



HAL
open science

Evolutionary response to coexistence with close relatives: increased resistance against specialist herbivores without cost for climatic-stress resistance

Mickael Pihain, Pille Gerhold, Alexis Ducouso, Andreas Prinzing

► To cite this version:

Mickael Pihain, Pille Gerhold, Alexis Ducouso, Andreas Prinzing. Evolutionary response to coexistence with close relatives: increased resistance against specialist herbivores without cost for climatic-stress resistance. *Ecology Letters*, 2019, 22 (8), pp.1285-1296. 10.1111/ele.13285 . hal-02181398

HAL Id: hal-02181398

<https://univ-rennes.hal.science/hal-02181398>

Submitted on 15 Jul 2019

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

**Evolutionary response to coexistence with close relatives:
increased resistance against specialist herbivores
without cost for climatic-stress resistance**

Mickael Pihain^{1,2}, Pille Gerhold², Alexis Ducouso³, Andreas Prinzing¹

¹ Research Unit “Ecosystèmes, Biodiversité, Evolution”, University of Rennes 1 / CNRS, 35042 Rennes, France

² Institute of Ecology and Earth Sciences, University of Tartu, 51014 Tartu, Estonia

³ BIOGECO, INRA, Université de Bordeaux, 33610 Cestas, France

Email addresses of authors:

Mickael Pihain: mickael.pihain@ut.ee

Pille Gerhold: pille.gerhold@ut.ee

Alexis Ducouso: alexis.ducouso@inra.fr

Andreas Prinzing: andreas.prinzing@univ-rennes1.fr

Corresponding author: Andreas Prinzing; andreas.prinzing@univ-rennes1.fr; Research Unit “Ecosystèmes, Biodiversité, Evolution”, University of Rennes 1 / CNRS, Rennes 35042, Campus Beaulieu, bât 14a, 35042 Rennes, France.

Short running title: Response to coexistence with relatives

Key words: adaptation; associational resistance; climatic-stress resistance; eco-evolutionary feedback; ecomorphology and chemical ecology; galls, ectophages and miners; phylogenetic diversity; multifunctional resistance; Sessile Oak (*Quercus petraea*); temperate forests

Type of article: Letters

Number of words in the abstract: 150, number of words in the main text: 4994.

Number of references: 68

Number of figures: 3

Number of tables: 3

Statement of authorship: AP and AD sampled leaves, and measured leaf-chemistry, MP measured leaf morphology and herbivore pressure. AD was responsible of measures of budburst and growth and provided data on provenance neighbourhoods and climates. MP, AP and PG wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

Data accessibility statement: The data supporting the results are archived in HAL <https://hal.archives-ouvertes.fr/hal-02062599>.

Abstract

Why can hosts coexist with conspecifics or phylogenetically proximate neighbours despite sharing specialist enemies? Do the hosts evolve increased enemy resistance? If so, does this have costs in terms of climatic-stress resistance, or in such neighbourhoods does climatic-stress select for resistances that are multifunctional against climate and enemies? We studied oak (*Quercus petraea*) descendants from provenances of contrasting phylogenetic neighbourhoods and climates in a 25-year-old common garden. We found that descendants from conspecific or phylogenetically proximate neighbourhoods had the toughest leaves and fewest leaf miners, but no reduction in climatic-stress resistance. Descendants from such neighbourhoods under cold or dry climates had the highest flavonol and anthocyanin levels, and the thickest leaves. Overall, populations facing phylogenetically proximate neighbours can rapidly evolve herbivore resistance, without cost to climatic-stress resistance, but possibly facilitating resistance against cold and drought via multifunctional traits. Microevolution might hence facilitate ecological coexistence of close relatives and thereby macroevolutionary conservatism of niches.

Introduction

Coexistence among conspecific or phylogenetically proximate plants (“phylogenetically proximate” from here on) has been suggested to be difficult due to increased herbivore pressure, but plant populations might respond to such coexistence by evolving increased herbivore resistance. Specifically, individuals of phylogenetically proximate plant species tend to share similar traits (Burns & Strauss 2011; Peterson 2011; Violle et al. 2011) and can be attacked by the same herbivore species (Brändle & Brandl 2006). This effect of phylogenetic proximity on herbivory is likely to be strongest in highly specialized herbivores (Nyman et al. 2006, Vialatte et al. 2010). Consequently, in phylogenetically proximate neighbourhoods, a focal host plant could be attacked by the herbivores of its neighbours, increasing herbivory on the focal plant (Yguel et al. 2011). It has been suggested that such increased herbivore pressure prevents coexistence of phylogenetically proximate individuals and leads to coexistence among phylogenetically distant species (Janzen 1970; Liu et al. 2012; we use the term “coexistence” sensu largo, i.e. including coexistence with conspecifics, Jiang et al. 2018). However, such neighbourhoods might also select for increased herbivore resistance. In phylogenetically proximate neighbourhoods, more resistant plants will survive better, have more chances to reach maturity and reproduce more, leading to a higher fitness than non-resistant plants. Plant resistances are often genetically determined and hence heritable, e.g. levels of flavonoids or anthocyanins or leaf morphology (e.g. Stevens & Lindroth 2005; Johnson et al. 2009). Overall, a phylogenetically proximate neighbourhood should select for genotypes that are resistant against herbivores, in particular against specialist herbivores. These selection pressures are particularly powerful in trees (Ersoz et al. 2010), where natural selection can shift frequencies of traits across a population within a fraction of a generation time (even if selection pressures might change even more rapidly, Rellstab et al. 2016). This rapid shift of the frequencies of traits is possible due to large population sizes (seeds and seedlings included), 99.9999 % mortality depending on heritable resistance traits, and a very high genetic variability among trees and among seeds of each tree (Shaw 1968; Zanetto & Kremer 1995; Klaper et al. 2001; Petit & Hampe 2006). Overall, our first hypothesis

is that tree species are not passively suffering from increased pressure by specialist herbivores in a phylogenetically proximate neighbourhood, but rather local populations are adapting to herbivory as a result of selection for herbivore resistance (Fig. 1).

If phylogenetically proximate neighbourhoods select for higher herbivore resistances they might indirectly select against capacities that are traded off against herbivore resistances such as the resistance to extreme climatic conditions. Specifically, resistance against herbivores might invoke multiple types of costs for the tree (Baldwin & Hamilton 2000; Koricheva 2002; Siemens et al. 2009). Investment in resistance against herbivores might hence be traded off against other capacities of trees. For instance, genotypes with increased energy investment into traits conferring herbivore resistance might have less energy available to invest into traits conferring other functions including competitiveness or climatic-stress resistance (Siemens et al. 2012; Alsdurf et al. 2013). Our second hypothesis is hence that phylogenetically proximate neighbourhoods indirectly select for reduced climatic-stress resistance due to a combination of two mechanisms: direct selection for genotypes of increased herbivore resistance (above hypothesis), and a trade-off between herbivore resistance and climatic-stress resistance of genotypes (Fig. 1). We expect this indirect selection to involve particular resistance traits that are energetically costly to a tree because they are produced in high quantities, such as anthocyanins or flavonols or morphological resistance traits (Feeny 1976).

