REVIEW AND SYNTHESES

Climate-driven diversity dynamics in plants and plant-feeding insects

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Abstract

The origin of species-rich insect–plant food webs has traditionally been explained by diversifying antagonistic coevolution between plant defences and herbivore counter-defences. However, recent studies combining paleoclimatic reconstructions with time-calibrated phylogenies suggest that variation in global climate determines the distribution, abundance and diversity of plant clades and, hence, indirectly influences the balance between speciation and extinction in associated herbivore groups. Extant insect communities tend to be richest on common plant species that have many close relatives. This could be explained either by climate-driven diffuse cospeciation between plants and insects, or by elevated speciation and reduced extinction in herbivore lineages associated with expanding host taxa (resources). Progress in paleovegetation reconstructions in combination with the rapidly increasing availability of fossil-calibrated phylogenies provide means to discern between these alternative hypotheses. In particular, the 'Diffuse cospeciation' scenario predicts closely matching main diversification periods in plants and in the insects that feed upon them, while the 'Resource abundance-dependent diversification' hypothesis predicts that both positive and negative responses of insect diversity are lagged in relation to host-plant availability. The dramatic Cenozoic changes in global climate provide multiple possibilities for studying the mechanisms by which climatic shifts may drive diversity dynamics in plants and insect herbivores.

Keywords

Climatic oscillations, coevolution, diversity dynamics, extinction, global flora, insect–plant interactions, lineages-through-time plot, niche conservatism, phylogeny, resource abundance.

INTRODUCTION

Terrestrial plants and the insects that feed upon them constitute one of the pivotal ecological and evolutionary interactions on the planet (Novotny *et al.* 2010). Both plants (Fiz-Palacios *et al.* 2011) and insects (Lewinsohn & Roslin 2008) are extremely diverse, and the immense number of species involved in complex trophic interactions has placed insect–plant networks in a central role in research on speciation and on the evolutionary assembly of trophic relationships (Futuyma & Agrawal 2009). A characteristic of insect–plant networks is specialisation with varying degrees, so that while most insect herbivores feed on single plant species or on groups of related plants, the diet of others may encompass numerous distantly related taxa (Novotny *et al.* 2010). Furthermore, while some insects clearly have been associated with their current host-plant taxa for tens of millions of years, phylogenetic studies have in most cases demonstrated that shifts among plant lineages are commonplace (Winkler & Mitter 2008). The role of such host shifts is still debated (Imada *et al.* 2011), but they could constitute an important driver of speciation in insect herbivores, and could therefore partly explain their present megadiversity (Winkler & Mitter 2008; Janz 2011).

The rise of molecular phylogenetics during the last 10 years, which finally enabled reliable comparisons of the diversification histories of plants and herbivores, led to a quick reassessment of old coevolutionary hypotheses on the assembly of insect–plant associations. The first victim was the 'Parallel cladogenesis' scenario, which postulated

that insect herbivores diversified simply by tracking speciation events in their host lineages; the hypothesis did not survive even the first demonstrations of highly disparate insect and plant phylogenies (Futuyma & McCafferty 1990). Broader analyses later also brought into question the classic 'Escape–and–radiate' hypothesis (Ehrlich & Raven 1964), which supposes that insect–plant communities are built by successive rounds of diversification; such alternating cycles could result if plants that evolve novel defence traits escape from herbivores and then undergo rapid speciation bursts, that are then slowed down when new insect groups colonise the new plant clade and diversify by shifting among the closely related young species. The escape–and–radiate hypothesis seems a poor explanation of the fact that species-rich insect phylogenies show repeated back-and-forth shifts among plant taxa (Winkler & Mitter 2008; Nyman *et al.* 2010), and that the most diverse herbivore communities are found on ecologically dominant and widespread plants rather than on rare ones (Lewinsohn *et al.* 2005).

A more realistic hypothesis seems to be the 'Resource archipelago scenario', which suggests that related plants – by being relatively similar in their physiological, morphological and ecological properties – form evolving islands and archipelagos in resource space, and phylogenetic niche conservatism in insects leads to host shifts or colonisations occurring preferentially – but not exclusively – among closely related plants (Brändle *et al.* 2008; Nyman 2010). The number of herbivore species on any given plant species or clade therefore depends on balances between *in situ* speciation and extinction, and

between colonisation from and desertion to other plants (Brändle *et al.* 2008; Nyman 2010). As both of these diversity balances probably are biased with respect to resource availability, the preferential accumulation of insects on common plants that have many relatives likely follows from a combination of herbivore niche conservatism and extreme variation in the abundance of distinct resources: Local abundances and range sizes of plant species can differ by multiple orders of magnitude (Brändle *et al.* 2008; Edwards *et al.* 2010), and global resource inequality is exacerbated by the fact that locally common plants often are also geographically widespread (Murphy *et al.* 2006).

