Exploring variation in the responses of tree species to climate across diverse montane forests in Taiwan

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Thesis abstract

Rapid climate change is impacting forest distribution, species composition and function globally. Although some overall patterns are emerging, many factors can interact with climate across different forest types and between individual trees, which can modify responses of trees to climate change. Our overall understanding of how forests are changing is incredibly limited, with a paucity of information from tropical and subtropical mountain regions. Given the need for substantial improvement to our understanding of the variation in responses of forests to climate change, this thesis sets out to evaluate our current knowledge and highlight the remaining gaps in our understanding. Specifically, this thesis aims to 1) determine the size and direction of species distribution shifts, 2) identify the extent to which tree functional traits are associated with distribution shifts and environmental variation, 3) quantify variation in functional traits across the elevation range of a widely distributed tree species (*Pinus taiwanensis*), and 4) quantify the variability in responses of the early stages of *P. taiwanensis* development to projected temperature changes. We found that high-elevation species shifted upwards but below the treeline, species shifted individualistically. Individual functional traits were poor predictors of individual species distribution shifts, but relationships between environment and function at the community-level were strong. Overall functional trait variation was high across the elevation range of *P. taiwanensis* and higher temperatures reduced the time to seedling emergence and promoted biomass gain, with seed elevation of origin also highly influential. These findings highlight the substantial variability possible in plant-climate relationships across a large elevational gradient spanning a broad range of forest types, highlighting that it should not be assumed that trees will react 'as one' to climate change. Ultimately, this information will allow improved estimation of the impacts of climate change on biodiversity and ecosystem function across tropical montane forests.

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Chapter 1

Quantifying the influence of climate on montane forest trees for more effective global change assessments

1.1 Climate change impacts on ecosystems and species

Ongoing global climate change is becoming an increasingly prevalent threat to the planet (IPCC 2021). Over the last 40 years, temperatures for each 10-year period have been higher than any decade previously since accurate temperature records began in 1850 (IPCC 2021). Since 1970, temperatures have risen at the fastest rate ever seen for a 50-year period over the last 2000 years and are predicted to rise to an average of 1 ^{o}C – 5.7 ^{o}C above pre-industrial levels by the year 2100 (IPCC 2021). Alongside rising global mean temperatures, increased frequency of extreme events such as wildfires, droughts and tropical storms are occurring and are expected to continue to increase in frequency over coming decades (Jump and Peñuelas 2005, Swain et al. 2020, IPCC 2021). Consequently, such changes to the climate are increasingly having widespread impacts on our natural systems, from the organism to the ecosystem level (Bellard et al. 2012, Sintayehu 2018, Arneth et al. 2020). The impacts of such changes will be particularly pronounced if the rate of climate change exceeds the pace at which organisms can respond (Ackerly et al. 2010). Understanding how biological systems are responding to these ongoing climatic pressures is of paramount importance for effective planning, management and conservation of natural resources.

As primary producers and a key component of habitat structure, plants form the fundamental basis of most terrestrial ecosystems, with changes in plant distribution, structure and function likely to have implications across trophic levels. It is well established that there is a close association between plants and environmental conditions (Hiesey et al. 1942, Woodward 1987a). In 1807, von Humboldt and Bonpland published their iconic *Tableau Physique*, which depicts the way that vegetation changes across gradients in climate, and became a key reference in the field of biogeography (Von Humboldt and Bonpland 1807, Moret et al. 2019). Variations in climatic conditions such as temperature and precipitation shape plant processes such as germination, growth, survival and functionality (Lloret et al. 2009, Standish et al. 2012, Merlin et al. 2015, Barga et al. 2017, Diaz et al. 2020), which can influence where plants grow across the landscape. However, climate change is disrupting the relationship between plant vital rates and landscape position. For some plants, climate change will cause conditions to become unfavourable and could result in local extirpation, as populations are unable to adapt to rapidly changing conditions (Davis and Shaw 2001). However, some plants may be able to persist under changing climate by shifting to more suitable habitats or adjusting to new conditions through genetic adaptation, phenotypic plasticity or both (Aitken et al. 2008, Corlett and Westcott 2013, Tito et al. 2021). Interspecific variation is likely in the ability of plants to persist and such changes could have widespread implications for overall community composition and ecosystem structure and function.

1.2 Impact of climate change on forests

Attention is increasingly being paid to the impact climate change is having on forests (Aitken et al. 2008, FAO and UNEP 2020, Abram et al. 2021, De Frenne et al. 2021, Lecina-Diaz et al. 2021). Spanning temperate, tropical and boreal systems, forests are a key terrestrial biome, covering around 30% of Earth’s land surface and providing globally important carbon storage, ecosystem services and biodiversity (Pan et al. 2011, Jenkins et al. 2013, Maréchaux et al. 2021). Changing climatic conditions will have substantial impacts on forests, with tropical forests in particular predicted to experience conditions within the next 100 years which have not existed on Earth for millennia (Corlett 2011). Climate change could affect forests through shifts in tree species distributions, community structure, phenology, demography and overall ecosystem function (Chmielewski and Rötzer 2001, Peñuelas et al. 2007, Harsch et al. 2009, Feeley et al. 2011, Ruiz-Benito et al. 2017a), with impacts likely to be common but varied.

Some overall patterns in the response of forest trees to climate change are emerging, but it is unclear how widespread and ubiquitous such changes are. For example, a global meta-analysis of 166 treelines found that over half migrated upward or poleward as they tracked shifting climatic zones (Harsch et al. 2009), whilst widespread forest decline and stress is common at the rear edges of species distributions, such as drought induced dieback which is occurring across Mediterranean forests (Jump et al. 2006, Sánchez-Salguero et al. 2012, Vilà-Cabrera et al. 2019). Despite the importance of forests and the increasingly prevalent threats to these habitats, our overall understanding the variation in responses of different tree dominated habitats to ongoing climate change is limited, resulting in poor insight for planning, conservation and management of these systems.

1.3 Impacts of climate change on mountain forests

Mountain forests are particularly vulnerable, comprising around 28% of forests (Price 2003), but holding disproportionally high levels of species richness and endemism and experiencing particularly large and rapid increases in temperature (Beniston et al. 1997, Nogués-Bravo et al. 2007, Jump et al. 2012, Rangwala and Miller 2012, Greenwood and Jump 2014). Vegetation communities across mountain slopes are strongly differentiated by temperature, which rapidly declines with increasing distance above sea level by around 5-6.5 °C per 1000 m of elevation gain (Colwell et al. 2008, Jump et al. 2009). Changes in climate could have disproportionately large impacts on mountain plant communities (Klein et al. 2004) as they are sensitive to temperature changes and have limited scope for upward migrations (Pauli et al. 2003). Mountain forests provide many key ecosystem functions and services, such as slope stabilisation and erosion prevention (Schönenberger et al. 2005, Stoffel et al. 2006), carbon sequestration (Peng et al. 2009) and hydrological cycling (Dirnböck and Grabherr 2000, Price 2003, Snyder et al. 2004). However, despite their value, research into the impacts of climate change on montane forests is limited compared to lowland areas (Greenwood and Jump 2014), restricting our ability to assess how these important systems are responding to change.

If montane plant communities are responding primarily to temperature changes, such as those occurring due to anthropogenic climate change, we may expect frequent upwards elevational shifts in mountain regions (Grace et al. 2002). Such upwards shifts have been observed, for example, a meta-analysis of a range of taxa and biomes suggested average upwards migrations of 11.1 m per decade (Chen et al. 2011) and a study of montane plant species in western Europe discovered even greater average upper range shifts of 29 m per decade over the last century (Lenoir et al. 2008) (*Fig.1.1*). However, limits on species’ ranges may not always be climatic (Ettinger et al. 2011) and temperature changes do not act on plants in isolation, meaning that responses of plants to climate change can be varied, with differing capacities to persist or migrate in response to similar changes in environmental conditions (Lenoir and Svenning 2015). Plant growth and survival can be limited by factors such as competition (Lewis and Tanner 2000, Coomes and Allen 2007), topography (Elsen et al. 2020) and anthropogenic influences (Vilà-Cabrera et al. 2019), alongside climate. Even treeline ecotones, which are expected to be primarily limited by temperature, have been showing variable responses to climate change due to local scale variations in environmental conditions (Greenwood et al. 2014, 2015, Morley et al. 2020).

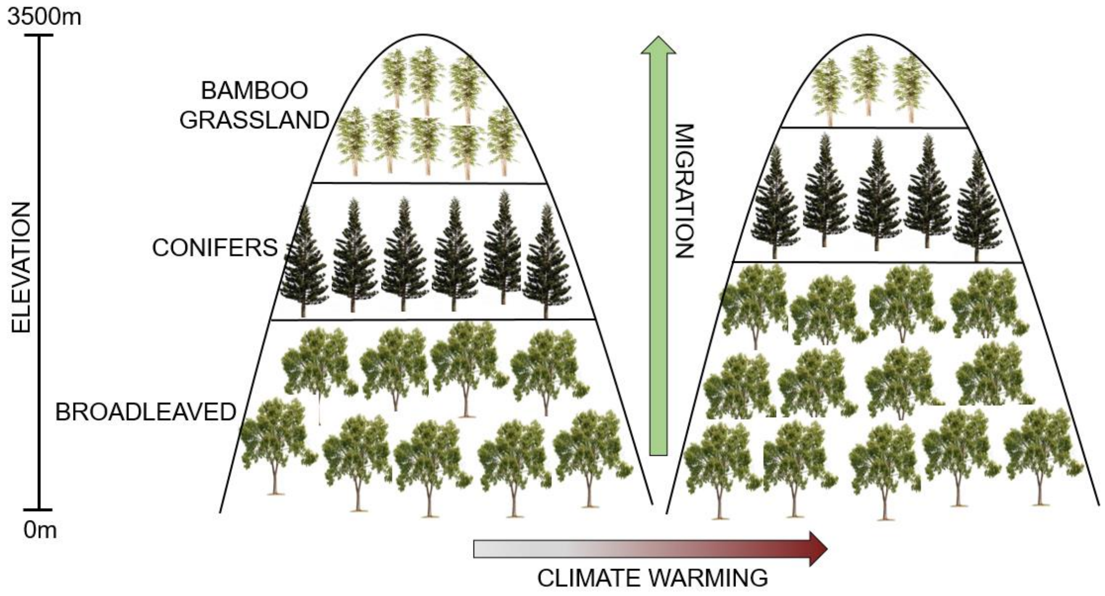

Fig.1.1: Expected migration of tree species distribution in response to ongoing climate change in Taiwan.

1.4 Variability in response of plants to environment

Across mountain regions there are many factors which can act alongside climate to influence where plants can grow from local to landscape scales (Jobbágy et al. 1996, Chen et al. 2011, Forero-Medina et al. 2011, Morley et al. 2018). Montane topography is typically complex and varied, driving differences in distributions and functions of plants due to factors such as slope gradient, aspect and substrate (De Frenne and Verheyen 2016, Lembrechts and Lenoir 2019, Midolo et al. 2019, Elsen et al. 2020). Edaphic conditions can vary, with differences in soil nutrient and water availability (van Breugel et al. 2018, Šípek et al. 2020) and differences in soil depth and bedrock stability. Variations can occur in biotic factors, such as intra- and interspecific competition, facilitation, disease and parasitism, which can shape plant communities (Lenoir et al. 2009, Máliš et al. 2016, Cadotte and Tucker 2017, Thakur and Wright 2017). As some species shift their distributions, the habitat suitability for others may change, impacting overall community composition (Greenwood et al. 2016). Alongside climate change, anthropogenic land use changes can also influence species distributions through disturbances and legacy effects (Vilà-Cabrera et al. 2019). Climate change itself is also complex, involving factors such as the amount and duration of rainfall, frequency and duration of fog, location of the cloud base, and seasonality (IPCC 2013a). High-altitudes may not always become more favourable to plants (Jump et al. 2012), with high variability in climatic and non-climatic factors across mountain regions likely to drive complex responses of tree species to climate change.

Substantial variations in responses of plants to environmental change are likely both within and between different species, due to different environmental pressures and varying characteristics and tolerances to changing conditions (Huntley 1991, Le Roux and McGeoch 2008, Kichenin et al. 2013, Rabasa et al. 2013, Smithers et al. 2018, Rosas et al. 2019). Considerable genetic and environmental variation can occur across individual species ranges, resulting in local and population level adaptations and responses to climate change (Howe et al. 2003, Savolainen et al. 2007, Reich and Oleksyn 2008, Matías and Jump 2014, Anadon-Rosell et al. 2020, Ignazi et al. 2020, Tito et al. 2021). Plants can have different physiological constraints throughout their life-span, resulting in differing responses to climate change across different life-stages (Chen et al. 2011). For example, seedlings can be particularly sensitive to changes in conditions compared to their adult counterparts (Karban and Thaler 1999, Jackson et al. 2009). A meta-analysis across different taxa found that, despite experiencing similar changes in temperature, 42-50% of species showed within species variability in their responses, due to additional influencing factors (Gibson-Reinemer and Rahel 2015). Particularly large intraspecific variation may be expected in heterogeneous environments and along environmental gradients (Körner 2007, Albert et al. 2011), due to the high topographic and climate variability. Identifying the extent to which species are responding predictably to climate change is essential for effective management and conservation.

Despite considerable variability in responses of trees to climate change, much of the research thus far on the impacts for forest trees has largely been biased towards the extremes of species ranges, overlooking changes spanning across elevational gradients (Lenoir et al. 2009). Impacts such as distribution shifts can be most obvious at range edges (Allen and Breshears 1998). However, environmental conditions at range edge ecotones often favour specialists (Fadrique et al. 2018), so changes in these areas may not be typical across ecosystems, resulting in bias in our understanding of the impacts of environmental change on forest systems (Boisvert-Marsh et al. 2014). Plant phenotypes can be different at range edges compared to mid-range individuals of the same species, as individuals are at their environmental stress tolerance limits (Ignazi et al. 2020). Species reorganisations and changes in abundance are possible across species ranges and are much less well understood (Lenoir et al. 2008, Rabasa et al. 2013). Shifts in abundance across forest habitats could foreshadow further changes (Estrada et al. 2016). For example, increased density of subalpine forests has been observed below the treeline, even when treelines themselves have not shifted (Bharti et al. 2012). Even subtle changes in community composition could alter overall ecosystem function (Ruiz-Benito et al. 2017b). For an accurate picture on changes occurring across montane forests, information is needed from different species, habitats and biomes (Fadrique et al. 2018).

1.5 Information gaps in the tropics and subtropics

With high variability in environmental conditions and climate, generalising patterns of climate impacts across regions may be misleading, as every mountain has a different suite of environmental and topographical conditions, and climate change is likely to affect these systems differently (Harsch et al. 2009, Antão et al. 2020, Comte and Lenoir 2020, Lenoir et al. 2020). Global averages may mask subtle differences between species and environments (Morley et al. 2018). Assessments of forest distribution shifts have thus far been biased towards temperate and boreal systems, largely from relatively accessible areas in Europe (e.g. Grabherr et al. 1994, Gehrig-Fasel et al. 2007, Harsch et al. 2009, Dirnböck et al. 2011, Ruiz-Labourdette et al. 2012). Studies on range shifts are limited across Asia, South America, Central Africa, Antarctica and Greenland (Lenoir and Svenning 2015). This spatial bias in data means that the tropics and subtropics remain underrepresented. Generalising patterns and processes from temperate and boreal sites may be misleading due to strongly contrasting conditions between systems.

Tropical forests hold the largest species diversity of any terrestrial environment (Potapov et al. 2012) and around 70% of the global forest carbon sink (Pan et al. 2011). Temperatures in the tropics do not vary hugely across latitudes, but rapidly decline with increasing altitude (Colwell et al. 2008, Jump et al. 2009), so subtle changes in climate could cause rapid shifts in montane community composition (McCarty, 2001). Tropical climates allow trees to persist at much higher altitudes than mountains at higher and lower latitudes, with the treeline isotherm of around 5-8 ^{o}C (Körner and Paulsen 2004) often not reached until around 3500 m (Paulsen and Körner 2014). Quantifying distribution shifts and their drivers may be particularly challenging in tropical forests (Esquivel-Muelbert et al. 2019), due to the high species diversity and complexity of biotic interactions at low latitudes (Schemske et al. 2009, Hargreaves et al. 2019), which results in multiple factors potentially interacting with temperature. The effects of climate change are also expected to be particularly pronounced across tropical forests (Sheldon 2019), with forecasts of seasons becoming more unpredictable in length and intensity (Neelin et al. 2006, Fu 2015).

Despite likely substantial changes, our understanding of the variability possible in responses to climate change within and between tropical tree species is limited. For example, our understanding of the variations in the early development of seedlings is particularly limited for tropical trees (Verdú and Traveset 2004, Bhadouria et al. 2016), restricting our ability to predict the distributions, composition and function of future forests. Information on variability in functional characteristics of plants is limited in the tropics (Wilson et al. 1999, Jetz et al. 2016 but see Poorter et al. 2008, Wright et al. 2010, Chaturvedi et al. 2011) and tropical and subtropical montane forest range shifts have also been poorly documented (although examples include Colwell et al., 2008; Fadrique et al., 2018; Feeley et al., 2011; Jump et al., 2012). As global environmental changes continue, further understanding is needed on the impacts across a wide spectrum of forest types and species, to allow us to prepare for the implications of such changes for biodiversity, ecosystem function and dependent human populations.

1.6 Trait based ecology and the impact of global change on forests

For effective predictions to be made on the impact of climate change on trees, we first need to understand fundamental patterns in nature and how patterns and processes are linked to climate (Sutherland et al. 2013). Plant functional traits may provide such an opportunity. Functional traits comprise the morphological, physiological and phenological characteristics of plants, and are considered to reflect relationships between plants and their environment (Violle et al. 2014, Bjorkman et al. 2018, Boonman et al. 2020). Functional traits can vary within and between species (Siefert et al. 2015) and across different habitats (Albert et al. 2010). Particularly large trait variation is expected for plants existing in highly heterogenous environments, along gradients in environmental conditions and for species occupying large distributional ranges (Körner 2007, Albert et al. 2011, Bussotti et al. 2015, Rosas et al. 2019, Anderegg et al. 2021).

Due to the expected link between traits and environment, plant functional traits have been suggested as a tool for forecasting responses of vegetation to environmental change (Lavorel and Garnier 2002, Violle et al. 2007, Pacifici et al. 2015, Estrada et al. 2016, Funk et al. 2017, MacLean and Beissinger 2017, Briscoe et al. 2019, Maréchaux et al. 2021). However, it is unclear how effective traits are at predicting changes across different contexts (Estrada et al. 2016, Beissinger and Riddell 2021, Fontana et al. 2021) and which traits may be most insightful when assessing distribution shifts (Estrada et al. 2016). Variability is likely in the relationship between functional traits and environment across different ecosystems (Schellenberger Costa et al. 2017) and the effectiveness of traits to predict changes potentially also varies between environments (Estrada et al. 2016, Beissinger and Riddell 2021, Fontana et al. 2021). Further information on the relationship between plant function and climate is needed for predictions to be made of the responses of vegetation communities to climate change.

1.7 Forests and climate across Taiwan

Straddling the Tropic of Cancer in the South China Sea, the island of Taiwan has a broadly subtropical climate, spanning from tropical at the southern tip of the island to alpine at high elevation (Greenwood et al. 2015). Mountains cover 74% of the island (Lu et al. 2001, Klose 2006), with the Central Mountain Range running north to south, rising to a maximum altitude of 3952 m a.s.l. at the peak of Yushan. Altitude is the main driver of temperature differences, whilst monsoons cause variations in rainfall (Li et al. 2013). There is a distinct temperature decline from the south to the north of the country, with wetter conditions in the east than the west, with an average of 2500 mm per year and 1500 mm per year respectively (Li et al. 2013). Taiwan experiences around two typhoons per year between June and September (Li et al. 2013), but these have been becoming more unpredictable in recent years.

Across Taiwan, natural forests are abundant, covering an area of 2.197 million hectares (Tsai 2021), predominantly located on steep slopes with poor access and areas protected for maintaining drinking water, soil and timber resources (Li et al. 2013). Large scale deforestation has occurred at low elevations, with areas below around 500 m a.s.l. now dominated by agriculture and urban areas (Li et al. 2013). Above this, local human influences are minimal, with generally low levels of human disturbance away from the main roads and trails, with the steep and dangerous terrain a major deterrent of forestry, tourism and agriculture. Forest types across Taiwan's Central Mountain Range are highly varied, spanning across different climatic zones. Evergreen broadleaved forests dominate at low elevations and transition into areas of mixed forest, deciduous broadleaved and evergreen broadleaved forest with increasing elevation (Li et al. 2013). These forests include genera such as *Ficus, Machilus, Castenopsis, Fagus* and *Quercus* (Li et al. 2013). Coniferous forest with abundant *Tsuga chinensis* and *Abies kawakamii* dominates at high elevations (Li et al. 2013). The *A. kawakamii* treeline is spatially variable (Greenwood et al. 2014), but sits around 2900- 3400 m a.s.l. Beyond this, *Yushania niitakayamensis* bamboo dominates the alpine grassland (Greenwood et al. 2014). Endemic species make up around 55% of the plants at the highest elevations in Taiwan (Jump et al. 2012).

Climate change is primarily affecting Taiwan through rising temperatures, with precipitation largely unchanged (Jump et al. 2012), but some evidence to suggest rainfall frequency, intensity and persistence has increased during typhoons, most likely due to a slowing of their movement over the island (Tu and Chou 2013). These rising temperatures are causing many plant species to rapidly migrate to higher elevations (Jump et al. 2012) with further upwards migrations predicted under climate change (Hsu et al. 2012). Increased rainfall could result in more frequent landslides, altering vegetation communities on slopes (Chou et al. 2011). Substantial upwards vegetation shifts are predicted to cause habitat fragmentation and the ranges of most forest types to shrink, with cypress and *Picea* forests particularly negatively affected (Hsu et al. 2012). Endemic species at high altitudes are likely to be threatened by encroachment from lower altitudinal species (Jump et al. 2012).

Research on Taiwan's mountain forests has primarily focussed on the high-altitude system. Altitude and sheltering have been identified as the primary influencing factors of distribution shifts at the *A. kawakamii* treeline (Huang 2002), with further advance expected as the climate warms due to a positive relationship between growth rate and air temperature (Greenwood et al. 2015). There is substantial spatial variation in treeline advance due to factors such as steep unstable topography, exposed aspects, soil quality, water availability and competition between trees and *Y. niitakayamensis* grassland and increasing forest density at the treeline (Greenwood et al. 2014, Morley et al. 2020). High altitude soils and rates of ecosystem processes at the alpine treeline have been found to be highly variable (Stoll 2022). Treeline advance has also been found to be an important factor altering the broader plant community, with species richness of epiphytic macro-lichens lower in rapidly advancing treelines

(Greenwood et al. 2016). Beyond the treeline, the upper distributional range limits of various alpine plant species in Taiwan have risen by around 3.6 m every year over the last century (Jump et al. 2012). However, quantitative data on observed shifts below the treeline and variability in responses of trees to climate change in Taiwan is very limited.

1.8 Thesis outline

Due to the current paucity of information on the impacts of environmental change on montane forests below the treeline in the tropics and subtropics, this thesis is a targeted attempt to address some of these information gaps by focussing on forests in the Central Mountain Range of Taiwan. The research presented here aims to characterise and quantify variability within and between species from the landscape to the individual organism scale. Through four data chapters, this thesis investigates broad-scale changes in species distributions across hyper-diverse montane forests. The primary goal of this work, which is to make significant contributions to the field of forest ecology and gain greater insights on the variations in responses of trees to climate change across diverse forest habitats.

To address the information gap of tree species distribution shifts below the treeline, this thesis aims to quantify individual tree species shifts and their potential drivers across different forest types at a landscape scale. To do this, Chapters 2 and 3 use a nation-wide forest inventory dataset from Taiwan (NFI), which was systematically sampled across the forested areas of Taiwan between the 9th August 2008 and 23rd January 2013 (*Fig.1.2*). Chapter 2 aims to assess broadscale patterns, focusing on estimating tree species distribution shifts across the Central Mountain Range. Building on these findings, Chapter 3 investigates the relationship between plant functional traits and climate and determines whether traits could be used as predictors of future distribution shifts.

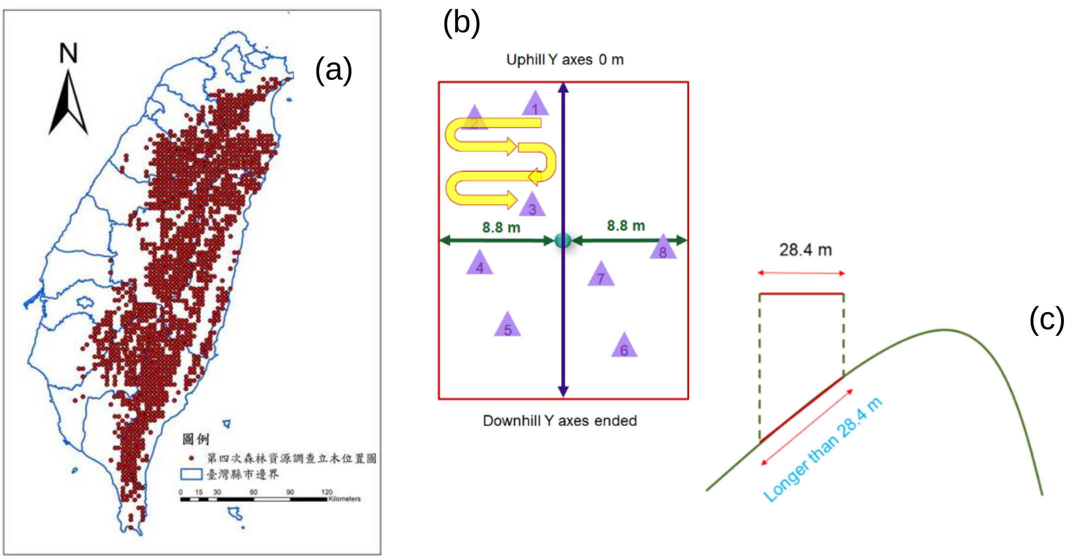

Fig.1.2: (a) Plot locations of the 4th National Forest Inventory of Taiwan and (b) Plot X axes run horizontally, divided into two sides of 8.8m and Plot Y axes run downslope. Sampling runs from the top left of the plot to the bottom right. (c) Representation of double sampling method and plot layout, where plot Y axes are adjusted according to the slope to ensure a standard plot size in remote sensing imagery and (Fig. credit: Taiwan team).

Greater insight is needed on variation across tropical elevation gradients to identify the environmental controls on vegetation and subsequently predict future impacts on community composition and ecosystem function. To gain insight on how much variability is possible within a single species and determine potential differences in response to climate change, Chapters 4 and 5 assess the variability of a widely distributed pine species, *Pinus taiwanensis* Hayata, across a diverse elevational gradient, for a more in-depth investigation of within species differences in plant-climate relationships. Chapters 4 and 5 focus on the Hehuanshan and Xueshan areas of Northern Taiwan (*Fig.1.3*), where *P. taiwanensis* is abundant. Chapter 4 considers variability in functional traits across an elevation gradient, assessing how plant function varies in response to diverse climatic and physiographic factors across a species distribution range. Chapter 5 assesses variability in the early developmental stages of seedlings to future climate scenarios, to determine how the vulnerable first stages of growth of the species respond to variations in climatic conditions, to foreshadow potential future impacts of climate change on forests.

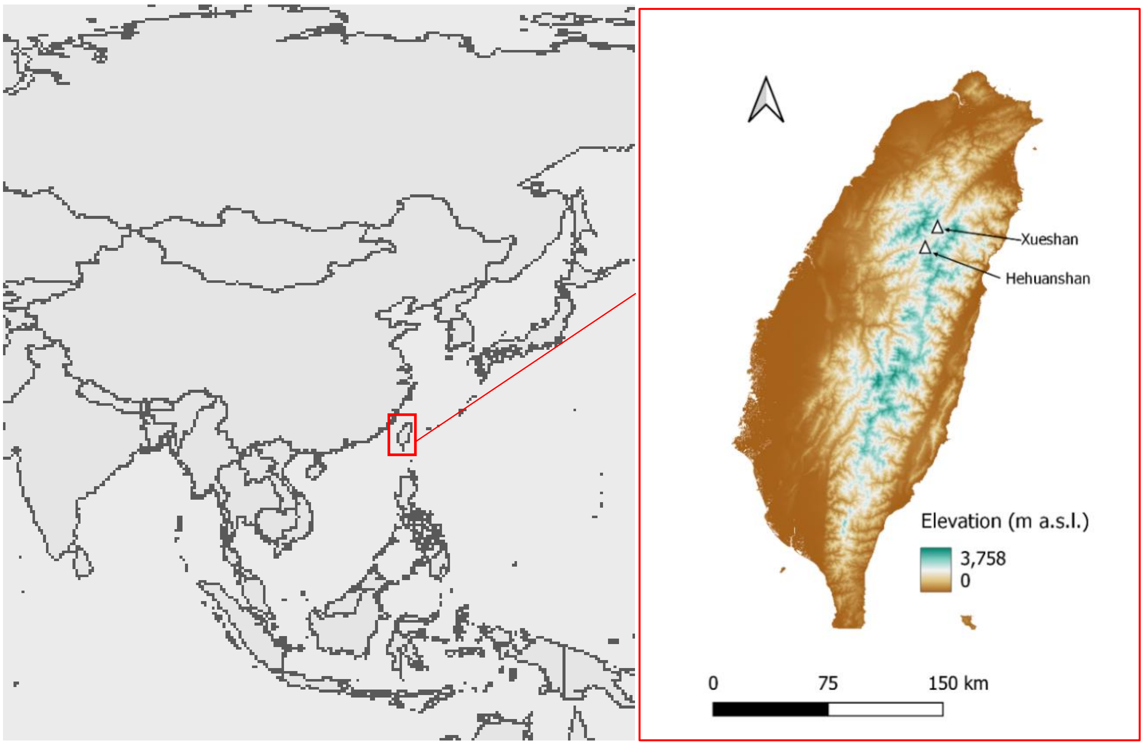

Fig.1.3: Location of Taiwan in South China Sea and a digital elevation model of Taiwan (meters above sea level) and the approximate locations of Xueshan and Hehuanshan, from which *Pinus taiwanensis* data were sampled.

This thesis concludes with Chapter 6, which explores the key theme of variability underpinning all chapters, summarises the advances made through this research and identifies areas for future investigation. Overall, this investigation of an understudied region will allow for improved understanding of tree species responses at a global scale.

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Chapter 2

Onward but not always upward: individualistic elevational shifts of tree species in subtropical montane forests

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Title: Onward but not always upward: individualistic elevational shifts of tree species in subtropical montane forests

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2.1 Abstract

Ongoing global climate change is driving widespread shifts in species distributions. Trends show frequent upwards shifts of treelines, but information on changes in montane forest below the treeline and in the tropics and subtropics is limited, despite the importance of these areas for biodiversity and ecosystem function. Patterns of species shifts in tropical and subtropical regions are likely to be more complex and individualistic than global averages suggest due to high species diversity and strong influence of competition, alongside direct climatic limitations on distributions. To address the question of how subtropical montane tree species are likely to move as climate changes, we used an extensive national forest inventory to estimate distribution shifts of 75 tree species in Taiwan by comparing the optimum elevation and range edges of adults and juveniles within species. Overall there was a significant difference in optimum elevation of adults and juveniles. Life stage mismatches suggested upward shifts in 35% of species but downward shifts of over half (56%), while 8% appeared stable. Upward elevation shifts were disproportionately common in high elevation species, whilst mid to low elevation species suggested greater variation in shift direction. Whilst previous research on mountain forest range shifts has been dominated by work addressing changes in treeline position, we show that although high elevation species shift up, below the treeline species may shift individualistically, heralding widespread changes in forest communities over coming decades. The wide variation of responses indicated is likely driven by individual species responses to interacting environmental factors such as competition, topography and anthropogenic influences across the broad range of forest types investigated. As global environmental changes continue, more detailed understanding of tree range shifts across a wide spectrum of forests will allow us to prepare for the implications of such changes for biodiversity, ecosystem function and dependent human populations.

2.2 Introduction

Ongoing global climate change is contributing towards widespread shifts in species distributions (Parmesan and Yohe 2003, Chen et al. 2011, Pecl et al. 2017, Lenoir et al. 2020), with movements to higher latitudes and elevations expected as species track warming climates (Gosz 1992, Morueta-Holme et al. 2015). Temperatures are predicted to rise to 1.5°C above pre-industrial levels by 2030 to 2052 (IPCC 2018), with mountain regions expected to experience temperatures up to three times higher than those recorded during the 20th Century (Nogués-Bravo et al. 2007). Evidence is accumulating of substantial shifts of montane forest tree distributions in response to climatic pressures (Harsch et al. 2009). The impacts of shifts can vary considerably across species ranges (Wallingford et al. 2020), with upwards shifts of trees threatening many endemic species frequently found at high elevations (Jump et al. 2012). Furthermore, changes in forest distribution and composition can decrease albedo (Pecl et al. 2017) and influence carbon sequestration (Kirby and Potvin 2007). Patchy coverage of assessments of montane forest shifts retards our understanding of the impacts changes are likely to have on biodiversity, ecosystem function and dependent human populations from local to global scales (but see Elsen et al. 2020). Accurate information on species distribution shifts is, therefore, urgently needed for improved bioclimatic modelling and to inform decisions on management, conservation, and policy.

While widespread upwards distribution shifts are reported for forest trees, research is largely based on studies of the treeline ecotone of Northern Hemisphere forests (e.g. Grabherr et al. 1994, Gehrig-Fasel et al. 2007, Harsch et al. 2009, Dirnböck et al. 2011, Ruiz-Labourdette et al. 2012), with more limited investigation of responses in tropical montane regions (Feeley et al. 2011, 2013, Feeley 2012, Duque et al. 2015, Fadrique et al. 2018, Pouteau et al. 2018). Tropical forests hold the largest species diversity of any terrestrial biome (Potapov et al. 2012), around 70% of the global forest carbon (Pan et al. 2011) and have key roles in stabilising soils (Nilaweera and Nutalaya 1999), maintaining soil fertility (García-Oliva et al. 1994) and regulating global water cycles (Snyder et al. 2004). Consequently, a greater understanding of tree species distributional changes and the implications on tropical ecosystem functioning is needed, due to a general lack of data, with few assessments in Asia, South America and Central Africa (Lenoir and Svenning 2015). Generalising patterns of range shifts across regions may be misleading, as environmental conditions vary and there is evidence to suggest climate change affects systems differently (Harsch et al. 2009, Antão et al. 2020, Comte and Lenoir 2020, Lenoir et al. 2020). In the tropics, temperatures do not vary greatly across latitude, but rapidly decline by around 5.2°C to 6.5°C every 1,000 m with increasing elevation (Colwell et al. 2008). Therefore, subtle climatic changes could cause rapid shifts in montane community composition (McCarty, 2001) and drive the establishment of novel species assemblages (Breshears et al. 2008, Gilman et al. 2010, Alexander et al. 2018). Tropical trees have already been observed living in sub-optimal conditions as they lag behind climate change, and could fall even further behind as climates rapidly alter (Feeley et al. 2011, Fadrique et al. 2018, Esquivel-Muelbert et al. 2019). The high species diversity and complexity of biotic interactions at low latitudes (Schemske et al. 2009) means that multiple factors are likely to interact with temperature, driving strongly individualistic species distribution shifts in tropical forests.

Whilst the general expectation is that species will migrate to higher elevations as the climate warms and bands of suitable environmental conditions shift upwards (Gosz 1992, Feeley 2012, Morueta-Holme et al. 2015), species distributions are limited by multiple interacting factors (e.g. Harsch et al. 2009, Ettinger et al. 2011, Wason and Dovciak 2017). Climate change is multifaceted and involves alterations to parameters including temperature mean and range, the amount and duration of rainfall, frequency and duration of fog, location of the cloud base, seasonality and frequency of extreme events (IPCC 2013b). Non-climatic factors such as local scale biotic interactions (Lenoir et al. 2009), physiological constraints (Chen et al. 2011), soil nutrient availability (van Breugel et al. 2018), presence and abundance of pests and diseases (Máliš et al. 2016), topography (De Frenne and Verheyen 2016, Lembrechts and Lenoir 2019, Elsen et al. 2020) and anthropogenic land use also influence species distributions (Vilà-Cabrera et al. 2019), and will affect species responses to changing climate. Although upwards species distribution shifts are commonly reported (e.g. Harsch et al. 2009, Feeley et al. 2011), studies have also identified downslope movements (Lenoir et al. 2010, Crimmins et al. 2011, Urli et al. 2014) or limited evidence of shifts altogether (Zhu et al. 2012). Large-scale downwards elevational shifts have been noted in some areas, such as in montane vegetation in California (Crimmins et al. 2011). Mountain regions typically have high habitat and environmental heterogeneity (e.g. Jobbágy et al. 1996, Morley et al. 2018), so individualistic shifts in montane forest tree species distributions could be particularly likely.

