

MICKAËL MATHIEU PIHAIN

The evolutionary effect of phylogenetic  
neighbourhoods of trees on their resistance  
to herbivores and climatic stress





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## LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following papers, which are referred to in the text by Roman numerals:

- I) **Pihain, M.**, Gerhold, P., Ducousso, A. & Prinzing, A. (2019). Evolutionary response to coexistence with close relatives: increased resistance against specialist herbivores without cost for climatic-stress resistance. *Ecology Letters* 22: 1285–1296, <https://doi.org/10.1111/ele.13285>.
- II) **Pihain, M.**, Prinzing, A., Ducousso, A., Courty, P.-E., Houet, T., Georges, R., Jambon, O., Musch, B. & Gerhold, P. (2021). Eco-evolutionary consequences of living with close relatives: Resistance to herbivores and climatic stress increases with investment into mycorrhiza in adult oaks. *Manuscript under review*.
- III) Prinzing, A., Ozinga, W.A., Brändle, M., Courty, P.-E., Hennion, F., Labandeira, C., Parisod, C., **Pihain, M.** & Bartish, I.V. (2017). Benefits from living together? Clades whose species use similar habitats may persist as a result of eco-evolutionary feedbacks. *New Phytologist* 213: 66–82, <https://doi.org/10.1111/nph.14341>.

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The author's contribution to the papers:

Was responsible for \*\*\*, contributed substantially \*\*, contributed \*

	I	II	III
Study design	**	**	*
Data collection	***	***	
Data analysis	***	***	
Manuscript preparation	***	***	*

# 1. INTRODUCTION

Among other pressures, forests are subjected to two ecological threats: herbivory, i.e. consumption of plant tissues by animals, and climatic stress. Herbivory can reach 100% during herbivore population outbreaks (Schowalter *et al.* 1986). Such herbivory pressure has been reported to reduce both the growth of individual trees and the entire forests (Schowalter *et al.* 1986; Dietze & Matthes 2014), and it can lead to tree mortality (Wulder *et al.* 2006; Meddens *et al.* 2012; Hultine *et al.* 2015). Trees are also affected by climatic stress such as chill, heat and drought (Bréda *et al.* 2006; Senf *et al.* 2020). Climatic stress has a negative impact on the physiology and performance of trees. For instance, drought increases the hydraulic resistance in the soil and at the soil-root interface, which induces stomatal closure resulting in reduced CO<sub>2</sub> assimilation, and might reduce tree growth (Bréda *et al.* 2006; McDowell *et al.* 2008). In case of severe drought, vessel embolisms can occur and lead to tree death (Condit *et al.* 1995; Mayr *et al.* 2002; Bréda *et al.* 2006; McDowell *et al.* 2008; Allen *et al.* 2010). Drought caused an excess of 500,000 ha of forest mortality between 1987 to 2016 in Europe (Senf *et al.* 2020).

Researches have shown that increasing species diversity decreases herbivory possibly due to ‘associational resistance’, i.e. the increased resistance of a focal tree species due to interactions with neighbouring tree species (Pimentel 1961; Jactel & Brockerhoff 2007; Vehviläinen *et al.* 2007; Barbosa *et al.* 2009; Abdala-Roberts *et al.* 2015). This associational resistance might be explained by the resource concentration hypothesis, which states that herbivores have a reduced chance to reach and stay in a patch where their host is less likely to be found (Root 1973; Hambäck *et al.* 2000). This reduced chance of herbivores to find their host might be due to host dilution (Castagneyrol *et al.* 2013) or due to the disruption of the visual and chemical cues used by herbivores by neighbouring trees (Barbosa *et al.* 2009). Neighbouring trees attacked by herbivores produce volatile organic compounds (VOC) that can induce the production of defences in a focal tree or attract natural enemies of the herbivores, thus reducing herbivory of the focal tree (Farmer 2001; Kessler 2001; Engelberth *et al.* 2004; Heil & Kost 2006; Kessler *et al.* 2006). The production of such VOCs seems to be higher in trees growing with heterospecific trees (Kigathi *et al.* 2013).

In addition to decreasing herbivory, tree-species diversity can decrease climatic stress or its effect on plants. For instance, tree-species diversity can increase drought resistance and resilience of trees (Pretzsch *et al.* 2013a, b; Kotlarz *et al.* 2018; Sousa-Silva *et al.* 2018; Jourdan *et al.* 2019, 2020; Grossiord 2020; Steckel *et al.* 2020; Vannoppen *et al.* 2020). This increased drought resistance and resilience can be explained by different mechanisms. Firstly, facilitation between tree species can occur, such as increased water availability for neighbouring trees by hydraulic lift, i.e. the release of water uptake from deep soil into upper soil layers (Dawson 1993; Caldwell *et al.* 1998; Zapater *et al.* 2011). Secondly, tree-species diversity might increase functional-trait diversity and thus the differentiation of tree rooting patterns, leading trees to better share the available water



(Schmid & Kazda 2001; Grossiord *et al.* 2015; Bello *et al.* 2019a). However, high tree-species diversity does not always increase resistance to herbivores or climatic stress. Specifically, it seems to depend on the identity of the tree species involved (Vehviläinen *et al.* 2007; Grossiord *et al.* 2014; Forrester *et al.* 2016; Bello *et al.* 2019b; Gillerot *et al.* 2021).

In mixed forests, the identity of the neighbouring tree species is important as they may be phylogenetically proximate or distant. During the previous 20 years, researchers have increasingly characterised communities by their measured the phylogenetic structure (Webb *et al.* 2002). Specifically, two communities of the same species richness can differ in phylogenetic structure. A community can be phylogenetically clustered, i.e. composed of phylogenetically proximate species; or a community can be phylogenetically overdispersed, i.e. composed of phylogenetically distant species. Phylogenetically proximate species tend to share similar traits and similar niches (Burns & Strauss 2011; Peterson 2011; Violle *et al.* 2011), in particular in undisturbed habitats like forests (Prinzing *et al.* 2021a).

Trees coexisting with phylogenetically proximate neighbours might encounter multiple problems (we use the term ‘coexistence’ *sensu largo*, i.e. conspecific and heterospecific co-occurring neighbours in direct contact and for decades). Firstly, such trees may suffer high herbivory pressure. As phylogenetically proximate species tend to have similar traits, they tend to share herbivore species (Ødegaard *et al.* 2005; Brändle & Brandl 2006; Burns & Strauss 2011; Dinnage *et al.* 2012). Therefore, trees coexisting with phylogenetically proximate neighbours experience increased herbivory as neighbouring species can act as a source of herbivores (Yguel *et al.* 2011; Dinnage 2013; Castagneyrol *et al.* 2014; Moreira *et al.* 2019). This effect of phylogenetic proximity on herbivores is strongest in specialised herbivores (Nyman *et al.* 2006; Vialatte *et al.* 2010; Grandez-Rios *et al.* 2015; Seifert *et al.* 2020). Secondly, trees coexisting with phylogenetically proximate neighbours may suffer increased climatic stress. The functional similarity between phylogenetically proximate neighbours results in that they share similar resource needs in space and time (Burns & Strauss 2011; Peterson 2011; Violle *et al.* 2011). Therefore they may suffer increased competition and in the case of resource limitation, they might experience increased abiotic stress (Wilson & Tilman 1991; Violle *et al.* 2011; Martínez-Vilalta *et al.* 2012). For instance, it has been shown that tree species coexisting with conspecifics, i.e. with phylogenetically proximate neighbours, suffer more from drought than with heterospecifics, i.e. with phylogenetically more distant neighbours (Pretzsch *et al.* 2013b). Overall, species coexisting with phylogenetically proximate neighbours might suffer increased herbivory and climatic stress.

The problems that trees coexisting with phylogenetically proximate neighbours encounter might prevent such coexistence and trees might coexist only with phylogenetically distant neighbours (Janzen 1970; Liu *et al.* 2012). Therefore, in nature, we should observe communities that are composed mostly of distantly related species. However, tree species do coexist with phylogenetically proximate neighbours, and surprisingly little is known about possible mechanisms permitting this coexistence. Here I argue that populations of trees may not be passively

suffering from increased pressure by herbivores in phylogenetically proximate neighbourhoods, but rather adapt by evolving increased resistance to herbivory.

The increased resistance to herbivory might have a cost for climatic stress resistance of trees. Coexistence with phylogenetically proximate neighbours might indirectly select against traits that are traded off against resistance to herbivory such as the resistance to climatic stress. Resistance to herbivory may be costly and involve multiple types of costs for trees, such as energy costs, opportunity costs and ecological costs (Baldwin & Hamilton 2000; Koricheva 2002; Strauss *et al.* 2006; Siemsen *et al.* 2009). For instance, tree species investing energy in resistance against herbivores might have less energy to spend in resistance against climatic stress (Siemsen *et al.* 2012; Alsdurf *et al.* 2013; Siemsen & Haugen 2013). Hence, if phylogenetically proximate neighbourhoods select for resistances against herbivores that are traded off against resistances to climatic stress, trees coexisting with phylogenetically proximate neighbours might be more resistant against herbivores but less resistant against climatic stress. However, resistances against herbivores may not automatically reduce resistances to climatic stress. This trade-off may depend on the type of resistances involved. Quantitative defences against herbivores, i.e. defences produced in high quantity to reduce the digestibility of plant tissues, have been shown to be multifunctional as they also increase resistance against climatic stress (Neilson *et al.* 2013). For instance, quantitative-chemical resistances such as tannins, anthocyanins and flavonols, or quantitative-morphological resistances like wax, increase the resistance against both herbivory and climatic stress (Jetter *et al.* 2000; Brennan & Weinbaum 2001a, b; Treutter 2006; Korn *et al.* 2008). Hence, if phylogenetically proximate neighbourhoods select for resistance that is multifunctional, species coexisting with phylogenetically proximate neighbours might be more resistant against both herbivory and climatic stress.

Tree populations coexisting with phylogenetically proximate neighbours may also evolve increased investment into mycorrhizae. Specifically, as a response to increased herbivory and climatic stress caused by phylogenetically proximate neighbourhoods, trees may invest into mutualists, such as mycorrhiza. Mycorrhizae are known to increase resistances against herbivores (Gehring & Whitham 2003; Gange *et al.* 2005; Koricheva *et al.* 2009) and climatic stress (Nelsen & Safir 1982; Ruiz-Lozano & Aroca 2010a, b). In addition, mycorrhizae provide nutrients and water to trees (van der Heijden *et al.* 2015; Garcia *et al.* 2016), which may indirectly enhance tree resistance against both herbivores and climatic stress. Under strong herbivory and climatic stress, trees investing much into mycorrhiza should hence survive better than trees investing little. Therefore, the investment into mycorrhizae should be selected under strong herbivory and climatic stress pressure, i.e. in phylogenetically proximate neighbourhoods. Hence, if phylogenetically proximate neighbourhoods select for increased investment into mycorrhizae, tree populations exposed to such neighbourhoods might be more resistant against both herbivory and climatic stress.