However, the world is not static, and the fossil record documents dramatic taxonomic and structural shifts in the global vegetation through time, most likely driven by large-scale changes in the Earth's climatic patterns (Morley 2007; Fiz-Palacios *et al.* 2011; Graham 2011) (Fig. 1). In rapidly changing conditions, geographic range shifts generally outpace adaptation (Crisp *et al.* 2004; Donoghue 2008), and the marked phylogenetic niche conservatism exhibited by many plant groups (Crisp *et al.* 2009) means that climatic changes can lead to concerted spread or contraction of whole plant clades. As a consequence, the diversity and availability of given plant groups may change drastically within evolutionarily short time periods (Crisp *et al.* 2004; Edwards *et al.* 2010), which should have a direct effect on insect herbivores associated with particular–expanding or declining– plant taxa. Indeed, a number of recent studies have begun to uncover a possible role of past climatic and vegetational shifts in insect diversification, many postulating a positive bottom-up effect via cyclic geographic fragmentation and reunification of host-plant lineages (hereafter termed 'Diffuse cospeciation,' McLeish *et al.* 2007; Micó *et al.* 2009; Voje *et al.* 2009; Strutzenberger & Fiedler 2011) or via an increase in host availability (hereafter termed 'Resource abundance-dependent diversity dynamics,' McKenna & Farrell 2006; Peña & Wahlberg 2008; Winkler *et al.* 2009).

Incorporating an effect of past climatic variability into hypotheses on diversification in plants and insects has great potential for advancing our understanding of both the generation and loss of biodiversity in these ecologically central networks. The recent influx of studies on the topic has been brought about by a confluence of methodological advances and progress in related fields: First, improvements in DNA sequencing methods and computing power, combined with new relaxed molecular-clock methods (Battistuzzi *et al.* 2011) and multiple fossil calibration points mean that ever larger, more densely sampled and more robust dated phylogenies that contain hundreds to thousands of species can be constructed (Hunt *et al.* 2007; Fiz-Palacios *et al.* 2011). Second, statistical innovations for inferring temporal variation and trait-associated shifts in diversification rates from phylogenetic trees make it possible to, for example, identify and compare periods of increased diversification within and between trophic levels (Moore & Donoghue 2009; Silvestro *et al.* 2011). Third, advances in paleobotany (McElwain & Punyasena 2007; Currano *et al.* 2010) in combination with improved paleoclimatic reconstructions (Zachos *et al.* 2008) and paleovegetation simulations (Salzmann *et al.* 2008) make it possible to reconstruct past changes in resource availability and distribution.

Here, we review the current evidence for the hypotheses that changes in resource availability and distribution, driven by shifts in global climate, are reflected in speciation–extinction and colonisation– desertion balances of plant-feeding insect clades, and that the direction and magnitude of the effects depend on the fates of the insects' current host-plants. The best possibilities for studying how
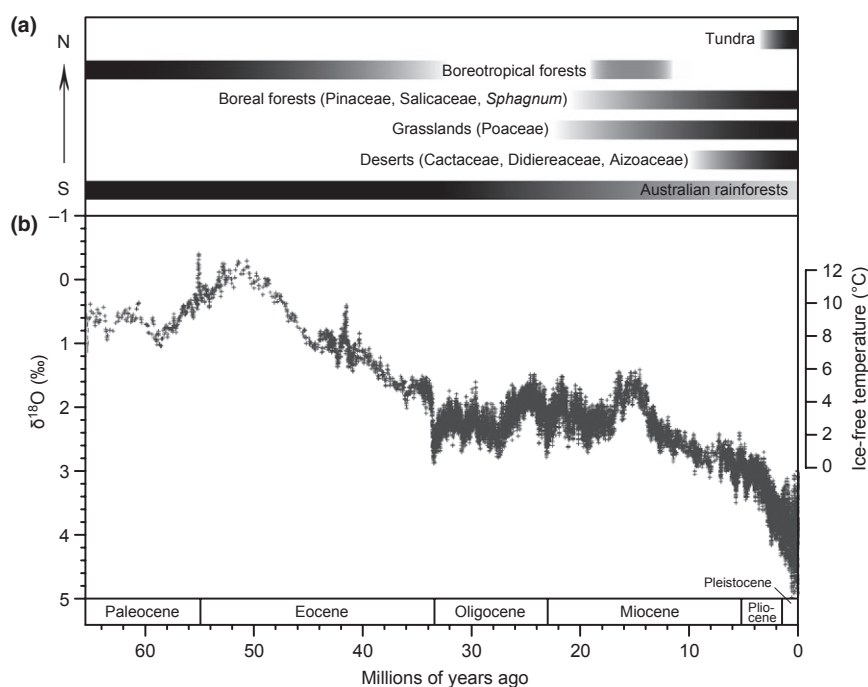
Figure 1 Major trends in global vegetation and climate during the Cenozoic. The rise and fall of several distinct biomes and vegetation zones (a), ordered roughly in a north-to-south direction, has closely followed changes in paleoclimate (b) estimated from relative proportions of different oxygen isotopes in samples of benthic foraminiferal shells (panel (b) modified, with permission, from Zachos *et al.* 2008). Examples of plant lineages that have experienced increases or declines in diversity and/or abundance are shown in parentheses after biome names in (a) (see main text for references). Note that the oxygen isotope proxy for global climate slightly overestimates the post-Eocene temperature drop due to formation of Antarctic and, later, Arctic ice sheets (Zachos *et al.* 2008).

climatic variation may influence diversity dynamics in plants and insect herbivores are provided by the dramatic changes that occurred in the global climate during the Cenozoic, which spans the *ca.* 65-million-year period from the end-Cretaceous mass extinction event to the present (Fig. 1). Below, we first outline the climatic history of the Cenozoic and review phylogenetic studies on how climatic shifts have influenced plant distributions and net diversification rates in different biomes across the globe. Thereafter, we detail the aforementioned processes ('Diffuse cospeciation' and 'Resource abundance-dependent diversity dynamics') that have been implicated as connectors of climate-driven changes in the geographic distribution, ecological dominance, and/or diversity of specific plant clades, and speciation/extinction balances in associated insect lineages. Finally, we describe conditions and methods that may allow us to discern between the alternative processes in a phylogenetic framework, and suggest further avenues of study in this young but rapidly advancing field of research.

