

Chapter 18

Latitudinal and Elevational Gradients in Plant Defences and Herbivory in Temperate Trees: Recent Findings, Underlying Drivers, and the Use of Genomic Tools for Uncovering Clinal Evolution



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Abstract Environmental gradients serve as powerful settings to elucidate the ecological and evolutionary processes driving changes in species diversity, trait evolution, and ecosystem function. Classic theory holds that stronger plant-herbivore interactions under more stable and warmer climates towards the equator and sea level have resulted in stronger selection on plant defences. We hereby address latitudinal and elevational gradients in plant defences and herbivory follow these predictions for a number of dominant taxa of temperate trees. Many of these taxa include species that span broad latitudinal and elevational ranges and thus represent useful models for testing clinal variation in plant defences and herbivory. First, we review recent studies testing for latitudinal and elevational gradients in temperate tree defences and herbivory. Second, we analyse these results in the light of classical theory and discuss potential deviations from expected patterns and candidate mechanisms. Third, we analysed the use of genomic tools for assessing the genetic basis of clinal evolution in plant defences, a promising alternative toward reducing inconsistencies and identifying commonalities in ecological and evolutionary processes. Our review indicates considerable variation in the strength and direction of elevational and latitudinal gradients in temperate tree defences and herbivory. Strikingly, patterns that are opposite to classic predictions are equally common and, in some cases, even more common than expected patterns. In light of these findings, we argue for a need to apply consistent methods across studies, conduct more comprehensive assessments of plant defensive phenotypes, and explicitly consider the role of abiotic factors. Furthermore, as future research closes these gaps, the adoption of genomic tools will open an unprecedented opportunity to launch a new generation of studies.

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To achieve this, there is a need to merge research on landscape genetics and ecological studies of plant-intraspecific clines in plant-herbivore interactions to unveil the genetic basis of clinal evolution in plant defences. Likewise, analyses of the molecular level evolution of target genes associated with plant defence also hold a large potential for assessing plant defence macro-evolutionary patterns along environmental clines. Applying these tools will help elucidate the mechanisms of adaptive evolution in plant defence along environmental clines and contribute to develop new theory by uncovering patterns not apparent previously from studies based solely on measurements of plant phenotypes and species interactions.

Keywords Clinal variation · Elevational gradients · Environmental gradients · Evolutionary genomics · Latitudinal gradients · Plant defence · Macroevolution

Environmental gradients have served as powerful settings to elucidate the ecological and evolutionary processes driving changes in species diversity, trait evolution, and ecosystem function (Dobzhansky 1950; Pianka 1966; Reich and Oleksyn 2004; Schemske et al. 2009). Latitudinal and elevational clines in biodiversity and species interactions have been especially well studied in this regard (Schemske et al. 2009; Sundqvist et al. 2013; Anstett et al. 2016), and although they differ in some aspects (see Moreira et al. 2018a), they are united under a common paradigm underscoring the role of abiotic controls over species abundances, diversity, and interaction strength. Under this framework, species interactions are predicted to be more intense under less seasonal and warmer climates found at lower latitudes and elevations, and this results in stronger selection on species traits (Schemske et al. 2009; Moreira et al. 2018a; Rasmann et al. 2014a; Mittlebach et al. 2007). In the case of plant-herbivore interactions, more intense and consistent patterns of herbivory under more stable and warmer climates toward the equator and sea level should result in stronger selection on plant defences (Rasmann et al. 2014a; Baskett and Schemske 2018). In turn, this is thought to have promoted plant (herbivory-based) niche differentiation, coexistence and speciation (Schemske et al. 2009; Kursar et al. 2009; Coley and Kursar 2014), and, indirectly, herbivore diversification (Futuyma and Agrawal 2009).

The mechanisms driving elevational and latitudinal variation in plant-herbivore interactions have been intensely debated, and a general consensus is yet to be reached (Anstett et al. 2016; Moreira et al. 2018a). The main reason has been the lack of consistency in the strength and direction of quantitative or qualitative variation in plant defences with latitude (Anstett et al. 2016; Moles et al. 2011) and elevation (Moreira et al. 2018a; Rasmann et al. 2014b). For example, Moles et al. (2011) found that merely 16% of studies conducted up to that date had found evidence that plants at lower latitudes were more defended than high-latitude plants, and a recent review by Moreira et al. (2018a) indicated that 66% of studies found that plants at low elevations were more highly defended than their high-elevation counterparts. A series of explanations have been put forward to account for these

inconsistent patterns, ranging from contrasting spatial and taxonomical scales of analyses across studies and insufficient quantification of different types of defensive traits and strategies to a lack of consideration of plant life histories and methodological inconsistencies (Anstett et al. 2016; Moreira et al. 2018a; Kooyers et al. 2017). Moreover, even though the influence of abiotic factors on herbivory is implicit in most research, only until recently studies began to explicitly address the influence of abiotic correlates of latitude and elevation (e.g. climate, soil variables) on plant defences and herbivory (Moreira et al. 2018a; Johnson and Rasmann 2011). Therefore, it has been difficult to identify the underlying factors dictating these disparate patterns (but see Galmán et al. 2018), and this has limited our understanding of the generative processes by which abiotic clines shape plant defences and herbivore pressure.

Another important consideration is that the literature on latitudinal and elevational gradients in plant-herbivore interactions has centred more frequently on herbaceous plants or shrubs, while studies performed on tree species have been relatively less common. Nonetheless, over 30% of the Earth's land surface is covered by forests (FAO 2012), and tree species account by and large most of the biomass in forested ecosystems (Grossman et al. 2018). In temperate regions, for example, there are a number of dominant tree taxa that cover large expanses of land and play preponderant role in shaping species interactions, evolutionary dynamics, and ecosystem function (e.g. *Quercus*, *Pinus*, *Betula*, *Salix*, among others). In addition, many of these temperate tree species span broad latitudinal and elevational ranges (e.g. *Pinus* (Moreira et al. 2014), *Quercus* (Galmán et al. 2019)) and therefore represent highly suitable models to test for clinal variation in plant defences and herbivore pressure. Addressing these patterns and their underlying drivers for temperate tree species is therefore needed to increase inference and achieve a more robust understanding of the evolutionary ecology of plant-herbivore interactions under a spatial context.