Alternatively, the same traits might confer resistance against herbivores and climatic-stress and selection for these traits by a phylogenetically proximate neighbourhood might either prevent or reinforce selection by climatic-stress. Anthocyanins and flavonols, for instance, have been shown to increase under both herbivore attack and climatic-stress due to frost or drought (Treutter 2006; Korn et al. 2008). Also tough, thick leaves rich in dry matter might resist both herbivores and climatic-stress. In such a case, two scenarios are possible. First, the double benefits from such multifunctional traits might reduce the costs of adaptation to climatic-stress in a neighbourhood that increases herbivore pressure, i.e. a phylogenetically proximate neighbourhood (Fig. 1). Second, the

signal of selection by climatic-stress might be obscured by selection of the same traits by herbivore pressure, i.e. in a phylogenetically proximate neighbourhood. Simply, climatic-stress is not needed for the evolution of such traits in a phylogenetically proximate neighbourhood, and herbivores from phylogenetically proximate neighbours are not needed in a stressful climate. To our knowledge, it has been little studied how selection due to climatic-stress interacts with selection due to herbivore pressure (Suzuki et al. 2014), or even conditions favouring herbivory. Our third hypothesis is hence that a phylogenetically proximate neighbourhood either prevents or reinforces the selection by climatic-stress for traits promoting climatic-stress resistance.

We tested the above hypotheses for sessile oak (*Quercus petraea*), one of the major forest trees across much of Europe, often growing with phylogenetically proximate neighbours, and suffering from climatic-stress (Cheaib et al. 2012). We used a 25-year common garden experiment from provenances of different phylogenetic neighbourhoods and climates (Appendix S1), permitting us to identify selection of genotypes in the provenances by characterising phenotypes of descendants in the common garden. Specifically, our hypotheses predict: (1) Descendants from provenances dominated by phylogenetically proximate neighbours experience little attack from specialist herbivores due to high levels of herbivore resistances (Fig. 1). (2) Provenances whose descendants have high levels of such herbivore resistances tend to have particularly low climatic-stress resistance, and these are the provenances dominated by phylogenetically proximate neighbours (Fig. 1). (3) Descendants from provenances of particularly harsh climates have tough and thick leaves rich in chemical resistance compounds – and the strength of this relationship is modified in provenances dominated by phylogenetically proximate neighbours (Fig. 1).

Methods

Sessile oak (*Quercus petraea*)

Sessile oaks are among the dominant late-successional tree species in forests across temperate Europe, often forming monospecific stands or growing together with other Fagaceae species (Ellenberg 1988). Sessile oaks suffer from a diverse and abundant herbivore fauna (Brändle & Brandl 2001), including both specialist species, such as miners and galls, and less specialised species such as ectophagous lepidoptera often capable of using multiple plant genera or even families (Gaston et al. 1992; Giffard et al. 2012). Southwood et al. (2004) show that all three groups are abundant on oaks, the ectophages mainly in May, galls and mines in August to October. Moreover, sessile oak is predicted to strongly suffer from future climate change towards the hot and dry range edge (Cheaib et al. 2012), while towards its continental and northern limit, it appears to be limited by cold and long winters (Sáenz-Romero et al. 2017). Vulnerability of a genotype to herbivores should be visible from increased damage, vulnerability to cold and long winters or hot and dry summers from a late bud burst, or from bud burst or growth that strongly responds to changes in ambient climate, as detailed below. Traits that may confer protection from herbivores, frost, heat or drought include leaves that are thick or tough, or rich in dry matter, in anthocyanins, flavonols, or tannins (Thomas et al. 2002; Cornelissen 2006; Korn et al. 2008; Nakabayashi et al. 2013).

The provenance experiment

We profited from a common garden experiment created by the French National Institute for Agricultural Research (INRA) in 1990 (Ducousso et al. 1996, Sinclair et al. 2015) and described in Appendix S2. We used phylogenetic distances in Yguel et al. (2011, details in Appendix S2) multiplied by the relative abundance of each trees species in each provenance (equivalent to abundance weighting in phylogenetic diversity measures) resulting in a gradient from zero to 48 million years.

We note that phylogenetic distance to *Q. petraea* does not always equal to phylogenetic diversity of the forest. For instance, a forest composed of 90% of *Q. petraea* and 10% *Fagus sylvatica* has identical phylogenetic diversity but much lower phylogenetic distance to *Q. petraea* than a forest of the inverse composition. We also characterised provenances by annual minimum and maximum temperatures and summer hydric deficit (Appendix S2). We selected 25 provenances, maximizing the variation in phylogenetic distance, while minimizing the geographic distance, hence mostly choosing pairs of provenances with contrasting phylogenetic distance that were geographically close. Also, in the common garden, we sampled trees from different provenances in spatial proximity. Each provenance is a replicate along a gradient of phylogenetic distances of parental neighbourhoods and parental climate, and trees were averaged within provenances to avoid pseudoreplication.

Sampling

In the common garden we sampled leaves from two trees from each of 21 provenances, and one tree from each of the remaining 4 provenances. Sampling was done in October 2015. We harvested leaves from branches of intermediate height of about 7-9 m. From each tree, we stored 40 leaves in a freezer at minus 18°C, and dried 50 flat leaves at ambient room temperature.

Measurements of herbivory

We assessed herbivory, using frozen leaves out of which we randomly selected 15 to 30 (variation imposed by technical constraints). As in Giffard et al. (2012), we discriminated three types of herbivory based on the feeding guild: (i) galls (ii) mines, i.e. galleries formed between the upper and the lower epidermis by insect larvae, and (iii) ectophagy, i.e. the partial or complete loss of leaf including epidermis. To quantify herbivory we first approximately quantified the surface of the leaf prior to damage by reconstructing the initial leaf shape before herbivory on a photocopy of the leaf.

We traced the drawing on a grid of points of 1x1cm² (Yguel et al. 2011). Then, we laid the grid on the leaf to quantify the area lost through ectophagy or leaf mines. Throughout, “area” was the number of points covering a given damaged or undamaged part of the leaf. We also counted the number of galls and leaf mines. For each leaf we calculated (i) the density of galls per cm² (ii) the proportion of area damaged by leaf mines, and (iii) the proportion of area damaged by ectophagy (we note that relationships observed for proportion of mined surface were consistent with numbers of mines per surface and average size of mines – the mined proportion of leaf surface integrates mine abundance and mine growth, appendix S3).

Proxies of climatic resistance

Climate is widely considered as a major control of the budburst of trees (Menzel 2000; Morin et al. 2010). Genotypes that are more resistant to cold winter temperatures burst buds earlier. Moreover, such resistant genotypes should also burst buds more independently of the ambient climate, resulting in low variation of budburst across the four common gardens. We thus used the budburst advancement, and coefficient of variation (CV) of budburst advancement across the four common gardens, as proxies of climatic-stress resistance. Budburst was recorded on a 0-5 ordinal scale where 0 is a dormant bud and 5 is a fully open bud (details in Sinclair et al. 2015, similar approaches in Crawley & Akhteruzzaman 1988; Tack et al. 2010). Budburst was surveyed already in 1995, but results were still applicable as relative budburst-rank of individual oak trees remains constant across years (Koenig et al. 2012). We calculated the CV of budburst for each provenance as the standard deviation of the budburst among the four common gardens divided by the mean. Climate is also considered to affect growth. Genotypes that are more resistant to climate grow independently of the ambient regional climate (Thomas et al. 2002). Growth was recorded as the height of trees after 10 years (starting from seeds) within each common garden in 2001, and we calculated the CV of growth across common gardens.

Measurements of leaf traits

We measured leaf chemical traits in the field. We measured an index of anthocyanins, flavonols and nitrogen status with an optical sensor based on the absorbance properties contained in the epidermis (Dualox 4 Force A; Louis et al. 2009; Cerovic et al. 2012). These measures are non-destructive and much more rapid than quantifying the within-leaf concentrations, but nevertheless strongly correlated to within-leaf concentrations (Goulas et al. 2004). Moreover, anthocyanins and flavonols reflect well overall polyphenol concentrations under comparable conditions (Scogings 2014). We measured three leaves per tree, between leaf veins on both leaf faces.