SETTING THE STAGE: GLOBAL CLIMATE AND VEGETATION DURING THE CENOZOIC

Plants colonised land in the Ordovician *ca.* 450 Mya, and vegetation as complex as the modern one has existed since the beginning of the Carboniferous, *ca.* 350 Mya (Cleal & Thomas 2009). However, the taxonomic composition of the terrestrial flora has changed radically multiple times, meaning that many once-dominant plant taxa have either gone extinct, or been reduced to an ecological role that represents just a shadow of their past glory (McElwain & Punyasena 2007; Nagalingum *et al.* 2011). The middle Paleozoic flora was dominated by seedless vascular plant taxa such as lycophytes, sphenophytes and tree ferns, but spore-producing lineages increasingly began to give way to gymnosperm seed plants towards the Permian (Cleal & Thomas 2009). This trend continued after the end-Permian mass extinction event 251 Mya, leading to a proliferation of conifers and ferns during the early Mesozoic (McElwain & Punyasena 2007; Cleal & Thomas 2009). Many of the aforementioned shifts in the Paleozoic and early Mesozoic flora happened cyclically or in asynchrony in different parts of the world, and in many cases were linked to climatic variation resulting from volcanism, glaciations, orogenies and palaeocontinental restructuring (Cleal & Thomas 2009).

From the perspective of the Earth's present flora, the single most important event in plant evolution was the rise of flowering plants during the latter half of the Mesozoic Era (Berendse & Scheffer 2009; Graham 2011). While the earliest angiosperm fossils date back to the early Cretaceous *ca.* 140 Mya, new molecular studies consistently place the origin of flowering plants at over 200 Mya (Smith *et al.* 2010), indicating that the 'angiosperm explosion' had a long fuse. After the apparently sluggish start, flowering plants began to diversify and to displace the mid-Mesozoic flora, which was a diverse mixture of gymnosperms and seedless plants that descended from survivors of the end-Permian and end-Triassic mass extinctions (Berendse & Scheffer 2009; Fiz-Palacios *et al.* 2011). Potential causes underlying the success of angiosperms have been extensively debated, but could include fortuitous preadaptation to the increasing environmental instability and rising average temperatures of the Cretaceous (Heimhofer *et al.* 2005), or intrinsic factors such as insect pollination, polyploidisation, or key innovations conferring competitive superiority (Crepet & Niklas 2009). Whatever the cause, after the K–Pg mass extinction angiosperm diversity rebounded faster than that of non-

angiosperm taxa, and flowering plants today make up nearly 90% of the plant species (Crepet & Niklas 2009), as well as the vast majority of the plant biomass (Berendse & Scheffer 2009).

Despite their collective success, angiosperms do not act as a coherent unit, and species numbers, diversification rates, geographic distributions, and overall ecological importance of particular flowering plant clades have risen and fallen differentially throughout the Cenozoic, evidently as a result of dramatic climatic changes during the last *ca.* 65 million years (Zachos *et al.* 2008). The warm and humid 'greenhouse' climate of the Paleocene and early Eocene was followed by a sustained albeit cyclic decline in global average temperatures (Fig. 1), and after the Oligocene, the climatic deterioration was aggravated by aridification in many parts of the world (Graham 2011), as well as by intermittent polar glaciations (Zachos *et al.* 2008).

Cenozoic climatic deterioration first led to range contractions in the extensive tropical and boreotropical forests that covered most of the globe (Morley 2007; Donoghue 2008), apparently triggering an extinction wave in warm-adapted plant lineages in high latitudes (Erkens *et al.* 2009; Antonelli & Sanmartín 2011) and later in Australia (Crisp *et al.* 2004). Northern boreotropical forests were slowly replaced by temperate mixed mesophytic forests (Donoghue & Smith 2004), which were, in turn, pushed southward by boreal forests (Taggart & Cross 2009) and fragmented by aridification-induced grassland expansions (Edwards *et al.* 2010; Strömberg 2011). As expected, phylogeny-based lineages-through-time (LTT) analyses have uncovered increased post-Eocene speciation in several plant taxa adapted to cool and dry environments. For example, temperate lineages in the Brassicaceae diversified rapidly during the early Oligocene, while speciation apparently was slower in the family's tropical sister clades (Couvreur *et al.* 2010). Similarly, Shaw *et al.* (2010) found that diversification of *Sphagnum* mosses, which nowadays form extensive peatlands across the Holarctic, kicked off in the Miocene when cooling intensified. In addition to the grass family Poaceae (Bouchenak-Khelladi *et al.* 2010), aridification-linked radiations have occurred in Mesoamerican *Bursera* trees (De-Nova *et al.* 2012), in multiple southern African plant lineages (Verboom *et al.* 2009), as well as in cacti, ice plants and agaves, three distantly related succulent plant groups that inhabit similar niches in deserts in different parts of the globe (Arakaki *et al.* 2011). Increased fire frequency due to longer dry seasons and ecological dominance of flammable C4 grasses may also have driven some diversifications that resulted in the widespread development of savanna systems and its rich associated biota (Simon *et al.* 2009). In some cases, dwindling temperatures combined with rapid orogenic activity to establish extensive cool high-altitude habitats (Graham 2011), with associated radiations, such as the genus *Lupinus* in the Andes (Hughes & Eastwood 2006).