In the current context of environmental change and the massive species loss, it becomes urgent to understand why some plant species persist and some go

extinct. Climate change is predicted to increase climatic stress in intensity and frequency (Zandalinas *et al.* 2021; “IPCC – Intergovernmental Panel on Climate Change” 2021). Therefore, plant species already under strong herbivory and climatic stress might be threatened and go extinct. In this context, species growing in phylogenetically proximate neighbourhoods might be of particular concern as such neighbourhoods increase both herbivory and climatic stress. However, I previously argue that phylogenetically proximate neighbourhoods might select for increased resistances against herbivory and climatic stress. Hence, species coexisting with phylogenetically proximate neighbours might be less vulnerable to environmental change and have a reduced risk of extinction.

The major aim of this thesis is to address the effect of coexistence with phylogenetically proximate neighbours on resistances against herbivory and climatic stress (**I, II**) and its consequences for responses to future environmental change (**III**). In **III**, data were collected from published papers and combined with databases, whereas in **I** and **II** data were collected in a common garden experiment originating from provenances of different phylogenetic neighbourhoods and climates, enabling us to identify the natural selection occurring in these neighbourhoods. Specifically, this thesis addresses the following questions:

- 1) Does coexistence with closely related neighbours select for increased morphological and chemical defences against herbivores? (**Paper I**)
- 2) Does coexistence with closely related neighbours indirectly select against resistance to climatic stress? (**Paper I**)
- 3) Does coexistence with closely related neighbours select for increased mycorrhiza-mediated resistance against both herbivory and climate stress? (**Paper II**)
- 4) Does coexistence with closely related neighbours reduce the risk of extinction under environmental change? (**Paper III**)

## 2. MATERIALS AND METHODS

### 2.1 Data collection

In papers **I** and **II** data were collected from a common garden experiment, where acorns of sessile oak (*Quercus petraea*) from different forest provenances across Europe were planted by the French National Institute for Agriculture, Food and Environment and by “Office National des forêts” in 1990. The common garden experiment aims to study the genetic variability of sessile oak across its distributional range. In papers **I** and **II**, the sampling was done in the common garden located in “La Petite Charnie” forest, in the western part of France (48° 05'12 "N, 0° 9'40" W).

Sessile oak is a suitable candidate species to test my hypotheses as it is a common tree species in Europe and often growing in both pure or mixed stands (Ellenberg 1988). It is known to suffer from an abundant and diverse herbivore fauna (Brändle & Brandl 2001), including both specialist and generalist herbivore species (Gaston *et al.* 1992; Giffard *et al.* 2012). Sessile oak is also known to profit from ectomycorrhizae (Courty *et al.* 2006, 2007; Leski *et al.* 2010; Yguel *et al.* 2014). In addition, it is predicted to be strongly negatively impacted by future climate change, especially by the increasing temperatures (Cheaib *et al.* 2012).

Provenances were forest parcels of 25 ha within forest stands. Tree species composition and abundance in each provenance have been recorded as *Quercus petraea*, *Quercus robur*, *Fagus sylvatica* and non-Fagaceae angiosperms (there were no gymnosperms in the provenances). For each provenance, the annual minimum and maximum temperature and the summer hydric deficit (potential evapotranspiration minus precipitation from June to August) were extracted from WORLDCLIM database (Fick & Hijmans 2017). In paper **I**, 25 provenances were selected in the common garden and in paper **II**, 30 provenances were selected. Provenances were selected by maximising the variation in phylogenetic distance (as defined below) in provenances and minimising the geographic distance by creating pairs of provenances geographically close with contrasting phylogenetic distances. In the common garden, two trees were sampled for each provenance.

In paper **III**, data were collected from published papers and the Dutch National Vegetation Database, focusing on angiosperm species in the Netherlands. Information of habitat use was taken from Ozinga *et al.* (2013). The position of each angiosperm species along environmental gradients was determined using Ellenberg indicator values (Ellenberg *et al.* 1992) and averaged across multiple plots. For a given gradient, the within-genus environmental variation was determined as the standard deviation across its constituent species. Within-genus variation of habitat use was calculated from the mean of standard deviation for different gradients. Local co-occurrence was taken from Prinzing *et al.* (2016). For each species, the average number of co-occurring congeners per plot was extracted from the Dutch National Vegetation Database, and then averaged within genera (see Prinzing *et al.* 2016 for more details).

## 2.2 Measurement of phylogenetic distances

In papers **I** and **II**, phylogenetic distance in each provenance was estimated from the mean distance between *Quercus petraea* and each tree species present in the provenance and weighted by its relative abundance. This measure is equivalent to abundance weighting in phylogenetic diversity measures. Phylogenetic distances were collected from Vialatte *et al.* (2010) and Xing *et al.* (2014). Vialatte *et al.* (2010) set the distance between two lineages of equal rank in the classification IV by Angiosperm Phylogeny Group to the crown age of the younger of the two lineages. This estimated crown-age describes the moment in the history of life when the two lineages were present for herbivore lineages. In paper **III**, the phylogenetic age of each genus present in the Netherlands was estimated using genus crown-age taken from Bartish *et al.* (2016) and Hermant *et al.* (2012).

## 2.3 Plant traits

### 2.3.1 Morphological traits

In paper **I**, leaf toughness, thickness and leaf dry matter content (LDMC) were assessed from leaves sampled in the common garden. Leaf toughness, thickness and LDMC are resistance traits used against herbivores and climatic stress. Leaf thickness was assessed on four randomly selected leaves per tree using a precision calliper (Thickness gauge glorythai, model number: BY01, Shantou, China). For each leaf, eight measurements were done avoiding the main veins. Then, the measurements were averaged per leaf, per tree and per provenance. Leaf toughness was assessed from randomly selected five leaves per tree using a durometer to measure the resistance to punching (ATG-50 Dial Tension Gauge Gram Force Meter Dual point 50g, Wenzhou, China). For each leaf, eight measurements were done avoiding the main veins. Again, the measurements were averaged per leaf, per tree and per provenance. LDMC was assessed using the five leaves used for leaf toughness measures. Per tree, the leaves were rehydrated and weighted together to obtain the wet weight. Then, the leaves were dried for 48 hours in an oven at 65 °C and reweighted to obtain the dry weight. LDMC was then calculated by dividing the dry weight by the wet weight. LDMC was then averaged across trees within provenances.

### 2.3.2 Chemical traits

In papers **I** and **II**, leaf chemical traits were measured right after the sampling of the leaves in the common garden. In both papers **I** and **II**, leaf chemical traits were measured on three undamaged leaves. In paper **I**, an index of anthocyanins, flavonols and nitrogen status was measured in October 2015 using an optical sensor based on leaf transmittance (Dualux 4 Force A; Louis *et al.* 2009; Cericovic

*et al.* 2012). Anthocyanins and flavonols are leaf chemicals used for the resistance against herbivores and climatic stress. The nitrogen status was measured to take into account the nutritional status of the trees in the later analyses as the nutritional status might influence the resistance to herbivory or climatic stress. In paper **II**, the leaf chlorophyll content (in  $\mu\text{g cm}^{-2}$ ) was measured in September 2018 using the optical sensor based on leaf transmittance (Dualex 4 Force A). Measures of leaf chlorophyll by Dualex 4 Force A are strongly correlated with extracted leaf chlorophyll (Cerovic *et al.* 2012). Leaf chlorophyll content might be destroyed by the production of reactive oxygen species induced by drought (Smirnoff 1993, 1995). Hence, measuring leaf chlorophyll content in September permits to estimate overall chlorophyll degradation induced in particular by drought period during summer.

### **2.3.3 Investment into mycorrhizae and mycorrhization rank**

In paper **II**, the investment of trees into mycorrhizae was inferred from the proportion of root tips with mycorrhizae and from the enzymatic activity of mycorrhizal root-tips.

The proportion of ectomycorrhizal root-tips and density of root tips were assessed using ground core taken in May 2018. Each ground core was homogenized by hand and 40 mL of the sample were then gently washed in tap water for 2 hours. Each washed sample was passed by two sieves of 4 mm and 1 mm mesh sizes, the first to retain big detritus and the second to retain fine roots and separate them from fine particles such as clay. Fine roots were collected manually from the 1 mm sieve, stored in a petri dish and photographed. In order to get manageable sub-sample and capture a sufficient amount of root tips, the photos of fine roots were analysed by applying a regular grid of 70 circles of 0.15 cm of radius, separated by 0.75 cm, on them, using ImageJ software (<https://imagej.net/ImageJ>). The number of circles containing root tips was recorded as “density of root tips”. The proportion of these root tips that have ectomycorrhizae was then recorded.

The ectomycorrhizal enzymatic activity was assessed from ground cores taken in September 2018. For each sample, 10 root tips with ectomycorrhizae were selected to measure their enzymatic activity using high-throughput microplate assays described in Courty *et al.* (2005). Enzymatic activities were expressed per unit of time and per unit of area to take into account root-tip size (projected area of the ECM root-tip, in  $\mu\text{mol min}^{-1} \text{mm}^{-2}$ ) as described in Courty *et al.* (2005) and were log-transformed to obtain an approximate Gaussian distribution. The enzymatic activity was measured for laccase (in  $\mu\text{mol min}^{-1} \text{mm}^{-2}$ ) as it plays an important role in the mobilisation of nutrients by ectomycorrhizae due to its capacity to break down lignin (Criquet *et al.* 1999; Courty *et al.* 2006). Enzymatic activity, proportion of ectomycorrhizal root-tips and root-tip density were then averaged for each tree and averaged across trees within provenances.

In paper **III**, the mycorrhization rank was extracted for each species present in the Netherlands from Hempel *et al.* (2013). Mycorrhization rank was defined

as 0 for non-mycorrhized species, 1 for species with mandatory mycorrhizal association, and 0.5 for species with facultative mycorrhizal association. The mycorrhization rank was then averaged across species within genera.

## **2.4 Resistance to herbivores and climatic stress**

### **2.4.1 Resistance to herbivores**

Resistance of trees to herbivores was inferred from low herbivory.