We measured leaf morphological traits in the laboratory. We assessed leaf thickness on four randomly selected leaves among the leaves studied for herbivory, i.e. using material that had been deep-frozen. We used a precision calliper (Thickness gauge glorythai, model number: BY01, Shantou, China). For each leaf, we measured the thickness at eight points between the main veins as recommended by Pérez-Harguindeguy et al. (2013). We averaged values per leaf, per tree and per provenance.

To assess leaf toughness we randomly selected five leaves per tree. Because Pérez-Harguindeguy et al. (2013) discourage the use of frozen leaves we used dried leaves which we rehydrated by letting them soak for 24 hours in tap water. Once rehydrated, we used a durometer to measure the resistance to punching (ATG-50 Dial Tension Gauge Gram Force Meter Dual point 50 g, Wenzhou, China) at eight points per leaf between the main ribs. Again, we averaged values per leaf, tree, and provenance.

To assess leaf dry matter content (LDMC) we used the five rehydrated leaves per tree having served for toughness measurements. We weighed them together, dried to weight-constancy during 48 hours in an oven at a temperature of 65 ° C and then reweighed to obtain dry weight (Pérez-

Harguindeguy et al. 2013). We calculated the LDMC dividing the dry weight by the wet weight of the five leaves. Then we averaged the LDMC across trees within provenances.

Statistical analyses

Throughout our analyses, information on descendants in the common garden was averaged within provenances. For our analyses, except for the exploratory analyses, we did corrections for multiple comparisons using the method of the false discovery rate, following Benjamini & Hochberg (1995), applied to each of the four groups of dependent variables (pressure by specialist herbivores, pressure by generalist enemies, morphological resistances, or chemical resistances).

Exploratory analyses

Soil types in provenances might influence phylogenetic distance of neighbourhoods, and select for different capacities of nitrogen acquisition. We therefore checked if the soil type of the provenances had an effect on leaf nitrogen status of the descendants or on the phylogenetic distance of the provenance neighbourhood. As there was no effect of soil type and as soil types were only known for 19 provenances we did not integrate soil type into our below models (Appendix S4).

Our measure of phylogenetic distance of the provenance neighbourhood is dependent on the abundance of different tree taxa in the provenances. We therefore checked with simple regressions the effect of abundances of individual taxa in the provenances on each variable of herbivory or herbivore resistances. We found that taxon abundances were always less significant than phylogenetic distance (Appendix S5). We hence used only phylogenetic distances in our models.

Relationships between the phylogenetic distance of provenance neighbourhoods and the herbivory or resistances against herbivores of descendants from these provenances

We performed multiple regressions to study the effect of phylogenetic distance of neighbourhood on herbivory or traits related to herbivore resistances (leaf toughness, leaf thickness, LDMC, anthocyanins and flavonols). We took into account multiple co-variables that might relate to phylogenetic distance in the provenance or nutritional quality of the descendants for herbivores: annual minimum and maximum temperatures, and summer hydric deficit in the provenances, budburst and the leaf nitrogen status of the descendants (Crawley & Akhteruzzaman 1988; Minkenberg & Ottenheim 1990).

Relationships between resistance against herbivores and climatic-stress resistance

We performed multiple regressions to study the effect of herbivore resistance (low proportion of ectophagy, low gall density, low proportion of leaf mines, leaf toughness, leaf thickness, LDMC, anthocyanins and flavonols) on climatic-stress resistance (bud-burst advancement, CVs of bud-burst and growth). We used leaf nitrogen status as a co-variable to avoid bias due to differences of nutrient availability for descendants from different provenances, as suggested by Koricheva (2002).

Relationships between phylogenetic distance of provenance neighbourhoods and climatic-stress resistance or resistance-related traits

We performed multiple regressions to study the effect of phylogenetic neighbourhood on climatic-stress resistance of descendants. We took into account the annual minimum and maximum temperature, summer hydric deficit in the provenances, and leaf nitrogen status of the descendants in the common garden as co-variables as explained before.

We performed multiple regressions to study the effect of phylogenetic neighbourhood and climate in the provenances, and the interaction between both, on traits potentially increasing climatic-stress resistance (anthocyanins, flavonols, leaf toughness, leaf thickness and LDMC), using the advancement of budburst and leaf nitrogen status as co-variables as before. Again, we included all three climatic variables into the model, together with corresponding interaction term. In order to not overload the model we applied a selection of the variables using the R function “step()”. This function uses a stepwise selection procedure, based on Akaike Information Criterion (Burnham & Anderson 2002). A positive interaction means that descendants from climatically stressful provenances have higher levels of a resistance-trait if neighbourhoods in these provenances are phylogenetically distant. Finally, we explored the indirect effect of phylogenetic neighbourhood on climatic-stress resistance mediated by resistance traits, using techniques from pathway analyses. This indirect effect is a compound path composed of two direct paths. Direct paths are usually characterised by standardized regression coefficients but these coefficients are inflated in models with interaction terms due to inevitable multicollinearity (Fletcher 2012). As t-values are not inflated (Friedrich 1982) we used them to quantify for each direct path its explained variance Pearson R^2 (as in Rosenthal 1991), and the compound paths as the product of the R^2 of the two direct paths. We applied the same procedure for the indirect effects of the interactions between phylogenetic neighbourhood and provenance climate on climatic-stress resistance mediated by resistance traits. We focused on explaining the climatic-stress resistance that was most strongly related to resistance traits, the coefficient of variation of budburst.

All statistical analyses were performed using R version 3.4.1. We verified assumptions of normality and variance homogeneity as follows. We identified residual outliers graphically checking for the normality of the residuals with the QQ plots and the weight of the residuals with the Cook's distance. A maximum of three outliers were excluded per analysis.

Results

Descendants from phylogenetically proximate neighbourhoods had increased resistances against leaf miners

Proportion of leaf-mines was highest in descendants from provenances with phylogenetically distant neighbourhoods but independent of climate. Attack by galls was independent of parental neighbourhood but highest in descendants from warm climates. Proportion of ectophagy was independent of parental environment (Tab. 1 and Fig. 2A). Leaves were softest in descendants from phylogenetically distant neighbourhoods and mildest temperatures (Tab. 1 and Fig. 2B).

Consistently, soft leaves had particularly high proportion of leaf mines ($T=-2.146$, $p=0.0466$, $\text{adjusted}R^2=0.20$, $df=17$, same co-variables as in above models). Leaves tended to be thinnest and poorest in dry matter in descendants from mildest temperatures. Anthocyanins or flavonols did not depend on parental environment (Tab. 1). Note that the effect of phylogenetic distance on proportion of leaf-mines might be driven by the phylogenetic distance of the heterospecifics: this effect was maintained after including conspecific abundance into the model (which only had a weak effect; Appendix S6). In contrast, the effect of phylogenetic distance on leaf toughness might be driven by both heterospecific distance and conspecific abundance: taken into account together these variables showed roughly similar, non-significant, effects (Appendix S6).

Resistances against leaf miners did not relate to climatic-stress resistance

Descendants with advanced budburst within the studied common garden, or with constant budburst across common gardens, had low gall density (Tab. 2, Fig. S7A and B). No relationships were observed for climatic-stress resistance as inferred from among-common-garden CV of growth of descendants, or for physical or chemical resistances, or the proportion of leaf mines (Tab. 2).

Descendants from phylogenetically proximate neighbourhood were no less resistant to climatic-stress than descendants from other neighbourhoods

The phylogenetic distance of the parental neighbourhood had no effect on the budburst advancement ($T=0.598$, $p=0.557$, adjusted $R^2=0.08$, $df=18$), the CV of budburst ($T=-0.178$, $p=0.861$, adjusted $R^2=0.47$, $df=17$) or the CV of growth ($T=0.417$, $p=0.682$, adjusted $R^2=-0.08$, $df=18$), nor did it change the relationship between temperature extremes in provenances and proxies of climatic-stress resistance (interaction terms in Appendix S8).

