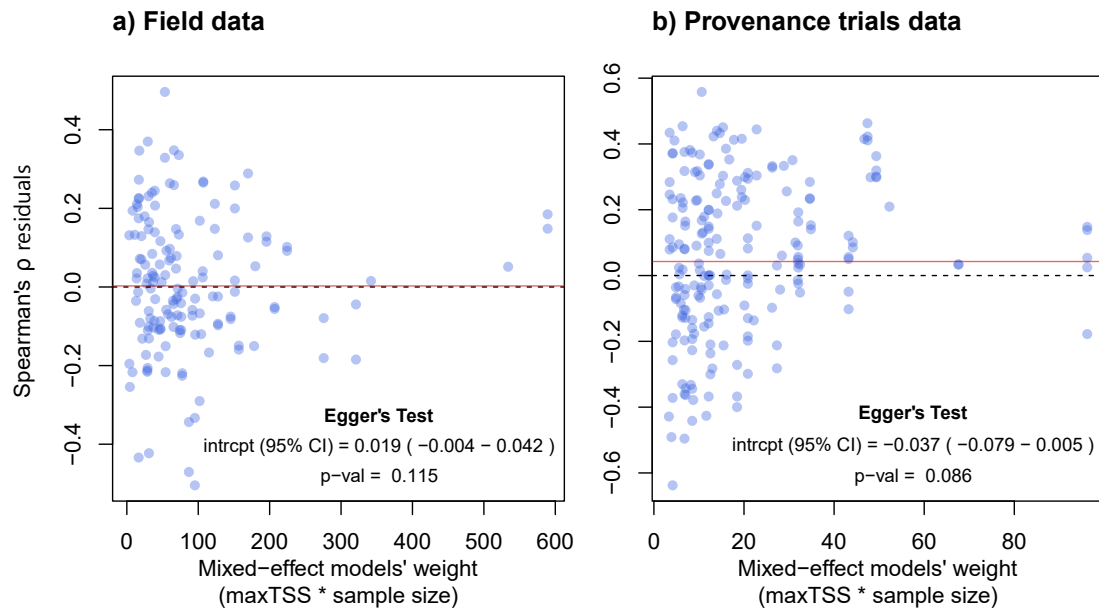## a) Field data   b) Provenance trials data

Figure III.5.1: *Funnel plots showing the relationship between mixed effect model' weight [i.e. maximum 'True Skill Statistic' (= TSS) multiplied by sample size used to compute the correlation] and null model' residuals for a) field data and b) common garden experiments data. The maximum TSS correspond to the highest TSS value found across each SDM's run per species. Red line indicates weighted mean Spearman' correlation estimated using the linear mixed-effect model. Horizontal dashed line indicates correlation equal to zero. Eggers' test estimates the significance of the intercept of a linear regression model using the residuals of the null model as dependent variable, and the model' weight as predictor. Non-significant intercepts obtained this way indicate no evidence of model weight to influence residuals.*
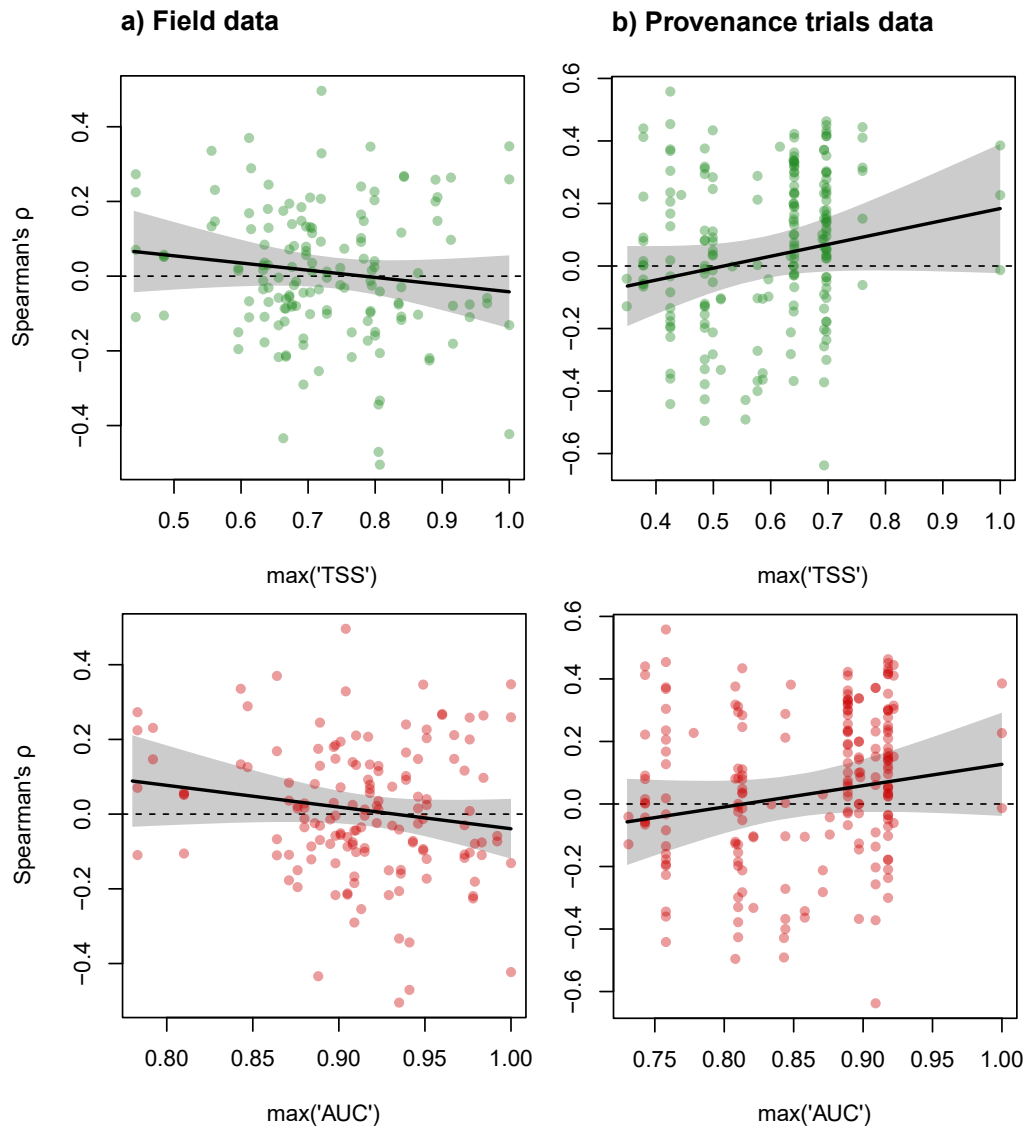
Figure III.5.2: *Linear relationship (and 95% CI) between Spearman correlations and indicators of SDMs precision [maximum 'True Skill Statistic' (=TSS) in green; maximum 'Area under the ROC Curve' (=AUC) in red] in a) field data and b) common garden experiments data. The maximum TSS and AUC correspond to the highest value found across each SDM's run per species. Models are obtained from unweighted linear mixed effect models using model precision as predictor (see description of the random component in the 'Methods' section). Horizontal dashed line indicates Spearman's correlation equal to zero. No significant slopes were detected.*