PROCESSES CREATING LINKS BETWEEN CLIMATIC SHIFTS AND DIVERSIFICATION IN PLANTS AND INSECTS

The total dependence of insect herbivores on the plants that they feed on means that their geographical distributions and population sizes will tend to track changes in the range and abundance of their hosts (Smith *et al.* 2011). Climatic shifts therefore may have influenced the balance between speciation and extinction in insect herbivores via an effect on the global flora in two main ways: an increase in insect net diversification could follow from cyclic climate-induced range fragmentation in their host species or clades ('Diffuse cospeciation';
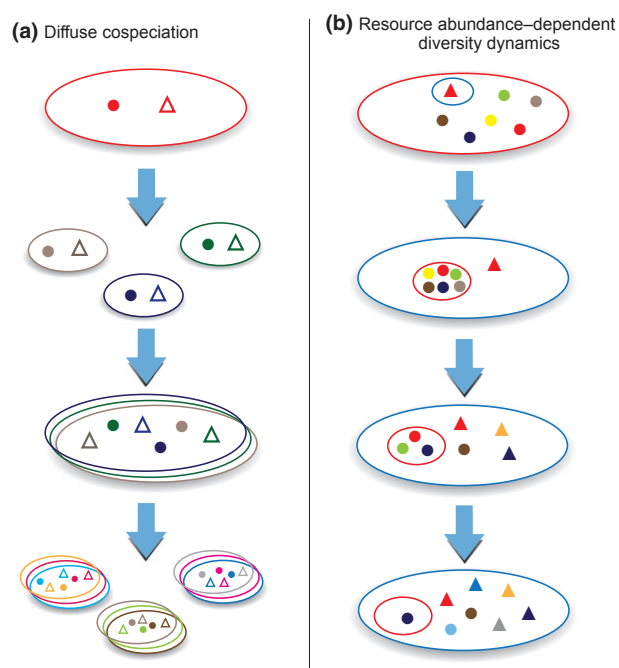
Figure 2 Conceptual illustration of the main processes by which climatic shifts can influence diversity dynamics in insect herbivores via effects on plants. In diffuse cospeciation (a), climatic oscillations induce fragmentation–fusion cycles in the geographic range of a plant clade. During fragmentation phases, associated herbivores (denoted by circles and triangles) speciate in parallel with their hosts; however, during rejoining phases herbivores colonize the newly formed relatives of their host plants. In resource abundance-dependent diversity dynamics (b), a climatic shift favors the *Blue* plant lineage at the expense of the *Red* lineage. Consequently, the insect community on *Red* starts declining, while the community on *Blue* becomes enriched due to increased speciation and reduced extinction probabilities, and colonisation by previously *Red*-adapted herbivores.

Fig. 2a), or from changes in overall host (or host clade) abundance and distribution ('Resource abundance-dependent diversity dynamics'; Fig. 2b).

Diffuse cospeciation

Although many speciation modes operate in plants, a considerable proportion of lineage splits probably occur allopatrically, i.e., as a result of geographic isolation of initially conspecific populations that over time diverge enough to become separate species (Moore & Donoghue 2007; Valente *et al.* 2010). Changes in climate can rapidly shift and fragment the geographic distributions of plant species (Rodríguez-Sánchez & Arroyo 2008; Alsos *et al.* 2009). Therefore, especially climatic fluctuations enforcing alternating range contractions and fusions have the potential to spur speciation in affected plant lineages (Fig. 2a). Diversification driven by climatic cyclicity has been found in many plant taxa that radiated during the Pleistocene (Valente *et al.* 2010; Levsen *et al.* 2012). However, more extended oscillations during the Oligocene and Miocene also appear to have played a role, for example, in the radiations of African rainforest trees (Couvreur *et al.* 2008) and the genus *Cyclamen* in the Mediterranean region (Yesson *et al.* 2009).

Assuming that speciation in plants is often allopatric, it can be argued that a large number of species in a given plant clade is indicative of an evolutionary history involving multiple cases of

population isolation following range fragmentations and/or dispersal events (Hughes & Eastwood 2006; Valente *et al.* 2010). Importantly, a complex geographic history of a plant lineage means that the phylogeography of associated herbivores may have been complicated as well (Micó *et al.* 2009; Procheş *et al.* 2009; Strutzenberger & Fiedler 2011), which could theoretically lead to plant–herbivore cospeciation. As mentioned above, extended parallel cladogenesis between plants and insects, which would require strict host specificity and an absence of host shifts and host-range expansions, has been refuted by molecular-phylogenetic studies (Winkler & Mitter 2008). Nevertheless, more 'diffuse' forms of cospeciation (Fig. 2a) could still operate. 'Diffuseness' to the process is brought about if herbivore species that have cospeciated with their host during a range fragmentation phase colonise the host's recently diverged relatives if given the opportunity during fusion phases. Such dietary expansions following range fusions seem reasonable considering that many insects specialise on distinct plant clades rather than on single plant species (Brändle *et al.* 2008; Novotny *et al.* 2010). An especially intriguing possibility is that, because fragmentation of the geographic distribution of a plant species or lineage can potentially simultaneously isolate populations of numerous insect associates (Aoki *et al.* 2011), cyclic speciation in plants could be amplified in the insects (Fig. 2a).

