Distantly related neighbours of host trees can prevent arthorpods from matching tree characteristics : a story of arthropod phenotypes and leaf damage on oak trees

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Distantly related neighbours of host trees can prevent arthropods from matching tree characteristics: a story of arthropod phenotypes and leaf damage on oak trees

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Dedicated to my cousin Kamalesh Sarkar

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Table of contents

French summary..... 01

Introduction..... 09

Amazing diversity of arthropods in forests..... 11
To be successful forest arthropods need to match to the characteristics of their host trees 11
It can be difficult for arthropods to match their host-tree characteristics 14
Objectives: revealing the patterns of matching of forest arthropods to host trees with increasing phylogenetic isolation of trees 17
Hypothesis: mechanisms such as reduced movements and information may reduce matching on phylogenetically isolated trees 18
Model system: arthropods on oaks 19
References 20

Chapter 1 Ectophagous herbivores do not profit from rich resources on phylogenetically isolated trees 31

Abstract 33
Introduction 34
Methods 38
Results 43
Discussion 49
Conclusions 55
Acknowledgements 55
Funding 55
References 56
Supplementary materials 62

Chapter 2 Where herbivores find their phenology match: Accessible trees bursting buds rapidly and predictably accumulate matching herbivore species 77

Abstract 79
Introduction 80
Methods 84
Results 88
Discussion 95

Conclusions 99
Acknowledgements 99
Funding 100
References 100
Supplementary materials 103

Chapter 3 Biogeographic rules of arthropod body-size across trees in a forest canopy..... 115

Abstract 117
Introduction 118
Methods 120
Results 123
Discussion 127
Conclusions 130
Acknowledgements 130
Funding 130
References 131
Supplementary materials 134

Discussion..... 151

The arthropod perspective 153
The tree perspective 156
Phylogenetic isolation: patterns and processes 160
Conclusion 161
References 162

French summary

Des voisins phylogénétiquement éloignés peuvent empêcher les arthropodes de concorder aux caractéristiques d'un arbre hôte : une histoire de phénotypes d'arthropodes et de dommages foliaires sur des chênes.

Les forêts jouent un rôle essentiel dans la biodiversité mondiale car elles abritent un large éventail d'espèces, notamment une grande diversité d'arthropodes herbivores. Ce haut niveau de diversité des arthropodes est dû à la diversité des microhabitats forestiers qui permettent la ségrégation et la coexistence des niches. La recherche en écologie des arthropodes forestiers se concentre sur l'étude de la spécialisation plante-hôte et de la ségrégation de niche. Les arthropodes herbivores sont séparés par les espèces d'arbres et les espèces d'arthropodes spécialisées peuvent être trouvées sur des arbres individuels dans une forêt mixte. Dans cette thèse, j'examine spécifiquement comment l'isolement et les autres caractéristiques des arbres matures affectent à la fois la diversité des arthropodes et l'évolution des traits chez les arthropodes et les arbres.

Pour réussir, les arthropodes, tels que les insectes et les araignées, doivent s'adapter aux caractéristiques de leurs arbres hôtes. Les arbres possèdent une série de caractéristiques uniques, telles que la forme et la taille des feuilles, la qualité nutritionnelle et le microclimat, qui peuvent varier d'une espèce à l'autre et même entre individus. Ces caractéristiques peuvent sélectionner et trier respectivement les génotypes et les espèces d'arthropodes correspondants. Pour maximiser leur bénéfice nutritionnel, les arthropodes doivent faire correspondre leur morphologie, leur physiologie et leur comportement aux caractéristiques de leurs arbres hôtes. Pour profiter des opportunités d'alimentation, les arthropodes doivent être synchronisés avec l'arbre hôte, le moment du débourrement et le développement des feuilles étant des facteurs clés. Le développement et le taux de croissance des arthropodes sont influencés par la température, les environnements plus chauds provoquant un développement plus rapide et une taille corporelle plus petite à maturité, tandis que les environnements plus frais peuvent ralentir leur développement. Par conséquent, les arthropodes doivent faire correspondre leur taille corporelle au microclimat de leur arbre hôte pour optimiser leurs possibilités et compléter leur développement. Ceci donne lieu à des schémas de taille corporelle similaires aux règles biogéographiques. En fin de compte, la variété des caractéristiques des arbres peut trier les espèces d'arthropodes correspondantes en communautés et promouvoir la diversité des arthropodes.

Les arthropodes sont confrontés à des défis dans l'adaptation des caractéristiques de leur arbre hôte en raison de divers facteurs tels que la concurrence, la pression ennemie, l'isolement et les changements dans l'association des arbres. Une concurrence et une pression ennemie élevées sur les arbres à haute qualité de ressources peuvent entraîner une diminution de la prise de nourriture, forçant les

arthropodes à se déplacer vers des arbres sous-optimaux où la concurrence et la pression ennemie sont plus faibles, ce qui provoque une diminution de l'adéquation entre les caractéristiques de l'arbre hôte et l'abondance des herbivores et des dommages aux feuilles. Un isolement spatial plus important des arbres hôtes pourrait forcer les arthropodes à s'installer dans des arbres sous-optimaux, car les arthropodes ont une capacité limitée de dispersion et de détection des indices olfactifs pour trouver les arbres dans l'espace. L'isolement peut agir sur les arthropodes forestiers à l'échelle des parcelles forestières et des arbres individuels dans une forêt continue composée de plusieurs espèces d'arbres. Les arthropodes forestiers peuvent avoir du mal à se déplacer entre des parcelles forestières fragmentées qui sont séparées dans l'espace par d'autres formes de terrain, par exemple des terres agricoles, qui sont habitables pour la plupart des arthropodes forestiers. Les arthropodes forestiers peuvent également avoir du mal à se déplacer entre les arbres lorsque ces derniers sont associés dans l'espace à des voisins phylogénétiquement éloignés. Une telle résistance associative des arbres peut isoler des herbivores spécialisés sur des arbres individuels. Ce type d'isolement est appelé isolement phylogénétique et il a été démontré qu'il était désavantageux pour les arthropodes à bien des égards. Cependant, nous ne savons pas si l'isolement phylogénétique rend difficile l'adaptation des arthropodes aux caractéristiques de leur arbre hôte.

Dans le cadre de cette thèse, je me concentre sur l'étude des effets de l'isolement phylogénétique sur l'appariement des caractéristiques des arbres hôtes par les arthropodes forestiers associés. J'émets l'hypothèse que l'isolement phylogénétique des arbres hôtes réduit l'appariement des caractéristiques des arbres par les arthropodes par une réduction de l'information disponible et des mouvements entre les arbres. Les trois catégories de caractéristiques de l'arbre hôte examinées dans cette étude sont la taille et la qualité des feuilles, la phénologie du débourrement et de l'avancement des feuilles, et la température.

J'ai étudié les arthropodes sur les chênes de la forêt de Rennes dans l'Ouest de la France, qui a un climat océanique tempéré. Les chênes étudiés appartiennent à deux espèces étroitement liées, *Quercus petraea* et *Q. robur*, et les arthropodes étudiés appartiennent à trois ordres : Lepidoptera (chenilles de papillons de nuit), Araneae (araignées de la canopée) et Heteroptera (espèces suceuses de feuilles et prédatrices). La forêt est divisée en 202 parcelles, où les chênes des parcelles dominées par les angiospermes sont entourés principalement d'arbres étroitement apparentés comme les châtaigniers, les hêtres et d'autres chênes, tandis que les chênes des parcelles dominées par les gymnospermes sont entourés principalement d'arbres lointainement apparentés comme le pin sylvestre et l'épicéa. Cela crée un gradient continu d'isolement phylogénétique des chênes dans la forêt, offrant une excellente occasion de tester l'effet de l'isolement phylogénétique sur l'appariement des caractéristiques de l'arbre hôte par les arthropodes.

J'ai découvert qu'il est difficile pour les arthropodes forestiers de correspondre aux caractéristiques des arbres hôtes isolés phylogénétiquement. Lorsque les arbres hôtes sont isolés phylogénétiquement, (i) l'herbivorie n'augmente plus proportionnellement à la taille des feuilles, (ii) la correspondance phénologique diminue, en particulier sur les arbres à éclatement rapide, et (iii) les relations température/taille changent.

(i) Chez les ectophages, l'utilisation proportionnelle de la taille des feuilles était réduite sur les arbres les plus isolés phylogénétiquement, et ce schéma était déterminé par l'herbivorie par individu en une année et l'abondance par feuille une autre année. Pour les galles et les mineuses des feuilles, aucun effet cohérent de l'isolement phylogénétique sur l'utilisation proportionnelle des ressources n'a été trouvé. Pour les parasitoïdes des ectophages, l'isolement phylogénétique a réduit l'utilisation proportionnelle des chenilles au cours de l'une des années d'étude.

(ii) Les herbivores correspondent à la date de débourrement des arbres sur le terrain (chenilles plus petites sur les arbres dont le débourrement est plus tardif), ce qui a également été confirmé dans le jardin commun (chrysalide plus tardive des chenilles des arbres dont l'avancement des feuilles est plus lent). Cette correspondance a disparu lorsque l'identité des espèces d'herbivores a été prise en compte. La taille des chenilles correspondait mieux à la date de débourrement sur les arbres à débourrement rapide, en particulier sur les arbres qui sont peu isolés ou dont la date de débourrement relative varie peu d'une année à l'autre. Il est important de noter que le taux d'herbivorie augmente avec le niveau de correspondance phénologique des herbivores.

(iii) La taille du corps des trois taxons (Lépidoptères, Aranéacées et Hétéroptères) est liée à la température de l'arbre hôte, et l'intensité, voire le signe, de cette relation varie selon les taxons et les années. Dans certains cas, l'isolement phylogénétique des arbres hôtes renforce le déclin de la taille du corps avec la température.

Ces résultats éclairent l'histoire de vie, l'évolution et la diversité des arthropodes. Tout d'abord, on pense généralement que le cycle biologique des arthropodes est déterminé par des facteurs tels que la qualité de la nourriture, les interactions biotiques et le microclimat. Pour les herbivores se nourrissant d'arbres à feuilles caduques, la phénologie de l'arbre hôte joue également un rôle important en sélectionnant certains génotypes. Je montre pour la première fois que la phénologie du débourrement sélectionne les espèces d'arthropodes au sein des espèces d'arbres, affectant ainsi la composition de la communauté sur les arbres individuels. En plus de la correspondance au moment du débourrement, j'ai constaté que les arbres hôtes avec des feuilles à développement rapide trient en faveur des espèces d'arthropodes à développement rapide. Par conséquent, le cycle de vie des arthropodes peut être

déterminé à la fois par la vitesse de débourrement et le développement des feuilles. Deuxièmement, les arthropodes pourraient évoluer vers une stratégie de couverture dans le cas d'une forte fluctuation de la période relative de débourrement des arbres hôtes d'une année sur l'autre. En cas de forte fluctuation, les herbivores sont incapables de s'adapter au moment du débourrement et, au lieu de cela, ils peuvent évoluer pour répartir le risque d'une mauvaise adaptation à la phénologie de l'arbre hôte. Cela implique d'avoir une gamme de dates d'éclosion dans une seule couvée pour augmenter la probabilité d'éclosion pendant le débourrement. Les études futures devraient examiner la variation de la date d'éclosion des œufs au sein des lots d'œufs pour mieux comprendre ce phénomène. Troisièmement, les arthropodes suivent les règles biogéographiques de la taille du corps même dans une forêt. J'ai constaté que les arbres hôtes avec des microclimats plus chauds peuvent trier pour les plus petites espèces d'herbivores et les plus grandes espèces de prédateurs. Les effets étaient renforcés sur les arbres phylogénétiquement isolés. Cela suggère que les arbres individuels dans une forêt peuvent fonctionner comme micro-archipels pour les arthropodes, où les arbres varient à la fois dans la température et le degré d'isolement. Quatrièmement, la diversité des arthropodes au sein d'une forêt peut être améliorée par le tri des arthropodes à travers une mosaïque de taille de feuille, de phénologie de développement des feuilles, de température et d'isolement phylogénétique des arbres hôtes. La ségrégation de niche est un mécanisme crucial qui permet à de nombreuses espèces de coexister dans un écosystème. J'ai découvert que les arbres forestiers trient les espèces d'arthropodes en fonction de divers facteurs, notamment les caractéristiques des feuilles, la phénologie du développement des feuilles, la température et l'isolement phylogénétique. Les résultats fournissent des preuves de multiples dimensions de niche qui jouent un rôle crucial dans le maintien de la diversité des arthropodes dans les forêts. Globalement, cette thèse améliore nos connaissances sur la biologie des arthropodes forestiers.

Ces résultats éclairent également l'évolution des arbres hôtes. Tout d'abord, les populations d'arbres dans lesquelles les individus sont souvent isolés phylogénétiquement peuvent évoluer pour avoir des feuilles plus grandes et un débourrement plus rapide. Ces caractéristiques peuvent améliorer la croissance de l'arbre, mais aussi attirer les herbivores. Cependant, l'attraction semble être entravée par l'isolement phylogénétique des arbres hôtes. Deuxièmement, les populations d'arbres dans lesquelles les individus sont souvent non-isolés phylogénétiquement peuvent évoluer pour dépendre de plus en plus des défenses constitutives. La théorie de la défense optimale prédit que les défenses constitutives seront favorisées dans les environnements où la pression des herbivores est élevée et prévisible. Pour les arbres non isolés phylogénétiquement, la pression des herbivores tend à être prévisible et à augmenter avec la taille des feuilles ou la vitesse de débourrement, ce qui rend ces arbres plus susceptibles de dépendre de défenses constitutives. Troisièmement, l'isolement phylogénétique des arbres semble conférer une résistance associative. L'association d'un arbre hôte avec des espèces d'arbres

phylogénétiquement éloignées peut réduire l'appariement des caractéristiques de l'arbre par les herbivores spécialistes, ce qui se traduit par une réduction de l'herbivorie. Quatrièmement, les arbres peuvent fluctuer le moment de leur débourrement d'une année à l'autre pour se défendre contre les herbivores. Cette fluctuation dans le timing relatif peut empêcher les herbivores de s'adapter et de profiter de la concentration de feuilles fraîches produite par un débourrement rapide. Dans l'ensemble, cette thèse améliore nos connaissances sur l'évolution des arbres hôtes.

Les modèles observés parmi les arbres phylogénétiquement isolés peuvent être expliqués par des processus déterministes. L'isolement phylogénétique des arbres est similaire à l'isolement biogéographique classique des espèces sur les îles. Tous deux entraînent une réduction de la richesse des espèces, des ressources inutilisées et la libération d'ennemis. Sur les îles, l'isolement biogéographique classique est expliqué par l'immigration et l'extinction stochastiques, tandis que des études antérieures sur l'isolement phylogénétique des arbres ont également expliqué les modèles par des processus stochastiques. Cependant, les résultats de cette thèse montrent que la correspondance réduite entre les herbivores et les traits des arbres sur les arbres plus isolés phylogénétiquement peut également être expliquée par des processus déterministes, les traits des espèces d'arthropodes étant importants dans ces processus. Dans l'ensemble, cette thèse améliore nos connaissances sur les modèles et les processus de l'isolement phylogénétique des arbres hôtes.

Dans l'ensemble, cette thèse a montré que l'isolement phylogénétique affecte les interactions entre les arthropodes et les arbres dans les forêts. Cet isolement empêche les arthropodes de choisir efficacement les arbres ayant des ressources abondantes, une phénologie et un microclimat adaptés, ce qui entraîne une réduction de l'herbivorie. L'isolement phylogénétique peut également affecter l'évolution des caractéristiques des populations d'arbres, permettant l'évolution de feuilles plus grandes, d'un débourrement plus rapide et d'une canopée plus fraîche. Ces arbres peuvent également bénéficier de défenses induites en réponse à une pression herbivore faible et imprévisible, tandis que ceux qui ont des voisins proches peuvent bénéficier davantage de défenses constitutives en raison d'une pression herbivore prévisible et élevée. De plus, la fluctuation du débourrement peut aider les arbres à éviter un excès d'herbivorie en rendant difficile l'adaptation des communautés d'herbivores. En conclusion, cette thèse souligne l'importance de considérer de multiples dimensions de niche telles que la taille des feuilles, la vitesse du débourrement, la prévisibilité du débourrement, et la température de la couronne, dans la compréhension des interactions entre les arthropodes forestiers et les arbres, et leur impact sur la diversité des arthropodes et l'évolution des traits tant chez les arthropodes que chez les arbres.

Introduction

Introduction

Amazing diversity of arthropods in forests

Forest ecosystems are important for global ecology and diversity as the trees represent a large portion of the biomass and forests are home to a large portion of the world's biodiversity. Especially herbivorous arthropods are species rich and these are in turn hosts to a myriad of parasitoids and parasites and predated on by many predators, including arthropods (National Research Council 1969; Lewinsohn et al. 2005; Smith et al. 2008; Basset et al. 2012; Staab and Schuldt 2020). This diversity is structured through species turnover (β-diversity) at global and local scale resulting from dispersal limitation and habitat filtering. Thus, insect communities differ between biogeographical regions and among forest types. But even within a single hectare of forest and among individual trees at the same site, there is considerable species turnover (Erwin et al. 2005). Importantly, many arthropods are coexisting on individual trees. This high degree of arthropod diversity in forests is related to the high diversity of microhabitats in forest that offer opportunities for niche segregation which promotes coexistence (Basset et al. 2012; Wehner et al. 2016; Swart et al. 2020; Habel et al. 2021). An important focus in forest arthropod research is niche segregation through host-plant specialization, specialization on plants parts, and feeding modes (Lewinsohn et al. 2005). As a result of host-plant specialization, each tree species is isolated for herbivorous arthropod species (Southwood and Kennedy 1983). It follows that individual trees of a particular tree species can be isolated to individuals of specialized arthropods species in a mixed forest (Vialatte et al. 2010). The arthropods also potentially affect tree diversification as trees may escape some herbivores by changing their defence against herbivorous arthropods (Ehrlich and Raven 1964). The arthropods further potentially contribute to the maintenance of tree diversity (Janzen 1970; Connell 1971). In particular the Janzen-Connell hypothesis posits that regeneration is difficult near conspecific trees because herbivorous arthropods from the conspecific tree are likely to attack the nearby seedlings (Basset et al. 2019). In my thesis, I focus on arthropods on mature trees, asking questions on how the isolation of individual trees interacts with other characteristics of trees (leaf size and quality, leaf developmental phenology, and microclimate) to ultimately affect arthropod diversity and trait evolution in arthropods and trees.

To be successful forest arthropods need to match to the characteristics of their host trees.

Trees show wide variation in characteristics, both among and within species. Tree species vary among others in morphology, physiology, phenology, and also microclimate. It is obvious that tree species vary in leaf shape and size (Sack and Frole 2006; Nicotra et al. 2011; Bhatia et al. 2021). Furthermore, the nutritional quality

of leaves differs among species as a result of difference in physiological process such as nitrogen assimilation and synthesis of defence chemicals (Lowman and Box 1983; Sariyildiz and Anderson 2005; Hättenschwiler et al. 2008; Asner et al. 2009; Abdala-Roberts et al. 2018). Species of deciduous trees also differ in the timing of budburst (when they get leaves in spring) and in the timing of leaf senescence (when leaves discolour and fall in autumn). For example, hornbeams usually burst buds earlier than oaks (Wesołowski and Rowiński 2006). Moreover, tree species differ in crown shape, attainable size, and capacity of water transportation, and these traits affect the microclimate in the crown (Gupta et al. 2018b). Usually it is colder within the crown of tree species that reflect more sun light or transpire more water (Lin and Lin 2010; Gupta et al. 2018a). These characteristics can also vary among individuals within a tree species, for example leaf morphology such as size, shape and toughness vary among individuals within a tree species (Pihain et al. 2019). This phenotypic variation among individuals within a population of tree results from the interplay between genetic and environmental variation. For example, the nutritional quality of leaves differs among individuals of a tree species as a result of differences in primary processes of growth, development and senescence i.e. intrinsic heterogeneity, and in response to biotic and abiotic stress, i.e. extrinsic heterogeneity (LeRoy et al. 2007; Osnas et al. 2018). Within-species variation in the timing of budburst is also well documented (Crawley and Akhteruzzaman 1988; Van Dongen et al. 1998; Visser and Holleman 2001; Wesołowski and Rowiński 2006; Cole and Sheldon 2017). This variation is known to be both due to genetic variation (Baliuckas and Pliura 2003) and environmental variation such as temperature and sun exposure (Marchand et al. 2020; Malyshev et al. 2022). The microclimate of tree crowns can vary between tree individuals as they vary in size and in the rate of transpiration. Larger trees tend to be less shaded by larger neighbours and to catch more wind that prevents crowns from heating up. Transpiration of water cools leaves as the water evaporates. Transpiration rates are higher when stomata are open and this thus also benefits photosynthesis, but it is risky because it can lead to water stress. Trees can also affect the natural enemy pressure on their herbivores by providing more or less shelter from natural enemies, by forcing them to feed for a longer time and thus expose them more to natural enemies, or by emitting herbivore induced volatiles that attract natural enemies such as parasitoids, predacious arthropods, and birds (Amo et al. 2013; Dicke 2015; Aartsma et al. 2017). Hence, there are many tree characteristics that can sort for various arthropod species matching these characteristics, and this may ultimately promote the diversity of arthropods.

Arthropods need to have adaptations to profit from variation in leaf characteristics. In general, leaves that have a higher nitrogen content, lower fibre content, and a lower concentration and diversity of defensive chemicals are more nutritious for arthropods (Mattson 1980; Coley 1983; Nascimento et al. 2017). Therefore, trees often are defended more against arthropods when they have reduced nitrogen content, and increased fibre content or defensive chemicals (Schoonhoven et al. 2005; Farha-Rehman et al. 2010). Arthropods on trees with lower leaf nitrogen content can perform

compensatory feeding to approach an optimal nitrogen intake, but this comes with the physiological costs of over-ingestion of other matter (Raubenheimer and Simpson 1993). It is difficult to chew or mine leaves with a higher fibre content, and to digest leaves with higher concentrations of defensive chemicals such as tannins and other phenolic compounds (Klocke and Chan 1982; Berenbaum 1983). Arthropods on leaves with higher fibre content should have harder mandible enabling them to chew or mine tough leaves (Chapman 1995; Kang et al. 1999; Hörnschemeyer et al. 2013). Arthropods also employ a variety of counter strategies to deal with chemical defences (Karban and Agrawal 2002). For example, arthropods that feed on trees with leaves with high tannin contents can maintain a more alkaline gut pH (high PH) which reduces the effectiveness of tannins in interfering with digestion (Martin et al. 1985; Barbehenn and Peter Constabel 2011). The indirect defences of trees can be mitigated by herbivores building shelters, anti-predator traits such as crypsis and aposematism (Singer et al. 2014), and even manipulating leaves to make them refrain from emitting herbivore induced volatiles (Takai et al. 2018). Therefore, in order to profit from the nutritional quality of the trees, the arthropods need to match their morphological, physiological and behavioural phenotypes with the characteristics of their host trees. Hence, the nutritional characteristics of the host trees can select for matching arthropod genotypes into population and sort for matching arthropod species into communities at the level of individual trees.

Arthropods need to have adaptations to profit from variation in tree phenology. Arthropods need to be able to profit from the window of opportunity that the phenology of the trees provide. To feed on trees, arthropods need to be synchronised with their host trees so that they are in the feeding stage at the time that the resources of the host trees are most profitable. For example, arthropods that feed on freshly-emerged leaves, must be in their feeding stage (such as caterpillar stage of Lepidoptera) around the time that their host trees burst buds (Feeny 1970; Forkner et al. 2004). If they develop earlier than the budburst, they will have nothing to feed on. If they develop too late, the leaves will have become too tough to chew and too chemically defended to digest (Hunter and Lechowicz 1992; Wesołowski and Rowiński 2006). The leaf development also selects arthropods to complete their feeding stage before the leaves cease to be profitable. Failing to do so might result in incomplete development or in smaller body size, both reducing arthropod fitness. In order to complete development in time, arthropods should develop rapidly on trees that develop their leaves rapidly. As arthropod are typically near their physiologically maximum growth rate, this means that rapid leaf development selects for smaller body size within species and sort for smaller body size among species. Altogether, in order to feed on fresh leaves and complete development, arthropods need to match the timing of budburst and the speed of leaf development of their host trees. Hence, the timing of budburst and the speed of leaf development of the host trees can select for matching arthropod genotypes into populations and sort for matching arthropod species into communities.

Arthropods need to have adaptations to profit from variation in the microclimate of the trees. The development of arthropods (transition through developmental stages) speeds up with an increase in temperature (Ju et al. 2011; Bjørge et al. 2018; Zhang et al. 2021). Hence, the development of arthropods can be faster on warmer trees than that on colder trees. While the growth of arthropods (rate of body mass gain) also speeds up with temperature, this effect is smaller than the effect on development, leading to smaller body size at maturity (Forster et al. 2011; Verberk et al. 2021). Larger species of arthropods require longer development, and may thus suffer more from faster development on warmer trees. Their growth may not be sufficient, and that can have negative fitness consequences such as reduced fecundity due to reduced adult body size. Furthermore, smaller-bodied species of arthropods usually develop rapidly, and may suffer from slower development on colder trees. They may not be able to complete their development, resulting in premature death. Even a little difference in average temperature over a time period can be crucial as it can result in a big difference in terms of degree days that they experience during their development (Chen et al. 2015; Pincebourde & Casas 2019). Therefore, arthropods should match their body size with the microclimate of their host trees i.e. larger species of arthropods would perform better on cooler trees, and smaller species on warmer trees. Hence, the microclimatic conditions of the host trees can select for matching arthropod genotypes into population and sort for matching arthropod species into communities. This could result in arthropod body size patterns similar to biogeographic rule such as Bergmann's, rule (smaller body size in warmer climates).

It can be difficult for arthropods to match their host-tree characteristics.

Competition and enemy pressure may make it difficult for arthropods to match the host-tree characteristics. As stated above, matching with host trees allows the arthropods to profit from the characteristics of the tree. However, as more herbivores gather at those more profitable trees, the profitability will be reduced by increased competition and natural enemy pressure (Gurevitch et al. 2000; Kaplan et al. 2014). Therefore, high rates of competition and enemy pressure on trees with high resource quality may not allow arthropods to gain much from moving to trees with profitable traits. For example, under high levels of competition, even arthropods with matching mandible or gut pH may not be able to ingest a sufficient amount of food to complete their development. Natural enemies often show functional responses, concentrating where prey density is highest (Schenk and Bacher 2002; Fernández-arhex and Corley 2003). As herbivores concentrate on trees with higher leaf quality, natural enemies will also concentrate on these trees, leading to higher predation and parasitation rates on these trees. Since this high enemy pressure increases the chance of being eaten before completing development, the enemy pressure reduces the overall advantage of feeding on such trees. In that case, the herbivorous arthropods may have a higher chance to complete their development on trees with suboptimal characteristics where

competition and enemy pressure are less intense. This can ultimately can result in reduced matching of host tree chrematistics with herbivore abundance and leaf damage.

Isolation may also make it difficult for arthropods to match with the host-tree characteristics. Arthropods need to be able to find the trees in space in order to match to the characteristics of their host trees. When the host trees are dispersed in space, the arthropods need higher dispersal capacity to find the trees. For active dispersers, higher dispersal capacity is associated with larger body size with stronger flight muscles and more stored energy for flight; in contrast, for passive dispersers, higher dispersal capacity requires a smaller body size that helps them float further on the wind (Jung and Croft 2001; Jenkins et al. 2007; Vialatte et al. 2010). Hence, arthropod species with limited dispersal capacity might often fail to find host trees to which they match better, especially when the host trees are dispersed in space. Furthermore, many arthropods find their host trees using olfactory and visual cues (Campbell and Borden 2006; Wenninger et al. 2009; L.Yv et al. 2015). When host trees are shorter than their neighbours or their odours is masked by other odours in the environment, they will be less apparent to herbivores. The arthropods then need well-developed sensory mechanisms to process such olfactory and visual cues to find matching host trees that are less apparent. Hence, arthropods with weak sensory mechanisms may fail to find a host tree, especially when the host trees are not apparent. Therefore, arthropods need matching dispersal and sensory phenotypes to find their host trees.

Isolation can act on forest arthropods at the scale of forest fragments. Forest arthropods may find it difficult to move between fragmented forest patches that are spatially separated by other land forms, for example agricultural land, which is inhabitable for most of the forest arthropods (Harris 1984; Didham et al. 1996, 1998; Bélanger and Grenier 2002; Liu et al. 2019). Reduction in arthropod movement by such spatial isolation may not allow arthropods to find patches where they match well the characteristics of the trees. In such a scenario, arthropods may also not leave trees with suboptimal characteristics given the uncertainty in finding a better matching tree. Such dispersal limitation and risk averse behaviour of arthropods may reduce matching host tree characteristics in fragmented forests. Indeed, in fragmented forests, reduced folivory does not appear to result from reduced leaf palatability; but to result from the changes in folivore assembly caused by the fragmentation (Silva and Simonetti 2009). Overall, forest arthropod separated by spatial distance of inhabitable other land forms finds it difficult to match the host-tree characteristics.