In papers **I** and **II**, three types of herbivory were discriminated based on feeding guilds: (1) galls that are growth deformities on leaf surface and produced by insect larva; (2) leaf mines that are galleries formed between leaf epidermis by insect larva; and (3) ectophagy that is the partial or complete loss of leaf including epidermis.

In paper **I**, herbivory was assessed from 15 to 30 leaves per tree and in paper **II** from 10 to 15 leaves per tree. Quantifying herbivory required the reconstruction of the initial leaf surface prior to the damages. The initial leaf surface was reconstructed by drawing on a grid of dots of  $1 \times 1 \text{ cm}^2$ . Then, the areas damaged by ectophages or leaf miners were assessed by counting the number of dots covering the damaged parts.

The number of galls and leaf mines was also counted. For each leaf, the density of galls and the density of leaf mines per  $\text{cm}^2$  was calculated as well as the proportion of area damaged by leaf miners and the proportion of area damaged by ectophages. Each measure of herbivory was then averaged per tree and per provenance.

### **2.4.2 Resistance to climatic stress or risk of extinction under environmental change**

In paper **I**, the resistance of trees to climatic stress was inferred from budburst advancement, low coefficient of variation of budburst and low coefficient of variation of growth. Specifically, the climate is considered to control the budburst and growth of trees (Menzel 2000; Thomas *et al.* 2002; Morin *et al.* 2010). Therefore, trees that are particularly resistant to cold winters should bud burst early. In addition, tree genotypes that are resistant to climatic stress should show a budburst and growth that is independent of local climate; hence, such genotypes should show low variation of budburst and growth across common gardens. Budburst was assessed on a 0–5 ordinal scale where 0 is a dormant bud and 5 is a fully open bud (Sinclair *et al.* 2015). Growth was recorded in 2001 as the height of the trees after 10 years in each of the four common gardens. The coefficients of variation of budburst and growth were calculated as the standard deviation among the four common gardens divided by the mean.

In paper **II**, resistance to climatic stress was inferred from the capacity of trees to maintain leaf chlorophyll during drought. Drought stress of the trees in the common garden was inferred from the air temperature at the surface of the crown at 1 p.m., i.e. the warmest period of the day, on the 1<sup>st</sup> of September, 2018. Air temperature at the surface of plants can be used as a proxy of drought stress (Courault *et al.* 1996; Holzman *et al.* 2021). Air temperature at the surface drives drought stress by increasing saturation water-vapour pressure and thereby saturation deficit of the atmosphere which increases water loss of plants by transpiration. Crown temperatures of trees within the common garden were extracted from remotely sensed data (Prinzing *et al.* 2021b) and detailed in Appendix S9 in **II**. From the same data set, the height and altitude of the trees in the common garden were extracted for later analyses.

In paper **III**, we considered the risk of extinction under environmental change, and we described species in the Netherlands rather than descendants from populations of *Q. petraea* across Europe. We inferred risk of extinction from a low population decline under environmental change during the 20<sup>th</sup> century. Population trends were extracted from Ozinga *et al.* (2009). These authors used the species occurrence in the Netherlands across a 1-km<sup>2</sup> grid during 1902–1949 and 1975–1998. A binary classification of the data was done so that species were considered as declining only if the number of grid-cell presences had declined by >25%.

## 2.5 Data analysis

To test whether the phylogenetic distance of provenance neighbourhoods selects for increased resistance to herbivores (**I**), multiple regressions were performed studying the effect of the phylogenetic distance of provenance neighbourhoods on the resistance to herbivores of trees in the common garden. For resistance to herbivores, proportion of ectophagy, proportion of leaf mines, gall density, leaf toughness, leaf thickness, LDMC, anthocyanins and flavonols were used. Co-variables potentially related to the phylogenetic distance of provenance neighbourhoods and the nutritional status of the trees in the common garden were taken into account (annual minimum and maximum temperatures, summer hydric deficit in provenances, budburst and leaf nitrogen status of trees in the common garden).

To test whether resistance to herbivores is traded off against resistance to climatic stress (**I**), multiple regressions were conducted studying the effect of resistance to herbivores on climatic stress resistance. High resistance to herbivores, was inferred from low herbivory (proportion of ectophagy, proportion of leaf mines, gall density) or high leaf toughness, leaf thickness, LDMC, anthocyanins and flavonols. High resistance to climatic stress were inferred from high advancement of budburst, or low the coefficient of variation of budburst and growth. The leaf nitrogen status of the trees in the common garden was used as a co-variable.

To test whether the phylogenetic distance of provenance neighbourhoods selects against resistance to climatic stress (**I**), multiple regressions were conducted



studying the effect of phylogenetic distance of provenance neighbourhoods on climatic stress resistance of trees in the common garden. Resistance to climatic stress was inferred from a high advancement of budburst, and a low coefficient of variation of budburst and growth. The annual minimum and maximum temperatures, summer hydric deficit in provenances and leaf nitrogen status of the trees in the common garden were taken into account as co-variables.

To test whether the phylogenetic distance of provenance neighbourhoods changes the selection by climate on traits (**I**), multiple regressions were conducted studying the effect of phylogenetic distance of provenance neighbourhoods and climate in provenances and their interaction on traits. For traits, we considered leaf toughness, leaf thickness, LDMC, anthocyanins and flavonols. The advancement of budburst and leaf nitrogen status of trees in the common garden were used as co-variables. All climatic variables (annual minimum and maximum temperatures, and summer hydric deficit) and their corresponding interaction with phylogenetic distance in provenances were included in the models. In order to not overload the models, a selection of the variables has been done using the R function 'step()'. This function uses a stepwise selection procedure, based on Akaike Information Criterion (Burnham & Anderson 2002).

To test whether the investment into mycorrhizae of trees in the common garden changes with the phylogenetic distance of provenance neighbourhoods (**II**), multiple regressions were conducted studying the effect of phylogenetic distance of provenance neighbourhoods on the investment into mycorrhiza. High investment into mycorrhizae was inferred from a high proportion of ectomycorrhizal root-tips and of laccase activity. The annual minimum and maximum temperatures, and summer hydric deficit in provenances were used as co-variables. A selection of the explanatory variables was conducted using the R function 'step()'.

To test whether the herbivory of trees in the common garden changes with their investment into mycorrhizae (**II**), multiple regressions were conducted studying the effect of mycorrhizae or root characteristics on herbivory. Herbivory was quantified as the proportion of leaf mines, density of galls or proportion of ectophagy. A high investment into mycorrhizae was inferred from a high proportion of ectomycorrhizal root-tips or a high laccase activity. Roots were characterized by their root-tip density. Tree height, altitude, crown temperature and budburst of trees in the common garden were taken into account as co-variables. Again, the explanatory variables were selected using the R function 'step()'.

To test whether the phylogenetic distance of the provenance neighbourhoods selects for increased resistance against herbivores (**II**), multiple regressions were conducted studying the effect of phylogenetic distance of provenance neighbourhoods on herbivory of trees in the common garden. For herbivory, was quantified as the per-leaf proportion of leaf mines or of ectophagy, or the density of galls. The annual minimum and maximum temperatures, and summer hydric deficit in provenances were used as co-variables. The explanatory variables were selected using the R function 'step()'.

To test whether trees with particularly high investment into mycorrhizae were more resistant to climatic stress (**II**), multiple regressions were conducted testing

whether the relationship between leaf chlorophyll content and crown temperature becomes less negative with high investment into mycorrhizae. Therefore, the interaction between crown temperature and mycorrhizae was included in the model. The models were performed separately for each mycorrhiza variable (mycorrhizal enzymatic activity and proportion of mycorrhizal root-tips) and the density of root-tips. For each regression, the height and the altitude of trees in the common garden were taken into account as co-variables. The explanatory variables were selected using the R function 'step()'.

To test whether the phylogenetic distance of the provenance neighbourhoods selects for increased resistance to climatic stress (**II**), one regression was conducted testing whether the relationship between leaf chlorophyll content and crown temperature becomes less negative with increasing phylogenetic proximity of the provenance neighbourhood. Therefore, the interaction between crown temperature and phylogenetic distance in provenance neighbourhoods was included into the model. The height and the altitude of trees in the common garden were taken into account as co-variables. The explanatory variables were selected using the R function 'step()'.

To test whether genera of species with a particularly high mycorrhizal association, have reduced risk of extinction (**III**), a regression was conducted testing whether the relationship between the within-genus proportion of species declining during the 20<sup>th</sup> century and the degree of intra-genus co-occurrence becomes more negative with increasing mycorrhizal association within genus. Therefore, the interaction term between within-genus co-occurrence and the mycorrhizal association was included in a model explaining the proportion of declining species. For mycorrhizal association, the mean mycorrhiza-ranking within genus was used.

To test whether genera in which species use the same habitat and co-occur with congeners have reduced risk of extinction (**III**), a regression was conducted testing whether the relationship between the proportion of declining species within genus during the 20<sup>th</sup> century and the similarity in habitat-use becomes more positive when the similarity in habitat use corresponds to high coexistence. Similarity in habitat use was inferred from a low variation (SD) in Ellenberg values of species within genera. Correspondence between similarity in habitat use and within-genus co-occurrence was quantified as small absolute residuals of the regression of within-genus co-occurrence on similarity in habitat use. The interaction between similarity in habitat-use and these absolute residuals was included in the model. Genus crown age and species richness were used as co-variables.

All analyses in papers **I** and **II** were done using the software R while the analyses in paper **III** were done using the software Statistica.

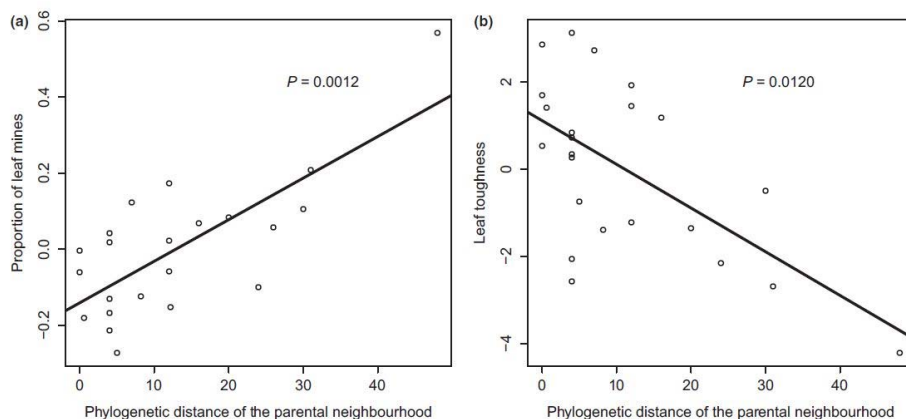
### 3. RESULTS

#### 3.1 Coexistence with closely related neighbours selects for increased morphological resistance against herbivores

The proportion of leaf mines was lowest in trees descending from provenances of phylogenetically proximate neighbourhoods (Fig. 1A). The density of galls and the proportion of ectophagy of trees in the common garden were not related to the phylogenetic distance of the provenance neighbourhoods (Table 1 in **I**).