Because postspeciational host shifts and extinctions can erode signs of cospeciation events over time (Nyman *et al.* 2010; Janz 2011), the best systems for studying climate-driven parallel speciation involve recently-diverged insect groups that are narrowly specialised in their host use. A particularly revealing example in this respect comes from a recent study by McLeish *et al.* (2007), who showed that diversification of Australian gall thrips in the genus *Kladothrips* mirrors the fragmentation history of their *Acacia* hosts: lineages inducing galls on *Acacia* section *Plurinerves* underwent a rapid speciation episode coinciding with the aridification of Australia during the last five million years, while diversification remained largely constant in lineages specializing on species in *Acacia* section *Juliflorae*. According to the authors, the underlying reason is that cyclic aridification led to alternating fragmentation/fusion phases in species of section *Plurinerves*, which inhabit mainly semi-arid habitats, while the ranges of the more arid-adapted species of section *Juliflorae* mainly remained unfragmented in the dry central plain of Australia.

An interesting parallel to this Australian pattern was found in Africa by Voje *et al.* (2009), who inferred that in African flightless bush crickets in the subfamily Phaneropterinae, forest- and savanna-adapted lineages differ in their main periods of diversification: The gradual and cyclic Plio-Pleistocene aridification of Africa first led to a burst of speciation in savannah-adapted bush crickets as a result of increasing habitat availability or complexity, while a second diversification wave in forest-associated lineages followed later, when forests became fragmented and restricted to mountainous areas.

Resource abundance-dependent diversity dynamics

An important unanswered question in macroevolutionary biology is whether the number of species that can coexist on a given resource is limited by ecological interactions, or whether communities remain unsaturated even as species diversity rises (Kisel *et al.* 2011). Ecological saturation has been suggested for a number of systems in which species-accumulation curves appear to level off after an initial period of rapid diversification (e.g., Linder 2008; Elias *et al.* 2009).

The frequent observation that extant insect communities are richest on common plants (Lewinsohn *et al.* 2005) indicates that resource-dependent diversity limits exist in insect–plant networks, but it also means that major changes in host availability should have a direct influence on the dynamics of speciation and extinction in insect taxa. Specifically, an increase in the abundance and geographic range of a host-plant lineage should enhance net diversification by facilitating speciation and decreasing extinction probabilities while, conversely, reductions in the global abundance of a plant group should lead to declining associate diversity (Fig. 2b). Especially the prevalence of extinction could be influenced simply by changes in insect population size (given that large populations are less likely to go extinct than small ones; Kisel *et al.* 2011), and average population sizes should correlate positively with host abundance (Smith *et al.* 2011). Climate-associated population expansions indeed have been found in two population-genetic studies that applied Bayesian skyline plots to reconstruct the late-Pleistocene demographic histories of two North American *Parnassius* butterflies (Schoville & Roderick 2009) and two *Castanopsis*-associated weevil species in Japan (Aoki *et al.* 2011). In both cases, the authors attributed the population increases to climatic shifts that favored the host lineages of the herbivores.

Grasses (family Poaceae) and grass-associated insects present one of the best systems for testing the possibility of accelerated insect diversification following a climate-driven increase in a plant group. Unlike most of their modern descendants, the first grasses probably inhabited the shady forest understory during the late Mesozoic and early Cenozoic (Bouchenak-Khelladi *et al.* 2010), while rapid diversification and major expansions of grass-dominated habitats did not occur until the Mio- or Pliocene, when especially the Poales rose to dominance in seasonally dry systems (Edwards *et al.* 2010). At present, grasses comprise over 10,000 species, and grasslands cover over 40% of the Earth's land area, typically in semi-arid regions on several continents (Strömberg 2011).

The late-Cenozoic expansion of grasslands had a major impact on the evolutionary trajectories of mammalian herbivores (Blois & Hadly 2009; Stadler 2011), and several recent studies have addressed how the spread of grass-dominated ecosystems influenced diversification patterns in plant-feeding insects. Peña & Wahlberg (2008) postulated that the diversification of butterflies in the tribe Satyrini, of which most rely on grasses for nutrition at the larval stage, was spurred by the main radiation of grasslands in the beginning of the Neogene (see also Price *et al.* 2011). Grassland expansion has also been implicated as a factor initiating or accelerating the radiations of leafcutter ants (Mueller & Rabeling 2008), planthoppers (Urban *et al.* 2010), leafhoppers (Zahniser & Dietrich 2010), and savanna-inhabiting lineages of African bush crickets (Voje *et al.* 2009).