Isolation can act on forest arthropods at the scale of individual trees within continuous forest consisting of multiple tree species. The likelihood of arthropods finding a particular tree may depend on the trees it is associated with. In this regard, there are two opposite lines of argument, namely ‘associational resistance’ (Atsatt and O’dowd 1976) and ‘associational susceptibility’ (Brown and Ewel 1987). ‘Associational resistance’ means that trees gain resistance to arthropod attack when they spatially

associate themselves with other tree species. In contrast, the 'associational susceptibility' means that trees risk susceptibility of arthropod attack when they spatially associate themselves with other tree species (Brown and Ewel 1987; Jactel et al. 2021). There are data to support both patterns. It is not clear why certain associations confer resistance to trees from damage caused by arthropods (associational resistance), while certain associations confer susceptibility (associational susceptibility). It can be that certain associations make it difficult for arthropods to find the trees, while other association make it easier. Perhaps in some cases the isolation effect of natural enemies is stronger than that of herbivores, so that enemy-release reverses the effect of isolation on herbivores. It is also possible that in some cases associated trees have other effects on focal trees (e.g. through competition or allelopathy) that make them more susceptible to arthropod attack. If reduced insect movements are responsible for associational resistance, especially angiosperm-gymnosperm associations might be advantageous for the trees (Jactel and Brockerhoff 2007).

More generally, it might be difficult for the arthropods to find host trees that are associated with phylogenetically distant neighbours. Many arthropods are specialists of one or a few usually closely related host plant species (Ehrlich and Raven 1964; Kennedy and Southwood 1984; Brändle and Brandl 2006; Seifert et al. 2020). Therefore, a larger number of arthropods can be expected to move between neighbouring trees that are phylogenetically closely related than between those that are phylogenetically distantly related (Vialatte et al. 2010). Furthermore, the phylogenetically distant neighbours could mask the olfactory and visual search cues of the focal tree (Castagneyrol et al. 2013; Binyameen et al. 2013), which may make it difficult for the arthropods to find the focal tree (Jactel et al. 2011; Salazar et al. 2016). Together, such neighbourhood of phylogenetically distant trees may function as a biological isolation for the arthropods of the focal tree (Vialatte et al. 2010; Liu et al. 2012). This type of isolation is called phylogenetic isolation (schematics of phylogenetically isolated and non-isolated tree in Fig. 1), and can be quantified as the mean phylogenetic distance of the focal host-tree with its spatial neighbours (Vialatte et al. 2010).

Phylogenetic isolation of trees has been shown to be disadvantageous for the arthropods in many ways. On more phylogenetically isolated trees, Vialatte et al. (2010) observed reduced richness and abundance of Heteroptera (true bugs). Furthermore, Yguel et al. (2011) observed reduced abundance of Lepidoptera (moth caterpillars) and reduced use of resources by them. Moreover, Grandez-Rios et al. (2015) found a reduced richness of herbivorous arthropods, in particular of specialist herbivores. However, we do not know whether phylogenetic isolation makes it difficult for the arthropods to match their host-tree characteristics.

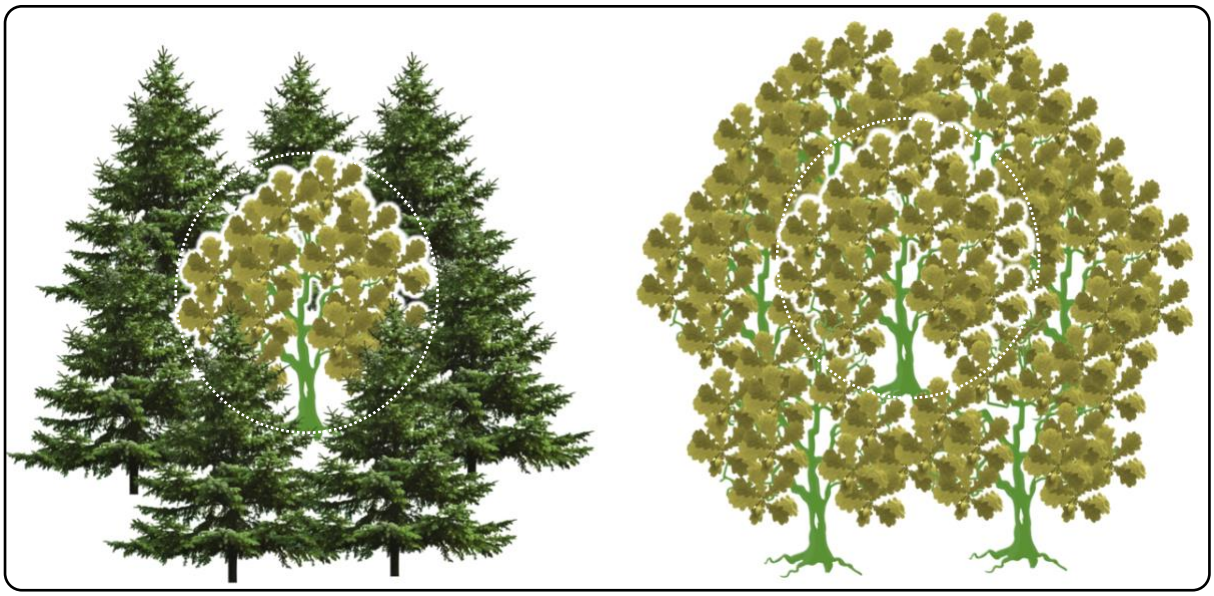

Fig. 1 A phylogenetically isolated tree (left) and a phylogenetically non-isolated tree (right). The isolated tree has spatial neighbours that are phylogenetically distant. Distantly related neighbours have different traits and harbour different arthropods than the focal tree. Distantly related neighbours also mask the odours of the focal tree.

Objectives: revealing the patterns of matching of forest arthropods to host trees with increasing phylogenetic isolation of trees

Spatial isolation of forest patches has been shown to reduce the matching of forest arthropods to their host tree characteristics. Phylogenetic isolation, a measurement of isolation at the scale of individual trees has been shown to affect forest arthropods in a similar way as isolation of habitat patches. Therefore, phylogenetic isolation of host trees may also make it difficult for forest arthropods to match the host-tree characteristics. However, it is not yet known whether isolation at the scale of individual trees can reduce matching of host-tree characteristics by associated arthropods. Hence, I investigated the effects of phylogenetic isolation on matching of host-tree characteristics by associated arthropods. Specifically, in chapter 1, I investigated the matching of leaf characteristics: increasing folivore abundance or leaf consumption with an increase in leaf size or quality. In chapter 2, I investigated the matching of caterpillar phenology with tree phenology. This included testing if phylogenetic isolation reduced the pattern of early development of arthropods on early bursting trees, as well as matching in terms of early pupation of arthropods from host trees that mature leaves early in the field (in common garden). In chapter 3, I investigated the matching of arthropod body size with tree temperature (decreasing arthropod body size with an increase in host-tree temperature) and phylogenetic isolation (extreme body sizes on more isolated trees).

Hypothesis: mechanisms such as reduction of movements and availability of information may reduce matching on phylogenetically isolated trees

Phylogenetic isolation of trees reduces matching of tree characteristics by associated arthropods through a reduction in the information about trees available to the arthropods and reduced among-tree movements. Phylogenetic isolation of trees can mask the olfactory and visual search cues for the arthropods. Therefore, the arthropods will have less reliable information about the characteristics of phylogenetically isolated trees, and hence it may be difficult for arthropods to find matching trees (Fig. 2). In addition, phylogenetic isolation of trees can reduce between-tree movement of arthropods. Arthropods may thus also find it difficult to find host trees that they match well under reduced among-tree movement (Fig. 2). Moreover, under reduced information and movement, arthropods may also find it risky to move away from host trees that they match poorly because of the high risk of finding nothing (Fig. 2). Altogether, phylogenetic isolation may weaken the matching of host-tree characteristics by associated arthropods.

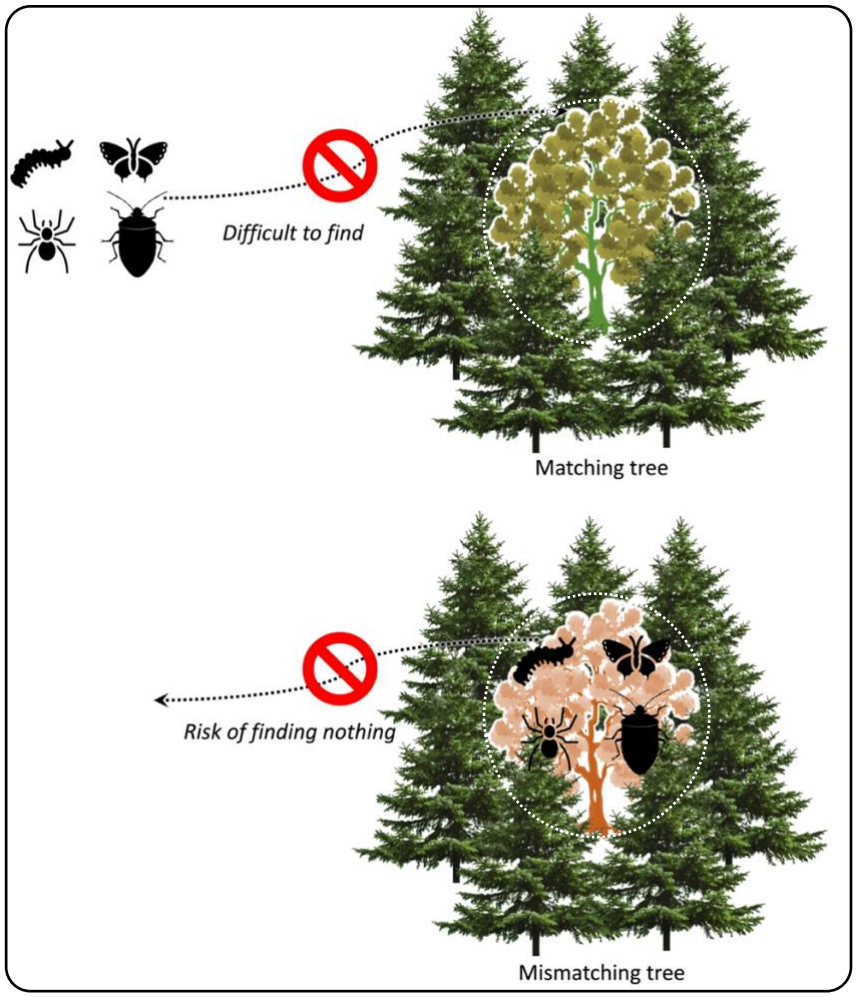

Fig. 2 Schematic representation of processes on phylogenetically isolated trees. Under reduced movement, arthropods find it more difficult to find and reach matching host-trees (top), and more risky to leave mismatching host-trees (bottom).

In this thesis, I focused on three categories of characteristics of host trees: leaf size and quality, budburst and leaf advancement phenology, and temperature. **I hypothesised that due to reduced movements and information, phylogenetic isolation of host trees prevents arthropods from matching – (1) leaf size and quality, (2) timing of budburst and speed of leaf development, and (3) temperature of the tree.** I developed these three hypotheses in detail separately in tree main chapters.

Model system: arthropods on oaks

A community of arthropods on oaks in a mixed forest is an excellent model to test these hypotheses. Oaks are among the most common trees of the temperate region, and they occur in oak stands as well as among neighbours that are phylogenetically distantly related (Vialatte et al. 2010). Oaks are particularly rich in arthropods, and may host about 5000 to 6000 species in a given region in North-West Europe (Kennedy and Southwood 1984; Dajoz 1998). Among oak individuals within a forest, there is often considerable variation in characteristics such as leaf size and quality, budburst and leaf-development phenology, and microclimate (Crawley and Akhteruzzaman 1988; Kleinschmit 1993; Visser and Holleman 2001; Roslin et al. 2006; Wesołowski and Rowiński 2006; Ranius et al. 2008; Uribe-Salas et al. 2008). Therefore, arthropods associated with oaks in a forest are exposed to wide variation in tree characteristics to match, and thus provide an excellent opportunity to test the effect of phylogenetic isolation on matching of host-tree characteristics.

I studied the arthropods on oaks in the forest of Rennes (48° 11' North, 1° 34' West; c. 90 m altitude), a temperate forest in Western France of about 3000 hectares with an oceanic climate (mean annual temperature 11.3 °C; cumulative annual rainfall 836 mm). The oaks were from two very closely related species - *Quercus petraea* and *Q. robur*. These two species can hybridize (Petit et al. 2004; Jensen et al. 2009), and support a very similar fauna of arthropods (e.g. Southwood et al. 2004; Gossner et al. 2015). Thus, in the context of this thesis, they could be treated as a single species. The studied arthropods were from three orders - Lepidoptera (folivorous moth caterpillars), Araneae (canopy spiders) and Heteroptera (both leaf sucking and predatory species). The forest is divided into 202 parcels which are dominated by either angiosperms or gymnosperms (Fig. 3). Oaks in the angiosperm-dominated parcels are surrounded mainly by closely related trees such as chestnuts (Castanea sativa), beech (Fagus sylvatica) and other oak trees (Vialatte et al. 2010). Whereas, oaks in the gymnosperm-dominated parcels are surrounded mainly by distantly related trees such as Scot's pine (Pinus sylvestris) and spruce (Picea abies). Thus, this forest makes it possible to obtain a wide range and continuous gradient of phylogenetic isolation of oaks.

Fig. 3 An angiosperm-dominated parcel (left) and a gymnosperm-dominated parcel (right) parcels of Forest of Rennes (image from Google Map).

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Chapter 1

Ectophagous herbivores do not profit from rich resources on phylogenetically isolated trees

Ectophagous herbivores do not profit from rich resources on phylogenetically isolated trees

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Abstract

Resource use by consumers across patches is often proportional to the quantity or quality of the resource within these patches. In herbivores, such proportional use of resources is likely to be more efficient when plants are spatially proximate, such as trees forming a forest canopy. However, resources provided by forest-trees are often not used proportionally. We hypothesised that proportional use of resources is reduced when host trees are isolated among phylogenetically distant neighbours that mask olfactory and visual search cues, and reduce herbivore movement between trees. Such phylogenetically distant neighbourhoods might sort out species that are specialists, poor dispersers, or have poor access to information about leaf quality. We studied individual oaks, their leaf size and quality, their herbivory and abundance of herbivores (mostly Lepidopteran ectophages, gallers and miners), and parasitism of herbivores. We found that leaf consumption by ectophages hardly increased with increasing leaf size when host trees were phylogenetically isolated. We found a similar effect on host use by parasitoids in 1 year. In contrast, we found no consistent effects in other herbivore guilds. Relative abundances of specialists and species with wingless females declined with phylogenetic isolation. However, resource use within each of these groups was inconsistently affected by phylogenetic isolation. We suggest that phylogenetic isolation prevents ectophages from effectively choosing trees with abundant resources, and also sorts out species likely to recruit in situ on their host tree. Trees in phylogenetically distant neighbourhoods may be selected for larger leaves and greater reliance on induced defences.

Keywords: Herbivore guilds, Leaf size/quality, Phylogenetic isolation, Parasitoids, Plant-animal interactions.

Introduction

Resource use by a community of consumers and their natural enemies is often proportional to the quantity or quality of the resource (Holling 1959; MacArthur and Pianka 1966; Emlen 1966; Fretwell and Lucas 1969; Gripenberg et al. 2010). For example, herbivory is higher on trees with larger leaves or higher leaf-nitrogen content (see Fig. 1 for conceptual representation, Moore and Francis 1991; Ruhnke et al. 2009). Such proportional use of resources by herbivorous insects could result from ovipositing females or foraging caterpillars choosing resource-rich trees (Faeth et al. 1981; Cornelissen and Stiling 2008). In addition, individual herbivores may be more reluctant to leave resource-rich trees than resourcepoor trees (Charnov 1976), thereby increasing their abundance on resource-rich trees. Moreover, individually, herbivores may consume more leaf area on trees with higher leaf quality. This is likely the case when individuals belong to species or genotypes that consume more (Wimp et al. 2004; Pilosof et al. 2017; Eisenring et al. 2021). Proportional use of resources is more likely when the trees are spatially close to each other, facilitating herbivore movements between trees. But even resources provided by forest-trees are often not used proportionally (Faeth et al. 1981; Courtney and Kibota 1990; Gripenberg et al. 2007; Kitamura et al. 2007; Craig and Itami 2008), and factors that reduce proportional use of resources on forest trees remain poorly understood.

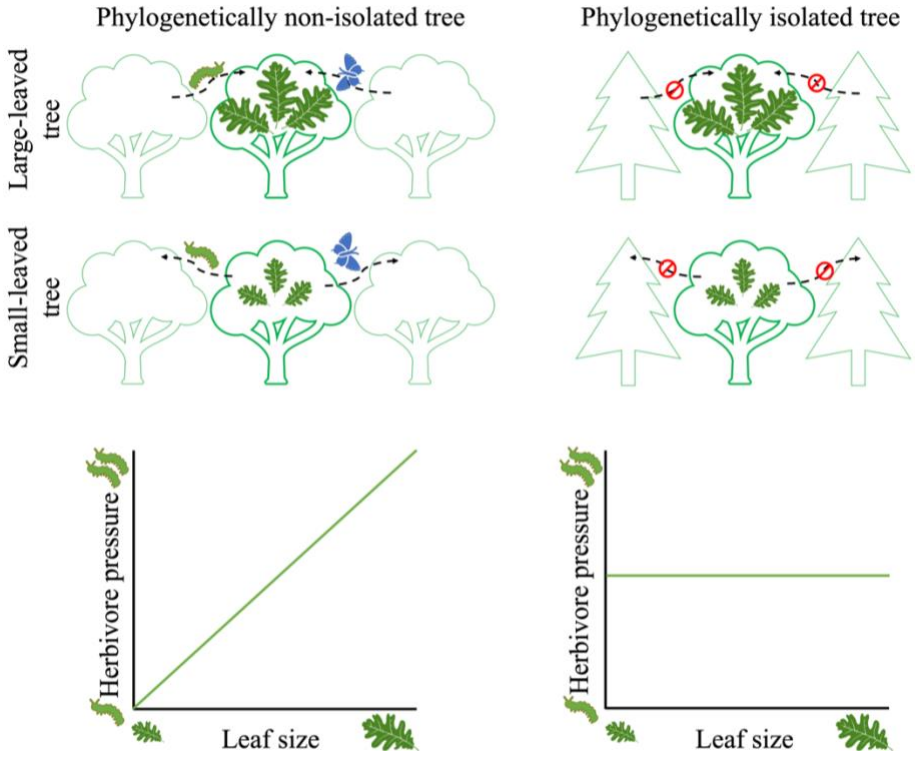

Fig. 1 Proposed processes (top row) and the resulting pattern of proportional use of resources (bottom row) on phylogenetically non-isolated (left) and phylogenetically isolated trees (right). If phylogenetic isolation of an individual tree reduces the rate of movement of ovipositing adults or larvae of herbivores that prefer large leaves, herbivore pressure will correlate less with leaf size on more phylogenetically isolated tree.

Forest trees can be phylogenetically separated from their spatial neighbours by millions of years of evolution ('phylogenetic isolation' from here on, Vialatte et al. 2010), and this may reduce proportional use of resources in herbivores. Many herbivores are specialised on one or a few usually closely related host plant species (Ehrlich and Raven 1964; Kennedy and Southwood 1984; Brändle and Brandl 2006; Seifert et al. 2020). Therefore, a larger number of herbivores can be expected to move between neighbouring trees that are phylogenetically closely related than between those that are phylogenetically distantly related (Vialatte et al. 2010). Hence, when phylogenetic isolation of a tree is high, herbivore movements between trees are expected to be scarce, compared to when phylogenetic isolation is low (Vialatte et al. 2010). In addition, phylogenetically distant neighbours could mask the olfactory and visual search cues of a focal tree (Castagneyrol et al. 2013; Binyameen et al. 2013), which may make the focal tree more difficult to detect for herbivores (Jactel et al. 2011; Salazar et al. 2016). This can reduce the immigration of ovipositing females and foraging larvae (Jactel et al. 2011). In addition, this masking of search cues may cause herbivores on phylogenetically isolated trees to be more reluctant to leave resource-poor trees (Charnov 1976; Stratton et al. 2019). Thus, both reduced movement and masking of search cues can reduce proportional use of resources (Fretwell and Lucas 1969). Consistently, more phylogenetically isolated trees have lower species richness and abundance of herbivorous Heteropteran (Vialatte et al. 2010), and reduced leaf consumption by ectophagous lepidopteran caterpillars (Yguel et al. 2011). However, reduced abundance does not indicate reduction in proportional use of resources (Fretwell and Lucas 1969; Kratina et al. 2009; Beest et al. 2016; Avgar et al. 2020). To our knowledge, effects of phylogenetic isolation on proportional use of resources have never been studied.

Phylogenetic isolation may reduce proportional use of resources by sorting out herbivore species with traits that facilitate it. Such traits could be (1) host plant specialisation, because specialised herbivores use host resources more efficiently (Gripenberg et al. 2010; Charlery de la Masselière et al. 2017), (2) ovipositing when information on leaf quantity or quality is available, i.e., developed leaves are present, as this would facilitate the choice of large and good quality leaves, and (3) strong dispersal capacity, because better dispersers are better able to select the most profitable trees. Phylogenetic isolation may sort out some of these herbivore traits. For example, when specialist herbivores are more affected by phylogenetic isolation than generalists, and when weaker dispersers have a lower chance of finding phylogenetically isolated trees (as indicated by Vialatte et al. 2010 for Heteroptera). Specialist herbivores could be more affected because they have lower chance to find phylogenetically isolated host tree as they are repelled by the odour from phylogenetically distant trees than their host tree species (Stratton et al. 2019). Moreover, optimal foraging theory (Charnov 1976) suggests that oak specialists will move less within forest stands where oaks are among phylogenetically distant trees than where oaks are among conspecifics. Thus, phylogenetic isolation may shape the

species composition in herbivore communities by sorting out species that would cause proportional use of resources.

Besides individual traits, herbivores can be characterised by guild membership, such as ectophages, leaf miners and leaf gallers. Such guilds might differ in the effect of phylogenetic isolation on their degree of proportional use of resources, as they differ in capacity of active dispersal (Peterson and Denno 1998; Asplen 2018), and in perception and processing of information on leaf size and quality (Bernays and Funk 1999; Javoiš et al. 2019). More specialised guilds such as leaf miners and leaf gallers (Novotny et al. 2010) are on average better at choosing plants on which their larvae perform best (Gripenberg et al. 2010), which should lead to more proportional use of resources. Different guilds can also differ in their responses to leaf quality. For example, leaf miners can locally modify the leaf's photosynthetic activity (Giron et al. 2007) and leaf gallers can modify the nutritional environment of their gall (Hartley and Lawton 1992), so that natural leaf quality is less relevant to them. Therefore, the ectophages that are poor at leaf modification might experience more selection to find host trees with large and high-quality leaves.

Parasitoids of herbivores often have close relationships with particular plant species (De Moraes et al. 1998; Bailey et al. 2009) as they are usually specialised on one or a few herbivore species (Schär and Vorburger 2013) which in turn are specialised on their host plants (Forister et al. 2015). Moreover, parasitoids can use the same olfactory and visual search cues as their host for finding the correct plants (Birkett et al. 2003; Aartsma et al. 2017). Therefore, the degree of phylogenetic isolation of the host tree might also affect proportional use of resources in parasitoids. This would be important because the parasitoids can partly regulate local herbivore abundances, and thus affect the exploitation of leaf resources of a tree (Hunter and Price 1992). Parasitoids are often able to track hosts by exploiting plant volatiles over large distances (Gossner et al. 2014; Aartsma et al. 2017), and may thus be less affected by isolation than herbivores. However, in the case of phylogenetic isolation, these volatile signals may be masked by volatiles of other plant species (Perfecto and Vet 2003), and this can cause reduced proportional use of resources in parasitoids. Moreover, given that a patch of resources is much smaller for the parasitoids (i.e. the herbivores) than that of the herbivores (i.e., the tree), parasitoids might also be more affected by phylogenetic isolation than herbivores. Yguel et al. (2014) showed that overall parasitism rate of caterpillars tends to be lower on more phylogenetically isolated trees, but such low parasitism rate does not exclude proportional use of resources. Whether proportional use of resources in parasitoids is affected by phylogenetic isolation among trees has so far not been addressed.

We studied the effects of phylogenetic isolation of host trees on proportional use of resources in associated herbivore guilds and parasitoids. As a model system, we used oaks (*Quercus petraea* (Matt.) Liebl*, Q. robur* L. and their hybrids) in a mixed forest and focused mainly on ectophages. We used a combination of raw data from earlier

publications and unpublished data (Table 1). We tested the prediction that phylogenetic isolation reduces the strength of the relationship between resource quantity/quality and resource use, i.e. the proportional use of resources. We investigated three levels of resource use: *per-leaf herbivory*, *per-individual herbivory* and *per-leaf abundance*. At the level of *per-leaf abundance*, we also explored whether the effect of phylogenetic isolation of host trees on proportional use of resources is found in particular among species that possess traits that facilitate it: host-plant specialisation, ovipositing when leaves are present (inferred from flying from June to October), or high dispersal capacity (inferred from large wingspan or absence of wingless females). We then tested whether phylogenetic isolation per se affects overall species composition, and in particular if phylogenetic isolation sorts out species with traits that facilitate proportional use of resources. We finally expanded the tests of whether phylogenetic isolation reduces proportional use of resources to two more herbivore guilds (leaf gallers and leaf miners, in terms of abundance) and to the parasitoids of ectophages (in terms of caterpillar use). For herbivores, we characterised resource quantity as leaf area, and resource quality as leaf dry matter content, carbon–nitrogen ratio (C:N) and total leaf phenolic content. For parasitoids, we characterised resource quantity as the density of ectophagous caterpillars. We also tested how resource use becomes less proportional with increases in two more commonly studied variables, isolation of the resource patch in space (distance to nearest oak), and the age of the resource patch (age of oaks), and explored if phylogenetic isolation can be explained by the proportion of pines.

Table 1 Overview of the data. Where *Italics* denotes a level of resource use. 1 = Yguel et al. 2011, 2 = Yguel et al. 2014, 3 = Vialatte et al. 2010. NA data were not available.

Data		Year:	2006	2010	2011
Insect group	Ectophages	*Per-leaf herbivory*	1	1	Unpublished
		Per-leaf abundance	NA	1	Unpublished
		Per-individual herbivory	NA	1	Unpublished
		Species traits in community	NA	Unpublished	Unpublished
	Leaf miner	*Per-leaf abundance*	NA	Unpublished	Unpublished
	Leaf galler	*Per-leaf abundance*	Unpublished	Unpublished	Unpublished
	Parasitoid	Abundance	NA	2	2
Leaf traits	Quantity	Leaf size	1	1	Unpublished
	Quality	LDMC	1	1	NA
		C:N	1	1	NA
		LPC	1	1	NA
Tree traits	Phylogenetic isolation		3	1	1
	Distance to nearest oak		3	1	1
	Circumference		3	1	1

Methods

Field site and study trees

Our study was conducted in the Forest of Rennes (48° 11' North, 1° 34' West; *c.* 90 m altitude), a temperate forest in Western France of about 3000 hectares with an oceanic climate (mean annual temperature 11.3 °C; cumulative annual rainfall 836 mm). The forest is divided into 202 parcels that are usually either dominated by oaks (*Q. petraea*, *Q. robur* and their hybrids) or pines (*Pinus sylvestris* L.). We studied pairs of oaks (avoiding cross-species pairs) with trees within a pair being only 30–150 m apart, one in an oak-dominated parcel, and the other in a pine-dominated parcel. Neighbouring trees were from 19 species, spanning a continuous range of phylogenetic distances from oak (Supplementary material 1, Table. S1). Pairs of study trees were spread across the entire forest. We studied the "First Set" of 9 pairs of adult oaks (producing acorns) in 2006 (earlier used in Vialatte et al. 2010; Yguel et al. 2011), and the "Second Set" of 11 pairs in 2010 and 2011 (earlier used in Yguel et al. 2011, 2014; see Table 1).

Neighbourhood and traits of study trees

For each study tree, we determined the degree of phylogenetic isolation, distance to the nearest oak, and circumference at breast height. In addition, crown position relative to dominant canopy and budburst phenology of each tree were recorded, as those are also known to affect herbivore abundance and herbivory (Crawley and Akhteruzzaman 1988; Eliason and Potter 2000; Castagneyrol et al. 2017; Barker et al. 2018; Ekholm et al. 2020; Faticov et al. 2020). Procedures and data sources are detailed below.

Degree of phylogenetic isolation for the First Set of trees had been calculated by Vialatte et al. (2010), and for the Second Set of trees by Yguel et al. (2011). Degree of phylogenetic isolation of each tree was calculated as mean phylogenetic distance to the trees with which its crown was in contact (Supplementary material 1). Phylogenetic distances to all species of trees growing in contact with study trees were quantified as in Supplementary material 1, Table S1. Understory trees (height < 6 m) were not considered because there is little exchange of insects between canopy and understory (Corff and Marquis 1999; Gossner et al. 2009).