Bias in research on forest tree species distribution shifts towards the extremes of species ranges overlooks changes occurring over the whole elevational gradient (Lenoir et al. 2009). Although changes in distribution are typically most obvious at ecotones (Gosz 1992), treeline changes do not necessarily translate to equivalent shifts of all species (Vitasse et al. 2012) or influence dynamics below the treeline. Environmental conditions at ecotones often favour specialists (Fadrique et al. 2018), so distributional changes here are unlikely to be typical of ecosystems as a whole. Species can respond individualistically to climate change (Huntley 1991, Rabasa et al. 2013), with differing capacities to persist or migrate in response to changing environmental conditions (Lenoir and Svenning 2015). Populations of the same species at different locations across the distribution range can also shift independently (Feeley 2012, Felde et al. 2012), with a meta-analysis of within-species range shifts finding that non-thermal factors considerably influenced patterns, with 42-50% of species showing individualistic shifts despite experiencing similar temperature increases (Gibson-Reinemer and Rahel 2015). Subtle changes within ranges, such as species redistributions or declines, are also likely (Lenoir et al. 2008) and could foreshadow future range shifts (Estrada et al. 2016). The conclusions drawn on forest shifts could, therefore, be substantially different depending on which area or species is assessed (Boisvert-Marsh et al. 2014). For an accurate picture on montane forest tree species distribution shifts, species-specific information is needed (Fadrique et al. 2018), from across the entire elevational gradient.

Given the paucity of information on range shits of tropical montane trees, we sought to determine if evidence exists for species-specific range shifts below the treeline and the extent to which shifts are uniform for the species or individualistic across the elevational gradient. We estimated tree species distribution shifts across an elevation gradient of diverse tropical mountain forests in Taiwan, using a country-wide multi-species forest inventory dataset. We tested the hypothesis that species at high elevations, which are most likely to be temperature limited, will shift upwards, but lower elevation species will display more complex, individualistic patterns due to the greater relative importance of biotic interactions below the treeline. We provide novel insight into distribution shifts of multiple species with elevation and their implications for forest communities in a subtropical montane forest system, contributing key information to better understand forest distribution shifts at a global scale.

2.3 Materials and methods

2.3.1 Study location

The island of Taiwan straddles the Tropic of Cancer at the margins of the South China Sea. Lowland climates are warm and humid and conditions range through temperate to alpine with increasing elevation in the Central Mountain Range. Elevation is the main driver of temperature differences, whilst monsoons cause substantial variations in rainfall within and between years (Li et al. 2013). Mountains cover 74% of the island (Lu et al. 2001), with over 200 peaks higher than 3,000 m a.s.l. (Li et al. 2013). Areas below around 500 m a.s.l. are dominated by urban and agricultural land uses following widespread deforestation, but natural forests are abundant above this elevation, transitioning from broadleaved to mixed and conifer forest with increasing elevation (Li et al. 2013). Landslides occur frequently due to steep topography and unstable geology interacting with earthquakes and typhoons (Lu et al. 2001). High elevation species in Taiwan have been shown to be predominantly shifting upwards (Jump et al. 2012, Greenwood et al. 2014, Morley et al. 2019), but there is a paucity of quantitative information on dynamics in the broader forest below the treeline.

2.3.2 Data

Analyses were undertaken using the 4th Taiwan National Forest Inventory (NFI), a systematic plot-based survey across the forested mountainous areas of Taiwan between the 9th August 2008 and 23rd January 2013 (*Fig.2.1*).

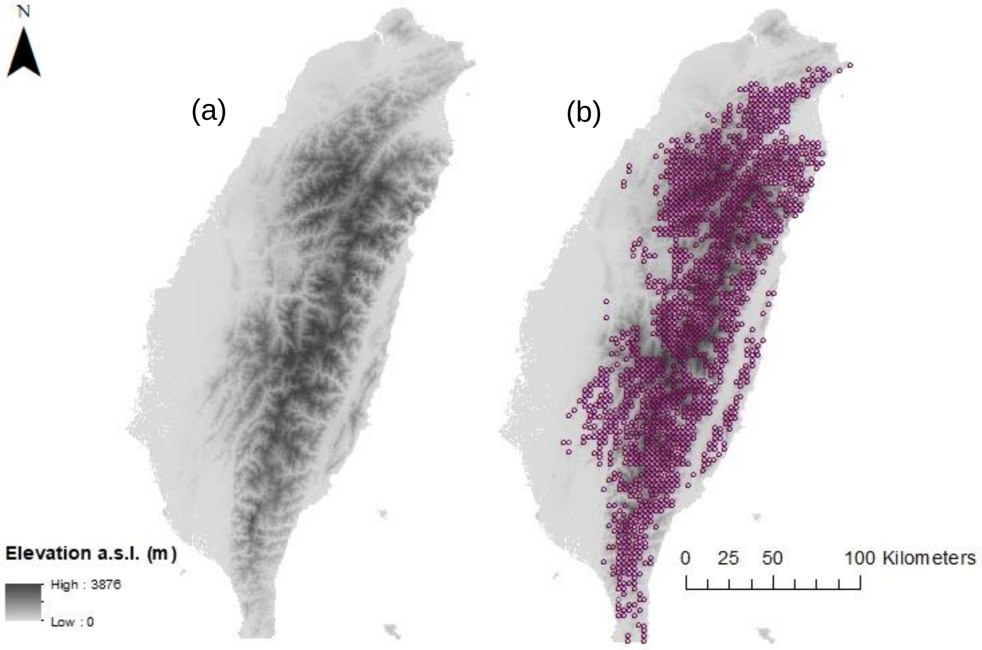

Fig.2.1: Digital elevation model of Taiwan (a) and the distribution of National Forest Inventory field plots (b).

Plots covered an elevation range from 0 - 3,769 m a.s.l. and had a mean spacing of 2,871 m between plots (spacing of 3,000 m in national forest areas and 1,500 m elsewhere). The NFI was spatially extensive, and comprised species information, tree measurements and environmental data over 1,564 plots, incorporating 86,306 trees and 516 species. Plots were approximately 0.05 ha (from 0.007 to 0.159 ha), with one plot side of 17.6m perpendicular to slope and the other side parallel with a variable size to maintain the projected plot area (*Fig.2.S1*). Within each plot, all trees > 5 cm diameter at breast height (dbh) measured at 1.3m were recorded, with data such as species, dbh and height collected (Table 2.S1). The elevation of each plot was recorded using a GPS.

Tree basal area (m^2) was calculated for each tree and summed to plot level (Kershaw et al. 2017). From the available data, we removed trees with missing elevation, dbh or xy plot coordinates; trees with dbh > 99.99% of values, as these trees had obvious measurement errors, plot x coordinates > 8.8 m and plot y coordinates > 99.99% to remove outliers; plots with basal area < 0.2 m^2 and > 99.99% of basal area, leading to a final number of 84,361 trees and 1,548 plots. We checked for plantation forests by identifying plots with > 90% basal area of commonly planted species *Taiwania cryptomerioides, Cryptomeria japonica* and *Chamaecyparis formosensis* and checked the coefficient of variation of dbh values. No plots were removed following this process, as only one plot was identified despite trialling less conservative parameter values for basal area (down to > 60%) and dbh coefficient of variation (up to < 0.3), and this plot also showed tree height variation from 5.8 m to 28 m, indicating that it is unlikely to have been planted.

2.3.3 Demographic analysis

To estimate the magnitude and direction of forest tree species distribution shifts at the range optima and range edges we used a demographic approach. A single survey was used to determine the distribution mismatch between adult and juvenile trees as a proxy for change, with juveniles considered to reflect more recent environmental conditions and adults reflecting historic conditions (Lenoir et al. 2009, Rabasa et al. 2013). Two methods of defining adult and juvenile life stages were compared. The first defined juveniles < 1st quartile of dbh values and adults > 1st quartile of dbh values, whilst the second used a species-specific approach, defining juveniles < 0.25 percentile of dbh values for each species and adults > 0.5 percentile. No seedlings were incorporated in the dataset, allowing us to reduce potential influence on the results of ontogenetic niche differentiation (different environmental requirements of different life stages of the same species) and potential time lags between environmental changes and tree responses (Werner 1984, Lenoir et al. 2009, Bertrand et al. 2011, Kroiss et al. 2015, Máliš et al. 2016, Alexander et al. 2018). The distribution of adult and juvenile trees across the landscape for each method was compared, showing similar patterns and therefore indicating that the two methods are unlikely to give substantially different results. However, the second approach was selected as it provides species-specific information and removes trees with intermediate size classes. Distributions were checked again to detect any obvious latitudinal biases in life stages, to determine whether there were any indications of species shifting latitudinally, but no patterns were observed. Data were converted to occurrence records and species selected for analysis if there were at least 30 plots containing the species at the juvenile life stage. The final dataset comprised 62,089 trees, 1,526 plots and 84 species.

To explore the shape of species presence along the elevation gradient, we used generalized additive models (GAMs), with most species displaying hump-shaped distributions. These distributions were tested using generalized linear models (GLMs), comparing linear models with quadratic models for each species and life stage. Pseudo R^2 values were calculated as 1 - (residual deviance/null deviance) to determine the predictive power of the models and models were compared using AIC (Akaike Information Criterion), with lower values suggesting a better fit (with a difference ≥ 2). In accordance with the assumption that species are generally most abundant in the centre of their range (Holt et al. 1997), only data from species which fitted the quadratic model better than the linear model were used for further analysis (75 out of 84 species). Predictions of probability of occurrence were generated for each species, from which, distribution graphs were created and range optima extracted (*Fig.2.S1a-c*). The difference in range optima between life stages was calculated for each species and a Wilcoxon signed rank test used to test the general trend of mismatches across all species.

To estimate changes in upper and lower range edges, a data exploration approach was used. We compared elevation at the range edges based on the raw data distributions using the 1st and 9th deciles of the elevation range as they provide a more robust indication of the range edge than extreme values (Lenoir et al. 2009). The difference in range edge positions between life stages was then calculated for each species and Wilcoxon signed rank tests used to test the overall mismatch across all species. All analyses were undertaken in R version 3.6.0 (R Core Team 2019).

2.4 Results

2.4.1 Differences between life stages at range optima

There was substantial variation in the magnitude and direction of mismatches in range optima between life stages for different species (*Fig.2.2*). Around one third of species (35%) had juvenile optima higher than adults, suggesting upward shifts. However, over half of modelled species (56%) had juvenile range optima at lower elevations than adult optima of the same species, suggesting downward shifts. Shifts in elevational optima between adults and juveniles ranged from 0 m to 390 m, with high variability in upward and downward shifts. Overall, there was a significant difference in the optimum elevation between life stages (V=679.5, p=0.002), with the juvenile median 50 m lower than the adult median. There was no difference in range optima between life-stages for 8% of species.

Evidence for upward elevation shifts was disproportionately common in high elevation species (blue to green in *Fig.2.2*). From the 15 species with adult optima > 2,000 m a.s.l., upwards shifts were indicated for 12 species, downward shifts for 2 species, whilst 1 remained stable. The species which showed evidence for downward shifts were predominantly from mid to low elevations, with 41 out of 43 species having adult optimum elevations < 2,000 m a.s.l. The species which showed no apparent mismatch between life stages were primarily mid-elevation species from the Lauracae, Theaceae and Juglandaceae families, with adult optimum positions ranging from 950 m to 2660 m.

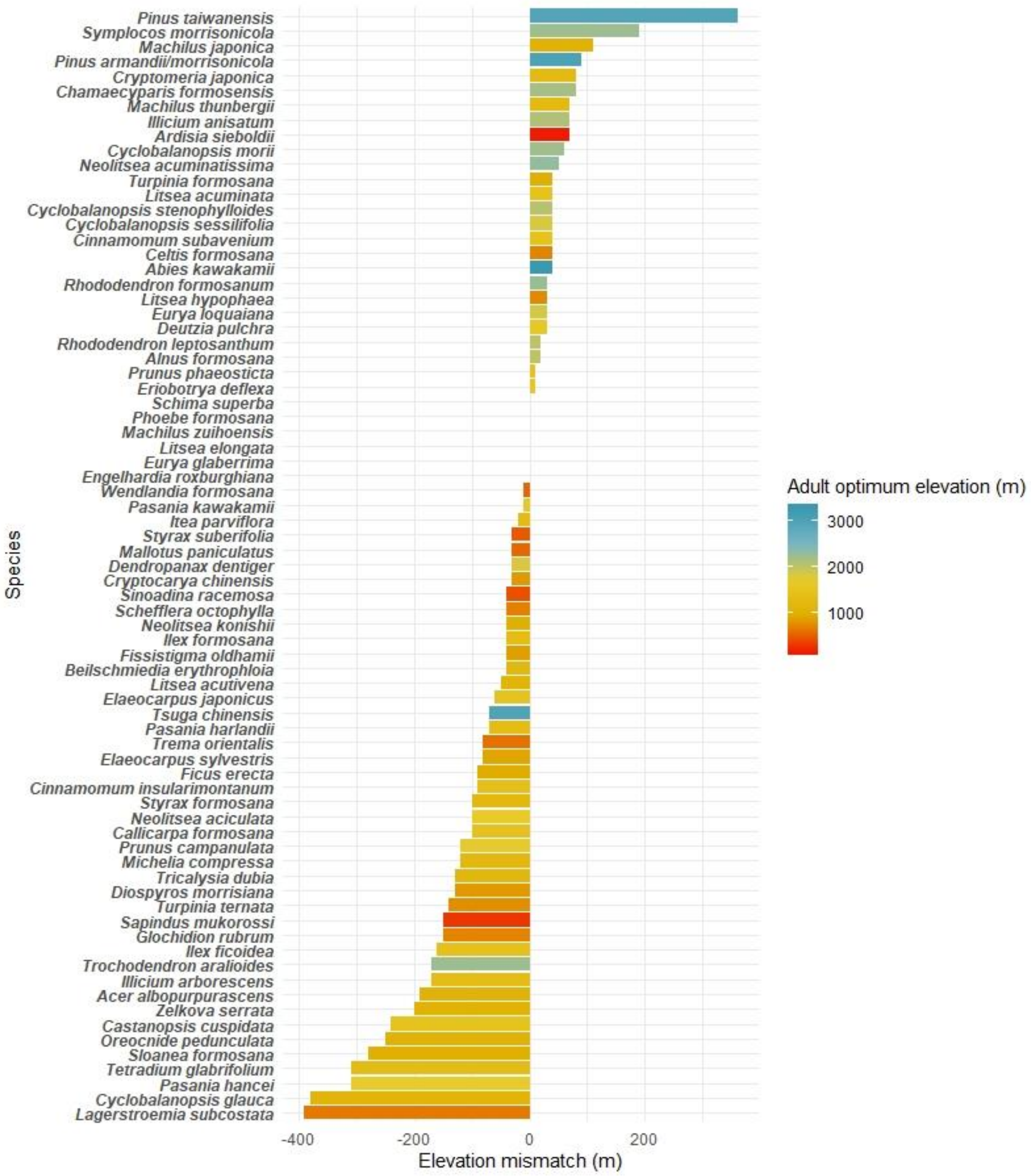

Fig.2.2: Shifts in optimum elevation (m) between adults and juveniles of 75 subtropical montane tree species calculated as optimum (juvenile) - optimum (adult), using modelled optimum elevations. Negative values indicate juveniles located at lower elevation than their adult counterparts, whilst positive values indicate juveniles located at higher elevations. Juveniles were located at lower elevations than adults for 42 species, higher elevations for 27 species, and at the same elevation for 6 species.

2.4.2 Differences between life stages at range edges

Species elevational ranges varied considerably in size (from 363 to 1,974 m), with species located at the high and low elevational extremes displaying the smallest ranges (*Fig.2.3*). Most species showed a mismatch between life stages at their lower and upper range edges (1st and 9th decile), with substantial variation between species. Mismatches suggested range expansions in 57% of species and range contractions in 43%. There were 17 species (22.67%) which had mismatches that implied range expansion at both range boundaries, with downward shifts at their lower range boundary and upward shifts at their upper range boundary.

The raw data trends were consistent with the model results. At the lower range edge, around two thirds of species (65.33%) had juvenile lower range edges below adults of the same species, suggesting potential downward shifts. Around a quarter of species (26.67%) had juveniles located higher than adults, suggesting upward shifts at their lower range edge. Mismatches in elevation ranged from 2.4 m to 482 m, with considerable variation in the sizes of mismatches in both upward and downward directions. There was no life stage mismatch at the lower range edge for 8% of species. However, overall, there was a significant difference in the lower range edge positions between life stages (V=1735.5, p=0.002), with the juvenile median 123.1 m lower than the adult median.

Over half of species (56%) showed mismatches suggesting downward shifts at the upper range edge, with juvenile upper range edges lower than adult upper range edges of the same species. Indications of upward shifts at the upper range edge were evident in 40% of species, with juveniles located higher than adults. Mismatches in elevation ranged from 4.3 m to 528.1 m, with considerable variation in the sizes of mismatches in both upward and downward directions. Overall considering all species, whilst the juvenile median was 13m higher than the adult median, there was no significant difference in the upper range edge positions between life stages (V=1614, p=0.0928).

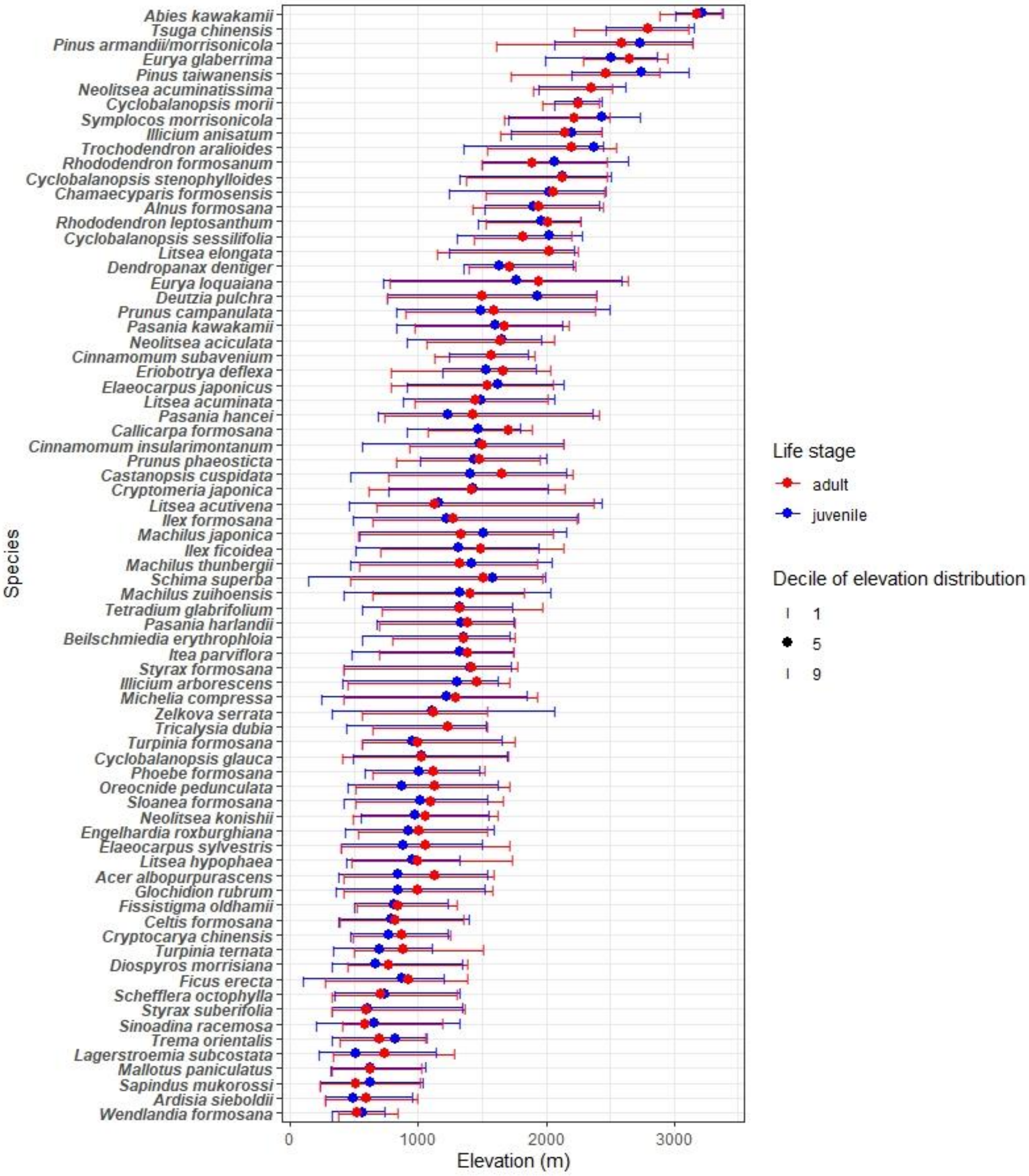

Fig.2.3: Comparison between juvenile (blue) and adult (red) presence records for 75 subtropical tree species with elevation using the 1st and 9th deciles as the range edges and the 5th decile as the range mid-point.

2.5 Discussion

By comparing the distribution of adult and juvenile life stages of 75 tree species across an elevation gradient from 0 to 3,769 m a.s.l covering a broad range of forest types, we provide evidence that suggests species distribution shifts along elevational gradients can vary considerably in tropical forests. While it is generally expected that species should shift to higher elevations in response to climate change (Chen et al. 2011), we found highly variable life stage mismatches in range optima and upper and lower range edge positions, with a tendency for juveniles to be located at lower elevations than their adult counterparts. While our evidence suggests high altitude species are largely shifting upwards, mid to low elevation species showed more idiosyncratic patterns. Downward shifts of range optima were more common and were concentrated in mid to low elevation forests where species diversity was higher. Our results suggest that migration could be a common response of montane forest tree species to environmental change, but that species move individualistically and are impacted by factors other than climate warming (Huntley 1991). Range optima and upper and lower range edges of individual species did not shift uniformly in terms of size or direction, and more species underwent range expansions than contractions. Mid-elevation species appeared to be more stable under climate change, with some showing no migrations and no associated population declines, and others displaying range expansions at both edges of their distributions.

The upslope movements at high elevations we observed are likely to have been facilitated by rising temperatures and the potential for trees to expand into non-forest areas, following the expectation that climate change drives species upwards as higher elevations become suitable for tree establishment and growth (Lenoir et al. 2009, Jump et al. 2012, Greenwood et al. 2014, Pouteau et al. 2018). Temperatures in Taiwan's Central Mountain Range have risen to around 1.05°C higher than the 1934-1970 average, with this warming already linked to rapid upwards migrations of high altitude plant species (Jump et al. 2012). Although the overall mismatch at the upper range boundary showed no significant difference across all species, critically, there was substantial difference at an individual species level. Upward shifts were the most common response of high elevation species, which is consistent with high altitude trees generally being more temperature limited than trees from warmer areas (Way and Oren 2010), high elevation montane environments warming at a faster rate than lower elevations (Pepin et al. 2015) and high elevation plant species likely to be competitively excluded under warmer temperatures (Alexander et al. 2015, Morley et al. 2020).

Our findings support much of the literature indicating widespread upwards shifts at the treeline (e.g. Grabherr et al. 1994, Gehrig-Fasel et al. 2007, Harsch et al. 2009, Dirnböck et al. 2011, Ruiz-Labourdette et al. 2012) and high elevation species shifting faster than mid to low elevation species (Lenoir et al. 2008). Furthermore, results based on forest inventory analysis here endorse assessments of treeline shifts in the same region based on aerial and satellite imagery (Greenwood et al. 2014). However, while upward shifts are indicated at the highest altitudes, the shifts in range optima that we identify below the treeline are highly individualistic, supporting the expectation that climatic warming can interact with a wide range of non-thermal factors to drive considerable variation in species distributional responses (Lenoir et al. 2010, Crimmins et al. 2011).

Competition for light and nutrients is a major limitation on tree growth and survival (Lewis and Tanner 2000, Coomes and Allen 2007), particularly in diverse tropical forests (Terborgh 2012). Shifts in distributions of some species can reduce the habitat suitability for others (Greenwood et al. 2016), with some species distributions lagging behind climate change whilst others respond more rapidly (Alexander et al. 2018, Lenoir et al. 2020). Ecotones can create barriers for movement, as conditions are typically different than in surrounding forest and can prevent some species colonising (Fadrique et al. 2018), while local variation in edaphic conditions can also restrict the expansion of some species distributions and promote the maintenance of others (Greenwood et al. 2014). Individualistic shifts of species can result in novel community compositions and biotic interactions which can, in turn, cause cascades of species distribution shifts (Huntley 1991, Gilman et al. 2010). Competitive interactions can be further influenced by alterations in plant phenology and physiology in response to climate change (Hughes 2000).

Certain functional traits may facilitate some species survival over others, with traits such as an ability to disperse and colonise new areas early, frequent reproduction and high fecundity likely to aid migrations to new areas (Angert et al. 2011, Alexander et al. 2018) and seed size and number and mode of reproduction likely to influence survival at a new site (Alexander et al. 2018). Effective dispersers may be able to track climate change and out-compete species which are responding more slowly (Urban et al. 2012). Two of the largest shifts in optimum elevation we observed were in *Pinus taiwanensis* and *Lagerstroemia subcostata***,** which are common to disturbed areas and habitat margins (Qin et al. 2007, Ruiz-Benito et al. 2015) indicating that they may be well equipped to respond to environmental changes. However, it is important to note that while we focus on distributional differences between life stages, establishment in a new site does not guarantee success as climate continues to change. For example, reductions in *P. taiwanensis* growth have been linked to increasing temperatures, suggesting that performance of established trees may decline under future climate (Ruiz-Benito et al. 2015). Future studies might further explore how altitudinal changes across life stages depend on key functional traits, with dispersal syndrome or ability to track climate change potentially being key plant strategies (Montoya et al. 2008, Ruiz-Benito et al. 2017b). For example, species able to migrate rapidly at high elevation have the potential to form outposts in advance of the current treeline where their establishment is facilitated by survival beyond the seedling life stage (Ewald 2012).

Our analyses show wide variation in responses of species across their range, with evidence suggesting the upper edge, optimum and lower edges moving in different directions or at different rates. Differences in shifts across the range of a single species are likely to be due to populations being affected by different processes and drivers of reproduction, dispersal, establishment and growth interacting across a species elevation range. Variation in local adaptation and phenotypic plasticity can cause populations of the same tree species to respond differently to the same environmental challenges (Matías and Jump 2012), with considerable variation in functional traits possible even within single species groups (Hulshof and Swenson 2010). Variations in abiotic environments (Rumpf et al. 2018) and micro-scale climatic conditions also influence where individuals are located (Lembrechts and Lenoir 2019). Mountain environments are highly heterogeneous, with areas of suitable habitat often separated by features such as valleys and outcrops, which restrict migrations (Alexander et al. 2018). Factors such as soil conditions, unstable bedrock, exposed aspects and steep gradients can limit migrations, and have already been linked to individualistic treeline advance in Taiwan (e.g. Greenwood et al. 2014, 2015), whilst disturbances such as avalanches and landslides can drive species downwards locally, even within the context of upward shifts facilitated by a warming climate (Cannone et al. 2007, Frei et al. 2010).

Across the region investigated, mid-elevation species appear well equipped to cope with changing climates, with some evidencing persistence and others an ability to migrate. Generalist species with large ranges are considered more likely to succeed under climate change than specialists with narrow ranges (Broennimann et al. 2006, Laurance et al. 2011). The species we observed that did not shift their elevational distributions were all from mid-elevations with large ranges, indicating that they may be able to persist over coming decades and following expectations that generalist species shift less than specialists (Lenoir et al. 2008). While some mid-elevation species look likely to maintain current distributions, others show potential to expand. Of the 17 species with mismatches that suggested range expansions with downwards shifts at their lower range boundary and upwards shifts at their upper range boundary, 11 were characteristic of Pasania–Elaeocarpus montane evergreen broadleaved cloud forest (1,200–1,600m a.s.l.) and 10 of Machilus-Castanopsis sub-montane evergreen broadleaved forest (400–1,800m a.s.l.), described by Li et al. (2013). However, such changes will be strongly determined over future decades by shifts in the cloud base, thickness, cover and water content (Ray 2013), which may differ locally due to variation from the East Asian Monsoon and the Massenerhebung effect (Schulz et al. 2017). The pattern of mid-elevation forests faring better than some others under climate change has previously been noted, such as *Pinus jeffreyi* in Nevada rapidly expanding at the mid-elevation point of its range (Gworek et al. 2007). Our results indicate that future forests in Taiwan may show a relative increase in more resilient mid-elevation species.

Whilst ecological and environmental factors influence species distributions, anthropogenic land-use changes also shape how species are located across the landscape and may have an important role in driving the complex species distribution shifts we observed. Around 60% of mountainous regions across the globe are exposed to intensive anthropogenic land use pressures (Elsen et al. 2020). Agricultural activities are creeping upwards in Taiwan as the human population grows (Chou and Tang 2016), with orchards, tea, vegetables and betel nut now planted locally at mid to high elevations (Lu et al. 2001). Tourism and recreation have also increased in recent decades in forested mountain regions, with associated development expanding, particularly along roads (Lu et al. 2001). Although large scale land-use change in the lowlands would most likely drive forests upwards (Guo et al. 2018a), small disturbances may allow certain species to colonise areas previously unavailable to them and temporarily increase species richness (Connell 1978, Molino and Sabatier 2001, Lembrechts et al. 2017).

Both historic forest cover and recent interventions can influence the rate of climate-driven shifts (Guo et al. 2018a), particularly at lower edges of species distributions (Vilà-Cabrera et al. 2019). Forests in Taiwan are mostly protected for water resources, slope stability and biodiversity, and there is a strong public appreciation for the value of forests (Lu et al. 2001). However, timber harvesting has occurred, and was particularly intense in some parts of the island during the 1940s (Lu et al. 2001). Localised forest thinning is undertaken for conservation purposes in some areas (Weng et al. 2007, Zhuang et al. 2014, Lin et al. 2015), providing potential for infilling from higher elevations. The legacy of past land use should not be overlooked in driving current forest composition and performance (Perring et al. 2016, 2018, Alfaro-Sánchez et al. 2019).

As the climate continues to change, information on the mechanisms, drivers and implications of forest redistributions are urgently needed. Here, we have addressed an important knowledge gap, demonstrating that tree distribution shifts in tropical montane forests are complex and are likely driven by more than direct effects of climate alone. We followed a similar, but adjusted, demographic approach used in previous studies (e.g. Lenoir et al. 2009, Vitasse et al. 2012, Rabasa et al. 2013), which can be applied to forest regions across the world to rapidly assess changes using a single survey in the absence of suitable historic records. Therefore, we suggest this approach will be particularly valuable in data poor regions, such as understudied tropical forests where one large-scale survey could indicate the magnitude and direction of potential tree species changes.

One argument against our interpretation of species distribution shifts could be that differences in the abundance and local distribution of adults and juveniles of a species can be linked to ontogenetic niche differentiation (Werner 1984, Bertrand et al. 2011). However, we argue that findings presented here can indicate anticipated changes through time because: (i) the observed directional patterns can be explained by climate change drivers, but they are not consistent with ontogenetic shifts (i.e. higher tolerance of juveniles than adults at high elevations (Lenoir et al. 2009); and (ii) we excluded seedlings that are expected to show the greatest ontogenetic niche differences not linked to temporal changes (Máliš et al. 2016). Further integrated analysis of climate, at both a micro and macro scale (Lembrechts and Lenoir 2019), landscape, land use history and species traits is valuable to provide greater detail. With predictions of future movements essential for effective conservation and resource management, further research into approaches such as trait based range shift predictions are needed (Pöyry et al. 2009, Angert et al. 2011, Estrada et al. 2016). Assessments combining multiple parts of species ranges are scarce (Lenoir and Svenning 2015), yet are much needed and important for gaining a thorough understanding of distribution shift dynamics.

2.5.1 Conclusions

Whilst previous predictions suggest widespread upwards shifts of tree species as the climate warms, trends of montane forest change in the tropics and sub-tropics are likely to be more complex than global averages suggest. Here, we estimated distribution shifts of 75 tree species in Taiwan to assess the extent to which species respond individualistically to current environmental changes. While frequent upward shifts were indicated for high elevation species, in contrast to expectations, we found evidence suggesting downward shifts to be widespread at mid to low elevations in subtropical montane forest. There was great variability in responses between species and across different parts of the ranges of single species. The wide variation of responses we identified is most likely driven by biotic interactions in high diversity forest and individual species and population responses to interacting environmental factors such as topography and anthropogenic influences. These factors are common to many other tropical and subtropical forests, suggesting such individualistic responses should be frequent and indicating a high likelihood of widespread forest community change over coming decades. With global environmental changes ongoing, accounting for complexity in shifts in montane forest species distributions is needed to provide insight on the implications for ecosystems and the people who depend on them.