In terms of morphological resistances, trees descending from phylogenetically proximate neighbourhoods had tougher leaves but had not thicker leaves or were not richer in dry matter content (Fig. 1B; Table 1 in **I**). Consistently, trees with tough leaves experienced low proportion of leaf mines ( $T = -2.146$ ,  $P = 0.0466$ , adjusted  $R^2 = 0.20$ ,  $d.f = 17$ ).

In terms of chemical resistances, anthocyanins and flavonols of trees in the common garden were not related to the phylogenetic distance of the provenance neighbourhoods (Table 1 in **I**).



**Figure 1.** Statistical effect of phylogenetic distance of provenance neighbourhoods on (A) the proportion of leaf surface covered by leaf mines, and (B) the leaf toughness of the trees in the common garden. Y-values give partial residuals, accounting for co-variables (annual minimum and maximum temperatures and summer hydric deficit in the provenances, advancement of budburst and leaf nitrogen status of the trees in the common garden), as explained in Table 1 in **I**. Data points are means across trees within provenances. See publication **I**.

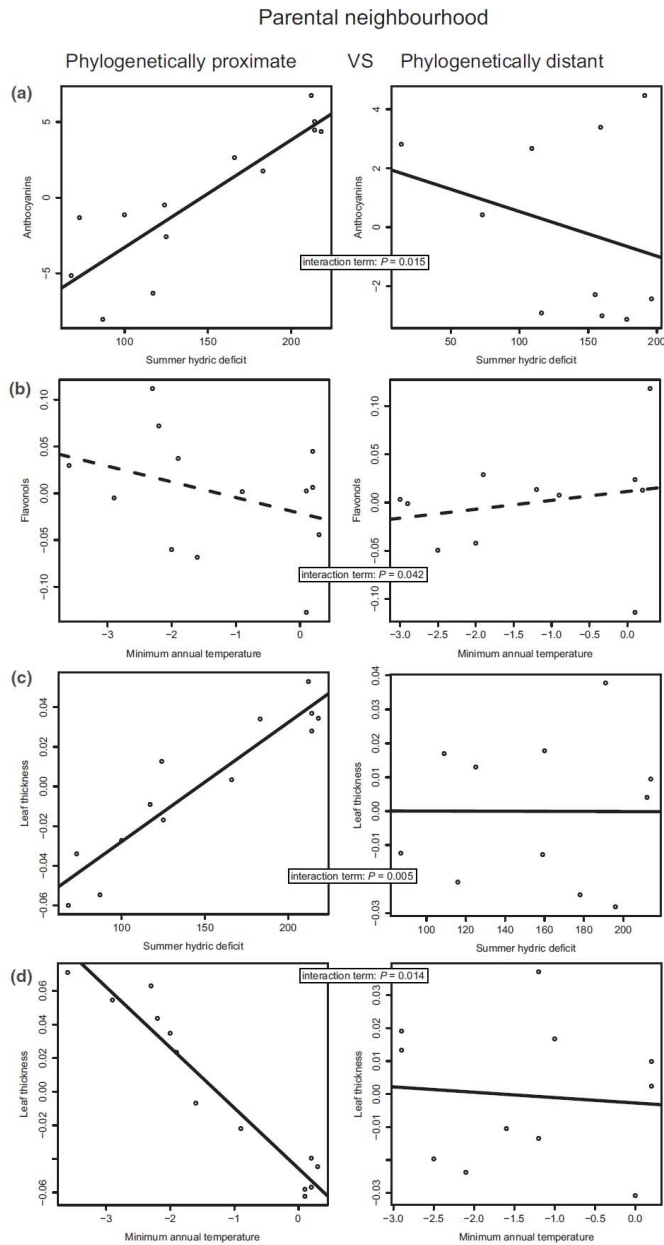
### **3.2 Coexistence with closely related neighbours does not indirectly select against resistance to climatic stress: no trade-off between resistances to herbivores and climatic stress**

No relationships were found between climatic stress resistances and the proportion of leaf mines (Table 1). Trees with particularly advanced budburst or with constant budburst experienced low gall density (Table 1; Fig. S7A, B in **I**). Trees with advanced budburst experienced a high proportion of ectophagy (Table 1; Fig. S7C in **I**), albeit this relationship disappeared after correction for false discovery rate. No relationships were found between climatic stress resistance and chemical or morphological resistances to herbivory (Table 1). Overall, the phylogenetic distance of the provenance neighbourhoods had no effect on climatic stress resistance (third paragraph in the result section of **I**).

Phylogenetically proximate neighbourhoods reinforce the selection by harsh climates on traits conferring climatic stress resistances. In particular, there were significant interactions between the phylogenetic distance of the provenance neighbourhoods and provenance climate on anthocyanins, flavonols and leaf thickness (Fig. 2; Table 3 in **I**). Specifically, traits of trees descending from phylogenetically proximate neighbourhoods reflected more the climatic stress in the provenance compared to trees descending from phylogenetically distant neighbourhoods (Fig. 2; Table 3 in **I**).

**Table 1.** Statistical effect of specialist and generalist herbivores, and of chemical compounds and morphological traits conferring herbivore resistance, of trees in the common garden on their climatic-stress resistance. Climatic-stress resistance is represented by the advancement of budburst of descendants in the “La Petite Charmie” common garden, by the coefficient of variation (CV) of budburst advancement, and by the CV of growth across four commons gardens. Multiple linear regression analyses accounting for the leaf nitrogen status of the trees in the common garden. LDMC = leaf dry matter content. Significant values are in bold (an asterisk indicates that the P values stay significant after correction using the false discovery rate). ‘Proportion’ refers to the proportion of the entire leaf surface affected by a type of herbivory. Data points are means across trees within provenances. See Table 2 in publication I.

	Specialist herbivores			Generalist herbivores		Chemical compounds			Morphological traits		
	Gall density	Proportion of leaf mines	Proportion of ectophagy	Anthocyanins concentration	Flavonols concentration	Leaf toughness	Leaf thickness	LDMC			
Advancement of budburst	T	-4.083	0.838	2.569	0.039	-0.092	-1.380	-0.883	0.713		
	P	<b>0.0005*</b>	0.412	<b>0.0175</b>	0.9690	0.9270	0.1820	0.3874	0.4836		
	Adj. R <sup>2</sup> of entire model	0.42	-0.006	0.27	-0.04	0.06	0.09	-0.005	0.07		
	d.f.	21	20	22	21	20	22	21	22		
CV of budburst	T	5.614	-0.926	-1.453	0.327	-0.798	1.719	0.993	-0.362		
	P	<b>&lt;0.0001*</b>	0.3660	0.1604	0.7470	0.4342	0.1002	0.3320	0.7211		
	Adj. R <sup>2</sup> of entire model	0.61	0.004	0.13	-0.03	0.10	0.09	0.008	-0.03		
	d.f.	22	20	22	21	20	21	21	21		
CV of growth	T	-0.690	0.251	0.442	0.098	-0.397	-0.478	0.272	-0.379		
	P	0.4982	0.8040	0.6630	0.9230	0.6952	0.6373	0.7880	0.7080		
	Adj. R <sup>2</sup> of entire model	-0.01	-0.088	-0.034	-0.07	-0.03	0.05	-0.07	-0.06		
	d.f.	20	18	21	21	20	21	21	21		



**Figure 2.** Interaction between the phylogenetic distance of the provenance neighbourhoods and the provenance climate on traits conferring resistance against climatic stress. Presented are significant (full lines) or marginally significant (dashed lines) interactions after correction for false discovery rate from Table 3 in **I**: phylogenetic distance (below vs above median) x (a) summer hydric deficit affecting anthocyanins, (b) minimum annual temperature affecting flavonols, (c) summer hydric deficit affecting leaf thickness and (d) minimum annual temperature affecting leaf thickness. Binary grouping for illustrative purposes, statistical tests treat phylogenetic distance, summer hydric deficit and minimum annual temperature as continuous variables. The values on Y-axis are the partial residuals, that is, accounting for the advancement of budburst and leaf nitrogen status of the trees in the common garden, as explained in Table 3 in **I**. Data points are means across trees within provenances. See publication **I**.

### **3.3 Coexistence with closely related neighbours selects for increased mycorrhiza-mediated resistance against both herbivory and climatic stress**

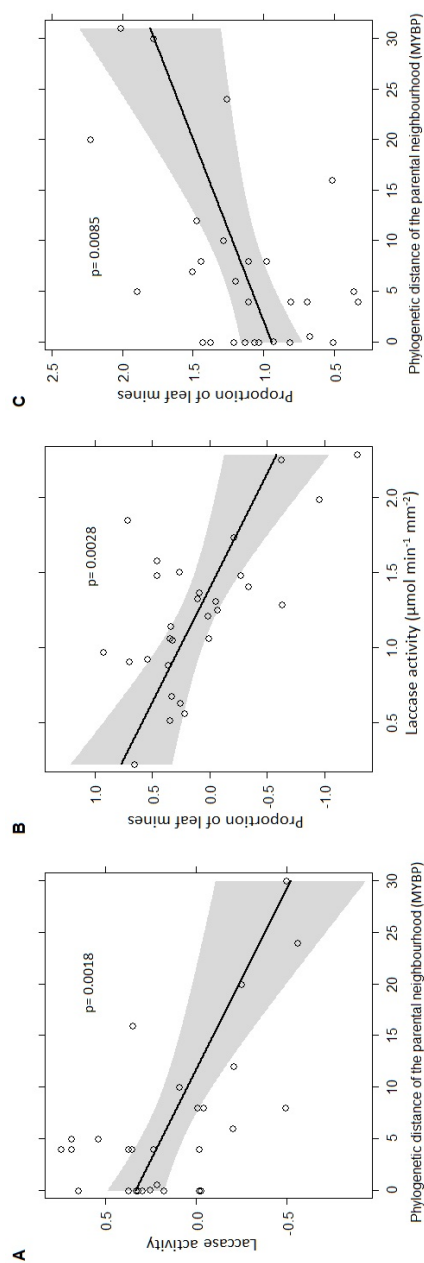
Multiple steps were needed to test whether coexistence among closely related species selects for increased mycorrhiza-mediated resistances against herbivores and climatic stress. Firstly, the statistical effect of the phylogenetic distance of provenance neighbourhoods on the investment of trees in the common garden into mycorrhiza was tested. The mycorrhizal enzymatic activity significantly decreases with the phylogenetic distance of the provenance neighbourhoods (Fig. 3A; Table S1 in **II**). In other words, trees descending from phylogenetically proximate neighbourhoods had significantly higher mycorrhizal enzymatic activity than trees descending from phylogenetically distant neighbourhoods. No relationships were found between the phylogenetic distance of provenance neighbourhoods and neither the proportion of mycorrhizal root-tips, nor the density of root tips (Table S1 in **II**).