Spatial distance from each study tree to the nearest adult oak was measured from trunk to trunk. This is not to be confused with the distance between two study trees in a pair. Rather, this distance is between one study tree and the nearest oak in its neighbourhood. Circumference of the study trees was measured at breast height. As larger trees tend to be older, the circumference is a good estimate of relative age of the trees for a given soil and macroclimate (Rozas 2003). According to local foresters,

absolute age was on average ca. 80 years in the First Set, and on average ca. 60 years in the Second Set of trees.

Whether the crown position of study trees was within or below the dominant canopy was noted for the First Set of trees. Trees of the Second Set were always located below the dominant canopy. Budburst phenology was monitored only for the Second Set of trees, in 2010 and 2011. From the beginning of March, the developmental stage of 10 random apical leaf buds from the upper stratum was determined on a three-rank scale once every 3 days using binoculars (Wesołowski and Rowiński 2006). Every sampling day, 10 new buds were randomly selected. From these data we inferred the date when a tree completed budburst, i.e., all 10 random buds of the tree had developed unfolded leaves. We then set the date when the first tree completed budburst as 0, and calculated the budburst of other trees relative to this tree in days.

Quantity and quality of leaf resources

We measured leaf area as a parameter of resource quantity, and leaf dry matter content (LDMC), leaf carbon to nitrogen ratio (C:N) and total leaf phenolic content as parameters of resource quality (Feeny 1970; Forkner et al. 2004; Schoonhoven et al. 2005). For the First Set of trees, we collected 30 leaves per tree between 16th August and 27th September 2006: 10 leaves were collected from each of 3 strata (upper exposed to sun, lower exposed to sun, and lower sheltered), and the leaf trait measurements were averaged per tree. For the Second Set of trees in 2010, a total of 40 leaves (20 from upper and 20 from lower stratum) were sampled from each tree both in the beginning of May and in the middle of September. We used spring samples for leaf quality measurements, and autumn sample for leaf size measurements. This was done because leaf quality in September might differ drastically from what herbivores experience in the beginning of Spring (Feeny 1970). Similar to 2010, 40 leaves were sampled from each tree in the middle of September in 2011, and used for leaf size measurement. In 2011, we did not sample leaves in spring and hence did not make any measurement of leaf quality.

Leaf area was estimated with a 1 × 1 cm^2 dot grid and quantified as the number of dots covering the whole leaf (as described in Yguel et al. 2011). To estimate the size of the whole leaf we manually reconstructed the missing part that was eaten by the ectophages.

To measure leaf quality, the leaves were cut longitudinally into two pieces. The piece without the main central vein was used to analyse LDMC and C:N, while the larger piece was used to analyse leaf phenolics. LDMC analyses were made following the protocol of Cornelissen et al. (2003). C:N analyses were made by “flash combustion” using a Carlo Erba NA1500 Series II elemental analyzer for the First Set of trees, and a PerkinElmer CHN PE 2400 for the Second Set of trees. For the analyses of leaf phenolics, the leaves were frozen and lyophilised for 36 h, and pooled per stratum to

obtain sufficient material. Leaf phenolics were characterised at the Polyphenols Biotech lab, Bordeaux (France), by spectrometry following the Folin–Ciocalteu indices method and expressed as the percentage of dry mass gallic acid equivalent (Singleton et al. 1999).

Herbivore abundance and herbivory

We studied the abundance of ectophages, leaf gallers and leaf miners to address the prediction developed in the Introduction. Abundance of ectophagous caterpillars on oaks peaks during the spring period (Southwood et al. 2004), and therefore we sampled caterpillars twice during the springs of 2010 and of 2011. The first sampling was done when all the study trees had just completed budburst, and the second was three weeks later. Each sample consisted of a two meters long branch, and from each study tree, one such sample was cut from the upper, and one from the lower stratum (both are sheltered). Samples were brought to the lab in plastic bags where the caterpillars were collected, and the leaves counted. To obtain *per-leaf abundance* of caterpillars, we divided the number of caterpillars collected from a tree by the number of leaves sampled. The leaf miners and leaf gallers are most abundant during the summer (West 1985), and hence we counted them from the leaves sampled for leaf area and herbivory measurements in September.

Apart from counting individuals, we studied herbivory caused by ectophages (Table 1). For this, we summed the values of missing leaf surface (see “Quantification of leaf resources”, see also Yguel et al. 2011) across all the leaves of a tree and divided that by the number of leaves to obtain *per-leaf herbivory*. We then divided these summed values by the number of caterpillars to obtain *per-individual herbivory*. We note that all our measures of herbivory are absolute surfaces, not proportions of leaf area, given that leaf area was the independent variable in later analyses. Our aim was to understand under which conditions the absolute amount of leaf material used increased with quantity or quality of leaves available, rather than the percentage (as in Yguel et al. 2011).

Parasitism of ectophagous caterpillars

The ectophagous caterpillars collected were visually searched for ectoparasitoids. We then reared the caterpillars and monitored emergence of endoparasitoids for five months from the day of sampling. The caterpillars were reared individually in Petri dishes at ambient temperature and were fed every two days with fresh oak leaves. We used absolute numbers of parasitised caterpillars observed per tree, not proportions of a given number of caterpillars parasitized, given that number of caterpillars was the independent variable in later analyses. Again, our aim was to understand under which conditions the caterpillar use in terms of absolute number increases with the total number of caterpillars present, rather than the parasitism rate (as in Yguel et al. 2014).

Ectophages species identification

After collection, all caterpillars were photographed and assigned to morphospecies based on visual assessment. Those that were successfully reared to adults in the lab were identified to species. Those individuals that died before eclosion (due to parasitism or other causes) were assumed to be of the same species as those that eclosed from the same caterpillar morphospecies. However, if the individuals that eclosed from a single morphospecies belonged to multiple species, we re-evaluated the caterpillar morphology taking into account the caterpillar-adult matches. Individuals that could not be identified in this way were not assigned to any species (43 out of 237 in 2010 and 22 out of 203 in 2011). We also gathered information on host-plant specialization, flight period, winglessness in females and wingspan from the websites Catalogue of the Lepidoptera of Belgium (De Prins and Steeman 2021), and Guide to the moths of Great Britain and Ireland (Kimber 2021). We considered species that are monophagous oak feeders as specialists, and species that fly between June and October as having direct information of final leaf size while ovipositing.

Statistical analyses

To test for effects of phylogenetic isolation of individual host trees on proportional use of resources, we used multiple linear regression models. For herbivores, we considered *per-leaf herbivory*, *per-individual herbivory* and *per-leaf abundance* as dependent variables that represent aspects of absolute leafresource use. These variables were then used in multiple regression models with a leaf trait (leaf area, LDMC, C:N, or phenolics), phylogenetic isolation, and the interaction between the leaf trait and phylogenetic isolation. Notably, in these models, the effects of leaf traits on leaf use represent the degree of proportional use of resources, while the interaction terms indicate the effects of phylogenetic isolation on proportional use of resources. For parasitoids, the dependent variable was the number of parasitised caterpillars, and predictors were the total number of caterpillars, phylogenetic isolation, and the interaction between the number of caterpillars and phylogenetic isolation. Tree pair was not included in the models because our analyses showed that resource use was not affected by pair (see Supplementary material 2, Table S2). These analyses were repeated including crown position for the First Set of trees, and budburst phenology for the Second Set of trees as co-variables in the models (phenology had not been recorded for the First Set, and crown position had been held constant in the Second Set). Accounting for these covariables did not change the general conclusions, but reduced the degrees of freedom, and is hence presented only in Supplementary material 3, Table S3. Finally, we repeated the initial models (the ones without the covariables), replacing phylogenetic isolation by either distance to the nearest oak, or by oak circumference (indicating age), as justified in the Introduction.

We note that *per-leaf herbivory* cannot exceed the area of the leaf, and number of parasitised caterpillars cannot exceed the total number of caterpillars, so that a

regression of, for instance, leaf area on herbivory area is constrained to be positive. We hence did not present these particular relationships, nor the R^2 of the total models, but our focus was on the interaction term, which is not affected by this constraint. Indeed, our hypotheses make predictions only about the interaction terms. We also note that multiple analyses were conducted on the effect of leaf quality, each accounting for different leaf characteristics. So, a correction for multiple testing might be warranted. However, even without correction we found only 2 significant interaction terms out of 21 in the main body of the manuscript (see Table 2) and hence conclude the absence of pattern, even without correction.

In ectophages, we explored whether proportional use of resources on phylogenetically non-isolated trees emerged in particular among species with certain traits. We therefore defined groups of species with a particular trait value, e.g., species that fly when the leaves are developed between June and October vs. other species. We then conducted for each of the two groups the initial model, i.e., *per-leaf abundance* explained by resource quantity or quality, and PI, and their interaction. We similarly divided the data into host-plant specialists and generalists, species with winged vs. wingless females, and species with below vs. above median wingspan.

To test for the contributions of different tree traits and leaf traits in shaping the species composition of ectophagous communities on individual trees, we performed a Permutational Multivariate Analysis of Variance (PERMANOVA) using the R package *vegan* (Oksanen et al. 2019). To test whether phylogenetic isolation sorts out certain species traits in ectophages, we used simple regressions: the dependent variable was the community weighted average value of the trait, using species abundance as a weight. In the calculus of community-weighted mean wingspan, we excluded species that have wingless females to ensure independence from the community-weighted mean of presence of wingless females. The predictor was the phylogenetic isolation of the trees. All statistical analyses were performed using R version 4.0.2 (R Core Team 2020). We used a normal error distribution as the residuals of our multiple regression analyses approached normality and homoscedasticity. If a model did not meet normality and homoscedasticity criteria even after removal of at most two influential data points, it was removed from the analyses (3 out of 51 models in the body of the manuscript). Influential data points were identified by the visual assessment of four plots: residuals vs fitted values, normal Q-Q, scale-location, and residuals vs leverage (with Cook's distance). We considered an interaction term significant only if it was significant after the removal of at most one influential data point and retained its significance after possible exclusion of a second influential data point.

Results

Overview of the data

Degree of phylogenetic isolation ranged from 5.71 to 106.67 million years in the First Set, and from 10 to 125.67 million years in the Second Set of trees, and varied continuously between the extremes (Supplementary material 4, Fig. S4.a). Spatial distance from each study tree to the nearest adult oak ranged from 2.5 to 18.9 m in the First Set and from 0.7 to 9.4 m in the Second Set of trees (Supplementary material 4, Fig. S4.b.). Circumference of the study trees ranged from 57.75 to 133.1 cm (mean 93.2 cm, SD = 22.4) in the First Set, and from 37.8 to 91.4 cm (mean 62.1 cm, SD = 16.7) in the Second Set of trees (Supplementary material 4, Fig. S4.c).

Per tree mean leaf area ranged from 17.57 to 53.40 cm^2 in the First Set of trees. In the Second Set, it ranged from 34.98 to 73.33 cm^2 in 2010, and from 49.40 to 83.65 cm^2 in 2011. Leaf size of a tree was positively correlated between 2010 and 2011 ($t = 3.247$, $p = 0.004$, $df = 20$). Mean LDMC ranged from 30.73 to 42.44% in the First Set of trees, and from 21.71 to 32.47% in the Second Set in 2010. Mean C:N ranged from 17.48 to 28.91 in the First Set, and from 9.41 to 13.65 in the Second Set in 2010. Mean leaf phenolics ranged from 3.04 to 10.01% in the First Set, and from 12.18 to 36.05% in the Second Set in 2010.

We found a total of 237 caterpillars on 9739 leaves in 2010, and 203 caterpillars on 14914 leaves in 2011. The *per-leaf abundance* of caterpillars ranged from 0.004 to 0.072 in 2010, and from 0.003 to 0.028 in 2011. Out of these two years, the *per-leaf abundance* of caterpillars was higher in 2010 (Welch Two Sample t-test $t = 2.989$, $df = 28.203$, p-value = 0.006). The species composition of ectophage caterpillars on different trees is given in Supplementary material 5, Table S5A. The information on wingspan, winglessness in females, flying period, host-plant specialization are given in Supplementary material 5, Table S5B. *Per-leaf abundance* of leaf miners ranged from 0.050 to 0.610 in 2010, and from 0.200 to 0.800 in 2011. *Per-leaf abundance* of leaf gallers ranged from 0.003 to 0.362 in 2006, from 0.000 to 0.366 in 2010, and from 0.000 to 0.800 in 2011. For the caterpillars, *per-leaf herbivory* ranged from 0.700 to 9.600 cm^2 in the First Set of trees. In the Second Set of trees, it ranged from 0.525 to 9.525 cm^2 in 2010, and from 0.425 to 10.600 cm^2 in 2011. *Per-individual herbivory* ranged from 21.197 to 418.5 cm^2 in 2010, and from 39.462 to 803.480 cm^2 in 2011. A total of 51 out of 206 caterpillars were parasitised in 2010 and 67 out of 203 in 2011.

Effect of phylogenetic isolation on proportional use of resources by ectophages

Phylogenetic isolation significantly reduced the proportional use of leaf size at all levels of leaf use: *per-leaf herbivory*, *per-individual herbivory* and *per-leaf abundance* (Fig. 2): the interaction term “leaf area × phylogenetic isolation” was significant and negative (Table 2). In particular, for *per-leaf herbivory* this reduction was significant in all the

study years i.e., for the First Set of trees in 2006 and for the Second Set in 2010 and in 2011 (Table 2, Fig. 2a). The levels of *per-individual herbivory* and *per-leaf abundance* were tested only for the Second Set of trees in 2010 and in 2011. For *per-individual herbivory*, the reduction was significant in 2011 but not in 2010 (Table 2, Fig. 2b). For *per-leaf abundance* (all species together), the reduction was significant in 2010 but not in 2011 (Table 2, Fig. 2c). In contrast, phylogenetic isolation did not significantly affect the proportional use of resource quality i.e., LDMC, C:N and phenolics (Table 2).

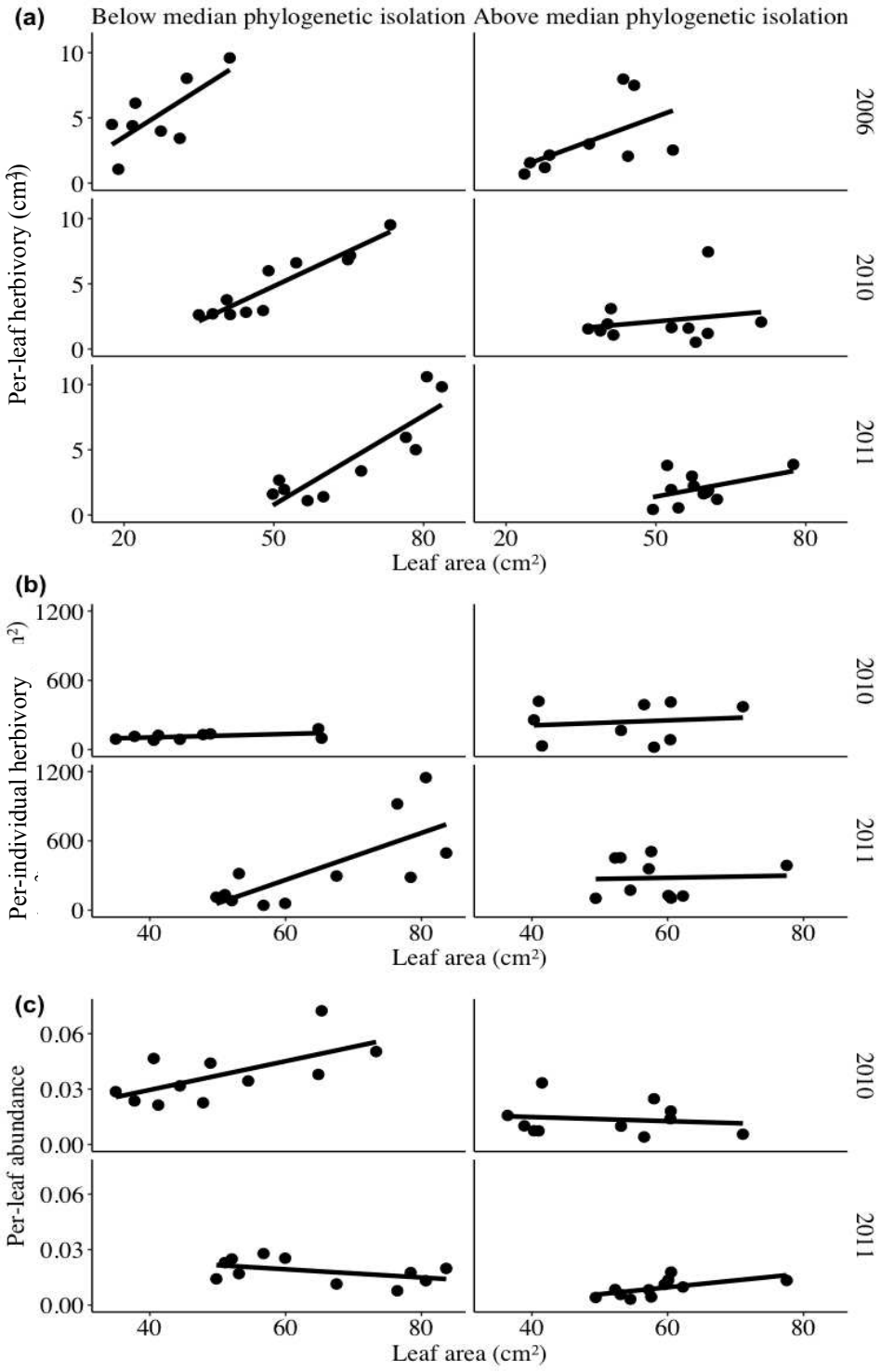

Fig. 2 Phylogenetic isolation of individual host trees significantly reduced proportional use of leaf area by ectophages. **a** Phylogenetic isolation significantly reduced the increase in *per-leaf herbivory* with an increase in leaf area in 2006 (interaction term phylogenetic isolation x leaf size: $t = -2.686$, $p = 0.019$, df = 13), 2010 ($t = -3.078$, $p = 0.006$, df = 18) and 2011 ($t = -2.122$, p=0.049, df=17). **b** Phylogenetic isolation significantly reduced the increase in *per-individual herbivory* with an increase in average leaf area in 2011 ($t = -2.329$, $p = 0.032$, df = 17). (**c**) Phylogenetic isolation significantly reduced the increase in *per-leaf abundance* with an increase in leaf area in 2010 ($t = -2.844$, $p = 0.011$, df = 18). Phylogenetic isolation is presented as binary in the figures, but is a continuous measure and statistically analysed as such.

Table 2 Statistical effects of phylogenetic isolation of individual host trees on proportional use of resources by associated insects – tested for ectophages, leaf gallers, leaf miners and parasitoids of ectophages. Proportional use of resources was considered in terms of resource quantity (leaf area) and quality (LDMC, C:N, LPC). For all three guilds of herbivores, proportional use of resources was studied at the level of *per leaf-abundance*, and for ectophages also at the level of *per-leaf herbivory* and *per-individua herbivory*. Proportional use of resources by parasitoids was studied at the level of caterpillar use. Note that the statistics given in the table are only for the interaction term in the models, but the models also accounted for the main effects of the variables in the interaction term. PI = phylogenetic isolation, LA = leaf area, LDMC = leaf dry-matter content, C:N = carbon-nitrogen ratio, LPC = leaf phenolics content, TC = Total caterpillars. *Italics* denotes a level of resource use. Bold denotes a significant *p* value.

Group	Use of	Effects of	Level	Trees:	First Set			Second Set					
				Year:	2006			2010			2011		
					t	*p*	*df*	*t*	*p*	*df*	*t*	*p*	*df*
Ectophages													
	Leaf size												
		LA × PI	*Per-leaf herbivory*		-2.686	**0.019**	13	-3.078	**0.006**	18	-2.122	**0.049**	17
			Per-individual herbivory			NA		0.538	0.597	18	-2.329	**0.032**	17
			Per-leaf abundance	All species		NA		-2.844	**0.011**	18	1.371	0.187	18
				Specialists		NA		-2.377	**0.029**	18	4.004	**<0.001**	18
				Generalists		NA		-1.442	0.166	18	-0.957	0.351	18
				Direct leaf info		NA		-1.007	0.327	18	1.403	0.178	18
				No direct leaf info		NA		-0.694	0.497	18	-0.771	0.451	18
				Winged females		NA		-2.602	**0.018**	18	0.817	0.424	18
				Wingless females		NA		-1.265	0.222	18	Invalid model		
				Small wingspan		NA		-1.317	0.205	17	-0.531	0.602	18
				Large wingspan		NA		-0.086	0.932	18	1.684	0.109	18
	Leaf quality												
		LDMC × PI	*Per-leaf herbivory*		0.619	0.546	14	0.739	0.470	18		NA	
			Per-individual herbivory			NA		-1.311	0.206	18		NA	
			Per-leaf abundance			NA		1.813	0.088	17		NA	
		C:N x PI	*Per-leaf herbivory*		-0.094	0.927	14	1.070	0.299	18		NA	
			Per-individual herbivory			NA		-0.582	0.568	18		NA	
			Per-leaf abundance			NA		-0.297	0.770	18		NA	
		LPC x PI	*Per-leaf herbivory*		0.532	0.603	14	1.301	0.210	18		NA	
			Per-individual herbivory			NA		-0.490	0.630	18		NA	
			Per-leaf abundance			NA		1.356	0.192	18		NA	
Leaf gallers													
	Leaf size												
		LA × PI	*Per-leaf abundance*		-0.618	0.547	14	0.074	0.942	17	-1.394	0.181	17
	Leaf quality												
		LDMC × PI	*Per-leaf abundance*		1.401	0.184	13	-0.398	0.696	15		NA	
		C:N x PI	*Per-leaf abundance*		0.373	0.715	13	5.579	**<0.001**	17		NA	
		LPC x PI	*Per-leaf abundance*		2.074	0.059	13	0.078	0.939	16		NA	
Leaf miners													
	Leaf size												
		LA × PI	*Per-leaf abundance*			NA		-1.167	0.259	17	-2.132	**0.048**	17
	Leaf quality												
		LDMC × PI	*Per-leaf abundance*			NA		Invalid model				NA	
		C:N x PI	*Per-leaf abundance*			NA		3.285	**0.005**	16		NA	
		LPC x PI	*Per-leaf abundance*			NA		Invalid model				NA	
Parasitoids													
	Caterpillars												
		TC x PI	Parasitised caterpillars			NA		-2.567	**0.020**	17	-0.755	0.460	0.46

Within the different groups, we found that among specialists, phylogenetic isolation significantly reduced proportional use of resources in 2010 but significantly increased it in 2011 (Table 2, Fig. 3a). Among species with winged females, phylogenetic isolation significantly reduced proportional use of resources in 2010 but not in 2011 (Table 2).

In both the years 2010 and 2011, phylogenetic isolation contributed the most to shape the species composition in ectophage communities on individual trees, albeit only significantly in 2010 (Supplementary material 6, Table S6). In particular, phylogenetic isolation significantly sorted out specialist ectophages in 2010 and 2011 (Table 3, Fig. 3b) and species with wingless females in 2010 (Table 3, Fig. 3c). An analysis based on the variable 'presence/absence of species with wingless females' using logistic regression leads to the same conclusion (Supplementary material 8).

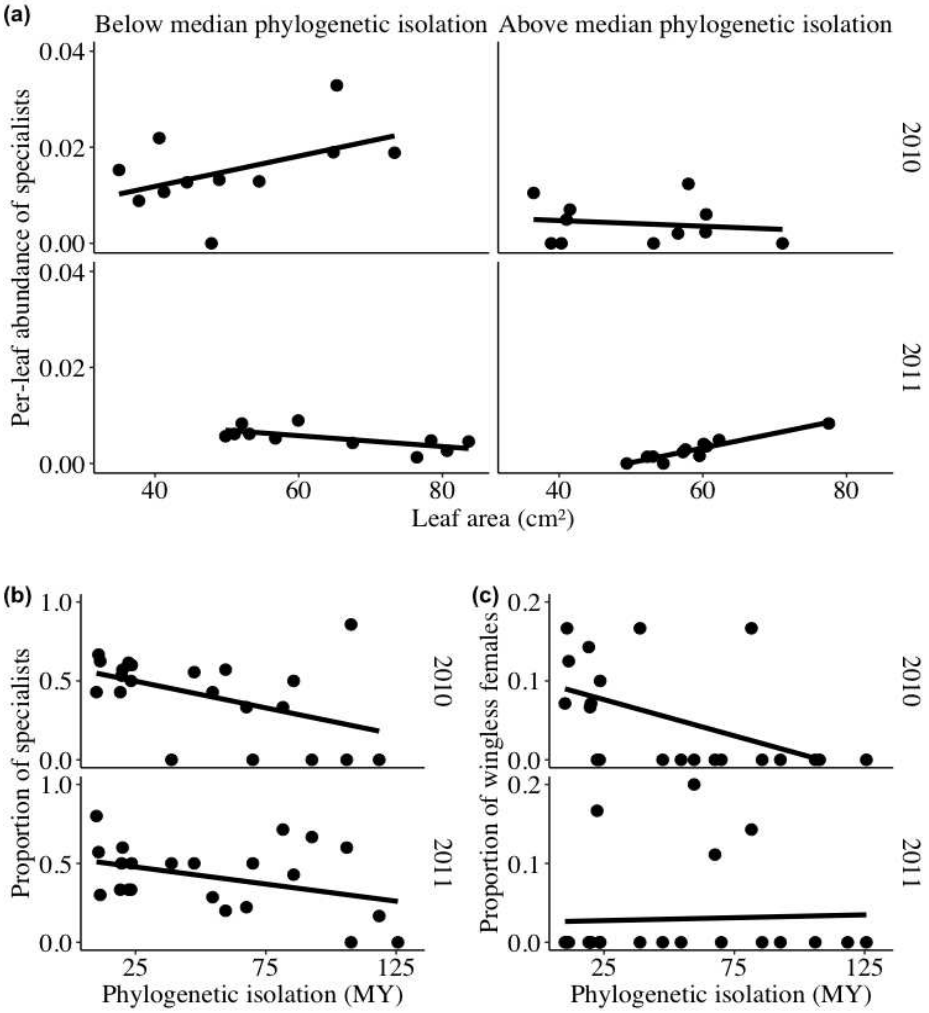

Fig. 3 Effect of phylogenetic isolation on subgroups of ectophages. **a** Phylogenetic isolation significantly reduced the increase in *per-leaf abundance* of specialists with an increase in leaf area in 2010 ($t = -2.377$, $p = 0.029$, df = 18), but significantly increased the same in 2011 ($t = 4.004$, $p < 0.001$, df = 18). See Table 2 for full analyses. **b** Phylogenetic isolation significantly reduced the proportion of specialists in both 2010 ($t = -2.301$, $p = 0.033$, df=19) and 2011 ($t=-2.281$, $p = 0.034$, df = 19). **c** Phylogenetic isolation significantly reduced the proportion of species that have wingless females in 2010 ($t = -2.535$, $p = 0.020$, df = 19). See Table 3 for full analyses.

Table 3 Effect of phylogenetic isolation of individual host trees on community-weighted means of multiple species traits of ectophagous herbivores, tested by simple regression analysis. Bold denotes a significant *p* value. See Fig. 3b for illustration.

Effects of phylogenetic isolation on	Year:	2010			2011		
		t	p	df	t	p	df
Proportion of specialists		-2.301	**0.033**	19	-2.281	**0.034**	19
Proportion of species that fly between June-October		-0.354	0.727	19	-1.281	0.216	19
Proportion of specis that have wingless females		-2.535	**0.020**	19	Invalid model		
Community weighted average wingspan		-0.617	0.544	20	0.092	0.927	20

Effect of phylogenetic isolation on proportional use of resources by leaf gallers

Phylogenetic isolation did not significantly affect the proportional use of leaf size by leaf gallers. This effect was consistently absent in both the First Set (in 2006) and the Second Set (both in 2010 and in 2011) of trees (Table 2). Proportional use of leaf quality was affected significantly only in 1 out of 6 cases (Table 2). The interaction term “C:N × phylogenetic isolation” was positive (Table 2). This reflects a reduction in proportional use of low C:N (i.e., high leaf quality) with phylogenetic isolation.

Effect of phylogenetic isolation on proportional use of resources by leaf miners

The effect of phylogenetic isolation on proportional use of leaf resources by the leaf miners was inconsistent. For the Second Set of trees, proportional use of leaf size was significantly reduced in 2011 but not in 2010 (Table 2). Proportional use of leaf quality was affected significantly only in 1 out of 3 cases (Table 2): in terms of low C:N in the First Set of trees in 2010.

Effect of phylogenetic isolation on proportional use of resources by parasitoids

Phylogenetic isolation significantly reduced the proportional use of ectophagous caterpillars (total number of caterpillars) by parasitoids in 2010 but not in 2011 (Table 2 Fig. 4). We note that this decline in use of abundant caterpillars in 2010 cannot be explained by the effect of phylogenetic isolation on caterpillar diversity, because phylogenetic isolation reduced caterpillar diversity ($p < 0.001$, $t = -4.12$, df = 20), and lower caterpillar diversity *in*creased the number of parasitised caterpillars ($p = 0.004$, $t = -3.31$, df = 19). We could not test for the effect of phylogenetic isolation on the proportional use of resource quality because we have no data on nutritional quality provided by the caterpillars.

