

Chapter 3

Sources of Variation in Defensive Traits in *Quercus* Species: Insights Gained from Research Spanning Individuals to Communities and Local- to Broad-Scale Factors



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3.1 Introduction

Quercus (Fagaceae) is a species-rich genus that includes close to 600 species of shrubs and trees distributed throughout the Northern Hemisphere [1–4], and as such represents one of the most diverse and broadly distributed tree genera with species occurring from the tropics to northern latitudes and from the Americas to Europe and Asia. Paleocological data indicate that the genus originated in America where highest levels of species richness are currently found at middle latitudes (Mexico), and subsequently spread to the Old World [2, 5]. Extant oaks are a dominant component of terrestrial vegetation in many temperate regions and are considered foundation species that support a high diversity of associated consumers and shape ecosystem functions in different types of temperate forests [6].

Throughout their distribution, oaks are attacked by a diverse fauna of vertebrate and invertebrate herbivores. Notorious examples in the New World include white-tail deer *Odocoileus virginianus*, the leaf-tying caterpillar *Psilocorsis quercicella*, the western tussock moth *Orygia vetusta*, and the gold-spotted oak borer *Agrilus coxalis* [7–10], whereas in the Old World common herbivores are the European roe deer *Capreolus capreolus*, the gypsy moth *Lymantria dispar*, the oak processionary *Thaumetopoea processionea*, the sycamore *Acrionicta aceris*, the pale tussock *Elkneria pudibunda*, the leaf miner *Ectoedemia albifasciella*, and the purple hair-streak *Favonius quercus* [11–13] (Fig. 3.1). There is strong evidence linking several of these herbivores, particularly in the case insects, and putative defensive traits for a

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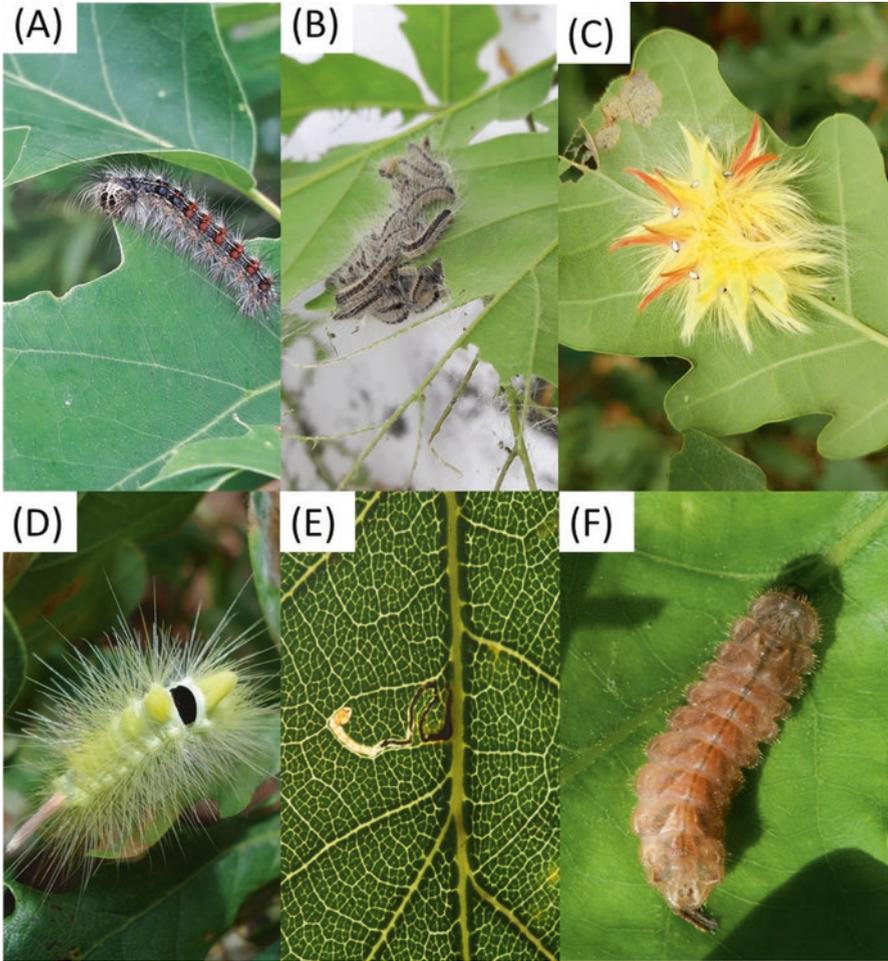