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2.8 Supplementary material

*Table 2.S1: Results of model selection of generalized linear models (glm) run for probability of occupancy of 84 species in the 4th Taiwan National Forest Inventory for each life stage across an elevation gradient. Model 1 is a standard glm and Model 2 is a glm with a quadratic term. *Higher pseudo R^2 value, **Lower Akaike information criterion (AIC) value.*

Species	**Life stage**	**Model**	**Pseudo R^2**	**AIC**
Acer albopurpurascens	Adult	1	0.03	580.4
		2	0.08*	550.4**
	Juvenile	1	0.03	417.8
		2	0.05*	412**
Castanopsis cuspidata	Adult	1	0.00	838
		2	0.04*	807.8**
	Juvenile	1	0.01	680.4
		2	0.03*	668.6**
Ardisia sieboldii	Adult	1	0.22	705.7
		2	0.23*	695.1**
	Juvenile	1	0.23	607.5
		2	0.25*	595.5**
Beilschmiedia erythrophloia	Adult	1	0.02	920.1
		2	0.14*	810**
	Juvenile	1	0.02	726.7
		2	0.09*	673.6**
Celtis formosana	Adult	1	0.11	632.3
		2	0.15*	603.8**
	Juvenile	1	0.09	461.8
		2	0.13*	441.7**
Callicarpa formosana	Adult	1	0.00	543.3
		2	0.12*	482.2**
	Juvenile	1	0.00	367.1
		2	0.08*	340.9**
Alnus formosana	Adult	1	0.05	974.5
		2	0.17*	852.9**
	Juvenile	1	0.03	536.9
		2	0.10*	500.9**
Chamaecyparis formosensis	Adult	1	0.09	884.7
		2	0.22*	760.3**
	Juvenile	1	0.08	571.5
		2	0.17*	518.3**
Abies kawakamii	Adult	1	0.65	185.4
		2	0.71*	157.2**

	Juvenile	1	0.61	135.8
		2	0.68*	113.1**
Cyclobalanopsis sessilifolia	Adult	1	0.01	467.9
		2	0.06*	447.3**
	Juvenile	1	0.01	319.1
		2	0.07*	303.7**
Cyclobalanopsis longinux	Adult	1	0.00	1156
		2	-0.13	1024**
	Juvenile	1	0.00	910.7
		2	0.09*	832.2**
Cleyera japonica	Adult	1	0.01	730.3
		2	0.03*	721.8**
	Juvenile	1	0.01	539.3
		2	0.01	537.4**
Cinnamomum subavenium	Adult	1	0.00	622
		2	0.10*	561.9**
	Juvenile	1	0.00	438.8
		2	0.11*	392.1**
Cryptomeria japonica	Adult	1	0.00	577.5
		2	0.02*	569.4**
	Juvenile	1	0.00	503.7
		2	0.03*	494.2**
Cyclobalanopsis glauca	Adult	1	0.02	746.7
		2	0.05*	728**
	Juvenile	1	0.04	626.1
		2	0.05*	620.6**
Cryptocarya chinensis	Adult	1	0.09	507.1
		2	0.18*	456.6**
	Juvenile	1	0.09	370
		2	0.16*	342.3**
Cinnamomum insularimontanum	Adult	1	0.00	627.3
		2	0.07*	584.1**
	Juvenile	1	0.00	503
		2	0.05*	482**
Cyclobalanopsis morii	Adult	1	0.10	546.4
		2	0.28*	439.6**
	Juvenile	1	0.10	331
		2	0.36*	240.5**
Daphniphyllum glaucescens	Adult	1	0.01	570.7
		2	0.02*	566.1**
	Juvenile	1	0.02	360
		2	0.03*	359.9**
Elaeocarpus japonicus	Adult	1	0.00	1020
		2	0.08*	937.4**

	Juvenile	1	0.00	739.2
		2	0.08*	679.4**
Dendropanax dentiger	Adult	1	0.02	502.6
		2	0.13*	446.9**
	Juvenile	1	0.01	348.6
		2	0.12*	313.8**
Elaeocarpus sylvestris	Adult	1	0.03	693.4
		2	0.06*	681**
	Juvenile	1	0.05	492.3
		2	0.08*	481.5**
Cyclobalanopsis stenophylloides	Adult	1	0.05	848.5
		2	0.14*	766.9**
	Juvenile	1	0.05	646
		2	0.14*	590**
Deutzia pulchra	Adult	1	0.00	505
		2	0.03*	490.2**
	Juvenile	1	0.00	389.6
		2	0.02*	383.7**
Diospyros eriantha	Adult	1	0.21	337.1**
		2	0.21	338.9
	Juvenile	1	0.26	274.4
		2	0.30*	262.6**
Diospyros morrisiana	Adult	1	0.08	638.5
		2	0.14*	599**
	Juvenile	1	0.09	412.3
		2	0.12*	399**
Engelhardia roxburghiana	Adult	1	0.06	858.7
		2	0.13*	797.8**
	Juvenile	1	0.05	664
		2	0.12*	622.1**
Ficus fistulosa	Adult	1	0.07	840.7**
		2	0.07	842.6
	Juvenile	1	0.10	692.1**
		2	0.10	694
Ficus erecta	Adult	1	0.05	423.7
		2	0.11*	399.5**
	Juvenile	1	0.07	295.2
		2	0.13*	276.2**
Glochidion rubrum	Adult	1	0.09	723.3
		2	0.13*	698.5**
	Juvenile	1	0.10	553.2
		2	0.12*	541.8**
Ficus septica	Adult	1	0.28	290.8
		2	0.30*	287.9**

	Juvenile	1	0.26	239.2**
		2	0.27*	240.3
Eurya loquaiana	Adult	1	0.01	1082
		2	0.06*	1035**
	Juvenile	1	0.01	840.9
		2	0.03*	824.2**
Fissistigma oldhamii	Adult	1	0.09	652.3
		2	0.17*	593.9**
	Juvenile	1	0.09	548.8
		2	0.17*	501.8**
Ilex ficoidea	Adult	1	0.00	567.3
		2	0.05*	541.3**
	Juvenile	1	0.01	421.9
		2	0.05*	407.6**
Eriobotrya deflexa	Adult	1	0.00	459.1
		2	0.07*	427.8**
	Juvenile	1	0.00	315.3
		2	0.14*	275.1**
Eurya glaberrima	Adult	1	0.20	396.4
		2	0.28*	359.5**
	Juvenile	1	0.17	293.8
		2	0.24*	271.9**
Litsea acuminata	Adult	1	0.00	1636
		2	0.21*	1288**
	Juvenile	1	0.00	1376
		2	0.15*	1174**
Lagerstroemia subcostata	Adult	1	0.19	1027
		2	0.25*	952.7**
	Juvenile	1	0.21	748.6
		2	0.23*	734.1**
Illicium anisatum	Adult	1	0.05	405.6
		2	0.13*	371.7**
	Juvenile	1	0.05	300.8
		2	0.11*	283.1**
Litsea hypophaea	Adult	1	0.07	605.4
		2	0.10*	589.9**
	Juvenile	1	0.08	496.7
		2	0.11*	478.3**
Itea parviflora	Adult	1	0.01	840
		2	0.12*	750.4**
	Juvenile	1	0.01	661.9
		2	0.07*	622.8**
Ilex formosana	Adult	1	0.00	443.7
		2	0.05*	426.7**

	Juvenile	1	0.00	322
		2	0.02*	318.3**
Illicium arborescens	Adult	1	0.00	381.2
		2	0.07*	357.9**
	Juvenile	1	0.01	326.6
		2	0.05*	315.6**
Litsea acutivena	Adult	1	0.02	527.5
		2	0.04*	515.4**
	Juvenile	1	0.02	417.1
		2	0.04*	409.9**
Litsea elongata	Adult	1	0.03	540
		2	0.12*	490.6**
	Juvenile	1	0.03	398.8
		2	0.15*	350.3**
Michelia compressa	Adult	1	0.01	989.5
		2	0.05*	957.9**
	Juvenile	1	0.02	645.7
		2	0.04*	633.6**
Machilus thunbergii	Adult	1	0.02	1551
		2	0.10*	1427**
	Juvenile	1	0.01	1261
		2	0.06*	1191**
Mallotus japonicus	Adult	1	0.12	429.4**
		2	0.12	431.4
	Juvenile	1	0.14	335.6**
		2	0.14	337
Machilus zuihoensis	Adult	1	0.02	1311
		2	0.10*	1200**
	Juvenile	1	0.01	1022
		2	0.08*	956.5**
Neolitsea aciculata	Adult	1	0.01	546.4
		2	0.12*	486.6**
	Juvenile	1	0.00	382.3
		2	0.07*	357.2**
Neolitsea acuminatissima	Adult	1	0.11	701.3
		2	0.22*	618.9**
	Juvenile	1	0.10	545.2
		2	0.18*	500.7**
Machilus japonica	Adult	1	0.04	1588
		2	0.08*	1528**
	Juvenile	1	0.01	1301
		2	0.03*	1275**
Mallotus paniculatus	Adult	1	0.22	886.7
		2	0.27*	831.6**

	Juvenile	1	0.17	599.3
		2	0.20*	574.9**
Mallotus philippensis	Adult	1	0.17	420.3
		2	0.17	419.6**
	Juvenile	1	0.19	285.9
		2	0.21*	281.7**
Pasania harlandii	Adult	1	0.01	558.9
		2	0.09*	515.6**
	Juvenile	1	0.01	400.6
		2	0.05*	384.6**
Oreocnide pedunculata	Adult	1	0.04	996.4
		2	0.10*	940.1**
	Juvenile	1	0.07	819.5
		2	0.10*	793**
Polyspora axillaris	Adult	1	0.00	649.2
		2	0.02*	639.1**
	Juvenile	1	0.00	485.5
		2	0.01*	483.6**
Pasania kawakamii	Adult	1	0.00	937.4
		2	0.08*	862.1**
	Juvenile	1	0.00	749.6
		2	0.08*	693.6**
Neolitsea konishii	Adult	1	0.04	655.1
		2	0.09*	624.3**
	Juvenile	1	0.05	508.9
		2	0.11*	477.8**
Phoebe formosana	Adult	1	0.04	512
		2	0.13*	465.6**
	Juvenile	1	0.03	378.2
		2	0.09*	355.2**
Pasania hancei	Adult	1	0.00	780.8
		2	0.03*	762.6**
	Juvenile	1	0.00	632.9
		2	0.02*	622**
Pinus taiwanensis	Adult	1	0.16	851.1
		2	0.18*	830.9**
	Juvenile	1	0.19	556.4
		2	0.20*	548.2**
Pinus armandii/morrisonicola	Adult	1	0.17	524.8
		2	0.19*	513.1**
	Juvenile	1	0.21	310.4
		2	0.23*	303.6**
Prunus campanulata	Adult	1	0.00	409.6
		2	0.04*	398.6**

	Juvenile	1	0.00	299.9
		2	0.02*	295.4**
Schima superba	Adult	1	0.00	661.7
		2	0.04*	635.5**
	Juvenile	1	0.00	498.3
		2	0.02*	493**
Rhododendron leptosanthum	Adult	1	0.04	785.3
		2	0.12*	721.8**
	Juvenile	1	0.03	655.3
		2	0.07*	628.3**
Rhododendron formosanum	Adult	1	0.06	451
		2	0.11*	428.5**
	Juvenile	1	0.05	376.4
		2	0.09*	363.1**
Schefflera octophylla	Adult	1	0.19	1201
		2	0.25*	1111**
	Juvenile	1	0.14	981.8
		2	0.18*	937.8**
Prunus phaeosticta	Adult	1	0.00	1041
		2	0.11*	927.1**
	Juvenile	1	0.00	734.5
		2	0.13*	643.3**
Sloanea formosana	Adult	1	0.04	551
		2	0.09*	523**
	Juvenile	1	0.06	368.4
		2	0.07*	363.3**
Sapindus mukorossi	Adult	1	0.21	450.9
		2	0.23*	441**
	Juvenile	1	0.17	300.6
		2	0.18*	298.5**
Sinoadina racemosa	Adult	1	0.12	350.3
		2	0.14*	345.1**
	Juvenile	1	0.13	283.1
		2	0.14*	279.3**
Tsuga chinensis	Adult	1	0.37	675.7
		2	0.41*	634.9**
	Juvenile	1	0.36	446.8
		2	0.43*	399.9**
Trochodendron aralioides	Adult	1	0.08	715.5
		2	0.16*	651.8**
	Juvenile	1	0.03	384.9
		2	0.08*	365.6**
Symplocos morrisonicola	Adult	1	0.07	431.3
		2	0.17*	388.4**

	Juvenile	1	0.07	299.9
		2	0.11*	289**
Tetradium glabrifolium	Adult	1	0.01	635.3
		2	0.07*	598.1**
	Juvenile	1	0.03	307.4
		2	0.05*	301.5**
Turpinia formosana	Adult	1	0.06	1030
		2	0.13*	959.8**
	Juvenile	1	0.05	859
		2	0.11*	801.1**
Styrax suberifolia	Adult	1	0.14	497.3
		2	0.16*	485.9**
	Juvenile	1	0.12	388.2
		2	0.13*	382.3**
Styrax formosana	Adult	1	0.01	479.1
		2	0.06*	458.6**
	Juvenile	1	0.02	348.1
		2	0.04*	342.7**
Trema orientalis	Adult	1	0.15	484.8
		2	0.21*	453**
	Juvenile	1	0.12	290.3
		2	0.16*	282.1**
Tricalysia dubia	Adult	1	0.02	532.8
		2	0.11*	485.1**
	Juvenile	1	0.03	377.6
		2	0.09*	357.7**
Wendlandia formosana	Adult	1	0.17	392.2
		2	0.23*	366.2**
	Juvenile	1	0.17	299.5
		2	0.25*	275.2**
Turpinia ternata	Adult	1	0.09	691.9
		2	0.13*	662.9**
	Juvenile	1	0.11	504
		2	0.15*	486.1**
Zelkova serrata	Adult	1	0.03	612.2
		2	0.10*	573.5**
	Juvenile	1	0.04	389.3
		2	0.06*	383.8**

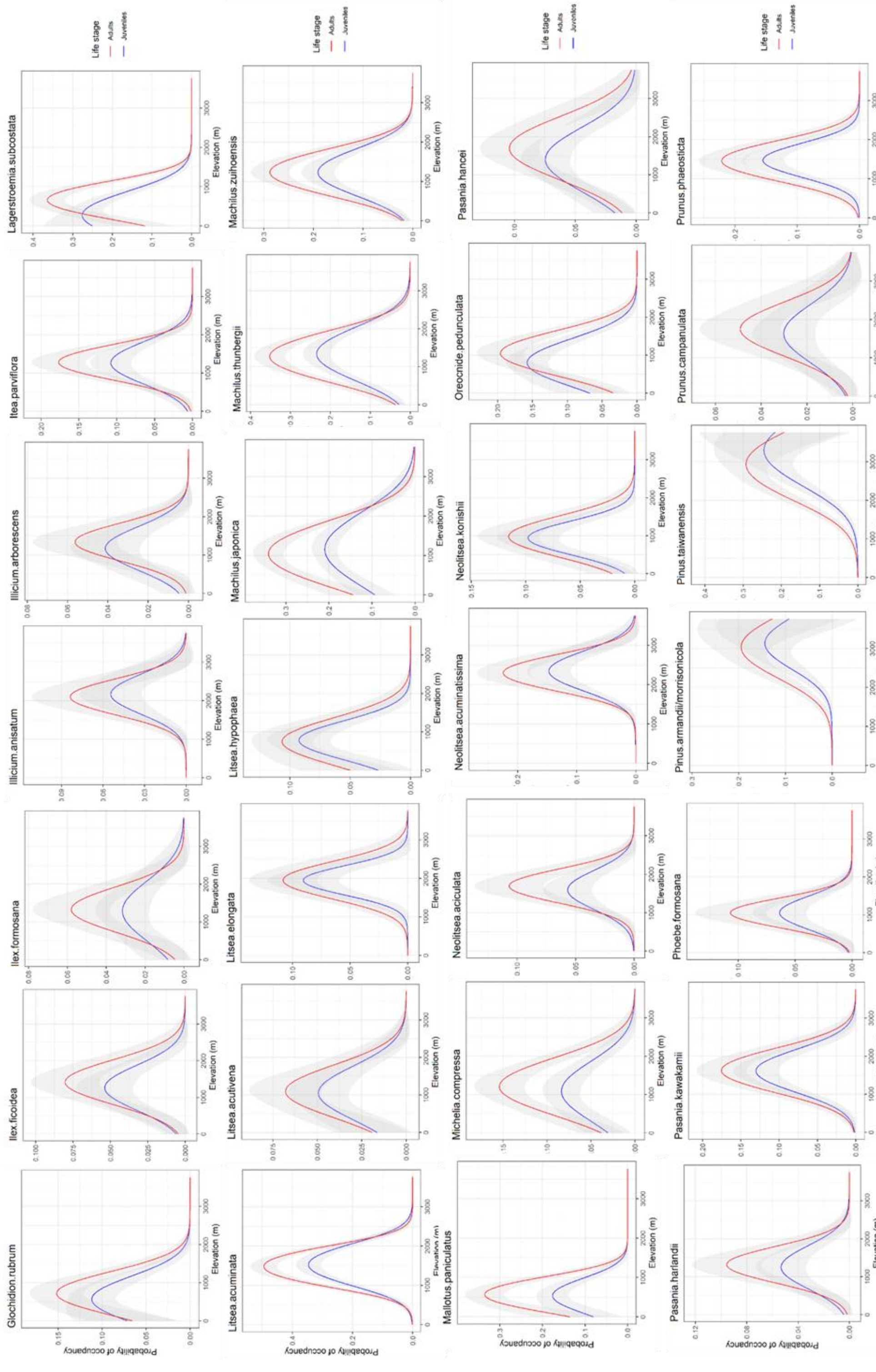

Fig.2.S1a: Probability of occupancy of 75 subtropical montane tree species over an elevation gradient in Taiwan. Red lines refer to the adult life stage and blue lines refer to the juvenile life stage. Grey shaded areas represent confidence intervals of estimates (1.96 standard deviations of the mean).

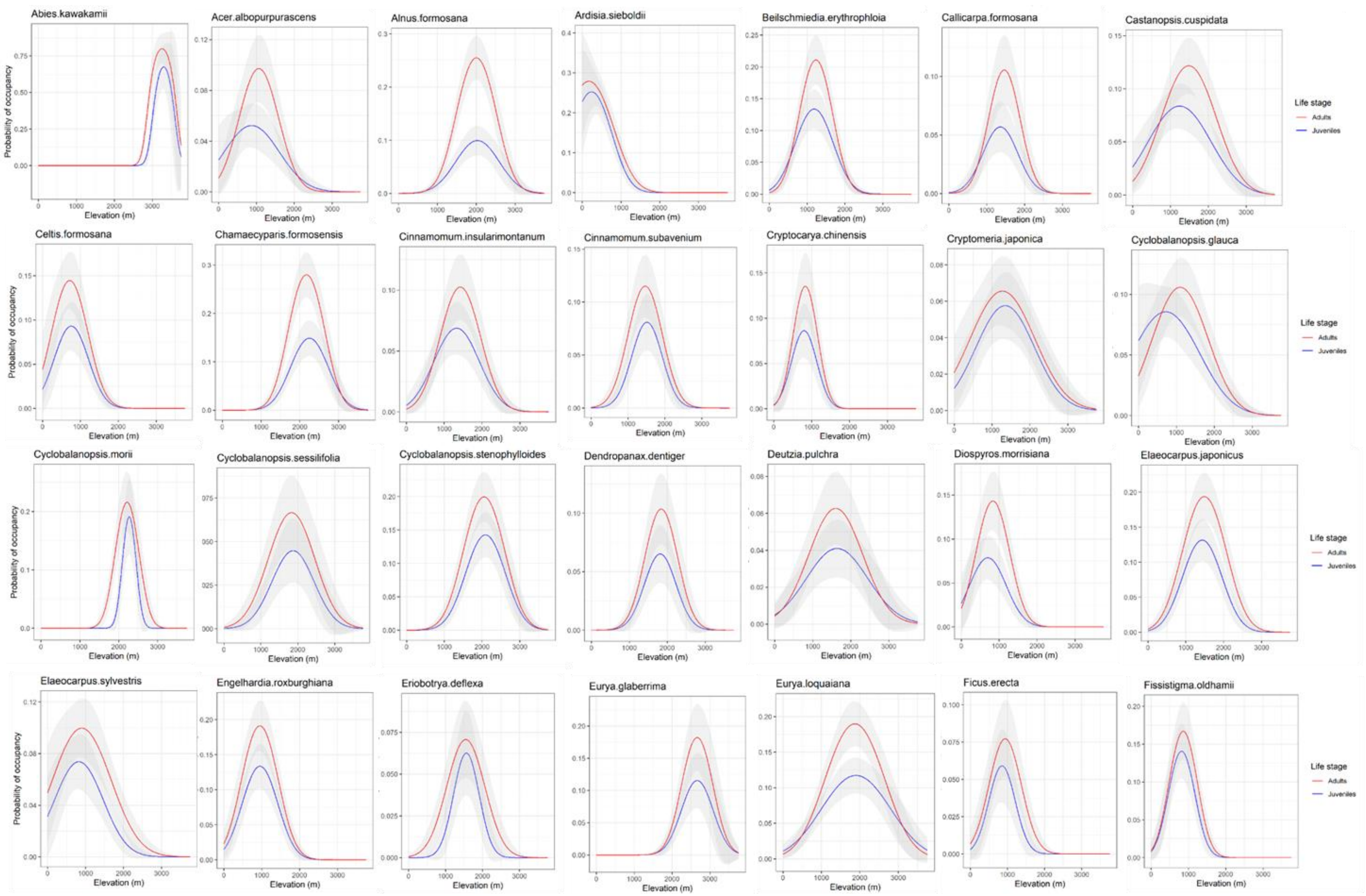

Fig.2.S1b: Probability of occupancy of 75 subtropical montane tree species over an elevation gradient in Taiwan. Red lines refer to the adult life stage and blue lines refer to the juvenile life stage. Grey shaded areas represent confidence intervals of estimates (1.96 standard deviations of the mean).

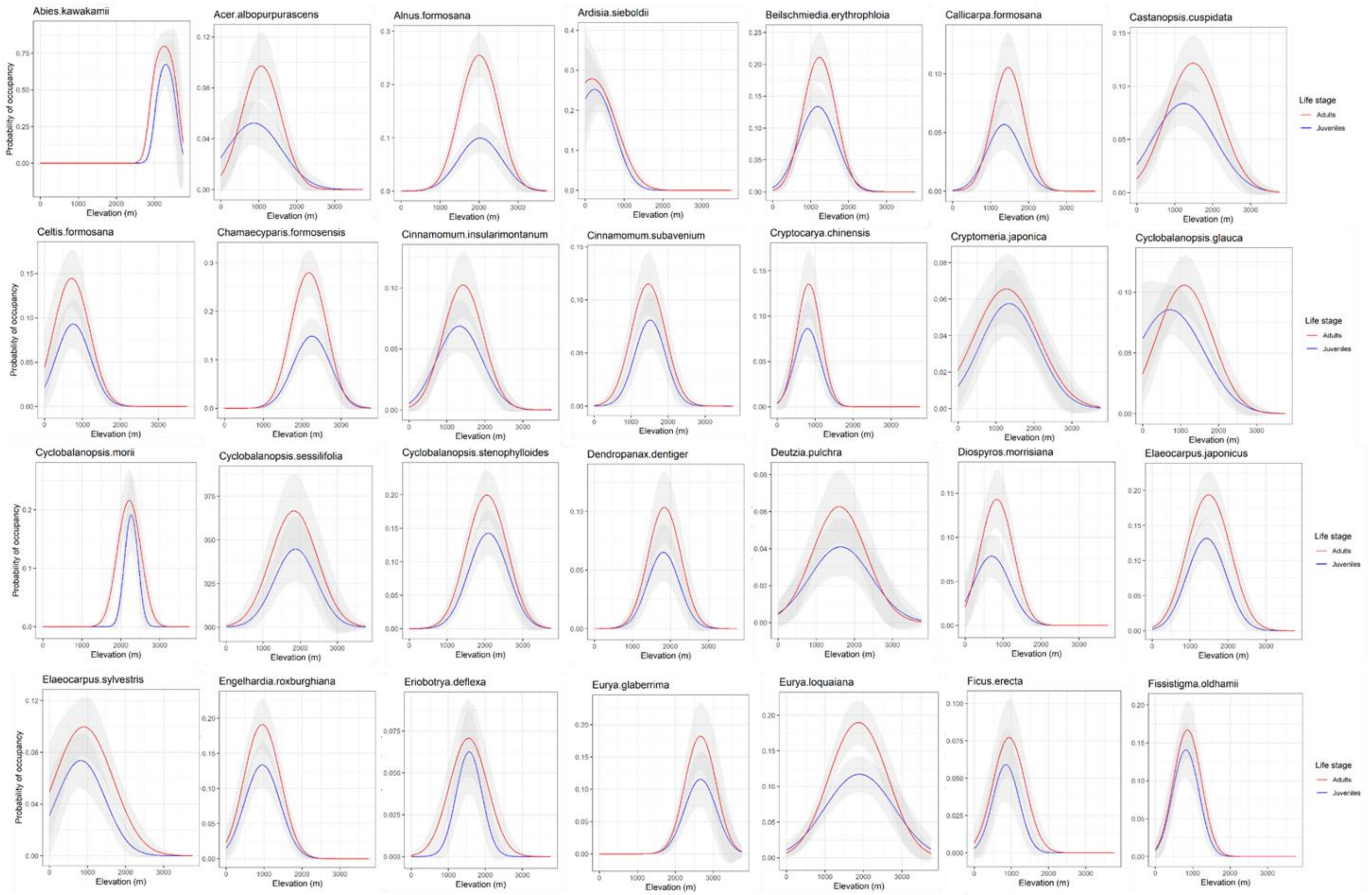

Fig.2.S1b: Probability of occupancy of 75 subtropical montane tree species over an elevation gradient in Taiwan. Red lines refer to the adult life stage and blue lines refer to the juvenile life stage. Grey shaded areas represent confidence intervals of estimates (1.96 standard deviations of the mean).

Chapter 3

Climatic drivers of variation in functional composition across diverse montane forests in Taiwan

3.1 Abstract

Since the geographical distributions of plant species are strongly influenced by climate, ongoing climate change has the potential to influence species distributions from local to global scales, bringing potential consequences for biodiversity and ecosystem function. Plant functional traits have often been used to characterise differences and predict changes in vegetation in response to environmental change, as they are expected to reflect plant-environment relationships. However, despite a strong theoretical link between functional traits and species distribution shifts, evidence of this relationship is limited. Improved understanding of climatic determinants of trait distributions are needed to assess the implications of climate change on ecosystems. Here, we aimed to address the question of whether individual traits can be used to predict species distribution shift size or direction and identify the extent to which plot-level functional composition is liked to environmental variables of temperature and precipitation across the Central Mountain Range of Taiwan. We linked estimated tree species distribution shift size and direction to species mean trait values derived from the TRY plant trait database for a range of functional traits associated with different plant strategies. Plot community weighted mean (CWM) values were then calculated and compared to temperature and precipitation. Although individual functional traits were poor predictors of distribution shift size and direction at the species level, relationships between temperature and precipitation and function were strong at the community-level. Although the variability observed in our findings highlights the challenges involved in using traits as predictors of species distribution shifts, the close relationships between environment and CWM values offers hope that traits may be useful in linking plant responses to environmental change at the community-level. Ultimately, traits may hold important insight into ecological processes and how they are changing over space and time, enabling better predictions to be made of the impacts of climate change on plant communities.

3.2 Introduction

The geographical distributions of plants are strongly controlled by climate (Woodward and Williams 1987, Pearson and Dawson 2003). Therefore, rapid and ongoing climate change has the potential to substantially affect plant species distributions and community composition over coming decades (Parmesan and Yohe 2003). As temperatures rise, species are frequently declining in abundance at the warm edge of their distribution range, where they exist at their drought tolerance limits, and shifting upward and poleward at their cool range edge to track changing environmental conditions (Gosz 1992, Grabherr et al. 1994, Parmesan and Yohe 2003, Harsch et al. 2009, Feeley et al. 2011, Ruiz-Labourdette et al. 2012, Morueta-Holme et al. 2015, Fadrique et al. 2018, Vilà-Cabrera et al. 2019). However, many factors can influence the abundance and distribution of species and interact with climate to drive complex distribution shifts. Species distributions can be strongly limited by factors such as competition, habitat modifications and dispersal barriers (Lenoir et al. 2010, Wiens 2011). Individual tree responses to climate change can vary over space and time and be driven by multiple interacting drivers (Kling et al. 2020), resulting in non-uniform distribution shifts (Buckley and Kingsolver 2012, O’Sullivan et al. 2021, Auld et al. 2022). Variations in conditions at the local-scale could cause differences in distribution shifts within a single species (O’Sullivan et al. 2021). Changes in abundance can occur within species ranges as well as changes to the overall distribution of species, affecting community composition (Williams and Jackson 2007, Lenoir et al. 2008, Estrada et al. 2016, Pecl et al. 2017, Chain-Guadarrama et al. 2018). Such changes in species distributions and plant community compositions could cause local extinctions (Wiens 2016) and substantially alter overall ecosystem function and ecological processes (Williams and Jackson 2007). However, our current understanding of the best ways to predict which species are likely to show climate induced distribution shifts is limited, resulting in poor capacity to plan for conservation and management (Angert et al. 2011).

Plant functional traits, defined as the morphological, physiological and phenological differences between plants, have been widely proposed as a tool for forecasting responses of vegetation to environmental change (Lavorel and Garnier 2002, Violle et al. 2007, Pacifici et al. 2015, Estrada et al. 2016, Funk et al. 2017, MacLean and Beissinger 2017, Briscoe et al. 2019, Maréchaux et al. 2021). Functional traits are considered to reflect plant-environment relationships, with variations possible in traits associated with growth, survival, fecundity and dispersal (e.g. Lavorel and Garnier 2002, Cornelissen et al. 2003, Bresson et al. 2011, Guerin et al. 2012, Reich 2014, Violle et al. 2014, MacLean and Beissinger 2017, Ruiz-Benito et al. 2017, Bjorkman et al. 2018, Boonman et al. 2020). Traits enabling rapid dispersal, such as small seed size and high seed number, along with frequent reproduction and high fecundity may aid migrations to new areas (Angert et al. 2011, Alexander et al. 2018), whilst seed size and number and mode of reproduction could influence survival at new sites (Alexander et al. 2018). Leaf traits such as length, thickness and area can reflect responses to environmental conditions, as they are linked to variation in factors such as light, temperature, nutrients, water availability and herbivory (Fonseca et al. 2000, Hanley et al. 2007, Wright et al. 2017). Traits such as density of stomata on leaves, xylem hydraulic vulnerability and leaf photosynthesis are closely aligned to water economy, reflecting plant-water relations and thus potentially important drought tolerance mechanisms (McDowell et al. 2022). Plant resource-use strategy traits such as specific leaf area (SLA), leaf dry matter content (LDMC) and wood density can be used to infer a more holistic view of plant approaches, from slow growth and persistence to fast and productive (Wilson et al. 1999, Roche et al. 2004, Poorter and Bongers 2006, Guo et al. 2018b, Rosas et al. 2021). Functional traits hold the potential to provide vital insight on changes in plant species distributions and abundance (MacLean and Beissinger 2017), particularly for trees, as their long regeneration times may result in limited opportunities to adapt to changing conditions (Butt and Gallagher 2018).

Although the theoretical link between plant functional traits and species distribution shifts is strong, evidence of this relationship is limited (e.g. Angert et al 2011, Estrada et al. 2016, Beissinger and Riddell, 2021). A meta-analysis testing the ability of traits to predict species distribution shifts in response to climate change for different taxa found that most traits had no significant link to shifts, whilst even those which showed significant trends explained a small portion of the overall variation in species distribution shifts (MacLean and Beissinger 2017). The link between distribution shifts and functional traits is likely to be complex and driven by multiple interacting factors (Estrada et al. 2016, MacLean and Beissinger 2017), with the effectiveness of traits to predict changes potentially also varying between contexts, scales and time periods (Estrada et al. 2016, Beissinger and Riddell 2021, Fontana et al. 2021). It remains unclear to what extent individual traits can be used as an effective tool for predicting changes in highly heterogenous environments with complex interacting drivers (Funk et al. 2017) and which traits are most closely associated with distribution shifts (Estrada et al. 2016). Consequently, there is a need to assess the relationship between functional traits and species distribution shifts across different traits and contexts to inform how best traits can be used to improve predictions of responses of plants to environmental change.

Since the effects of individual functional traits on plant performance can vary between different environmental contexts, predicting how species may respond to climate change requires an understanding of how functional traits relate to the environment (McGill et al. 2006). It is likely that variability exists in the relationship between functional traits and environment across different ecosystems (Schellenberger Costa et al. 2017). Since environmental predictors are typically measured at the plot or site level and plant functional trait values are generally given at the species level (Miller et al. 2019), interactions between traits and environment may be more easily detectable if considered at the community scale. Typically, such approaches involve calculating trait community weighted means (CWM), potentially alongside trait diversity, to provide a measure of variability around mean values (Lepš et al. 2006). Associations between functional trait composition and environment may foreshadow changes in ecosystem function over coming decades, potentially altering processes such as the ability of trees to fix and store carbon (Vanderwel et al. 2013, Yuan et al. 2018). Even subtle differences in the values of key functional traits could have considerable impacts for overall function (Ruiz-Benito et al. 2017b), but our current understanding of how functional trait composition is changing is generally very limited (Vilà-Cabrera et al. 2015, Zhang et al. 2018). Without clarity on the link between traits and environment, it becomes difficult to reliably use plant traits to understand and predict distribution shifts across different systems and foreshadow changes in function over coming decades.

Given the need to better understand the relationship between plant functional traits and plant-environment relationships, including responses of vegetation to ongoing climate change, we aimed to determine whether traits can be linked to observed distribution shifts and the extent to which key trait values correlate to environmental variables of temperature and precipitation. With trait based approaches gaining increasing interest as a way to tractably reduce biological complexity to address global change questions, a wide range of plant functional trait data are now being made publicly available in global plant trait databases such as TRY (Kattge et al. 2020). Such databases allow global trait-based investigations and comparisons across species and biomes and enable us to explore patterns and relationships between plant function and environment (Violle et al. 2014). Here, we focus on tree species across an elevation gradient of diverse subtropical mountain forests in Taiwan. We focussed on key traits which we expect may have an influence on distribution shifts and function-environment relationships; (1) the resource-use strategy traits of SLA, LDMC, wood density and relative plant growth rate, (2) the reproductive traits of seed spread rate, shape, area, dry mass, number per plant, germination rate, germination lag time and seedbank longevity, (3) the leaf physiology traits of area, length, fresh mass, dry mass and thickness, (4) root traits of length and belowground relative growth rate and (5) water economy traits of stomata density, conductance and surface area, leaf photosynthesis rate and xylem hydraulic vulnerability. These traits were chosen as they are related to the primary axes of functional trait variation, are available for many species (Westoby 1998, Mokany et al. 2015) and have the potential to be closely linked to environmental conditions. Our objectives were (1) to determine whether functional traits can effectively predict shift size or direction at the species level, and (2) identify whether variation in environmental variables of temperature and precipitation are associated with differences in trait composition at the plot level.

3.3 Methods

3.3.1 Study location

Taiwan is a mountainous subtropical island, lying south-east of mainland China in the South China Sea. Conditions in the lowlands are warm and humid, consistent with the island's position on the Tropic of Cancer. Mountains make up 74% of the island (Lu et al. 2001), with conditions transitioning to a cooler temperate, then alpine environment, with increasing elevation above sea level (Li et al., 2013). Widespread deforestation for urban and agricultural developments has occurred at low elevations, but natural forests are abundant from around 500 m a.s.l. Evergreen broadleaved forests dominate at low elevations, which then transition into areas of mixed forest, deciduous broadleaved and evergreen broadleaved forest with increasing elevation (Li et al., 2013). Coniferous forest dominates at high elevations, stretching to the treeline at around 3000 m a.s.l. (Li et al., 2013).

3.3.2 Data

Data were obtained from the 4th Taiwan National Forest Inventory (NFI), the TRY plant trait database (Kattge et al. 2011) and CHELSA BIOCLIM (Karger et al. 2017b, a). The NFI is a systematic plot-based survey of the forests in Taiwan undertaken between the August 2008 and January 2013, comprising species information, tree measurements and environmental data for 86,306 trees and 516 species over 1,564 plots. NFI plots covered an elevation range from 0 to 3769 m a.s.l. and were approximately 0.05 ha, with one plot side of 17.6 m perpendicular to slope and the other side parallel with a variable size to maintain the projected plot area. Within each plot, all trees > 5 cm diameter at breast height (dbh) measured at 1.3 m were recorded. The elevation of each plot was recorded using a GPS.

For species with > 10 observations in the NFI (342 species), trait data were requested from the TRY global plant trait database. The following traits were selected; SLA, LDMC, wood density, relative plant growth rate, seed spread rate, seed shape, seed area, seed dry mass, seed number per plant, seed germination rate, seed germination lag time, seedbank longevity, leaf area, leaf length, leaf fresh mass, leaf dry mass, leaf thickness, root length, belowground relative growth rate, stomata density, stomatal conductance, stomata surface area, leaf photosynthesis rate and xylem hydraulic vulnerability. Needle leaf trait data from *Pinus taiwanensis* trees in Taiwan were also added to the dataset (O’Sullivan et al. 2022). Raster layers were downloaded from CHELSA BIOCLIM of mean annual air temperature averaged over 1 year (^oC) and annual precipitation amount accumulated over 1 year (kg m^{-2}, which is equivalent to mm since 1 mm of rain over 1 m^2 = 1 litre of water, and 1 litre water = 1 kg). These rasters were then cropped to Taiwan’s geographical extent and extracted for the central point of each NFI plot.

3.3.3 Analyses

To assess the frequency of trait data availability in TRY, we calculated how many species had ≥ 1 measurement per trait. We also investigated how many species had ≥ 20 measurements per trait, as 20 records provides a greater representation across individuals for mean value calculations and has been reported as the minimum acceptable threshold to capture intraspecific trait variation (Kattge et al. 2011, 2020). To minimise statistical issues encountered when dealing with small sample sizes, we only considered traits which had at least one record from ≥ 30 species for further analysis. This included SLA, LDMC, wood density, log seed dry mass, leaf area, leaf length, stomata conductance and leaf photosynthesis. Three outliers > 99.85% of SLA values were removed due to values being unexpectedly and unrealistically large compared to other values for the species.

A demographic approach was used to estimate forest tree species distribution shifts at the species level. Using the NFI, we identified the mismatch in distributions between adult and juvenile trees of the same species, as a proxy for change, where juveniles reflect more recent environmental conditions and adults reflect historic conditions (Lenoir et al. 2009, Rabasa et al. 2013). Using the diameter at breast height (dbh) as a measure of size, adults were defined as > 0.5 percentile of dbh values for that species and juveniles as < 0.25 percentile of the dbh values (O’Sullivan et al. 2021). We included all species which had juveniles present in ≥ 10 plots. We considered the median elevation for the species distribution as an approximation of the optimum elevation for growth of that species, based on the assumption that most species show a curved shaped distribution as they are most abundant at the centre of their range (Holt et al. 1997). We calculated the median elevation of conspecific adults and juveniles, compared the median position for adults and juveniles for each species and calculated the shift size (m) and direction (upwards, downwards, no shift). No shift was defined as species which had 0m difference between their adult and juvenile life stage. Due to small sample sizes, species which did not shift their distribution were removed from analyses.

For each species, mean values for each functional trait were calculated. Species with ≥ 1 observation for a given trait were included in analyses. Species which showed 0 m difference in their optimum position between adult and juvenile life-stages were excluded from analyses due to small sample sizes. Only traits with ≥ 20 species were included for further investigation to avoid running analyses with small sample sizes, resulting in leaf thickness, leaf photosynthesis and stomata conductance being excluded from analyses at this stage. For the remaining traits, linear models with normal distribution of residuals were used to assess the influence of trait values on shift size and logistic regression used to assess the influence of trait values on shift direction. Our results obtained here were compared to an alternative approach of calculating the optimum position of species ranges using linear models with a quadratic term (*Fig.3.S1, Table 3.S1*, O'Sullivan et al. 2021), with similar patterns detected, but sample sizes too small for this approach to produce model results which could be reliably used.