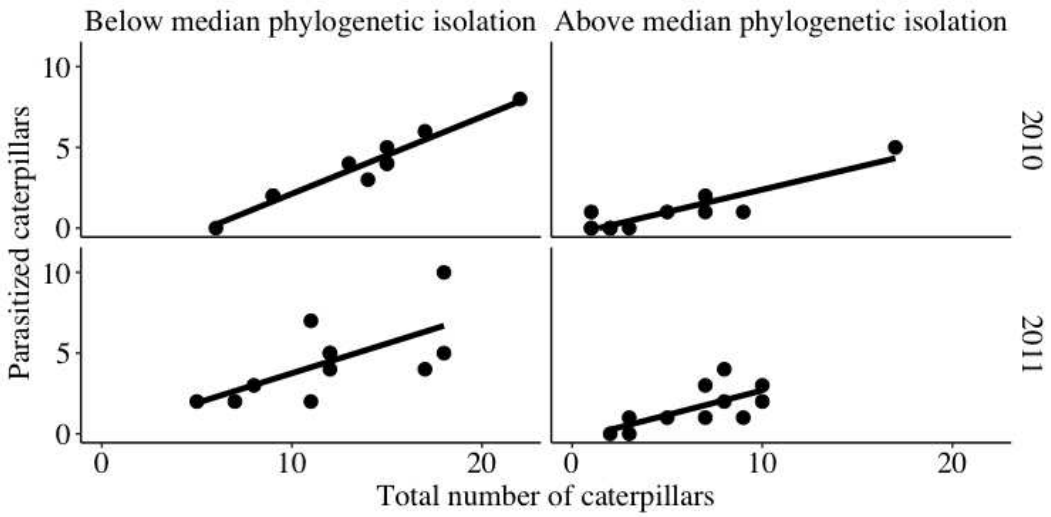

Fig.4 Phylogenetic isolation of individual host trees significantly reduced proportional use of caterpillars by parasitoids in 2010. The increase in number of parasitised caterpillars with an increase in total number of caterpillars was less for phylogenetically isolated trees in 2010 (t=− 2.567, p=0.02, df=17), but not in 2011 (t=− 0.755, p = 0.460, df = 18). Note that the given statistics are for the interaction term 'total number of caterpillars *phylogenetic isolation'. Phylogenetic isolation is presented as binary in the figures, but is a continuous measure and statistically analysed as such.

Effect of isolation of resource patch in space and of age of the resource patch on proportional use of resources

Proportional use of resources was not affected consistently by isolation of resource patches in space, i.e. distance to nearest oak. Only 4 out of 36 models were significant – 1 for ectophages, 2 for leaf gallers, 1 for leaf miners and 0 for parasitoids (Supplementary material 7A, Table S7A.a). The two effects on leaf gallers varied between years. In 2006, distance to nearest oak statistically reduced the proportional use of leaf size by leaf gallers, whereas in 2010 it reduced that of a quality parameter (low C:N). Proportional use of resources was never affected by the age of the resource patch, i.e. age of oaks measured by its circumference (Supplementary material 7A, Table S7A.b). Overall, none of these variables affected proportional use of resources as consistently as did phylogenetic isolation. We finally note that the percentage of pines had a weaker effect than phylogenetic isolation (Supplementary material 7B, Table S7B).

Discussion

We hypothesized that proportional use of resources by herbivores and parasitoids would be reduced among more phylogenetically isolated trees as it reduces between-tree movement and masks search cues. We tested this hypothesis in three guilds of herbivores—ectophages, leaf gallers, and leaf miners, and in parasitoids of ectophages. As predicted, we found that in ectophages the proportional use of leaf

size was reduced on more phylogenetically isolated trees in terms of *per-leaf herbivory* in all years tested. This pattern of *per-leaf herbivory* appeared to be driven by *per-individual herbivory* in 2011, and by *per-leaf abundance* in 2010. Patterns of *perleaf abundance* in 2010, in turn, appeared to be driven by (1) an increase in abundances with leaf size on phylogenetically non-isolated trees in species that are specialists or have winged females in 2010, and (2) the decline of relative abundances of specialists and species with wingless-females on isolated trees in 2010. For leaf gallers and leaf miners, we did not find a consistent effect of phylogenetic isolation on proportional use of resources. For parasitoids of ectophages, phylogenetic isolation reduced the proportional use of caterpillars in one of the study years, and this cannot be explained by the finding that caterpillar diversity reduced parasitism. In contrast to the significant effects of phylogenetic isolation, we found no support for the further hypotheses of effects of spatial isolation from to the nearest oak or of tree age on proportional use of resources, and effects of phylogenetic isolation could not be explained simply by the proportion of pines.

Limitations

Our study inevitably has limitations. First, we studied the relationship between resource use and resource quantity or quality but did not directly study the processes that might drive resource use, such as movements or information usage by individuals. However, in comparable situations, such patterns have indeed been shown to result from movements or information usage. For instance, some studies showed that the usage of volatile compounds emitted by trees helps herbivores to discriminate between host trees (Jactel et al. 2011; Ghirardo et al. 2012; Binyameen et al. 2013; Conchou et al. 2017). Moreover, we studied traits of ectophage species (for example, host-plant specialisation), which indirectly permits us to address the underlying mechanisms. Second, we interpret high herbivory as a sign of high use of rich leaf resources—but it may also be a sign of compensatory feeding on poor-quality leaves (Raubenheimer and Simpson 1993). We cannot exclude a minor contribution of such compensatory feeding to our herbivory scores, but consider a major contribution unlikely: compensatory feeding should decrease with leaf quality, but we found no negative relationship between herbivory and leaf quality. Third, phylogenetic isolation might represent nothing more than an effect of the percentage of pine trees, the most abundant and phylogenetically most distant tree species in our study. However, replacing the phylogenetic isolation by % pines mostly reduced significances (Supplementary material 7, Table 7B). Therefore, the observed effects of phylogenetic isolation on proportional use of resources are more than a pine-effect. Finally, herbivory can also be due to herbivores other than Lepidoptera caterpillars, notably certain Symphyta (Hymenoptera), Coleoptera and Orthoptera (Heil 2004; Martin et al. 2009). However, in this region, caterpillars are known to be by far the dominant ectophage herbivores (personal observations and Southwood et al. 2004; Yguel et al. 2011). Moreover, Symphyta caterpillars were not observed.

How could phylogenetic isolation have reduced proportional use of leaf size by ectophages?

On phylogenetically isolated trees, herbivory by ectophages did not increase proportionally to leaf size, in either of the study years. First, we had hypothesised that phylogenetic isolation of host trees might reduce the movement of specialized ectophages between neighbouring trees (Kennedy and Southwood 1984; Brändle and Brandl 2006; Gilbert and Webb 2007; Stratton et al. 2019). In this case, individual large-leaved trees would receive fewer ectophages from their neighbours when they are more phylogenetically isolated from their neighbours (suggested by Vialatte et al. 2010). This effect should be especially pronounced for more specialized herbivore species (demonstrated for Heteroptera by Vialatte et al. 2010). As outlined above, declines of overall proportional use of resources in terms of *per-leaf abundance* were consistent with the patterns of absolute and relative abundance of specialists.

Second, the distantly related neighbours of phylogenetically isolated trees might mask the olfactory and visual cues of the focal tree (Binyameen et al. 2013), reducing information available to herbivores. Hence, ectophages could find it more difficult to identify and reach large-leaved trees when the trees are more phylogenetically isolated (Jactel et al. 2011; Salazar et al. 2016). Furthermore, on small-leaved trees, the odour from the distantly related neighbours might discourage individual ectophages from leaving its host tree (Charnov 1976). Overall, when ectophages visit and test phylogenetically isolated trees at a lower rate or have less information about other potential host trees, they are less likely to show proportional use of resources. This should only play a role for herbivores that oviposit when developed leaves are present, which could give them direct information about the size and quality of leaves. However, the effect of phylogenetic isolation on proportional use of resources did not differ between the species that have direct leaf size information during oviposition and species that do not have it.

Third, herbivory by ectophages might not increase proportionally with leaf size on phylogenetically isolates trees due to poor sorting of phenotypes of ectophage species. If phylogenetic isolation of individual host trees reduces the influx of individual ectophages, it will also reduce the influx of phenotypes, which serve as the raw material for the sorting of those phenotypes that fit best to the local environment (a process operating both within and across species; Vellend 2016). With less raw material, phenotype sorting might be poor on more phylogenetically isolated trees. Hence, on large-leaved trees that are phylogenetically isolated, there might be fewer ectophages that are large and capable of eating much and thereby tracking large leaves. However, we did not find any effect of phylogenetic isolation on average body size (wingspan), nor did phylogenetic isolation affect the proportional use of leaf size by species with below or above median body size.

Fourth, abundances of ectophages may be abundant on some trees due to high in situ reproduction rather than immigration. In this scenario, larger leaves might allow larger populations to develop when the trees are phylogenetically non-isolated. This scenario would require that leaf size of a tree is correlated between years, which we found. The scenario would predict phylogenetic isolation of host trees to decrease relative abundances of species that are likely to reproduce in situ on their host tree: wingless-female species or oak specialists (being unable to use neighbouring non-oak trees). We indeed found decreases in relative abundances of these groups with phylogenetic isolation, in particular in 2010, the year in which ectophage abundances did not increase proportionally with leaf size on phylogenetically isolated trees. Moreover, the importance of in-situ reproduction is further underlined by the fact that even species in which ovipositing females do not have information on leaf size also showed proportional use of resources suggests an important role for in situ recruitment.

Overall, these four processes should facilitate using leaves proportional to their size on phylogenetically nonisolated trees. In theory we could have expected the opposite: that phylogenetically isolated trees harbour species that are very good at finding suitable trees and that may be able to use leaves proportional to their size even among phylogenetically isolated trees. Consistently, we did find more species with winged females on phylogenetically isolated trees. Nevertheless, leaves were used proportionally to their size only on the phylogenetically non-isolated trees. Altogether, that leaves are not used proportionally to their size on phylogenetically isolated trees cannot be explained by particular groups of ectophages becoming incapable of using leaves proportionally to their size, but possibly by a relative decline in those groups that might be best at using leaves proportionally to size.

Why was proportional use of resources achieved in terms of *per-leaf abundance* in one year, but by *per-individual herbivory* in the other?

Patterns of proportional use of resources at the level of *per-leaf herbivory* by ectophages were reflected in patterns of *per-leaf abundance* in 2010, and in patterns of *per individual herbivory* in 2011. As outlined before, caterpillar abundance on non-isolated trees being proportional to leaf size suggests an establishment of little dispersive ectophages recruiting in situ on their host tree so that abundances on that tree correspond to the quantity of resources it offers. In contrast, patterns of per ectophage herbivory suggest sorting of ectophage phenotypes by the leaf traits. Thus, within ectophage species, trees with larger leaves would accumulate ectophage genotypes that consume more leaf surface, or across ectophage species, those species that consume more leaf surface. The importance of these two groups of processes may depend on the overall abundance of ectophages, which was significantly higher in 2010 than in 2011. High abundance might trigger negative density-dependent interactions among ectophages such as direct resource competition, increased defences of the shared host, or attraction of shared natural enemies (Birkett et al. 2003; Staudt and Lhoutellier 2007; Faiola and Taipale 2020;

Collie et al. 2020). These negative density-dependent interactions, in turn, may push ectophages to leave host trees, and find new host trees (Charnov 1976; Vialatte et al. 2010). Phylogenetic isolation may then hamper these processes, in particular in a high-abundance year like 2010. The same negative density-dependent processes among abundant ectophages also reduces the amount of resources available per ectophage (Collie et al. 2020). As a result, in a high abundance year, increased leaf area per tree may not correspond to increased leaf area available per ectophage, and hence not sort for ectophage phenotypes that are capable of eating more. Overall, the high total abundance of ectophages in 2010 might possibly explain why ectophage abundance, but not per ectophage herbivory increased with leaf area on non-isolated trees (and inversely for 2011).

Why did phylogenetic isolation not affectthe ectophage's proportional use of leaf quality?

We suggest that proportional use of leaf quality by ectophages was not affected by phylogenetic isolation because there was no proportional use of leaf quality. When proportional use of leaf quality is absent, it cannot be affected by phylogenetic isolation. Proportional use of leaf quality may be absent when information on leaf quality is insufficient. This is most obvious for herbivores that oviposit during the winter when there are no leaves in the trees (Sarvašová et al. 2020). Even herbivores that oviposit in late summer and overwinter as eggs to hatch in spring (Du Merle 1988) may face a poor correlation between leaf quality in summer and that in spring of the next year. Even in the same season, leaf quality does not correlate perfectly among years (Gripenberg et al. 2007). Such poor correlation might be caused in part by the tree's responses to herbivory: trees are known to respond to herbivory by reducing their leaf quality for herbivores (Kant et al. 2015; Volf et al. 2021). Therefore, herbivorous adult insects not emerging in spring might lack sufficient information on quality of leaves available to larvae in spring. This problem might be particularly strong in trees that suffer much from herbivory, which are often phylogenetically non-isolated trees (Yguel et al. 2011). For this reason, resource quality might not be tracked even on non-isolated trees.

Why did phylogenetic isolation not reduce proportional use of resources by leaf gallers and leaf miners?

Proportional use of resources by leaf gallers and leaf miners was not consistently affected by phylogenetic isolation of individual host trees. This is consistent with lack of effects of phylogenetic isolation on overall abundance of leaf miners and leaf gallers in the study system (Hidasi-Neto et al. 2018). Perhaps miners and gallers do not respond to the parameters tested. Absence of proportional use of leaf size was surprising, given reported preferences for large leaves in leaf miners (Faeth 1991). Endophages might have little to no need of choosing trees with a particular leaf quality, because they can strongly improve it locally (Cornell 1989; Hartley 1998; Nyman and

Julkunen-Tiitto 2000; Giron et al. 2007; Kaiser et al. 2010). Perhaps other leaf traits such as toughness that limit oviposition and mine initiation are more important to endophages (Faeth 1985; Pihain et al. 2019). Even when endophages do track resources, it might be easier for them to overcome the effect of phylogenetic isolation than it is for ectophages if they i.e. experience less dispersal limitation. Specifically, many leaf gallers are known for their high dispersal capacity (Gilioli et al. 2013). In addition, this high dispersal limits in situ reproduction on host trees and therefore adjustment of abundances to resources available on a tree (Connor et al. 1983).

Why did parasitoids use hosts proportionally in only one of the two study years?

The proportional use of ectophagous caterpillars by parasitoids was reduced by phylogenetic isolation of individual host trees in 2010, but not in 2011. This pattern of 2010 cannot be explained by high caterpillar diversity possibly reducing parasitism (Stireman III and Singer 2003), as we have demonstrated that phylogenetic isolation reduced caterpillar diversity and would thus have increased parasitism on phylogenetically isolated trees, not decreased it. One possible explanation could be the higher abundance of ectophagous caterpillars in 2010 (Yguel et al. 2014). Effect of abundance may be predicted from optimal foraging theory: many parasitoid species exhibit a type III functional response to host density (Morrison and Strong 1980; Fernández-arhex and Corley 2003; Veldtman and McGeoch 2004), which means that resource use increases with resource abundance only above a certain threshold of resource abundance. In our case, such high levels of abundances of ectophages might have been reached only in the high abundance year, and even then, only on the phylogenetically non-isolated trees. Our data thus suggest that parasitoids track the abundance of ectophage hosts only during years of high overall ectophage abundance and among trees with high ectophage abundance (phylogenetically non-isolated). We finally note that parasitism not only increases in a uniformly closely related tree neighbourhood, it also increases in a uniform community of host caterpillars.

What are the potential consequences for trees that are phylogenetically isolated?

The fact that ectophagy mostly does not increase with leaf area on phylogenetically isolated trees, may be both advantageous and disadvantageous for the trees. On the one hand, it may be advantageous because when herbivores cannot feed more on large-leaved trees, trees might then benefit more from large leaves. Such leaves can help to reduce water loss (Wang et al. 2019). Hence, phylogenetically isolated trees can be expected to grow larger leaves. Consistently, Castagneyrol et al. (2017) found that specific leaf area increases with phylogenetic isolation of individual host trees. On the other hand, the fact that ectophagy mostly does not increase with leaf area on phylogenetically isolated trees may also be disadvantageous for the trees, as it renders attacks by ectophages unpredictable. Unpredictable attacks select for induced defences because constitutive defence would be a waste of resources when there is

no attack. However, when there is an attack, induced defences may be costlier than constitutive defences (Pigliucci 2001; Perkovich and Ward 2021). Overall, for a tree, the advantages and disadvantages of growing in a phylogenetically distant neighbourhood might possibly equal out, but the selection pressures on leaf area and defence traits are likely to be different.

Conclusions

Overall, we find that proportional use of resources declines with phylogenetic isolation of host trees. It does so in the herbivore guild that is least capable of moving between, detecting and manipulating host trees — the ectophages. Ectophagous herbivores consume more on large-leaved trees, either by establishing in larger numbers of individuals (2010), or by establishing individual phenotypes that consume more (2011). But this proportional use of resources happens only as long as neighbouring trees are phylogenetically proximate, in 2010 likely because in such neighbourhoods species accumulate that are most likely to recruit locally — species specialized on oaks or having wingless females. Parasitism could partly counteract proportional use of resources on trees in phylogenetically proximate neighbourhoods, because high densities of ectophages attract more parasitoids, at least during high-abundance years. Lack of proportional use of resources in leaf miners and leaf gallers might be due to their ability to improve resource quality within trees, and due to their limited in situ recruitment on trees. Finally, the negative effect of phylogenetic isolation of trees on proportional use of resources by ectophages suggests that tree populations in phylogenetically distant neighbourhoods might be selected for larger leaves and greater reliance on induced defences.

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Supplementary materials

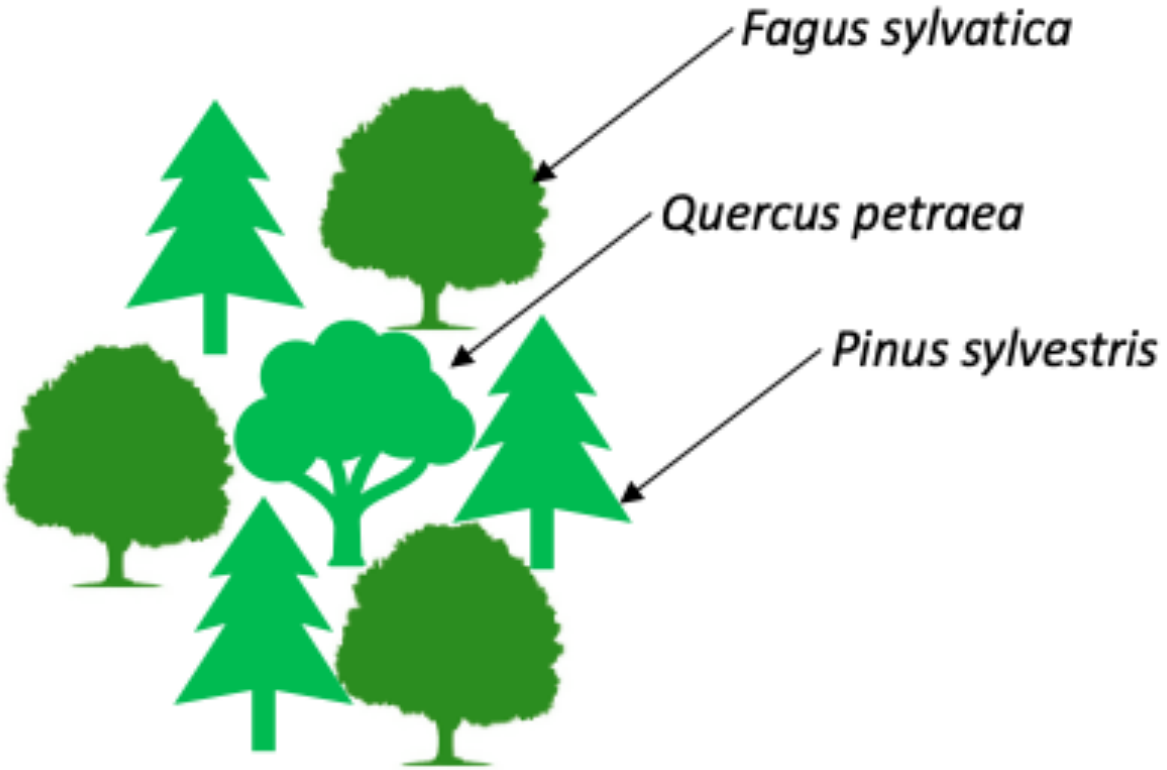
Supplementary material 1. Phylogenetic distances and calculation of phylogenetic isolation

Phylogenetic distance between two tree species is the estimated time (in MYBP) since the evolutionary establishment of the clades of a given neighbouring tree species and of oaks. These phylogenetic distances were taken from Vialatte et al. (2010) and Yguel et al. (2011), based on Magallon et al., 1999, Manos et al., 1999, Wikström et al., 2001, Poinar et al., 2007. Note that this is not the most recent common ancestor, as this would give gymnosperms such as pines an extreme weight (Savard et al., 1994), and would essentially render our parameter a simple percentage of pines in the surroundings of the oaks. Rather, this is the age when both sister clades had established their particular characteristics as hosts for insects (i.e. phylogenetic crown-age of the younger of the two lineages and not stem age). Thus, phylogenetic distance corresponds to the smaller of the two crown ages of the two lineages involved (i.e. of oak and of the other tree species) at the corresponding phylogenetic rank (ranks within Angiosperms inferred from APG 2003, 2009, and checked against 2016).

Table S1: Phylogenetic distance between oaks and other trees in our data set based on crown ages (taken from Vialatte et al. 2010 and Yguel et al. 2011).

Species	Phylogenetic rank of separation with oak						Distance (MY)
Chamaecyparis sp.	Spermatophytes	-	-	-	-	-	140
Pinus sylvestris	Spermatophytes	-	-	-	-	-	140
Abies sp.	Spermatophytes	-	-	-	-	-	140
Ilex sp.	Angiosperms	Asterids	-	-	-	-	128
Tilia sp.	Angiosperms	Rosids	Malvids	-	-	-	89.5
Salix caprea	Angiosperms	Rosids	Fabids	Malpighiales	-	-	68
Populus tremula	Angiosperms	Rosids	Fabids	Malpighiales	-	-	68
Rhamnus sp.	Angiosperms	Rosids	Fabids	Rosales	-	-	58.5
Prunus sp.	Angiosperms	Rosids	Fabids	Rosales	-	-	58.5
Sorbus sp	Angiosperms	Rosids	Fabids	Rosales	-	-	58.5
Pyrus sp.	Angiosperms	Rosids	Fabids	Rosales	-	-	58.5
Malus sp.	Angiosperms	Rosids	Fabids	Rosales	-	-	58.5
Ulmus minor	Angiosperms	Rosids	Fabids	Rosales	-	-	58.5
Alnus glutinosa	Angiosperms	Rosids	Fabids	Fagales	Betulaceae	-	54
Corylus avellana	Angiosperms	Rosids	Fabids	Fagales	Betulaceae	-	54
Betula sp.	Angiosperms	Rosids	Fabids	Fagales	Betulaceae	-	54
Carpinus betulus	Angiosperms	Rosids	Fabids	Fagales	Betulaceae	-	54
Fagus sylvatica	Angiosperms	Rosids	Fabids	Fagales	Fagaceae	Fagus	40
Castanea sativa	Angiosperms	Rosids	Fabids	Fagales	Fagaceae	Castanea	40

Degree of phylogenetic isolation of a tree was calculated as mean phylogenetic distances to the trees with which its crown was in contact (or the projections of crowns of trees on the ground were in contact). Hence, the formula to calculate the phylogenetic isolation of an oak is $Phylogenetic\ isolation = \frac{\sum_{i=1}^{n} Phylogenetic\ distance}{n}$; where n is the number of trees in crown contact of that oak. As an example, the case given in the figure below is a *Quercus petraea* surrounded by 3 *Pinus sylvestris* and 3 *Fagus sylvatica*. So, the total number of trees in crown contact with the oak is 6. Phylogenetic distance between a *Quercus petraea* and a *Pinus sylvestris* is 140 MY, and between a *Quercus petraea* and a *Fagus sylvatica* is 40 MY. Hence, the phylogenetic isolation of this oak will be $\frac{140+140+140+40+40+40}{6} = 90$ MY .



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Supplementary material 2. Effects of tree pairs on resource use

Species composition and abundance of insects may vary spatially in a forest, so that more proximate trees have more similar insect communities. Therefore, we selected trees that differ in phylogenetic isolation in pairs of spatially proximate trees, rather than selecting the trees randomly (Legendre et al. 2004). To test whether the tree pair defines the various level of use of resources by ectophages, leaf gallers, leaf miners and parasitoids of ectophagous caterpillars, we performed an ANOVA. We found that pair did not significantly affect herbivore abundance or herbivory (Table S2). So, we do not account for "pair" in further analyses.

Table S2. Results of ANOVA testing for the effect of tree pair on various level of use of resources by ectophages, leaf gallers, leaf miners and parasitoids of ectophagous caterpillars.

Group	Dependent variable	Year	DF	F	p
Ectophages	*Per-leaf herbivory*	2006	8	1.574	0.256
		2010	10	0.378	0.932
		2011	10	0.381	0.930
	Per-individual herbivory	2010	10	0.873	0.581
		2011	10	1.390	0.298
	Per-leaf abundance	2010	10	0.214	0.989
		2011	10	0.986	0.505
Leaf gallers	*Per-leaf abundance*	2006	8	1.239	0.376
		2010	10	1.472	0.267
		2011	10	1.584	0.231
Leaf miners	*Per-leaf abundance*	2010	10	1.033	0.475
		2011	10	0.719	0.695
Parasitoids	Parasitised caterpillar	2010	10	0.699	0.710
		2011	10	0.756	0.667

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Supplementary material 3. Influence of crown position and budburst phenology on the effect of phylogenetic isolation on proportional use of resources

Crown position and budburst phenology did not change the overall effect of phylogenetic isolation on proportional use of resources. After accounting for crown position and budburst phenology, phylogenetic isolation still statistically reduced the tracking of leaf size and not leaf quality by ectophages. Specifically, for ectophages, tracking of leaf size was still reduced at *Per-leaf herbivory* level in all three years, and at *Per-individual herbivory* level in 2011 but not in 2010 - only the signal at the level of *Per-leaf abundance* was lost. In addition, for ectophages, phylogenetic isolation still consistently did not affect the proportional use of leaf quality. For leaf gallers and leaf miners, phylogenetic isolation still did not consistently affect the proportional use of

resources. Moreover, for parasitoids, phylogenetic isolation still affected the proportional use of caterpillars in 2010 but not in 2011. Overall, the models accounting for the effects of crown position and budburst phenology (Table S3) support the results of the models that do not account for these co-variables (Table 2).

Table S3. Statistics of the multiple linear regressions that accounted for the effects of crown position (in 2006) and budburst phenology (in 2010 and 2011). Note that the statistics given in the table is of only the interaction term in a model, but the models also account for the main effects of the variables in the interaction term and the variable given in the column 'Accounted for'. LA = leaf area, LDMC = leaf dry-matter content, C:N = carbon-nitrogen ratio, LPC = leaf phenolics content, TC = total caterpillars, PI = phylogenetic isolation, CP = crown position, BB = budburst.

Group	Use of	Dependent variable	Effects of	Year	Accounted for	t	*p*	DF
Ectophages	Leaf size	*Per-leaf herbivory*	LA × PI	2006	CP	-2.495	**0.028**	12
			LA × PI	2010	BB	-3.315	**0.004**	17
			LA × PI	2011	BB	-2.193	**0.043**	16
		Per-individual herbivory	LA × PI	2010	BB	-0.956	0.352	17
			LA × PI	2011	BB	-2.518	**0.023**	16
		Per-leaf abundance	LA × PI	2010	BB	-1.166	0.260	17
			LA × PI	2011	BB	1.490	0.154	17
	Leaf quality	*Per-leaf herbivory*	LDMC × PI	2006	CP	0.435	0.672	11
			LDMC × PI	2010	BB	0.739	0.470	17
			C:N × PI	2006	CP	-1.408	0.187	11
			C:N × PI	2010	BB	1.011	0.326	17
			LPC × PI	2006	CP	0.165	0.872	13
			LPC × PI	2010	BB	1.352	0.194	17
		Per-individual herbivory	LDMC × PI	2010	BB	-0.721	0.481	17
			C:N × PI	2010	BB	-0.460	0.651	17
			LPC × PI	2010	BB	-0.300	0.768	17
		Per-leaf abundance	LDMC × PI	2010	BB	1.171	0.259	16
			C:N × PI	2010	BB	-0.120	0.906	16
			LPC × PI	2010	BB	1.278	0.219	16
Leaf gallers	Leaf size	*Per-leaf abundance*	LA × PI	2006	CP	-0.512	0.617	13
			LA × PI	2010	BB	-0.379	0.709	16
			LA × PI	2011	BB	-1.579	0.133	17
	Leaf quality	*Per-leaf abundance*	LDMC × PI	2006	CP	0.763	0.459	13
			LDMC × PI	2010	BB	1.610	0.127	16
			C:N × PI	2006	CP	0.459	0.654	13
			C:N × PI	2010	BB	5.419	**<0.001**	16
			LPC × PI	2006	CP	1.824	0.093	12
			LPC × PI	2010	BB	0.980	0.342	16
Leaf miners	Leaf size	*Per-leaf abundance*	LA × PI	2010	BB	-0.694	0.498	16
			LA × PI	2011	BB	-0.983	0.339	17
	Leaf quality	*Per-leaf abundance*	LDMC × PI	2010	BB	0.671	0.512	16
			C:N × PI	2010	BB	1.238	0.233	17
			LPC × PI	2010	BB	2.096	0.052	17
Parasitoids	Caterpillars	Parasitised caterpillars	TC × PI	2010	BB	-2.173	**0.044**	17
			TC × PI	2011	BB	-0.003	0.998	17

Supplementary material 4. Distribution of phylogenetic isolation, distance to the nearest oak and oak circumference

In our data, the phylogenetic isolation of individual trees, their distance to the nearest oak and oak circumference had continuous distributions (Fig. S4), and were treated as such in our analyses. Phylogenetic isolation has a binary representation in the illustrations in the main body of the article (Fig. 1, 2, 3 and 4) only to permit an easier interpretation.