Fig. 3.1 (a) The gypsy moth *Lymantria dispar* (Photo credit: Thomas Damestoy), (b) the oak processionary *Thaumetopoea processionea* (Photo credit: Thomas Damestoy), (c) the sycamore *Acronicta aceris* (Photo credit: Bastien Castagneyrol), (d) the pale tussock *Elkneria pudibunda* (Photo credit: Bastien Castagneyrol), (e) the leaf miner *Ectoedemia albifasciella* (Photo credit: Ayco Tack), and (f) the purple hairstreak *Favonius quercus* (Photo credit: Ayco Tack)

number of oak species [14–18]. These include physical traits such as toughness, fiber content, and trichomes [8, 19, 20], chemical traits such as phenolic compounds (e.g. tannins; [10, 15, 17, 18]), and phenological traits such as leaf longevity and timing of leaf senescence [21].

Research on oak anti-herbivore defences over the last half century spans more than 60 species, ranging from perennial shrubs to deciduous trees found in plant communities that range from montane tropical forests to temperate deciduous forests or Mediterranean-type vegetation [8, 18]. Much of this work has focused on

correlations between insect attack and several of the above-mentioned oak traits. For example, studies have looked at associations between chemical defences and herbivore abundance or performance [14, 16, 22], leaf phenological escape from herbivory [21, 23], as well as landscape-scale (e.g. patch-level or fragment) spatial variation in chemical defences [24, 25]. In most of these cases, studies have usually focused on one or two co-occurring oak species at the local scale, though recent efforts have been made to address broader-scale (biogeographic) patterns in defences within-species as well as across a number of species or clades using phylogenetic methods. Examples of the latter include work on oak defences along climatic or latitudinal gradients [17, 19, 26], elevational gradients [27, 28], as well as continental-scale comparisons [18].

Knowledge gained thus far from these studies has shed light into the importance of diverse biotic and abiotic contributors to intra- and inter-specific variation in oak putative defensive traits. We hereby seek to summarize this rich body of research by describing the most relevant findings on patterns of variation in oak defences, ranging from individual- to community-level variation and spanning local-scale to broad-scale patterns. In each case, we analyse and synthesize the most important underlying biotic and abiotic factors shaping these patterns, and, in doing so, provide an integrative view of sources of variation shaping intra- and inter-specific variation in oak anti-herbivore defences. In addition, we also point at potential linkages across scales to be addressed in future work.

3.2 Local and Landscape-Level Sources of Variation in Oak Defences

3.2.1 Individual- and Population-Level Variation

3.2.1.1 Plant Genetic Variation

Intra-specific variation in plant defences occurring at the level of individual plants can be genetically- or environmental-based [29–31]. To date, however, relatively few studies have assessed patterns of genetically-based intra-specific variation in oak defensive traits. Despite this, there are a few recent studies reporting on intra-specific variation in chemical defences for a handful of species, most of which have measured phenolic compounds. For example, Damestoy et al. [32] found that the concentration of leaf total phenolics in *Q. robur* exhibited significant (three-fold variation) across a pool of 30 genotypes sourced from a single site. In addition, Solla et al. [33] found significant genotypic variation in leaf phenolic concentration within populations *Q. ilex*, but variation among several populations was low and not statistically significant. Although in combination these studies report on intra-specific variation for merely two oak species, results suggest genetically-based variation in oak chemical defences in both cases, either within or among populations. These results are comparable to levels of intra-specific genetic variation in

chemical defences (including phenolics) reported for other better studied taxa of temperate trees such as *Pinus* [31, 34, 35], *Salix* [30, 36, 37], and *Populus* [29, 38, 39]. Accordingly, further investigations spanning other oak species are necessary to gain a better understanding of patterns of intra- and inter-specific variation in *Quercus* defences, its underlying biotic and abiotic correlates, and its ecological implications [40].