However, the Cenozoic climatic shifts also led to increases in other plant taxa, with similar consequences for their insect associates. Winkler *et al.* (2009) showed that in the species-rich leaf-mining agromyzid fly genus *Phytomyza*, shifts from host plants in Ranunculaceae to hosts belonging to asterid herb families elevated net diversification rates in multiple independent cases. The authors concluded that the diversification of asterid-associated *Phytomyza* lineages was driven by the increase in abundance, geographic distribution, and diversity of their host plants after the middle Miocene, when the spreading of open grass- and herb-dominated environments in the North Temperate Zone favored herbaceous asterids. Accelerated diversification in response to climate-induced resource increases also has been suggested for South American

Cephaloleia leaf beetles on *Heliconia* (McKenna & Farrell 2006) during the Oligocene, and for Holarctic nematine sawflies on *Salix* (Nyman *et al.* 2010) during the late Cenozoic.

DISCERNING BETWEEN THE ALTERNATIVES

The alternative processes by which climatic shifts could affect insect herbivore diversification are not mutually exclusive and could in many cases act in concert or in sequence (McKenna & Farrell 2006; Peña & Wahlberg 2008). Furthermore, as the aforementioned case of African bush crickets (Voje *et al.* 2009) shows, diversification bursts in closely related, but differentially specialised, lineages can be not only asynchronous, but also driven by different mechanisms. Last, changes in geographic distributions, extinctions and shifts in diet breadth or host-plant use by insect lineages most likely lead to cospeciation events being observable only for a relatively short time (cf. McLeish *et al.* 2007), meaning that even true diffuse cospeciation processes may be difficult to identify reliably by comparing phylogenies of species-rich plant and insect groups, which necessarily include increasingly old divergences towards the root.

Despite these caveats, it seems that in some situations it will be possible to distinguish between the alternatives based on phylogenetic information, because different processes should lead to differing levels of congruence between the species numbers and diversification times of interacting plant and insect groups. In general, diffuse cospeciation is likely to lead to a closer correspondence of species numbers in interacting clades than if insect diversification is driven by plant clade abundance alone. More importantly, long-term diffuse cospeciation should result in roughly parallel lineages-through-time curves and a clear overlap in the main diversification periods across trophic levels (Fig. 2a), whereas insect diversity responses could lag considerably behind changes in resource abundance, especially when environmental changes are fast (Fig. 2b). The underlying explanation for this is that speciation and extinction on, as well as colonisation and desertion of, specific plant clades are likely to be stochastic and relatively slow processes. Positive (speciation and colonisation credits) and negative (extinction and desertion debts) diversity lags would therefore constitute macroevolutionary analogues of 'immigration credit' and 'extinction debt,' concepts that are used to describe delayed responses in community diversity following shifts in metapopulation structure and habitat availability on ecological time scales (Jackson & Sax 2009).

Comparisons of chronograms and lineages-through-time plots provide an efficient way to test for congruence in temporal trajectories of diversification in interacting plant and insect lineages. Extensive overlaps in divergence times – suggestive of diffuse cospeciation – have been found, for example, between *Conicobruchus* seed beetles and their hosts in the leguminous tribe Indigofereae (Kergoat *et al.* 2011), between pierine butterflies and their Brassicales hosts (Wheat *et al.* 2007), as well as between geometrid *Eois* moths and South American *Piper* plants (Strutzenberger & Fiedler 2011).

However, most studies have found that insect clades are millions of years younger than the plant clades on which they feed (Gómez-Zurita *et al.* 2007), suggesting that diffuse cospeciation is restricted to special cases involving specialist insects that have colonised the host clade prior to the plants' main radiations (e.g., McLeish *et al.* 2007; Kergoat *et al.* 2011), while delayed diversity responses predominate. Along the same lines, a few studies have detected colonisation lags, i.e., that plant clades tend to be colonised only after they have become abundant and widespread (McKenna *et al.* 2009; Winkler *et al.* 2009; Ohshima *et al.*

2010). An interesting analog to this has also been found on a larger, biome-level scale: Hawkins & DeVries (2009; Hawkins 2010) proposed that delayed colonisation and diversification underlie the depauperate lepidopteran faunas of extra-tropical regions, i.e., that originally (and predominantly) warm-adapted lepidopteran lineages have not yet had enough time to diversify in colder areas of the globe; instead, extra-tropical lepidopteran taxa are found in scattered locations on the overall lepidopteran phylogeny, and these groups are characterised by shallow divergence times (see also Condamine *et al.* 2012).

FUTURE DIRECTIONS

The recent surge of studies on links between climatic shifts and diversity dynamics in plants and insects has uncovered multiple cases in which diversification and/or extinction can be attributed to climatically induced range fragmentation, or to changes in the amount of available resources. Nevertheless, the field is still relatively young and, consequently, many questions remain unanswered.

One of the main questions concerns the mechanism by which new species arise. Diffuse cospeciation events are by definition allopatric, but the speciation mode is not so clear in situations in which diversification is driven by a change in the amount of resources. In these cases, the question is whether an apparently climate-associated radiation of a given plant lineage was caused by ecological speciation following minor niche shifts, or whether the speciation burst simply resulted from increased opportunities for allopatric speciation following geographic range expansion (Moore & Donoghue 2007; Linder 2008; Kisel *et al.* 2011)? The corresponding question arises whenever an increase in the spread and diversity of a plant clade appears to have triggered a delayed radiation in insect associates, because the underlying speciation process can be ecological, i.e., driven by host shifts across the species of the plant lineage (Wheat *et al.* 2007; Condamine *et al.* 2012) or non-ecological, following increased possibilities for geographical isolation (Nyman *et al.* 2010; Imada *et al.* 2011; see also Janz 2011). The relative frequency of these speciation modes can be studied by analyzing recent speciation events on densely sampled time-calibrated insect phylogenies that include data on host use and geographic ranges (McKenna & Farrell 2006; Winkler & Mitter 2008; Nyman *et al.* 2010). Additional insights could be gained by targeting insect taxa that occur on related plant clades that exhibit contrasting patterns of species numbers and overall abundance, while taking into account the possibility of marked long-term abundance changes (Rodríguez-Sánchez & Arroyo 2008; Taggart & Cross 2009).