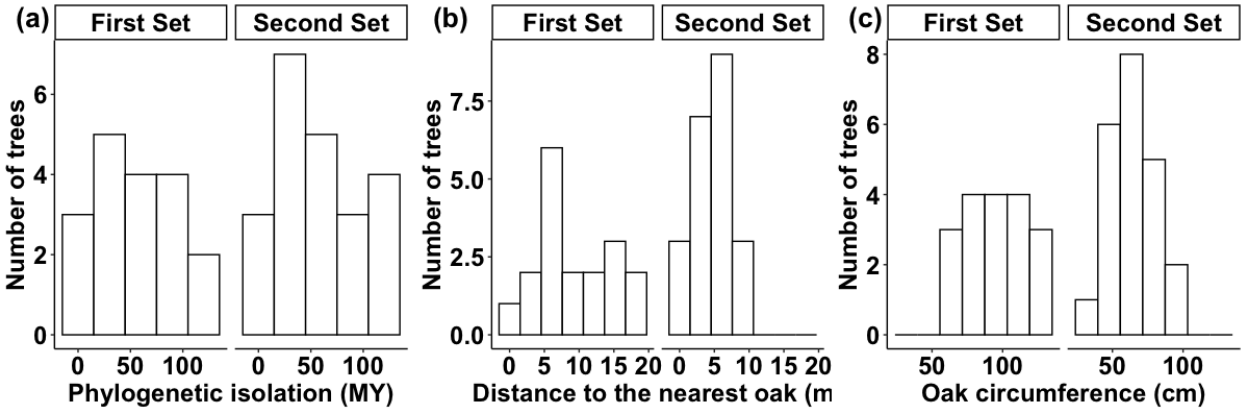


Fig. S4: The distribution of (a) phylogenetic isolation, (b) distance to the nearest oak, and (c) oak circumference for First Set (studied in 2006) and Second Set of trees (studied in 2010 and 2011). The phylogenetic isolation ranged from 5.71 to 106.67 million years in First Set, and from 10 to 125.67million years in Second Set of trees. The spatial distance from the study trees to the nearest adult oak ranged from 2.5 to 18.9 m in First Set and from 0.70 to 9.40 m in Second Set of trees. The circumference of the study trees was measured at breast height, and ranged from 57.75 to 133.1 cm in First Set, and from 37.8 to 91.4 cm in Second Set of trees.

Supplementary material 5. Community composition and species traits of ectophages

Table S5A: Community composition of ectophages

Year	Tree	*Acrobasis consociella*	*Acrobasis repandana*	*Aglia tau*	*Agriopis aurantiaria*	*Aleimma loeflingiana*	*Archips Podana*	*Archips sp*	*Biston strataria*	*Carcina quercana*	*Catocala promissa*	*Catocala sponsa*	*Conistra sp*	*Cyclophora linearia*	*Ennomos quercinaria*	*Epirrita autumnata*	*Erannis defoliaria*	*Eupithecia abbreviata*	*Eupithecia sp*	*Eupsilia transversa*	*Hedya nubifera*	*Lymantria dispar*	*Lymantria monacha*	*Operophtera brumata*	*Orgyia antiqua*	*Orthosia cerasi*	*Orthosia incerta*	*Orthosia munda*	*Pammene argyrana*	*Phycita roborella*	*Poecilocampa populi*	*Polyploca ridens*	*Spilonota ocellana*	*Tortrix viridana*	*Undetermined*	*Ypsolopha parenthesella*	*Ypsolopha ustella*	*Zeiraphera isertana*
2010	2.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	4	5	1	0	2
	2.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
	4.1	0	0	0	1	0	0	4	0	2	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	2	0	0	0	0	0	0	1	1	0	0	1
	4.2	0	0	0	0	0	1	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	1
	5.1	0	0	0	0	0	0	4	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	2	0	0	0	0	0	0	2	3	1	1	1
	5.2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	2	0	0	0	0	0	0	0	0	0	1	0	3	1	1	0	0
	6.1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	3	0	0	0	0	0	0	0	3	1	0	0
	6.2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
	7.1	0	2	0	0	1	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0	0	0	0	0	0	0	2	0	0	0
	7.2	0	0	0	0	0	0	2	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	1
	8.1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	2	2	0	0	0
	8.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
	9.1	0	0	0	1	0	0	6	1	0	0	0	3	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	1	0	0	2	0	0	0
	9.2	0	0	0	0	0	0	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0
	10	0	0	0	1	0	1	8	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	1	6	1	0	0
	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0
	13	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	0	0	0	0	3	0	0	0	1	0	0	1	4	1	0	0	1
	13	0	1	0	2	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	3	0	0	0	0	0	0	0	2	5	0	0	0
	14	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	3	1	0	0
	14	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
	X.1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	1	0	0	0	0	0	0	0	6	2	0	0	1
	X.2	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2011	2.1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0
	2.2	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	4.1	0	0	0	0	0	0	0	0	3	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	2	3	0	0	0
	4.2	0	0	0	1	0	0	0	0	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
	5.1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	1	1	0	0	1
	5.2	2	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	1	5	2	0	1
	6.1	2	0	0	0	0	0	2	0	2	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0
	6.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0
	7.1	0	0	0	0	0	0	2	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	5	0	0	0
	7.2	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	0	0	0	0	0	0	0	2	0	0	0
	8.1	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1	0	0	0	0	0	1	0	0
	8.2	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	2	1	0	0
	9.1	0	0	0	0	0	0	3	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	1	5	0	0	2
	9.2	1	0	0	1	0	0	1	0	2	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0
	10	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	1	0	0	0	1	0	1	2	0	0
	10	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	1	3	0	0	1
	13	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	2	7	0	0	0
	13	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	3	2	0	0	0
	14	0	0	0	0	0	0	3	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	3	1	0	0	0	0	0	0	9	0	0	0
	14	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	3	0	0	0
	X.1	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	3	0	0	0
	X.2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0

Table S5B: Traits of ectophage species that are present in the community. Information are taken from the websites Catalogue of the Lepidoptera of Belgium (De Prins and Steeman 2021), and Guide to the moths of Great Britain and Ireland (Kimber 2021).

Species	Average wingspan (mm)	Host-plant specialisation	Fly between June-October	Wingless females
Acrobasis consociella	20.5	Specialist	Yes	No
Acrobasis repandana	22.5	Specialist	Yes	No
Aglia tau	72.0	Generalist	No	No
Agriopis aurantaria	31.0	Generalist	No	Yes
Aleimma loeflingiana	16.5	Generalist	Yes	No
Archips Podana	22.0	Specialist	Yes	No
Archips sp	20.8	Specialist	Yes	No
Bena bicolorana	42.5	Specialist	Yes	No
Carcina quercana	19.0	Generalist	Yes	No
Catocala promissa	62.5	Specialist	Yes	No
Catocala sponsa	65.0	Specialist	Yes	No
Conistra sp	33.9	Generalist	No	No
Cyclophora linearia	29.5	Specialist	Yes	No
Ennomos quercinaria	46.0	Generalist	Yes	No
Epirrita autumnata	42.0	Generalist	Yes	No
Erannis defoliaria	35.0	Generalist	No	Yes
Eupithecia abbreviata	20.5	Generalist	No	No
Eupithecia sp	17.5	Generalist	No	No
Eupsilia transversa	37.0	Generalist	No	No
Hedya nubifera	18.0	Generalist	Yes	No
Lymantria dispar	43.5	Generalist	Yes	No
Lymantria monacha	40.0	Generalist	Yes	No
Operophtera brumata	25.0	Generalist	No	Yes
Orgyia antiqua	27.5	Generalist	Yes	Yes
Orthosia cerasi	37.0	Generalist	No	No
Orthosia incerta	37.5	Generalist	No	No
Orthosia munda	41.0	Generalist	No	No
Pammene argyrana	11.5	Specialist	No	No
Phycita roborella	26.5	Specialist	Yes	No
Poecilocampa populi	37.5	Generalist	No	No
Polyploca ridens	32.5	Specialist	No	No
Spilonota ocellana	14.5	Generalist	Yes	No
Tortrix viridana	20.5	Specialist	Yes	No
Ypsolopha parenthesel	18.0	Generalist	Yes	No
Ypsolopha ustella	17.5	Specialist	No	No
Zeiraphera isertana	17.0	Specialist	Yes	No

References:

De Prins W, Steeman C (2021) Catalogue of the Lepidoptera of Belgium. https://projects.biodiversity.be/lepidoptera/. Accessed 24 Feb 2022

Kimber I (2021) UKMoths | Guide to the moths of Great Britain and Ireland. https://ukmoths.org.uk/. Accessed 24 Feb 2022

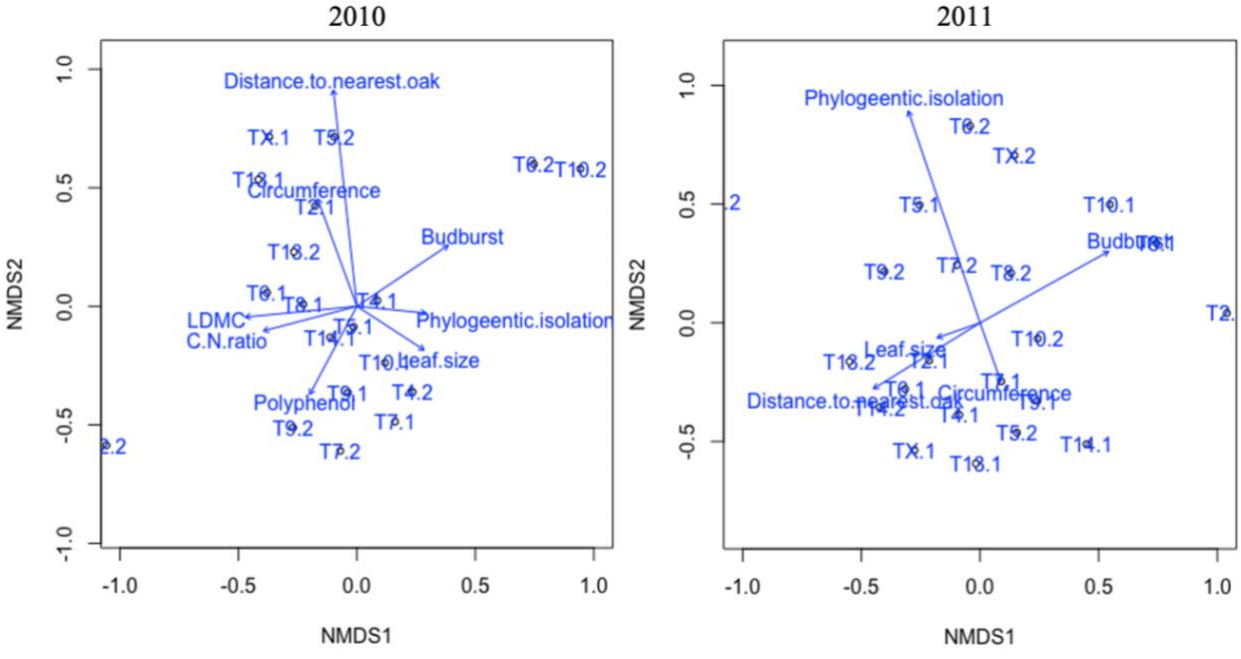
Supplementary material 6. Role of different tree traits and leaf traits to shape species composition in ectophage communities

In both the years 2010 and 2011, phylogenetic isolation has contributed the most to shape the species composition in ectophage communities on individual trees, albeit only significantly in 2010.

Table S6: Contributions of different tree traits and leaf traits to shape the species composition of ectophagous communities on individual trees. Tested by a Permutational Multivariate Analysis of Variance (PERMANOVA) using the R package *vegan*. PI = phylogenetic isolation, DIS = Distance to nearest oak, TC = Tree circumference, BB = budburst, LA = leaf area, LDMC = leaf dry-matter content, C:N = carbon-nitrogen ratio, LPC = leaf phenolics content

Effects of Year:	2010						2011					
	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
PI	1	0.537	0.537	1.934	0.089	**0.040**	1	0.308	0.308	1.363	0.064	0.213
DIS	1	0.444	0.444	1.600	0.073	0.110	1	0.273	0.273	1.208	0.057	0.260
TC	1	0.281	0.281	1.011	0.046	0.422	1	0.179	0.179	0.793	0.037	0.616
BB	1	0.193	0.193	0.695	0.032	0.753	1	0.203	0.203	0.898	0.042	0.549
LA	1	0.134	0.134	0.481	0.022	0.893	1	0.250	0.250	1.108	0.052	0.374
LDMC	1	0.283	0.283	1.018	0.047	0.408	NA	NA	NA	NA	NA	NA
C:N	1	0.177	0.177	0.638	0.029	0.781	NA	NA	NA	NA	NA	NA
LPC	1	0.397	0.397	1.429	0.066	0.158	NA	NA	NA	NA	NA	NA
Residuals	13	3.611	0.278	0.596			16	3.616	0.226	0.749		
Total	21	6.058	1.000				21	4.830	1.000			

The figure represents the ordination plots of Nonmetric Multidimensional Scaling (NMDS), where datapoints are individual trees, and the arrows represent a tree trait or a leaf trait.



Supplementary material 7. Effects of distance to the nearest oak, oak circumference and percentage pines in the neighbourhood on proportional use of resources

(A) Distance to the nearest oak and oak circumference: We compared effects of phylogenetic isolation of individual host trees on the proportional use of resources to that of two more commonly studied variables, isolation in space and availability of the resource in time. Isolation in space was measured as the spatial distance of the study oaks to its nearest adult oak. We used circumference of the tree at breast height as a proxy of the age of a tree. Neither the distance to the nearest oak (Table S7A.a), nor the circumference of the trees (Table S7A.b) showed consistent significant effect on proportional use of resources. Note that the statistics given in the table is of only the interaction term in a model, but the models also accounted for the main effects of the variables in the interaction term. LA = leaf area, LDMC = leaf dry-matter content, C:N = carbon-nitrogen ratio, LPC = leaf phenolics content, TC = total caterpillars, DIS = distance to the nearest oak, OC = oak circumference.

Table S7A.a: Effects of distance to the nearest oak on proportional use of resources.

Group	Use of	Dependent variable	Effects of	Year	t	*p*	DF
Ectophages	Leaf size	*Per-leaf herbivory*	LA × DIS	2006	1.532	0.148	14
			LA × DIS	2010	-1.010	0.326	18
			LA × DIS	2011	-1.039	0.312	18
		Per-individual herbivory	LA × DIS	2010	0.487	0.633	17
			LA × DIS	2011	-0.887	0.387	18
		Per-leaf abundance	LA × DIS	2010	-0.778	0.447	18
			LA × DIS	2011	0.713	0.485	18
	Leaf quality	*Per-leaf herbivory*	LDMC × DIS	2006	0.569	0.579	13
			LDMC × DIS	2010	0.143	0.888	17
			C:N × DIS	2006	-0.588	0.567	13
			C:N × DIS	2010	1.049	0.310	16
			LPC × DIS	2006	0.166	0.871	14
			LPC × DIS	2010	-0.921	0.369	18
		Per-individual herbivory	LDMC × DIS	2010	-2.672	**0.016**	18
			C:N × DIS	2010	1.893	0.075	18
			LPC × DIS	2010	Invalid model		
		Per-leaf abundance	LDMC × DIS	2010	1.371	0.188	18
			C:N × DIS	2010	-1.227	0.236	18
			LPC × DIS	2010	0.882	0.389	18
Leaf gallers	Leaf size	*Per-leaf abundance*	LA × DIS	2006	-2.783	**0.016**	13
			LA × DIS	2010	0.541	0.595	17
			LA × DIS	2011	Invalid model		
	Leaf quality	*Per-leaf abundance*	LDMC × DIS	2006	0.653	0.525	14
			LDMC × DIS	2010	-1.757	0.097	17
			C:N × DIS	2006	0.943	0.362	14
			C:N × DIS	2010	2.927	**0.009**	17
			LPC × DIS	2006	0.792	0.442	14
			LPC × DIS	2010	-1.997	0.063	16
Leaf miners	Leaf size	*Per-leaf abundance*	LA × DIS	2010	0.541	0.595	17
			LA × DIS	2011	-1.536	0.143	17
	Leaf quality	*Per-leaf abundance*	LDMC × DIS	2010	-1.757	0.097	17
			C:N × DIS	2010	2.927	**0.009**	17
			LPC × DIS	2010	-1.997	0.063	16
Parasitoids	Caterpillars	Parasitised caterpillars	TC × DIS	2010	-0.673	0.509	18
			TC × DIS	2011	-1.075	0.299	16

Table S7A.b: Effects of oak circumference on proportional use of resources.

Group	Use of	Dependent variable	Effects of	Year	t	*p*	DF
Ectophages	Leaf size	*Per-leaf herbivory*	LA × OC	2006	1.444	0.171	14
			LA × OC	2010	-0.266	0.793	18
			LA × OC	2011	1.907	0.074	17
		Per-individual herbivory	LA × OC	2010	1.489	0.156	16
			LA × OC	2011	0.716	0.483	18
		Per-leaf abundance	LA × OC	2010	-0.988	0.336	18
			LA × OC	2011	-0.380	0.708	18
	Leaf quality	*Per-leaf herbivory*	LDMC × OC	2006	-0.805	0.434	14
			LDMC × OC	2010	0.935	0.363	17
			C:N × OC	2006	0.213	0.834	14
			C:N × OC	2010	-0.402	0.692	17
			LPC × OC	2006	-1.910	0.077	14
			LPC × OC	2010	0.290	0.775	18
		Per-individual herbivory	LDMC × OC	2010	Invalid model		
			C:N × OC	2010	0.800	0.434	18
			LPC × OC	2010	Invalid model		
		Per-leaf abundance	LDMC × OC	2010	0.808	0.430	18
			C:N × OC	2010	-0.770	0.451	18
			LPC × OC	2010	0.036	0.972	18
Leaf gallers	Leaf size	*Per-leaf abundance*	LA × OC	2006	-0.334	0.743	14
			LA × OC	2010	-1.489	0.155	17
			LA × OC	2011	Invalid model		
	Leaf quality	*Per-leaf abundance*	LDMC × OC	2010	Invalid model		
			LDMC × OC	2006	-1.743	0.105	13
			C:N × OC	2006	0.913	0.377	14
			C:N × OC	2010	1.211	0.243	17
			LPC × OC	2010	Invalid model		
			LPC × OC	2006	-0.419	0.682	14
Leaf miners	Leaf size	*Per-leaf abundance*	LA × OC	2010	-1.489	0.155	17
			LA × OC	2011	-1.225	0.237	17
	Leaf quality	*Per-leaf abundance*	LDMC × OC	2010	Invalid model		
			C:N × OC	2010	1.211	0.243	17
			LPC × OC	2010	Invalid model		
Parasitoids	Caterpillars	Parasitised caterpillars	TC × OC	2010	-1.909	0.073	17
			TC × OC	2011	-1.060	0.303	18

(B) Percentage pines in the neighbourhood: Phylogenetic isolation is the mean phylogenetic distance to the neighbours and the value can be determined mainly by the neighbours having large phylogenetic distance to the focal tree. Our focal oak has the maximum phylogenetic distance to pines (among the neighbouring trees). Hence, we compared effects of phylogenetic isolation of individual host trees on the proportional use of resources to that of percentage of pines in the neighbourhood. We conducted these analyses for all groups of insects (extophages, leaf gallers, leaf miners and parasitoids), but not for the subgroups within ectophages. We found that percentage pine has a weaker effect than phylogenetic isolation. Percentage

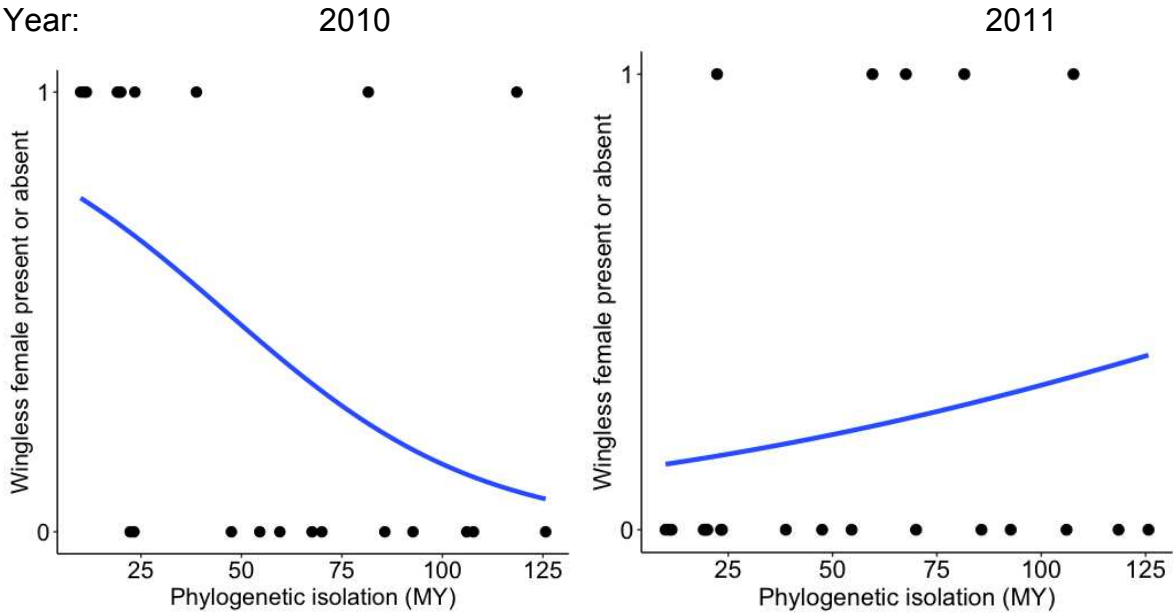
pines has a significant interaction effect only in 6 out of 35 cases (Table S7B), whereas phylohenetic isolation has a significant interaction effect in 9 out of those 35 cases (Table 2). In the 6 cases where both phylogenetic isolation and percentage pines have a significant interaction effect, there are 4 cases where phylogenetic isolation has a smaller p-value than percentage pines (compare between Table 2 and Table S7B). Hence, Phylogenetic isolation explains proportional use of resources more consistently and more strongly than percentage pines in the neighbourhood. Note that the statistics given in the table is of only the interaction term in a model, but the models also accounted for the main effects of the variables in the interaction term. LA = leaf area, LDMC = leaf dry-matter content, C:N = carbon-nitrogen ratio, LPC = leaf phenolics content, TC = total caterpillars, % Pines= percentage pines.

Table S7B: Effects of percentage of pines on proportional use of resources.

Group	Use of	Dependent variable	Effects of	Year	t	*p*	DF
Ectophages	Leaf size	*Per-leaf herbivory*	LA × % Pines	2006	-0.031	0.975	14
			LA × % Pines	2010	-3.159	**0.005**	18
			LA × % Pines	2011	-2.538	**0.021**	17
		Per-individual herbivory	LA × % Pines	2010	0.549	0.590	18
			LA × % Pines	2011	-2.197	**0.042**	17
		Per-leaf abundance	LA × % Pines	2010	-2.268	**0.037**	17
			LA × % Pines	2011	1.390	0.181	18
	Leaf quality	*Per-leaf herbivory*	LDMC × % Pines	2006	0.555	0.588	14
			LDMC × % Pines	2010	0.389	0.702	18
			C:N × % Pines	2006	-0.452	0.658	14
			C:N × % Pines	2010	1.158	0.262	18
			LPC × % Pines	2006	0.338	0.740	14
			LPC × % Pines	2010	0.744	0.467	18
		Per-individual herbivory	LDMC × % Pines	2010	-1.342	0.197	17
			C:N × % Pines	2010	-0.545	0.592	18
			LPC × % Pines	2010	-0.403	0.692	18
		Per-leaf abundance	LDMC × % Pines	2010	1.417	0.174	17
			C:N × % Pines	2010	0.209	0.837	17
			LPC × % Pines	2010	0.615	0.615	18
Leaf gallers	Leaf quality	*Per-leaf abundance*	LA × % Pines	2006	-0.686	0.504	14
			LA × % Pines	2010	0.222	0.827	17
			LA × % Pines	2011	0.222	0.827	17
	Quality	*Per-leaf abundance*	LDMC × % Pines	2006	0.867	0.400	14
			LDMC × % Pines	2010	Invalid model		
			C:N × % Pines	2006	0.987	0.340	14
			C:N × % Pines	2010	5.473	**<0.001**	17
			LPC × % Pines	2006	1.018	0.326	14
			LPC × % Pines	2010	Invalid model		
Leaf miners	Leaf size	*Per-leaf abundance*	LA × % Pines	2010	-1.155	0.263	18
			LA × % Pines	2011	-1.179	0.255	17
	Leaf quality	*Per-leaf abundance*	LDMC × % Pines	2010	0.4	0.694	18
			C:N × % Pines	2010	1.505	0.150	18
			LPC × % Pines	2010	1.351	0.194	17
Parasitoids	Caterpillars	Parasitised caterpillars	TC × % Pines	2010	-2.436	**0.026**	17
			TC × % Pines	2011	-0.904	0.378	18

Supplementary material 8. Logistic regression of presence/absence of species with wingless females

We conducted a logistic regression to test for an effect of phylogenetic isolation on the presence of species with wingless females. Phylogenetic isolation had a negative effect in 2010 (z = -2.079, p = 0.038, df = 20), but no effect in 2011 (z = 0.834, p = 0.404, df = 20).



Chapter 2

Where herbivores find their phenology match: Accessible trees bursting buds rapidly and predictably accumulate matching herbivore species

Where herbivores find their phenology match: Accessible trees bursting buds rapidly and predictably accumulate matching herbivore species

Soumen Mallick, Freerk Molleman, Benjamin Yguel, Jörg Müller, Romain Georges, Stéphanie Llopis, Marjorie Levant, Frédéric Jean, Yasin Gundesli and Andreas Prinzing

Abstract

In deciduous trees, herbivorous insects must match their phenology to that of the trees to have access to suitable food, but succeed doing so only on some trees. We hypothesize that phenology matching is favoured by rapid budburst, attraction of matching herbivores from spatially or phylogenetically proximate trees, and accumulation of matching herbivores on trees that burst buds predictably across years, i.e. that across years consistently occupy the same bud-bursting rank among conspecifics. We studied caterpillars on oaks across three years. Caterpillar size in the field matched bud-burst phenology, and pupation date in the lab matched leaf advancement in the field. Relationships disappeared after accounting for species identity of caterpillars. Caterpillar sizes matched budburst best on trees that were both, rapidly bursting and either proximate to neighbours (spatially or phylogenetically), or bursting buds consistently across years. Trees on which caterpillar size matched budburst better suffered more herbivory. We suggest that matching of caterpillars to present tree phenology is achieved by sorting of matching species into communities over years. Trees can avoid this sorting by growing far from conspecifics or closely related species or by bursting slowly and unpredictably across years, two aspects of plant phenology that have been largely overlooked.

Keywords: budburst, leaf advancement, species sorting, phylogenetic isolation, plant-animal interactions, oak

Introduction

A central theme in studies of plant-herbivore interactions is the matching of phenologies between the plant and the herbivores. For example, deciduous trees have budburst followed by major changes in leaf quality (Hunter & Lechowicz 1992; Wesołowski & Rowiński 2006), and many herbivorous insects need to time their phenology to match this tree phenology in order to be able to feed on fresh leaves (Feeny 1970; Forkner *et al.* 2004). Lepidoptera can match phenology through matching phenology of egg-hatching, overwintering larvae breaking diapause, or adult flight period, and also through movements of flying females, ballooning larvae or even crawling larvae. This phenology matching is thought to be affected mainly by the climate change (Visser & Holleman 2001; Singer & Parmesan 2010; Ekholm 2017). However, even under the same climate in the same site, host plants often vary dramatically in their phenology; for example, individual oak trees within a given forest and during a given year show substantial variation in their timing of budburst (Crawley & Akhteruzzaman 1988; Van Dongen *et al.* 1998). But very few studies tried to understand how herbivores respond to this variation among trees. Does the budburst phenology of individual trees select for matching individuals within populations or for matching species within communities? Are these responses ongoing or have they accumulated over the past years? Can certain tree characteristics or those of the neighbouring trees facilitate or hinder such matching of herbivores to tree phenology? Does matching represent a success of herbivores to follow trees in time, or of trees to exclude non-matching herbivores?