Crucially, research on elevational and latitudinal gradients in plant defences and herbivory has a deeply rooted evolutionary perspective (Dobzhansky 1950; Schemske et al. 2009; Endler 1977). Paradoxically, clinal evolution of species traits is often implied in these studies but relatively few have involved explicit evaluations of evolutionary processes. The most notable exception to this is classical (and a number of more recent) studies involving common garden and reciprocal transplant experiments to test for population differentiation along (e.g. elevational) clines (reviewed by Cheplick 2015). Still, much of this research has focused largely on plant traits associated with adaptation to abiotic factors (Clausen et al. 1947; Linhart and Grant 1996), and the fewer studies addressing clinal adaptation to biotic factors have mostly focused on traits associated with competition and to some extent also pollination (Cheplick 2015). In contrast, tests of local adaptation to herbivores and pathogens are far less common (Abdala-Roberts and Marquis 2007; Lowry et al. 2019), and this bias is also markedly reflected in research on latitudinal and elevational gradients. As a result, very few studies have involved direct and explicit evaluations of the evolution of plant defences along elevational and latitudinal clines (but see Pellissier et al. 2014). Generally speaking, a number of analytical tools

have flourished over the last decade which can be used to detect loci (e.g. defensive genes) under selection both within and across plant taxa. These range from genome-wide association analyses within species (e.g. De Kort et al. 2014) to molecular analyses pinpointing macro-evolutionary patterns of selection on plant defences across plant taxa (Carmona et al. 2019). Still, many of these methods have rarely been applied to plant genes associated with biotic defence under the geographic context of latitudinal and elevational gradients, thus pointing at a highly promising but yet unrealized research opportunity.

In this chapter, we focus on the evolutionary ecology of latitudinal and elevational gradients in plant defences and herbivory associated with long-lived temperate trees, though the arguments and conclusions drawn from our review in general terms extend to plant species of any life form. First, we review a suite of studies conducted over the last decade testing for latitudinal and elevational gradients in defences and herbivory for several genera of temperate trees which have served as model systems. Second, we compare these results to classical predictions on latitudinal and elevational gradients in herbivore pressure and discuss the observed patterns. Here we also include an explicit consideration of abiotic controls over clinal variation in plant traits and herbivory, which a few recent studies have addressed. Third, we discuss classic and modern approaches that have been used to study the evolutionary implications of clinal variation in plant defences. Here we emphasize the potential application of genomic tools to measure and understand adaptive evolution of plant defences along ecological gradients, and provide examples of ways in which they can be used to address questions at both the micro- and macro-evolutionary level.

Latitudinal and Elevational Gradients in Plant-Herbivore Interactions in Temperate Trees

We next review the main findings from studies on latitudinal and elevational gradients in plant defences and herbivory for several key genera of temperate trees, mainly oaks (*Quercus* spp.) for which much of the recent work has focused, and to some extent also other groups such as birches (*Betula* spp.), pines (*Pinus* spp.), and beeches (*Fagus* spp.). We focus on these taxa for two reasons. First, they lend themselves to robust tests of intraspecific clines in plant defences and herbivory and their underlying micro-evolutionary processes because they include a number of dominant species spanning broad latitudinal and elevational ranges. For example, *Quercus* and *Pinus* span both tropical and temperate latitudes and up to 3000 m in elevation, covering a vast diversity of abiotic (e.g. climatic) and biotic conditions (Moreira et al. 2014; Cavender-Bares 2019). Second, they provide useful models for assessing macro-ecological and macro-evolutionary patterns of clinal variation because their constituent species vary substantially in their latitudinal and elevational distributions (i.e. large cross-species variation along both geographical axes increasing power of

analyses). In addition, working with groups of congeneric species allows for tight controls of ecological variation and phylogenetic relatedness among taxa.

Latitudinal and Elevational Variation in Defences in Temperate Trees

A total of 15 studies spanning 97 species have assessed latitudinal and elevational gradients in defences in temperate trees, of which 80% have involved chemical defences (Fig. 18.1a). Of this total, oaks (*Quercus* spp.) have been the most frequently studied group (53% of studies, 63 species), followed by pines (*Pinus* spp., 33% of studies, 20 species) and birches (*Betula* spp., 13% of studies, three species). A number of these studies have found support for the classic prediction that plants at low latitudes and elevations have higher levels of defences in response to more intense herbivore pressure (Anstett et al. 2016; Rasmann et al. 2014a), namely, 33% of latitudinal studies and 40% of elevational studies. Nonetheless, a moderate amount of studies have found either no evidence of latitudinal (17%) or elevational (20%) clines in defences, and a substantial number of other studies have found, contrary to expectations, greater levels of defences at higher latitudes (50%) or elevations (40%).

Variation among studies in the strength and direction of latitudinal and elevational gradients in plant defences could be explained by differences in the type and identity of plant defensive correlates measured as well as the resolution of chemical analyses (Anstett et al. 2016; Moreira et al. 2018a). For example, the identity of specific types of secondary compounds and their role in herbivore resistance is often not assessed as studies typically bin multiple types of compounds into broad classes which may mask clines that are apparent only when looking at individual compounds or groups of compounds (Anstett et al. 2014, 2015). Recent studies with temperate trees that have measured multiple types of secondary compounds (5 studies, 33% of total reported above) highlight this point, as clinal patterns often vary among compound groups or individual compounds (e.g. phenolics, terpenes). Likewise, the functional role of these compounds in determining herbivore resistance for a given plant species or group of related species is often not assessed but rather assumed based on correlations or evidence from other systems without actual documentation of effects on herbivore performance (Anstett et al. 2016).

In addition, plant macronutrients can also predict herbivory (Mattson 1980; Agrawal 2007) and exhibit latitudinal and elevational gradients (e.g. Reich and Oleksyn 2004). Two recent studies with temperate trees reported that the concentration of leaf phosphorus and nitrogen (two limiting macronutrients for herbivores) in *Q. robur* trees increased towards higher latitudes (Moreira et al. 2018b) and elevations (Abdala-Roberts et al. 2016a). In both cases, however, nutritional traits were not associated with leaf damage suggesting they did not influence clines in herbivory. In addition, Garibaldi et al. (2011a) observed that foliar phosphorus content in *Nothofagus pumilio* forests of the northern Patagonian Andes (Argentina) increased