Plot functional composition was assessed for log seed dry mass, wood density, leaf area, leaf length, SLA and LDMC. Tree basal area (m^2) was calculated for each tree in the NFI and summed to the plot level (Kershaw et al. 2017). For each trait, plots were filtered so that only plots with ≥ 70% of basal area with trees with trait data were included. To assess the relationship between traits and environmental variables at an ecosystem scale, community weighted means (CWM) were used, as they combine multiple species trait values to account for the variation in function at the community-level, enabling comparisons with environmental data gathered at the ecosystem scale (Miller et al. 2019). CWM were calculated for each plot by determining the mean functional trait values of all tree species in a plot, weighted by the abundance of each species (Lavorel et al. 2008, Miller et al. 2019) using the equation:

$$\frac{\Sigma\ (species\ mean\ trait\ value\ x\ species\ N\ per\ plot)}{total\ N\ per\ plot}$$

Functional dispersion (FD), which is the weighted mean distance of individual species to the centre value of all species in the plot (Pakeman 2014), was also assessed and calculated using the 'FD' package (Laliberte and Legendre 2010, Laliberté et al. 2014) (*Fig.3.S2, Fig.3.S3* and Table 3.S2). Linear models were used to assess the influence of plot temperature and precipitation on CWM and FD to assess the trait dominance and function between plots and the variability in trait values at the plot-level to link this to environmental variation. Global models including temperature, precipitation and their interaction were run and models compared using the 'MuMIn' package (Barton 2020). The most parsimonious models were chosen within two Akaike information criterion (AIC) units of the lowest AIC model and fitted via maximum likelihood (ML). Model residuals were checked to ensure they met test assumptions. All analyses were done in R (R Core Team 2021).

3.4 Results

3.4.1 Functional trait data availability

Of the 342 NFI species investigated, 211 (62%) had ≥ 1 record in the TRY database for SLA, wood density, leaf area, leaf thickness, seed dry mass, LDMC, leaf length, leaf photosynthesis rate per leaf area, stomata conductance, xylem hydraulic vulnerability, stomata density, seed germination rate, plant relative growth rate or seedbank longevity. No records were available for the remaining traits requested from the TRY plant trait database. Data availability differed considerably between traits, ranging from 2 species with ≥ 1 record for plant growth rate and seedbank longevity to 123 species with ≥ 1 SLA record (*Fig.3.1*). The mean number of species with ≥ 1 record for a given trait was 47. Considering the threshold of ≥ 20 measurements per species for more insightful mean estimates and intraspecific analyses (Kattge et al. 2011, 2020), the number of species with sufficient data availability was substantially reduced, ranging from 0 species with ≥ 20 records for plant growth rate, seedbank longevity, seed germination rate, xylem hydraulic vulnerability and stomata density to 10 species with ≥ 20 SLA records.

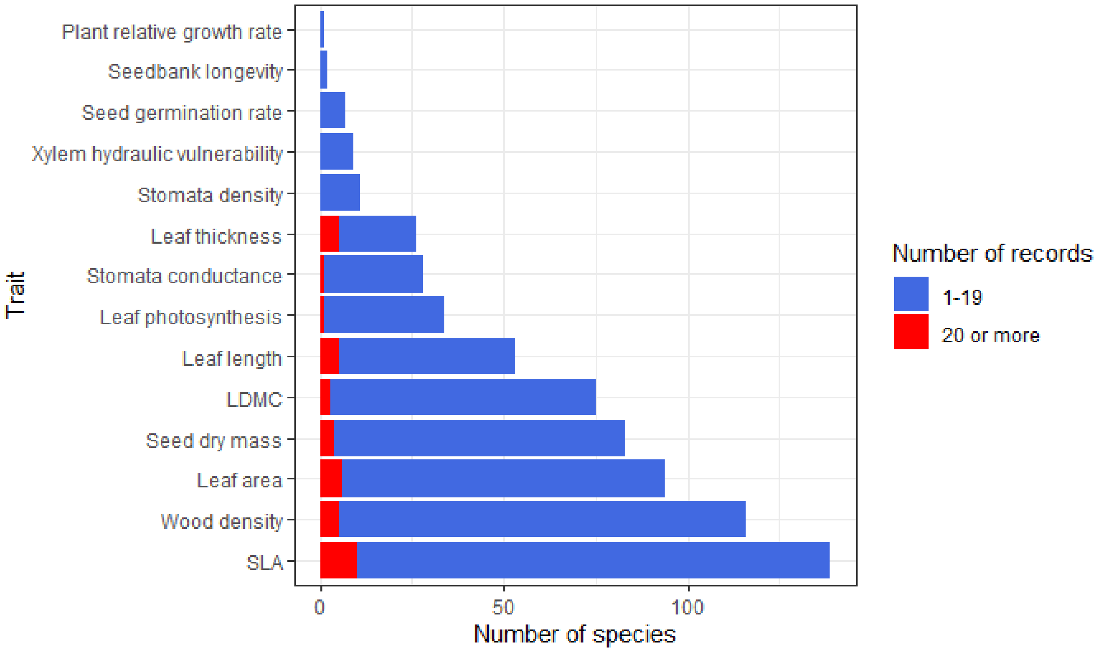

Fig.3.1: The number of species with ≥ 10 observations in the 4th Taiwan National Forest Inventory (NFI) and with 1-19 records in the TRY plant trait database (blue) and ≥ 20 records in TRY (red) for each trait investigated.

3.4.2 Variation in trait values with shift size and direction

There was substantial variation in trait values among all traits investigated, with coefficients of variation ranging from 14-135% (*Fig.3.2,* Table 3.1). Leaf area was particularly variable between species, with the highest value for the large leaved species *Macaranga tanarius* 1757 times larger than the smallest value. LDMC was the least variable trait, with the largest value two times higher than the smallest value. There were no significant relationships between traits and shift size or direction for any of the traits investigated. For shift size, R^2 values ranged from 0.01% to 3.21% and for shift direction R^2_{McFadden} values ranged from 0.01% to 4.56%.

Table 3.1: Linear and logistic regression model results of functional trait values from the TRY plant trait database for species in the 4th National Forest Inventory for Taiwan (NFI), considering the influence of trait values on species distribution shift size and direction at the species range optimum. Coefficient of variation (CV) also provided. SLA = specific leaf area. LDMC = leaf dry matter content.

Trait	**Model**	**R^2 or R^2_{McFadden}**	**Model output**	**Estimate**	**CV**	**Units**
Log seed dry mass	Shift size ~	0.0005 (0.05%)	F=0.017, df=1, 36, p= 0.898	142.76	0.58	g
	Shift direction ~	0.0069 (0.69%)	z= -0.596, df=37, p= 0.551	-0.53		
Wood density	Shift size ~	0.0046 (0.46%)	F=0.2146, df=1, 47, p=0.645	90.94	0.25	g cm^{-3}
	Shift direction ~	0.0049 (0.49%)	z=-0.534, df=48, p=0.593	-1.54		
Leaf area	Shift size ~	0.0001 (0.01%)	F=0.005, df=1, 43, p= 0.946	135.20	1.35	mm^2
	Shift direction ~	0.0061 (0.61%)	z=-0.563, df=44, p=0.574	-0.26		
Leaf length	Shift size ~	0.0236 (2.36%)	F=0.5314, 1, 22, p=0.474	145.93	0.63	mm
	Shift direction ~	0.0456 (4.56%)	z=-1.049, df=23, p=0.294	0.44		
SLA	Shift size ~	0.0026 (0.26%)	F=0.156, df=1, 60, p=0.694	136.53	0.33	mm^2 mg^{-1}
	Shift direction ~	0.0014 (0.14%)	z= -0.331, df=61, p=0.741	-0.28		
LDMC	Shift size ~	0.0321 (3.21%)	F=1.029, df=1, 31, p=0.3182	288.49	0.13	mg g^{-1}
	Shift direction ~	0.0001 (0.01%)	z=-0.046, df=32, p=0.963	-0.69		

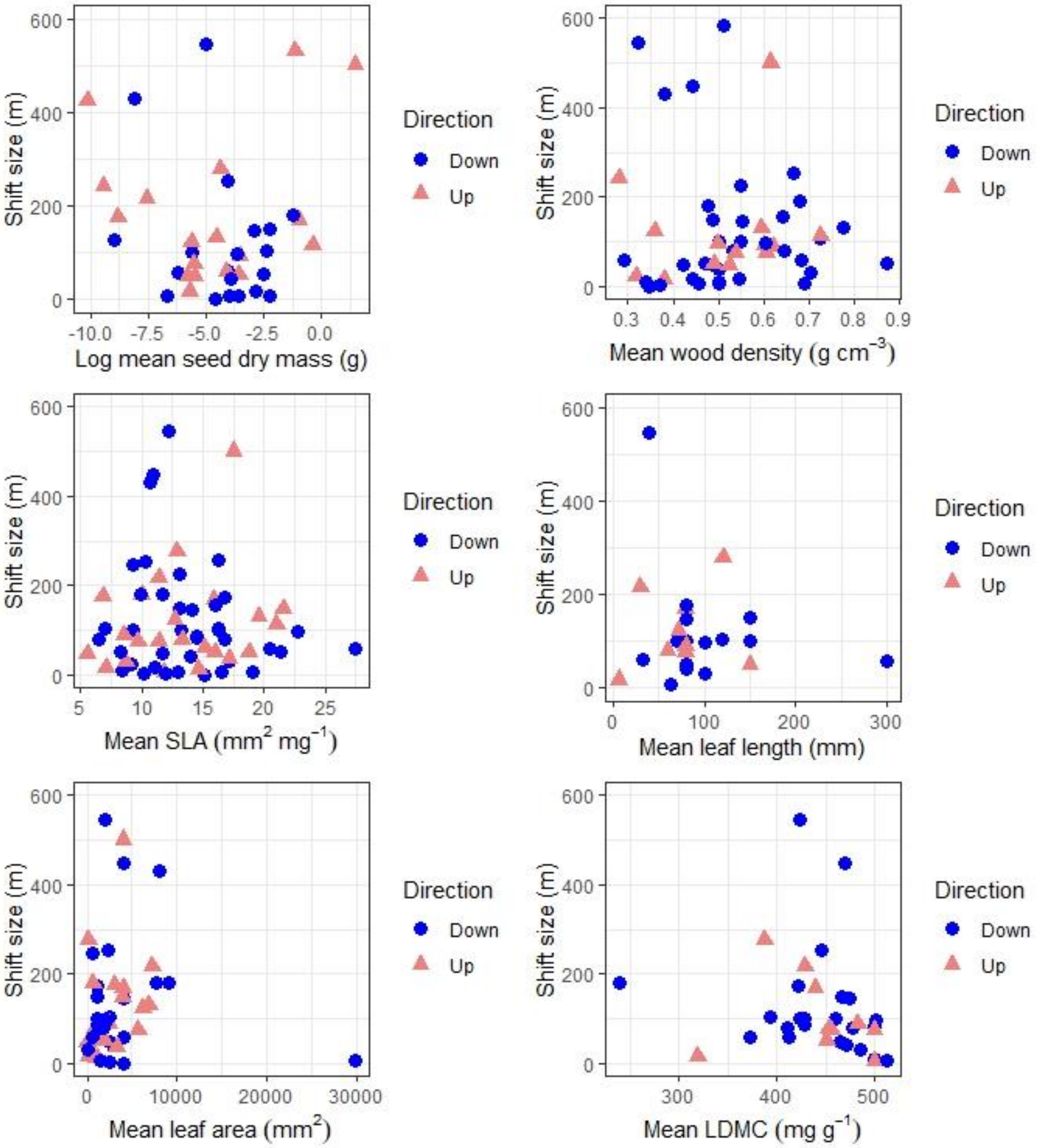

Fig.3.2: Mean species trait values taken from the TRY plant trait database in relation to elevational distribution shift size (m a.s.l.) and direction (down = to lower elevation or up = to higher elevation) for tree species in the 4th Taiwan National Forest Inventory (NFI). SLA = specific leaf area. LDMC = leaf dry matter content.

3.4.3 Functional composition variation in relation to environmental variables

There was substantial variation in plot CWM values among all traits investigated. Temperature had a substantial influence on trait CWM values and was included in the best fit model for all traits (*Fig.3.3, Fig.3.4,* Table 3.2). Temperature alone was the best indicator of CWM values for log seed dry mass and wood density. Precipitation and temperature explained leaf area, leaf length and SLA CWM values, whilst adding the interaction between these two variables resulted in a better fit model for LDMC CWM. Seed dry mass, SLA, leaf length and leaf area generally increased with increasing temperature, whilst wood density, leaf thickness and LDMC decreased. CWM significantly varied with precipitation for SLA, leaf area and LDMC, with SLA and leaf area generally declining with increasing precipitation, whilst LDMC increased (*Fig.3.5, Fig.3.6*, Table 3.2). Plot-level FD values also varied among traits, with patterns also linked to temperature and precipitation (*Fig.S2, Fig.S3,* Table S2).

Table 3.2: Linear model results of plot-level community weighted mean (CWM) functional trait values from the TRY plant trait database for species in the 4th National Forest Inventory for Taiwan (NFI) with environmental variables of temperature, precipitation and their interaction from CHELSA BIOCLIM layers. The simplest model within two AIC units from the best fit model were selected. Coefficient of variation (CV) also provided. SLA = specific leaf area. LDMC = leaf dry matter content.

Trait	**Selected model**	**R^2**	**Model output**	**Estimates**	**CV**	**Units**
Log seed dry mass	~temperature	0.031	F=5.533, df=1, 173, p=0.020	-6.283	0.46	g
Wood density	~temperature	0.016	F=3.067, df=1, 194, p=0.082	0.566	0.19	g cm^{-3}
SLA	~ temperature + precipitation	0.187	F=28.25, df=2, 246, p=<0.001	10.000, 9.641	0.28	mm^2 mg^{-1}
Leaf length	~temperature + precipitation	0.188	F=12.94, df=2, 112, p<0.001	38.492, 31.543	0.57	mm
Leaf area	~temperature + precipitation	0.143	F=16.46,, df=2, 198, p<0.001	49.494, 309.440	0.89	mm^2
LDMC	~temperature + precipitation + temperature * precipitation	0.061	F=3.012, df=3, 139, p=0.032	207.112, 195.529, 195.423	0.10	mg g^{-1}

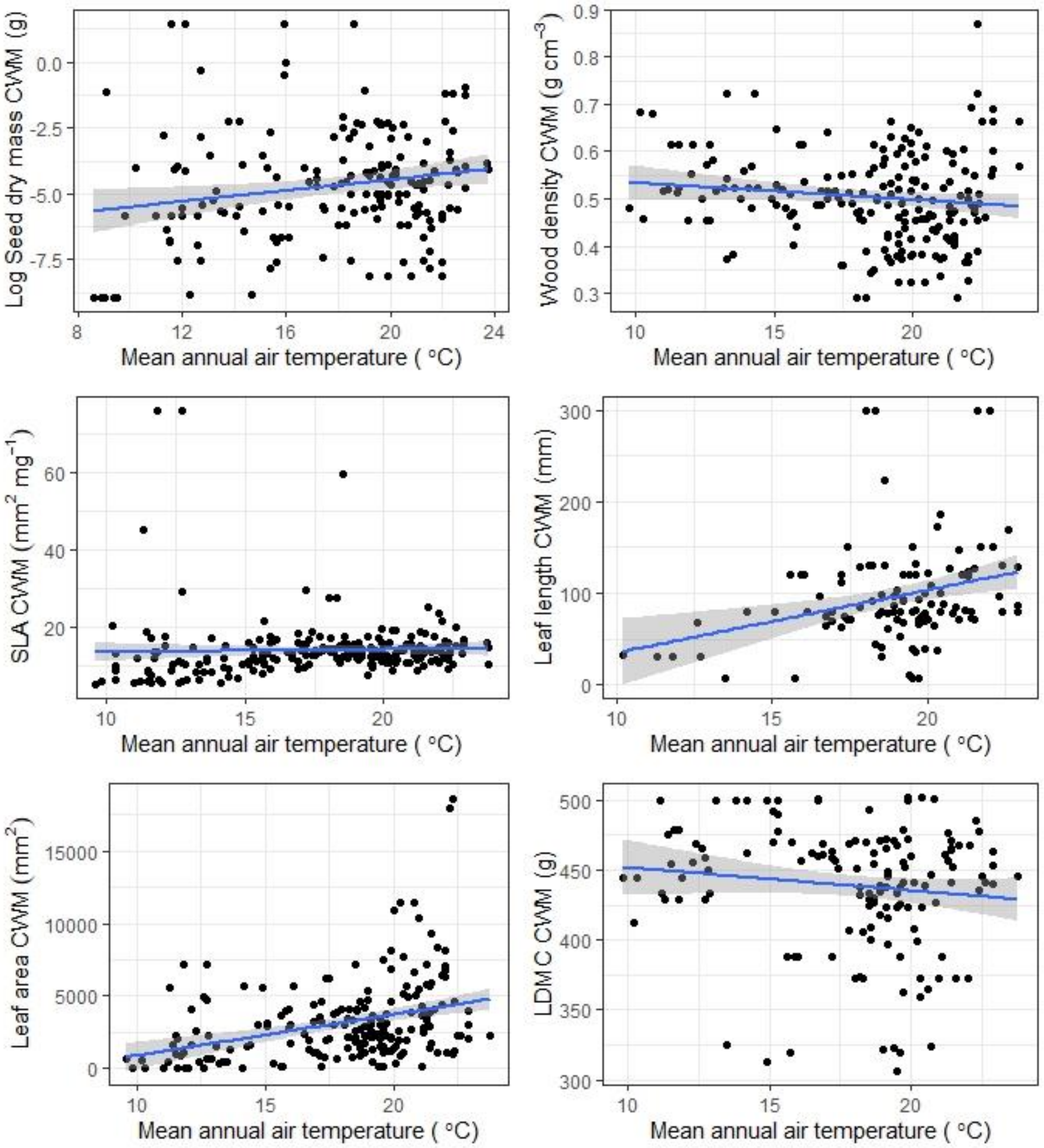

Fig.3.3: Mean annual air temperature at plot centre (^{o}C) and plot community weighted mean (CWM) functional trait values for plots in the 4th Taiwan National Forest Inventory for trees with traits in the TRY plant trait database. SLA = specific leaf area. LDMC = leaf dry matter

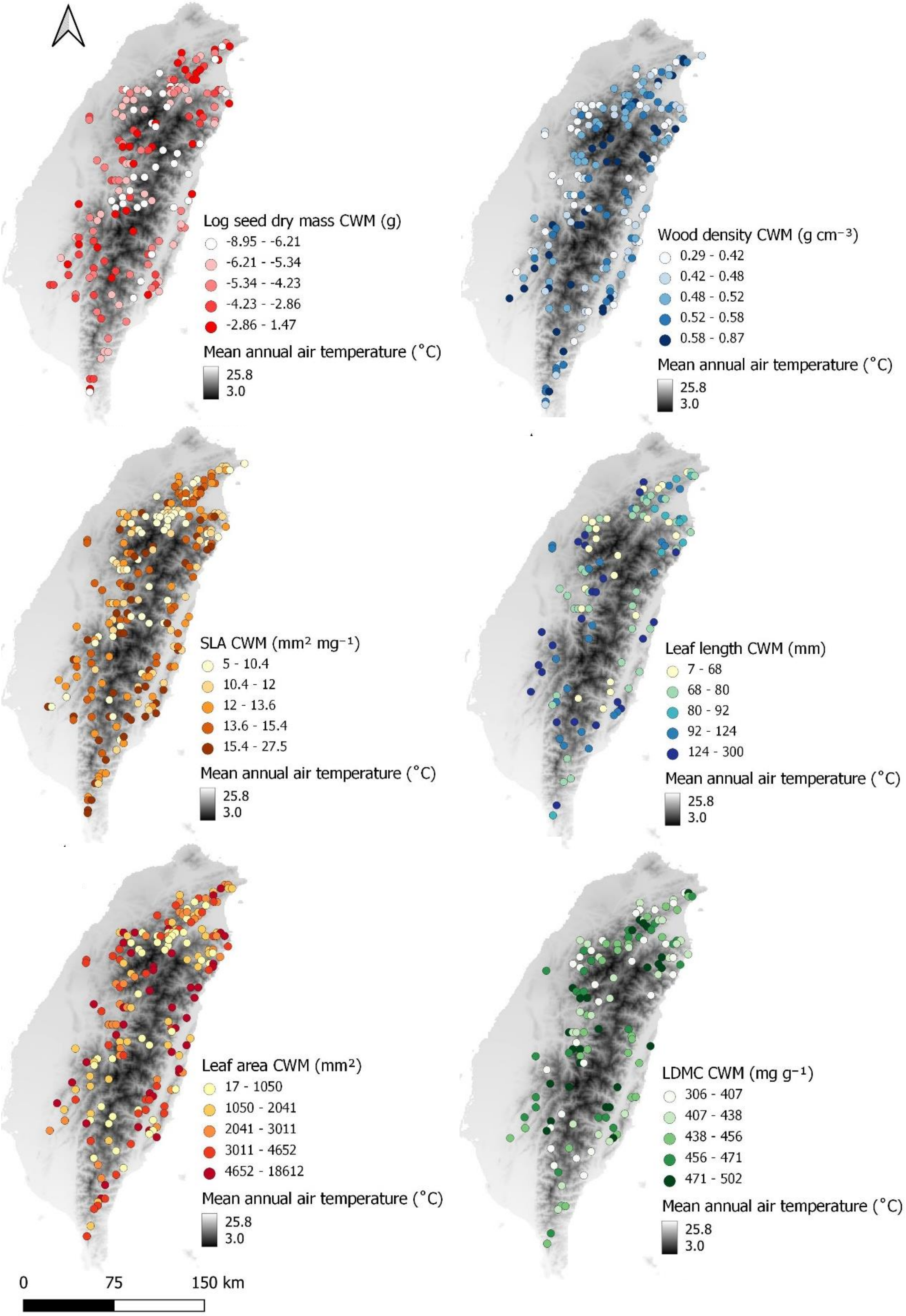

Fig.3.4: Spatial distribution of tree species community weighted means (CWM) of plots in the 4th Taiwan National Forest Inventory (NFI) for traits in the TRY plant trait database plotted against mean annual air temperature (^{o}C) from CHELSA (Karger et al. 2017b, a). SLA = specific leaf area. LDMC = leaf dry matter content.

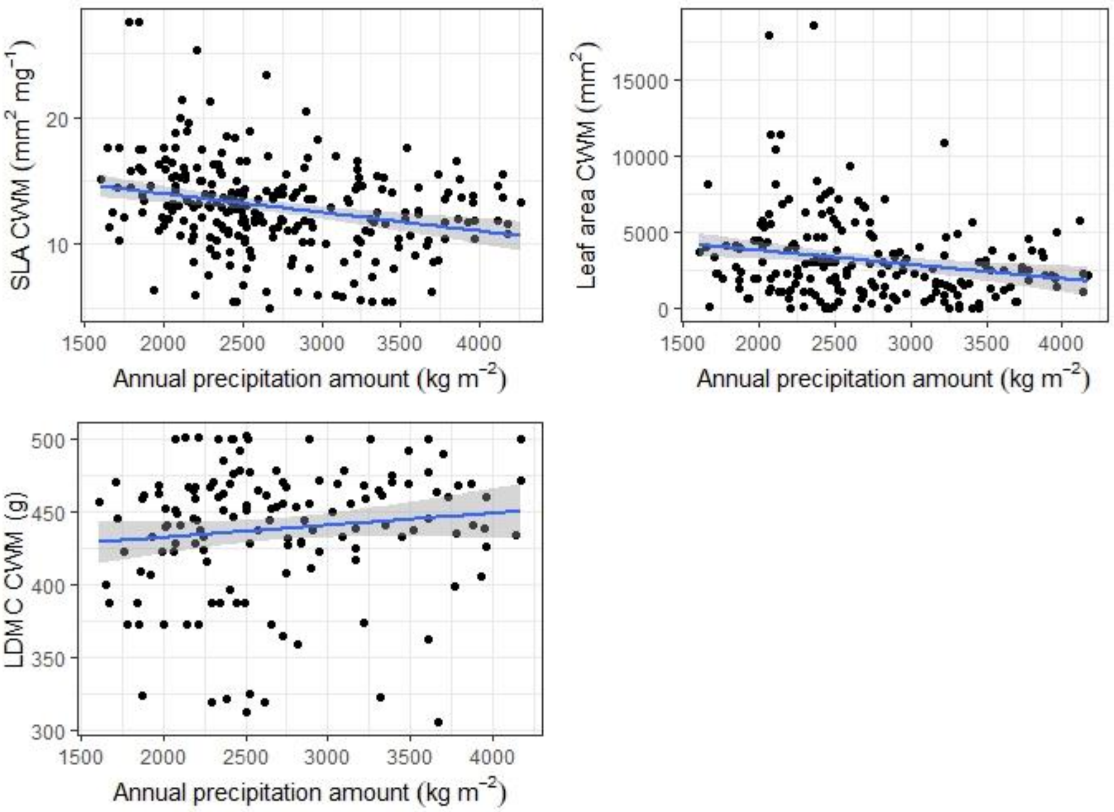

Fig.3.5: Annual precipitation amount at plot centre (kg m^{-2}) and plot community weighted mean (CWM) functional trait values for plots in the 4th Taiwan National Forest Inventory for trees with traits in the TRY plant trait database. SLA = specific leaf area. LDMC = leaf dry matter content.

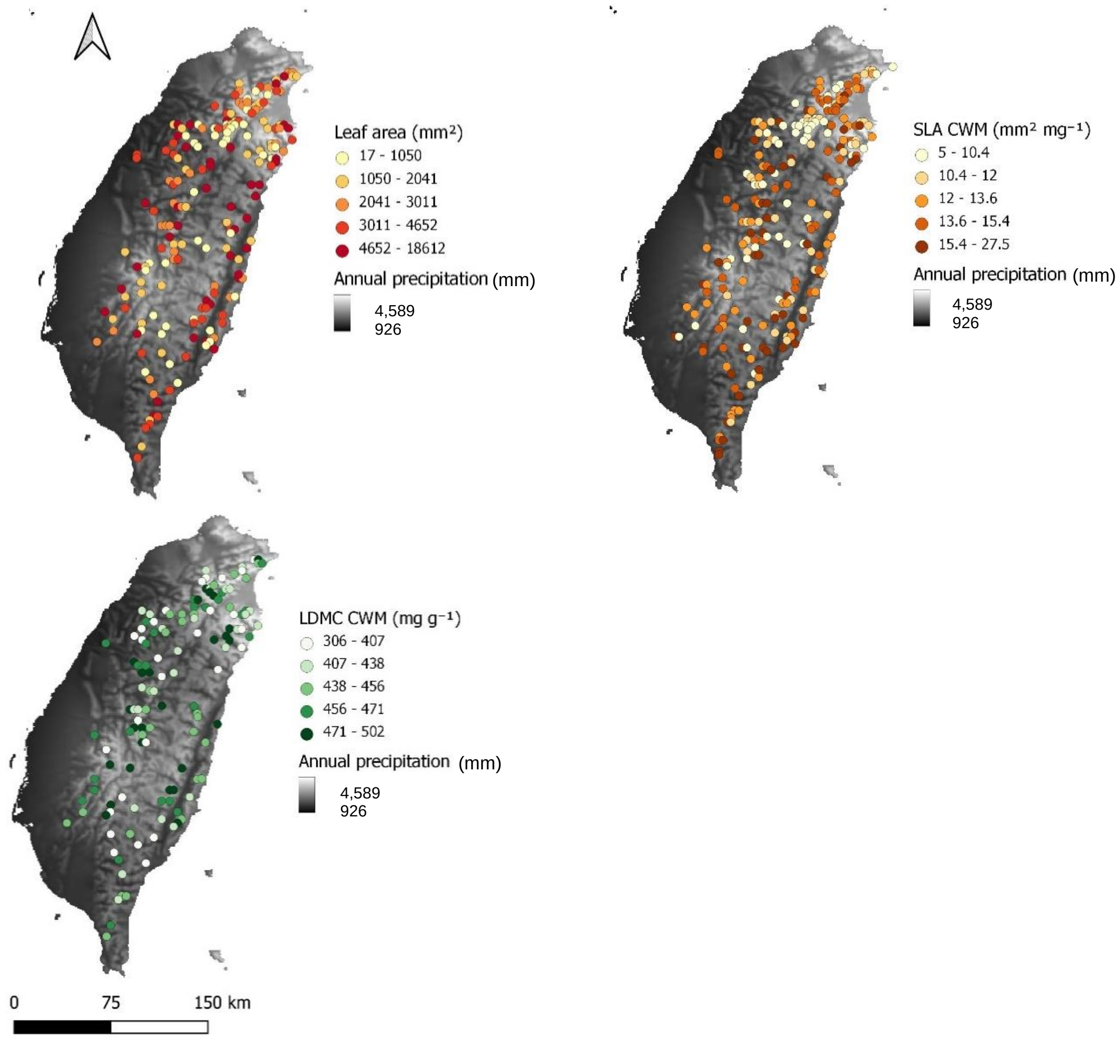

Fig.3.6: Spatial distribution of tree species community weighted means (CWM) of plots in the 4th Taiwan National Forest Inventory (NFI) for traits in the TRY plant trait database plotted against annual precipitation amount (mm) from CHELSA (Karger et al. 2017b, a). SLA = specific leaf area. LDMC = leaf dry matter content.

3.5 Discussion

Our findings suggest that individual functional traits are poor predictors of distribution shift size and direction at the species level, but that relationships between environment and function exist at the community-level across the broad range of forest types investigated. Temperature influenced function at the plot level, with precipitation also important for driving variation in several traits. Despite the challenges we have identified in using traits as predictors of individual species distribution shifts, the relationships between environment and community-level traits offers evidence that traits may be useful in linking plant responses to environmental change at the plot-level.

3.5.1 Functional traits as predictors of individual species shift size and direction

It may be unsurprising that clear relationships between individual trait values and distribution shifts at the species level were not found, as the assumption that a link between distribution shifts and mean species functional traits will be detectable may be an over-simplification of ecological complexity. Species do not exist in isolation from one another, with biotic interactions likely to drive varied responses of trees to climate change (Lenoir et al. 2009, Gilman et al. 2010, Alexander et al. 2015). Differences may occur in the size and direction of distribution shifts of populations of the same species across their distribution range, due to variations in local-scale conditions (O’Sullivan et al. 2021), whilst different life-stages of individuals could also respond differently to the same environmental pressures (Oldfather et al. 2021). As some trees shift their distributions, the habitat suitability for others could change (Greenwood et al. 2016), resulting in novel community compositions and biotic interactions which could interact to drive complex and varied species distribution shifts (Huntley 1991, Gilman et al. 2010, Alexander et al. 2015). Competition for light and nutrients are key limitations on tree growth and survival (Lewis and Tanner 2000, Coomes and Allen 2007), particularly in hyper-diverse forests (Terborgh 2012). Yet, such factors are likely to have substantial spatial variability, resulting in non-uniformity in environmental conditions across species ranges. Plant functional traits may also be variable across sites which have different land-use legacies (Alfaro-Sánchez et al. 2019), with variation in historic climate, pest outbreaks and anthropogenic land uses potentially influencing functional trait expression. Generalisations at the species-level using range optima may poorly explain distribution shifts of species occupying highly heterogenous environments. Considering changes in trait values from across multiple species within communities may provide a more accurate account of the variability in species re-organisations across the broad forest environment.

Species distribution shifts may be challenging to detect using functional traits when working with single traits in isolation (MacLean and Beissinger 2017, Beissinger and Riddell 2021). Trade-offs in resource-use strategy occur between species, within-species and across the life-span of individuals, with variation in survival, reproduction and growth (Laughlin et al. 2020). For example, if a trait positively influenced reproduction (such as rapid seed development or widespread seed dispersal), it is unclear what the impact would be on other traits, such as those which influence persistence or growth. Across individual species ranges, traits can vary substantially (O’Sullivan et al. 2022), driven by variation in factors such as competition (Boucher et al. 2013, Cárdenas et al. 2014), disturbances (Mayfield et al. 2006) and abiotic conditions (Körner 2007, Boucher et al. 2013, Asner et al. 2014). Growth-survival trade-offs are also common across the lifespan of long-lived species such as trees, which could influence functional trait values between individuals (Laughlin et al. 2020). The approach of using mean trait values may also be misleading, as large intraspecific differences could result in mean values poorly reflecting the variability in trait values across individual species ranges (Messier et al. 2010, Ahrens et al. 2021, Anderegg et al. 2021). Variation may be particularly high for widely distributed species and across heterogenous environments and environmental gradients, making individual trait approaches particularly challenging in these environments (O’Sullivan et al. 2022).

3.5.2. Variation in function across temperature and precipitation gradients

Despite challenges linking individual traits to individual species shifts, the close link between temperature and precipitation and functional trait values across the diverse montane forests investigated offers reassurance that traits may be an appropriate and useful tool for assessing plant-environment responses. Over recent years, rising temperatures and changes in precipitation associated with climate change have been experienced across Taiwan (Jump et al. 2012, Tu and Chou 2013), which are already thought to be causing many plant species to rapidly shift their distributions (Jump et al. 2012, Greenwood et al. 2016, Morley et al. 2020, O’Sullivan et al. 2021). Such changes in climate can influence overall ecosystem function, such as through altering tree demographic rates (Allen et al. 2015), forest productivity (Ruiz-Benito et al. 2014) and carbon cycling (Frank et al. 2015). Therefore, a strong association between environment and plot-level functional composition potentially foreshadows changes in function over coming decades due to shifts in species abundance and diversity at the community-level, irrespective of shifts in overall species ranges. Such changes in functional trait composition could be driven by processes such as tree mortality (Ruiz-Benito et al. 2017b), which are likely to be slow and gradual, resulting in small changes potentially remaining undetected when considering individual species in isolation. However, even subtle and small changes in the dominance of functional traits at the plot-level could influence plot-level functioning, for example, changes in tree leaf mass per area could result in changes in carbon gain (Ruiz-Benito et al. 2017b). Over time, changes in abundance and diversity could cause subsequent shifts in overall ecosystem functioning as environmental conditions change. Greater understanding of changes in functional trait composition will be crucial for detecting potential changes in overall ecosystems functioning.

3.5.3 Challenges and future directions

Ultimately, trait data can be time-consuming to collect across multiple species. It is possible that variability in data availability between traits may further affect our ability to detect relationships between traits and distribution shifts. Despite increasing trait data availability, databases such as TRY are far from complete, with considerable variability in data coverage between species and traits (Kattge et al. 2020). Whilst some traits were relatively well represented, such as SLA, wood density and leaf area, others, such as seedbank longevity and plant growth rate had poor coverage. For any given trait, species mostly had fewer than 20 observations, which is considered the minimum sample size for capturing within species trait variability (Kattge et al. 2011, 2020). Consequently, most species mean trait values were based on small sample sizes, which may provide a poor representation of the variability which exists across individual species ranges (O’Sullivan et al. 2022). Restricted data availability for many traits results in more widely available traits receiving greater focus, potentially limiting our ability to use traits to capture the fundamental components which influence plant distribution shifts across different contexts. For example, drought is likely to be a key factor influencing distribution shifts under warming temperatures of rear edge populations (Sánchez-Salguero et al. 2012), making hydraulic traits important to quantify (Rosas et al. 2021), whilst in other contexts plants may be limited by their ability to disperse, making dispersal capacity, seedbank longevity and habitat breadth important to consider (Estrada et al. 2015).

Although some authors argue that traits are too complex to provide meaningful insight on species distribution shifts (Angert et al. 2011), abandoning trait based approaches completely may miss opportunities to provide vital insight for management (MacLean and Beissinger 2017) and improve our understanding of biological complexity. Methods are needed which utilise current trait data to optimise their use for addressing global change questions. One such avenue for future research is building on our understanding of trait coordination among plants, to provide greater insight into trade-offs and plant-environment relationships (Yang et al. 2018, Maynard et al. 2022) such as through plant trait network analysis (He et al. 2020). Further understanding is needed on how plant responses to climate are influenced by biotic interactions, meaning that considering changes at the plot-level could be particularly insightful. Quantifying community-level functional traits across successive forest inventories could provide insight into shifts in forest function (Yuan et al. 2020). Traits could also be incorporated into distribution shift assessments through approaches such as joint species distribution models (Tikhonov et al. 2020) or experimental approaches of comparing plant responses to current and future competitors (Alexander et al. 2016). Quantifying the marginality of species across forest habitats may provide further insight into future species distribution shifts and changes in abundance. Such analyses could assess the spread of functional trait values within plots to determine whether individual species means are closer to the plot functional centre or margin, with high or low trait indicating the potential for a shift in plot-level function over coming decades. Developing analyses approaches such as those outlined here will enable us to improve our understanding of how functional traits may reflect plant ecological processes and their change over space and time.