A community of herbivores could have a phenology that matches that of its host tree due to the selection of matching individuals within populations or due to the sorting of matching species within communities. The relative importance of population vs. community-level processes in ecology remains poorly understood (Leibold & Chase 2017). We predict that if this phenology matching of herbivores reflects a selection of individuals within populations, the signal of matching should be maintained even after statistically accounting for species identity of herbivores. In contrast, if it reflects a sorting of species within communities the signal should disappear. These processes of selection or sorting might be ongoing or have accumulated through the past years (Joshi *et al.* 2003; Bazykin & Kondrashov 2011). Ongoing selection or sorting may for instance be due to influx or mortality of herbivores during the current year (Saccheri & Hanski 2006). Influx could be due to strong attraction of matching herbivores; whereas, mortality of mismatching herbivores will result in exclusion (see Fig. 1a). This ongoing selection and sorting could accumulate through past years when a given tree *in situ* harbours a local population or community of herbivores (Fig. 1b). Local populations ("demes") on individual trees have indeed been demonstrated (Mopper 1996; Mopper & Strauss 1998), in particular in herbivores with sedentary females (Van Dongen *et al.* 1998), or where adults move little (Schneider 1984), and also in common herbivores of oak (Molleman *et al.* 2022). We predict that if the matching of herbivores to tree

phenology reflects accumulated selection or sorting, phenology of herbivores should still match that of their respective host tree after transfer of the herbivores into standard laboratory conditions (common garden). In contrast, if it reflects only ongoing selection or sorting, phenologies should match the laboratory condition rather than initial host trees.

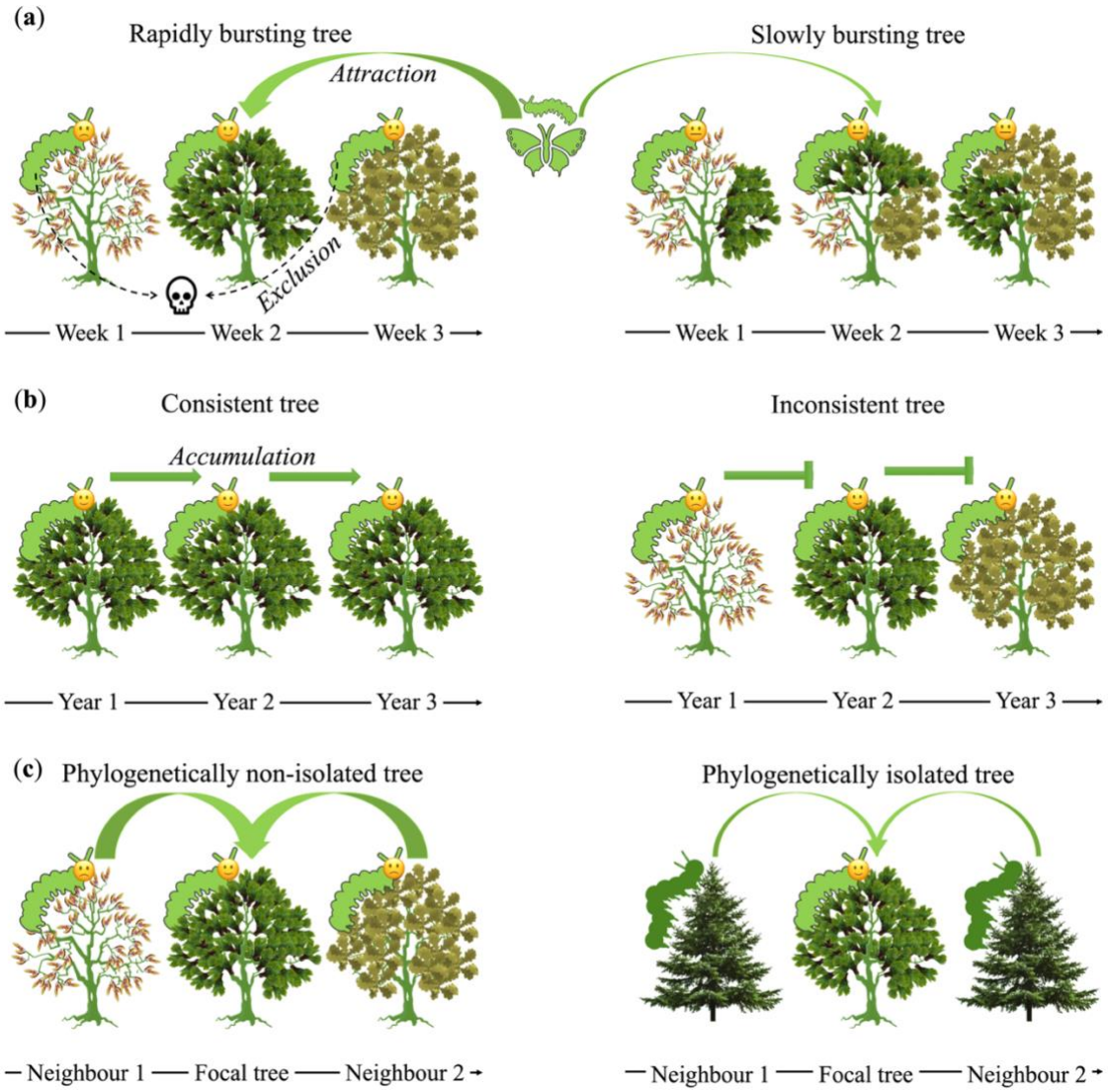


Fig. 1 Three ways how tree characteristics can favour matching of budburst timing by herbivores. **(a)** Rapid bursting of trees. A rapidly bursting tree (left) has the highest concentration of freshly emerged leaves at a given moment. Highest concentration attracts young herbivores in a developmental stage where they need freshly emerged leaves (happy herbivores). Herbivores arriving earlier or later (unhappy herbivores) are strongly mismatching with the emergence stage of the leaves and are hence excluded (skull). On a slowly bursting tree (right), such attraction and exclusion of herbivores are weak (emotionless herbivores). **(b)** Consistent budburst across years (e.g. consistently being the first tree to burst). In case of consistent budburst (left), matching budburst in one year ensures matching budburst in next years. Thus the tree accumulates matching herbivores. In case of inconsistent budburst (right), such accumulation is absent. **(c)** Phylogenetically non-isolated neighbourhood. In case of phylogenetically non-isolated trees (left), young herbivores that do not match the budburst of a host tree can easily move to a neighbouring host tree that matches. In case of phylogenetically isolated trees (right), such movement of herbivores is rare as the neighbouring trees are not suitable hosts for the herbivores of the focal tree.

Beside the timing of budburst, trees in a forest also vary drastically in their speed of budburst (Denéchère *et al.* 2021), and we hypothesize that higher speed may increase the level of phenology matching. Higher speed of budburst increases homogeneity of budburst within a crown i.e. all the buds burst around the same time (Quiring 1993; Quiring & McKinnon 1999). The rapidly bursting trees thus offer a high concentration of freshly emerging leaves to herbivores that match phenology, but herbivores that do not match experience a scarcity of edible leaves (see Fig. 1a). As a consequence, we hypothesize that matching herbivores are attracted by rapidly bursting trees, whereas the mismatching ones are excluded. Accumulating through years, such selective attraction and exclusion of herbivores would result in efficient selection of matching individuals within populations or sorting of matching species within communities (Fig. 1b). However, these mechanisms may or may not be effective everywhere. While exclusion may operate universally as mismatching herbivores might simply die or move away, attraction requires that herbivores can easily move between trees (Fig. 1c). Therefore, we hypothesize that attraction will not be effective when the host trees are isolated either in terms of spatial distance to a conspecific tree or in terms of phylogenetic distance to the spatially proximate neighbours (Vialatte *et al.* 2010). We also hypothesise that accumulation of local selection or sorting across years will not be effective when the trees are unpredictable from the point of view of herbivores: trees that vary their relative timing of budburst across years, e.g. a tree being the first to burst buds in one year while being average in another year. This variation will generate fluctuation in selection pressure on herbivores: the individuals or species that matched tree phenology well in one year will not match in the next year. We hence predict that herbivores should match tree phenology more on rapidly bursting trees, in particular if these trees are spatially or phylogenetically proximate to neighbours or show little variation in relative timing of budburst among years.

Trees might suffer or profit from phenology matching by herbivores. While intuitively herbivores matching their host trees might be considered as an adaptation of the herbivores, this cannot be taken for granted (Visser & Gienapp 2019). Despite increasing the fitness of individual herbivores, phenology matching may not affect the population demography (Reed *et al.* 2013), and hence, the rate of herbivory. We hypothesize that the abundance of the herbivores and the rate of herbivory on individual trees increases with the level of phenology matching if the matching results mainly from ongoing attraction of matching herbivores and accumulation of past selection or sorting of matching herbivores. We alternatively hypothesize that the abundance and herbivory on individual trees decreases with the level of phenology matching if the matching results mainly from the ongoing exclusion of non-matching herbivores.

Phenology matching is often measured as degree of synchrony between two events (e.g. budburst and egg-hatching), but this has been criticized, because some time gap

may actually optimize developmental success (Visser *et al.* 2012; Visser & Gienapp 2019). Such success can be measured as body size: herbivores matching the phenology of an early bursting tree should reach large body size early. However, body size is usually not used to interpret phenology because it is not a distinct phenological event like egg hatching (but see Osorio-Canadas *et al.* 2016). In addition, body size measurement excludes the herbivores that rapidly die due to major mismatch of phenology; for example, hatching long before budburst. Nevertheless, body size gives meaningful information on the success of those that survived. Moreover, body size is sometimes biologically more relevant as information about phenology than is egg hatching. A large mismatch between timing of egg hatching and budburst could be a success for herbivore species that overwinters as larvae (Rozsypal *et al.* 2013). Furthermore, body size allows to study the whole community of herbivores in the field while monitoring the egg hatching is possible only for a single (or few) species with wingless females (Visser *et al.* 2006). This restriction to only one or few species is little helpful when dealing with a study system in which many species do not rely on egg-hatching in spring to achieve phenology matching and species sorting is an essential process. Therefore, we studied the body size of caterpillars across all species, and not the egg hatching.

We studied the phenology matching between oak (*Quercus petraea* (Matt.) Liebl*, Q. robur* L. and their hybrids) trees and caterpillar communities (free-living and semi-concealed Lepidoptera) in a forest in western France. For these trees we determined the relative timing, speed and among-year consistency of budburst, and leaf advancement, and for the caterpillars collected from these trees we recorded body size and, in a common garden in the lab, day of pupation. Our study trees were selected to vary widely in their degree of isolation both in terms of spatial distance to a conspecific tree and in terms of phylogenetic distance to the spatially proximate neighbours. We asked the following questions: (1) Do the communities of caterpillars develop early on early bursting trees, and is this attributable to selection of individuals within species or sorting of species within communities? (2) Have communities of caterpillars from trees with leaves that become tough and unpalatable early been selected to pupate early? (3) Do the herbivores match tree phenology more on rapidly bursting trees, in particular if these trees are spatially or phylogenetically proximate to neighbours or show little among-year variation in timing of budburst relative to other trees? (4) Does herbivory on a tree increase or decrease with the degree to which herbivores match the tree's phenology? We also explored tree characteristics driving species composition of caterpillars in order to understand whether early or late tree phenology relate to different species compositions.

Methods

Field site and study trees

Our field site was the Forest of Rennes (48° 11′ North, 1° 34′ West; *c.* 90 m altitude), a temperate forest in Western France. The forest has an oceanic climate with mean annual temperature of 11.3°C and cumulative annual rainfall of 836 mm. The 3000-hectare forest is divided into 202 parcels most of which are either dominated by oaks (*Q. petraea*, *Q. robur /petraea* hybrids) or pines (*Pinus sylvestris* L.). We studied pairs of oaks, one oak from an oak-dominated parcel, and the other from a pine-dominated parcel. We avoided cross-species pairs. Trees within a pair were only 30-150 meters apart, and pairs were spread across the entire forest. We studied eleven pairs in 2010 and 2011 (earlier used in Yguel et al. 2011 and 2014), and twelve pairs in 2019. Eight of the pairs of 2019 trees had been used during the earlier years, non-used pairs had become unavailable due to forestry activities.

Tree isolation was measured both in terms of spatial distance to nearest oak and in terms of phylogenetic distance to the spatially proximate neighbours. The spatial distance to a conspecific tree was measured from trunk to trunk. This measurement is not to be confused with the distance between two study trees in a pair. Rather, this distance is between one focal tree and the nearest oak in its neighbourhood. The focal trees were growing in the neighbourhood of a total 19 other species, spanning a continuous range of phylogenetic distances from oak (Supplementary material 2, Table. S2). The phylogenetic distance of the focal tree to the spatially proximate neighbours was averaged across trees in crown-contact with the focal tree to obtain “phylogenetic isolation”. Understory trees (height < 6 meters) were not considered because there is little exchange of herbivores between canopy and understory (Corff and Marquis 1999; Gossner et al. 2009).

Determining tree phenology

Early-spring tree phenology was determined as timing of budburst. During each study year, bud development was monitored once every 2-3 days from the beginning of March until all the trees had completed budburst. On every sampling day, ten buds from the upper stratum and ten buds from the lower stratum were randomly selected, and their developmental stage was determined using binoculars. The determination of bud development was done on a three-rank scale (Wesołowski & Rowiński 2006) – a score of 0 for a closed bud, a score of 1 for a bud with folded leaves, and a score of 2 for a bud with unfolded leaves. Hence, the range of budburst score for a tree was between 0 to 40 – 0 when all twenty buds are closed, and 40 when all twenty buds having unfolded leaves.

We defined “date of budburst” as the date when a tree had reached the midpoint of budburst, i.e. a score of 20. Many trees reached this score in-between our visits and so we had to interpolate the date of budburst. To interpolate the timing of budburst, for each tree we fitted a linear regression of the budburst scores against sampling dates – from the last day when the tree last had a score of 0 to the first day when it reached the score of 40 for the first time. We then entered “20” as a result of this linear regression and resolved for “date”. We defined “speed of budburst” as the slope of the above regression line, i.e. the increment in budburst score per day.

The “heterogeneity of budburst” of a tree was determined as the standard deviation of budburst score of individual buds (0 or 1 or 2) per sampling dates and then averaged across dates (of budburst score of tree >0 and <40) within a year. To determine “consistency of budburst” of a tree across years, we first calculated for that tree the standard deviation of midpoint dates of budburst (as defined above) across years, and then took the reciprocal. Of course, a given tree will burst buds earlier in a warmer spring, but might from the point of view of herbivores still be consistently the last tree (for instance) to burst. In order to quantify this consistency in *relative* budburst date we set in every year, the midpoint of budburst of the first tree as 0.

We measured late-spring phenology as the leaf advancement of the trees. In deciduous trees, budburst is followed by a major decrease in leaf quality (Feeny 1968; Harper 1989; Hunter & Lechowicz 1992), and herbivores need to complete feeding before the leaves become unprofitable (Feeny 1968, 1970; Chen *et al.* 2003). To quantify pressures on herbivores to rapidly complete development, we quantified the leaf characteristics at a given point of time. We collected 20 leaves (10 from upper and 10 from lower stratum) from each of the trees between 17th-18th June. We measured the toughness, thickness and chemical composition of the leaves just after the collection in the field. The chemical composition estimation was done in the field using Dualex – a leafclip sensor which measures chlorophyll, nitrogen balanced index, flavonols, and anthocyanins (Goulas *et al.* 2004). Dualex measurements of Flavonols and anthocyanins represent measurements of extractable polyphenols (Cartelat *et al.* 2005). We then measured the leaf dry matter content (LDMC) in the lab. The leaves were first dried in an oven, then weighed (dry mass), then soaked in water for 24 hours and weighed again (wet mass). The dry matter content was calculated as the ratio between the dry mass and wet mass. Finally, we conducted a principal component analysis with all the above variables of leaf state. More than 80% of the variation was explained by PC1, which had positive loadings from toughness, thickness, flavonol, anthocyanin and leaf dry matter content and negative loadings from chlorophyll and nitrogen-balance index. Hence, we used the values of PC1 as leaf advancement scores, i.e. the leaves are more tough and thick and likely had higher overall polyphenol content.

Caterpillar sampling and rearing

In 2010, 2011 and 2019, we sampled caterpillars when all the study trees had just completed budburst. In 2010 and 2011, all trees were sampled once within a span of two days. A sample consisted of two two-meters long branches, one from the upper stratum and the other from the lower stratum. In 2019, each tree was sampled two times, once from the upper stratum and another time from the lower stratum, and the sampling was completed within a span of seven days. The order of stratum was randomly selected, and the cut branches were up to one meter long. In all years, the cut branches were brought to the lab in plastic bags, and searched for caterpillars. As justified in the Introduction, our primary interest was in the body size of the caterpillars. We photographed the caterpillars two days after collection and then measured the length of the caterpillars from their images. For imaging, we waited until the caterpillar rests in a linear posture to avoid the effect of caterpillar movement on length measurements. The advantage of such length measurements is that they do not depend on the gut-filling of a given caterpillar at a time of measure. The images were analysed using ImageJ – an open-sourced image analysis software. We subsequently reared the larva to adulthood and made species determination (details in Supplementary material 3). Some caterpillars turned out to be parasitized of and were excluded in later analyses as parasitization can reduce caterpillar growth (Morales *et al.* 2007).

In 2019, we also monitored the timing of pupation of collected caterpillars, which is a distinct phenological event. Monitoring of timing of pupation was not limited to the above-mentioned samples taken shortly after budburst, but also included samples taken later. We started sampling when the first tree started bursting bud and continued sampling until mid-May. The sampling was done two to three times a week, and only a fraction of study trees was sampled on a sampling day. All caterpillars were reared in standard laboratory conditions in a common garden, and always fed with freshly emerged leaves from common sources. We recorded pupation every one-two days.

Determining herbivore pressure

Higher density of caterpillars can cause more harm to the trees; hence we studied caterpillar density as a parameter of herbivore pressure on the trees. The caterpillar density on a tree was calculated by dividing the number of caterpillars collected by the number of leaves the caterpillars were collected from. In this calculation, we included all the sampling performed during 2019 (see “Caterpillar sampling and rearing”). For 2010 and 2011, we included a second sampling which was done after three weeks of the above-mentioned post-budburst first sampling (see “Caterpillar sampling and rearing”).

Caterpillar abundance is not the only determinant of harm caused by the caterpillars. Fewer caterpillars of larger-bodied species could cause more herbivory than many caterpillars of smaller-bodied species. Hence, in 2010 and 2011 we also studied the rate of herbivory as another parameter of herbivore pressure on the trees. To determine the rate of herbivory, forty leaves (twenty from upper stratum and twenty from lower stratum) were collected from each tree in mid-September. Leaf area was estimated with a 1 × 1-cm^2 dot grid and quantified as the number of dots covering the whole leaf (as described in Yguel et al. 2011). We manually reconstructed for each leaf the missing part that was presumably eaten. We separately summed the area of the whole leaves and the missing parts across forty leaves of each tree. The rate of herbivory on a tree was calculated by dividing the summed area of missing parts by the summed area of the whole leaves.

Data analyses

To test for the matching between the timing of budburst of the host trees and the body size of the caterpillars, we conducted simple linear regressions separately for each year. The regressions explained the average caterpillar lengths on individual trees at the time of sampling (when all the trees completed budburst) by the budburst date of each tree (midpoint of budburst). To determine to what extent this relationship is driven by species sorting, the analyses were repeated accounting for the species identity of the caterpillars. First, to account for the species identity, we conducted an analysis of variance (ANOVA), where the individual caterpillar length was explained by the species identity. Then, we collected the signed residuals from the ANOVA, and treated that as the species-corrected length of the caterpillars. Finally, similar to the initial approach, the species-corrected lengths of the caterpillars were averaged per tree and then explained in a simple linear regression by the day of the year when individual trees reached their midpoint of budburst.

To test for matching between the leaf advancement of the host trees in the field and the timing of pupation of the caterpillars in standard lab condition in a common garden, we conducted a simple linear regression (was done only for 2019, as explained above). The regression explained the average timing of pupation in the lab of caterpillars initially sampled from a given tree by the leaf advancement score of that tree in the field in mid-June (when many caterpillars were pupating). To test if this relationship is driven by species sorting, we followed the similar procedure as stated in the previous paragraph. We recall that all caterpillars in the laboratory had received fresh leaves, independent of the advancement of their host tree in the field.

We tested the relationship between the speed of budburst and the level of budburst-phenology matching by the caterpillars, and how this relationship depends on one of the tree characteristics of interest (spatial isolation, phylogenetic isolation, or the between-

year consistency of budburst). We first calculated the level of budburst-phenology matching and then conducted generalised linear mixed models. We determined the level of budburst-phenology matching on individual trees as the reciprocal of the absolute residuals of the above simple linear regression that explains the average length of the caterpillars by the day of the year when individual trees reached their midpoint of budburst. This variable of "budburst-phenology matching" had a half-normal distribution. Hence, we log transformed this variable with natural base of log. The generalised linear mixed models explained the log-transformed level of budburst-phenology matching by the speed of budburst, one of the tree characteristics, and the interaction between the speed of budburst and the involved tree characteristic. To conduct the generalised linear mixed models, we used the function *geeglm* from the R-package *geepack* (Yan & Fine 2004; Højsgaard *et al.* 2006). This approach allowed us to avoid the overfitting of the models. In these models, we separately used the study year and the tree identity as 'identity' (similar to random effects in mixed models). Because the results of both approaches lead to the same general conclusions, results of the analyses with tree identity as random effects is given only in Supplementary material 4.

We then tested for the effects of phenology matching on the herbivore pressure on individual trees, using linear mixed models. The models explained the caterpillar abundance or the rate of herbivory by the log transformed level of budburst-phenology matching. We used the study year as a random effect.

All statistical analyses were performed using R version 4.2.1 (R Core Team 2022). We used a normal error distribution as the residuals of the models approached normality and homoscedasticity. Influential data points were identified by the visual assessment of four plots: residuals vs fitted values, normal Q-Q, scale-location, and residuals vs leverage (with Cook's distance). At most one influential data point was removed from any analyses.

We finally explored the factors driving species composition of herbivores. Contributions of different tree characteristics were tested using Permutational Multivariate Analysis of Variance (PERMANOVA), under the R package *vegan* (Oksanen et al. 2019).

Results

Data overview

Distance to nearest oak ranged between 0.7 to 16.8 meters. Phylogenetic isolation ranged between 10 to 125.67 millions of years. Timing of budburst ranged between 105 to 130 calendar days in 2010, 91 to 99 calendar days in 2011, and 92 to 115 calenddays in 2019. Speed of budburst was measured as score gain per day (as explained in

Methods) which ranged between 2.61 to 6.55 in 2010, 2.77 to 5.85 in 2011, and 1.24 to 2.99 in 2019. Caterpillar average length per tree ranged between 2.15 to 10.91 mm in 2010, 1.90 to 18.66 mm in 2011, and 5.65 to 14.52 mm in 2019. The average timing of pupation in a standard laboratory condition ranged between 142 to 182 calendar days in 2019. Rate of herbivory ranged between 0.010 to 0.143 in 2010, 0.009 to 0.138 in 2011. Data used in this study is given in Supplementary material 1, Table S.1a and the correlations between variables is summarised in Supplementary material 1, Table S.1b.

Just when all the trees had completed budburst, 147 caterpillars were collected from 4730 leaves in 2010, 121 caterpillars from 7099 leaves in 2011, and 219 caterpillars from 11293 leaves in 2019. In addition, during the subsequent sampling, 90 caterpillars were collected from 5009 leaves in 2010, 82 caterpillars from 7815 leaves in 2011, and 308 caterpillars from 24900 leaves in 2019. We found a total of 46 species, all the species were not present every year. The community composition of caterpillars are summarised in Supplementary material 3, Table S3. Study year was the strongest determinant of the community composition; among the tree characteristics only the timing of budburst had a significant effect (Supplementary material 3). The caterpillar abundance per tree ranged between 0.004 to 0.072 caterpillars per leaf in 2010, between 0.003 to 0.028 in 2011, and between 0.004 to 0.067 in 2019.

Phenology matching by herbivore communities in individual trees

Average caterpillar size in the field decreased with a delay in the budburst of the host tree. This relationship was marginally significant in 2010, and highly significant in 2011 and 2019 (Fig. 2a, Table 1a). However, when accounting for the species identity of caterpillars, the relationship disappeared for 2010 and 2019, and the level of significance was reduced for 2011 (Fig. 2b, Table 1a).

Average timing of pupation in standard laboratory condition in a common garden was earlier when the leaf advancement score of the host tree in the field was high i.e. when the leaves were more tough or more bitter when samples at a common point in time (Fig. 2c, Table 1a). Again, when accounting for the species identity of caterpillars, the relationship disappeared (Fig. 2d, Table 1a). Note that advancement of leaves in mid-June was not related to the date of budburst of the same trees ($t = -1.373$, $p = 0.187$, $df = 18$, adj. $R^2 = 0.04$).

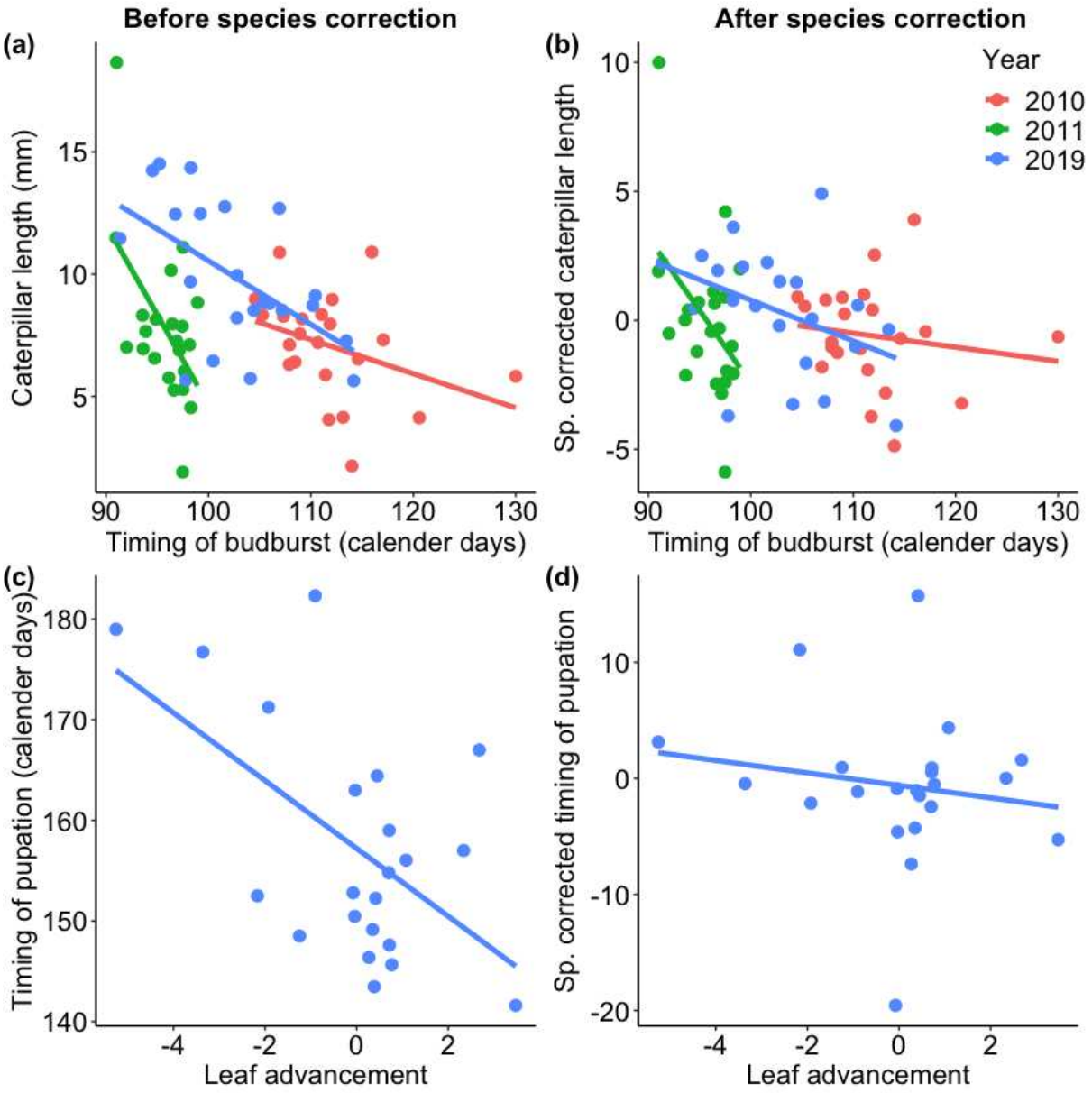


Fig. 2 Phenology matching by herbivore communities in individual host trees in the field (a-b) and in the laboratory (c-d). (**a**) Relationship between caterpillar length in late spring in the field and timing of budburst in 2010 (t = -1.742, p = 0.097, df = 20, adj. R^2 = 0.088), 2011 (t = -2.853, p = 0.010, df = 20, adj. R^2= 0.254), and 2019 (t = -2.978, p = 0.007, df = 20, adj. R^2 = 0.273). (**b**) as (a) but after correcting caterpillar length for species identity by taking residual length, in 2010 (t = -0.687, p = 0.500, df = 20, adj. R^2 = -0.026), 2011 (t = -2.151, p = 0.044, df = 20, adj. R^2 = 0.147), and 2019 (t = -1.998, p = 0.060, df = 20, adj. R^2 = 0.125). (**c**) Relationship between timing of pupation in the laboratory and leaf advancement in the field in 2019 (t = -2.973, p = 0.008, df = 20, adj. R^2 = 0.272; leaf advancement quantified as scores on Principal Component ordination, higher advancement of leaves corresponds to lower nutritional quality for herbivores). (**d**) as (c) but after correcting pupation date for species identity by taking residual length, in 2019 (t = -0.712, p = 0.485, df = 20, adj. R^2 = -0.024).