A phylogenetically proximate neighbourhood reinforces the selection by harsh climates on anthocyanins, flavonols and leaf thickness.

We observed significant interactions between phylogenetic distance of the parental neighbourhood and the parental climate on anthocyanins, flavonols and leaf thickness (Tab. 3). Specifically, stress due to high summer hydric deficit corresponded to an increase of anthocyanins concentration and leaf thickness of descendants from phylogenetically proximate but not distant neighbourhoods (Tab. 3, Fig. 3A and C). Stress due to low minimum annual temperatures corresponded to a strong increase of flavonols concentration and leaf thickness of descendants from phylogenetically proximate but not distant neighbourhoods (Tab. 3, Fig. 3B and D), albeit the effect on flavonols became marginally significant after correction for false discovery rate. Compound paths never exceeded $R^2=0.018$ suggesting no mediation by resistance traits between provenance neighbourhoods and climatic-stress resistance of descendants. (Note that *direct* effects of provenance climate on climatic-stress resistance did exist, Appendix S8).

Discussion

Overall, we found that descendants from phylogenetically proximate neighbourhoods differ from descendants from phylogenetically distant neighbourhoods in multiple ways. We acknowledge that our study has a number of limitations. First, there were no gymnosperms in the provenances used for this study. Castagneyrol et al. (2014) show that specialist-herbivore abundance on angiosperms starts to decrease when the phylogenetic distance of the neighbourhood differs from zero, while generalist abundance remains constant until the phylogenetic neighbourhood includes gymnosperms. Our results are hence appropriate mainly for specialist herbivores. Secondly, we do not have information about the pressure of herbivores in the provenances. Explaining herbivore resistances of a genotype from a phylogenetically proximate neighbourhood by herbivore pressure remains an interpretation. Such interpretation is a plausible one given that herbivore pressure does reflect phylogenetic composition of a forest (Brändle & Brandl 2006; Nyman et al. 2006; Yguel et al. 2011). Moreover, we inferred climatic-stress resistance from a limited number of proxies, i.e. budburst and growth and their coefficients of variation, proxies that certainly do not reflect all aspects of climatic-stress resistance. Nevertheless, budburst and growth are sensitive to factors limiting the distributional range of our study species, i.e. extreme winter and summer temperatures and drought (Menzel 2000; Morin et al. 2010). Finally, a trade-off between resistance against climatic-stress and against herbivores might be masked by other trade-offs such as between resistance to climatic-stress and pathogens. However, in our study, visible fungal pathogens covered only less than one percent of the leaves. A trade-off between resistance against bacteria and against climatic-stress cannot be excluded but should hide a trade-off between herbivore resistances and climatic-stress resistance only if bacteria attack oaks mainly in a phylogenetically distant neighbourhood, which should be tested in future studies.

Coexistence with phylogenetically proximate neighbours selects for genotypes that are morphologically resistant against one type of specialist herbivore. We had hypothesized that plants

from phylogenetically proximate neighbourhoods have evolved increased herbivore resistance because of the increased pressure of herbivores in such neighbourhood (Yguel et al. 2011). Consistent with the hypothesis we found that genotypes from such neighbourhoods are particularly resistant against leaf miners. Gaston et al. (1992) show that leaf miners are mostly specialists, probably because they are internal feeders and hence have to adapt to the specific leaf morphology and chemistry of their host plant (Cornell 1989). A major resistance against several miner species are tough leaves: tough leaves prevent adult females from piercing the leaf epidermis to oviposit their egg inside the leaf, or they prevent larvae that hatch on the leaf surface from entering inside the leaf. Cornelissen (2006) indeed shows that tougher leaves exhibited lower density of leaf miners. Consistently, we found that genotypes from phylogenetically proximate neighbourhoods have tougher leaves and that tough leaves are particularly little attacked by leaf miners. Equally consistently, we found that genotypes from phylogenetically proximate neighbourhoods are not particularly strongly resistant against ectophages, being usually less specialized due to their external feeding mode (Gaston et al. 1992). Low specialization permits the use of relatively distantly related host plants across Angiosperms, and consistent with that, Grandez-Rios et al. (2015) show that ectophages are not affected by the phylogenetic neighbourhood. Selection for plant defences against ectophages should hence not differ among phylogenetic neighbourhoods. Inconsistent with the hypothesis we found that genotypes from phylogenetically proximate neighbourhoods are not particularly resistant against another type of specialist enemies: galls (itself consistent with Yguel et al. [2014] showing that gall abundance does not depend on host phylogenetic isolation). Possibly, any effect of parental neighbourhood is overridden by the observed effect of parental temperatures on gall resistance. Finally, inconsistent with the hypothesis we found that genotypes from phylogenetically proximate neighbourhoods are not particularly resistant in terms of chemical compounds. Neilson et al. (2013) have suggested that chemical compounds are multifunctional - in the absence of herbivores they might serve other purposes than herbivore resistance. Herbivory in a

phylogenetically proximate neighbourhood hence might not increase selection for the chemical compounds.

Coexistence with phylogenetically proximate neighbours does not indirectly select against climatic-stress resistance because resistances against specialist herbivores are not traded off against climatic-stress resistance. We had hypothesized that if phylogenetically proximate neighbourhoods select for higher herbivore resistances they might indirectly select against capacities that are traded off against herbivore resistances such as climatic-stress resistance. The first part of this hypothesis, on selection of herbivore resistances, is equal to hypothesis 1 and has been treated before. We will here discuss the second and third part, i.e. a trade-off between resistances against herbivores and climatic-stress, and an indirect selection against climatic-stress resistance by phylogenetically proximate neighbourhoods. Consistent with the trade-off part of the hypothesis we found a tendency of delayed budburst in trees that are more resistant against ectophages, albeit other proxies of climate resistance did not respond. Delayed budburst represents an opportunity cost by delaying photosynthesis (Koricheva 2002). However, this trade-off might not lead to an indirect selection against climatic-stress resistance in a phylogenetically proximate neighbourhood as such neighbourhood did not select for increased resistance against ectophages. Inconsistent with the trade-off part of the hypothesis we found no negative relationships between resistances against leaf miners, including leaf toughness, and climatic-stress resistance. There might be no trade-off because resistance to leaf miners and to climatic-stress occur at different moments: Leaf toughness – a resistance against leaf miners - develops in a climatically favourable period for oaks in spring and in early summer. In contrast, climatic-stress limiting budburst operates in late winter. Oaks might therefore invest into the resistance against leaf miners in spring and summer and later on invest in climatic-stress resistance, without any direct trade-off among them. In addition, inconsistent with the trade-off part of the hypothesis we found no trade-off between chemical compounds and climatic-stress resistance. Neilson and al. (2013) have suggested that the multifunctionality of chemical resistances such as anthocyanins can offset the cost of plant chemical resistance. Also,

opposite to the trade-off part of the hypothesis, we found a positive relationship between resistances against galls and against climatic-stress in terms of early budburst. Crawley & Akhteruzzaman (1988) have shown that some gall species prefer oaks that burst buds late, possibly because such oaks are more favourable for adult female gall wasps. Finally, we found no evidence in favour of the third part of the hypothesis, i.e. an indirect selection against climatic-stress resistance in phylogenetically proximate neighbourhoods. This is consistent with the absence of trade-offs between resistances against miners and against climatic-stress, and with the absence of selection for resistance against ectophages in such neighbourhoods.