Secondly, the statistical effect of investment of trees in the common garden into mycorrhizae on herbivory was tested. Trees with particularly high mycorrhizal enzymatic activity experienced a low proportion of leaf mines (Fig. 3B; Table 1 in **II**). No relationships were found between either the proportion of mycorrhizal root-tips or the density of root tips and either the herbivory variables (Table 1 in **II**).

Thirdly, the statistical effect of the phylogenetic distance of provenance neighbourhoods on the herbivory of trees in the common garden was tested. Consistent with the previous results, trees descending from phylogenetically proximate neighbourhoods experienced a low proportion of leaf mines (Fig. 3C; Table 2 in **II**). No relationships were found between the phylogenetic distance of the provenance neighbourhoods and the gall density or the proportion of ectophagy of the trees in the common garden (Table 2 in **II**).

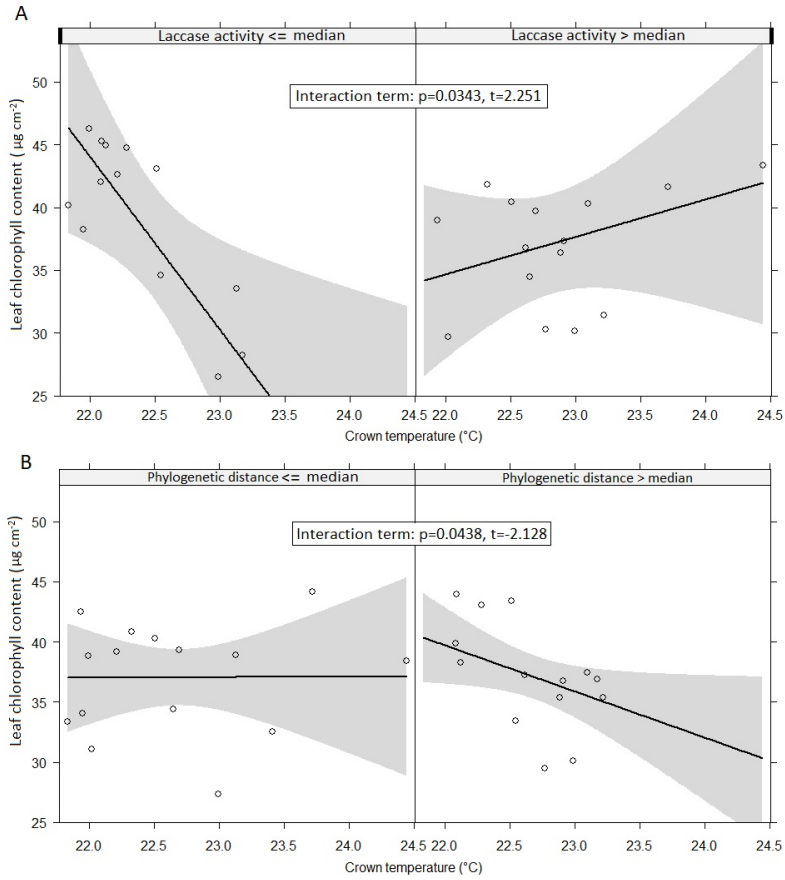
Fourthly, the statistical effect of the investment of trees in the common garden into mycorrhizae on their resistance to climatic stress was tested. There were significant positive interactions between mycorrhizae and the crown temperature of the trees on their leaf chlorophyll content (Fig. 4A; Table 3 in **II**). Trees with high mycorrhizal enzymatic activity, proportion of mycorrhizal root-tips or density of root tips experienced low chlorophyll reduction under increased crown temperature (Fig. 4A; Table 3 in **II**).

Finally, the effect of the phylogenetic distance of provenance neighbourhoods on the resistance to climatic stress of trees in the common garden was tested. There was a significant negative interaction between the phylogenetic distance of the provenance neighbourhoods and the crown temperature of the descendant trees on their leaf chlorophyll content (Fig. 4B; Table S5 in **II**). In other words, trees descending from phylogenetically proximate neighbourhoods experienced a low chlorophyll reduction under increased crown temperature (Fig. 4B; Table S5 in **II**).



**Figure 3.** Relationship of the phylogenetic distance of the neighbourhood in provenances and leaf miners attacks on trees in the common garden as mediated by the mycorrhizal enzymatic activity. The laccase enzymatic activity of mycorrhiza of oak descendants decreases with the phylogenetic distance of the provenance neighbourhood (A). The proportion of leaf mines on oak descendants decreases with the laccase enzymatic activity (B). The proportion of leaf mines on oak descendants increases with the phylogenetic distance of the provenance neighbourhood (C). Y-values are the partial residuals, accounting for co-variables, as explained in Tables 1, 2 and 3 in **II**. Data points are means across descendants within provenances. See publication **II**.



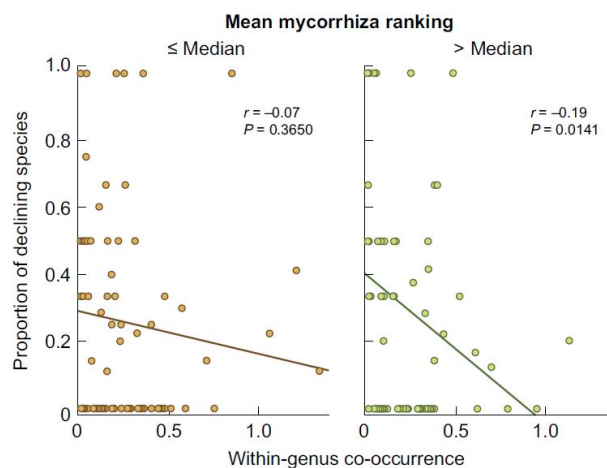


**Figure 4.** The relationship between crown temperature and leaf chlorophyll content of oak descendants in the common garden changes (A) with laccase enzymatic activity, and (B) with the phylogenetic distance of the provenance neighbourhood. Y-values are partial residuals, accounting for co-variables (crown temperature, tree height, altitude and block), as explained in Tables 4 and S4 in II. Data points are means across descendants within provenances. Binary grouping for illustrative purposes, statistical tests treat phylogenetic distance, laccase activity and their respective interaction with the crown temperature as continuous variables. Note that laccase activity is higher in descendants from provenances with phylogenetically proximate neighbourhoods. In the illustrated case, the median of the laccase enzymatic activity = 1.18 and the median of the phylogenetic distance = 4. See publication II.

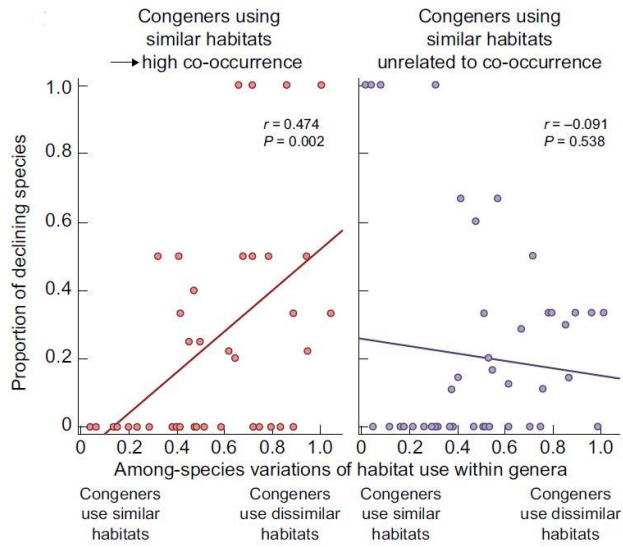
### 3.4 Coexistence with closely related neighbours reduces the risk to go extinct under environmental change

The effect of mycorrhizal association on the relationship between the proportion of declining species and the degree of coexistence with closely related neighbours was tested. The mycorrhizal association was inferred from the mean mycorrhiza ranking within genus as explained in the Materials and Methods section. The degree of coexistence with closely related neighbours was inferred from the degree of co-occurrence with congeners. There was a significant negative interaction between coexistence with congeners and the mycorrhizal association rank on the proportion of declining species (Fig. 5). Specifically, genera whose species are coexisting with closely related neighbours have a reduced proportion of declining species only in genera with particularly high mycorrhizal association.

The effect of coexistence between closely related neighbours on the relationship between the proportion of declining species and the similarity in habitat use among close relatives was tested. There was a significant interaction between similarity in habitat-use among congeners and how this similarity increases coexistence with congeners on the proportion of declining species (Fig. 6). Specifically, the similarity in habitat-use within genus reduces the proportion of declining species only when increased similarity among congeners relates to increased co-occurrence among congeners.



**Figure 5.** A high degree of intra-genus coexistence corresponds to a low proportion of declining species within a genus, provided that its species are colonized by mycorrhizas (above median mycorrhization rank, right graph, versus left graph). Median of mean mycorrhiza ranking = 0.8. Data points are angiosperm genera studied in the Netherlands. The intra-genus coexistence was inferred from the number of fellow congeners with which an average species will co-occur on an average plot (from Prinzing *et al.*, 2016). See publication III.



**Figure 6.** Genera in which species use similar habitats have a low proportion of declining species during the 20<sup>th</sup> century provided that similarity in habitat use among corresponds to high coexisting of congeners. Data points are angiosperm genera studied in the Netherlands. See publication **III**.