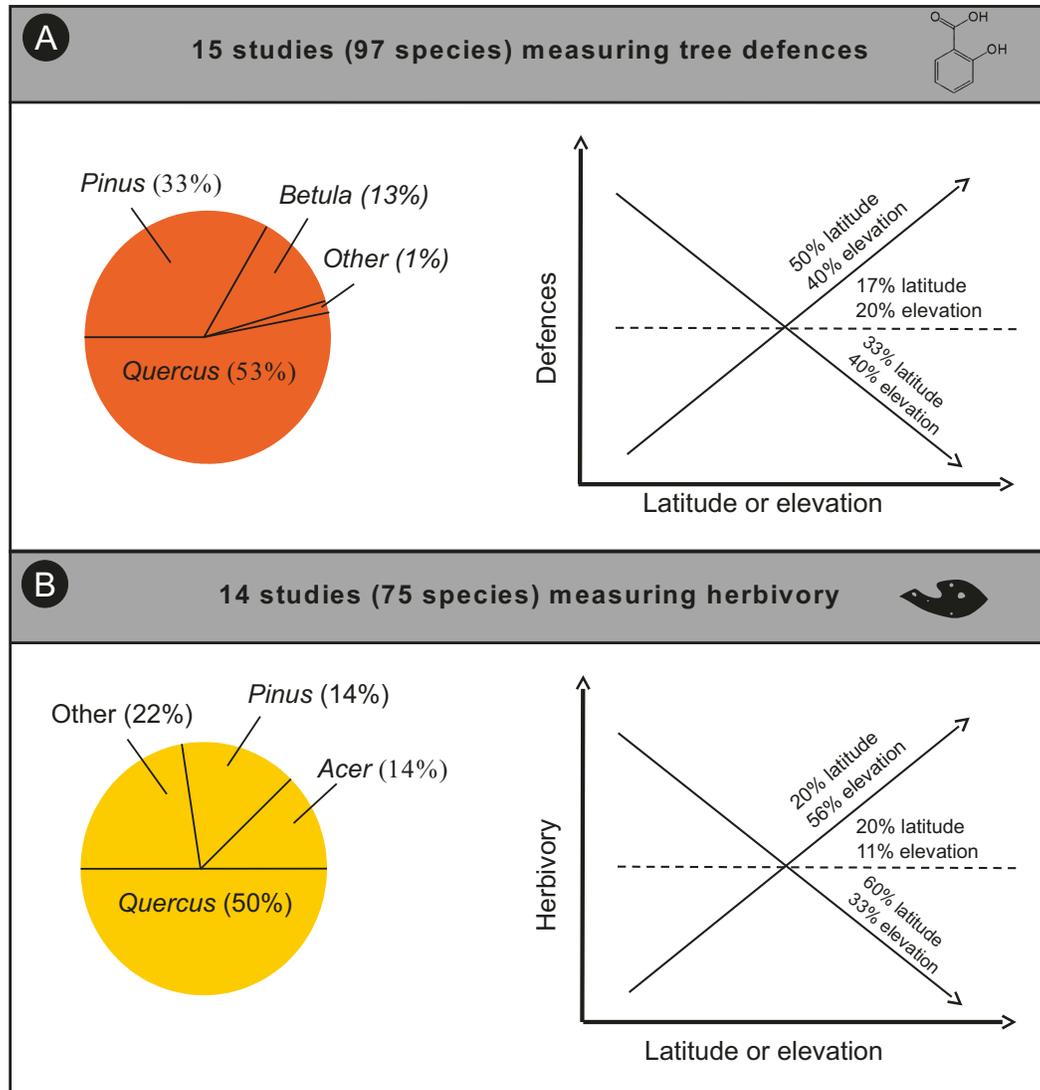


Fig. 18.1 Summary of the number of studies testing for latitudinal or elevational gradients in defences (a) and herbivory (b) in temperate tree species. The percent of studies showing expected (negative) vs. unexpected (neutral, positive) latitudinal or elevation gradients are shown, as well as percent of studies by tree taxa

from low- to high-elevation sites, but again leaf herbivory and phosphorus concentration were not significantly correlated. Although these studies did not find evidence suggesting that plant nutrients influence clines in herbivory, more studies are still needed. For example, plant exhibit strategies associated with resorption and reallocation of nutritional traits from herbivore-damaged to undamaged tissues (Frost and Hunter 2008; Moreira et al. 2012), and these mechanisms could be under selection by herbivores and vary along ecological gradients of herbivore pressure (or abiotic conditions; see ahead). Therefore, a detailed quantification of both sec-

ondary metabolites and nutrients in plant tissues is necessary to better characterize gradients in defence and, more broadly, overall plant quality for herbivores (Marquis et al. 2012) to herbivores along ecological gradients.

A more comprehensive assessment of traits associated with different defensive strategies may also increase our understanding of latitudinal and elevational gradients in plant defence and explain variation in the observed patterns. Defensive strategies such as tolerance (e.g. regrowth capacity or overcompensation in reproduction (Carmona et al. 2011)), induced defences (Karban 2011), and indirect defences (i.e. used to recruit predators and parasitoids (Agrawal 2011)) may also exhibit clinal variation. There may be trade-offs between defensive strategies (Agrawal 2000), such that two or more defensive traits or strategies may negatively covary along latitudinal or elevational gradients such that considering them separately may lead to an erroneous or incomplete understanding of observed patterns. For example, constitutive and induced defences frequently trade off (Moreira et al. 2014; Koricheva et al. 2004; Kempel et al. 2011; Rasmann and Agrawal 2011; Rasmann et al. 2015), and shifts in the relative allocation to each strategy may occur along an ecological gradient. Plants growing in resource-poor and stressful environments found at high latitudes or elevations should be selected for increased allocation to constitutive defences, as the cost of replacing tissues consumed by herbivores is higher under low resource conditions (Coley et al. 1985; Endara and Coley 2011). For example, Moreira et al. (2014) found that levels of constitutive resin in 18 pine species increased at higher latitudes and elevations, whereas the inducibility of these traits increased toward the equator. It is also possible, however, that environments with low herbivore pressure typically found at high latitudes or elevations should select for low constitutive and high induced defences because the costs of continuously producing the former are high when damage is low. Supporting this alternative, Galmán et al. (2019) recently found that oak species with high elevational ranges exhibited a greater inducibility of phenolic compounds (hydrolysable tannins).

More studies differentiating constitutive and induced defences are needed in temperate trees (and other life forms as well) to assess these proposed mechanisms for ecological gradients in plant defensive strategies. In addition, we are unaware of studies testing for latitudinal or elevational clines in direct and indirect defences in trees (see Rasmann et al. 2014c; Pellissier et al. 2016 for examples with herbaceous species), representing another overlooked axis of plant defensive strategies. Similarly, trade-offs between tolerance and resistance (Fineblum and Rausher 1995; Agrawal et al. 1999) may lead to covariation in these defensive strategies along ecological gradients. Only two studies to date have tested for and not found trade-offs in these two plant strategies along latitudinal (Więski and Pennings 2014) or elevational (Dostálek et al. 2016) clines, and both involved herbaceous species. We are aware of no clinal studies on tolerance and resistance with long-lived plants, particularly temperate trees.

Latitudinal and Elevational Variation in Herbivory in Temperate Trees

A total of 14 studies spanning 75 species have assessed latitudinal and elevational gradients in herbivory for temperate trees, all of which have involved leaf damage by insects (Fig. 18.1b). Of this total, again oaks (*Quercus* spp.) by far have been the most frequently studied group (50% of studies, 57 species), followed by pines (*Pinus* spp. 14% of studies, three species) and maples (*Acer* spp., 14% of studies, two species). Several of these papers have found support for the prediction that plants at low latitudes and elevations have higher herbivore pressure, namely, 60% of latitudinal studies and 33% of elevational studies. As for plant defences, however, a substantial number of studies have found either no evidence of latitudinal (20%) or elevational (11%) clines in herbivory, and a number of other studies have found, contrary to expectations, greater levels of herbivory at higher latitudes (20%) and elevations (56%). Taken together, these results indicate considerable deviations in the predicted patterns of elevational and latitudinal variation in herbivore attack, which would presumably lead to concomitant variation in clinal patterns for plant defences.