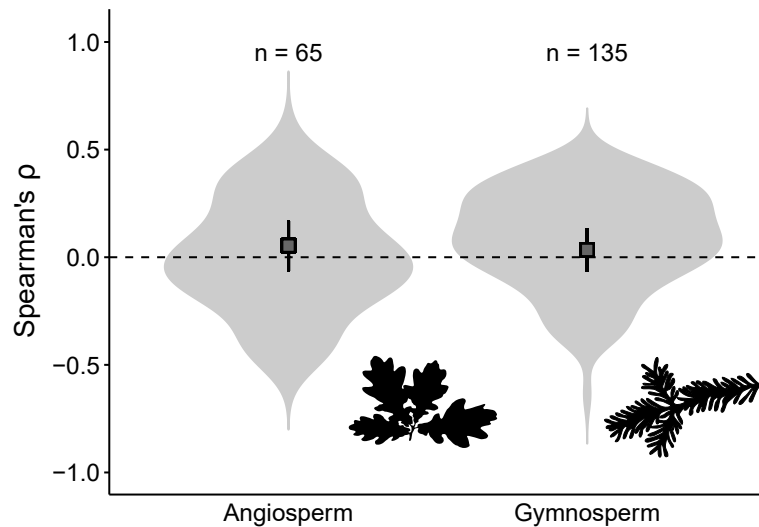**a) Field data**
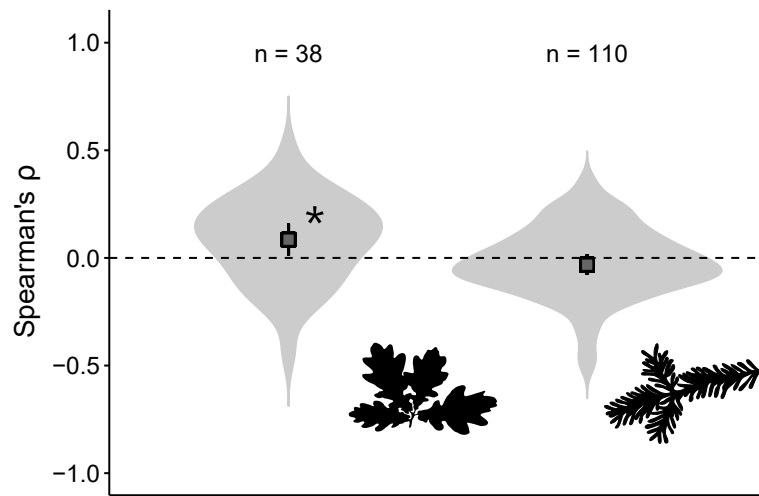
b) Provenance trials data

Figure III.5.3: *Distribution of Spearman's correlation coefficients between species' probability of occurrence and individual fitness across the main taxonomic group (angiosperm and gymnosperm) (violin plot) for a) field data and b) common garden experiments data. Grey squared points indicate mean pooled effect (and 95% CI) obtained from mixed-effect models using response taxonomic group as predictor (n = number of pairwise correlations). Horizontal dashed line indicates Spearman's correlation equal to zero. Significance between groups (*) (p-val = .01) was only detected in field data. Taxonomic group was the only predictor retained in the stepwise backward selection in field data. Credit: Ferran Sayol / PhyloPic (Quercus and Abies silhouettes) under a CC0 Public Domain Dedication License.*