3.2.1.2 Environmental-Based Variation and Plant Plasticity

Induced defensive responses to biotic or abiotic factors have been evaluated for several oak species, among which the effects of resource availability and herbivory have received the most attention (see studies in Hunter [41]). In the case of resource availability, a study by Forkner and Hunter [42] evaluated the effects of soil nutrients and found that addition of fertilizer caused a reduction in leaf tannin concentration and an increase in leaf chewer, phloem feeder, and leaf miner abundance for *Q. rubra* and *Q. prinus*. In addition, a previous study reported that soil fertilization weakened induced resistance to herbivory in these species [43], which in combination with the latter study indicates soil resource controls over both constitutive and induced defences in these species. These results agree with findings of studies with other tree species [29, 31] and are consistent with plant defence theory in that plants growing under resource-rich environments grow faster and allocate less resources to defences (“Resource Availability Hypothesis”, [44]). Other studies with oaks have tested for effects of additional sources of abiotic variation, in some cases showing inconsistent patterns. For example, with respect to water availability, Castagneyrol et al. [25] found that leaf physical defences in *Q. robur* were not significantly influenced by artificial irrigation, whereas Schwanz et al. [45] reported for the same species that drought stress reduced the activities of antioxidative enzymes in leaves. In addition, Barber and Marquis [46] found that leaves on *Q. alba* trees exposed to high light availability were better defended (higher toughness and content of phenolics) than leaves on trees under shaded conditions. These findings are consistent with findings for other temperate and tropical tree species suggesting that photo-induction of these secondary metabolites is relatively common [47, 48]. Overall, findings concerning effects of nutrient availability are in agreement with plant defence theory, whereas effects of water and light availability are less consistent and may vary as a function of the type of secondary metabolites and their propensity for photo-induction (e.g. phenolics). Provided the importance of phenolic compounds as putative defensive traits in oaks, investigating the concurrent and interactive effects of multiple sources of resource availability (e.g. light, water and nutrients) for a larger number of species will yield insight on how the abiotic environment shapes oak defence investment.

3.2.1.3 Plant Ontogenetic Variation

Ontogenetic variation combines genetically-determined effects as well as plasticity responses to changing biotic and abiotic pressures over plant development. Although there is little work on ontogenetic variation in oak defences, a couple of recent studies by our group point at interesting results that merit further attention. Specifically, we found that levels of leaf physical and chemical defences in *Q. robur* were in most cases significantly higher in saplings than in adult reproductive trees, whereas insect leaf herbivory was correspondingly lower in saplings than in adult trees, a pattern that was possibly explained by differences in defence levels [24]. Similarly, in a recent study including eight oak species sampled throughout the Iberian Peninsula we also found that the concentration of chemical defences was higher for saplings than for adult trees [49]. However, in this case we found no significant effect of plant ontogeny on insect leaf herbivory [49]. Another study by Wang et al. [50] similarly found that saplings of *Q. variabilis* had a higher concentration of leaf chemical defences compared to mature trees across populations. These results could be seen as consistent with theory, as defence levels for long-lived plants are expected to decline from saplings to more advanced stages of adult life [51]. Overall, these findings point at ontogeny as an important source of variation in oak defences deserving further attention in other species to unveil ontogenetic trajectories in oak defensive investment. Multi-species experiments explicitly testing for plant ontogeny including multiple developmental stages as well as a more detailed control of early life stages (seedlings to saplings) under natural field conditions would provide a good step in this direction.