Plausible explanation for the observed variation in patterns of herbivory (and, as a result, plant defences), common to all plant type studies (not only trees), is that herbivore pressure is not always adequately or consistently measured (Zvereva and Kozlov 2019), and the identity of the attacking herbivores is frequently not assessed (Anstett et al. 2016; Moreira et al. 2018a). Herbivore species or guilds may vary in their susceptibility to changing abiotic conditions and may therefore exhibit different (in some cases contrasting) patterns of abundance and damage on focal host plants along environmental clines (Rasmann et al. 2014b; Anstett et al. 2014, 2015; Pennings et al. 2009). Consequently, pooling damage by multiple types of herbivores may obscure the detection of significant patterns only apparent when differentiating damage by each attacker (Anstett et al. 2016; Moreira et al. 2018a; Abdala-Roberts et al. 2015). Recent studies with temperate trees measuring multiple attackers (5 studies, 36% of total reported above) highlight this point, as clinal patterns in herbivory or abundance commonly vary among herbivore species or guilds (e.g. chewers, miners, sap-feeders). For example, Andrew and Hughes (2005) found that the amount of herbivory by sap-sucking and mining insects on *Acacia falcata* trees increased toward more temperate latitudes, whereas chewing herbivory increased toward tropical latitudes. Similarly, Nakamura et al. (2014) found that herbivory by chewing, mining, and galling insects in beech (*Fagus crenata*) in Japan exhibited contrasting latitudinal patterns. Insect miner and galler densities were higher at lower latitudes, whereas leaf-chewer damage herbivory was greater at higher latitudes (Nakamura et al. 2014).

These inconsistencies or coarseness in herbivory measurements explained above have likely also obscured our understanding of how clines in herbivore pressure shape concomitant clines in plant defences. A number of studies have demonstrated that herbivore species from different guilds can exert selective effects on different

plant traits or select on the same trait but in a different manner (e.g. Juenger and Bergelson 1998; Carmona and Fornoni 2013; Wise and Rausher 2013). It is therefore plausible for variable or opposing selection by multiple herbivores to lead to unexpected patterns in the strength and direction of latitudinal (Anstett et al. 2014; Moreira et al. 2015; Abdala-Roberts et al. 2016b) and elevational (Descombes et al. 2017; Pellissier et al. 2012) gradients in plant defences. Relatedly, recent work analysing community-level variation in herbivore traits has shown that insect herbivore diet breadth increases with latitude (Forister et al. 2015; Salazar and Marquis 2012) and elevation (Rasmann et al. 2014a; Pellissier et al. 2012). This could result in latitudinal and elevational changes in herbivore selection on plant traits given that specialist herbivores might select for different plant defensive traits or strategies than generalists (Ali and Agrawal 2012). However, these studies have been restricted to herbaceous plants and virtually nothing is known about this for temperate trees.

Abiotic Controls over Plant Defences and Herbivory Along Latitudinal and Elevational Clines

Abiotic conditions represent a third type of factor which may modulate plant-herbivore interactions along environmental gradients. Although the influence of abiotic factors is implicit in research on latitudinal and elevational gradients in plant-herbivore interactions, paradoxically, relatively few studies have explicitly addressed their influence (e.g. climate, soil nutrients (Johnson and Rasmann 2011; Moreira et al. 2018b)). The implicit assumption has been that abiotic conditions (primarily associated with climate) affect herbivore population sizes and feeding season length, and this then shapes herbivore pressure and selection intensity on plant defences (Anstett et al. 2016). However, recent studies with temperate trees assessing the influence of abiotic correlates (e.g. Galmán et al. 2018; Abdala-Roberts et al. 2016a; Garibaldi et al. 2011a; Loughnan and Williams 2019) suggests that this situation is more complex than previously envisioned and that there may be alternative scenarios. For example, Abdala-Roberts et al. (2016a) reported that climatic factors shaped elevational gradients in insect herbivory and chemical defences in *Q. robur*, but such effects were independent of each other (i.e. climate effects on one had no implications on the other). On the other hand, Garibaldi et al. (2011b) found that insect leaf damage in *N. pumilio* decreased with latitude and such gradient was not attributable to climatic effects on plants and herbivores. In addition, also with *Q. robur*, Moreira et al. (2018b) reported that, rather than abiotic factors shaping latitudinal variation in herbivory and in turn defences in this oak species, climate and soil variables influenced plant chemical defences and such effects indirectly shaped the latitudinal gradient in herbivory. Finally, some studies have simply found no influence of latitudinal variation in abiotic factors (e.g. climate) on concomitant patterns of insect herbivory (Moreira et al. 2018b) or defences (Galmán et al. 2019) in temperate trees. For example, in a greenhouse experiment using 1-year-old plants

from 18 oak species, Galmán et al. (2019) reported that oak species growing at higher elevations exhibited a greater inducibility of phenolic compounds, but climatic factors (average climatic niches) did not explain this pattern.

Interestingly, recent work by Mikhail Kozlov and collaborators (2013, 2015) across multiple years elucidated interactions between climatic factors and latitudinal clines in herbivory by different insect guilds for birch trees (*Betula pendula* and *B. pubescens*). For example, the abundance of leaf miners in these two birch species significantly decreased with latitude during cold years but was independent of latitude during warm years (Kozlov et al. 2013). However, the load or density of sap-feeders in these two birch species decreased with increasing latitude in typical summers but increased towards the pole in an exceptionally hot summer (Kozlov et al. 2015) (for examples with herbs, see Anstett et al. 2015; Abdala-Roberts et al. 2016b). These studies emphasize the value of addressing abiotic factors, differentiating damage by multiple herbivore guilds, and assessing temporal variation in such associations in order to elucidate the influence of abiotic controls over latitudinal and elevational gradients in plant-herbivore interactions. Although there has been success in using these observational approaches to understand the concurrent effects of abiotic factors—including our own work in oaks (e.g. Moreira et al. 2018b; Abdala-Roberts et al. 2016a)—experimental manipulations of abiotic drivers are also needed to better understand their influence on species interactions and assess causality.

Evolutionary Studies of Latitudinal and Elevational Gradients in Plant Defences

The central tenet of research on latitudinal and elevational gradients is that stronger herbivore pressure towards lower latitudes and elevations has selected for higher plant defences (Schemske et al. 2009; Baskett and Schemske 2018; Rasmann et al. 2014b). Accordingly, most studies to date have measured proxies of plant defences (e.g. chemical and physical) and imply that observed patterns reflect concomitant variation in biotic selective regimes along elevational (reviewed by Moreira et al. 2018a) or latitudinal (reviewed by Schemske et al. (2009) and Mittlebach et al. (2007)) gradients. Although increasing spatial scale and replication along a sampled gradient allow to more robustly ascertain the evolutionary dynamics shaping biogeographical patterns of plant-herbivore interactions (Anstett et al. 2016), to date relatively few studies have used approaches and methods to explicitly measure the evolutionary mechanisms and implications of clinal variation in herbivory (and abiotic factors) for plant defences.