## 4. DISCUSSION

This thesis has shown that trees descending from phylogenetically proximate neighbourhoods had increased resistance against one type of herbivore, the leaf miners, and this resistance seems to be due to higher leaf toughness. Trees descending from phylogenetically proximate neighbourhoods were no less resistant against climatic stress and there was no trade-off between resistances to herbivores and climatic stress compared to trees from phylogenetically distant neighbourhoods. Trees descending from phylogenetically proximate neighbourhoods reflected most strongly the climatic stress in the provenance (I). Trees descending from phylogenetically proximate neighbourhoods had high mycorrhizal enzymatic activity. Trees with particularly high mycorrhizal enzymatic activity were more resistant to leaf miners. Consistently, trees descending from phylogenetically proximate neighbourhoods experienced less attacks by leaf miners. Trees with a particularly high mycorrhizal enzymatic activity, or a high proportion of ectomycorrhizal root-tips, had increased maintenance of chlorophyll under heat. Consistently, trees descending from phylogenetically proximate neighbourhoods had increased maintenance of chlorophyll under heat (II). Co-occurrence of species within a genus is high when species within genera use similar habitats. Angiosperm species co-occurring with congeners had a reduced risk of extinction only in genera with a high degree of association with mycorrhizae. Finally, genera in which species use similar habitats had reduced risk of extinction, only when similarity in habitat use corresponds to high co-occurrence of species within genera (III).

### 4.1 Coexistence with closely related neighbours selects for increased resistance against herbivores

This thesis hypothesized that coexistence with closely related neighbours selects for increased resistance against herbivores, in particular against specialist herbivores. Confirming this hypothesis, this thesis has shown that trees descending from phylogenetically proximate neighbourhoods were more resistant against one type of herbivore, the leaf miners, due to increased leaf toughness. Cornelissen (2006) has already shown that tougher leaves experienced a low density of leaf miners, but has not related this pattern to selection pressures. Leaf miners are mostly specialist herbivores and as internal feeders they must be adapted to leaf morphology and chemistry (Cornell 1989; Gaston *et al.* 1992). As specialist herbivores, they may be able to use closely related tree species only. Therefore, leaf miners should be concentrated in forest patches rich in closely related hosts, i.e. in phylogenetically proximate neighbourhoods, leading to strong selection pressure and explaining why trees from such neighbourhoods are more defended against leaf miners.

Trees descending from phylogenetically proximate neighbourhoods were not particularly resistant against ectophagous insects. Ectophagous insects are usually less specialised than leaf miners because they are external feeders (Gaston *et al.* 1992). As ectophagous insects are less specialised, they can use relatively more distantly related neighbouring trees. Ectophagous insects seem not to be affected by the phylogenetic distance of the neighbourhood (Grandez-Rios *et al.* 2015; but see Yguel *et al.* 2011 working on a much larger range of distances than we did). Hence, there should be no difference in the herbivory pressure caused by ectophagous insects in phylogenetically proximate or distant neighbourhoods. Therefore, tree resistance against ectophagous insects should be the same among phylogenetic neighbourhoods, which justifies the absence of increased resistance against ectophagous insects in trees descending from phylogenetically proximate neighbourhoods.

Inconsistent with my hypothesis, trees descending from phylogenetically proximate neighbourhoods were not particularly resistant against gall insects, which are specialist herbivores. Gall insects are so specialised that they can create their own environment within leaves and counter leaf resistance (Gaston *et al.* 1992) which possibly explains the absence of increased resistance in trees descending from phylogenetically proximate neighbourhoods. Moreover, Yguel *et al.* (2014) show that the phylogenetic distance of the neighbourhoods does not decrease gall abundance suggesting that gall insects are able to track their host even in phylogenetically distant neighbourhoods so that the selection by galls on oaks does not differ between phylogenetically distant and proximate neighbourhoods. Also, inconsistent with my hypothesis, trees descending from phylogenetically proximate neighbourhoods had no increased chemical resistance. Chemical compounds such as tannins, anthocyanins or flavonols can be multi-functional and can be used to respond to other pressures than herbivory (Treutter 2006; Korn *et al.* 2008; Neilson *et al.* 2013). Hence, increased herbivory in phylogenetically proximate neighbourhoods might not select for increased chemical resistance.

#### **4.2 Coexistence with closely related neighbours does not indirectly select against resistance to climatic stress: no trade-off between resistances to herbivores and climatic stress**

This thesis hypothesized that coexistence with closely related neighbours indirectly selects against resistance to climatic stress that is traded off against resistance to herbivory. Descendants from closely related neighbourhoods indeed showed increased resistance against leaf miners due to increased leaf toughness. However, inconsistent with the trade-off hypothesis, no negative relationships were found between resistance against leaf miners or leaf toughness and resistance against climatic stress. This absence of trade-off might result from the time gap

between resistance against leaf miners and climatic stress. Leaf miners are attacking trees in spring and summer therefore leaf toughness is important during this period. Climatic stress resistance was inferred from the advancement of budburst, and climatic stress limiting budburst occurs in late winter. Therefore, trees can invest in both resistances without any direct trade-off between them. Absence of trade-off might also result from the multifunctionality of morphological resistances (Jetter *et al.* 2000; Brennan & Weinbaum 2001a, b). In addition, there was no trade-off between chemical compounds and climatic stress resistances. Again, the lack of this trade-off might be explained by the multifunctionality of chemical compounds (Treutter 2006; Korn *et al.* 2008; Neilson *et al.* 2013). Also, inconsistent with the trade-off hypothesis, this thesis has even shown a positive relationship between resistance against galls and climatic stress as inferred from the advancement of budburst. Specifically, trees with particularly high resistance against late frost bud burst early and experience few gall attacks. This result is compatible with Crawley & Akhteruzzaman (1988) showing that galls prefer trees with late budburst. Overall, there was no trade-off between resistance against herbivores and climatic stress and therefore no indirect selection against resistance to climatic stress in phylogenetically proximate neighbourhoods.

Finally, trees descending from particularly cold winters or dry summers had increased flavonols, anthocyanins and leaf thickness only when in the provenance the tree neighbourhood was phylogenetically proximate. As explained above, these chemical and morphological resistances are suggested to be multifunctional. Hence, coexistence with closely related neighbours seems to reinforce the selection by climatic stress for multifunctional resistances due to increased herbivory in such neighbourhoods. This reinforcement of selection by climatic stress might be possible due to the double benefits of multifunctional resistances that might reduce the costs of adaptation to climatic stress in environments increasing herbivory, i.e. phylogenetically proximate neighbourhoods. In addition, climatic stress might in turn reinforce the selection pressure by herbivores. White (1984) has suggested that climatic stress can increase the availability of nitrogen in the leaves of stressed plants, which may increase herbivory and hence reinforce herbivory selection pressure. Overall, multifunctional resistances against both herbivory and climatic stress might be high in trees coexisting with closely related neighbours.

In addition, as phylogenetically proximate neighbourhoods seem to increase the selection for resistances that are multifunctional due to increased herbivory, the tree-genotypes selected in such neighbourhoods might be resistant to both herbivores and climatic stress even in absence of the latter. In other words, climatic stress might not be needed for the evolution of multifunctional resistance to climatic stress. If so, the coexistence with closely related neighbours, by increasing herbivory, might select for tree genotypes resistant to climatic stress even in non-stressful climate. Therefore, monospecific forests or composed of closely related species might be able to cope with future climate stress.

### **4.3 Coexistence with closely related neighbours selects for increased mycorrhiza-mediated resistances against both herbivory and climatic stress**

This thesis hypothesized that coexistence with closely related neighbours selects for increased mycorrhiza-mediated resistances against both herbivory and climatic stress. Consistently, this thesis has shown that trees descending from phylogenetically proximate neighbourhoods had increased investment into mycorrhizae and were particularly resistant against leaf miners and heat-induced drought. Specifically, trees with particularly high investment into mycorrhizae were more resistant against leaf miners but no more resistant against galls or ectophagous insects.

This result is consistent with Koricheva *et al.* (2009) showing that mycorrhizae do not affect galls because galls can counter tree resistance (Gaston *et al.* 1992). Koricheva *et al.* (2009) also show that mycorrhizae had a negative effect on generalist ectophagous insects and a positive effect on specialist ectophagous insects. Hence, the observed absence of the effect of mycorrhizae on ectophagous insects suggests that the measure of ectophagy used in this thesis regroups both generalist and specialist ectophagous insects. In addition, the observed increased tree resistance against leaf miners is consistent with Koricheva *et al.* (2009) showing that mycorrhizae have a negative effect on leaf miners. Mycorrhizae are known to increase induced resistance against herbivores (Pozo & Azcón-Aguilar 2007; Wang *et al.* 2015; Meier & Hunter 2018). In addition, mycorrhizae are known to provide nutrients to trees which might help trees to produce costly resistances that are known to impede specialist herbivores – the quantitative resistances (Ali & Agrawal 2012; van der Heijden *et al.* 2015; Garcia *et al.* 2016). Therefore, coexistence with closely related neighbours seems to select for increased investment into mycorrhizae, which in turn increases resistance against leaf miners, potentially by increasing induced quantitative resistances.

Trees descending from phylogenetically proximate neighbourhoods had increased investment into mycorrhizae, leading to increased maintenance of chlorophyll during heat. The common garden of “La Petite Charnie” is characterized by temperate, oceanic climate, therefore high temperatures are unlikely to exceed the thermal tolerance of chlorophyll and damage it directly. Instead, a high temperature increases leaf desiccation by increasing the water saturation deficit of the air (Anderson 1936), which in turn leads to the production of reactive oxygen species able to destroy leaf chlorophyll (Smirnoff 1993, 1995). Mycorrhiza might increase resistance to desiccation, firstly, by increasing water uptake (Marulanda *et al.* 2003), which might enable trees to avoid leaf desiccation. Secondly, mycorrhizae can provide nitrogen to trees (Courty *et al.* 2010), which might help trees to compensate for the destruction of chlorophyll by producing new chlorophyll as chlorophyll is nitrogen-based. Finally, mycorrhizae can increase antioxidant resistances (Wu *et al.* 2014), which might counteract the production of reactive oxygen species and avoid chlorophyll destruction. Therefore, coexistence with closely related neighbours, by increasing climatic stress,

seems to select for increased investment into mycorrhizae leading to increased resistance against drought.

Mycorrhizae seem to be multifunctional as they increase the resistance to both herbivores and climatic stress. This multifunctionality of mycorrhizae might explain the fact that mycorrhizae are selected and conserved across evolution and contribute to the fact that more than 80% of the plants have mycorrhizae. Despite this positive side, the investment of trees into mycorrhizae might be costly. Trees are allocating a part of their carbon into mycorrhizae in exchange for the supply of other nutrients by mycorrhizae (Nehls *et al.* 2001). Yet, this allocated carbon to mycorrhizae will not be used for tree metabolism (Nehls *et al.* 2001), which might limit tree growth. Therefore, having a high mycorrhization or high mycorrhizal activity, selected for in a phylogenetically proximate neighbourhood, might be hard to bear for trees in terms of carbon allocation.