3.2.2 Plant Community-Level Variation

3.2.2.1 Plant Neighbourhood Effects

Plants are embedded in diverse communities where the presence of conspecific and heterospecific neighbours around a focal plant can greatly affect growth, survival and reproduction of individual plants [52, 53], as well as the strength of plant-herbivore interactions [54–56]. For example, the fact that the relative frequency of a particular host plant species is lower in heterospecific relative to conspecific neighbourhoods results in a lower likelihood of herbivore attack on this focal species (Resource Concentration Hypothesis; [57]). Similarly, herbivore attack on focal plants may decrease in species mixtures due to the presence of one or more heterospecific neighbours, which either attract herbivores or somehow interfere with herbivore location of the preferred host plant (i.e. associational resistance; [58]). Studies have also reported that the diversity or species composition of plant neighbourhoods can indirectly affect herbivory on focal plants by modifying plant nutritional quality (e.g. physical traits and secondary metabolites; [59–62]). For

example, competition for resources or facilitation among heterospecific plants may alter plant growth or the nutritional value of plant tissues to herbivores [63, 64].

A number of studies have evaluated the effects of population- and community-based habitat heterogeneity on oak defences and herbivory, most focusing on pedunculate oak *Q. robur* due to its broad distribution and dominant status in temperate forests of Western Europe. For example, in a recent observational study, we found that leaf physical and chemical defences in *Q. robur* did not vary between stands with a lower vs. high frequency of this species [24]. In contrast, leaf herbivory on this species was (as expected) lower in low-frequency stands and this pattern was apparently not associated with the measured leaf traits [24]. In a similar study, Castagneyrol et al. [65] found that leaf physical defences in *Q. robur* were greater in pure stands of this species relative to mixed stands, but defence levels varied depending on the canopy stratum, suggesting an influence of microhabitat abiotic conditions. Although some leaf traits were correlated with herbivory in this study, tree diversity effects on insect herbivory were only partially driven by variability in oak leaf traits [65]. In another study, Castagneyrol et al. [25] conducted a manipulative experiment with varying levels of tree species richness and found that leaf physical defences in saplings of *Q. robur* trees planted in mixtures varied depending on the tree species neighbour identity though in most cases defences were higher in oak monoculture stands. Counter to expectations, leaf trait variation again was independent of herbivory. Together, these studies provide evidence of emergent neighbourhood effects on English oak defences and herbivory, though patterns of variation in defence and herbivory appear to be uncoupled in some cases suggesting that other (unmeasured) defensive traits could be playing a role. Further tests of this type are needed for other oak species found in different community types in order to start unveiling relevant community-level predictors of variation in oak defences and herbivory.

3.2.2.2 Landscape-Level Variation

To date, most oak studies have centred on arthropod community variation at the landscape level [11, 66, 67] whereas less attention has been given to oak defensive traits, a key component needed to explain spatial herbivory or arthropod community structure. Initial work by M. Hunter, although conducted at a local (rather than landscape) scale, pointed at the importance of associating spatial variation in arthropod community structure and oak defences. For example, Hunter et al. [68] found within-stand correlations of opposing sign between oak (*Q. velutina* and *Q. rubra*) leaf secondary chemistry and densities of leaf-chewing and leaf-mining insects, but no correlation with sap-sucking insects. Leaf-chewers were negatively associated with secondary metabolite concentrations, whereas leaf-miners were positive associated with these traits suggesting that this guild obtains benefits against natural enemies from a diet high in secondary metabolites [69]. A couple of recent studies have explicitly addressed landscape-level variation in oak defences. In one of these studies, Maldonado-López et al. [70] found that the concentration of secondary

metabolites in *Q. castanea* did not vary as a function of fragment size. Given that leaf damage by insect leaf-chewers did depend on fragment size, these findings suggest that differences in herbivory were underlain by other unmeasured leaf traits or abiotic factors [70]. In contrast, Cuevas-Reyes et al. [71] found higher levels of secondary metabolites *Q. deserticola* in large than in small fragments, and that spatial variation in some groups of phenolic compounds was correlated with mistletoe infection. Insect herbivory and mistletoe infection were in turn negatively and positively correlated (respectively) with the concentration of secondary metabolites in this oak species [71], suggesting causal linkages between oak defences and these consumers across sites.