There is a long history of research testing for plant adaptive differentiation along environmental clines (reviewed by Cheplick (2015) and Linhart and Grant (1996)), with a number of early studies focusing on elevational gradients (e.g. Clausen et al. 1940, 1947, reviewed by Cheplick 2015). Several complementary approaches have been used to this end, from analyses that correlate environmental and genetic

variation or differentiation (e.g. Gould et al. 2013) to manipulations involving common garden or reciprocal transplant experiments (reviewed by Cheplick 2015 and Hargreaves et al. 2019), and to a lesser extent studies testing differences in the strength of regression-based estimates of phenotypic selection on focal traits along ecological clines (e.g. Etterson 2004; Toju and Sota 2006). To date, however, experimental studies along latitudinal and elevational gradients have focused mostly on plant adaptation to abiotic factors (e.g. climate or soil conditions Cheplick 2015; Pellissier et al. 2014), whereas fewer have addressed the influence of biotic factors. Exceptions to this include work on population differentiation in growth-related traits associated with competition or reproductive traits (e.g. flowering time or floral morphology) implicitly related to pollinator selection (e.g. Gould et al. 2013; Anderson et al. 2015; Berardi et al. 2016; Hirano et al. 2017, reviewed by Hargreaves et al. 2019). In contrast, studies of this nature addressing plant anti-herbivore defensive traits are rare, with only two recent exceptions involving reciprocal transplant studies showing that plant population differentiation in direct (Lowry et al. 2019) and indirect (Kergunteuil et al. 2019) defences along elevational gradients is associated with concomitant variation in plant fitness (see also Lowry et al. 2019). At the same time, whereas number of studies have measured plant-herbivore trait differentiation with respect to multispecies interactions under a spatial context (nonadditive or diffuse selection; Thompson 2005), most of this work has not involved ecological gradients, at least not explicitly. Finally, studies testing for latitudinal or elevational clines in phenotypic selection by herbivores on plants are virtually absent except for one study measuring selective effects of herbivory on plant reproductive output (Sandring et al. 2007), and we are aware of no studies measuring latitudinal or elevational variation in herbivore selection on putative plant defensive traits. Importantly, all of such studies have involved herbaceous plants, whereas tree species have been largely neglected.

Although common garden and reciprocal transplant experiments represent a powerful tool for testing plant adaptive differentiation to biotic and abiotic factors along geographical clines (Hargreaves et al. 2019), they are logistically demanding and impose constraints on the number of replicates that could ideally be established along the gradient, as well as replication within each location (Kawecki and Ebert 2004). In the case of long-lived plants, they may be further limited due to the difficulty of assessing lifetime or long-term measurements of fitness. Similarly, while it is also desirable to measure plant performance or fitness over several seasons to provide a more robust assessment of local adaptation, long-term measurements are often not feasible. More broadly, by testing for differences between selected points along the gradient, this approach also imposes a discretization of continuous ecological variation found along clines which may limit an assessment of the full range of trait variation and its underlying (continuous) drivers. On the other hand, regression-based methods used to estimate phenotypic selection on target traits are easier to implement methodologically and logistically, and a large number of estimates for multiple populations can allow to analyse continuous variation along a studied gradient. However, temporal replication of selection measurements is also desirable to better characterize selective regimes (Schemske and Horvitz 1989;

Siepielski et al. 2009; Ehrlén 2014), and even in the few cases where this has been addressed, inference about long-term patterns is often limited. Furthermore, intrinsic ecological noise in some systems may be substantial such that patterns of temporal variation in phenotypic selection may not be informative about observed adaptive population differentiation.

In addition to transplant experiments and regression-based measurements of phenotypic selection, the use of genetic markers has proven highly useful in relating genetic population differentiation with estimates of phenotypic selection on target traits or fitness measurements in experimental studies along ecological gradients (e.g. Lowry et al. 2019; Hirano et al. 2017; Schemske 1984; Anderson and Geber 2010). More recently, high-throughput sequencing has allowed to identify genomic regions, groups of genes, or specific genes underlying plants traits (reviewed by Bazakos et al. 2017), and these data can be analysed with respect to variation in biotic or abiotic factors to elucidate the genetic basis of adaptive differentiation along ecological clines (e.g. Tiffin and Ross-Ibarra 2014; Hoban et al. 2016; Wang et al. 2018). In particular, genomic tools can be used to measure the genetic signature of natural selection on targeted genes associated with plant resistance to herbivory across multiple populations (of a single species) or across species within a given clade. These methods, however, are currently unexploited in gradient studies (see De Mita et al. 2013; Dalongeville et al. 2018) and could represent a powerful option for assessing micro- and macro-evolutionary patterns associated with variation in biotic and abiotic selective pressures along latitudinal and elevational clines.

Elevational and Latitudinal Gradients in Plant Defences Through a Genomic Lens

We depart from the general observation that few studies have explored patterns of clinal selection on plant defensive traits at the molecular level (Züst et al. 2012; Brachi et al. 2015). Based on this, we elaborate on methodological and analytical approaches in evolutionary genomics (at micro- and macro- evolutionary levels) that can be used to unveil clinal patterns of adaptive evolution in plant defences (and, in the same way, plant enemy counterdefences). These methods can be applied to any plant species, though there are several criteria of taxa selection (see ahead) that can be followed to maximize the power of these analyses.

Assessing Micro-evolutionary Patterns of Clinal Variation in Plant Defences

Research on landscape genomics has played a fundamental role in detecting loci under selection and identifying environmental variables acting as selective sources while simultaneously considering genome-wide demographic effects such as gene

flow, genetic drift, bottlenecks, and inbreeding (Schoville et al. 2012; Allendorf et al. 2010; Luikart et al. 2003; Stinchcombe and Hoekstra 2008). Broadly speaking, this approach involves in situ sampling of several individuals from multiple populations along a heterogeneous landscape (e.g. across contrasting habitats or along environmental clines), sometimes also involving ex situ sampling of source populations under controlled (e.g. greenhouse or common garden) conditions to minimize environmental effects (Fig. 18.2a, b) and the genotyping of all individuals at many independent loci (i.e. a genome scan). This scan may or may not include candidate genes underlying traits of interest (Fig. 18.2c). Following from this, the level of genetic