Closer integration of fossils, paleoclimatic reconstructions, species distribution models and genetic data is also desirable in the future, because in isolation each of these research fields can tell only part of the whole story. Potent illustrations of the benefits to be gained from combining these various approaches are provided in the highly interdisciplinary studies by Alsos *et al.* (2009) and Levsen *et al.* (2012) on the past, present and future of the arctic-alpine dwarf willow *Salix herbacea* L. and two North American *Populus* species, respectively. The first step toward extending such analyses to multitrophic communities have been taken by Aoki *et al.* in a set of papers on the Pleistocene history of Japanese broad-leaved forests and several weevil species associated with the dominant trees (summarised in Aoki *et al.* 2011). In these studies, the effects of climatic shifts were modeled via the plants, but species distribution models can also be applied directly to insects: Vila *et al.* (2011) used phylogeny-based reconstructions of ancestral thermal tolerances and host-plant associations of *Polyommatus* butterflies to demonstrate that the Bering land bridge (and later Bering Strait) acted as a climatic filter regulating eastward dispersal of *Polyommatus* species from Asia to the New World: The earliest transcontinental dispersals (*ca.* 10–2.5 Mya) occurred in warm-loving lineages that fed on fabaceous hosts, while the latest migrants (<1.1 Mya) were cold-adapted groups associated with boreal or subarctic plant taxa such as *Vaccinium* (Ericaceae) and *Primula* (Primulaceae). Given that climatically mediated dispersal limitation or facilitation can have a major influence on the prospects for diversification in differentially specialised insects (see also Hines 2008; Ohshima *et al.* 2010), these approaches deserve wider application.

Because of the novelty of the field, phylogenetic studies on climatic effects on diversification in insects and plants have thus far focused on restricted sets of interacting taxa. Fortunately, the immense diversity of both plants and insects provides nearly unlimited possibilities for synthesizing information from multiple groups in order to gain more general insights into these questions (*cf.* Verboom *et al.* 2009; Arakaki *et al.* 2011). The fact that the insect community feeding on any given plant group is typically composed of multiple unrelated taxa that have colonised the plant lineage at different times (Gómez-Zurita *et al.* 2007; Nyman 2010) provides a crucial component of replication, which is needed to test specific hypotheses concerning the timing and mechanisms of diversification. A particularly relevant methodological advance in this area was recently published by Silvestro *et al.* (2011), as their Bayesian approach allows for using a meta-analytical framework for testing hypotheses invoking spatial and temporal trends in speciation and extinction rates. Such meta-analyses could, for example, be used to combine the aforementioned case studies of grassland-associated insect taxa into a single analysis. Importantly, only a fraction of grassland-associated insect groups have hitherto been subjected to thorough phylogenetic analyses; potential species-rich targets for additional cross-taxon studies include hesperiine butterflies (Warren *et al.* 2009), elachistine moths (Kaila 2011), several groups of grass-feeding beetles (Micó *et al.* 2009), and – naturally – grasshoppers (Chintauan-Marquier *et al.* 2011). Studies on grassland insects could fruitfully be augmented by analyses of herbivores associated with succulent plant groups that underwent aridification-driven radiations contemporaneously with the Poaceae (Arakaki *et al.* 2011). Corresponding multi-taxon studies testing for a connection between host abundance and insect net diversification are possible also, for example, for herbivores associated with Pinaceae (Brändle *et al.* 2008) and the genus *Salix* (Nyman *et al.* 2010), both of which presumably benefited from the late-Cenozoic expansion of the Boreal Forest biome (Donoghue 2008; Taggart & Cross 2009; Crisp & Cook 2011). A particularly interesting backdrop for synthetic insect analyses would be provided by the rediversification of cycads, which occurred concurrently in many parts of the world following expansions of seasonal tropical and subtropical areas from the late Miocene onwards (Nagalingum *et al.* 2011).