3.5.4 Conclusion

The research in this chapter set out to explore the relationship between traits and distributional shifts of tree species across forests in Taiwan and the links between forest functional composition and climate. Our results suggest that individual functional traits are likely to be weak predictors of distribution shifts at the species level across the highly heterogenous forests investigated, but that close relationships between environmental variation and trait values exist at the plot-level. Ultimately, traits are not a panacea and have their limits as an explanatory tool. However, close relationships between environmental variation and trait values at the plot level suggest that traits are useful for reducing complexity and linking form and function. Understanding how forest function is changing is crucial in the context of ongoing global change. Functional trait data hold considerable power to enable us to predict the functional impacts of changing species distributions. However, improved understanding is needed of what traits can and cannot tell us and how they can most effectively be used. Work is needed to increase data availability of traits across under-represented species and biomes and explore methods of how best to utilise these data to provide useful information on plant function and how it relates to environmental change. Improved understanding of the links between plant communities, traits and ecological processes, could provide vital insight into the structure and function of ecological communities, enabling predictions on how they are changing over space and time over coming decades.

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3.7 Supplementary material

3.7.1 Individual trait values with shift size and direction

The results obtained here were compared to an alternative approach of calculating the optimum position of species range distributions using linear models with a quadratic term (O'Sullivan et al. 2021), but similar patterns were obtained (*Fig.3.S1*). Models were run for all traits, but sample sizes of < 20 for all traits except SLA means that model results should be treated with caution (Table S1).

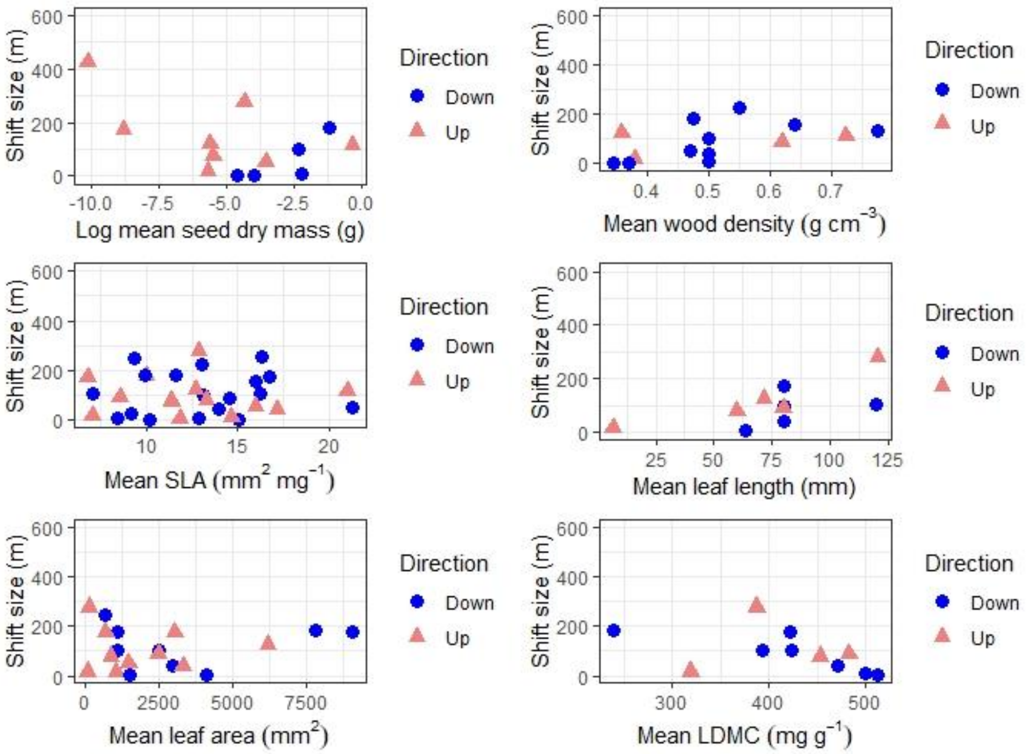

Fig.3.S1: Mean species trait values taken from the TRY plant trait database in relation to elevational shift size (m a.s.l.) and direction (down = to lower elevation or up = to higher elevation) for tree species in the 4th Taiwan National Forest Inventory (NFI). Species distribution shift size and direction extracted from O'Sullivan et al. 2021. SLA = specific leaf area. LDMC = leaf dry matter content.

Table 3.S1: Linear and logistic regression model results of functional trait values from the TRY plant trait database for species in the 4th National Forest Inventory for Taiwan (NFI), considering the influence of trait values on species distribution shift size and direction at the species range optimum (O’Sullivan et al. 2021). *Coefficient of variation (CV) also provided. SLA = specific leaf area. LDMC = leaf dry matter content.*

Trait	**Model**	**R^2 or $R^2_{McFadden}$**	**Model output**	**Estimate**	**CV**	**Units**
Log seed dry mass	Shift size ~	0.2348	F=3.376, df=1, 11, p=0.093	1.65	0.62	g
	Shift direction ~	0.2067	z=-1.512, df=12, p=0.131	-2.223		
Wood density	Shift size ~	0.2293	F=3.869, df=1, 13, p=0.071	212.46	0.25	g cm^{-3}
	Shift direction ~	0.0008	z=0.125, df=14, p=0.900	-0.732		
Leaf area	Shift size ~	0.0102	F=0.176, df=1, 17, p=0.680	100.203	0.97	mm^2
	Shift direction ~	0.0061	z=-1.222, df=18, p=0.222	0.787		
Leaf length	Shift size ~	0.4337	F=6.127, df=1, 8, p=0.038	-23.0311	0.42	mm
	Shift direction ~	0.0597	z=-0.839, df=9, p=0.402			
SLA	Shift size ~	0.0001	F=0.003, df=1, 29, p=0.959	104.953	0.29	mm^2 mg^{-1}
	Shift direction ~	0.0032	z=-0.364, df=30, p=0.716	0.101		
LDMC	Shift size ~	0.2180	F=2.509, df=1, 9, p=0.148	299.8874	0.20	mg g^{-1}
	Shift direction ~	0.0044	z=-0.252, df=10, p=0.801	0.273281		

3.7.2 Functional dispersion with temperature and precipitation

There was substantial variation in plot functional dispersion (FD) values among all traits investigated (*Fig.3.S2, Fig.3.S3,* Table 3.S2). Precipitation alone was the best indicator of FD values for SLA and LDMC. Temperature alone was the best indicator of FD values for leaf length, leaf area and wood density, with FD generally increasing with increasing temperature. Precipitation alone was the best indicator of FD values for SLA and LDMC, with FD generally increasing with increasing precipitation amount. Precipitation and temperature together explained log seed dry mass.

Table 3.S2: Linear model results of plot-level functional dispersion (FD) of functional trait values from the TRY plant trait database for species in the 4th National Forest Inventory for Taiwan (NFI) with environmental variables of temperature, precipitation and their interaction from CHELSA BIOCLIM layers. The simplest model within two AIC units from the best fit model were selected. Coefficient of variation (CV) also provided. SLA = specific leaf area. LDMC = leaf dry matter content.

Trait	**Selected model**	**R^2**	**Model output**	**Estimates**	**CV**	**Units**
Log seed dry mass	~temperature + precipitation	0.07	F=6.594, df=2, 171, p= 0.002	0.149, 0.145	0.28	g
Wood density	~temperature	0.08	F=16.78, df=1, 194, p=<0.001	0.147	0.34	g cm^{-3}
SLA	~precipitation	0.03	F=7.445, df=1, 247, p=0.007	0.258	0.23	mm^2 mg^{-1}
Leaf length	~temperature	0.13	F=17.09, df=1, 112, p=<0.001	0.012	0.36	mm
Leaf area	~temperature	0.12	F=27.15, df=1, 198, p<0.001	0.089	0.39	mm^2
LDMC	~precipitation	0.03	F=4.115, df=1, 141, p=0.044	0.250	0.27	mg g^{-1}

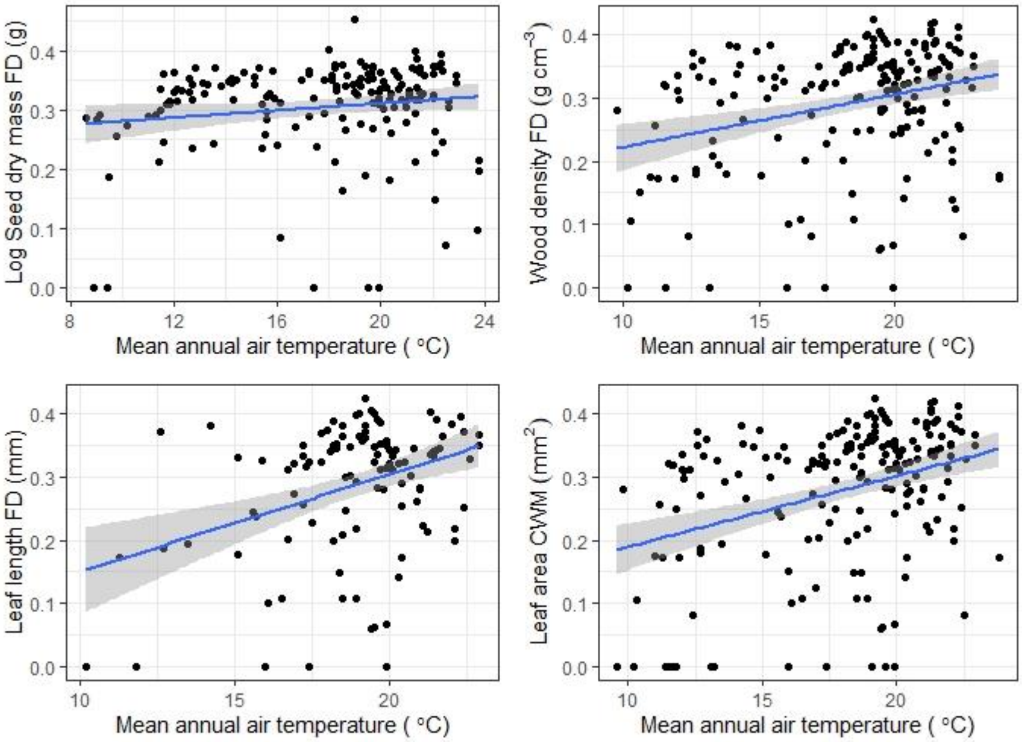

Fig.3.S2: Mean annual air temperature at plot centre (°C) and plot trait functional dispersion (FD) values for plots in the 4th Taiwan National Forest Inventory for trees with traits in the TRY plant trait database. SLA = specific leaf area. LDMC = leaf dry matter content.

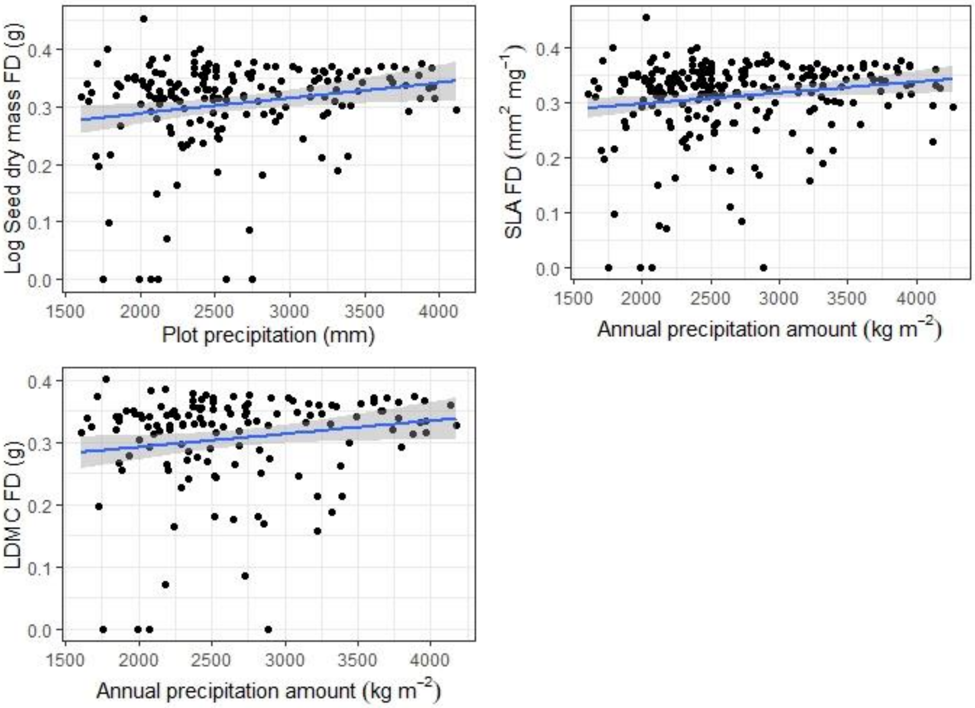

Fig.3.S3: Annual precipitation amount at plot centre (kg m^{-2}) and plot trait functional dispersion (FD) values for plots in the 4th Taiwan National Forest Inventory for trees with traits in the TRY plant trait database. SLA = specific leaf area. LDMC = leaf dry matter content.

3.7.3 Supplementary material references

O'Sullivan, K. S. W. et al. 2021. Onward but not always upward: individualistic elevational shifts of tree species in subtropical montane forests. - Ecography (Cop.). 43: 1–12.

Chapter 4

High intraspecific trait variation results in a resource allocation spectrum of a subtropical pine across an elevational gradient

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Title: High intraspecific trait variation results in a resource allocation spectrum of a subtropical pine across an elevational gradient

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4.1 Abstract

Aim: Plant functional traits are broadly used to quantify and predict impacts of climate change on vegetation. However, high intraspecific trait variation can bias mean values when few measurements are available. Here, we determine the extent of individual leaf trait variation and covariation across a highly heterogeneous environmental gradient for a widely distributed subtropical pine. We demonstrate the implications of trait variation for characterising species by assessing data availability and variability across the Pinus genus.

Location: Central Mountain Range, Taiwan. Taxon: Pinus taiwanensis Hayata (Pinaceae).

Methods: We measured eight functional traits suggested to reflect plant strategies: needle length, area, thickness, dry and fresh mass, stomatal row density (SD), leaf dry matter content (LDMC) and specific leaf area (SLA). We examined trait variation in response to climatic and physiographic factors across an elevational gradient of 495– 3106 m a.s.l. using linear mixed effects models (LMMs). Intraspecific trait covariation was explored using principal component analyses (PCAs) and LMMs. Descriptive statistics were calculated for Pinus records in the global TRY plant trait database.

Results: Intraspecific variability among traits was high (CV 20%– 44%) and predictable with elevation (generally $p < 0.05$, with declining needle size and LDMC with elevation and increasing SD). However, 41%– 92% of variance was un-explained by topography. Sixty- five percent of variation was explained by two trait covariation axes, with predictable changes with elevation ($p < 0.001$). Pinus data availability in TRY was low. Across traits, only 12.5%– 53% of species had sufficient sample sizes for intraspecific analyses.

Main conclusions: We show substantial trait variation for a single species, here likely driven by temperature differences and additional biotic and abiotic drivers across the elevational range. Improved understanding of the extent and implications of intraspecific variability is necessary for reliable quantifications and predictions of the impacts of environmental change, especially in understudied, hyper- diverse ecosystems such as tropical forests

4.2 Introduction

Identifying fundamental patterns in nature and understanding their causation is key to predicting responses of ecosystems to ongoing global change (Sutherland et al. 2013). Plant functional traits are broadly used to predict the impacts of climate change on vegetation, as they reflect responses of plants to environmental conditions (Lavorel and Garnier 2002, Cornelissen et al. 2003, Violle et al. 2014, Ruiz-Benito et al. 2017b, Bjorkman et al. 2018, Boonman et al. 2020). However, assessments using traits typically compare values between species, despite intraspecific differences likely to have widespread influences on community responses to environmental change (Albert et al., 2011; Boucher et al., 2013; De Bello et al., 2011; Fajardo & Siefert, 2016; Kichenin et al., 2013; Niinemets, 2014; Rosas et al., 2019; Siefert et al., 2015; Soudzilovskaia et al., 2013; Vilà-Cabrera et al., 2015). Intraspecific functional trait differences have been linked to variation in, amongst others, plant range shift capacity (Ozinga et al. 2009, Angert et al. 2011, Estrada et al. 2016), competitive ability (Bohner and Diez 2020) and performance under recent climate warming (Ruiz-Benito et al. 2017b). Information on intraspecific trait variation and how it connects to environment will enable more accurate predictions to be made of the impacts of environmental change on plant distributions, physiology, growth, community structure and ecosystem functioning (Bjorkman et al., 2018; Lavorel & Garnier, 2002; Lecerf & Chauvet, 2008; Midolo et al., 2019; Myers-Smith et al., 2019; Violle et al., 2012; Wang et al., 2018).

Across local and regional scales, intraspecific trait variation can be driven by differences in biotic interactions (Boucher et al. 2013, Cárdenas et al. 2014), abiotic conditions (Asner et al., 2014; Boucher et al., 2013; Körner, 2007; Lambrecht & Dawson, 2007), genetics (Albert et al., 2010; Jung et al., 2010), management (Kahmen et al. 2002), disturbances (Mayfield et al. 2006), forest stand structure (Vilà-Cabrera et al. 2015) and tree size (Iida et al. 2014). A multi-species analysis indicated that up to 40% of overall variation of some plant traits occurs within species (Kattge et al., 2011), whilst a global meta-analysis attributed 25% of variation within communities and 32% of variation between communities to intraspecific trait differences (Siefert et al. 2015). Wide differences between individuals may cause variation around species means to be as informative as mean values themselves (Messier et al. 2010, Ahrens et al. 2021, Anderegg et al. 2021). Yet, intraspecific trait data availability is limited, with even some of the most data rich species having only moderate coverage in the TRY global plant trait database and uneven data availability between traits, species, communities and regions (Grime, 2006; Niinemets, 2014). Uncritical use of trait data in multi-species analyses risks comparing species with small or widely varying sample sizes that overlook inherent intraspecific variation, with particular care needed when analysing trait data compiled from different sites and time periods (Niinemets, 2014).

Particularly large intraspecific variation is expected in heterogeneous environments, along environmental gradients and in species with large distribution ranges (Albert et al., 2011; Anderegg et al., 2021; Bussotti et al., 2015; Körner, 2007; Rosas et al., 2019). With marked and rapid declines in temperature with increasing distance above sea level, elevation gradients provide an ideal opportunity to test plant responses to different environmental conditions (McGill et al. 2006, Malhi et al. 2010). Across elevation gradients, after controlling for physiographic factors such as slope and aspect, plant functional traits are expected to vary in response to factors such as declining air temperature and atmospheric pressure, and increasing solar radiation with increasing elevation (Körner et al., 1986; Körner, 2007; Sundqvist et al., 2011). Plants at higher altitudes are typically smaller, with smaller and thicker leaves (Bresson et al., 2011; Körner, 2007) and fewer stomata than their low elevation counterparts, reflecting restricted water availability (Schoettle and Rochelle 2000) and low temperatures at high elevations (Körner, 2007).

Whilst there are some common trends in plant trait variation across elevation gradients, information is limited on how consistent these fundamental patterns are, restricting our ability to make predictions of how vegetation might change under different environmental conditions. Elevational patterns can be complex and non-linear, with traits influenced by several interacting drivers such as competition, ecosystem productivity, soil moisture and fertility, clear-sky turbidity, hours of sunshine, wind, season length, geology and human land use (Körner, 2007; Sundqvist et al., 2013). Mountains are highly heterogeneous, with environmental controls differing across local, regional and continental scales (Jobbágy et al. 1996, Sundqvist et al. 2013, Morley et al. 2018, Midolo et al. 2019). Fundamental elevational trends may not hold across latitudes, with information on trait variation in the tropics limited compared to temperate northern hemisphere regions (Wilson et al. 1999, Jetz et al. 2016, but see Chaturvedi et al., 2011; Poorter et al., 2008; Wright et al., 2010). Rapid declines in temperature in the tropics by around 5.2°C to 6.5°C every 1,000 m a.s.l. with increasing elevation (Colwell et al. 2008), along with high species diversity and ecological trade-offs (Boucher et al., 2013; Wright, 2002), may decouple trait variation from expected trends.

Leaf traits are commonly used to describe physiological differences and ecological strategies among plants (Westoby 1998, Westoby et al. 2002, Grime 2006, Poorter and Bongers 2006, Zanzottera et al. 2020), as they are fundamental for gas and water exchange, carbon assimilation and photosynthesis (Smith et al. 1997, Donnelly et al. 2016, Dong et al. 2020). Leaves can be quick and easy to measure, which is an advantage in remote and challenging areas to access such as tropical mountains (Westoby 1998, Weiher et al. 1999, Garnier et al. 2001). Leaves can vary in size and in anatomical features such as stomatal density along environmental gradients, reflecting differences due to genetics and phenotypic plasticity (Donnelly et al. 2016). Plant traits often strongly covary, with suites of traits reflecting different resource-use strategies and providing greater insight on plant strategies than considering traits in isolation. The leaf economic spectrum (LES) is broadly used to describe plant ecological approaches spanning from fast returns on investments to slow growth and persistence (Fajardo & Siefert, 2018; Messier et al., 2017; Niinemets, 2014; Pan et al., 2020; Wright et al., 2004, 2005). The LES is often quantified through the metrics of specific leaf area (SLA) and leaf dry matter content (LDMC), with low SLA and high LDMC associated with persistence and high SLA and low LDMC associated with short-lived and productive strategies (Guo et al., 2018; Poorter & Bongers, 2006; Roche et al., 2004; Wilson et al., 1999). However, large differences between individuals may result in intraspecific differentiation in resource allocation strategies, and hence position along the LES, which may complicate comparison of trait-environment relationships across species (Fajardo & Siefert, 2016, 2018; Messier et al., 2018; Niinemets, 2014). Determining the extent to which intraspecific variation follows broad LES patterns and identifying whether traits covary predictably will provide a better understanding of the links between vegetation and environment, enabling more accurate predictions to be made of the impacts of environmental change.

Given the need to better understand intraspecific trait variability and its potential drivers across different environmental conditions, we sought to determine the extent to which fundamental patterns in leaf trait variation are consistent across space for a very widely distributed subtropical pine species. By focussing on needles, as fundamental components of conifer physiology, we aimed to capture variation in size dimensions and other characteristics associated with phenotypic plasticity and genetic adaptations (Donnelly et al. 2016). To better understand implications of trait covariation, we explored the extent to which the LES holds within this species and its predictability with elevation. The *Pinus* genus is diverse and globally distributed (Ioannou et al. 2014). Therefore, to demonstrate the implications of trait variation for characterisation of the species and the wider genus, we determined how well represented individual *Pinus* species are by trait data and compared variability within traits between congeneric species. Specifically, we sought to determine: 1) To what extent traits vary predictably across the range of *Pinus taiwanensis*, 2) whether the measured traits covary, or if lack of covariation leads to changing relationships between traits across the range and, 3) if variability within traits restricts our ability to use species-level trait values to represent a species or differentiate between others within the genus.

4.3 Materials and Methods

4.3.1 Study system and species

Pinus taiwanensis Hayata (Pinaceae) is widespread across the island of Taiwan, where it is generally considered endemic, although closely related species are found in mainland China and Japan (Fu et al. 1999). The species spans diverse climatic and habitat conditions, extending over an exceptionally large range in the Central Mountain Range, spanning from around 500 to 3,200 m a.s.l. (“Taiwan National Forest Inventory (4th)” 2013) Taiwan is a subtropical island, experiencing warm and humid conditions, which transition through temperate to alpine with increasing elevation (Li et al. 2013). At low elevations (below 500 m a.s.l.), urban and agricultural land dominates following widespread deforestation, but natural forests are abundant above this height, transitioning from evergreen broadleaved forests into areas of mixed forest, deciduous broadleaved and evergreen broadleaved forest at higher elevations (Li et al. 2013). Whilst *P. taiwanensis* is found scattered through mixed forest and open habitat at lower elevations, it typically increases in abundance and occurs in monodominant stands at high elevations (Li et al. 2013). As an early successional species, it primarily favours light and humid conditions (Cai and Liu 2017), regenerating quickly on disturbed land (Chou et al. 2009).

4.3.2 Site selection and sampling

Mature adult trees > 10 cm diameter at breast height (dbh) were sampled between 7th and 30th November 2019 across an elevation gradient in the northern part of Taiwan’s Central Mountain Range (*Fig.4.1, Table 4.S1*). Sample sites were identified from local knowledge of the species distribution and selected to achieve even sampling across the elevation gradient. Sites ranged from 495 m to 3,106 m a.s.l. and included monodominant stands, mixed forest and scattered individual trees in open habitat, due to changes in forest composition and increasing abundance of *P. taiwanensis* with elevation preventing sampling from forests with consistent structure. Coordinates were recorded at each sampling location and elevation, aspect and terrain slope extracted from a high-resolution Digital Elevation Model (NASA JPL shuttle mission, 30 m pixel size) for each sampling location. Several branches were collected per tree, selecting the highest accessible branches (largely 10-30m above the ground) with fully expanded, mature, sun leaves (Cornelissen et al. 2003). Branches were transported to the laboratory in sealed poly bags containing a small piece of moist filter paper (Kitajima and Poorter 2010). A total of 92 trees were sampled across 15 sites, with minimum 2 and maximum 12 trees per site.

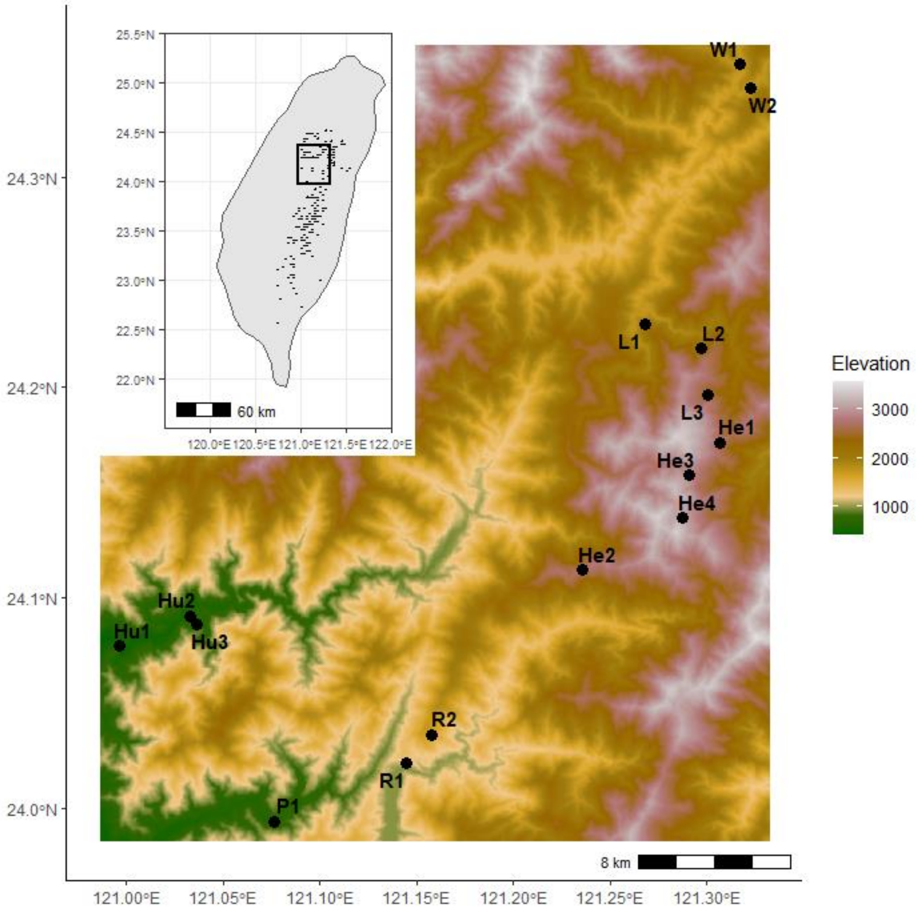

Fig.4.1: Locations and elevation (m a.s.l.) of *Pinus taiwanensis* sample sites in the northern part of the Central Mountain Range of Taiwan. Inset map shows the distribution of *P. taiwanensis* based on sample location and presence records in the Taiwan National Forest Inventory (*Taiwan National Forest Inventory (4th),* 2013). Location name information in Table 4.S1. Projection: WGS 84 / UTM zone 51N.

4.3.3 Needle trait measurements

Five leaves were randomly selected per tree for functional trait measurements. Eight functional traits were measured: needle thickness (mm), area (mm^2), length (mm), fresh and dry mass (mg), specific leaf area (SLA, mm^2 mg^{-1}), leaf dry matter content (LDMC, mg g^{-1}) and stomatal row density (SD, per mm^2). These traits were chosen as they have previously been associated with high intraspecific trait variation (Siefert et al. 2015), ecological changes along elevation gradients (Bresson et al., 2011; Körner, 2007; Schoettle & Rochelle, 2000), sensitivity to environmental variation (Donnelly et al. 2016) and LES strategies of growth and survival (Wright et al., 2004). We hypothesised that needle size (length, thickness and mass) would reduce with increasing elevation due to temperature limitation. We hypothesised that stomatal row density would decline with increasing elevation as a response to water limitation. We hypothesised that SLA and LDMC would show opposite trends, with increasing SLA and decreasing LDMC with elevation. Needle thickness was measured at the centre of the needle using digital callipers (0.1mm precision), length using a ruler and area using the Apple iOS iPad application Leafscan (Anderson and Rosas-Anderson 2017). Abaxial and adaxial longitudinal stomatal rows were counted using a microscope (Donnelly et al. 2016). Fresh mass was obtained from a further 20 randomly selected needles weighed at 0.1g precision, as the mass of individual needles was too small to be detected on the balance available to us in the field. Needles were stored in individual tea bags to air dry, further dried in an oven at 60^{o}C for several days then weighed to 0.001g precision. Individual needle fresh mass was estimated by calculating the difference in fresh and dry mass of the bulk sample, dividing by N=20 and adding to individual needle dry needle mass measurements.

SLA, the ratio of leaf surface area to dry mass, was calculated:

$$SLA = \frac{\pi\, rl + 2\, rl}{m}$$

where r = thickness, l = length and m = dry mass, to account for the curved shape of pine needles (Donnelly et al. 2016). LDMC, the ratio of leaf dry to fresh mass, was expressed as dry mass (mg) proportional to fresh mass (g) (Wilson et al. 1999, Vaieretti et al. 2007, Pérez-Harguindeguy et al. 2013). SD per leaf was calculated as:

$$SD = \frac{abaxial\ stomatal\ rows\ +\ adaxial\ stomatal\ rows}{2\ x\ needle\ area}$$

4.3.4 Additional trait data

To assess intraspecific needle trait data availability more broadly, the number of data records listed in the TRY global plant database were obtained for the key needle traits of thickness, length, LDMC and SLA across the *Pinus* genus.

4.3.5 Analysis

Trait variation was initially explored using descriptive statistics (minimum, maximum, mean, standard deviation, coefficient of variation (CV) and 95% confidence intervals (CI)). To further explore the variation between needle functional traits and topographic variables of elevation, slope and aspect, we fitted linear mixed effects models (LMMs). All traits met test assumptions according to diagnostic plots on model residuals. Global models included fixed effects of elevation, aspect (as four cardinal directions; north, east, south and west) and terrain slope and random effects of individual trees. Elevation and slope were scaled and aspect was modelled as categorical as it is a circular variable. We incorporated pairwise interactions based on our expectation of interactive effects of topography on trait values. Variance inflation factors of the linear predictors were checked for multi-collinearity, with values between 1 and 2 suggesting no multi-collinearity (Zuur et al. 2010). Guided by our expectation of changing trait values with elevation, all models included elevation, but differed in their inclusion of slope and aspect and their interaction with elevation. Models were ranked by Akaike information criterion (AICc) from lowest to highest. The most parsimonious models were selected, within two AIC units of the lowest AIC model, and fitted via maximum likelihood (ML). The percentage contribution of fixed and random effects (Pseudo-$R^2_{\text{conditional}}$) in explaining functional trait variation was calculated (Nakagawa and Schielzeth 2013). A paired samples Wilcoxon test was used to compare abaxial and adaxial SD.

To assess trait covariation in multidimensional space across the full elevation range, we performed a principal component analysis (PCA). The first two components with eigenvalues >1 were retained for further inspection and analysis (Zwick and Velicer 1986). LMMs were run using component axes as the response and elevation, slope and aspect as predictors, with tree as a random factor. Both component axes met test assumptions according to diagnostic plots on model residuals.

To assess intraspecific needle trait data availability in TRY, we extracted needle length, thickness, LDMC and SLA for individual *Pinus* species. We quantified how many species had publicly available records for each trait and the mean number of measurements per trait. We calculated how many species had ≥ 20 measurements per trait and the proportion of species with records with ≥ 20 measurements, as this measurement intensity has been reported as the minimum acceptable threshold to capture intraspecific variation (Kattge et al., 2011; Kattge et al., 2020). We further investigated a subset of the *Pinus* species with ≥ 20 records, selecting the nine most well represented species for each trait except LDMC where only five species had ≥ 20 records. We extracted the minimum, median and maximum value for each species and trait, calculated the mean for the *Pinus* genus and compared this to our *P. taiwanensis* data. All analyses were carried out in R version 4.1.1. (R Core Team 2021) using the packages ‘lme4’ (Bates et al. 2015), ‘lmerTest’ (Kuznetsova et al. 2017) and ‘MuMIn’ (Barton 2020).

4.4 Results

There was substantial intraspecific variation in all traits in *P. taiwanensis*, with coefficients of variation ranging from 20-44% (*Fig.4.2, Table 4.S2*). Needle dry mass was particularly variable across the gradient, with the highest value eighteen times larger than the smallest value. SLA increased by a factor of ten over the gradient, fresh mass and SD increased by a factor of nine and thickness increased by a factor of eight. Needle area and LDMC increased five-fold and length four-fold over the gradient.

4.4.1 Topographic variation in functional traits

In general, needles became smaller, had higher SD and lower LDMC with increasing elevation, although there was considerable variation around this pattern (*Fig.4.2*). Fixed and random (tree) effects (Pseudo-$R^2_{\text{conditional}}$) accounted for 47-95% of the model variance, comprising 0.07-59% of variance from fixed effects and 24-57% from random effects (*Table 4.1*). There were significant elevation main effects for all traits. Needle size was generally negatively associated with elevation, with significant elevation effects for length (t=-23.89, p<0.001), area (t=-11.14, p<0.001), fresh mass (t=-5.00, p=0.014), dry mass (t=-2.03, p=0.027) and thickness (t=0.03, p=0.006). Models of needle length, area, fresh mass and dry mass were improved with the inclusion of aspect as a fixed effect, with smaller leaves on east facing slopes (*Fig.4.S1, Table 4.S3*). Slope gradient, and the interaction between slope and aspect, further explained differences in fresh and dry mass, with marginally lighter needles on slopes with moderate gradients (15-25^{o}) (*Fig.4.S2, Table 4.S3*). Overall, fixed (topographic) effects captured substantial variation in needle size, explaining over half of the variance in needle length (59%), over a quarter of the variance in fresh mass (38%) and dry mass (29%), and 22% of the leaf area variance. Variation in needle thickness was less strongly linked to topography, with fixed effects of elevation, aspect, slope and the interaction between aspect and slope explaining 15% of variance.