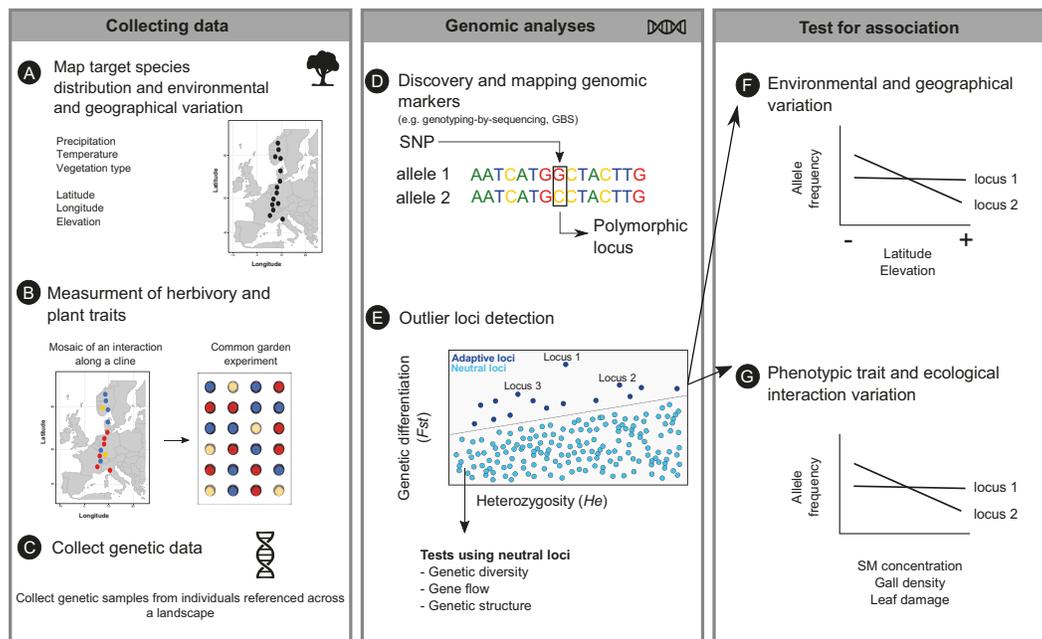


Fig. 18.2 Workflow depicting approach for testing latitudinal or elevational gradients in selection on target plant genes coding for putative defensive traits and their underlying correlates (i.e. herbivory and/or abiotic factors). **(a)** Collecting information about target species distribution along the gradient as well as geographical and environmental information. **(b)** In the field, sample individuals along the gradient to record phenotypic values for putative defensive traits (e.g. leaf toughness, trichome density, secondary metabolites concentration “SM”), measurements of antagonistic interaction strength (e.g. infection rate, amount of leaf damage). In parallel, collect seeds from sampled individuals in the field to conduct a common garden experiment to test for population differentiation in putative defensive traits as well as to conduct trait measurements to be used in testing for associations between allele frequencies, trait values, and environmental factors and herbivory (or pathogen infection). **(c)** Collect genetic samples. **(d)** Discover and map genomic markers using procedures such as genotyping-by-sequencing (GBS). **(e)** Use these data to perform an outlier loci test to detect candidate loci under selection. Non-outlier loci evolving under neutral evolution can be used in complementary tests. **(f)** A negative association between allele frequency of a locus previously detected under selection and latitude or elevation would be indicative of clinal variation in selection (i.e. as shown for locus 2). **(g)** An association between allele frequency for a given outlier locus and the phenotypic values (from field sampling or common garden experiment) of a putative defensive trait (e.g. SM) would provide evidence that a given locus codes for the plant trait measured (e.g. locus 2), whereas correlations between allele frequency and the amount of leaf damage or performance by herbivores or pathogens would suggest a role in resistance for the locus

differentiation across populations can be estimated (Fig. 18.2d; see Stinchcombe and Hoekstra 2008; Sork et al. 2013). With this approach, loci are assumed to evolve by natural selection if they are strongly differentiated among populations (outlier values of the coefficient of population differentiation, F_{st}) when compared with selectively neutral regions (Fig. 18.2e; see Allendorf et al. 2010; Luikart et al. 2003). Next, statistical associations between allelic frequencies of loci detected under selection (i.e. loci with outlier F_{st} values) and environmental variables can be used to unveil potential sources of selection (Fig. 18.2f, g). For more detailed technical considerations, see De Mita et al. (2013) and Dalongeville et al. (2018).

By applying the above procedure under a gradient-explicit framework, the frequency of alleles of outlier loci can be tested against herbivory (or plant pathogen infection) across populations as a preliminary assessment of their potential adaptive value in the context herbivore resistance, as well as with latitude or elevation to assess the magnitude and direction of clinal variation in allele frequencies (Fig. 18.2f, g). Likewise, multiple regression or structural equation modelling can also be used to assess correlations between allele frequencies and biotic factors (herbivory, pathogen infection), as well as abiotic (e.g. climatic) variables, and tease apart the relative influences of these environmental drivers (see 2.3 on the importance of considering abiotic factors). Further work with candidate loci significantly associated with latitude or elevation and with herbivory could include tests of their functional role in herbivore resistance by means of genome-wide associations with putative defensive traits, ideally under a common garden setting (e.g. de Villemereuil et al. 2016). In addition, gene mapping based on quantitative genetic approaches can be used to corroborate the genetic basis and function of such candidate genes by using linkage disequilibrium mapping and QTL mapping (Stinchcombe and Hoekstra 2008), as well as with gene knockout experiments (e.g. gene editing using CRISPR Bortesi and Fischer 2015).

This landscape genomics approach has been used for a number of tree species to discover candidate genes coding for traits associated with water-use efficiency, abiotic-related stress responses, as well as wood quality or density. Most of the traits looked at in these studies are linked to adaptation to abiotic factors (e.g. temperature, humidity) and to resource use and acquisition (De Kort et al. 2014; Eckert et al. 2010; Jaramillo-Correa et al. 2015; Manel et al. 2012). Similarly, a number of studies with herbaceous species have tested for associations between outlier loci and abiotic environmental variables in the context of adaptation to climatic change (Lee and Mitchell-Olds 2012; Bragg et al. 2015; Clark et al. 2007; Bergelson et al. 2001). Unfortunately, few of these studies have looked at genes and traits putatively associated with plant-enemy interactions (but see Brachi et al. 2015), despite the fact that these genes frequently exhibit high levels of polymorphisms across populations (Clark et al. 2007; Bergelson et al. 2001). Consequently, we know very little about the landscape genomics of plant-enemy interactions (Brachi et al. 2015), particularly under ecological gradients.

Employing landscape genomics research to uncover loci coding for plant traits presumed to be involved in herbivore (or pathogen) resistance in plants can provide a useful way forward to detect loci under selection, their role in herbivore resistance,

and identify biotic (and/or abiotic) agents of selection, including different plant enemy taxa or guilds. Accordingly, as the number of elevational and latitudinal studies utilizing these approaches accrues, including work involving multispecies comparisons (e.g. Manel et al. 2012), we will start to gain knowledge on candidate genes, underlying traits, and ultimately a better understanding of clinal micro-evolutionary patterns in plant defence.

Assessing Macro-evolutionary Patterns of Clinal Variation in Plant Defences

The preceding section addressed genetic and genomic approaches at the population level to detect ongoing micro-evolutionary patterns of selection. We next introduce comparative approaches to detect signatures of selection at the species level that can inform on macro-evolutionary clinal patterns of adaptive evolution in plant defences.