Overall, there have been few studies over the last two decades addressing landscape level variation in oak secondary chemistry and this appears to hold true for other tree species [41]. Thus, whereas early work pointed at the importance of investigating the relationships between arthropod community structure and oak (and other tree taxa) secondary chemistry in a spatially-explicit manner [72], since then there has been little progress in addressing this challenge. Nonetheless, the few studies conducted to date involving non-oak species have found patterns that suggest a link between spatial variation in herbivory, tree (secondary and primary) chemistry, and soil nutrient levels [41, 73]. Investigating these links at the landscape level will allow to assess the feedbacks between consumer effects, oak chemistry, and ecosystem processes (nutrient dynamics; [41]).

3.3 Broader-Scale Sources of Variation in Oak Defences

3.3.1 Regional to Global Patterns

3.3.1.1 Latitudinal and Elevational Gradients

Environmental gradients have played an important part in the study of spatial variation in species interactions, particularly plant-herbivore interactions [74, 75]. Classical hypotheses hold that stronger herbivore pressure under more stable climates towards the equator and sea level has resulted in stronger biotic selection on plant defensive traits [75, 76]. Although a number of empirical studies have found support for this pattern, recent syntheses on latitudinal (reviewed by Moles et al. [76] and Anstett et al. [77]) or elevational (reviewed by Rasmann et al. [78] and Moreira et al. [79]) studies show mixed evidence for the predicted patterns.

Pertaining latitudinal gradients, Pearse and Hipp [17] found that constitutive leaf defences in 56 oak species were higher at lower latitudes, and that these latitudinal gradients were strongly predicted by climate. However, a closer look at studies addressing intra-specific clines reveals substantial variation among species. For example, Wang et al. [50] similarly reported that constitutive chemical defences (and insect herbivory) in *Q. variabilis* trees increased with decreasing latitude, a pattern that was strongly associated with latitudinal variation in climatic conditions.

In contrast, we reported that levels of constitutive leaf defences in *Q. robur* populations decreased with decreasing latitude and that this pattern was associated with higher insect herbivory at lower latitudes [26]. Importantly, our results also indicated climatic and soil variables predicted latitudinal variation in oak defences, and that this cline in defences in turn shaped the latitudinal gradient in herbivory from the “bottom-up” [26]. Finally, Loughnan and Williams [80] recently reported that constitutive physical defences and herbivory in leaves of *Q. garryana* were best explained by climatic variation (spring precipitation), but did not vary significantly with latitude.

With respect to elevational gradients, we recently found that constitutive chemical defences in leaves of eight oak species in the Iberian Peninsula increased towards higher elevations [49]. In another study, we found that inducibility of chemical defences (but not constitutive defences) in leaves of 18 oak species increased towards higher elevations, and that this gradient was not explained by climatic predictors [28]. Finally, in another recent study [27] we found that constitutive chemical defences and insect herbivory on leaves of *Q. robur* trees increased towards higher elevations, and abiotic factors explained elevational variation in leaf defences and herbivory, but in an independent manner (i.e. abiotically-determined clines in herbivory and defences are not related to each other).

Overall, latitudinal variation in oak defences fits the prediction of increasing defences towards the equator, although there is considerable variation among species in the strength and sign of latitudinal gradients. Elevational work, on the other hand, similarly shows considerable variation among species, in some cases being supportive but in other not of theory predicting increasing defences at lower elevations. Abiotic factors (climate, soil conditions) appear to be important third-party factors affecting clinal variation in herbivory, oak defences or both, and should therefore be included in future work to better explain underlying forces shaping pattern variability.