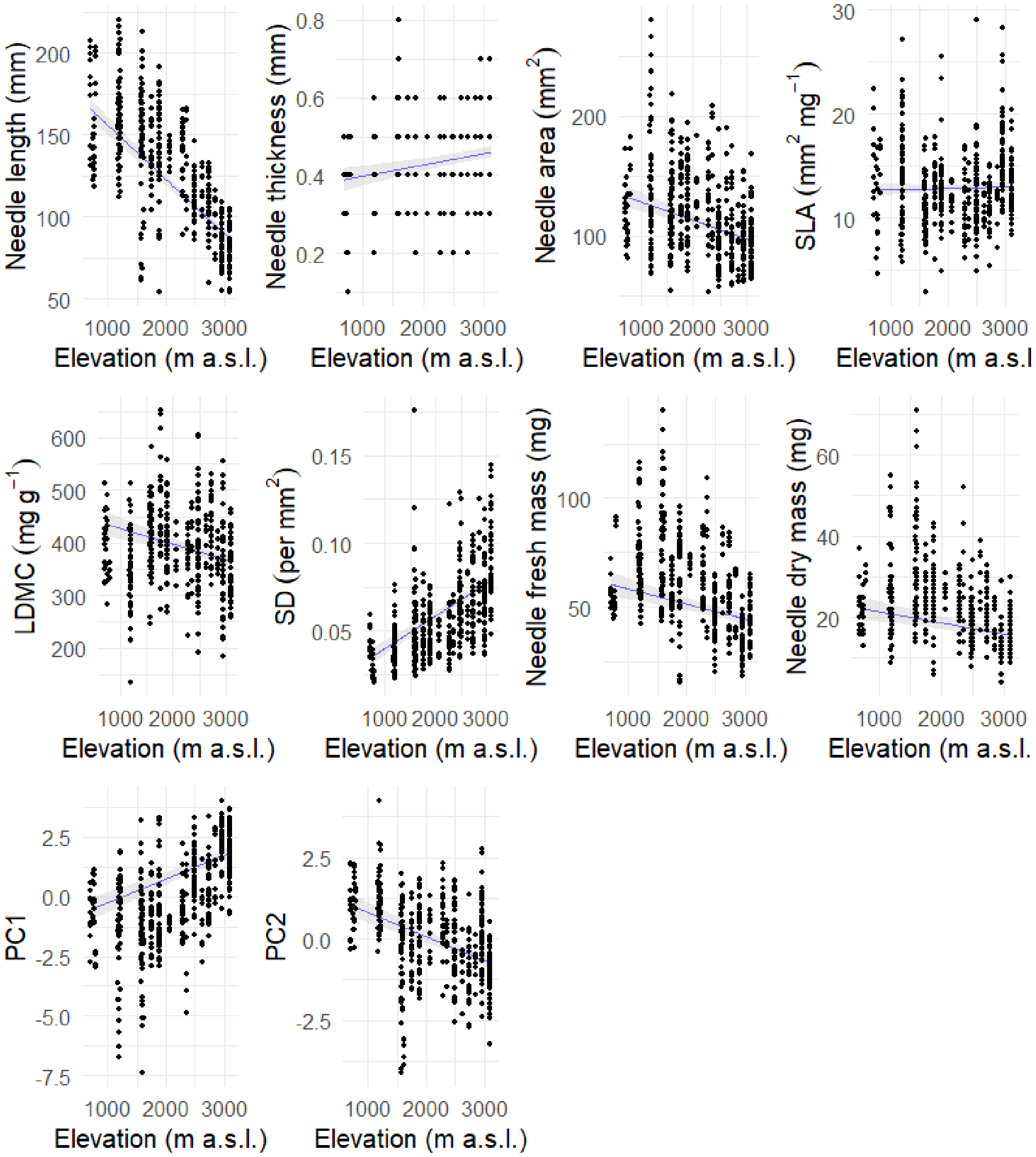

Fig.4.2: *Pinus taiwanensis* needle trait values per tree along an elevation gradient from samples taken in the Central Mountain Range of Taiwan. Blue lines represent predicted relationships based on linear mixed effect models, omitting any interaction terms for the purposes of graphical representation. Grey shaded areas show 95% confidence intervals. SLA = Specific leaf area, LDMC = leaf dry matter content, SD = stomatal density.

Table 4.1: Summary of the selected models for each trait measured on Pinus taiwanensis needles sampled from the Central Mountain Range of Taiwan. Selected models were the simplest model with the lowest AIC which still included elevation as a predictor. More complex models were chosen only if they reduced AICc by >2 from a simpler model.

Trait	**Model**	**ΔAIC**	**Elevation results**		**Pseudo - $R^2_{conditional}$**	**Variance (%)**		**Unit**
			Scaled estimate	**p**		**Fixed**	**Random (tree)**	
Length	~elevation + aspect	0.00	-23.89	<0.001	0.84	59	24	mm
Thickness	~elevation + aspect + slope + aspect*slope	0.00	0.03	0.006	0.52	15	36	mm
Area	~elevation + aspect	0.68	-11.14	<0.001	0.61	22	39	mm^2
SLA	~elevation	1.22	0.10	0.739	0.47	0.07	47	mm^2 mg^{-1}
LDMC	~elevation + aspect + elevation*aspect	0.00	-21.41	0.020	0.57	8	49	mg/g
SD	~elevation + aspect	0.00	0.01	<0.001	0.64	38	26	per mm^2
Fresh mass	~ elevation + aspect + slope + aspect*slope	0.00	-5.00	0.014	0.95	38	57	mg
Dry mass	~elevation + aspect + slope + aspect*slope	0.00	-2.03	0.027	0.76	29	46	mg
PC1	~elevation + aspect + slope + aspect*slope	0.00	0.77	<0.001	0.77	42	35	
PC2	~elevation	0.59	-0.55	<0.001	0.67	19	49	

SD was positively associated with increasing elevation, with a significant elevation effect (t=0.01, p<0.001). The SD model was improved by including aspect, with higher SD on east facing slopes (*Fig.4.S1*). Fixed effects of elevation and aspect explained 38% of the observed SD variation. SD was significantly higher on the abaxial than the adaxial side of the needle, with a mean of 0.033 and 0.025 per mm^2 respectively (V = 79307, p<0.001). Resource-use strategies varied over the elevation gradient, with a significant decline in LDMC (t=-21.41, p=0.020) with increasing elevation. Including slope and aspect, and their interaction, improved model fit, explaining 8% of the variance in LDMC. However, SLA did not significantly vary with elevation (t=0.334, p=0.739) with only 0.07% of the variance explained by elevation. LDMC was marginally lower on east facing slopes (*Fig.4.S1*).

4.4.2 Covariation among functional traits

The first two component axes of the full PCA together explained 65% of the variance (*Fig.4.S3*). The first axis (PC1) showed a clear negative association with needle size (length, area and mass) and explained 46% of the total variance. The second axis (PC2) was negatively correlated with needle thickness and SD and accounted for 19% of the total variance. Needle area and length were tightly paired, with close positive associations also present for mass and LDMC (*Figs.4.S3 and 4.S4*). PC1 significantly increased with elevation (t=4.994, p<0.001), with slope, elevation and aspect fixed effects explaining 42% of the variance and differences between trees attributed to 35% of the variance (Table 4.1, *Fig.4.2*). PC2 significantly declined with increasing elevation (t=-4.878, p<0.001), with elevation explaining 19% of the variance and differences between trees explaining 49% (Table 4.1, *Fig.4.2*).

The TRY database held information on 123 *Pinus* species, with 78 species (63%) having at least one measurement for needle length, thickness, SLA and/or LDMC and 45 species (37%) having no data for any of these traits (Tables 4.S4 and 4.S5). The number of species with ≥ 20 trait measurements varied from 5 to 27 species, comprising 12.5-53% of species with > 0 measurements. The mean number of measurements per species was generally < 20, with only needle thickness having a mean > 20. The extent of intraspecific trait variability differed considerably between species. For the subset of *Pinus* species we investigated further, the difference between the maximum and minimum species trait values ranged from 31 to 266 mm for needle length, 0.19 to 0.75 mm for needle thickness, 244 to 517 mg g^{-1} for LDMC and 8 to 52 mm^2 mg^{-1} for SLA (*Fig.4.3*). Most species and traits had much smaller sample sizes than our *P. taiwanensis* data, suggesting variability is likely to be underestimated in many cases.

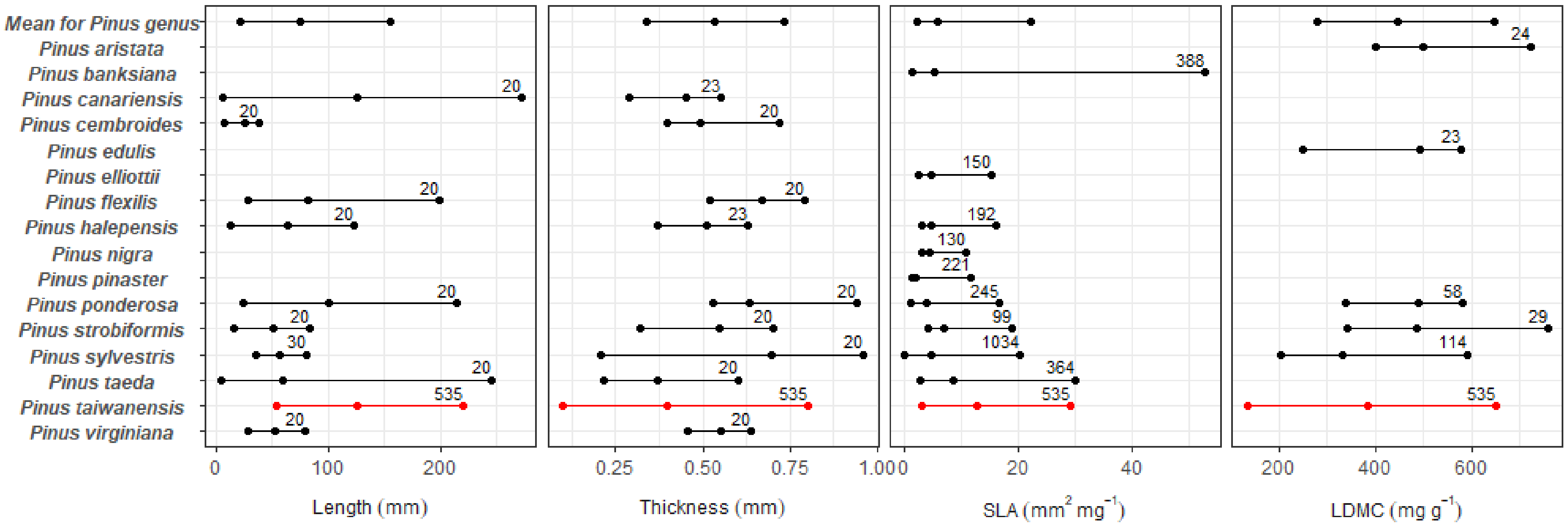

Fig.4.3: Minimum, median and maximum needle length, thickness, specific leaf area (SLA) and leaf dry matter content (LDMC) for *Pinus* species in the TRY global plant trait database. Labelled numbers represent the number of measurements available in TRY for each species and trait. The nine most data rich species are included for each trait except LDMC, where only 5 species had ≥ 20 measurements and thus met the threshold outlined in (Kattge et al., 2011; Kattge et al., 2020).

4.5 Discussion

We observed large intraspecific needle trait variation in *P. taiwanensis* across its broad elevational range. As expected, directional changes linked to elevation were identified, aligning with ecological theory that species traits vary across elevation gradients (e.g. Campetella et al., 2019; Körner, 2007; Sundqvist et al., 2013) and plant function determines species distributions (Hulshof et al. 2013). A spectrum of resource allocation was present across the elevation gradient, suggesting resource-use trade-offs acting across the species range (Fajardo and Siefert 2018). However, the strength of elevational trends varied between traits, with slope and aspect accounting for a portion of the variation, and often substantial unexplained variance. Our findings agree with suggestions that intraspecific differences contribute an important component of functional trait variability (Ahrens et al., 2021; Albert et al., 2010; Violle et al., 2012). We provide evidence that pronounced intraspecific variation in resource allocation strategy can occur, likely associated with high environmental heterogeneity across a species range (*Fig.4.2*). Such variability could potentially impact our ability to forecast responses of species to environmental change, since local-scale drivers might significantly modify LES-climate relationships within and between species. Furthermore, we illustrate the risk of not considering intraspecific variation when using published trait data by highlighting considerable trait variation within and between species across the *Pinus* genus in conjunction with overall low numbers of reported trait values and variability likely to often be underestimated (*Fig.4.3*). Uncritically deriving and employing mean species trait values to predict community responses to ongoing climate change risks inadequately describing key functional differences between populations and individuals within and between species.

4.5.1 Variation in functional traits across the species range

Elevation strongly influenced needle size, with trees from low elevations having larger needles (length, area and mass) than those at higher elevations. Needle size is typically influenced by the most limiting environmental factor (Schoettle and Rochelle 2000), with small leaves expected for plants experiencing extreme drought (Meier and Leuschner 2008), high or low temperature, nutrient shortages or high-radiation (Pérez-Harguindeguy et al. 2013). Our findings follow expectations of patterns across elevation gradients, with needle size likely to be largely temperature driven, since plant productivity is tightly coupled with air temperature and low elevation sites in our study region are characterised by warmer temperatures (Hatfield & Prueger, 2015; Körner et al., 1986; Wright et al., 2017). Large needles at lower elevation suggest water availability is sufficient to prevent desiccation despite high temperatures (Scoffoni et al. 2011), with mean annual rainfall in the lowlands as high as 3,756 mm per year (Shiau and Huang 2015). Trees at low elevations may be maximising resource capture when availability is high.

Unexpectedly, SD increased with elevation. Trees are expected to restrict water loss at high elevations (Schoettle and Rochelle 2000), where humidity and rainfall are typically low (Körner, 2007; Leuschner, 2000). Declining SD with elevation has been observed in conifers, such as *P. flexilis* (Schoettle and Rochelle 2000), *P. contor*ta and *Abies lasiocarpa* in the dry Mid-Southern Rocky Mountains (Hultine and Marshall 2000). With high humidity across the elevation gradient in Taiwan, low SD is unlikely to be a drought response *per se* (Beerling and Chaloner 1993, Luomala et al. 2005). However, it may be linked to water economy, as stomata may close due to high vapour pressure deficit or temperatures rising above plant photosynthesis thresholds in the humid tropics (Oren et al. 1999, Doughty and Goulden 2009, Duursma et al. 2014). Changes in CO_2 partial pressure may be influential, with SD increasing as CO_2 partial pressure declines towards higher elevation and plants maximise carbon gain (Woodward and Bazzaz 1988, Mott 2009, Pato and Obeso 2012). Additionally, a trade-off may exist between SD and stomata size, with small stomata able to respond more rapidly to changing conditions, but present in higher densities (Wang et al., 2014). Our findings more closely match responses of *P. roxburghii* in the Himalayas and *P. koraiensis* and *Picea crassifolia* in similar systems in China, attributed to factors such as changes in temperature, light, humidity and CO_2 concentration with elevation (Gou et al. 2005, Zhou et al. 2012, Tiwari et al. 2013). Trade-offs between water and CO_2 availability across the species range are likely to vary between temperate and tropical systems and could be further explored through common garden and controlled environment experiments to identify the extent of environmental and genetic drivers.

Aspect differences further explained some of the observed needle trait variation for all traits except SLA, whilst slope influenced needle thickness and mass. Smaller needles and higher SD were observed on east facing slopes, whilst larger needles were common to moderately steep slopes (~15-25^{o}). High variability in vegetation across Taiwan’s mountain forests has been linked to slope and aspect differences, with east and south facing slopes experiencing the greatest gains in forest area through treeline advance between 1963 and 2016 (Morley et al. 2020), and moderately steep, east facing slopes experiencing the highest seedling recruitment (Greenwood et al. 2014, 2015). These differences are likely driven by variation in factors such as microclimate (Lembrechts and Lenoir 2019) and soil moisture across different topographies (Körner, 2007; Lambrecht & Dawson, 2007), resulting in variations in stand development, composition and interspecific competition which likely further influence trait variation (Vilà-Cabrera et al. 2015). However, uneven sampling across slope and aspect categories across the elevation range, due to local variation in the distribution of the species, must also be considered, with elevational effects potentially masking slope and aspect differences.

Despite significant associations of traits with elevation, slope and aspect, unexplained trait variation ranged from 41-92%. Such variability is unsurprising given the high environmental variability across the elevation range in this highly topographically variable environment. Needle thickness was particularly poorly explained by elevation, slope and aspect (15% of variance). Although the positive correlation between LDMC and needle thickness may suggest an association between thickness and other measures of needle size, needle thickness is generally considered independent from other traits and more complex (Roche et al. 2004). However, it may be linked to drought, nutrient shortages, older leaves (Roche et al. 2004, Pérez-Harguindeguy et al. 2013) or herbivore defence (Hanley et al. 2007). Along with SD, needle thickness was a key contributor to the second component axis (PC2), suggesting a link between water availability and needle thickness, perhaps driven by factors such as soil and microclimate. Identifying the sources of additional key influential factors acting along with elevation related temperature changes to drive trait expression will provide more accurate insights on plant responses to environment.

The high variation among the resource-use traits of LDMC and SLA suggests a spectrum of resource allocation within the species. LDMC and SLA were related, following the widely accepted expectation that these traits show opposite trends to one another, as observed in the global LES (Wilson et al. 1999). However, overall, LDMC and SLA were poorly explained by differences in topography (fixed effects variance 8% and 0.07% respectively), suggesting a substantial contribution from alternative (unaccounted for) factors. Elevation appeared influential in resource allocation, with significant declines with increasing elevation of LDMC and the PC2 axis of variation, and a significant increase in PC1 with elevation. Differentiation with temperature and water appear likely, due to the close association of PC1 and needle size (length, area and mass) and PC2 with needle thickness and SD. However, observed intraspecific trait patterns may be linked to local scale biotic interactions varying with elevation, as

P. taiwanensis occurs in mixed stands at low elevations and monoculture at higher elevations (Boucher et al., 2013; Cárdenas et al., 2014) and interspecific interactions are considered to be stronger towards lower elevations (Hargreaves et al. 2019). The decline in LDMC with elevation suggests a shift in resource-use strategy from productive at low elevations to persistence at high elevations. Whilst the SLA and LDMC variability we observe is consistent with the LES, the relationship is likely driven by local-scale factors rather than climate, allowing contrasting strategies under similar climatic conditions across elevations. Thus, LES-climate relationships alone may be only partially informative given the importance of local-scale factors in driving resource allocation. Ultimately, these variations in resource-use strategy could substantially impact the response of individuals to changes in environment and climate.

4.5.2 Implications of trait variation

Differences in function are relevant in the context of community assembly, population dynamics and ecosystem processes under ongoing environmental change, with populations of the same species capable of responding differently (Bolnick et al. 2011, Kichenin et al. 2013, Siefert et al. 2015, Vilà-Cabrera et al. 2015, Rosas et al. 2021, Tito et al. 2021). For example, intraspecific variation in root and leaf traits can drive differences in soil stability (Ali et al. 2017), rates of leaf litter decomposition (Lecerf and Chauvet 2008) and radial growth rates (Laforest-Lapointe et al. 2014). Whilst the extent of intraspecific variation will differ between species, traits and ecological contexts (Kattge et al., 2011; Vilà-Cabrera et al., 2015), our current understanding of these differences is limited. Across species ranges there are many factors that can make sites suitable for species persistence or migration, resulting in disparities between observations and predictions on species range shifts within and between species (Bohner and Diez 2020, O’Sullivan et al. 2021). However, low-elevation populations are likely to be at greatest risk of elevated vulnerability to rising temperatures, with populations of *P. taiwanensis* growing in warmer conditions at lower elevations showing reduced growth and poor overall performance compared to their higher elevation counterparts (Ruiz-Benito et al. 2015). With many trees now situated in rapidly changing conditions (Feeley et al. 2011, Fadrique et al. 2018, Esquivel-Muelbert et al. 2019), greater understanding is needed of the drivers of key functional differences, the variability around mean trait values and the interaction between climatic and local-scale factors with traits for community and ecosystem level impacts to be accurately predicted.

Although collecting new intraspecific trait data will not always be possible (Albert et al., 2011; Martin et al., 2017), the TRY global plant trait database provides an opportunity to rapidly quantify intraspecific differences. Yet, many species do not have sufficient data for accurate assessments of intraspecific trait variability, making uncritical comparisons of mean trait values for many species ineffective for addressing differences at the local scale, along heterogeneous environmental gradients and the regional scale for broadly distributed species. Across the *Pinus* genus, species frequently had insufficient data for intraspecific comparisons and where sufficient data were available, we demonstrate considerable trait variation within and between species. Whilst 20 measurements has been reported as the minimum acceptable threshold to capture intraspecific variation (Kattge et al., 2011; Kattge et al., 2020), larger sample sizes may be required for highly variable species. For example, *P. taiwanensis* represented by mean leaf length in Huisun Forest would give a value of 178.7mm, whilst a mean from the highest sample location on Hehuanshan would be 46% lower at 82.6mm. Taking population means rather than species means (Albert et al., 2010) or including the standard deviation with mean estimates will improve the species averaging method (Messier et al. 2010). Capturing variability in key areas and across environmental gradients will allow more accurate predictions to be made of changes in vegetation and the ecological implications of key functional differences (Albert et al., 2011; Martin et al., 2017; Messier et al., 2010; Siefert et al., 2015; Siefert & Ritchie, 2016; Vilà-Cabrera et al., 2015; Yang et al., 2018).

Here, we demonstrate the extent of trait variation across the full elevation range of a particularly widely distributed pine, *Pinus taiwanensis*. Whilst research on trait variation frequently focusses on differences between species, we provide evidence of large intraspecific needle trait and resource-use strategy variation, with substantial differences between individuals linked to elevational temperature variation and interacting drivers likely further contributing to variation. We illustrate the risk of underestimating variability, which could have substantial implications for species comparisons, particularly in highly heterogenous environments. Functional variation is crucial to understand and account for in the context of using mean species traits to predict population resilience, distribution shifts, conservation and management. With intraspecific variation emerging as a fundamental component of functional trait differences, improved understanding of variation across wide environmental gradients will provide critical insight on changes in vegetation over coming decades.

4.6 Data availability statement

The *Pinus taiwanensis* trait dataset used here is available at DataSTORRE at the University of Stirling (http://hdl.handle.net/11667/188) and has been submitted to the TRY global plant trait database.

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4.8 Supplementary material

Table 4.S2: Location, elevation, slope and aspect information of Pinus taiwanensis sample sites in the Central Mountain Range of Taiwan.

Site code	Region	Mean elevation (m a.s.l.)	Slope gradient (º)	Aspect (º)	Coordinates
Hu1	Huisun Forest	495	19	46	N24º04.647’ E120 º59.684’
P1	Puli	690	14	356	N23º59.723’ E121º04.572’
Hu3	Huisun Forest	770	19	269	N24 º 05.308’ E121 º 02.084’
Hu2	Huisun Forest	752	22	66	N24 º 05.308’ E121 º 02.084’
R1	Ren’ai township	1199	29	174	N24 º 01.44’, E121 º 08.656’
R2	Ren’ai township	1597	21	152	N24 º 02.250’ E121 º 09.392’
W1	Wuling farm	1759	30	100	N24 º 21.474’ E121 º 18.711’
W2	Wuling farm	1885	24	297	N24 º 20.785’ E121 º 19.058
L1	Lishan	2073	23	288	N24 º 14.040’ E121 º 15.859’
L2	Lishan	2303	46	343	N24 º 13.358’ E121 º 17.617’
L3	Lishan	2494	13	93	N24 º 12.048’ E121 º 17.848’
He1	Hehuanshan	2616	35	127	N24 º 10.686’ E121 º 18.251’
He2	Hehuanshan	2731	34	153	N24 º 06.999’ E121 º 14.038’
He3	Hehuanshan	2959	23	108	N24 º 09.759’ E121 º 17.337’
He4	Hehuanshan	3106	25	71	N24 º 09.758’ E121 º 17.336’

Table 4.S3: Maximum, minimum, mean, standard deviation, coefficient of variation (CV) and 95% confidence intervals of Pinus taiwanensis needle trait measurements from sample sites in the Central Mountain Range of Taiwan.

Needle trait	Minimum	Maximum	Mean	Standard deviation	CV (%)	95% CI	Unit
Length	54.00	220.00	125.87	36.06	29	122.58, 129.17	mm
Area	53.00	280.00	116.49	36.72	32	116.48, 116.50	mm^2
Fresh mass	15.25	140.35	58.04	20.64	36	56.15, 59.92	mg
Dry mass	4.00	71.00	22.61	9.86	44	21.71, 23.51	mg
Thickness	0.10	0.80	0.43	0.10	23	0.42, 0.43	mm
SD	0.02	0.18	0.06	0.02	33	0.05, 0.06	mm^2
LDMC	134.43	651.77	386.97	75.88	20	381.20, 392.74	mg g^{-1}

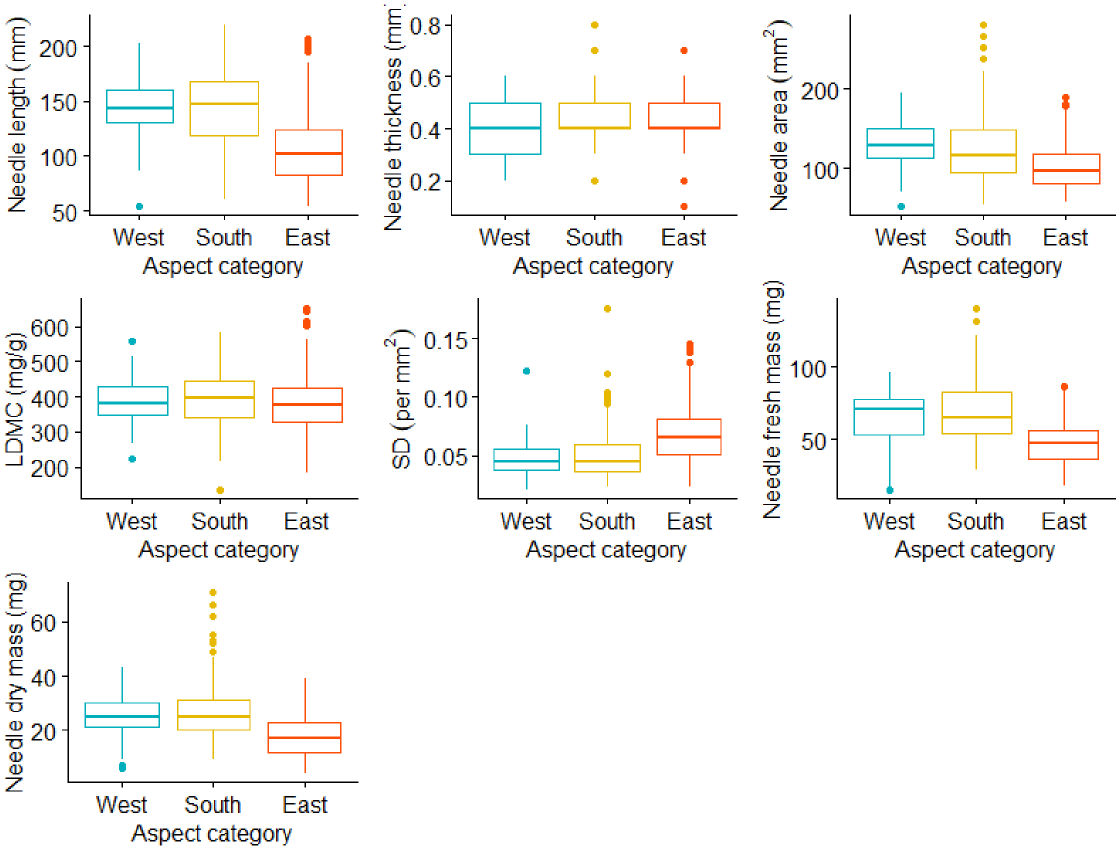

Fig.4.S1: *Pinus taiwanensis* needle trait values across aspects from samples taken in the Central Mountain Range of Taiwan. SLA = Specific leaf area, LDMC = leaf dry matter content, SD = stomatal density

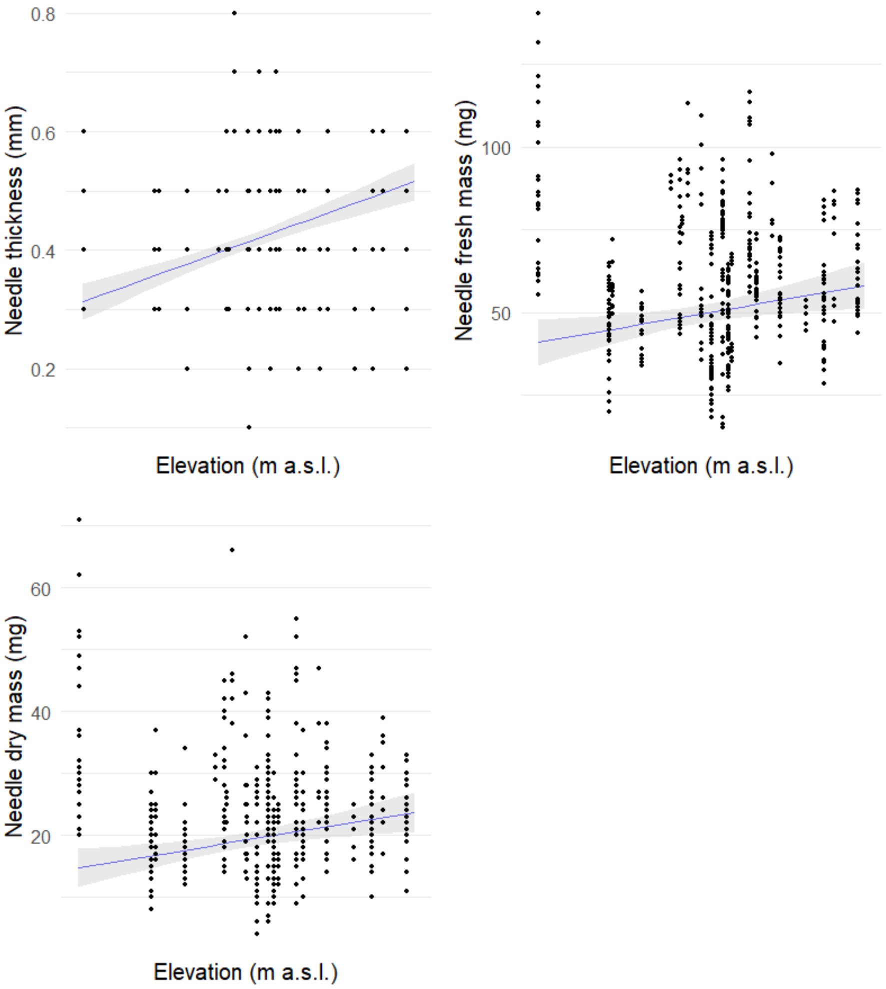

Fig.4.S2: *Pinus taiwanensis* needle trait values per tree with slope angle for samples taken in the Central Mountain Range of Taiwan. SLA = Specific leaf area, LDMC = leaf dry matter content, SD = stomatal density

Table 4.S3: Summary of the selected models which included slope and aspect for each trait measured on Pinus taiwannsis needles sampled from the Central Mountain Range of Taiwan. Selected models were the simplest model with the lowest AIC which still included elevation as a predictor. More complex models were chosen only if they reduced AICc by >2 from a simpler model. Aspect results give significance of differences between groups.

Trait	**Model**	**Aspect results**			**Slope results**		
		p (south and west)	**p (south and east)**	**p (west and east)**	**p**	**Scaled slope estimate**	**Unit**
Length	~ elevation + aspect	0.1204	0.0457	0.0010	NA	NA	mm
Thickness	~ elevation + aspect + slope + aspect*slope	0.4217	0.2468	0.8718	0.0006	0.047	mm
Area	~ elevation + aspect	0.4448	0.1889	0.0752	NA	NA	mm^2
LDMC	~ elevation + aspect + elevation*aspect	0.1600	0.2421	0.6154	NA	NA	mg/g
SD	~ elevation + aspect	0.0398	0.5294	0.0089	NA	NA	per mm^2
Fresh mass	~ elevation + aspect + slope + aspect*slope	0.8300	0.0009	0.0121	0.1826	4.021	mg
Dry mass	~elevation + aspect + slope + aspect*slope	0.6392	0.0019	0.0365	0.1204	2.109	mg

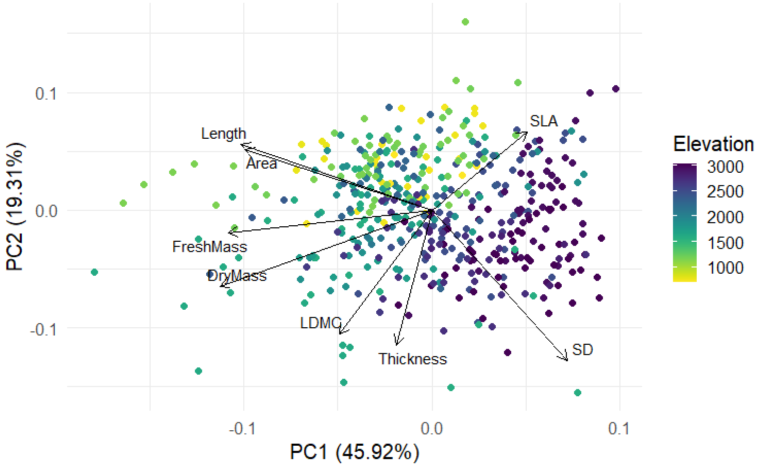

Fig.4.S3: The first two components of principal component analyses (PCA) of *Pinus taiwanensis* needle trait values taken across an elevation gradient in the Central Mountain Range of Taiwan. Elevation given in m a.s.l.

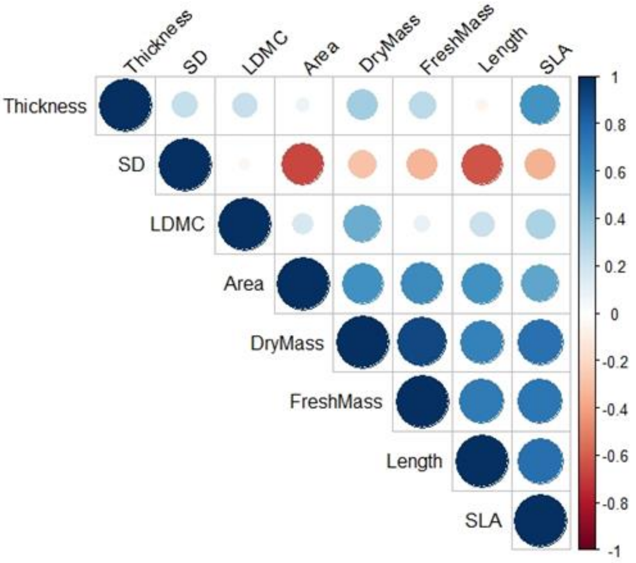

Fig.4.S4: Correlation matrix of *Pinus taiwanensis* needle traits from samples across the elevation range in the Central Mountain Range of Taiwan.

Table 4.S4: Number of species with records, number and percentage of species which met the threshold of =>20 measurements (Kattge et al. 2011, 2020) and the mean number of measurements for Pinus species within the TRY database with records for needle thickness, length, leaf dry matter content (LDMC) and specific leaf area (SLA).

Trait	**Number of species with records**	**Number of species with =>20 records**	**% species with =>20 records**	**Mean number of measurements**
Needle thickness	17	7	53	22
Needle length	72	7	12.5	4
LDMC	17	5	29	12
SLA	54	27	50	18.5

Table 4.S5: Number of publicly available measurements on members of the Pinus genus in the TRY database for several commonly measured needle leaf traits.