Just as clinal variation in herbivore pressure has likely selected for concomitant clines in plant defensive gene variation within species (see Sect. 4.1), we could also expect a gradient in the signature of selection across species with contrasting latitudinal distributions (Fig. 18.3). Under this context, the expectation would be that rates of adaptive evolution in genes associated with plant defence are higher for species distributed at lower latitudes and elevations, as a consequence of more intense herbivore or pathogen selection on the defensive traits they code for. This prediction could be tested by comparing the rates of adaptive evolution of target genes underlying plant defensive traits across a number of plant taxa and from this infer clinal variation in the signature of selection on such genes. One way of measuring gene adaptive rates is in terms of the ratio of non-synonymous (dN, i.e. those affecting protein structure and function) to synonymous (dS, i.e. those not affecting protein function and evolve neutrally) mutations in such genes (Yang and Bielawski 2000; Li et al. 1985). If herbivore and pathogen pressure strengthen with decreasing latitude and elevation, then beneficial mutations in defensive genes should be more frequently fixed by selection in species found at lower latitudes and elevations. Therefore, non-synonymous mutations that increase the defensive value of a particular gene (i.e. substitution resulted in a beneficial mutation) should have a higher probability of spreading through a plant population and therefore become fixed more often at lower latitudes and elevations, than synonymous mutations (Yang and Bielawski 2000). Accordingly, the signature of selection estimated as the ratio $\omega = dN/dS$ should be higher than 1 at lower latitudes (e.g. for tropical vs. temperate lineages), i.e. selection favours fixation of non-synonymous mutations (dN) at a rate above neutral expectations (dS), a pattern indicative of so-called positive selection. Conversely, $\omega < 1$ would be indicative of “negative” or “purifying” selection which acts against (i.e. purging) non-synonymous mutations more strongly relative to neutral mutations. Finally, when $\omega = 1$ (i.e. equal rates of dS and dN), this indicates lack of selection on phenotypic variation at the codon level

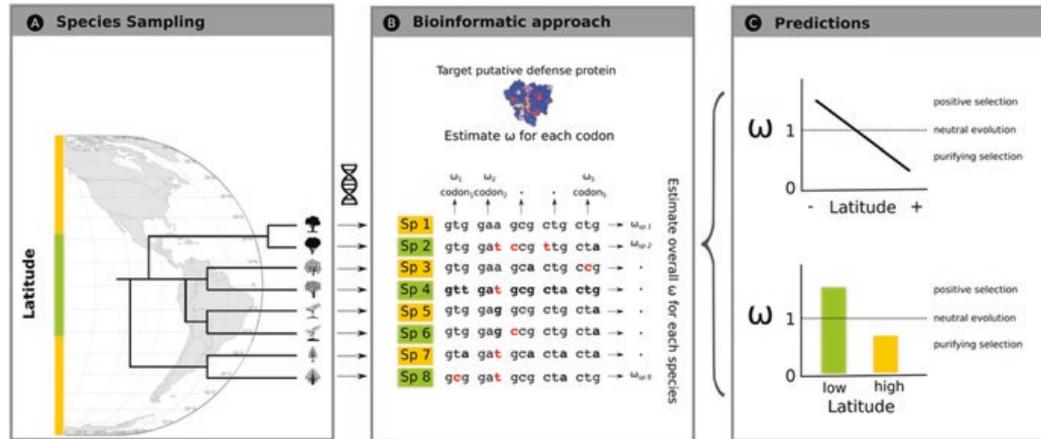


Fig. 18.3 (a) Sampling sister species with contrasting latitudinal or elevational distributions (minimizing species overlap as much as possible) while controlling for ecological and evolutionary factors (e.g. age, life form, effective population sizes, etc.). Species with tropical distributions are in green, whereas those with boreal and austral distributions are in yellow. (b) Sequencing and aligning orthologous target defensive gene (e.g. class I chitinase; protein illustration taken from Bishop et al. 2000; red dots within the protein denote detected sites under positive selection). Multiple alignment and phylogenetic tree are used by PAML to assess the signature of selection ($\omega = dN/dS$) at the codon level (i.e. sites within protein assuming equal evolutionary rates across species; horizontal axis of variation) and species level (ω is averaged across codons within the sequence for each species). Nucleotide bases in bold indicate mutations, and non-synonymous mutations are denoted in red, whereas synonymous mutations are in black. (c) Upper panel shows a negative association between ω averaged estimates for each species (i.e. vertical axis of variation in B), and latitude or elevation will indicate that species distributed at higher latitudes or elevations have lower rates of adaptive evolution of defence genes than those found at lower latitudes or elevations. More sophisticated PAML models (e.g. branch-site and clade models) can incorporate both axes of variation to test for contrasting patterns of positive selection at the site level among different groups of species (e.g. grouped into low or high latitude based on their distribution). (c) Lower plot depicts results from a more detailed analysis combining site- and species-level variation (branch-site and clade models in PAML) which allows to explicitly test whether the signature of positive selection is higher for species evolving at lower latitudes than those evolving at higher latitudes

implying that non-synonymous mutations evolve neutrally (Yang and Bielawski 2000; Li et al. 1985).

Genomic and statistical tools have been used to test for latitudinal gradients in evolutionary rates of neutral genetic markers in plants (Wright et al. 2003, 2006; Davies et al. 2004), but to our knowledge have not been used to test for macro-evolutionary patterns of clinal evolution for genes associated with anti-herbivore defences. To achieve this, we envision a procedure that would involve a phylogenetically controlled selection of plant taxa (e.g. congeneric species) with contrasting latitudinal or elevational ranges and with little overlap in their latitudinal or elevational distribution ranges (Fig. 18.3a; Wright et al. 2006; Gillman et al. 2009). The selection of candidate species should ideally also account when possible for other confounding factors such as life form (e.g. sample only tree species), mating system, and functional traits (e.g. shade tolerance, resource acquisition strategies).

Another important criterion would be to choose common species with large populations in order to control for effects of genetic drift caused by small effective population sizes (Wright et al. 2006). For each species, the same putative defensive ortholog gene (i.e. a gene that descends from a common ancestral form) must be sequenced to then perform a multiple alignment that is used, in combination with a phylogenetic tree of the studied taxa (Fig. 18.3a), to assess the signature of selection (ω) across species at the protein site level (i.e. codon) (Fig. 18.3b), as well as to compare the signature of selection among sites between previously determined groups of species (Yang and Bielawski 2000). Currently, the debate on methods to assess the molecular signature of selection is ongoing and leading to improvements of these statistical tools (Kosakovsky Pond and Frost 2005), and in some cases the best option has been to report results from simultaneously competing procedures (for a discussion on relevant methods, see Kosakovsky Pond and Frost 2005; Kosakovsky Pond et al. 2005). We next provide a closer look at one of these approaches based on Phylogenetic Analysis by Maximum Likelihood (PAML) (125), which is one of the oldest, most widely used, and best documented methods. It also has a relatively easy implementation (e.g. included in Biopython, and ETE tool) and is under constant update.