#### **4.4 Coexistence with closely related neighbours reduces the risk of extinction under environmental change**

This thesis hypothesized that species coexisting with closely related neighbours have reduced risk of extinction. According to the hypothesis, angiosperm species coexisting with closely related neighbours have a reduced risk of extinction but only when such species have a strong mycorrhizal association. As seen in the previous section mycorrhizae increase the resistance to climatic stress. Closely related neighbours might share similar mycorrhizae (Ishida *et al.* 2007) and thus act as a source of mycorrhizae. In such a case, species coexisting with closely related neighbours might have increased mycorrhizal association. As seen previously, mycorrhizae may help their host to better resist climatic stress. Climate change is predicted to increase climate stress in intensity and frequency (Zandalinas *et al.* 2021; IPCC 2021). Therefore, species coexisting with closely related neighbours may have a reduced risk of extinction under climate change due to increased access to mycorrhizal association, which may increase resistance to climate stress.

In addition, this thesis has shown that the use of similar habitats within genera reduces the proportion of declining species only when the use of similar habitats corresponds to high local co-occurrence. This result suggests that the evolutionary conservation of habitat use within genera reduces the risk of population decline by increasing local co-occurrence with congeners. Again, this increased co-occurrence of species with congeners, i.e. closely related neighbours, may facilitate the exchange of mycorrhizae between congeners which may increase their resistance to climatic stress. Mycorrhizae may also facilitate the exchange of resources between neighbouring congeners via the common mycorrhizal network (Selosse *et al.* 2006; Walder *et al.* 2015), which might increase tree resistance to climatic stress. Therefore, species using similar habitats and co-occurring with closely related neighbours might have a reduced risk of extinction under climate change due to increased mycorrhiza-mediated resistance to climate stress.



## 5. CONCLUSION

This thesis suggests that trees coexisting with closely related neighbours are evolving increased resistance against herbivores and without cost for resistance to climatic stress. Trees coexisting with closely related neighbours are also evolving increased mycorrhiza-mediated resistances against both herbivory and climatic stress. Species coexisting with closely related neighbours have a reduced risk of extinction under climate change.

These results suggest that under strong selection pressure trees are able to adapt rapidly increased resistances. Contrary to common belief, trees may not require several generations to adapt. Specifically, trees have long generation times, rendering adaptation to rapid environmental change impossible if adaptation requires multiple generations. However, adaptation may occur within less than entire generation time. Ersoz *et al.* (2010) has shown that selection pressures in trees are particularly powerful and can shift trait frequencies within populations within less than a generation. This rapid adaptation is possible due to large population sizes, an extremely high mortality based on heritable resistances and a very high genetic variability among trees but also among seeds of the same tree (Shaw 1968; Zanetto & Kremer 1995; Klaper *et al.* 2001; Petit & Hampe 2006). This within-generation adaptation might have implications for forest responses to future climate. Even if tree species adaptation is not sufficiently fast to entirely track climate change (Rellstab *et al.* 2016), this adaptation might still enable tree populations to partly respond to the ongoing climate change.

These results may also have implications for understanding the coexistence of closely related species. Coexistence of closely related species is suggested to be difficult among others due to increased herbivory and climatic stress (Janzen 1970; Webb *et al.* 2002; Liu *et al.* 2012). This thesis shows that coexistence with closely related species may be possible as species can adapt to increased herbivory and climatic stress. Species adaptations to increased herbivory and climate stress might hence facilitate their coexistence with close relatives and possibly explain the existence of naturally monospecific forests or such dominated by a single lineage (Gromtsev 2002).

These results may also have implications for management of forests under climate change. Climate change is predicted to increase climatic stress in intensity and frequency (Zandalinas *et al.* 2021; IPCC 2021). The increased multi-functional resistances such as mycorrhiza-mediated resistances to climatic stress might enable trees to persist under climate change. If so, foresters may find tree genotypes adapted to future climatic stress in monospecific forests or such composed of closely related species. In addition, tree genotypes resistant to herbivores may be found in such forests. Therefore, planted monospecific forests might be less attacked by herbivores if tree genotypes have been selected from forests composed of closely related species.

Overall, this thesis shows that coexistence with closely related neighbours might be facilitated through an eco-evolutionary feedback, i.e. changes in ecological interactions of trees induce evolutionary change in trees, which in turn changes the ecological interactions of trees. This thesis may help to understand forest responses to climate change and suggests ways to maintain the use of native tree species in forestry rather than replace them by exotics.

## SUMMARY

Herbivory and climatic stress are known to negatively impact trees and forests. Researches have shown that increasing tree-species diversity by creating mixed forests seems to decrease herbivory via associational resistance and decrease climatic-stress effects via facilitation. However, these effects are species dependent and no clear general pattern was established. In mixed forests, the identity of the neighbouring tree-species is important, as they may be phylogenetically closely related or distantly related to the focal tree. It has been shown that closely related species tend to share similar traits and are therefore used by the same herbivores and exploit resources like water at similar depths and times. Species coexisting with closely related neighbours may hence suffer particularly high herbivory and competition for limited resources. Therefore, coexistence with closely related neighbours has been suggested to be difficult and species may coexist rather with distantly related neighbours. Yet, in nature we observe forests composed mostly of closely related species and we do not understand the mechanisms.

In this thesis, I argue that firstly, trees can adapt to increased herbivory by evolving increased morphological or chemical resistances. Hence, phylogenetically proximate neighbourhoods might select for increased resistance against herbivores. Secondly, this selection for increased resistances against herbivores might be traded-off against resistances to climatic stress. Therefore, phylogenetically proximate neighbourhoods might indirectly select against climatic stress resistance. Thirdly, trees may also adapt to increased herbivory and climatic stress by evolving increased investment into mycorrhizae, as mycorrhizae are known to increase resistances to both herbivory and climatic stress. Therefore, phylogenetically proximate neighbourhoods might select for increased investment into mycorrhizae. Fourthly, I argue that species already under high herbivory and climatic stress may have an increased risk of extinction under environmental change. Hence, phylogenetically proximate neighbourhoods might increase the risk of extinction under environmental change. Alternatively, evolved resistances to herbivory and climate stress in species growing in phylogenetically proximate neighbourhoods may render these species more resistant against environmental change in general. Specifically, this thesis addresses the following questions:

- 1) Does coexistence with closely related neighbours select for increased morphological and chemical defences against herbivores?
- 2) Does coexistence with closely related neighbours indirectly select against resistance to climatic stress?
- 3) Does coexistence with closely related neighbours select for increased mycorrhiza-mediated resistance against both herbivory and climate stress?
- 4) Does coexistence with closely related neighbours increase or decrease the risk of extinction under environmental change?

To study questions 1–3, I used a common garden experiment of 30-years-old sessile oak (*Quercus petraea*) descending from provenances of contrasting phylogenetic neighbourhoods and climates. This common garden experiment permits to identify the natural selection for resistances to herbivory and climate stress by phylogenetic neighbourhoods. To study the question 4, I used data from published papers and from the Dutch National Vegetation Database of hundreds of plant genera across the Netherlands to identify the effect of coexistence with close relatives on the risk of extinction of plant genera under environmental change.

This thesis shows that trees descending from phylogenetically proximate neighbourhoods experienced lower attacks by leaf miners due to increased leaf toughness, but not chemical resistance. This result suggests that coexistence with closely related neighbours selects for increased resistance against specialist herbivores via increased morphological resistance.

This thesis shows that there was no evidence for a trade-off between resistance to herbivores and climatic stress. Trees descending from phylogenetically proximate neighbourhoods were no less resistant to climatic stress. Trees descending from cold and dry climates had increased resistances against climatic stress provided the neighbourhood was phylogenetically proximate. These results suggest that coexistence with closely related neighbours does not indirectly select against resistance to climatic stress. Instead, coexistence with closely related neighbours seems to reinforce the selection by climatic stress for resistances having multiple functions.

This thesis shows that trees descending from phylogenetically proximate neighbourhoods had increased mycorrhizal enzymatic activity and such trees experienced lower attacks by leaf miners. Trees with particularly high mycorrhizal enzymatic activity or proportion of mycorrhizal root-tips had better maintenance of chlorophyll under heat. Also, trees descending from phylogenetically proximate neighbourhoods had better maintenance of chlorophyll under heat. These results suggest that coexistence with closely related neighbours selects for increased investment into mycorrhizae, which increases the resistance against both specialist herbivores and climatic stress. Again, this selection seems to favour resistances that are multifunctional, i.e. mycorrhiza-mediated resistance against both herbivores and climatic stress.

Finally, this thesis shows that plant genera in which species co-occur had lower proportions of species declining under environmental change in the Netherlands during the 20<sup>th</sup> century – provided that their constituent species have high mycorrhizal association. Moreover, the use of similar habitats within genera reduces the proportion of declining species in the Netherlands, provided that the use of similar habitats corresponds to high local co-occurrence with congeners. These results suggest that the evolutionary conservation of habitat use within genera reduces the risk of population decline by increasing co-occurrence with congeners. This increased co-occurrence with congeners might increase the access to mycorrhizae, which may increase the resistance to climatic stress.

Overall, this thesis adds insights to the mainstream of community ecology by suggesting that tree species can rapidly adapt to increased herbivory and climatic stress in phylogenetically proximate neighbourhoods by evolving increased resistances. These adaptations might facilitate the coexistence with closely related neighbours. These adaptations of trees in phylogenetically proximate neighbourhoods might facilitate responses to future environmental changes.

## SUMMARY IN ESTONIAN

### **Puude fülogeneetilise naabruse evolutsiooniline mõju vastupanuvõimes herbivooridele ja kliimamuutustele**

Herbivooria ja kliimamuutused mõjutavad negatiivselt nii üksikuid puid kui ka terveid metsi. On leitud, et suurema liigirikkusega segametsades on vähem herbivooriat puude suurema vastupanuvõime tõttu herbivooridele ja nõrgem kliimamuutuste mõju tänu kasulikele biotilistele interaktsioonidele. Herbivooria ja kliimamuutuste mõju on aga liigispetsiifiline, mistõttu üldist mustrit ei ole siiani leitud. Segametsades tuleks herbivooria ja kliimamuutuste uurimisel arvesse võtta fülogeneetiline naabus ehk uuritava puuisendi naabruses kasvavate teiste puuisendite liigiline identiteet, sest need võivad olla uuritava puuga kas lähedalt või kaugelt suguluses. Lähisugulastel on üldiselt sarnased tunnused, mistõttu lähisugulased võivad olla toidutaimeks samadele herbivooridele ning konkureerida samade limiteerivate ressursside pärast. Seetõttu võivad lähisugulastest koosnevas naabruses kasvavad puud herbivooria ja kliimamuutuste läbi rohkem kannatada. Lähisugulastest naabruses kasvamist peetakse seepärast keeruliseks ning arvatakse, et liigid eelistavad kasvada pigem kaugelt suguluses olevate liikide naabruses. Looduses leidub aga palju lähisugulasliikidest koosnevaid metsi, kusjuures selliste metsade tekkimise mehhanismid on ebaselged.