Species	**Needle thickness**	**Needle length (with and without petiole)**	**LDMC**	**SLA (with and without petiole)**
Pinus albicaulis	0	2	0	2
Pinus amamiana	0	0	0	2
Pinus aristata	0	3	72	50
Pinus arizonica (including subsp. cooperi and var stormiae)	0	2	0	0
Pinus armandii (including var. dabeshanensis)	2	6	2	2
Pinus attenuata	0	4	0	0
Pinus attenuradiata	0	0	0	0
Pinus ayacahuite	0	0	0	0
Pinus balfouriana (including subspp. austrina and balfouriana)	0	2	0	0
Pinus banksiana	0	4	0	389
Pinus bhutanica	0	0	0	0
Pinus brutia (including vars. eldarica and pityusa)	0	2	0	0
Pinus bungea	0	0	0	1
Pinus bungeana	0	4	0	2
Pinus canariensis	43	20	0	47

Pinus caribaea (including vars. bahamensis and hondurensis)	0	2	0	1
Pinus cembra	0	2	10	11
Pinus cembroides (including var. bicolor)	0	22	0	40
Pinus clausa	0	4	0	58
Pinus contorta (including vars. contorta, latifolia and murrayana)	0	6	0	66
Pinus coulteri	0	2	0	1
Pinus cubensis	0	0	0	0
Pinus culminicola	0	0	0	0
Pinus dalatensis	0	0	0	0
Pinus densata	0	2	0	0
Pinus densiflora	0	6	0	0
Pinus devoniana	0	0	0	0
Pinus douglasiana	0	0	0	0
Pinus durangensis	0	0	0	0
Pinus echinata	0	8	0	1
Pinus edulis	0	2	69	53
Pinus edunata	0	0	0	0
Pinus elliottii (incouding var. densa)	0	6	0	120
Pinus engelmannii	0	3	0	0
Pinus fenzeliana	0	4	0	0
Pinus flexilis (including var. reflexa)	40	22	0	48
Pinus georginae	0	0	0	0
Pinus gerardiana	0	4	0	0
Pinus glabra	0	3	0	62
Pinus greggii	0	0	0	0
Pinus hakkodensis	0	0	0	0
Pinus halepensis	42	25	5	196
Pinus hartwegii	0	0	0	0
Pinus heldreicichii	3	8	0	12
Pinus henryi	0	2	0	0
Pinus herrerae	0	0	0	0
Pinus hwangshanensis	0	0	0	0
Pinus jaliscana	0	0	0	0
Pinus jeffreyi	0	3	0	7
Pinus kesiya (including vars. kesiya and langbianensis)	1	2	1	1
Pinus koraiensis	7	5	12	13

Pinus krempfii	0	0	0	0
Pinus lambertiana	0	2	0	2
Pinus latteri	0	2	0	0
Pinus lawsonii	0	0	0	0
Pinus leiophylla (including var. chihuahuana)	0	2	0	0
Pinus longaeva	0	2	0	0
Pinus luchuensis	0	0	0	0
Pinus lumholtzii	0	0	0	0
Pinus luzmariae	0	0	0	0
Pinus massoniana	7	5	12	24
Pinus maximartinezii	0	0	0	0
Pinus maximinoi	0	0	0	0
Pinus merkusii	0	0	0	0
Pinus monophylla	0	2	0	4
Pinus montezumae	0	0	0	0
Pinus monticola	0	2	0	7
Pinus morrisonicola	0	2	0	0
Pinus mugo (including subsp. mugo)	0	7	0	1
Pinus muricata	0	2	0	1
Pinus nelsonii	0	0	0	0
Pinus nigra (including subspp. dalmatica, laricio, nigra, pallasiana and salzmannii)	0	14	0	128
Pinus occidentalis	0	0	0	0
Pinus oocarpa	0	0	0	0
Pinus pallasiana	0	0	0	0
Pinus palustris	0	4	2	77
Pinus parviflora (including var. pentaphylla)	0	4	0	0
Pinus patula (including var. longipedunculata)	0	0	0	1
Pinus peuce	4	2	2	2
Pinus pinaster (including subspp. escarena and pinaster)	22	5	0	225
Pinus pinceana	0	0	0	0
Pinus pinea	2	2	0	27
Pinus pister	0	0	0	34
Pinus ponderosa (including var. scopulorum)	42	23	174	247

Pinus praetermissa	0	0	0	0
Pinus pringlei	0	0	0	0
Pinus pseudostrobus (including var. apulcensis)	0	0	0	0
Pinus pumila	0	0	0	6
Pinus pungens	0	3	0	1
Pinus quadrifolia	0	3	0	0
Pinus radiata	0	4	0	88
Pinus remota	0	0	0	0
Pinus resinosa	0	2	0	29
Pinus rigida	0	5	0	10
Pinus rigidrt	0	0	0	0
Pinus roxburghii	0	2	0	0
Pinus rzedowskii	0	0	0	0
Pinus sabiniana	0	2	0	1
Pinus schwerinii	0	0	0	0
Pinus serotina	0	6	2	9
Pinus sibirica	0	4	0	0
Pinus squamata	0	0	0	0
Pinus strhinicum	0	0	0	0
Pinus strobiformis (including subsp. veitchii)	40	22	87	99
Pinus strobus (including var. chiapensis)	0	4	15	79
Pinus sylvestriformis	0	0	0	0
Pinus sylvestris (including vars. hamata, mongholica and mongolica)	34	32	440	1171
Pinus tabuliformis (including var. mukdensis)	18	4	17	35
Pinus taeda	40	26	0	31
Pinus taiwanensis (including var. damingshanensis)	0	6	0	0
Pinus tecumumanii	0	0	0	0
Pinus teocote	0	0	0	0
Pinus thunbergii	0	4	0	3
Pinus torreyana (including subsp. insularis)	0	2	0	1
Pinus tropicalis	0	2	0	0
Pinus urcinata (including subsp. uliginosa)	0	2	10	68

Pinus virginiana	40	24	0	42
Pinus wallichiana	0	4	0	0
Pinus wangii	0	2	0	0
Pinus x murraybanksiana	0	0	0	0
Pinus x rhaetica	0	0	0	0
Pinus x sondereggeri	0	0	0	0
Pinus yunnanensis (including var. pygmaea)	0	6	0	0

Chapter 5

Impacts of predicted climate change on recruitment across the distribution range of a subtropical pine

5.1 Abstract

Ongoing climate change is having widespread impacts on global plant species distributions. Seedling life stages are particularly sensitive to changes in climate and can influence species distributions and abundance at the population and community scale. Yet, our current understanding of variability in and drivers of responses of seedlings to climate change is limited, resulting in patchy understanding of how populations may respond to rising temperatures across species ranges. To address this information gap, we assessed the responses of the early life stages of a widely distributed subtropical conifer *Pinus taiwanensis* across an elevation gradient to projected changes in climate. Seeds from low-, mid- and high-elevation trees were grown in controlled climate chambers representing current climate conditions at the 1st and 9th deciles of the species elevational distribution and future projected temperature increase of 5 °C from worst-case scenario predictions of warming above pre-industrial levels in East Asia. We investigated seed germination rates, time to emergence, survival, investment in roots vs shoots and leaf traits of length, thickness and stomatal density. We found considerable variation in the responses of *P. taiwanensis* seedlings across the broad elevation range to projected changes in temperature. Following expectations of higher temperatures promoting seedling growth, we found that increased temperature significantly reduced the time to emergence and promoted greater biomass gain. However, seed elevation of origin was highly influential in deciding the percentage of seeds which emerged, with poor germination from low-elevation seedlings and consistently higher performance in terms of germination percentage and biomass allocation from mid-elevation seedlings than high-elevation seedlings, particularly under the warmest temperatures. We demonstrate substantial variation in the response of a single species to changes in temperature linked to range location. Our findings highlight that it should not be assumed that populations across a species range will react 'as one' to environmental changes. Greater understanding is needed of the variability in early seedling development for reliable forecasts to be made of the potential impacts of climate change on species distributions.

5.2 Introduction

Climate is a key factor influencing the distributions of plant species globally (Woodward 1987b, Diamond 2018). Variations in temperature are highly influential in deciding plant germination, growth and survival (Lloret et al. 2009, Standish et al.

2012), and can therefore influence species distributions and abundance at the population and community scale (Walck et al. 2011). With climate change expected to continue into coming decades (IPCC 2021), considerable alterations to the distribution of species are likely to occur, with frequent upward latitudinal and altitudinal shifts already observed (e.g. Grabherr et al. 1994, Harsch et al. 2009, Feeley et al. 2011, Ruiz-Labourdette et al. 2012, Fadrique et al. 2018). However, responses to environmental change are not uniform, with variation possible in the early growth and development of seedlings between species and across space and time, due to different environmental pressures and tolerances (Arft et al. 1999, Matías and Jump 2014). Ultimately, intraspecific differences in responses to climate change can cause variations in the size and direction of distribution shifts (Morin and Thuiller 2009, O’Sullivan et al. 2021) and result in important variations in the ability of populations to persist (Fox et al. 2019). For accurate predictions to be made of the impacts of rapidly changing climate on forest tree species distributions, information is needed on variations in seedling establishment under different environmental conditions. This information will improve our understanding of population dynamics during a key developmental bottleneck (Ibáñez et al. 2007, Meineri et al. 2013, Matías and Jump 2014, Copenhaver-Parry et al. 2020).

The early life stages of plants are fundamental to population dynamics, affecting progression to adulthood and success during later life (Ibáñez et al. 2007, Vanderwel et al. 2013). Seedlings are at particular risk of mortality during their transition from germination to emergence (James et al. 2013), and continue to be vulnerable once established due to their limited root system, minimal stored resources and susceptibility to attack from insects and pathogens (Karban and Thaler 1999, Jackson et al. 2009). Seedlings experience different environmental conditions to their adult counterparts due to their limited development, can be more responsive to changes in environmental conditions and often occupy more specific niches than adult trees (Comita and Engelbrecht 2014, Greenwood et al. 2015, Smithers et al. 2018). Climate change can also impact seedlings indirectly through the conditions experienced by the maternal plant (Meineri et al. 2013), with variation in dispersal ability, persistence in the soil seedbank and the size, number and maturity of seeds (Walck et al. 2011, Anadon-Rosell et al. 2020). Understanding the mortality risk during the early stages of growth is particularly important for abundant species within existing communities (Diaz et al. 2020), as they have the potential to have a disproportionately large influence on future forest composition and function. Since seedlings could be particularly vulnerable under climate change and strongly influence species distributions over coming decades, information on responses of early life stages of plants to climate change is urgently needed.

There are two main responses of plants to climate change that can enable populations to persist; shifting to more suitable habitats or adjusting to new conditions through genetic adaptation, phenotypic plasticity or both (Aitken et al. 2008, Corlett and Westcott 2013, Tito et al. 2021). For long-lived species such as trees, existing resilience to environmental conditions through phenotypic plasticity alongside adaptation from standing genetic variation could be crucial for populations to survive into coming decades, as the rate of climate change may outpace their capacity to migrate (Aitken et al. 2008, Matías and Jump 2014, Canham and Murphy 2017, Liang et al. 2018, Vizcaíno-Palomar et al. 2020). Whilst climate change will affect species differently (Smithers et al. 2018), considerable genetic and environmental variation can also occur across individual species ranges, resulting in local and population level adaptations and responses to changing environmental conditions (Howe et al. 2003, Savolainen et al. 2007, Reich and Oleksyn 2008, Matías and Jump 2014, Anadon-Rosell et al. 2020, Ignazi et al. 2020, Tito et al. 2021). Variation can occur in seedling recruitment and survival (Cavieres and Arroyo 2000), with differences in factors such as time to emergence (Verdú and Traveset 2004), investment in roots vs shoots (Lloret et al. 1999) and density of stomata affecting seedling success (Premoli and Brewer 2007, Donnelly et al. 2016). Notable phenotypic differences may occur at the margins of species distributions, where individuals typically experience the most stressful environmental conditions, resulting in differences compared to individuals at the core of distributions (Ignazi et al. 2020). Variability is expected to be particularly high in species with wide distribution ranges (Matías and Jump 2014), as they demonstrate germination success under a broad range of conditions (Cavieres and Arroyo 2000). However, quantification of variation in response to future climates across individual species ranges are limited, resulting in limited understanding of how climate change may influence regeneration across different populations of the same species (Reich and Oleksyn 2008, Valladares et al. 2014).

For more accurate predictions to be made on future species distributions, information is needed on both the variation in responses of forest trees to climate change and the drivers behind these differences, particularly in the tropics and subtropics (Lenoir and Svenning 2015, Uriarte et al. 2018). Whilst higher temperatures could accelerate rates of physiological processes and primary productivity, providing a competitive advantage (Girardin et al. 2010, Hatfield and Prueger 2015), trees may be constrained by their response to increased temperatures by water limitation where water demand increases and availability declines or becomes less predictable (McDowell et al. 2010, Sánchez-Salguero et al. 2012). Trade-offs between growth and survival are likely, which could result in substantial variation in functional strategies between individuals, and ultimately, differences in responses to climate change (Seiwa 2007, Matías and Jump 2014). Although warming temperatures may be expected to enhance recruitment at the coldest parts of the species distribution range and reduce recruitment at the warmest parts (Matías and Jump 2014), climate change is complex and interactions with non-climatic drivers can result in non-uniform and individualistic responses (O’Sullivan et al. 2021). Our understanding of the variations in the early development of seedlings is particularly limited for tropical trees (Verdú and Traveset 2004, Bhadouria et al. 2016), restricting our understanding of how tropical ecosystems will respond to climate change.

Experimentally manipulating climate provides a powerful tool to identify potential responses of plants to climate change, independent of potential confounding effects such as biotic interactions or habitat characteristics (Lloret et al. 2009). Given the need to better understand intraspecific variability in recruitment and responses to climate change across the tropics and subtropics, we investigated the capacity of the early life stages of a widely distributed subtropical conifer, *Pinus taiwanensis*, across a wide elevational distributional range in Taiwan to tolerate projected temperature increases under climate change. We focus on the most vulnerable stages for trees; germination, seedling early growth and survival. We aimed to address the following questions; (1) do seedlings from maternal plants from high-, mid- and low-elevations differ in their regeneration capacity? (2) do seedlings show different responses to predicted future temperatures than current temperatures? (3) is seed elevation of origin modulating seedling responses to future temperatures?

5.3 Materials and Methods

5.3.1 Study system and species

Pinus taiwanensis Hayata (Pinaceae) is widespread across the island of Taiwan, inhabiting diverse climatic and habitat conditions across the Central Mountain Range. Considered a Taiwanese endemic (Fu et al. 1999), the species extends over an exceptionally large elevation range from around 500 to 3,200 m a.s.l. (data extracted from 4th Taiwan National Forest Inventory, see Chapters 2 and 3). This elevational range equates to a temperature range of approximately 13.5 ° C, given an altitudinal lapse rate of -0.5 ° C 100 m^{-1} for Taiwan (Guan et al. 2009). Taiwan has a subtropical climate, with warm and humid conditions in the lowlands that span through temperate to alpine conditions at higher altitudes (Li et al., 2013). The lowlands are dominated by urban and agricultural areas, but natural forests predominate across the mountainous terrain, transitioning through subtropical to temperate forest types (Li et al., 2013). *P. taiwanensis* increases in abundance with elevation, found scattered through mixed forest and open habitat at low elevations and in monodominant stands at high elevations (Li et al. 2013). It is an early successional species, primarily favouring high light and humidity (Cai and Liu 2017) and is able to regenerate quickly on disturbed land (Chou et al. 2009). Data from Alishan meteorological station indicate that temperatures in Taiwan in 2012 were around 1.05°C higher than the 1934-1970 average, whilst precipitation remained largely unchanged (Jump et al. 2012).

5.3.2 Seed source

Unopened pine-cones were collected from mature adult trees between 7th and 30th November 2019 across an elevation gradient of 1,198-3,032 m a.s.l. in the northern part of Taiwan's Central Mountain Range. Sites included monodominant stands, mixed forest and scattered individual trees in open habitat, due to changes in forest composition and increasing abundance of *P. taiwanensis* with elevation preventing sampling from forests with consistent structure. A total of 11 maternal trees were sampled across three elevation categories; low, medium and high. Multiple cones were sampled per tree, with 3 trees sampled at low-elevation, 4 at mid-elevation and 11 at high-elevation. Rare cone production at low-elevations constrained the number of maternal trees for seed collection in this region. Seeds were extracted by heating cones under lamps in well ventilated boxes for several days until they opened and seeds were released, rotating the position of cones once per day to allow approximately even heating across cones. Seeds were weighed to 0.001 g precision in batches of 10 and mean seed mass and standard deviation in grams calculated for each elevation category (low = 8 ± 3 mg, mid = 11 ± 5 mg, high = 8 ± 2 mg). This approach was used to keep the temperature within a reasonable range expected for the species under natural conditions (approximately 10-30°C), as previous experimental trials found that seeds heated in an oven at 50-60°C did not germinate when planted. Once extracted, seeds were stored in paper bags in a fridge at 6°C until sowing.

5.3.3 Experimental design

The experiment was conducted in Snijders Scientific controlled environment chambers at the University of Stirling Controlled Environment Facility. To test the effect of temperature on recruitment of seedlings, four chambers (1.8 m x 0.75 m x 1.2 m) were used to simulate different temperature scenarios. Two main factors were considered (i) elevation of seed source, with three levels, low-, mid- and high-elevation; and (ii) temperature, with four levels, current temperature at high elevation (Current High), projected future temperature at high elevation (Future High), current temperature at low elevation (Current Low) and projected future temperature at low elevation (Future Low) (*Fig.5.1*).

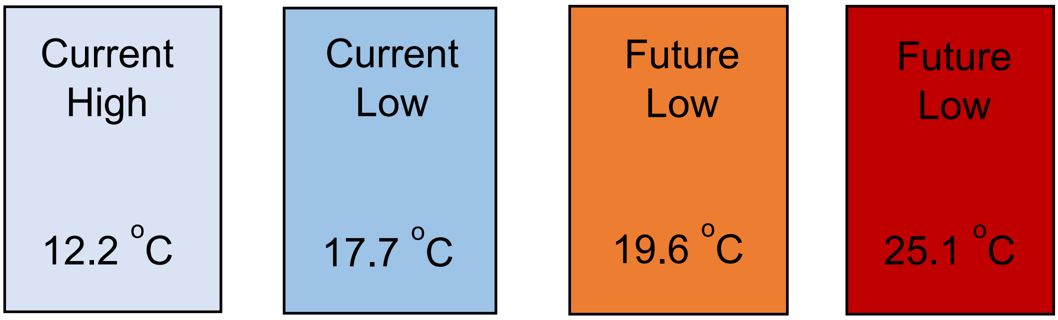

Fig.5.1: Growth chamber daytime temperature scenarios for *Pinus taiwanensis* seedlings. Current High = current temperature at high elevation, Future High = projected future temperature at high elevation, Current Low = current temperature at low elevation, Future Low = projected future temperature at low elevation.

Each chamber was allocated a temperature derived from mean monthly records between 1981-2010 (Taiwan Central Weather Bureau 2020) during the *P. taiwanensis* growing season of March to November (Liu et al. 2018). The mean temperature of the three hottest months from Alishan weather station (2,413m a.s.l.) were used to simulate the mean hottest conditions plants currently experience. High and low elevation temperatures were derived by calculating the 1st and 9th deciles of the elevation range of the seed samples (1,381 and 2,849 m a.s.l) and calculating the difference in temperature from Alishan using the lapse rate in Taiwan of - 0.5 °C for every 100 m elevation gain (Guan et al. 2009). Temperatures were lowered at night, calculated as the mean minimum monthly temperatures from the hottest three months in 2009 and 2010 (July-September), adjusted for the elevational lapse rate. Projected future temperatures were calculated from IPCC 2013 worst-case scenario RCP8.5 of 5.5 °C warming above pre-industrial levels in East Asia in June – August (IPCC 2013b). The worst-scenario was chosen to assess the maximum influence changes in temperature will have on seedlings. To account for current temperatures already being above pre-industrial levels, we selected projected temperatures which were 5 ^{o}C higher than current temperatures. Chosen temperatures were as follows; Current High, 12.2 ^{o}C day, 7.8 ^{o}C night, Future High, 19.6 ^{o}C day, 15.1 ^{o}C night, Current Low, 17.7 ^{o}C day, 13.3 ^{o}C night and Future Low, 25.1 ^{o}C day, 20.6 ^{o}C night. Relative humidity was kept constant at 88%, calculated as the mean at Alishan weather station over the *P. taiwanensis* growth period of March-November. Light intensity was set to the maximum photosynthetic photon flux density for the chambers (around 272 µmol m^{-2} s^{-1} approximately 15 cm above plants) to reflect conditions likely to be experienced by tropical seedlings developing in tall vegetation or understory (Chazdon and Fetcher 1984, Lin et al. 2003). Daily sunshine duration was set to 12 hours, gradually rising at dawn and decreasing at dusk for 1 hour.

Seeds from different trees were pooled into low-, mid- and high-elevation experimental populations. Seeds for experimental investigation were then selected at random. A total of 570 seeds were sown, comprising 224 each from mid- and high-elevation populations and 122 from low-elevation populations, due to restricted seed availability at low elevations. For mid- and high-elevation seeds, 4 seeds were sown per pot, and for low-elevation seeds, 2 seeds were sown in most pots and 3 seeds were sown in 10 of the pots. This resulted in a total of 56 seeds sown per temperature regime for high- and mid-elevation seeds and 26 low-elevation seeds sown in the Current High and Future High chambers, and 35 low-elevation seeds in the Current Low and Future Low chambers. Seeds were sown in root trainer tubes cut from poly-pipe (15 x 15 x 25cm) with a layer of gravel and a metal mesh bottom to aid drainage and a high nutrient compost and sand mix at a 3:1 ratio. Given restrictions on the import of live soil and the need to facilitate mycorrhizal inoculation, pots were irrigated at the start of the experiment with an inoculum made from soil collected near Scots pine (*P. sylvestris*) trees on the University of Stirling campus. For each pot, 150 ml of filtered soil solution was administered on the day of sowing, created from 4 kg soil and 95 g fine roots macerated in 4 litres of water for two days, following a similar procedure to Matías and Jump (2014). Thereafter, pots were watered at least once per week to maintain soil moisture at 25-30% throughout the experiment (Liu et al. 2018). Soil moisture over the surface 5 cm of each pot was measured fortnightly throughout the experiment using a SM200; Delta-T devices; values were recorded 2 days after irrigation events and the first measurements taken 2 weeks after sowing.

Pots were randomly allocated to chambers, ensuring an even distribution of pots from each elevation. Pot positions were rotated randomly twice throughout the experiment, to account for any differences in conditions within the chambers. Seedling emergence was monitored daily until no new seedlings emerged. To maximise experimental population size, where more than one seedling germinated in a pot, additional seedlings were transplanted to new pots and their transplantation status recorded, resulting in one seedling per pot in the final experimental set up. Seedling survival was recorded weekly throughout the experiment.

All surviving seedlings were harvested 24 weeks after sowing. Seedlings were carefully excavated from their pots and divided into above and below ground parts. Aboveground was defined as all plant material above the soil surface. Final shoot and root length were measured, roots were then washed and patted dry, and samples weighed to obtain root and shoot fresh biomass (0.1 mg precision). Two fully expanded leaves were randomly selected from each seedling to assess leaf trait variability. Needle length was measured using a ruler and thickness at the centre of the needle using digital callipers (0.01 mm precision). A microscope was used to count abaxial and adaxial longitudinal stomatal rows (Donnelly et al. 2016). Needle area was derived from needle length and thickness measurements as:

$$Needle\ area = \mathrm{\pi rl} + \mathrm{2rl}$$

where r = thickness and l = length, to account for the curved shape of pine needles (Donnelly et al. 2016). Roots and shoots, along with leaves which were removed for leaf trait measurements, were air dried in paper bags within boxes filled with silica gel for 10 days. Samples were weighed to obtain root and shoot dry biomass (0.0001 g precision). Seed import, storage and seedling experimental, harvesting, and disposal procedures were carried out in strict accordance with licensing conditions agreed with Science and Advice for Scottish Agriculture (SASA) under licence PH/2/2019.

5.3.4 Data analysis

Linear models (LMs) and linear mixed effects models (LMMs) with normal distribution of residuals were used to assess the influence of elevation of origin and chamber temperature as a categorical variable on seedling performance. Whether the seedlings had been transplanted to new pots or not was also incorporated as a fixed predictor in LMs and a random effect in LMMs. LMs were used to model log seedling time to emergence, log final height, root length, log total biomass and root/shoot ratio. LMMs were used to model soil moisture and leaf traits of length, thickness, area and stomatal density, fitted via restricted maximum likelihood (REML). Models were ranked from lowest to highest AIC, with the most parsimonious models selected within two AIC units. Significance of predictors was tested using the 'pbkrtest' package for LMMs and ANOVAs for LMs, comparing models with and without predictors in question.

To test for differences in seedling germination and survival between chambers and elevations, we used generalized linear models (GLM) with a binomial distribution and logit link function, to account for differences in sample sizes between groups. The models with the lowest AIC were selected and the chi-squared test statistic, p-value and pseudo-R^2 obtained using the 'nagelkerke' function in the 'rcompanion' package. All analyses were undertaken using R (R Core Team 2021).

5.4 Results

5.4.1 Seedling germination rate and time to emergence

A total of 209 seedlings emerged between 10 and 110 days after sowing (*Fig.5.2,* Table 5.1). Percentage germination significantly differed between elevation bands (χ^2=157.75, p<0.001, df=2), with the highest percentage germination for mid-elevation populations (54%) followed by high-elevation populations (37%). Low-elevation populations had a low percentage germination rate of five seedlings, comprising 4% of the seeds planted. Due to the small number of low elevation seedlings which germinated, only data from mid- and high-elevation seedlings were used for further analysis. There was no significant difference in germination percentage between chambers, with 47% in the coldest chamber, transitioning to 43%, 41% and 33% with increasing chamber temperature. Seedling time to emergence was significantly influenced by chamber temperature (F=233.9, df=3, 206, p<0.001), but did not significantly differ between mid- and high-elevation samples (29.4 ± 20.0 and 28.3 ± 19.9 days respectively) (*Fig.5.2,* Table 5.1). Emergence was faster in hotter chambers, with an increase of 41 days between the mean time to emergence for the hottest chamber and the coldest chamber.

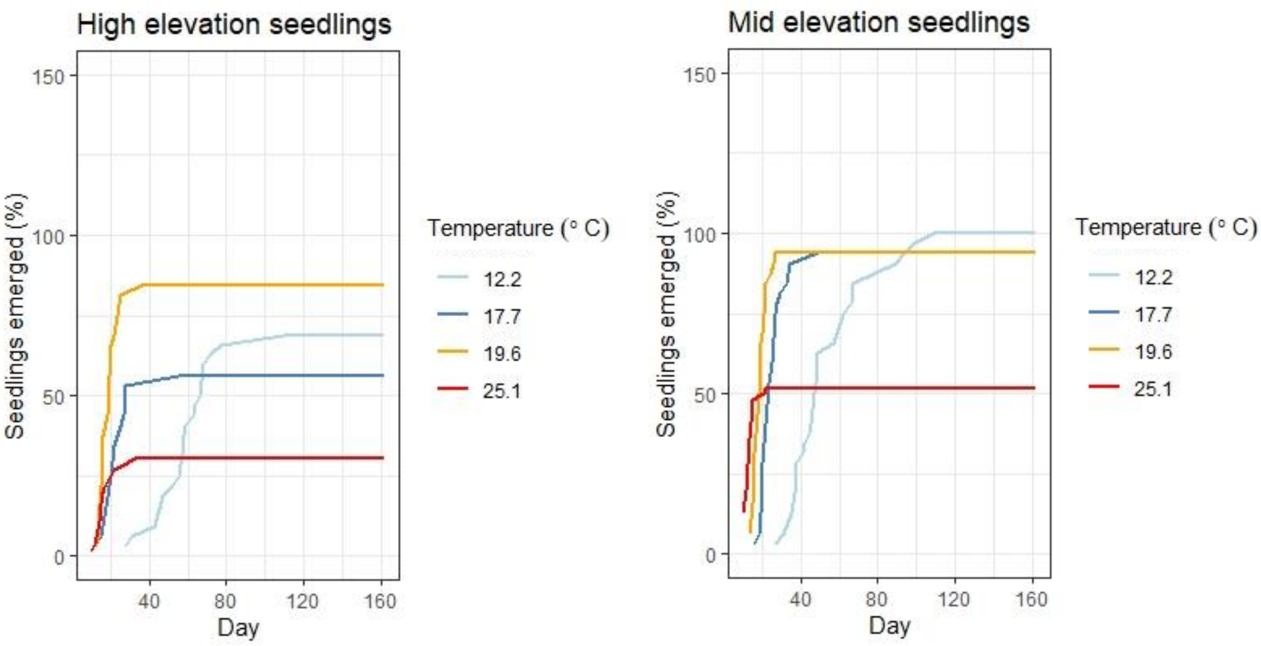

Fig.5.2: Cumulative seedling emergence curves of *Pinus taiwanensis* seedlings from mid- and high-elevation across four temperature chambers throughout the duration of the controlled environment experiment (time to emergence in days).

Table 5.4: Selected models and results for survival, germination and time to emergence of Pinus taiwanensis *seedlings from low-, mid- and high-elevation planted in controlled environment conditions across four temperature chambers. AUC = area under curve.*

Selected model	**Predictors**	**Fixed effects estimates**	**Model results**	**AUC or R^2**
Survival ~ elevation	Elevation	Mid = 1.792 High = 1.744	χ^2=0.014, p=0.906	AUC = 0.62
Germination ~ elevation	Elevation	Low = -2.322 Mid = 3.892 High = 1.946	χ^2= 157.75, df=2, p<0.001	R^2 = 0.51
Log time to emergence ~ temperature	Temperature	12.2^{o} = 3.976 17.7^{o} = -0.830 19.6^{o} = -1.064 25.1^{o} = -1.325	F=233.9, df=3, 206, p<0.001	R^2 = 0.77

5.4.2 Seedling survival

From the seedlings which emerged, 179 survived at the end of the experiment with an overall survival rate of 86%. Whilst differences in elevation were a better explanation for variations in survival rate than chamber temperature, overall there was no significant influence of elevation on seedling survival (χ^2=0.014, p=0.906).

5.4.3 Biomass allocation

Final biomass at harvest was influenced by chamber temperature and elevation of the maternal plant (*Fig.5.3,* Table 5.2). Seedlings were significantly taller in hotter chambers (F=25.21, df=3, p=0.001) with significantly longer roots (F=75.49, df=3, p<0.001). Seedlings from mid-elevations were significantly taller (F=5.20, df=1, p=0.02) with longer roots (F=5.02, df=1, p=0.03). Transplanting seedlings resulted in significantly shorter roots (F=16.45, df=1, p<0.001). Total biomass, expressed as the shoot and root dry weight at harvest, significantly increased with chamber temperature (F=44.50, df=3, p<0.001), as did the allocation of biomass to roots (root/shoot ratio) (F=28.38, df=3, p<0.001). Total biomass was higher for mid-elevation seedlings (F=7.27, df=1, p=0.01). Seedlings which were not transplanted had significantly higher root/shoot ratio (F=5.08, df=1, p=0.03) and total biomass (F=9.11, df=1, p=0.003).

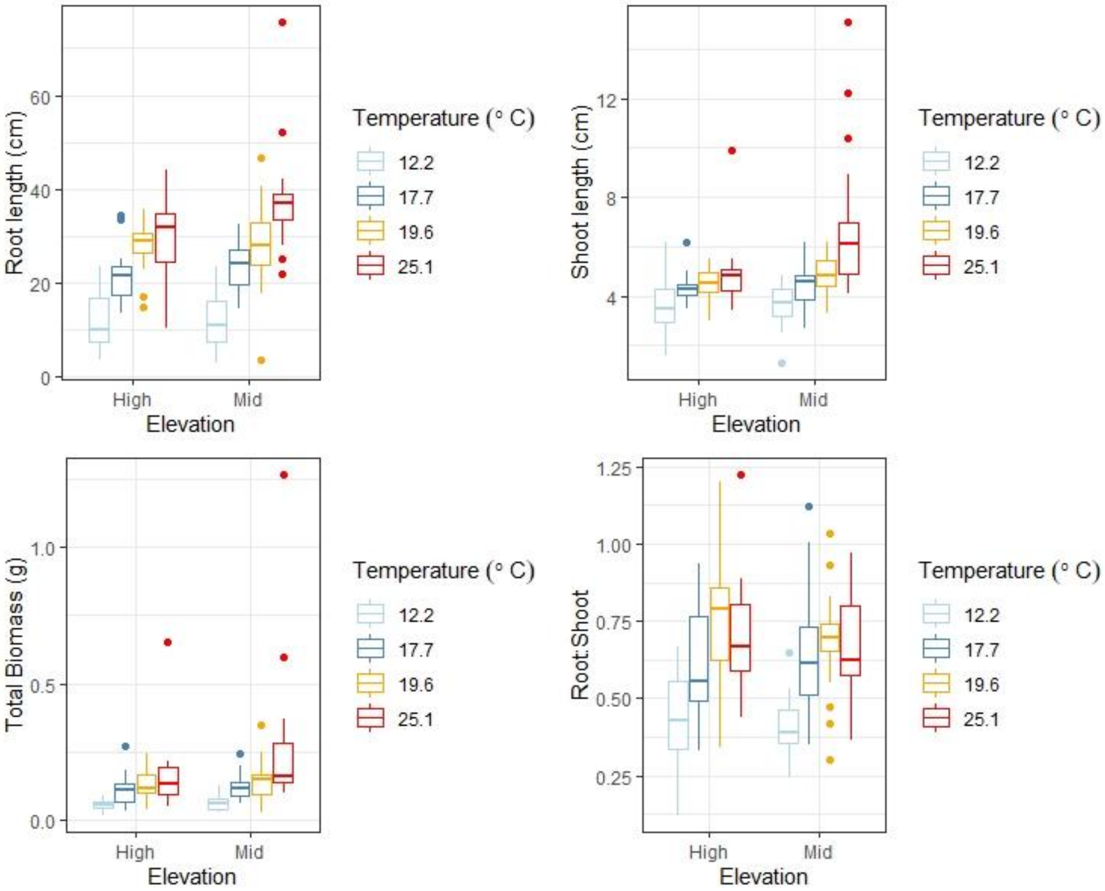

Fig.5.3: Values at harvest of root length, shoot length, total biomass and root/shoot ratio of *Pinus taiwanensis* seedlings from mid- and high-elevation forests planted in controlled environment conditions across four temperature chambers.

Table 5.5: Selected models and results for final biomass traits at harvest of Pinus taiwanensis seedlings from mid- and high-elevation planted in controlled environment conditions across four temperature chambers.

Selected model	**Overall model results**	**Predictors**	**Fixed effects estimates**	**Individual predictor results**	**R^2**
Log final seedling height ~ temperature + elevation	F=20.82, df=4, 166, p<0.001	Temperature	12.2° = 1.20 17.7° = 1.40 19.6° = 1.48 25.1° = 1.68	F=25.206, p=0.001, df=3	0.33
		Elevation	Mid = 1.20 High = 1.29	F=5.2018 p=0.02383, df=1	
Final root length ~ temperature + elevation + transplanted	F=47.81, df=5, 165, p=<0.001	Temperature	12.2° = 12.26 17.7° = 23.38 19.6° = 29.06 25.1° = 34.98	F=75.486, p<0.001, df=3	0.59
		Elevation	Mid = 14.75 High = 12.26	F=5.020, p=0.026, df=1	
		Transplanted	Yes = 12.26 No = 7.79	F=16.453, p<0.001, df=1	
Log final total biomass~ temperature + elevation + transplanted	F=29.19, df= 5, 165, p<0.001	Temperature	12.2°=-2.96 17.7° =-2.26 19.6° =-2.07 25.1° =-1.76	F=44.497, p<0.001, df=3	0.47
		Elevation	Mid = -2.75 High = -2.96	F=7.271, p=0.008, df=1	
		Transplanted	Yes = -3.19 No = -2.96	F=9.11, p=0.003, df=1	
Final root/shoot ratio~ temperature + transplanted	F=21.59. df=4, 166, p<0.001	Temperature	12.2°=0.45 17.7° =0.66 19.6° = 0.75 25.1° =0.70	F=28.382, p<0.001, df=3	0.34
		Transplanted	Yes = 0.39 No = 0.45	F=5.075, p=0.026, df=1	

5.4.4 Needle leaf traits

Needle leaf traits were influenced by chamber temperature, seed elevation of origin and transplantation status (*Fig.5.4,* Table 5.3). Stomatal density significantly declined with increasing chamber temperature (F=6.34, df=3, p<0.001) and mid-elevation samples had significantly lower stomatal density than high-elevation populations (F=15.07, p<0.001, df=1). Needle length significantly increased with temperature (F=38.44, df=3, p<0.001) and was higher for mid-elevation seedlings (F=11.09, df=1, p<0.001). Needle thickness significantly differed between chamber temperatures, but with no clear linear trend (F=9.73, df=3, p<0.001) and was higher for mid-elevation seedlings (F=16.90, df=1, p<0.001). Needle area significantly differed between chamber temperatures, with larger needle area for seedlings in the hottest chamber (F= 16.81, df=3, p<0.001) and was higher for mid-elevation seedlings (F= 17.22, df=1, p<0.001).

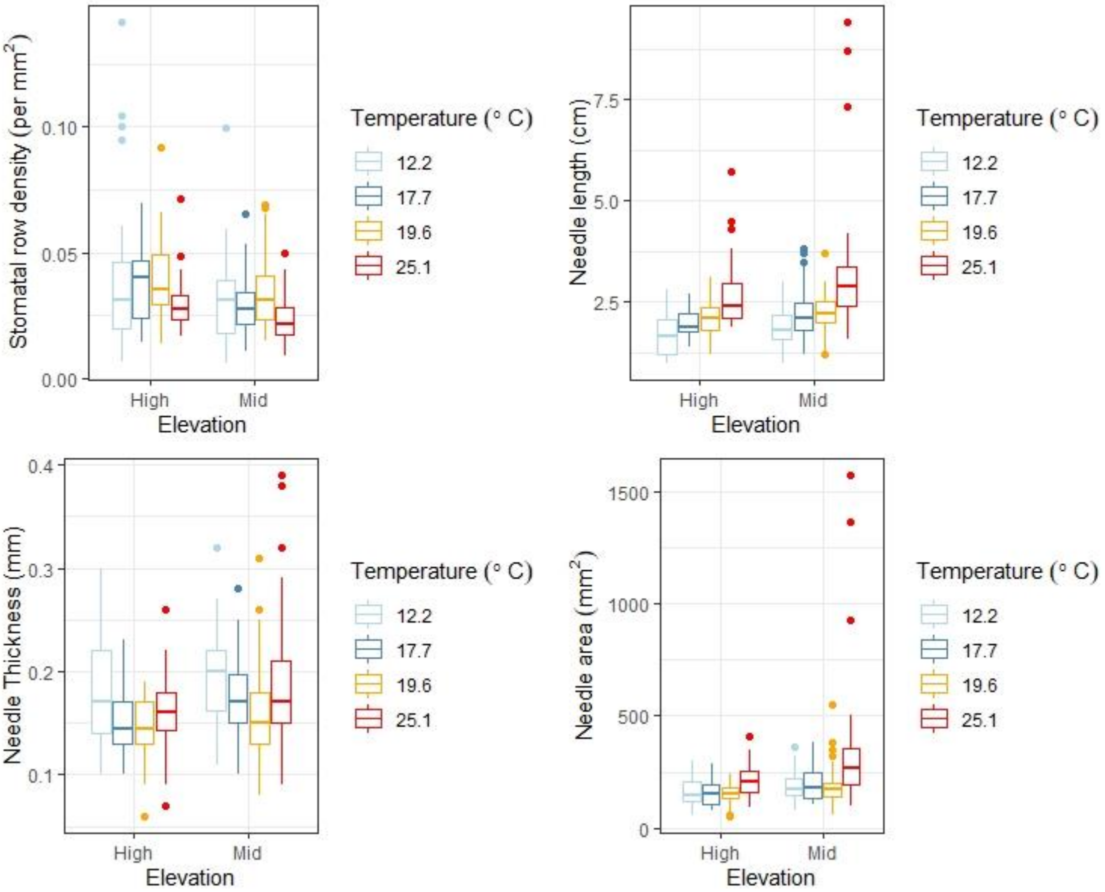

Fig.5.4: Values at harvest of stomatal row density (SD), needle length and needle thickness of *Pinus taiwanensis* seedlings from mid- and high-elevation forests planted in controlled environment conditions across four temperature chambers.