Specifically, PAML combines Markov chains and maximum likelihood to model the substitution process at the codon level and maximize the estimation of dN and dS and, consequently, ω (for details, see Yang and Bielawski 2000; Yang 2007). This approach can provide a detailed assessment of variation in ω among protein sites across species (Fig. 18.3b; free-ratio model (Nielsen and Yang 1998)), and also of variation in the signature of selection across sites within a protein to detect specific sites under positive selection and estimating the proportion of sites under positive selection (Fig. 18.3b). One way of testing whether defensive genes evolve faster at lower latitudes (or elevations) using this method would be to test for an association between the overall signature of selection estimated for each species ($\omega_{sp1} \dots \omega_{spn}$; using free-ratio models) against latitude or elevation (Fig. 18.3c, regression-type plot) (Yang 1998). It should be noted, however, that the signature of selection on protein sites under positive selection could be masked by strong purifying selection acting on most sites to maintain protein structure and function. This may lead to an underestimation of positive selection or to ambiguity in the interpretation of clinal patterns in the signature of selection, as values could result from weakening of purifying selection rather than due to positive selection (particularly when ω values do not exceed 1). Despite this caveat, evidence that ω increases (over and above 1) toward lower latitudes and elevations can be taken as good evidence of higher rates of evolution of putative defensive genes.

More advanced PAML models (branch-site and clade models) are capable of testing whether the pattern of ω at the site level within a protein is different between groups of species (Zhang et al. 2005; Weadick and Chang 2012). For example, previous studies have reported contrasting levels of positive selection on the visual pigment rhodopsin in cichlids species evolving in rivers vs. lakes (Schott et al. 2014) and on defensive protein class I chitinase between sexual and asexual *Oenothera* species (HerschGreen et al. 2012). We suggest that these types of models could be

used to test whether specific plant defence genes differ in their rates of evolution in response to latitude or elevation by coding species as low- or high-latitude (or elevation) groups. The basic prediction would be that the overall estimation of ω for a defensive protein shared by a group of species from lower latitudes or elevations will be higher ($\omega > 1$, indicating positive selection) than the ω estimated for the same protein for a group of species distributed at higher latitudes or elevations (Fig. 18.3c, lower plot). In this case, and in contrast to the former approach based on regression-type analyses which requires limited overlap in latitudinal distributions among species (see above), one criterion for species selection could be that they naturally fall into different groups (low vs. high latitude) and within each group species would have roughly similar distributions in order to increase the power of this type of categorical analysis.

Codon-based models such as PAML as well as others such as HyPhy (Kosakovsky Pond et al. 2005) have been key to study the signature of selection on defensive genes implicated at different stages of the plant's immune system response (HerschGreen et al. 2012; Tiffin and Moeller 2006; Mondragón-Palomino et al. 2002; Brunner et al. 2013). Here we suggest that the same tools can be used to test for latitudinal and elevational hypotheses, for which there are clear predictions but contradictory empirical evidence. Genomic and bioinformatics tools can provide a large number of datasets to test at genome-wide scale (Carmona et al. 2019). The potential to reveal macro-evolutionary patterns of latitudinal gradient on defence genes at the genomic level (i.e. hundreds of defence genes) lies in the use of customized scripts that automatize PAML analyses or by using packages designed to run such analyses (Maldonado et al. 2016; Webb et al. 2017).

Integrating Species Interactions and Genomics Research in Gradient Studies

Our revision highlights considerable variation in patterns (i.e. direction) of elevational and latitudinal gradients in temperate tree defences and herbivory. Notably, only a third of the studies reviewed found support for the prediction of increased tree defences towards lower latitudes and elevations, though considerably more (about two thirds) found support for increasing herbivory towards lower latitudes. Likewise, only a third of the studies found higher herbivory at lower elevations. Moreover, patterns that are opposite to classic predictions, i.e. increasing defences and/or herbivory towards higher latitudes and elevations, were equally common and in some cases more common than expected patterns. These patterns are similar to results from previous meta-analyses including all plant life forms (e.g. Moles et al. 2011) and highlight that the current paradigm of geographical gradients in plant-herbivore interactions needs to be revised and calls for investigating likely sources of inconsistencies.

It is important to note that conclusions from qualitative reviews (such as this chapter) and meta-analyses should be made with caution given substantial differences across studies in experimental design and methodology, not to mention a number of other particularities of each study and model system used, including substantial differences in the latitudinal or elevational ranges of the studied species. Accordingly, recent work and our current analysis points to the necessity of increasing the methodological consistency across studies (e.g. herbivory and trait measurements (Anstett et al. 2016)), improving the methods for plant trait quantification (e.g. analytical resolution of chemical analyses (Anstett et al. 2016)), as well as a more comprehensive assessment of plant defensive phenotypes (e.g. multiple defensive traits (Moreira et al. 2018a)). In addition, we also argue that an explicit consideration of abiotic correlates of elevational and latitudinal gradients is essential.

As research on plant-herbivore latitudinal and elevational gradients closes these gaps by converging on similar methodologies as well as accounting for sources of biotic and abiotic variation, the adoption of genomic tools will open an unprecedented opportunity to launch a new generation of studies. One key realization is the need to merge research on landscape genetics with ecological studies of plant-intraspecific clines in plant-herbivore interactions. Surprisingly, landscape genetic work has barely been applied to plant defences (but rather mostly to traits mediating abiotic tolerance (Sork et al. 2013)) and has usually not explicitly addressed elevational and latitudinal gradients. A huge opportunity therefore lies for unlocking the potential of these genomic tools towards unveiling the genetic basis of clinal evolution in plant defences. Specifically, we envision future work on focal plant species coupling complementary approaches where consistent phenotypic measurements are taken along gradients and in common gardens with source populations, followed by genomic analyses to discover relevant and genetic manipulations to confirm the ecological and adaptive role of targeted plant defensive traits. In doing so, there is a need to fine-tune the criteria for taxa selection in order to increase the power of these studies while expanding this research to other tree taxa (e.g. under a phylogenetically controlled framework) that could be good models in order to reach reliable generalizations.

Species-level analyses of molecular evolution hold a similarly large potential for assessing plant defence macro-evolutionary patterns along environmental clines. Applying these proteomic-based evolutionary analyses provides a powerful approach to studying the genetic and molecular basis of plant defence macro-evolutionary patterns and in doing so test classic predictions about the evolutionary consequences of biotic and abiotic forcing along latitudinal or elevational clines. This includes tests of plant defence co-evolutionary models (e.g. Endara et al. 2017) and theory on rates of gene evolution (e.g. Wright et al. 2003, 2006) in the context of latitudinal and elevational gradients. In doing so, we can address whether rates of clinal evolution are faster for defensive vs. nondefensive (e.g. genes associated with physiological responses to abiotic stress or baseline rates (Wright et al. 2003)) and uncover sources of variation in the rates of clinal evolution of different families of defensive genes. Finally, results from applying these tools and methods to elucidate latitudinal or elevational macro-evolutionary patterns in plant defence can also con-

tribute to develop new theory by uncovering patterns not apparent previously from studies based on measurements of plant traits and species interactions.

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