Käesolevas töös püstitati esiteks hüpotees, et puud kohanevad suurenenud herbivooria ja kliimamuutustega morfoloogiliste ja keemiliste kaitsemehhanismide abil. Seega võiks lähisugulasliikidest naabus selekteerida herbivooriavastaste kaitsemehhanismidega genotüüpe. Teiseks arvati, et herbivooria vastane kaitse võiks olla lõivsuhtes kliimamuutuste vastase kaitsega. Sellepärast võiks lähisugulastest koosnev naabus kaudselt selekteerida nõrgema kliimamuutuste vastase kaitsega genotüüpe. Kolmandaks eeldati, et puud kohanevad suurenenud herbivooria ja kliimamuutustega mükoriisa abil, sest mükoriisa tugevdab taimedel nii herbivooria kui ka kliimamuutuste vastast kaitset. Seega võiks lähisugulastest koosnev naabus selekteerida genotüüpe, mis investeerivad rohkem mükoriissasse. Neljandaks püstitati hüpotees, et tugeva herbivooria ja kliimamuutuste all kannatavatel taimedel on suurem tõenäosus keskkonnamuutuste korral välja surra. Sellisel juhul oleks lähisugulasliikidest koosnevas naabruses suurem väljasuremise oht. On aga ka võimalik, et herbivooria ja kliimamuutuste vastased kaitsemehhanismid muudavad lähisugulasliikidest naabruses kasvavad taimed keskkonnamuutustele vastupidavamaks.

Täpsemalt uuritakse käesolevas töös:

- 1) Kas lähisugulasliikidest koosnev naabus selekteerib tugevamate morfoloogiliste ja keemiliste herbivooriavastaste kaitsemehhanismidega genotüüpe?
- 2) Kas lähisugulasliikidest koosnev naabus selekteerib kaudselt nõrgema kliimamuutuste vastase kaitsega genotüüpe?

- 3) Kas lähisugulasliikidest koosnev naabrus selekteerib genotüüpe, mille suurem mükoriissus suurendab vastupanuvõimet herbivooriale ja kliimamuutustele?
- 4) Kas lähisugulasliikidest koosnev naabrus vähendab liigi väljasuremise riski keskkonnamuutuste korral?

1–3 hüpoteesi testimiseks koguti andmeid 30 aasta vanusest välieksperimentidist kivitammega (*Quercus petraea*). Eksperimenti rajamiseks kasutati erineva fülogeneetilise naabruse ja kliimaga metsadest pärit tammetõrusid üle Euroopa. Välieksperiment võimaldab uurida erinevate kaitsemehhanismidega genotüüpide looduslikku valikut erineva fülogeneetilise naabruse puhul. 4. hüpoteesi testimiseks kasutati andmebaasi *Dutch National Vegetation Database*, et uurida fülogeneetilise naabruse mõju keskkonnamuutuste poolt tingitud liikide väljasuremisele.

Käesoleva töö tulemusena selgus, et lähisugulasliikide naabrusest pärinevatel puudel olid paksemad lehted ja vähem lehtedes kaevandavaid putuk-herbivoore, kuid erinevust keemilises kaitstes ei õnnestunud tõestada. Sellest järeldub, et lähisugulasliikidest koosnev naabrus selekteerib genotüüpe, mis suurendavad spetsialistidest herbivooride vastast morfoloogilist kaitset.

Selgus ka, et herbivooriavastase kaitse ja kliimamuutuste vastase kaitse vahel puudub lõivsuhe. Lähisugulasliikide naabrusest pärinevatel puudel polnud nõrgem kliimamuutuste vastane kaitse. Külmast ja kuivast kliimast pärinevatel puudel oli tugevam kaitse juhul, kui nad pärinesid lähisugulasliikide naabrusest. Sellest järeldub, et lähisugulasliikidest koosnev naabrus ei selekteeri kaudselt nõrgema kliimamuutuste vastase kaitsega genotüüpe. Lähisugulasliikidest koosnev naabrus pigem tugevdab kliimamuutuste vastast kaitset juhul, kui kaitse on multifunktsionaalne.

Lähisugulasliikide naabrusest pärinevatel puudel oli suurem mükoriisa ensümaatiline aktiivsus ja neil oli vähem lehtedes kaevandavaid putuk-herbivoore. Suurema mükoriisa ensümaatilise aktiivsusega või suurema hulga mükoriissete juuretippudega puud suutsid kõrgetel temperatuuridel paremini klorofüllil säilitada. Klorofüllil säilitamise võime oli suurem ka lähisugulasliikide naabrusest pärinevatel puudel. Sellest järeldub, et lähisugulaslastest koosnev naabrus selekteerib genotüüpe, mis investeerivad rohkem mükoriisasse, mis omakorda suurendab nende genotüüpide vastupanuvõimet spetsialistidest herbivooridele ja kliimamuutustele. Selles selektsioonis eelistatakse multifunktsionaalseid kaitsemehhanisme, st. mükoriisast tingitud kaitsemehhanisme nii herbivooride kui ka kliimamuutuste vastu.

Käesolevas töös selgus ka, et 20. sajandil esines Madalmaades nendes taimeperekondades, mis kasvasid lähisugulasliikidest koosnevas naabruses, vähem keskkonnamuutuste poolt tingitud liikide väljasuremist juhul, kui liigid olid mükoriissed. Lisaks selgus, et sama kasvukohta eelistavate taimeperekondade liikidel oli väiksem väljasuremise risk juhul, kui kasvukohas kasvati koos lähisugulasliikidega. Sellest järeldub, et kasvukoha evolutsiooniline konservatiivsus taimeperekondades vähendab populatsioonide kahanemise riski. Lähisugulaste

koos esinemine suurendab samas mükoriissust, mille abil tugevneb kliimamuutuste vastane kaitse. Sellepärast on sama kasvukohta eelistavatel ja lähisugulaste naabruses kasvavatel liikidel kliimamuutuste korral tõenäoliselt väiksem risk väljasuremiseks.

Käesoleva töö põhjal võib järeldada, et lähisugulasliikidest koosnevas naabruses suudavad puud kiiresti arendada välja suurema herbivooria ja kliimamuutuste vastase kaitse. Nende kaitsemehhanismide olemasolu soosib lähisugulaste naabruses kasvamist. Sellepärast on võimalik, et lähisugulasliikide naabrusest pärinevad puud suudavad tuleviku keskkonnamuutustega paremini toime tulla.



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## **PUBLICATIONS**

## CURRICULUM VITAE

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### Education

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### Publications

- Pihain, M.**, Prinzing, A., Ducousso, A., Courty, P.-E., Houet, T., Georges, R., Jambon, O., Musch, B. & Gerhold, P. (2021). Eco-evolutionary consequences of living with close relatives: Resistance to herbivores and climatic stress increases with investment into mycorrhiza in adult oaks. *Manuscript under review*.
- Deniau, **M.**, **Pihain, M.**, Béchade, B., Jung, V., Brunellière, M., Gouesbet, V. & Prinzing, A. (2021). Seeds and seedlings of oaks suffer from mammals and molluscs close to phylogenetically isolated, old adults. *Annals of Botany*, 127: 787–798.
- Pihain, M.**, Gerhold, P., Ducousso, A. & Prinzing, A. (2019). Evolutionary response to coexistence with close relatives: increased resistance against specialist herbivores without cost for climatic-stress resistance. *Ecology Letters*, 22: 1285–1296.
- Prinzing, A., Ozinga, W.A., Brändle, M., Courty, P.-E., Hennion, F., Labandeira, C., Parisod, C., **Pihain, M.** & Bartish, I.V. (2017). Benefits from living together? Clades whose species use similar habitats may persist as a result of eco-evolutionary feedbacks. *New Phytologist*, 213: 66–82.

### Honours & awards

- 2018 Dora Plus activity 1.1 grant (short study visits) to participate at the II Joint Congress on Evolutionary Biology in Montpellier, France.
- 2018 Erasmus+ grant student mobility for studies at the University of Rennes 1, France, from September 2018 to June 2019.
- 2018 Grant from OSUR (Earth Sciences and Astronomy Observatory, Rennes, France).
- 2017 Dora Plus activity 1.1 grant (short study visits) to participate at the symposium of RENECOFOR in Beaune, France.

### Projects in progress

PRG741: “Comparative studies on insects: focus on body size (1.01.2020–31.12.2024)”, Toomas Tammaru, University of Tartu, Faculty of Science and Technology, Institute of Ecology and Earth Sciences.

### Completed projects

PUT1006: “Macroecological and evolutionary determinants of community phylogenetic and functional diversity (1.01.2016–31.12.2019)”, Pille Gerhold, University of Tartu, Faculty of Science and Technology, Institute of Ecology and Earth Sciences.

### Presentations

- 2019 **Pihain, M.**, Gerhold, P., Ducouso, A. & Prinzing, A. (2018). Evolutionary response to coexistence with close relatives: increased enemy defence, different response to climate, but no costs for climatic tolerance. International conference on ecological sciences. Rennes, France. Pp. 241–241.
- 2018 **Pihain, M.**, Ducouso, A., Kremer, A., Gerhold, P., Jaquiery, J. & Prinzing, A. (2018). Manipulate biotic neighbourhood to facilitate adaptation to abiotic stress: Do phylogenetically distant neighborhood select for more tolerant oak genotypes? *II Joint Congress on Evolutionary Biology*. Montpellier, France. Pp. 71–71.
- 2017 **Pihain, M.**, Ducouso, A., Kremer, A., Gerhold, P., Jaquiery, J. & Prinzing, A. (2017). *Manipuler le voisinage biotique pour augmenter la résistance abiotique: Est-ce que les chênes en voisinage phylogénétiquement éloigné supportent mieux les stress abiotiques?* Symposium of 25 years of RENECOFOR. Beaune, France. Pp. 42–42.
- 2017 Prinzing, A., Deniau, M. & **Pihain, M.** (2017). Evolutionary neighbourhood and climate interact to select for heritable defense phenotypes: anthocyanin and flavonoid contents and inducibility. *19<sup>th</sup> International Botanical Congress*. Shenzhen, China. Pp. 409–409.

## DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS

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