Coexistence in phylogenetically proximate neighbours can reinforce the selection by climate for biochemical compounds and one morphological trait, possibly reflecting increased pressure from herbivores. We had hypothesized that in phylogenetically proximate neighbourhoods, the increased herbivore pressure can reinforce or prevent the selection pressure by climatic-stress on particular traits conferring multiple resistances. As mentioned above, we found no supporting results for the “prevent” version of the hypothesis. Consistent with the “reinforce” version of the hypothesis we found that genotypes from cold-winter provenances have high levels of flavonols and thick leaves (known to increase frost resistance, Korn et al. 2008; González-Zurdo et al. 2016) - provided that the neighbourhood in the provenances was phylogenetically proximate. We found that genotypes from dry summer provenances had high levels of anthocyanins and thick leaves (known to increase water stress resistance, Chalker-Scott 1999; Ennajeh et al. 2010) – provided that the neighbourhood in the provenances was phylogenetically proximate. White (1984) suggests that climatic-stress increases the availability of nitrogen in leaves of stressed plants, which will increase herbivory and reinforce their selection pressure on plants. Resistance traits against cold stress and drought stress should hence be particularly important in plants exposed to high enemy pressure in a phylogenetically proximate neighbourhood.

Our results may have implications for understanding coexistence among phylogenetically proximate individuals (Prinzing et al. 2017, Gerhold et al. 2018). It has been suggested that coexistence of phylogenetically proximate individuals is prevented by increased herbivore pressure and competition, leading to coexistence among phylogenetically distant species (Janzen 1970; Webb et al. 2002; Liu et al. 2012). Our study shows that another response to coexistence among phylogenetically proximate individuals might be an adaptation to increased herbivore pressure. This adaptation to neighbourhoods seems to be no less important than adaptation to climates (Tab. 1), and seems to come without costs, at least in terms of climatic tolerance. We might hence hypothesize that adaptation to phylogenetically proximate neighbours facilitates their coexistence. Future studies should try to identify the importance of multifunctionality of chemical compounds possibly enabling plants to be jacks-of-all-trades and to coexist among phylogenetically proximate individuals. Our results also imply that while the response to coexisting close relatives has no costs for climatic-stress resistance, it might change the evolutionary response of one trait to climate. Future studies should identify what exactly causes this change, e.g. whether rather the action of enemies or of mutualists changes the selection pressure by climate.

Acknowledgements:

We thank Julie Jaquiéry, Jean-Pierre Caudal and Fouad Nassur for their help in sampling. We thank the PlantaComp project and in particular Antoine Kremer. We thank Julie Jacquéry for extensive discussion and improving the manuscript. We thank the two anonymous referees for improving the manuscript and their comments on this manuscript. This work was supported by an Estonian Research Council (grant PUT1006). MP and PG thank the Estonian Government for continuously keeping up our hopes about raising research funding to 1% of GDP.

References

Alsdurf, J.D., Ripley, T.J., Matzner, S.L., Siemens, D.H. (2013). Drought-induced trans-generational tradeoff between stress tolerance and defence: consequences for range limits? *Aob Plants*: 5, plt038.

Baldwin, I.T., Hamilton, W. (2000). Jasmonate-induced responses of *Nicotiana sylvestris* results in fitness costs due to impaired competitive ability for nitrogen. *Journal of Chemical Ecology*: 26, 915-952.

Benjamini, Y., Hochberg, Y. (1995). Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society*: 57, 289-300.

Brändle, M., Brandl, R. (2001). Species richness of insects and mites on trees: expanding Southwood. *Journal of Animal Ecology*: 70, 491-504.

Brändle, M., Brandl, R. (2006). Is the composition of phytophagous insects and parasitic fungi among trees predictable? *Oikos*: 113, 296-304.

Burnham, K.P, Anderson, D.R. (2002). *Model selection and multimodel inference*, 2nd edition. Springer.

Burns, J.H., Strauss, S.Y. (2011). More closely related species are more ecologically similar in an experimental test. *Proceeding of the National Academy of Sciences of the United States of America*: 108, 5302-5307.

Castagneyrol, B., Jactel, H., Vacher, C., Brockerhoff, E.G., Koricheva, J. (2014). Effects of plants phylogenetic diversity on herbivory depend on herbivore specialization. *Journal of Applied Ecology*: 51, 134-141.

- Cerovic, Z.G., Masdoumier, G., Ghozlen, N.B., Latouche, G. (2012). A new optical leaf-clip meter for simultaneous non-destructive assessment of leaf chlorophyll and epidermal flavonoids. *Physiologia Plantarum*: 146, 251-260.
- Chalker-Scott, L. (1999). Environmental significance of anthocyanins in plant stress responses. *Photochemistry and photobiology*: 70, 1-9.
- Chebib, A., Badeau, V., Boe, J., Chuine, I., Delire, C., Dufrêne, E. *et al.* (2012). Climate change impacts on tree ranges: model intercomparison facilitates understanding and quantification of uncertainty. *Ecology Letters*: 15, 533-544.
- Cornelissen, T. (2006). Herbivory by leaf miners on Florida scrub oaks. Thesis University of South Florida. Accessed Nov. 19th 2018 at <http://scholarcommons.usf.edu/etd/2491>
- Cornell, H.V. (1989). Endophagy-ectophagy ratios and plant defense. *Evolutionary Ecology*: 3, 64-76.
- Crawley, M.J., Akhteruzzaman, M. (1988). Individual variation in the phenology of oak trees and its consequences for herbivorous insects. *Functional Ecology*: 2, 409-415.
- Ducousso, A., Guyon, J.-P., Kremer, A. (1996). Latitudinal and altitudinal variation of bud burst in western populations of sessile oak (*Quercus petraea* (Matt) Liebl). *Annals of Forest Science*: 53, 775-782.
- Ellenberg, H.H. (1988). *Vegetation Ecology of Central Europe*, 4th edition. Cambridge University Press.
- Ennajeh, M., Vadel, A.M., Cochard, H., Khemira, H. (2010). Comparative impacts of water stress on the leaf anatomy of a drought-resistant and a drought-sensitive olive cultivar. *Journal of Horticultural Science & Biotechnology*: 85, 289-294.
- Ersoz, E.S., Wright, M.H., González-Martínez, S.C., Langley, C.H., Neale, D.B. (2010). Evolution of disease response genes in Loblolly pine: Insights from candidate genes. *Plos One*: 5, e14234.

Feeny, P. (1976). Plant apparency and chemical defense. *Biochemical Interaction Between Plants and Insects*: 10, 1-40.

Fletcher, T.D. (2012). QuantPsyc: Quantitative Psychology Tools. R package version 1.5.

<https://CRAN.R-project.org/package=QuantPsyc>

Friedrich, R.J. (1982). In defense of multiplicative terms in multiple regression equations. *American Journal of Political Science*: 26, 797-833.

Gaston, K.J., Reavey, D., Valladares, G.R. (1992). Intimacy and fidelity: internal and external feeding by British microlepidoptera. *Ecological Entomology*: 17, 86-88.

Gerhold, P., Carlucci, M.B., Procheş, S., Prinzing, A. 2018. The deep past controls the phylogenetic structure of present, local communities. *Annual Review of Ecology, Evolution, and Systematics*: 49, 477-499.

Giffard, B., Jactel, H., Corcket, E., Barbaro, L. (2012). Influence of surrounding vegetation on insect herbivory: A matter of spatial scale and herbivore specialisation. *Basic and Applied Ecology*: 13, 458-465.

González-Zurdo, P., Escudero, A., Babiano, J., García-Ciudad, A., Mediavilla, S. (2016). Costs of leaf reinforcement in response to winter cold in evergreen species. *Tree Physiology*: 36, 273-286.

Goulas, Y., Cerovic, Z.G., Cartelat, A., Moya, I. (2004). Dualex: a new instrument for field measurements of epidermal ultraviolet absorbance by chlorophyll fluorescence. *Applied Optics*: 10, 4488-4496.