3.3.1.2 Continental-Scale Patterns

Plant intra- and inter-specific patterns of defence investment can be strongly shaped by historical processes [81–83]. For example, biogeographical studies involving large-scale comparisons of Nearctic (i.e. North America) and Palearctic (i.e. northern Eurasia) for several plant taxa have shed light into how historical processes have shaped current patterns of defensive investment, including extinction rates, demographic history, and the history of colonization of plant and herbivore species [84–87].

In the case of oaks, phylogenetic and paleobotanical data suggest that the center of diversification of *Quercus* spp. is at middle latitudes of America [2, 5]. Some of these species subsequently migrated to the Old World prior to the break-up of land bridges linking the northern continents, whereas others (e.g. red oaks) evolved too late to cross [2, 5]. Research holds that extinction rates of temperate tree species (including oaks) have been lower and plant and herbivore rates of recolonization

have been higher for the Nearctic compared to the Palearctic since the last glacial period [84, 85]. Following from this, a stronger recent history of herbivore pressure in the Nearctic would result in oak species from this region being more heavily defended than their Palearctic counterparts. However, a recent study of ours showed that Nearctic oak species exhibited higher levels of lignins, but lower levels of condensed tannins, compared with Palearctic oak species [18], the latter compounds typically correlating more strongly with herbivore resistance. The lack of information on the history of herbivore pressure for different regions makes it difficult to establish predictions. Still, with increasing oak paleoecological and phylogenetic data progress can be made in understanding how historical factors operating at broad scales have shaped macro-evolutionary patterns of oak defences across different biogeographical regions.

3.3.1.3 Effects of Insularity

Insular systems have proven highly useful for elucidating the ecological and evolutionary mechanisms shaping biodiversity [88, 89], species interactions [90, 91], and trait evolution [92]. With respect to plant-herbivore interactions, islands frequently have low abundances and diversity of vertebrate and invertebrate herbivores relative to their mainland counterparts because of dispersal limitation and habitat filtering, which presumably results in lower levels of herbivory relative to mainland regions [88, 93, 94]. As a result, insular plants are expected to show lower levels of physical (e.g., spines, thorns) and chemical (e.g., secondary metabolites) defences than their mainland counterparts [93, 95–97].

Despite these predictions, recent studies have been unresponsive of these expectations with insular plants having higher (rather than lower) levels of physical and chemical traits putatively associated with herbivore resistance (e.g. [98–101]). For example, we found that insular populations of holm oak (*Q. ilex*) exhibited expectedly lower insect leaf herbivory, but instead higher chemical defences (condensed tannins) than their mainland counterparts [101]. This suggests that insularity effects on herbivory and the measured leaf traits appear to be uncoupled. Furthermore, abiotic factors did not explain differences in either leaf traits or herbivory between mainland and island populations, pointing to other unmeasured drivers of oak defensive investment. Expanding this work to include other oak species would allow for better generalization and understanding of insularity effects on oak defences, possibly revealing contrasting evolutionary histories depending on the underlying drivers and historical processes driving plant-herbivore interactions for each of the studied oak taxa.

3.3.1.4 Effects of Urbanization

Urbanization usually leads to significant changes in local environmental conditions (e.g. increasing temperatures and levels of CO₂) which can dramatically alter the quantity, availability, as well as temporal and spatial distribution of biotic and abiotic conditions needed to support plant and animal communities [102, 103]. For plant-herbivore interactions, a number of studies conducted over the last two decades have reported on patterns of insect herbivory and plant defensive traits on trees and herbaceous plants along urban-rural gradients [104, 105]. The overall patterns have been inconclusive; some studies have reported increased insect herbivory and defences in urban areas relative to rural habitats [106, 107], whereas other studies have found the opposite pattern [108–110].