Table 1: (a) Phenology matching - explaining caterpillar length in the field by timing of budburst separately for each study year, and timing of pupation in the laboratory by leaf advancement in 2019. These univariate analyses were done once before correcting caterpillar length or timing of pupation for species identity (left), and once after correcting it by taking residual length or residual timing (right). Before species correction, caterpillar length reduced with a delay in timing of budburst in 2010 (only marginally), 2011 and 2019. After species correction, caterpillar length did not reduce advanced when the trees had more advanced leaf with a delay in timing of budburst in 2010; it reduced in 2011 and 2019 (only marginally), but the relationship became weaker compared to the relationships before species correction. Before species correction, timing of pupation in the laboratory advanced when the trees in the field had more advanced leaves in mid-June. This relationship disappeared after species correction. **(b)** Explaining phenology matching of herbivores, i.e. increased caterpillar length on early bursting trees as described in (a). Phenology matching is explained by speed of budburst, a tree characteristic (distance to nearest oak or phylogenetic isolation or consistency of budburst) and the interaction between the speed of budburst and the tree characteristic. As justified in the Methods, we used Generalized Estimation Equation Solver (GEE) for these analyses. Phenology matching increased with budburst speed of oak trees that are spatially proximate to other oaks, phylogenetically proximate to neighbours, or burst buds consistently across years (interaction terms of three models in the left column, respectively from top to down). Relationships disappear after correcting for species identity of the herbivores, except for the case of spatially proximate to other oaks (right column). **(c)** Explaining herbivore abundance per leaf and rate of herbivory by phenology matching of herbivores, i.e. increased caterpillar length on early bursting trees. These univariate analyses also were done once before correcting for herbivore species identity (left), and once after correcting it (right). Phenology matching did not predict herbivore abundance, but the rate of herbivory increased at higher phenology matching. Accounting for herbivore species identity did not change the relationships.

		Before species correction				After species correction			
(a)	Matching of	t	*p*	df	adj. R^2	t	*p*	df	adj. R^2
	caterpillar length with timing of budburst								
	Year 2010	-1.742	*0.097*	20	0.088	-0.687	0.500	20	-0.026
	2011	-2.853	**0.010**	20	0.254	-2.151	**0.044**	20	0.147
	2019	-2.978	**0.007**	20	0.273	-1.998	*0.060*	20	0.125
	timing of pupation with leaf advancement								
	Year 2019	-2.973	**0.008**	20	0.272	-0.712	0.485	20	-0.024

(b)	Effects on phenology matching of	Wald	*p*	df	adj. R^2	Wald	*p*	df	adj. R^2
	Distance to nearest oak model			62	0.142			62	0.025
	speed of budburst	29.1	**<0.001**			0.11	0.740		
	distance to nearest oak	53.1	**<0.001**			0.03	0.870		
	speed of budburst : distance to nearest oak	26.6	**<0.001**			0.14	0.710		
	Phylogenetic isolation model			62	0.059			62	0.068
	speed of budburst	8.98	**0.003**			17.92	**<0.001**		
	phylogenetic isolation	2.07	0.150			24.04	**<0.001**		
	speed of budburst : phylogenetic isolation	7.75	**0.005**			2.59	0.110		
	Budburst consistency model			55	0.062			55	0.008
	speed of budburst	12.92	**<0.001**			1.21	0.270		
	consistency of budburst	16.62	**<0.001**			1.75	0.190		
	speed of budburst : consistency of budburst	7.48	**0.006**			0.56	0.460		

(c)	Effects of phenology matching on	t	*p*	df	adj. R^2	t	*p*	df	adj. R^2
	herbivore abuncance	0.800	0.428	62	0.009	1.630	0.108	62	0.035
	rate of herbivory	2.090	**0.043**	41	0.088	3.010	**0.004**	41	0.164

Effects of tree characteristics on the relationship between phenology matching and speed of budburst

We quantified phenology matching as the inverse of the absolute residuals of mean caterpillar size versus budburst date. Phenology matching overall was not correlated to speed of budburst (Table S1b). Nevertheless, phenology matching increased with speed of budburst when focal oaks were either close to another oak, were surrounded by oaks or closely related tree species (low phylogenetic isolation), or had high budburst consistency; in the opposite conditions, phenology matching even decreased with speed of budburst (Fig. 3, Table 1b). The signals of tree characteristics (distance to nearest oak, phylogenetic isolation, and budburst consistency) disappeared when accounting for the species identity of herbivores (Fig. 3, Table 1b).

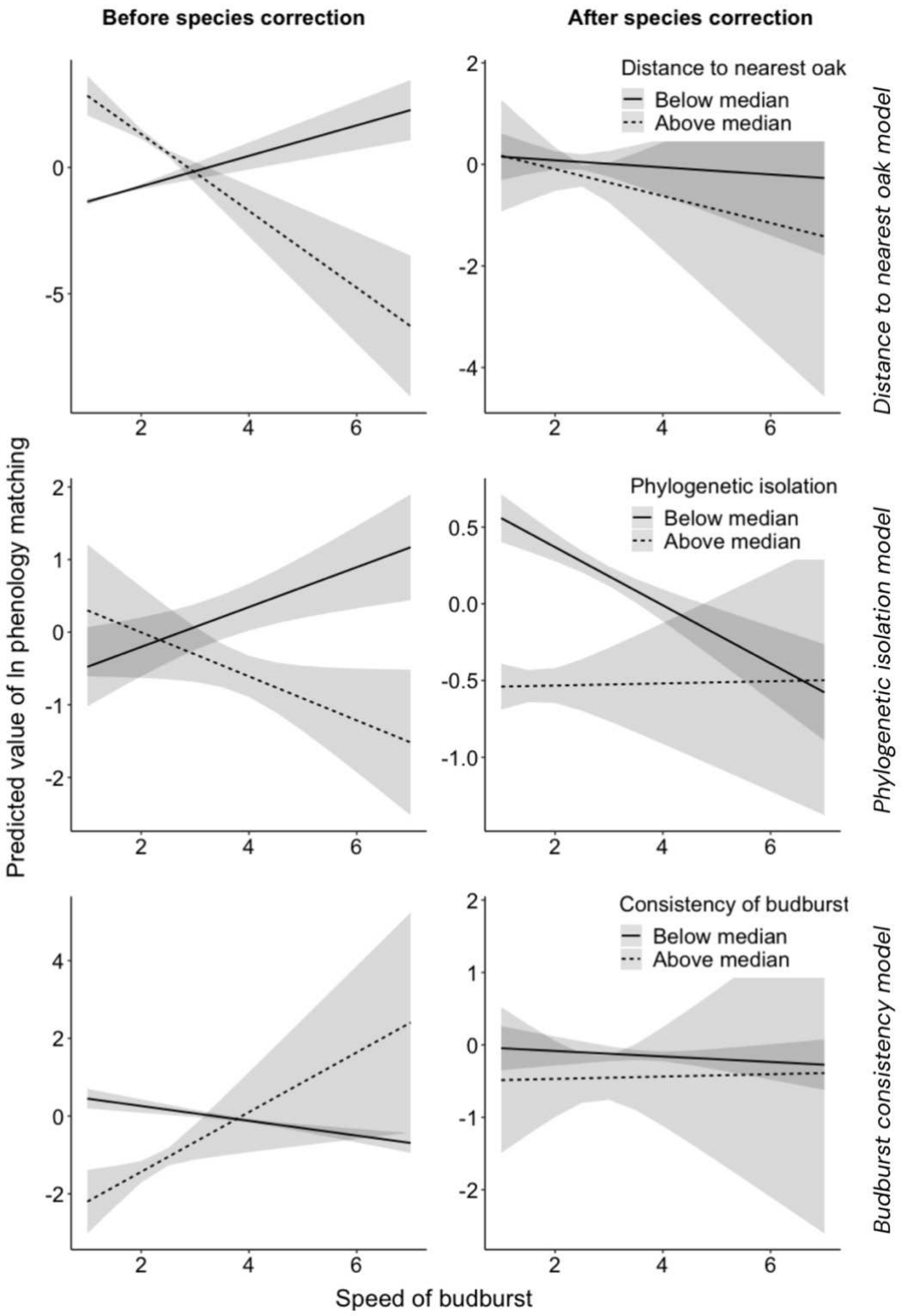


Fig. 3 Explaining phenology matching of herbivores, i.e. increased caterpillar length on early bursting trees as depicted in Fig. 2 (left graphs, y axes). Phenology matching increases with budburst speed (x axis) of oak trees that are spatially proximate to other oaks, phylogenetically proximate to neighbours, or burst buds consistently across years (straight lines in top middle and bottom graphs, respectively). Relationships disappear after correcting for species identity of the herbivores (right

graphs). The statistics of the interaction terms i.e. speed of budburst and one of the tree characteristics are as follows – for top-left wald = 26.60, p <0.001; for top-right wald = 0.14, p = 0.710; for middle-left wald = 7.75, p 0.005; for middle-right wald = 2.59, p = 0.110; for bottom-left wald = 7.48, p 0.006; and for bottom-right wald = 0.03, p = 0.860.

Effects of phenology matching on herbivore pressure of individual trees

The matching of herbivores to budburst was not related to their abundance (Fig. 4, Table 1c). Accounting for the species identity of herbivores did not change this pattern (Fig. 4, Table 1c). However, more matching of herbivores to budburst increased rate of herbivory (Fig. 4, Table 1c). This relationship became stronger when accounting for the species identity of herbivores (Fig. 4, Table 1c).

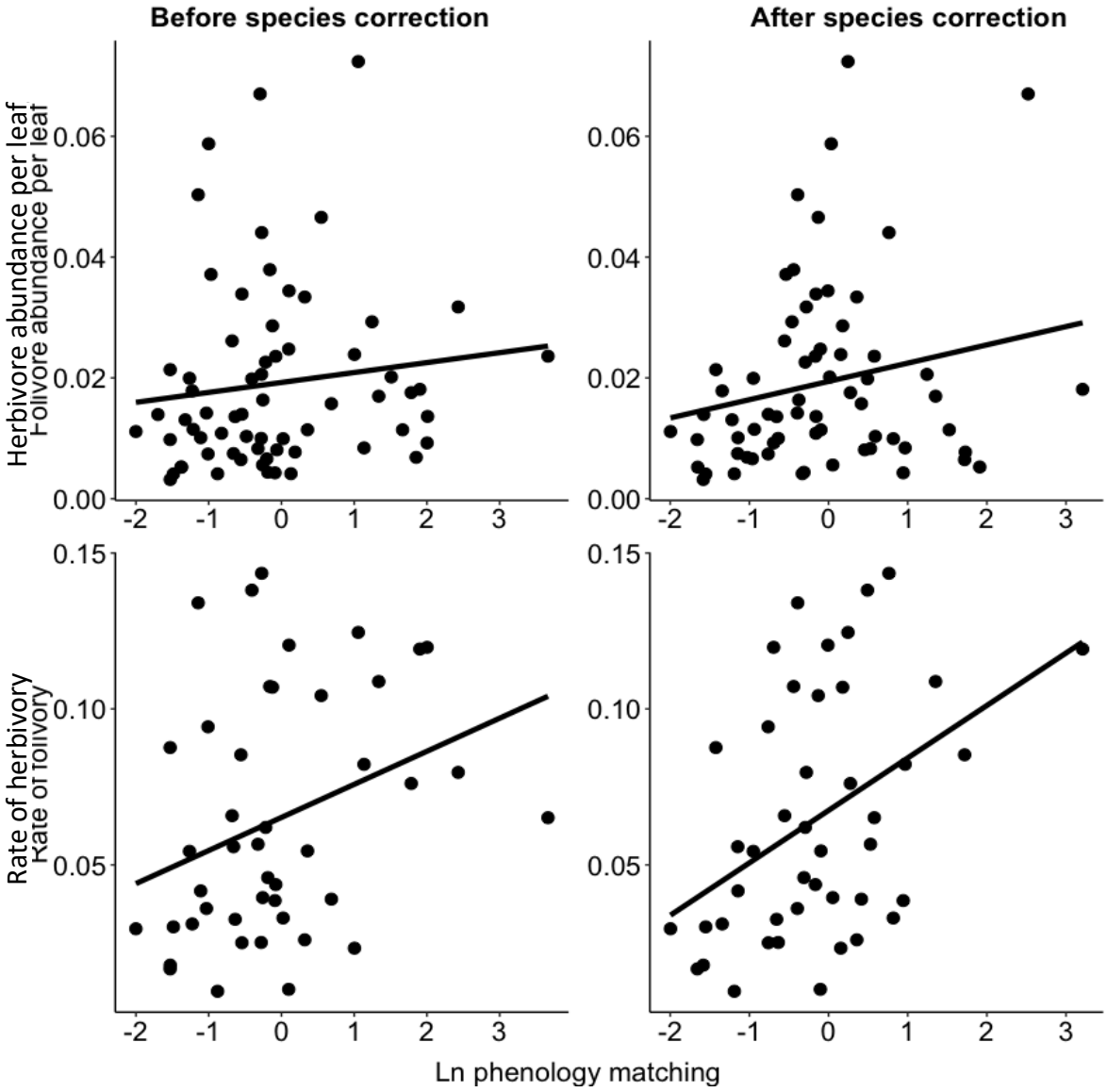


Fig. 4 Explaining herbivore abundance per leaf (top graphs, y axis) and rate of herbivory (bottom graphs, y axis) by phenology matching of herbivores (x axes), i.e. increased caterpillar length on early bursting trees as depicted in Fig. 2. Again, before (left) and after (right) accounting for herbivore species identity. Phenology matching did not predict herbivore abundance, but the rate of herbivory increased at higher phenology matching. Accounting for herbivore species identity did not change the relationships. The statistics are as follows – for top-left t = 0.800, p = 0.428, df = 62, adj. R^2 = 0.009; for top-right t = 1.630, p = 0.108, df = 62, adj. R^2 = 0.035; for bottom-left t = 2.090, p = 0.043, df = 42, adj. R^2 = 0.088; for bottom-right t = -3.010, p = 0.004, df = 41, adj. R^2 = 0.164.

Discussions

Results overview

We tested to what extent the matching of budburst date and caterpillar size, and of leaf advancement and pupation date is due to selection of matching individuals within species or sorting of matching species into communities; and to what extent such matching reflects ongoing and past selection or sorting. We explored how the matching of caterpillar size to budburst date is affected by tree characteristics. We found that herbivores matched the tree budburst date in the field (smaller caterpillars on trees with later budburst), and that this was also maintained in the common garden (later pupation in a common garden of caterpillars from trees with slower leaf advancement). This appeared to be due mainly to sorting of phenology matching species into communities rather than to selection of matching individuals within species because significant matching could no longer be detected when species identity of herbivores was taken into account. To test for tree characteristics that could affect this matching, we then quantified for each tree the degree of matching as the deviation from the regression line of caterpillar size explained by budburst date. Caterpillar size matched budburst date better on rapidly bursting trees, especially on the trees that are little isolated (other oaks nearby, or neighbours were of species that are on average closely related to oak), or show little variation in the relative budburst date across years. As phenology matching was mainly due to sorting of species into communities and matching was affected by tree characteristics, caterpillar community composition was also affected by budburst date (Supplementary material 3). Importantly, the rate of herbivory increased with the level of phenology matching by herbivores: trees have reason to prevent herbivores from matching tree phenology.

Limitations

Our study inevitably has limitations. First, we studied pattern of matching, not the likely processes that cause it; attraction (information perception, movement, decision making etc. of flying moths, ballooning larvae), exclusion (mortality of mismatched caterpillars),

and accumulation of past attraction and exclusion. Therefore, any inferences on processes are speculative. Second, future studies should verify whether leaf maturation rate is consistent among years so that it can select/sort for caterpillar development as our results suggest. Furthermore, to test how robust this result is, data from multiple years is needed to test if pupation in the lab matches leaf-maturation in the field consistently among years. Nevertheless, this matching between pupation in lab and leaf maturation in the field in 2019 is in agreement with the effect of among-year consistency of budburst: both are indicative of selection or sorting in the past. Third, Lepidoptera caterpillars are only part of the herbivores that feed on oak or any other tree. Although, some sawfly larva feed on oak leaves, caterpillars are responsible for most of the leaf damage in oaks in Northern Europe (Glavendekić & Medarević 2010). In our sample, only 1.32% of the larva were of sawflies. Furthermore, Lepidoptera caterpillars may be representative of other herbivores that need to match phenology. Finally, some of the effects we found are significant but still explain only a limited amount of variance (e.g. phenology matching was significantly explained by the interaction of speed of budburst and phylogenetic isolation, but the model explained only 5.9% variation in phenology matching). We do not pretend having found all drivers of matching of caterpillar communities to the phenology of their host tree. Also, the amounts of variances that we explain are not smaller than in earlier studies on phenology matching, and focussing on variation across years rather than across trees (Crawley & Akhteruzzaman 1988; Watt & McFarlane 1991).

Explanations

We found that communities of herbivores match the phenology of individual trees; is this due to selection of individuals into populations or sorting of species into communities? The signal of phenology matching disappeared when accounting for species identity of herbivores. This was the case both in the field (caterpillar size) and in standard laboratory conditions in a common garden (pupation date). If selection of phenology-matching individuals within populations played a dominant role in phenology matching (due to formation of local demes, Mopper 1996), the phenology matching should not have disappeared after species correction. Therefore, the phenology matching by herbivores appears to reflect mainly sorting of matching species within communities. This is further supported by our finding that budburst phenology is the key determining factor of herbivore species composition into communities on individual host trees (Supplementary material 3). Similarly, Crawley & Akhteruzzaman (1988) found that phenology affected herbivore species composition on individual trees. However, other studies did not detect an effect of budburst phenology on caterpillar community composition (Molleman et al. 2022). We stress, however, that the relationship between phenology matching of herbivores and herbivory became stronger after correcting for species identity, and some

of the other relationships only declined without becoming non-significant. These observations would be consistent with formation of local demes on trees.

Is the observed matching of herbivore phenology to tree phenology due to present or past processes? We found that after transfers of the herbivores into standard laboratory conditions in a common garden, the phenology of herbivore communities still matched that of their respective host tree (before species correction). Notably, timing of budburst was not related to leaf maturation, so that any relationship between pupation date and leaf maturation cannot be explained by a correlation between budburst date and pupation date. This maintenance of signal in a common garden thus reflects a strong outcome of selection and sorting that accumulated throughout the past years (de Villemereuil *et al.* 2016). Without selection and sorting by past leaf maturation, the herbivores would match the laboratory conditions rather than initial host trees. This also implies that many herbivore species on a given tree form a local community of persistent phenology. Extensive changes in species composition occur between years (Supplementary material 3), but these changes likely reflect replacement of species of early (or late) phenology by other species of early (or late) phenology.

Why did phenologies of herbivores match best on rapidly bursting trees : attraction of matching herbivores, or exclusion of mismatching herbivores, or their accumulation over past years? First, phenology matching overall was not correlated to speed of budburst, instead, rapid budburst favoured phenology matching by herbivores only under certain conditions. Given that exclusion may operate universally as mismatching herbivores might simply die or move away, it is less likely that exclusion plays an important role here. Second, rapid budburst favoured phenology matching by herbivores especially on the trees that are not isolated either in terms of spatial distance to a conspecific tree or in terms of phylogenetic distance to the spatially proximate neighbours. This strengthening of signal with spatial or phylogenetic proximity could result from increased accessibility of host trees from neighbours through effective attraction (suggested by Vialatte *et al.* 2010). Third, rapid budburst favoured phenology matching by herbivores especially on the trees that time their budburst consistently between years. As explained in the introduction, this strengthening of signal with consistency in timing of budburst between years could result from accumulation of local selection or sorting across years (Mopper & Strauss 1998). Altogether, these observations suggest that ongoing attraction of matching herbivores and the accumulation of local selection or sorting over past years both contribute to the herbivores better matching the phenology of rapidly bursting trees.

Is phenology matching good for the herbivores (as suggested by Visser & Gienapp 2019) or for the trees due to exclusion of non-matching herbivores? As explained above, ongoing exclusion is unlikely to explain the phenology matching we found, and so trees

might not profit. As also explained, phenology matching probably mainly resulted from attraction of matching individuals or species, and from accumulation of past selection or sorting of matching individuals or species. Strong attraction should hence increase the abundance of herbivores. However, we did not observe an increase in abundance of herbivores with an increase in the level of phenology matching. If past selection and sorting of herbivores accumulate to result in bigger herbivores on earlier bursting trees, this means that these particular herbivores had eaten a lot (Posledovich *et al.* 2015). This is consistent with the observed increase in rate of herbivory with an increase in the level of phenology matching. Increased herbivory for an equal number of herbivores indicates more food intake per herbivore, likely increasing its body size at pupation and hence fitness. Hence, our study supports what was so far only assumed (for example, Visser & Gienapp 2019; Ekholm *et al.* 2020): that the phenology matching is good for the herbivores and bad for the trees, albeit it is good only at the level of the herbivore individuals, not populations.

Implications

What should the trees do to avoid excessive herbivory caused by phenology-matching herbivores? First, matching herbivores are attracted by rapid budburst. So, slowing down the speed of budburst and thus increasing within-crown budburst heterogeneity could reduce the attraction of matching herbivores. Consistently, Quiring (1993) found that higher within-crown budburst heterogeneity reduces herbivory by first-instar caterpillars (albeit not in second-instar, which might possibly profit from the scattered presence of buds across a prolonged time in slowly bursting trees). Second, attraction of matching herbivores is highly effective when the tree is surrounded by conspecifics or phylogenetically proximate species. Growing far from conspecifics or phylogenetically proximate species might attract fewer matching herbivores. Consistently, Yguel *et al.* 2011 found lower herbivore pressure on phylogenetically isolated trees. Third, predictability of timing of budburst across years lead to local populations or communities of herbivores better matching the phenology of individual trees. Therefore, fluctuating budburst across years may be a strategy trees could employ to reduce phenology matching and thus herbivory (see also Crawley & Akhteruzzaman 1988; Rousi & Heinonen 2007). Altogether, to avoid excessive herbivory, trees should grow far from conspecifics or closely related species or burst buds slowly across a crown and inconsistently among year, especially when herbivore pressure is high. This speed and consistency of plant phenology have been little considered so far in the phenology literature, which is mainly focused on timing (Van Asch & Visser 2007).

It seems that trees can avoid high herbivory by slowing down the speed of budburst or by fluctuating relative timing of budburst among years or growing far from closely related

species, but why do many trees not do so? There may exist various costs for the trees associated with each of these options. First, slowing down the speed of budburst requires some buds to burst earlier than others, which might reduce the performance of the tree. Earlier bursting buds are more susceptible to be damaged by late frost (Svystun *et al.* 2021) while later bursting buds suffer from the shading by the leaves of the earlier bursting buds (Carabelli *et al.* 2007) and miss opportunities for growth. Second, fluctuating timing of budburst relative to other trees might cost energy for the trees. To advance budburst in the following year, trees might first need to advance leaf senescence in the current year (Marchand *et al.* 2020), which may reduce the energy production in the current year. Third, growing far from closely related species may increase the inter-specific competition and reduce the support from mutualists. These costs might outweigh the benefits due to reduced matching by herbivores.

Conclusions

Our unique approach to study the phenology matching by the whole community of herbivores revealed that present phenology matching on individual trees results mainly from sorting of matching species within communities during past years. We also showed that trees can avoid extensive herbivory by disrupting the process of sorting matching herbivores. Trees can do so by growing far from conspecifics or closely related species, or alternatively by slowing down the budburst speed and varying budburst timing relative to conspecifics across years. Speed and between-year consistency relative to conspecifics are two aspects of plant phenology that should be considered more in studies on plant phenology, so far strongly focused on absolute timing of the moment when on average, buds have reached a certain stage.

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Supplementary materials

Supplementary material 1. Data used, and correlations table

Table S1.a: Data used

Data that were used in this study is given in the below table where leaf advancement is a PCA of several leaf quality parameters (details given in the Methods section), and Sp. corrected values are the signed residuals of an ANOVA of caterpillar length (or pupation timing) against species identity of the herbivore.