Grandez-Rios, J.M., Bergamini, L.L., De Araujo, W.S., Villalobos, F., Almeida-Neto, M. (2015). The effect of host-plant phylogenetic isolation on species richness, composition and specialization of insect herbivores: A comparison between native and exotic hosts. *Plos One*: 10, e0138031.

- Janzen, D.H. (1970). Herbivores and the number of tree species in tropical forests. *The American Naturalist*: 104, 501–508.
- Jiang, L., Shi, C., Ye, M., Xi, F., Cao, Y., Wang, L., et al. (2018). A computational-experimental framework for mapping plant coexistence. *Methods in Ecology and Evolution*: 9, 1335-1352.
- Johnson, M.T.J., Agrawal, A.A., Maron, J.L., Salminen, J.-P. (2009). Heritability, covariation and natural selection on 24 traits of common evening primrose (*Oenothera biennis*) from a field experiment. *Journal of Evolutionary Biology*: 22, 1295-1307.
- Klaper, R., Ritland, K., Mousseau, T.A., Hunter, M.D. (2001). Heritability of phenolics in *Quercus laevis* inferred using molecular markers. *Journal of Heredity*: 92, 421-426.
- Koenig, W.D., Funk, K.A., Kraft, T.S., Carmen, W.J., Barringer, B.C., Knops, J.M.H. (2012). Stabilizing selection for within-season flowering phenology confirms pollen limitation in a wind-pollinated tree. *Journal of Ecology*: 100, 758-763.
- Koricheva, J. (2002). Meta-analysis of sources of variation in fitness costs of plant antiherbivore defenses. *Ecology*: 83, 176-190.
- Korn, M., Peterek, S., Mock, H.P., Heyer, A.G., Hinch, D.K. (2008). Heterosis in the freezing tolerance, and sugar and flavonoid contents of crosses between *Arabidopsis thaliana* accessions of widely varying freezing tolerance. *Plant, Cell & Environment*: 31, 813-827.
- Louis, J., Meyer, S., Maunoury-Danger, F., Fresneau, C., Meudec, E., Cerovic, Z.G. (2009). Seasonal changes in optically assessed epidermal phenolic compounds and chlorophyll content in leaves of sessile oak (*Quercus petraea*): towards signatures of phenological stage. *Functional Plant Biology*: 36, 732-741.
- Liu, X., Liang, M., Etienne, R.S., Wang, Y., Staehelin, C., Yu, S. (2012). Experimental evidence for a phylogenetic Janzen-Connell effect in a subtropical forest. *Ecology Letters*: 15, 111-118.

Menzel, A. (2000). Trends in phenological phases in Europe between 1951 and 1996. *International Journal of Biometeorology*: 44, 76–81.

Minkenbergh, O.P.J.M., Ottenheim, J.J.G.W. (1990). Effect of leaf nitrogen content of tomato plants on preference and performance of a leafmining fly. *Oecologia*: 83, 291-298.

Morin, X., Roy, J., Sonié, L., Chuine, I. (2010). Changes in leaf phenology of three European oak species in response to experimental climate change. *New Phytologist*: 186, 900-910.

Nakabayashi, R., Yonekura-Skakibara, K., Urano, K., Suzuki, M., Ymada, Y. *et al.* (2013). Enhancement of oxidative and drought tolerance in *Arabidopsis* by overaccumulation of antioxidant flavonoids. *The Plant Journal*: 77, 367-379.

Neilson, E.H., Goodger, J.Q.D., Woodrow, I.E., Moller, B.L. (2013). Plant chemical defense: at what cost? *Trends in Plant Science*: 18, 250-258.

Nyman, T., Farrell, B.D., Zinovjev, A.G., Vikberg, V. (2006). Larval habits, host-plant associations, and speciation in nematine sawflies (Hymenoptera: Tenthredinidae). *Evolution*: 60, 1622-1637.

Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P. *et al.* (2013). New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*: 61, 167-234.

Peterson, A.T. (2011). Ecological niche conservatism: a time-structured review of evidence. *Journal of Biogeography*: 38, 817-827.

Petit, R.J., Hampe, A. (2006). Some evolutionary consequences of being a tree. *Annual Review of Ecology, Evolution, and Systematics*: 37, 187-214.

Prinzing A., Ozinga, W. Brändle, M. Courty, P.-E. Hennion F., Labandeira C., Parisod C., Pihain, M., Bartish I. (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

Rellstab, C., Zoller, S., Walthert, L., Lesur, I., Pluess, A.R., Graf, R. *et al.* (2016). Signatures of local adaptation in candidate genes of oaks (*Quercus* spp.) with respect to present and future climatic conditions. *Molecular Ecology*: 25, 5907-5924.

Rosenthal, R. (1991). *Meta-analytic procedures for social research*. Volume 6. Sage Productions, London, p18.

Sáenz-Romero, C., Lamy, J.-B., Ducouso, A., Musch, B., Ehrenmann, F., Delzon, S. *et al.* (2017). Adaptive and plastic responses of *Quercus petraea* populations to climate across Europe. *Global Change Biology*: 23, 2831-2847.

Scogings, P., Siko, S., Taylor, P. (2014). Calibration of a hand-held instrument for measuring condensed tannin based of UV- and red-excited fluorescence. *African Journal of Range & Forage Science*: 31, 55-58.

Shaw, M.W. (1968). Factors affecting the natural regeneration of sessile oak (*Quercus petraea*) in North Wales. *Journal of Ecology*: 56, 647-660.

Siemens, D.H., Duvall-Jisha, J., Jacobs, J., Manthey, J., Haugen, R., Matzner, S. (2012). Water deficiency induces evolutionary tradeoff between stress tolerance and chemical defense allocation that may help explain range limits in plants. *Oikos*: 121, 790-800.

Siemens, D.H., Haugen, R., Matzner, S., Vanasma, N. (2009). Plant chemical defence allocation constrains evolution of local range. *Molecular Ecology*: 18, 4974-4983.

Sinclair, F.H., Stone, G.N., Nicholls, J.A., Cavers, S., Gibbs, M., Butterill, P. *et al.* (2015). Impacts of local adaptation of forest trees on associations with herbivorous insects: implications for adaptive forest management. *Evolutionary Applications*: 8, 972-987.

Southwood, T.R.E, Wint, G.R.W., Kennedy, C.E.J., Greenwood, S.R. (2004). Seasonality, abundance, species richness and specificity of phytophagous guild of insects on oak (*Quercus*) canopies. *European Journal of Entomology*: 101, 43-50.

Stevens, M.T., Lindroth, R.L. (2005). Induced resistance in the indeterminate growth of aspen (*Populus tremuloides*). *Oecologia*: 145, 297-305.

Suzuki, N., Rivero, R.M., Shulaev, V., Blumwald, E., Mittler, R. (2014). Abiotic and biotic stress combinations. *New Phytologist*: 203, 32-43.

Tack, A.J.M., Ovaskainen, O., Pulkkinen, P., Roslin, T. (2010). Spatial location dominates over host plant genotype in structuring an herbivore community. *Ecology*: 91, 2660-2672.

Thomas, F.M., Blank, R., Hartmann, G. (2002). Abiotic and biotic factors and their interactions as causes of oak decline in Central Europe. *Forest Pathology*: 32, 277-307.

Tobar, R., Azcon, R., Barea, J.M. (1994). Improved nitrogen uptake and transport from ¹⁵N-labelled nitrate by external hyphae of arbuscular mycorrhiza under water-stressed conditions. *New Phytologist*: 126, 119-122.

Treutter, D. (2006). Significance of flavonoids in plant resistance: a review. *Environmental Chemistry Letters*: 4, 147-157.