As is often the case in evolutionary research, studies have tended to focus on cases in which speciation rates seem to have increased, but it should be remembered that the link between insect diversification and host plant abundance also could operate in the opposite direction, such that herbivore extinction would be accelerated on plant lineages experiencing declines as a result of climatic changes. A recent, albeit

biotically induced, analog can be seen in North America, where the accidentally introduced fungus *Cryphonectria parasitica* (Murrill) Barr triggered continent-wide population collapse of the previously-dominant American chestnut [*Castanea dentata* (Marsh.) Borkh.], ultimately driving at least five specialised insect species to extinction within a hundred years (Wagner & Van Driesche 2010). Studying past extinctions based on phylogenetic information alone is difficult (Quental & Marshall 2010; Morlon *et al.* 2011), but periods of mass extinction can result in characteristic 'broom-and-handle' shaped phylogenetic trees and accompanying plateaus in lineages-through-time plots (Crisp & Cook 2009). The best model system for studying co-extinctions is perhaps presented by the collapse of Australian rainforests (Fig. 1): Crisp *et al.* (2004) found evidence for increased extinction rates after the mid-Cenozoic in Australian plant lineages adapted to aseasonal-wet conditions, and Crisp & Cook (2009) later demonstrated that lineages-through-time plots of Australian and African legumes exhibit the telltale signs of coincident mass extinctions at the end of Eocene. Corresponding studies on associated insects are lacking, but considering that the current extent of the Australian aseasonal-wet biome represents a mere fraction of that in the early Cenozoic (Morley 2007), finding signs of an ancient extinction wave in herbivores would be anticipated. Tests of increased extinction following resource declines could most likely also be done using herbivore lineages associated with plant clades that suffered during the post-Eocene demise of high-latitude boreotropical forests (e.g., Donoghue 2008; Erkens *et al.* 2009; Antonelli & Sanmartín 2011; Condamine *et al.* 2012).

CONCLUSIONS

The ability to construct robust and densely sampled time-calibrated phylogenetic trees for ever larger clades based on ever larger amounts of DNA sequence data has revolutionised the field of evolutionary insect–plant research: while even just a few years ago researchers were limited to performing topological comparisons of restricted plant and insect groups, species-rich fossil-calibrated chronograms now facilitate increasingly sophisticated analyses of temporal correspondence in the diversification times of interacting taxa. When combined with fossil data, paleoclimatic reconstructions, and simulated changes in geographical ranges, a whole new suite of possibilities for inferring evolutionary forces emerges.

One of the main consequences of dated phylogenies has been increased interest in the effects of abiotic changes on the balance between speciation and extinction, or the so-called Court Jester model of diversity dynamics (Benton 2009; Ezard *et al.* 2011; Stadler 2011). Clear evidence for climatically driven radiations (Couvreur *et al.* 2010; Arakaki *et al.* 2011), extinctions (Crisp & Cook 2009), and even diversity rebounds (Nagalingum *et al.* 2011) indeed have been found in numerous plant clades.

In entomological research, the new 'abiotic' approach contrasts with a long tradition of focusing on radiations resulting from ecological opportunity provided by colonisation of novel resources (Ehrlich & Raven 1964; Janz 2011). Nevertheless, evidence is now accumulating that ecological opportunity may arise purely fortuitously, from climatic shifts that favor the insects' host plants (Peña & Wahlberg 2008; Winkler *et al.* 2009). It should be noted that although climatic effects on insects are indirect and may in many cases lag millions of years behind plant clade resources, the underlying mechanisms involved are essentially identical to those of plants: Positive or negative shifts in net

diversification can ensue from a combination of phylogenetic conservatism in niche or habitat use (*cf.* Donoghue 2008; Crisp *et al.* 2009), and changes in the geographic distribution and/or overall abundance of suitable resources (*cf.* Linder 2008; Rodríguez-Sánchez & Arroyo 2008).

Range and abundance shifts caused by changes in climate are naturally unlikely to be the only drivers of diversity dynamics; one of the main tasks in the future is therefore to uncover the possible ways in which climatic variation interacts with other extrinsic abiotic forces such as plate tectonics and orogenies (Moore & Donoghue 2007; Elias *et al.* 2009; Micó *et al.* 2009), with intrinsic innovations of novel adaptive traits, as well as with biotic coevolutionary drivers that are likely to arise in species-rich insect–plant networks (Futuyma & Agrawal 2009; Novotny *et al.* 2010; Condamine *et al.* 2012). The key to achieving these goals – in addition to a tighter integration of geology, paleontology, ecological niche modeling, and genetics – is to combine hitherto separate phylogenetic studies into larger synthetic analyses that test specific hypotheses in a meta-analytical framework. Although the development of statistical tools for such analyses has only just begun (Silvestro *et al.* 2011), we predict that this research field will explode in the near future.

The taxonomic and ecological diversity of plants and insect herbivores makes them ideal groups for broad multi-taxon analyses, but the research questions and analytical settings can and should be expanded to other plant-dependent insects such as pollinators (Hines 2008; Smith *et al.* 2011) and decomposers (Baselga *et al.* 2011). Even more intriguing is the possibility that climatically driven diversification of insect herbivores may trickle up to higher levels in the food web (McLeish *et al.* 2010; Nicholls *et al.* 2010).

In conclusion, long-term shifts in the global climate evidently have influenced the balance between diversification and extinction in many plant and insect groups, but gaining a coherent view of how and when climatic variation drives diversity dynamics in complex ecological networks will require combining information from multiple disparate research disciplines and species-rich taxa. While the scale of the task is daunting, there is clearly a pressing need for such knowledge in a world in which human-induced global warming is reverting late-Cenozoic biome expansions by enforcing changes in the distributions of whole ecosystems (Taggart & Cross 2009), and in which habitat destruction and the spread of anthropogenic biomes at the expense of natural communities (Ellis *et al.* 2010) threatens the very existence of innumerable plant and insect species (Fonseca 2009).

AUTHORSHIP

The project was initiated by TN and NW. TN led the writing, but all authors contributed to writing and to the development of ideas herein.

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