There have been a few recent studies looking at effects of urbanization on oak defences. For example, in a recent study we found that *Q. robur* trees found in urban locations had lower levels of chemical defences and leaf chewer herbivory [110]. In contrast, urban trees had increased levels of leaf nutrients (nitrogen and phosphorus) compared to trees in natural forest locations [110]. Urbanization effects on chemical defences (but not herbivory) were in turn associated with urban to rural changes in CO₂ concentrations [110]. Although there have been other studies measuring urban-rural gradients in oak herbivory [111], one of these reporting on 10 temperate tree species (including *Q. robur*; [108]) these have not measured plant defensive traits. Pending further studies with additional oak species, evidence thus far for *Q. robur* suggests that oak defences are relaxed in urban environments whereas leaf nutrients increase, presumably leading to an overall increase in plant quality. More work is needed, however, to gain a clearer understanding of which are the most important biotic or abiotic correlates of urbanization effects on oak defence investment.

3.3.2 Phylogenetic Patterns

In recent decades, due to technological advances in molecular biology, ecologists have begun to consider the influence of phylogenetic relatedness among taxa on current patterns of inter-specific variation in plant defence allocation [82, 112, 113]. Ehrlich and Raven's classic work [114] predicted that (1) more closely related plant species should share similar defensive chemistry, (2) more derived species should be more highly defended, and (3) closely related herbivores are expected to feed on closely related plants as a result of co-evolutionary arms races between trophic levels [115]. In this sense, insightful studies by Pearse and Hipp with 56 oak American species found a strong phylogenetic signal in plant physical and chemical defences, as well as in leaf herbivory [8, 17]. However, a recent study by our group including 18 oak species from America and Eurasia found no phylogenetic signal in constitutive chemical defences (phenolic compounds) and their inducibility [18], suggesting that phylogenetic patterns of variation in oak defences do not follow predictions

by classic co-evolution models, at least for the studied species. While these findings should be taken with caution given the limited number of species studied, they also highlight the need to develop an expanded view of macro-evolutionary patterns of plant defences. Such views should consider alternative scenarios that depart from classic plant-herbivore coevolutionary theory (e.g. herbivore resource tracking, see Endara et al. [116]), as well as other ecological forces (e.g. abiotic factors) which might influence in the evolution of plant defences, independently of herbivore pressure [8].

3.4 Linkages Across Scales: Oaks as Model System

Oaks, together with other taxa of widespread, dominant trees, represent a good ecological model for integrating research across levels of study. Their high taxonomical and functional diversity allows for intra- and inter-specific comparisons to test for different mechanisms of biotic and abiotic control over tree defensive investment, whereas their status as foundational and dominant species implies strong local and landscape-level associations between oak defences, arthropod community structure, and ecosystem processes. In addition, this genus contains numerous species with contrasting distributions (e.g. latitudinally or elevationally) which serves the goal of assessing both local (e.g. using sympatric species) and broad-scale (e.g. comparisons across species with contrasting distributions) factors. For example, future work can assess patterns of both intra-specific (genetic) and inter-specific variation in defences, herbivory, and herbivore community structure for groups of co-existing oak species found in similar habitat types. Results can yield insight into the linkages between and relative contributions of intra- vs. inter-specific variation in oak defences and their implications for arthropod community structure [40]. Studies could involve both observational and experimental studies manipulating oak species (as well as that of other common co-occurring tree species) composition or phylogenetic diversity to connect these ecological patterns to evolutionary history. Likewise, expanding on this to address the ecosystem consequences of oak defence variation would involve measurements of nutrient cycling and decomposition to understand the linkages between oak intra- and inter-specific variation in tissue chemistry and ecosystem processes [41, 117]. Finally, also expanding from the previous examples, studies assessing these intra- and inter-specific sources of oak defence variation under different habitats or community types (e.g. along gradients or contrasting habitat types) are needed to understand how abiotic factors shape oak defences [118], as well as its associations with herbivory and herbivore community structure [118, 119]. These types of studies could also involve manipulations of abiotic factors and herbivory to assess their relative importance in shaping oak defence investment [120]. Work could make use of either natural and human-impacted or transformed (e.g. urban) habitats to test for anthropogenic controls over biotic and abiotic factors shaping oak defensive traits.

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