Table 5.6: Selected models and results for leaf traits at harvest of Pinus taiwanensis seedlings from mid- and high-elevation planted in controlled environment conditions across four temperature chambers.

Selected model	**Predictors**	**Fixed effects estimates**	**Individual predictor results**	R^2
Stomatal density (SD) ~ temperature + elevation +(1|transplanted)	Temperature	12.2° = 0.04 17.7° = 0.04 19.6° = 0.04 25.1° = 0.03	F=6.34, df=3, p<0.001	0.10
	Elevation	Mid = 0.03 High = 0.04	F=15.07, p<0.001, df=1	
Needle length~ temperature + elevation + +(1|transplanted)	Temperature	12.2° = 1.60 17.7° = 1.94 19.6° = 2.02 25.1° = 2.83	F=38.44, df=3, p<0.001	0.29
	Elevation	Mid = 1.87 High =1.60	F=11.09, df=1, p<0.001	
Needle thickness~ temperature + elevation + +(1|transplanted)	Temperature	12.2°= 0.18 17.7° = 0.15 19.6° = 0.14 25.1° = 0.16	F=9.73, df=3, p<0.001	0.13
	Elevation	Mid = 0.20 High = 0.18	F=16.90, df=1, p<0.001	
Needle area~ temperature + elevation + +(1|transplanted)	Temperature	12.2°= 140.98 17.7° = 281.95 19.6° = 141.74 25.1° = 252.52	F= 16.81, df=3, p<0.001	0.17
	Elevation	Mid = 196.57 High = 140.98	F= 17.22, df=1, p<0.001	

Mean soil moisture was 41% ± 9% from week 3-5, reflecting soil water-saturation which is not uncommon for this typhoonal system (Lin et al. 2003). For the rest of the experiment, from week 7-23, mean soil moisture was 25% ± 6% (*Fig.5.S1*). No plants experienced drought conditions.

5.5 Discussion

We found considerable variation in the responses of *P. taiwanensis* seedlings to projected changes in temperature across the elevation range of the species. Following expectations of higher temperatures promoting seedling growth, we found that increased temperature significantly reduced the time to emergence and promoted greater biomass gain. Once established, seedling survival was high, highlighting the importance of success at the pre-emergence phase of plant development for survival through to the seedling life stage (James et al. 2013). However, seed elevation of origin was highly influential in deciding the percentage of seeds which emerged, with poor germination from low elevation seedlings and consistently higher performance in terms of germination percentage and biomass allocation from mid- than high-elevation seedlings, particularly under the warmest temperatures. Our findings highlight the variability possible in the responses of the early stages of growth of a tree species to changes in climate, with the potential for widespread impacts on forests globally over the next century.

Our findings of higher temperatures promoting faster seedling emergence suggest that the early stages of *P. taiwanensis* growth may be highly sensitive to climate change. Emerging early can allow seeds to develop greater resistance to adverse conditions at an earlier stage (Matías and Jump 2014), increased growth and fecundity (Verdú and Traveset 2004) and a competitive advantage (Ross and Harper 1972). This faster emergence, along with potentially accelerated rates of physiological processes and faster primary productivity under higher temperatures (Girardin et al. 2010, Hatfield and Prueger 2015), was associated with higher values for final seedling height, root length and total biomass in warmer chambers. Despite *P. taiwanensis* generally being cold adapted, the optimum temperature for germination could be higher than expected, indeed some Arctic tundra species have been found to germinate best at 20-30 ^{o}C (Sayers and Ward 1996, Milbau et al. 2009). Therefore, we might expect higher temperatures to have a positive effect on germination and biomass accumulation for some individuals during the early stages of plant development.

This enhanced effect of increased temperatures, however, was not consistent for seeds harvested across the elevation range, following expectations of variation in development and responses to climate change between populations. Notably, seedlings from low-elevation populations showed very low germination rates across all temperature scenarios, suggesting the potential for reduced regeneration of these populations over coming decades. This low germination rate means we could not adequately quantify the likely impacts of differences in temperature to the later stages of growth of low-elevation seedlings. Overall, mid-elevation populations had higher total percentage germination and higher final root and shoot length, total biomass and needle size at harvest than high-elevation seedlings. Developing biomass quickly can allow increased nutrient acquisition, and thus more nutrient allocation to new growth (Hawkins et al. 1999). Rapid biomass gain could provide plants with greater resilience to adverse conditions at an earlier stage due to more stored resources and a larger stature. The enhanced growth of mid-elevation populations was particularly pronounced under the warmest temperatures, suggesting that mid-elevation populations may experience the most biomass gain in response to rising temperatures compared to their high-elevation counterparts.

The differences observed in early seedling growth between temperatures and elevations suggest variations in resource strategies in response to different pressures and tolerances. Seedlings exposed to higher temperatures displayed greater investment in roots than shoots, suggesting a shift in resource-use strategies with increasing temperature. Investing in roots over shoots can be a response to high temperatures (Girardin et al. 2010), as it allows plants to maximise soil nutrient and water capture (Lloret et al. 1999, Leuschner et al. 2007) and investing less in leaves can result in smaller leaf surface area, resulting in reduced water loss from leaves (Scoffoni et al. 2011). Roots are potentially more costly to produce in terms of carbon than leaves or stems, so plants may invest more in roots when they are not receiving sufficient resources from their aboveground components (Leuschner et al. 2007) or when nutrients such as nitrogen are low (Tateno et al. 2004). Soil moisture was not limiting throughout the experiment, so our findings may reflect a mechanism aimed to compensate for high evaporation rates when temperatures are high, resulting in increased belowground biomass production (Lloret et al. 1999).

Indications of a potential response of maximising water capture and reducing loss were mirrored through significantly higher stomatal row density for high-elevation seedlings compared to mid-elevation seedlings and the declining stomatal row density with increasing chamber temperature. Increasing stomatal density with elevation has been observed in adult *P. taiwanensis* trees and attributed to water economy (O’Sullivan et al. 2022), as stomata can close when vapour pressure deficit is high or temperatures rise above photosynthesis thresholds (Oren et al. 1999, Doughty and Goulden 2009, Duursma et al. 2014). Our findings for seedlings are remarkably similar to those of adults of the same species growing in situ (O’Sullivan et al. 2022), suggesting stomatal row density patterns are maintained throughout the life cycle of the species and that population differences across the elevation gradient may be important for driving differences in plant phenotype (Premoli and Brewer 2007). The differences observed in stomatal density between chamber temperatures could indicate a degree of phenotypic plasticity relating to water economy. The distribution and abundance of stomata on leaves is strongly influenced by genetics, but it can also be affected by environmental variables (Premoli and Brewer 2007). Therefore, variation in temperature could be driving morphological changes between high- and mid-elevation seeds, as plants respond to changing conditions over multiple generations.

Whilst unmeasured here, conditions experienced by the parent plant during seed development can be highly influential for seedling success (Daws et al. 2006). Compared to high-elevation seedlings, the relatively warmer temperatures during seed development for mid-elevation seedlings may have allowed seeds to develop more stored resources at an earlier stage than those from higher elevations, providing plants with increased resilience (Daws et al. 2006). Seed mass varied between elevations, with mean seed mass 1.4 times higher for mid-elevation seeds than high- or low-elevation seeds, suggesting that mid-elevation seeds typically stored more resources. Conditions experienced by the parent plants may still have been responsible for the lower germination rates of low-elevation seedlings. *P. taiwanensis* is largely cold adapted and is considered drought sensitive (Liu et al. 2019), meaning that seeds developing on maternal plants at low elevations are likely to have been more heat stressed than their higher elevation counterparts. Poor performance of low elevation trees has already been observed in previous work showing reduced growth of *P. taiwanensis* individuals in warm, low-elevation forests compared to higher elevation trees (Ruiz-Benito et al. 2015). With few trees with cones available to sample at low-elevations, it is also possible that these results have been influenced by stochastic variation resulting from a collection bias towards trees with available seeds.

The notable differences in response of seedlings from different elevations suggest variation in response to different selective drivers across the elevation gradient. Factors such as local scale competition could influence reproductive efforts, as variations occur in forest composition and structure across the elevation gradient investigated (Rodman et al. 2021). Populations at the edges of species distributions exist at the boundaries of their environmental tolerance and are typically present in lower densities and have reduced fecundity (Case and Taper 2000). The poor performance of the early growth of these marginal populations may herald *P. taiwanensis* population declines at the lower portion of the species distribution range over coming decades. The lower range boundary of *P. taiwanensis* is already estimated to have shifted to higher elevations by around 500m over recent years

(O’Sullivan et al. 2021). Trade-offs occur between growth and survival, with investment in one process often bringing costs for the other (Arft et al. 1999, Seiwa 2007, Matías and Jump 2014). Therefore, trees exposed to stressful conditions, such as drought, may divert their resources away from reproduction in order to persist, or alternatively, they may invest heavily in reproduction, at the cost of increased risk of mortality (Pérez-Ramos et al. 2010, Vilà-Cabrera et al. 2014, Lauder et al. 2019). It is possible that both these processes occur, as anecdotally, many low-elevation trees had no cones whilst others had large cone crops. It is also possible that low-elevation populations are being sustained through potentially higher quality seed flow from higher elevations, with trees performing poorly once established (Haldane 1956). As temperatures continue to rise, drought tolerant or warm-adapted species may show greater success in low elevation forests, potentially further exacerbating the stress on *P. taiwanensis* through interspecific competition (Liu et al. 2019).

The finding of mid-elevation populations performing well under warming has been mirrored in montane populations of the winter deciduous tree *Nothofagus pumilio* in South America (Ignazi et al. 2020). Whilst there is an assumption that species will migrate upwards (e.g. Harsch et al. 2009, Feeley et al. 2011, Fadrique et al. 2018), it is possible that mid-elevation populations could outcompete those at higher elevations. Rising temperatures may result in complex responses, with non-uniform shifts in the distributions of many tree species already estimated for this system (O’Sullivan et al. 2021). However, it is also possible that temporary enhancements in growth due to elevated temperatures may not necessarily result in long term benefits at the population scale due to negative implications for reproduction (Diemer 2002).

Experimental work provides an important opportunity to understand fundamental elevational differences in performance. However, many other factors play a role in how such differences might play out in the field. Differences in topography, soil nutrient availability, biotic interactions and human disturbances can also influence species distributions (Enric et al. 2009, Holtmeier and Broll 2011, Walck et al. 2011, Liang et al. 2018, van Breugel et al. 2018, Lembrechts and Lenoir 2019, Elsen et al. 2020). Although Taiwan has high humidity across the elevation range, droughts can also impact environments which are not typically water limited (Allen et al. 2010) and soil moisture in the field does not necessarily directly relate to rainfall, due to differences in soil depth and substrate. Climate change is driving increased frequency and intensity of extreme events, such as typhoons (Chiang and Chang 2011) and is altering seasonality (Qian and Zhang 2015), which could further drive events such as droughts to become more common. It is possible that differences in genotype were also responsible for observed variation in early development (Verdú and Traveset 2004). Local adaptations arise as a function of the interplay between genetics and environment (Valladares et al. 2014) and gene flow can be greater between populations which share an elevation band than nearby populations at a different elevation, suggesting that genetic differentiation of the species with elevation is possible (Premoli and Brewer 2007). Local adaptations could also allow some persistence of populations over coming decades (Hampe and Jump 2011).

5.5.1 Conclusions

Here, we demonstrate wide variation in early seedling development across the elevation range of a widely distributed pine, *P. taiwanensis*. The evidence we provide suggests that projected temperature changes are likely to influence seeding early growth, with variation across the species range, likely due to genetic and phenotypic differences between individuals. The greatest resilience is likely for mid-elevation forests, with low-elevation seeds showing poor germination, potentially foreshadowing population declines at the lower range margin over coming decades. This effect may be regulated to some extent by increased speed of emergence in response to higher temperatures providing greater resources to plants at an earlier developmental stage. Local adaptations could also allow some persistence, whilst variations in additional influences on seedling establishment and survival across the elevation range are likely to play a role. By demonstrating the variability possible in the early growth of a single species, we highlight the importance of understanding and quantifying differences for accurate predictions of future species distributions. Differences in response to climate across populations and developmental stages means that observed distribution shifts may be highly variable. Ultimately, the sensitivity we demonstrate of the early stages of growth of a tree species to changes in climate could foreshadow widespread changes in global forests over the next century. Greater understanding is urgently needed of the variability in early seedling development for reliable forecasts to be made of the potential impacts of climate change on species distributions.

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5.7 Supplementary material

5.7.1 Soil moisture

For measurements on week 7 of the controlled environment experiment and thereafter, 53% had soil moisture content of 25-30%, whilst 71% of measurements had soil moisture content between 20-35% (*Fig.5.S1, Table 5.S1*). Soil moisture was significantly different across temperatures (F=6.953, p<0.001, df=3) and over time (weeks) (F=13.848, p<0.001, df=2), whilst transplanting also significantly influenced soil moisture (F=257.80, p<0.001, df=1). Differences between pots (random effect) explained 19% of the observed variation whilst temperature, elevation and transplantation status explained 47%.

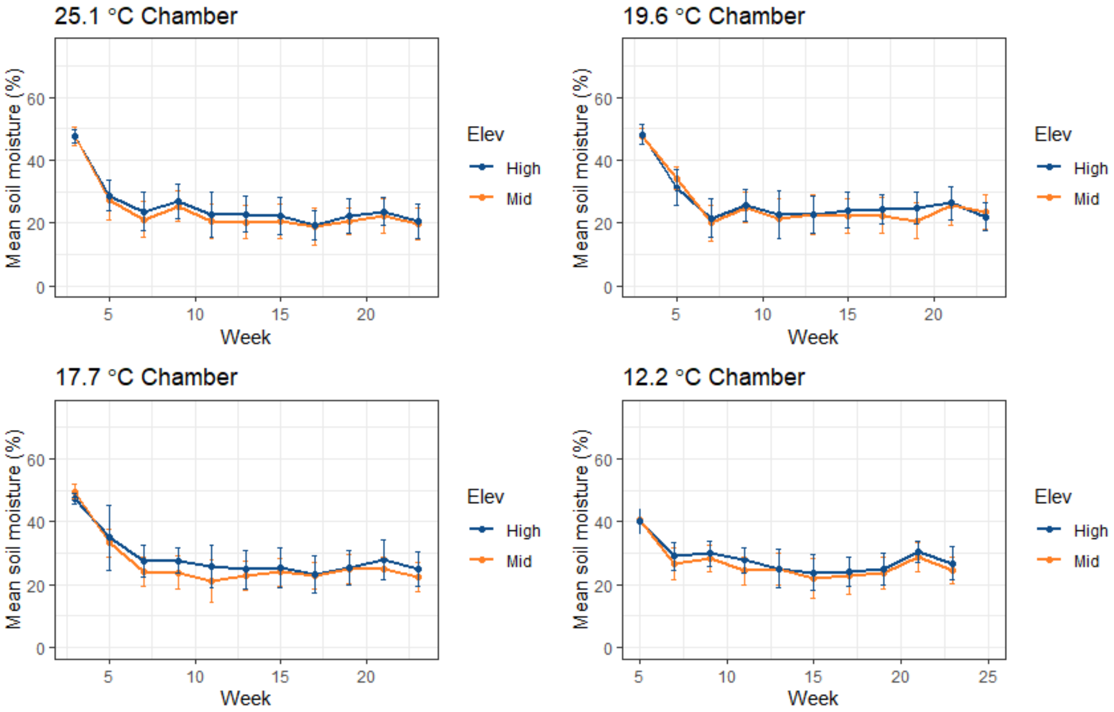

Fig.5.S1: Mean percentage soil moisture for high- and mid-elevation *Pinus taiwanensis* seedlings in each pot in each controlled environment chamber over the duration of the experiment.

Table 5.S1: Selected models and results for soil moisture and relative growth rate (RGR) of Pinus taiwanensis seedlings from mid- and high-elevation planted in controlled environment conditions across four temperature chambers.

Selected models	**Model output**	**Predictors**	**Fixed effects estimates**	**Individual predictor effects**	**R2**
Soil moisture~ temperature + transplanted + week + (1|plant)		Temperature	12.2º = 26.69049 17.7º = 26.26394 19.6º = 25.74723 25.1º = 24.1461	F=6.953, df=3, p<0.001	0.63
		Transplanted	Yes = 19.50997 No = 26.69049	F=257.80, df=1, p<0.001	
		Week	0.06896	F=13.848, df=1, p<0.001	
RGR ~ temperature + elevation + week	F=30.18, df=5, 1127, p<0.001	Temperature	12.2º = 48.6483 17.7º = 38.4391 19.6º = 32.7524 25.1º = 27.6248	F=30.675, p<0.001, df=3	0.12
		Elevation	Mid = 44.7269 High = 48.6483	F=7.149, p=0.008, df=1	
		Week	-1.3919	F=98.66, p<0.001, df=1	

5.7.2 Seedling growth rate

Seedling height was recorded every two weeks, starting six weeks after sowing. RGR was calculated for seedlings between 3 and 5cm height, to capture the same growth phase for plants in each chamber, as:

$$RGR = \frac{height - previous\ height}{previous\ height}\ x\ 100$$

RGR was modelled using a LM due to variance of the random effect close to zero and a lower Akaike information criterion (AIC) for a LM than LMM. Seedling RGR significantly declined over time (weeks) (F=98.66, p<0.001, df=1) and with increasing chamber temperature (F=30.675, p<0.001, df=3), and was significantly lower for mid- than high-elevation populations (F=7.1493, p=0.008, df=1) (*Fig.5.S2*, *Table 5.S1*).

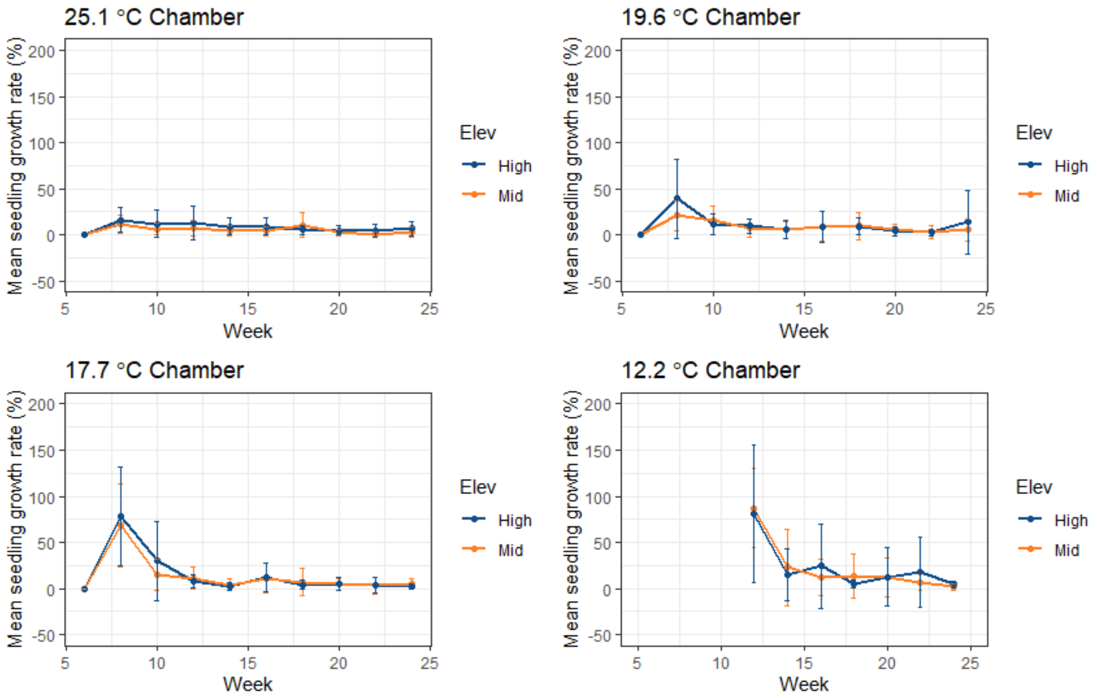

Fig.5.S2: Mean *Pinus taiwanensis* seedling heights for high- and mid-elevation seedlings in each controlled environment chamber (heights >=3cm) and seedling growth rate over time (weeks) (seedlings >3cm).

Chapter 6

Relationships between subtropical trees and climate and future directions for more effective global change assessments

6.1 Introduction

The threat of ongoing climate change to our natural environment and the people who depend on it is continuing to rapidly accelerate. Greater understanding is urgently needed of the impact climate change is having on the functioning of ecosystems for effective mitigation to be implemented (Bergstrom et al. 2021). Mountain forests are particularly vulnerable to climate change as they have disproportionally high levels of species richness and endemism, are experiencing particularly large and rapid increases in temperature and are understudied compared to their low elevation counterparts (Beniston et al. 1997, Nogués-Bravo et al. 2007, Jump et al. 2012, Rangwala and Miller 2012, Greenwood and Jump 2014, Verrall and Pickering 2020). Across the tropics and subtropics, information on changes to forests is limited, despite the importance of these environments for carbon storage, biodiversity and broader ecosystem services (e.g. García-Oliva et al., 1994; Nilaweera & Nutalaya, 1999; Pan et al., 2011; Potapov et al., 2012; Snyder et al., 2004). Given substantial information gaps, this thesis set out to overcome limitations in our ability to quantify and predict impacts of environmental change from the species to the ecosystem scale across a diverse subtropical montane system in Taiwan. Across four data chapters, the research outlined here has provided important insights enabling a better understanding of differences in the relationships between plants and climate, both within and between tree species. Ultimately, the findings outlined here have furthered our understanding of subtropical montane tree responses to climate change. Such information will allow for global comparisons to be made and provide more accurate insight to make more reliable predictions of changes across different ecosystems over coming decades.

6.2 Quantifying species distribution shifts

Although global trends in species distribution shifts have frequently shown upwards shifts of treelines (e.g. Harsch et al. 2009), Chapter 2 provided evidence for greater complexity in responses of trees to climate change (O'Sullivan et al. 2021). By considering a broad range of tree species occurring across a subtropical elevation gradient, we evidenced wide variation of distribution shifts between tree species, with upwards shifts common to high-elevation species, but more varied responses including frequent downwards shifts for mid to low elevation tree species. These varied responses are likely to be due to climatic warming interacting with non-thermal factors to drive variation in species distributional responses (Lenoir et al. 2010, Crimmins et al. 2011). Such individualistic responses of trees to climate change are likely to be common across complex tropical and subtropical systems and could have substantial implications for biodiversity and ecosystem functioning. For example, upwards shifts of trees can threaten endemic species at high elevations (Jump et al. 2012), whilst changes in overall forest distribution and composition can decrease albedo (Pecl et al. 2017) and influence carbon sequestration (Kirby and Potvin 2007). Our findings in Chapter 2 provided novel insight into the extent to which subtropical tree species respond individualistically to climate change within and between species. A better understanding of the variability in climate responses will ultimately enable more accurate estimations to be made of the implications of such changes at the ecosystem scale.

Further work is needed to determine the variability in tree species distribution shifts across different mountain systems. Such work could utilise existing forest inventory datasets across key areas, potentially comparing historic and contemporary records if data are available and collected in comparable ways (Shoo et al. 2006, Hassall and Thompson 2010), or using a demographic approach if only one survey is available (Lenoir et al., 2009). Here we had access to extensive field data, but travel to and from plot locations can bring substantial financial and time costs (McRoberts and Tomppo 2007). The limitations of collecting field data have been made increasingly paramount due to Covid-19 travel restrictions and the accelerating climate crisis requiring a reconsideration of the how and when field data area collected. Remote sensing may provide an opportunity to rapidly increase the efficiency and spatial and temporal scope of forest distribution shift assessments (Chambers et al. 2007, Xie et al. 2008) and has been used to assess changes such as greening (Gartzia et al. 2016, Carlson et al. 2017, Bolton et al. 2018) and treeline shifts (Zhang et al. 2009, Arekhi et al. 2018), and has the potential to be used to quantify changes at forest trailing edges (Vilà-Cabrera et al. 2019) and in forest density (Zhang et al. 2009). Integrating remote sensing data with targeted field surveys could upscale our ability to detect species distribution shifts within forests, providing greater understanding of changes occurring across different regions and biomes.

6.3 Drivers of species distribution shifts

Chapter 3 aimed to understand whether the differences observed in distribution shift size and direction observed in Chapter 2 were due to fundamental characteristics of plants. Plant functional traits provide an opportunity to assess the drivers of differences in plants across the landscape (Grime 1977, Niinemets 2014a, Fajardo and Siefert 2016). Therefore, Chapter 3 linked differences in shift size and direction to key functional trait values and assessed whether functional trait differences were related to variation in temperature and precipitation. Although we found close associations between functional trait composition and temperature and precipitation, individual traits were poor predictors of distribution shifts at the species level. Relationships between individual species distribution shifts and individual trait values may be challenging to detect since species have multiple traits with resource-use trade-offs, variations in traits within species and exist within complex and variable environments. However, the close relationships we observed between environmental variables and function suggest that we may see changes in abundance and diversity as the climate changes, with potential implications for overall forest function (Ruiz-Benito et al. 2017b). Chapter 3 provided new insight into the limitations and opportunities of trait data to predict future distribution shifts in a subtropical system, with close associations between climate and community-level function.

A key research priority going forward is to identify methods which can provide reliable predictions of species distribution shifts. Since climate is an important driver shaping plant species distributions (Woodward and Williams 1987, Pearson and Dawson 2003), we can expect climate change to substantially influence plant distributions. Therefore, research needs to focus on understanding plant-climate relationships. Open-access climate data provide an excellent basis for assessing broad-scale variations at the landscape scale, whilst elevation data can also generally be used as a reliable proxy for differences in temperature (see temperature maps in Chapter 3). However, weather station data may not match conditions actually experienced by plants at the local-scale growing within forests (De Frenne and Verheyen 2016), due to complex topography and variation in environmental conditions (Lambrecht and Dawson 2007, Morley et al. 2018, Midolo et al. 2019). Future research which integrates measures of climate at a micro and macro scale may provide improved insight of drivers of variations in local and regional conditions and how this influences processes at the individual and population scale (Lembrechts and Lenoir 2019, Maynard et al. 2022).

Alongside climate, additional biotic and abiotic drivers can affect species distributions (Liang et al. 2018), plant functional traits (Boucher et al. 2013) and seedling establishment and development (Enric et al. 2009, Walck et al. 2011). The combination of factors affecting plants is likely to vary across species ranges, with different trade-offs occurring between populations, resulting in varied responses to climate change (Seiwa 2007, Matías and Jump 2014). Modelling climatic drivers alongside factors such as habitat disturbances, land-use change and land-use legacies may be beneficial, as past land-use may affect tree responses (Alfaro-Sánchez et al. 2019, Zhang et al. 2021). For example, this could be done by uniting species distribution shift information with historic and current land-use maps. Further work could investigate how biotic factors can influence plant responses to climate change. Quantifying shifts in tree basal area could provide insight on changes in density, infilling and competition, providing greater insight on species co-existence than presence records data alone. Combining species distribution shift information with invasive species records, such as *Leucaena leucocephala* in Taiwan (Chen et al. 2012, Lu et al. 2013), could provide further insight into interspecific competition between sites. Predictions of species responses to climate change will be more insightful if we can quantify multiple potential drivers of distribution shifts.

Our findings in Chapter 3 highlight the need for further research into trait-based plant species range shift predictions. Our findings effectively demonstrate that functional trait-based methods offer an opportunity to link plant patterns and processes to environmental change, but it remains unclear the most insightful method of doing this. Considering changes in plant species diversity and abundance at the ecosystem scale may provide greater insight than assessing single species in isolation, as they may more accurately capture within species variability in distribution shifts. For example, this could be done through repeat forest inventories (e.g. Feeley et al. 2013), such as comparing plot-level community weighted mean (CWM) trait values over successive surveys, or by using comparisons of distributions of adult and juvenile trees as a proxy for change over time (e.g. Lenoir et al. 2009) and integrating CWM data with life-stage data. A marginality approach may also be useful, as species which are likely to shift their distributions may have trait values which are particularly high or low compared to other nearby trees. Exploring trait-based methods, alongside targeted data collection across key biomes and taxa, will improve our ability to understand plant function and how it relates to climate change.

6.4 Functional trait variability across a single species

To better understand species distribution shifts and predict future responses of forests to climate change, it is necessary to determine patterns and processes and consider the mechanisms driving them (Sutherland et al. 2013). This formed the basis of the work investigating the widely distributed conifer *Pinus taiwanensis* across the substantial elevational distribution range in which is occupies in Taiwan (Chapters 4 & 5).

By investigating *P. taiwanensis* needle leaf traits in Chapter 4, we showed substantial functional trait variation, likely driven by temperature differences and additional biotic and abiotic drivers across the elevational range (O'Sullivan et al. 2022). Intraspecific variability among traits was high and predictable with elevation. However, much of the variability was un-explained by differences in elevation, slope and aspect, suggesting that additional biotic and abiotic drivers also influence needle trait characteristics across the elevation gradient investigated. Data availability and variability of records from the TRY global plant trait database for the Pinus genus were generally very low, with few species having sufficient records to accurately characterise their intraspecific trait variability. Our findings in Chapter 3 provide novel insight into the extent of needle trait and resource-use strategy variation across the elevation range of a particularly widely distributed tree species, with substantial differences between individuals linked to elevational temperature variation and interacting drivers likely further contributing to variation. However, we also outlined an important information gap, with improved understanding of the extent and implications of intraspecific variability necessary for reliable quantifications and predictions of the impacts of environmental change on plant communities to be made, especially in understudied, diverse ecosystems.

Our findings in Chapter 4 highlight that caution is needed when using single values to convey trends, patterns and responses to climate for entire species. Incorporating measures of variability, such as standard deviations or functional dispersion may more accurately reflect plant trait variation (Laliberte and Legendre 2010, Pakeman 2014), whilst combining measurements across multiple parts of species ranges may also be important (Lenoir and Svenning 2015). Focussing data collection across key areas expected to have particularly high intraspecific variability, such as environmental gradients, will allow more accurate predictions to be made of changes in vegetation and the ecological implications of key functional differences

(Albert et al. 2011, Martin et al. 2017, Yang et al. 2018). Improved understanding of the extent and implications of intraspecific variability is necessary for reliable quantifications and predictions of the impacts of environmental change on vegetation, especially in understudied and diverse ecosystems such as tropical forests.

6.5 Variability in responses to climate across a single species

Using experimental warming to assess *P. taiwanensis* early growth provided us with greater clarity on variability in and drivers of responses of seedlings to climate change. Seedling life stages are particularly sensitive to changes in climate and can influence species distributions and abundance at the population and community scale. In Chapter 5, we found considerable variation in the responses of *P. taiwanensis* seedlings across the broad elevation range to projected changes in temperature. Following expectations of higher temperatures promoting seedling growth, we found that increased temperature significantly reduced the time to emergence and promoted greater biomass gain. However, seed elevation of origin was highly influential for the percentage of seeds which emerged, with poor germination from low elevation seedlings and consistently higher performance in terms of germination percentage and biomass allocation from mid-elevation seedlings than high-elevation seedlings, particularly under the warmest temperatures. These findings provide further evidence that species are unlikely to react uniformly to environmental changes, with differences detectable in plant responses even during the most vulnerable, early stages of plant development.

Leading on from this work, future research focussing on disentangling genetic and environmental components of variability in climate change responses, such as through local adaptation and phenotypic plasticity, would be beneficial (Valladares et al. 2014, Razgour et al. 2019). Since conditions experienced by the parent plant during seed development can be highly influential for seedling success (Daws et al. 2006), research into genetic differentiation of the species with elevation could be important (Premoli and Brewer 2007). Assessments of seedling responses to variation in climate in-situ could further aid our understanding of key driving factors of fundamental plant variation. For example, transplantation studies could simulate responses of plants under new climate conditions with novel competitors, providing further insight on drivers of plant responses to climate than temperature alone (Alexander et al. 2015). Greater understanding of the variability in early seedling development will provide more reliable forecasts to be made of the potential impacts of climate change on species distributions.

6.6 Synthesis and conclusions

Across all four data chapters, we provided evidence of close associations between climate and plant function, suggesting that we can expect a strong influence of changing climate on plants over coming decades. Functional traits of plants were tightly correlated with variation in temperature, and to a lesser extent, precipitation. In Chapter 3, we found a close association between plot-level tree functional trait composition and air temperature, whilst Chapter 4 provided evidence of an influence of elevation on *P. taiwanensis* needle traits, with elevation generally considered a good proxy for differences in temperature. As an example, the trait of stomatal row density was closely linked to temperature differences, with remarkably similar patterns between *P. taiwanensis* adult trees (Chapter 4) and seedlings (Chapter 5), with more stomatal rows at higher elevations and when temperatures were lower suggesting a response of maximising water capture and reducing water loss. Alongside phenotypic plasticity and adaptation which may be occurring, climate change could have direct effects on plant performance, as evidenced in Chapter 5 with higher temperatures resulting in faster seedling biomass gain. The work outlined in this thesis contributes significantly towards our understanding of fundamental relationships between plants and climate, enabling more accurate predictions of how plants may respond to climate change.

Elevation was also a key driver of observed variation in plant function and responses to climate. Our findings suggest that mid-range species and individuals could show the greatest resilience compared to those at range edges as the climate continues to change. In Chapter 2, we provided evidence which suggested that mid-elevation species could be more stable under climate change, as some showed no migrations and no associated population declines, and others displayed range expansions at both edges of their distributions. Then, in Chapter 5, we found that mid-elevation individuals of *P. taiwanensis* had higher total percentage germination and higher final root and shoot length, total biomass and needle size at harvest than high-elevation seedlings, with particularly large increases under the warmest temperatures, suggesting an enhancement in growth of mid-elevation individuals under climate change. These patterns linked to range position may be related to plant strategy, as generalist species with large ranges are considered more likely to succeed under climate change than specialists with narrow ranges (Broennimann et al. 2006, Laurance et al. 2011) and rapid biomass gain could provide plants with greater resilience to adverse conditions at an earlier stage due to more stored resources and a larger stature. This thesis offers novel insights into key differences to expect in the responses of plants to climate change across different parts of their distributional range.

Although not explicitly quantified here, additional interacting drivers are likely to have a substantial influence on plant responses to climate change. Our findings in Chapter 2 of high-elevation species typically shifting upwards but species from mid to low elevations showing more variation in shift direction is likely to be due to high elevation trees being temperature limited, but lower elevation trees being exposed to more variation in limiting factors, such as biotic interactions and disturbances. Competition, alongside resource-use trade-offs, were highlighted as potentially important factors limiting our ability to detect relationships between individual traits and individual species distribution shifts in Chapter 3. In Chapter 4, variation in functional traits were related to topographic variables of elevation, slope and aspect, but considerable trait differences were unexplained by these factors alone, suggesting that further drivers are acting to shaping intraspecific trait variation. By identifying the extent to which fundamental variation in plants and their responses to climate change are linked to climate and topography across an elevation range, we have provided novel insight into where information is missing on additional drivers of variation.

With evidence accumulating for widespread changes across forests globally, information is needed on plant-climate relationships to effectively plan for inevitable changes over coming decades. A theme which consistently emerged across all four data chapters was that high variability in function and responses to climate is common both within and between tree species. These findings provide further evidence that species are unlikely to react ‘as one’ to environmental changes, with differences detectable in plant responses even during the most vulnerable, early stages of plant development. However, we also found patterns which were consistent between chapters, such as close relationships between plants and climate and variability which is predictable across elevation. Additional factors such as competition, habitat disturbance and land-use legacies were potentially interacting with climate to drive observed variability. The research outlined in this thesis provides a significant contribution to our overall understanding of plant-climate relationships across diverse forest habitats. Ultimately, these contributions will enable improved understanding of the impacts of climate change on montane forest ecosystems and the factors that drive these patterns.

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