Vialatte, A., Bailey, R., Vasseur, C., Matocq, A., Goßner, M., Everhart, D., Vitrac, X., Belhadj, A., Ernoult, A., Prinzing, A. (2010) Phylogenetic isolation of host trees affects assembly of local Heteroptera communities. *Proceedings of the Royal Society, Series B*: 227, 2227-2236

Violle, C., Diana, R., Nemergut, D.R., Pu, Z., Jiang, L. (2011). Phylogenetic limiting similarity and competitive exclusion. *Ecology Letters*: 14, 782-787.

Webb, C.O., Ackerly, D.D., McPeck, M.A., Donoghue, M.J. (2002). Phylogenies and community ecology. *Annual Review of Ecology and Systematics*: 33, 475-505.

White, T.C.R. (1984). The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. *Oecologia*: 63, 90-105.

Yguel, B., Bailey, R., Tosh, N.D., Vialatte, A., Vasseur, C., Vitrac, X. *et al.* (2011). Phytophagy on phylogenetically isolated trees: why hosts should escape their relatives. *Ecology Letters*: 14, 1117-1124.

Yguel, B., Bailey, R., Villemant, C., Brault, A., Jactel, H., Prinzing, A. (2014). Enemy release of insect herbivores on phylogenetically isolated trees: why phytophages should follow plants escaping their relatives? *Oecologia*: 176, 521-532.

Zanetto, A., Kremer, A. (1995). Geographical structure of gene diversity in *Quercus petraea* (Matt.) Liebl. I. Monolocus patterns of variation. *Heredity*: 75, 506-517.

Accepted manuscript

Tables

Table 1. Effect of phylogenetic distance of parental neighbourhood and of climate (annual minimum and maximum temperatures, summer hydric deficit) in provenances on herbivory and herbivore resistances of oak descendants in the common garden. Linear regressions with co-variables (advancement of budburst and leaf nitrogen status of the descendants in the common garden). LDMC= leaf dry matter content. Significant values are in bold (an asterisk indicates the p value that 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 descendants within provenances.

	Dependent variables	Adj. R ² of entire model	df	Phylogenetic distance of parental neighbourhood		Tmin		Tmax		Summer hydric deficit	
				T	p	T	p	T	p	T	p
Specialist herbivores	Gall density	0.53	18	0.923	0.3681	1.132	0.2725	2.490	0.0228*	-1.282	0.2160
	Proportion of leaf mines	0.57	15	4.005	0.0012*	0.916	0.3743	-1.681	0.1135	-0.807	0.4325
Generalist herbivores	Proportion of ectophagy	0.13	16	0.045	0.9643	-0.150	0.8829	0.682	0.5050	-0.705	0.4911
Chemical compounds	Anthocyanins concentration	0.41	17	-0.548	0.5907	-1.316	0.2058	0.927	0.3669	0.751	0.4632
	Flavonols concentration	-0.09	16	0.128	0.9001	-1.009	0.3280	-0.397	0.6969	0.911	0.3757
Morphological traits	Leaf toughness	0.63	16	-2.832	0.0120*	-2.256	0.0384	3.372	0.0039*	-0.969	0.3469
	Leaf thickness	0.48	18	-1.716	0.1034	-1.976	0.0637	1.836	0.0829	1.080	0.2943
	LDMC	0.17	17	0.007	0.9948	-1.863	0.0799	0.930	0.3653	0.749	0.4641

Table 2. Effect of herbivory or herbivore resistances of the descendants on their climatic-stress resistance. Climatic-stress resistance is represented by advancement of budburst of descendants in the Petite Charnie common garden, coefficient of variation (CV) of budburst advancement and CV of growth across four common gardens. Multiple linear regression analyses accounting for leaf nitrogen status of the descendants in the common garden. LDMC= leaf dry matter content. Significant values are in bold (an asterisk indicates the p value that 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 descendants within provenances.

		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	0.0005*	0.412	0.0175	0.9690	0.9270	0.1820	0.3874	0.4836
	Adj. R ² of entire model	0.42	-0.006	0.27	-0.04	0.06	0.09	-0.005	0.07
	df	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	<0.0001*	0.3660	0.1604	0.7470	0.4342	0.1002	0.3320	0.7211
	Adj. R ² of entire model	0.61	0.004	0.13	-0.03	0.10	0.09	0.008	-0.03
	df	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 ² of entire model	-0.01	-0.088	-0.034	-0.07	-0.03	0.05	-0.07	-0.06
	df	20	18	21	21	20	21	21	21

Table 3. Effect of phylogenetic distance of parental neighbourhood, the parental climate (summer hydric deficit, annual minimum and maximum temperature), and the interaction between them on traits of the descendants conferring resistance against climatic-stress, accounting for the advancement of budburst and leaf nitrogen status of the descendants in the common garden. Multiple linear regression analyses across data points that are means across descendants within provenances. The variables of the models have been selected by multiple-step AIC procedure. Significant values are in bold (an asterisk indicates the p values that stay significant after correction using false discovery rate with $\alpha=0.05$ and a cross for $\alpha=0.1$).

			Phylo dist	Summer hydric deficit	Summer hydric deficit:phylo dist	Tmax	Tmax:phylo dist	Tmin	Tmin:phylo dist
Chemical compounds	Anthocyanins concentration	T	-1.586	2.715	-2.736	0.994	1.718	-3.472	
		p	0.133	0.016*	0.015*	0.336	0.106	0.003*	
		Adj. R ² of entire model				0.65			
	Flavonols concentration	df				15			
		T	2.052					-1.993	2.190
		p	0.055+					0.062+	0.042+
	Adj. R ² of entire model				0.19				
	df				18				
Morphological traits	Leaf toughness	T	0.882	0.0328	-1.563	3.723		-2.068	
		p	0.392	0.747	0.139	0.002*		0.056+	
		Adj. R ² of entire model				0.51			
	Leaf thickness	df				15			
		T	3.122	3.787	-3.288	3.068		-4.893	2.741
		p	0.007*	0.002*	0.005*	0.007*		0.0002*	0.014*
		Adj. R ² of entire model				0.70			
		df				16			
	LDMC	T				4.022		-5.684	
p					0.0008*		0.00002*		
Adj. R ² of entire model					0.67				
	df				18				

Figure legends

Figure 1. Our hypotheses. A conspecific or phylogenetically proximate neighbourhood (broadleaf trees as opposed to needle trees) increases pressure by specialist herbivores (caterpillar size) on a focal tree (broadleaf tree). Hypothesis 1 states that such neighbourhood selects for increased investment into resistance against specialist herbivores (thick arrows towards caterpillars). Hypothesis 2 states that traits conferring resistance to herbivores are distinct (red arrows) from those conferring resistance to climate (blue arrows), resulting in a trade-off between both (arrow size) and an indirect selection against resistance to climatic-stress in a conspecific or phylogenetically proximate neighbourhood (bottom graph). Hypothesis 3 suggests that traits are multifunctional and confer resistance against both, herbivory and climatic-stress (yellow arrows). In the illustrated case, resistance to climatic-stress is less costly in a conspecific or phylogenetically proximate neighbourhood as here the resistance trait also serves to resist herbivore pressure, facilitating selection by climatic-stress for this multifunctional resistance trait (bottom graph).

Figure 2. Effect of phylogenetic distance of parental neighbourhood in provenances on (A) the proportion of leaf surface covered by leaf mines, and (B) the leaf toughness of the descendants 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 descendants in the common garden), as explained in Tab. 1. Data points are means across descendants within provenances.

Figure 3. Interaction between the phylogenetic distance of the parental neighbourhood and the parental 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: 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. The values on Y-axis are the partial residuals, i.e. accounting for the advancement of budburst and leaf nitrogen

status of the descendants in the common garden, as explained in Tab. 3. Data points are means across descendants within provenances.

Accepted manuscript

Figures

Figure 1

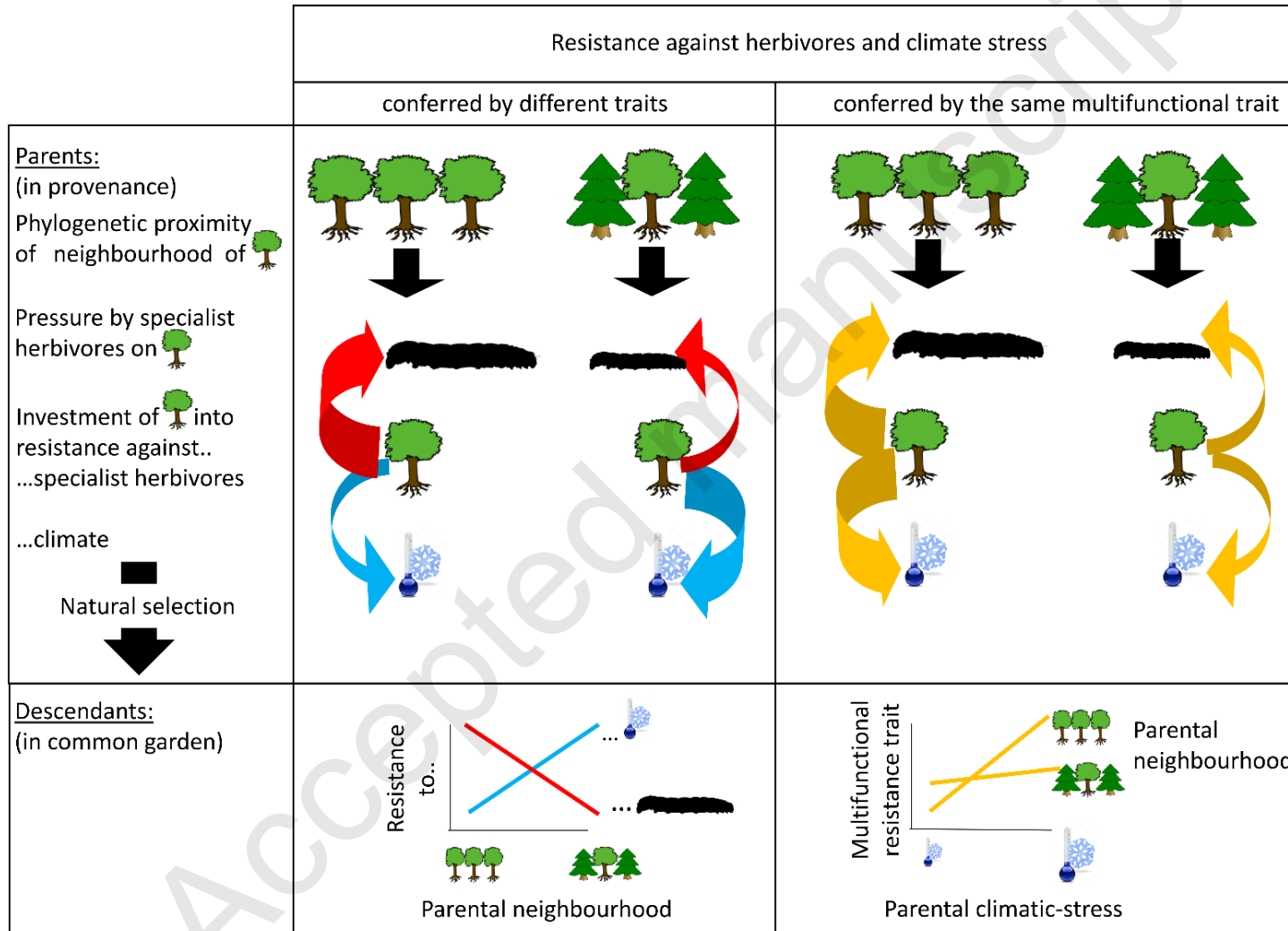


Figure 2

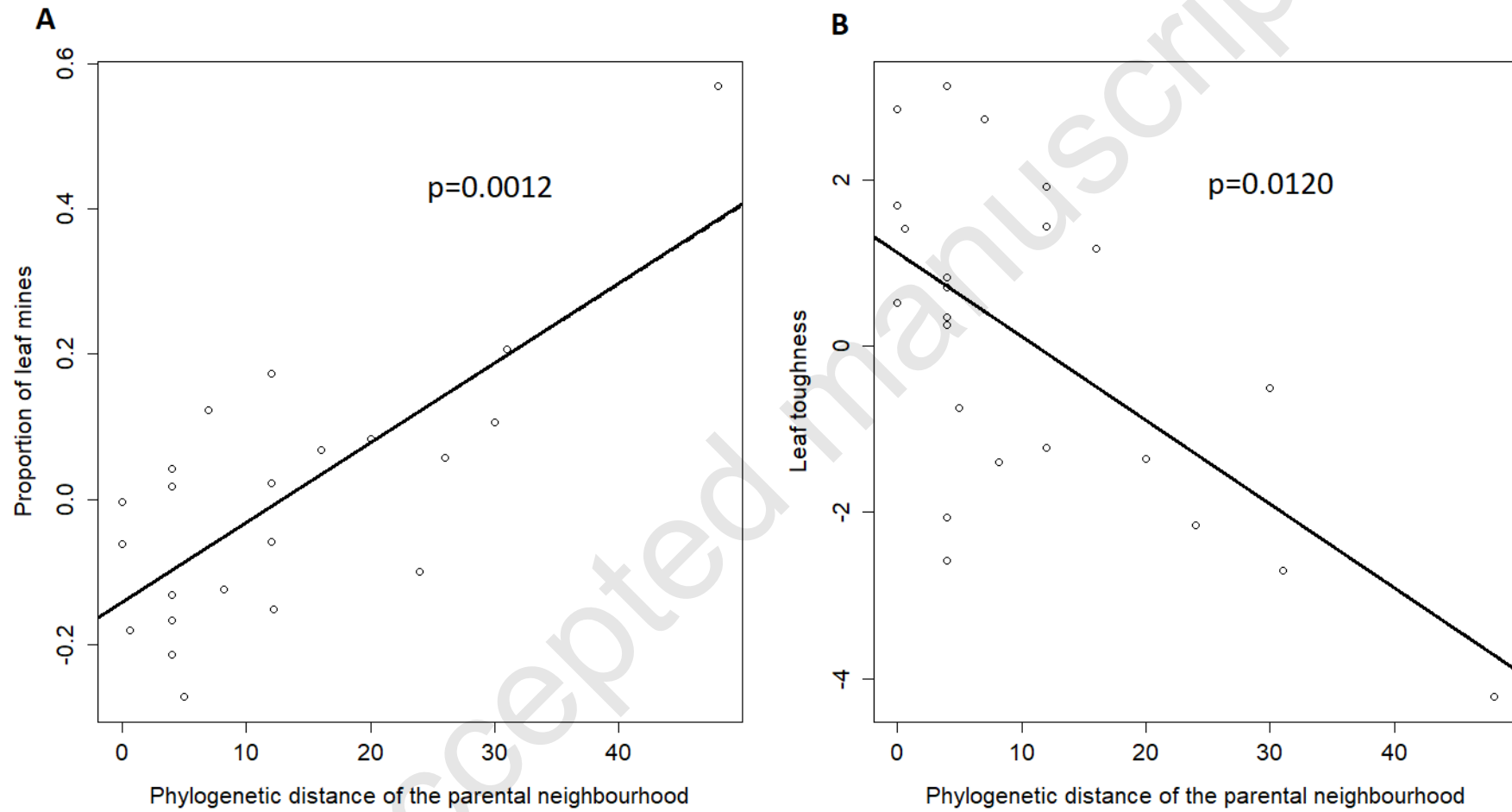


Figure 3