Year	Tree ID	Distance to nearest oak (m)	Phylogenetic isolation (MY)	Budburst timing (calendar days)	Budburst speed	Budburst heterogeneity	Budburst consistency	Leaf advancement	Caterpillar length (mm)	Sp. corrected caterpillar length	Pupation timing (calendar days)	Sp. corrected pupation timing	Caterpillar abundance	Rate of herbivory
2010	2.1	7.1	23.50	112	3.65	0.109	0.323	NA	7.96	0.410	NA	NA	0.034	0.120
2010	2.2	4.0	92.67	112	3.55	0.127	0.113	NA	4.05	-3.730	NA	NA	0.010	0.042
2010	4.1	5.7	19.14	107	4.04	0.119	0.128	NA	10.89	-1.805	NA	NA	0.050	0.134
2010	4.2	4.6	107.71	108	6.55	0.055	0.184	NA	7.11	-1.041	NA	NA	0.016	0.039
2010	5.1	1.2	22.33	111	3.73	0.133	0.143	NA	8.35	1.003	NA	NA	0.038	0.107
2010	5.2	8.3	47.50	114	4.97	0.082	0.117	NA	2.15	-4.865	NA	NA	0.021	0.088
2010	6.1	2.9	38.80	111	3.33	0.166	0.321	NA	5.88	-1.915	NA	NA	0.023	0.062
2010	6.2	8.1	125.67	113	4.36	0.081	0.147	NA	4.14	-2.810	NA	NA	0.007	0.094
2010	7.1	1.7	10.80	108	3.48	0.133	0.175	NA	6.41	-1.248	NA	NA	0.029	0.107
2010	7.2	2.0	59.56	105	3.99	0.075	0.632	NA	8.99	0.910	NA	NA	0.025	0.010
2010	8.1	1.1	54.56	115	4.45	0.102	0.075	NA	6.53	-0.707	NA	NA	0.018	0.119
2010	8.2	9.4	118.50	117	3.10	0.175	0.080	NA	7.31	-0.440	NA	NA	0.010	0.033
2010	9.1	0.7	19.64	109	4.43	0.091	0.210	NA	7.56	0.887	NA	NA	0.032	0.080
2010	9.2	6.1	67.56	121	3.43	0.133	0.141	NA	4.12	-3.210	NA	NA	0.014	0.025
2010	10.1	2.7	11.43	105	3.40	0.147	0.258	NA	8.33	0.546	NA	NA	0.072	0.125
2010	10.2	4.2	85.67	116	5.90	0.044	0.092	NA	10.91	3.900	NA	NA	0.004	0.030
2010	13.1	4.9	10.00	111	3.30	0.148	0.183	NA	7.20	-1.094	NA	NA	0.024	0.065
2010	13.2	7.0	81.56	109	3.56	0.152	0.519	NA	8.17	0.251	NA	NA	0.033	0.026
2010	14.1	6.0	23.27	108	2.61	0.216	0.161	NA	6.31	-0.847	NA	NA	0.044	0.143
2010	14.2	6.8	106.05	130	6.14	0.060	0.091	NA	5.83	-0.638	NA	NA	0.006	0.039
2010	X.1	4.9	20.00	107	4.84	0.106	0.364	NA	8.28	0.791	NA	NA	0.047	0.104
2010	X.2	3.6	70.00	112	4.43	0.100	0.113	NA	8.97	2.540	NA	NA	0.007	0.056
2011	2.1	7.1	23.50	96	2.87	0.395	0.323	NA	5.76	-0.438	NA	NA	0.006	0.085
2011	2.2	4.0	92.67	98	3.21	0.385	0.113	NA	5.28	-2.397	NA	NA	0.004	0.046
2011	4.1	5.7	19.14	94	5.85	0.167	0.128	NA	7.66	0.402	NA	NA	0.020	0.138
2011	4.2	4.6	107.71	94	3.63	0.277	0.184	NA	6.95	-2.125	NA	NA	0.004	0.009
2011	5.1	1.2	22.33	97	3.69	0.255	0.143	NA	6.89	-2.830	NA	NA	0.009	0.120
2011	5.2	8.3	47.50	98	3.62	0.249	0.117	NA	6.03	-1.963	NA	NA	0.024	0.023
2011	6.1	2.9	38.80	95	3.78	0.323	0.321	NA	8.15	0.701	NA	NA	0.017	0.109
2011	6.2	8.1	125.67	97	3.52	0.237	0.147	NA	1.90	-5.880	NA	NA	0.003	0.018
2011	7.1	1.7	10.80	92	3.53	0.228	0.175	NA	7.01	-0.509	NA	NA	0.020	0.054
2011	7.2	2.0	59.56	91	4.10	0.196	0.632	NA	18.67	9.995	NA	NA	0.011	0.030

(Continued)

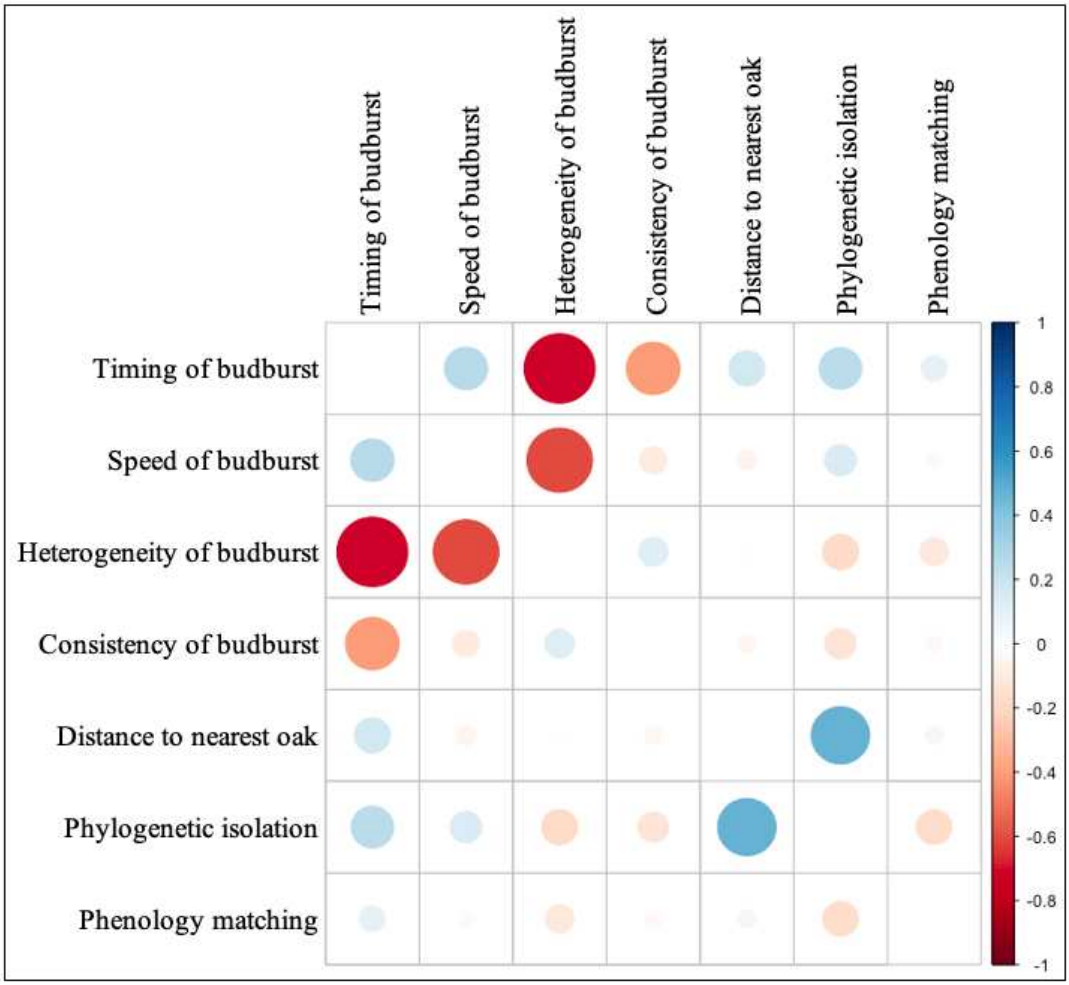
Year	Tree ID	Distance to nearest oak (m)	Phylogenetic isolation (MY)	Budburst timing (calendar days)	Budburst speed	Budburst heterogeneity	Budburst consistency	Leaf advancement	Caterpillar length (mm)	Sp. corrected caterpillar length	Pupation timing (calendar days)	Sp. corrected pupation timing	Caterpillar abundance	Rate of herbivory
2011	8.1	1.1	54.56	98	3.00	0.296	0.075	NA	4.54	-2.057	NA	NA	0.008	0.057
2011	8.2	9.4	118.50	97	3.40	0.360	0.080	NA	7.25	-0.313	NA	NA	0.008	0.082
2011	9.1	0.7	19.64	94	3.52	0.321	0.210	NA	8.32	0.014	NA	NA	0.024	0.044
2011	9.2	6.1	67.56	99	4.33	0.221	0.141	NA	8.84	1.991	NA	NA	0.018	0.031
2011	10.1	2.7	11.43	91	3.38	0.308	0.258	NA	11.49	1.906	NA	NA	0.018	0.076
2011	10.2	4.2	85.67	97	2.99	0.376	0.092	NA	5.26	-2.457	NA	NA	0.014	0.033
2011	13.1	4.9	10.00	96	2.77	0.498	0.183	NA	10.16	1.112	NA	NA	0.014	0.036
2011	13.2	7.0	81.56	97	3.48	0.350	0.519	NA	7.87	0.900	NA	NA	0.010	0.025
2011	14.1	6.0	23.27	95	3.95	0.290	0.161	NA	6.56	-1.209	NA	NA	0.026	0.066
2011	14.2	6.8	106.05	98	3.71	0.224	0.091	NA	11.10	4.210	NA	NA	0.010	0.017
2011	X.1	4.9	20.00	96	3.51	0.310	0.364	NA	7.96	0.662	NA	NA	0.011	0.054
2011	X.2	3.6	70.00	98	3.80	0.239	0.113	NA	7.11	-1.006	NA	NA	0.004	0.039
2019	2.1	7.3	23.50	99	1.24	0.523	0.323	0.765	12.48	2.081	146	-0.538	0.034	NA
2019	5.1	1.2	22.33	105	1.37	0.363	0.143	0.268	8.86	-1.655	146	-7.371	0.029	NA
2019	5.2	7.9	47.50	110	1.83	0.203	0.117	-0.077	9.12	0.587	153	-19.562	0.016	NA
2019	6.1	1.9	38.80	98	1.54	0.319	0.321	0.348	5.67	-3.702	149	-4.276	0.014	NA
2019	6.2	6.0	125.67	107	1.58	0.231	0.147	0.416	12.70	4.910	152	15.722	0.005	NA
2019	7.1	1.7	10.80	103	1.45	0.320	0.175	0.716	8.21	-0.208	148	0.899	0.010	NA
2019	7.2	7.1	59.56	95	1.70	0.385	0.632	3.473	14.25	0.477	142	-5.277	0.011	NA
2019	8.1	1.2	54.56	114	2.99	0.084	0.075	-3.360	5.64	-4.080	177	-0.452	0.007	NA
2019	8.2	9.2	118.50	107	1.56	0.293	0.080	-1.925	8.52	-3.146	171	-2.144	0.007	NA
2019	9.1	1.3	19.64	104	2.40	0.196	0.210	-2.166	5.73	-3.247	153	11.070	0.013	NA
2019	9.2	6.1	67.56	106	1.68	0.252	0.141	0.448	8.81	0.057	164	-1.485	0.011	NA
2019	10.1	3.0	11.43	95	1.49	0.435	0.258	0.383	14.52	2.511	143	-1.060	0.059	NA
2019	10.2	4.3	85.67	110	1.82	0.234	0.092	2.676	8.72	-1.009	167	1.575	0.008	NA
2019	13.1	4.9	10.00	102	1.77	0.272	0.183	-0.042	12.77	2.245	150	-0.894	0.037	NA
2019	13.2	6.1	81.56	98	2.33	0.189	0.519	0.700	14.36	3.610	155	-2.439	0.011	NA
2019	15.1	2.4	16.00	91	1.64	0.422	NA	1.080	11.46	2.235	156	4.349	0.067	NA
2019	16.1	2.1	27.56	100	1.76	0.261	NA	0.710	6.45	0.563	159	0.533	0.005	NA
2019	16.2	7.6	97.43	104	1.56	0.226	NA	-0.905	8.52	1.475	182	-1.151	0.004	NA
2019	17.1	5.0	45.00	98	1.88	0.255	NA	-1.246	9.69	0.775	149	0.936	0.021	NA
2019	17.2	13.7	109.23	97	1.73	0.284	NA	2.336	12.45	1.930	157	0.000	0.008	NA
2019	18.1	16.8	68.50	113	2.59	0.082	NA	-5.254	7.27	-0.362	179	3.128	0.020	NA
2019	18.2	14.2	65.00	103	1.73	0.274	NA	-0.032	9.95	1.510	163	-4.615	0.014	NA

Table S1.b: Correlation table

	Timing of budburst	Speed of budburst	Heterogeneity of budburst	Consistency of budburst	Distance to nearest oak	Phylogenetic isolation	Phenology matching
Timing of budburst		**0.260**	**-0.710**	**-0.400**	0.180	**0.250**	0.090
Speed of budburst	**0.019**		**-0.610**	-0.100	-0.060	0.140	-0.030
Heterogeneity of budburst	**<0.001**	**<0.001**		0.120	-0.010	-0.180	-0.110
Consistency of budburst	**<0.001**	0.384	0.364		-0.040	-0.130	-0.040
Distance to nearest oak	0.108	0.626	0.937	0.716		**0.480**	0.040
Phylogenetic isolation	**0.023**	0.213	0.147	0.255	**<0.001**		-0.180
Phenology matching	0.407	0.803	0.364	0.757	0.701	0.118	

p values

r values



Supplementary material 2. Phylogenetic distances and calculation of phylogenetic isolation

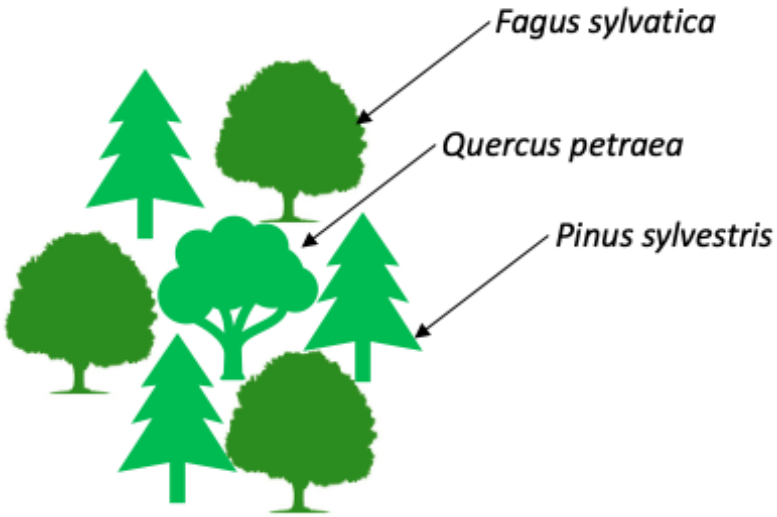
Phylogenetic distance between two tree species is the estimated time (in MYBP) since the evolutionary establishment of the clades of a given neighbouring tree species and of oaks. These phylogenetic distances were taken from Vialatte et al. (2010) and Yguel et al. (2011), based on Magallon et al., 1999, Manos et al., 1999, Wikström et al., 2001, Poinar et al., 2007. Note that this is not the most recent common ancestor, as this would give gymnosperms such as pines an extreme weight (Savard et al., 1994), and would essentially render our parameter a simple percentage of pines in the surroundings of the oaks. Rather, this is the age when both sister clades had established their particular characteristics as hosts for insects (i.e. phylogenetic crown-age of the younger of the two lineages and not stem age). Thus, phylogenetic distance corresponds to the smaller of the two crown ages of the two lineages involved (i.e. of oak and of the other tree species) at the corresponding phylogenetic rank (ranks within Angiosperms inferred from APG 2003, 2009, and checked against 2016).

Table S2: Phylogenetic distance between oaks and other trees in our data set based on crown ages (taken from Vialatte et al. 2010 and Yguel et al. 2011).

Species	Phylogenetic rank of separation with oak						Distance (MY)
Chamaecyparis sp.	Spermatophytes	-	-	-	-	-	140
Pinus sylvestris	Spermatophytes	-	-	-	-	-	140
Abies sp.	Spermatophytes	-	-	-	-	-	140
Ilex sp.	Angiosperms	Asterids	-	-	-	-	128
Tilia sp.	Angiosperms	Rosids	Malvids	-	-	-	89.5
Salix caprea	Angiosperms	Rosids	Fabids	Malpighiales	-	-	68
Populus tremula	Angiosperms	Rosids	Fabids	Malpighiales	-	-	68
Rhamnus sp.	Angiosperms	Rosids	Fabids	Rosales	-	-	58.5
Prunus sp.	Angiosperms	Rosids	Fabids	Rosales	-	-	58.5
Sorbus sp	Angiosperms	Rosids	Fabids	Rosales	-	-	58.5
Pyrus sp.	Angiosperms	Rosids	Fabids	Rosales	-	-	58.5
Malus sp.	Angiosperms	Rosids	Fabids	Rosales	-	-	58.5
Ulmus minor	Angiosperms	Rosids	Fabids	Rosales	-	-	58.5
Alnus glutinosa	Angiosperms	Rosids	Fabids	Fagales	Betulaceae	-	54
Corylus avellana	Angiosperms	Rosids	Fabids	Fagales	Betulaceae	-	54
Betula sp.	Angiosperms	Rosids	Fabids	Fagales	Betulaceae	-	54
Carpinus betulus	Angiosperms	Rosids	Fabids	Fagales	Betulaceae	-	54
Fagus sylvatica	Angiosperms	Rosids	Fabids	Fagales	Fagaceae	Fagus	40
Castanea sativa	Angiosperms	Rosids	Fabids	Fagales	Fagaceae	Castanea	40

Degree of phylogenetic isolation of a tree was calculated as mean phylogenetic distances to the trees with which its crown was in contact (or the projections of crowns of trees on the ground were in contact). Hence, the formula to calculate the

phylogenetic isolation of an oak is $Phylogenetic\ isolation = \frac{\sum_{i=1}^{n} Phylogenetic\ distance}{n}$; where n is the number of trees in crown-contact of that oak. As an example, the case given in the figure below is a *Quercus petraea* surrounded by 3 *Pinus sylvestris* and 3 *Fagus sylvatica*. So, the total number of trees in crown contact with the oak is 6. Phylogenetic distance between a *Quercus petraea* and a *Pinus sylvestris* is 140 MY, and between a *Quercus petraea* and a *Fagus sylvatica* is 40 MY. Hence, the phylogenetic isolation of this oak will be $\frac{140+140+140+40+40+40}{6} = 90\ MY$.



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Supplementary material 3. Species determination, community composition and its determinants

Species determination

All caterpillar photographs were assigned to morpho-species. Those that were successfully reared to adults in the lab were identified to species. In 2010 and 2011, those individuals that died before eclosion (due to parasitism or other causes) were initially assumed to be of the same species as those that eclosed from the same caterpillar morpho-species. However, if the individuals that eclosed from a single morpho-species belonged to multiple species, we re-evaluated the caterpillar morphology taking into account the caterpillar-adult matches. Individuals that could not be identified in this way, were assigned to an 'undetermined' species (43 out of 237 in 2010 and 22 out of 203 in 2011). In 2019, those individuals that died before eclosion (n = 292) were identified by individual barcoding (Savard et al. 1994; Magallon et al. 1999; Manos et al. 1999; Wikström et al. 2001; THE ANGIOSPERM PHYLOGENY GROUP 2003, 2009; Vialatte et al. 2010; Yguel et al. 2011; The Angiosperm Phylogeny Group et al. 2016).

Table S3: Community composition of herbivores on individual trees just after budburst of all the trees.

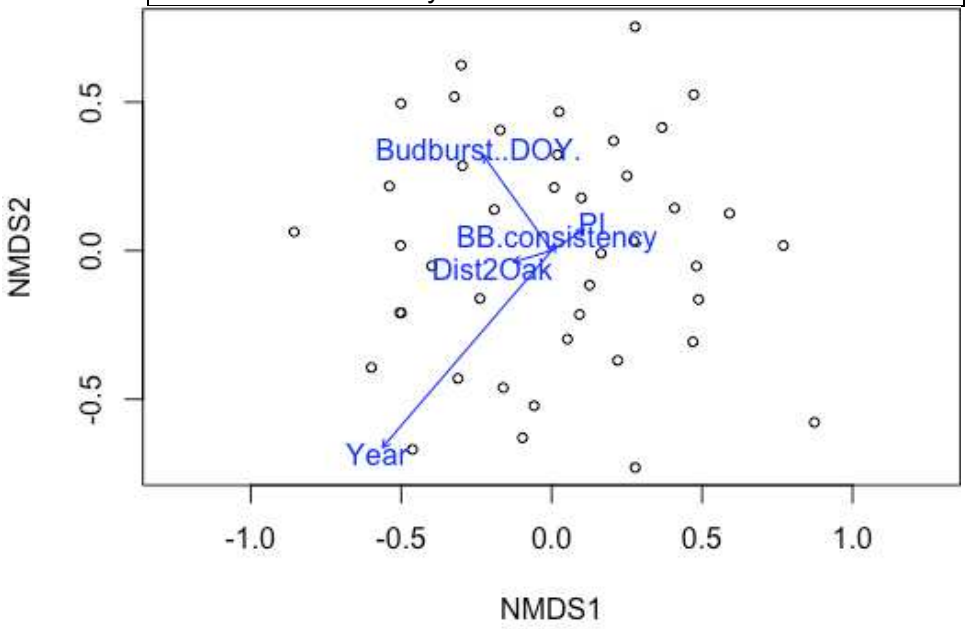
Year	Tree	*Acrobasis consociella*	*Acrobasis repandana*	*Agriopis aurantaria*	*Agriopis marginaria*	*Aleimma loeflingiana*	*Amphipyra pyramidea*	*Anorthoa munda*	*Archips Podana*	*Archips sp.*	*Carcina quercana*	*Catocala promissa*	*Catocala sponsa*	*Coleophora sp.*	*Conistra erythrocephala*	*conistra sp.*	*Conistra vaccinii*	*Cosmia trapezina*	*Ditula angustiorana*	*Ennomos quercinaria*	*Epirrita dilutata*	*Erannis defoliaria*	*Eudemis porphyrana*	*Eudemis profundana*
2010	2.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2010	2.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2010	4.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
2010	4.2	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2010	5.1	0	0	0	0	0	0	0	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0
2010	5.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2010	6.1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2010	6.2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2010	7.1	0	1	0	0	1	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2010	7.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
2010	8.1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0
2010	8.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2010	9.1	0	0	0	0	0	0	0	0	2	0	0	0	0	0	3	0	0	0	0	0	0	0	0
2010	9.2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0
2010	10.1	0	0	1	0	0	0	0	1	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0
2010	10.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2010	13.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
2010	13.2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2010	14.1	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2010	14.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2010	X.1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2010	X.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
2011	2.1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
2011	2.2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0
2011	4.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
2011	4.2	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0
2011	5.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2011	5.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2011	6.1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2011	6.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2011	7.1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0
2011	7.2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2011	8.1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0
2011	8.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2011	9.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2011	9.2	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2011	10.1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
2011	10.2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0
2011	13.1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
2011	13.2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2011	14.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
2011	14.2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2011	X.1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
2011	X.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2019	2.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	2
2019	5.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2019	5.2	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2019	6.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2019	6.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2019	7.1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0
2019	7.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2019	8.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2019	8.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
2019	9.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2019	9.2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
2019	10.1	1	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
2019	10.2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
2019	13.1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
2019	13.2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
2019	15.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2019	16.1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
2019	16.2	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0
2019	17.1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
2019	17.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0
2019	18.1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2019	18.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

(continued)

Year	Tree	*Eupithecia abbreviata*	*Eupithecia sp.*	*Euproctis chrysorrhoea*	*Gypsonoma dealbana*	*Hedya nubifera*	*Lymantra monacha*	*Lymantria dispar*	*Lymantria monacha*	*Operophtera brumata*	*Orthosia cerasi*	*Pammene argyrana*	*Phycita roborella*	*Polyploca ridens*	*Spilonota ocellana*	*Teleiopsis diffinis*	*Tortricidae sp.*	*Tortricodes alternella*	*Tortrix viridana*	*Undetermined*	*Ypsolopha alpella*	*Ypsolopha parenthesella*	*Ypsolopha ustella*	*Zeiraphera isertana*
2010	2.1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	4	2	0	0	0	1
2010	2.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
2010	4.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
2010	4.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0
2010	5.1	0	0	0	0	0	1	0	0	0	2	0	0	0	0	0	0	0	0	3	0	1	0	0
2010	5.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0
2010	6.1	0	0	0	0	1	0	0	0	0	2	0	0	0	0	0	0	0	0	2	0	1	0	0
2010	6.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
2010	7.1	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0
2010	7.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
2010	8.1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	2	1	0	0	0	0
2010	8.2	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
2010	9.1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2010	9.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0
2010	10.1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0
2010	10.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
2010	13.1	0	0	0	0	1	0	0	0	0	2	0	0	0	1	0	0	0	3	0	0	0	0	0
2010	13.2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	2	0	0	0	0
2010	14.1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0	0
2010	14.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
2010	X.1	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0
2010	X.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2011	2.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
2011	2.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
2011	4.1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	2	1	0	0	0	0
2011	4.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
2011	5.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
2011	5.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1
2011	6.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
2011	6.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
2011	7.1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	3	0	0	0	0
2011	7.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
2011	8.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
2011	8.2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0
2011	9.1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	3	0	0	0	1
2011	9.2	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2011	10.1	0	0	0	0	0	0	0	0	0	4	0	0	0	1	0	0	0	0	1	0	1	0	0
2011	10.2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	1
2011	13.1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0
2011	13.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0
2011	14.1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	5	0	0	0	0
2011	14.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2011	X.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
2011	X.2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0
2019	2.1	0	0	0	1	0	0	0	0	7	0	0	1	0	1	1	0	1	0	5	1	1	0	0
2019	5.1	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	3	0	0	0	2
2019	5.2	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	1	1	0	12	0	0	1	2
2019	6.1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	3	0	0	0	1
2019	6.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
2019	7.1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	3	0	0	0	0
2019	7.2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2019	8.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
2019	8.2	0	0	0	1	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0
2019	9.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0	0	0	0
2019	9.2	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0
2019	10.1	0	0	1	0	0	0	0	0	4	1	0	0	0	0	0	0	0	0	2	0	0	0	1
2019	10.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
2019	13.1	0	0	0	1	0	0	0	0	5	0	0	1	0	0	0	1	3	0	5	0	1	0	4
2019	13.2	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	2	0	0	0	0
2019	15.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	3
2019	16.1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
2019	16.2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	2	0	0	0	0
2019	17.1	1	0	0	0	0	0	0	0	2	0	0	1	0	0	0	0	0	0	6	0	1	0	1
2019	17.2	1	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	1	0	1	0	0	1	0
2019	18.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
2019	18.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0

Contributions of different tree characteristics and leaf characteristics to shaping the species composition of herbivore communities on individual trees as identified by Permutational Multivariate Analysis of Variance (PERMANOVA), using the R package *vegan* (Oksanen et al. 2019). Herbivore species composition on individual host trees was mainly determined by the study year. Among the tree characteristics, the budburst phenology is the key determining factor of herbivore species composition into communities on individual host trees.

	NMDS1	NMDS2	r^2	*p*
Year	-0.647	-0.762	0.57	**<0.001**
Timing of budburst	-0.579	0.815	0.12	**0.087**
Distance to nearest oak	-0.958	-0.288	0.01	0.763
Phylogenetic isolation	0.833	0.553	0.01	0.775
Budburst consistency	0.403	0.915	0.00	0.993

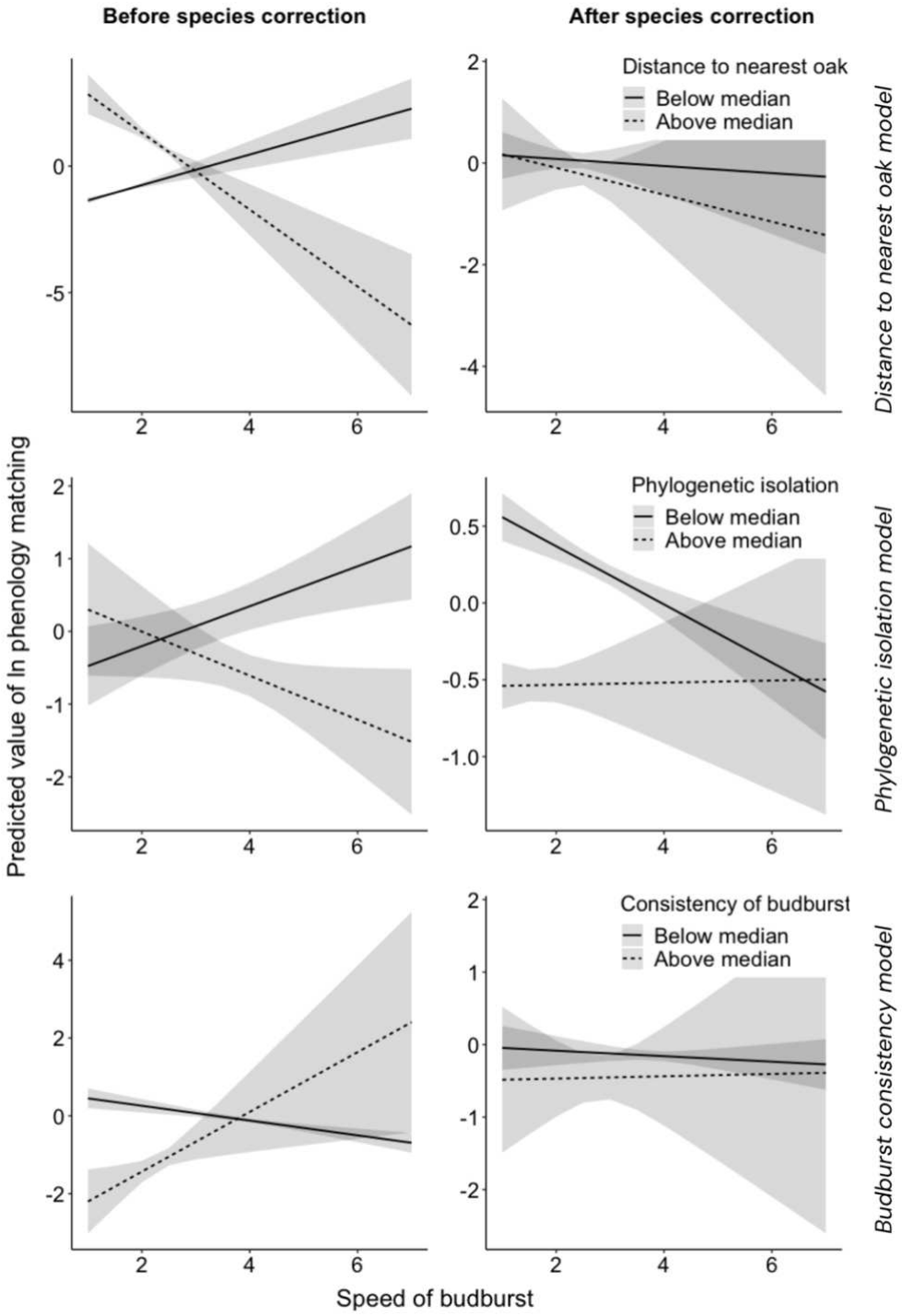


Supplementary material 4. Statistical effects of tree characteristics on the relationship between phenology matching and speed of budburst, using tree as random effect

As justified in the Methods, we studied the effects of tree characteristics on the relationship between phenology matching and speed of budburst using separately tree identity and the study year as random effects. The results of the analyses with study year as random effects are given in the main text (Fig. 3 and Table 1b). The results of the analyses with tree identity as random effects are given in this table. Phenology matching increased with speed of budburst under low distance to nearest oak (significant), or low phylogenetic isolation (marginally significant), or high consistency of budburst across years (marginally significant). The signals of tree characteristics (distance to nearest oak, phylogenetic isolation, and budburst consistency) disappeared when accounting for the species identity of herbivores. Overall, results

from both the approaches lead to the same general conclusions on the interaction terms.

	Before species correction				After species correction			
Effects on phenology matching of	Wald	*p*	df	adj. r^2	Wald	*p*	df	adj. r^2
Distance to nearest oak model			62	0.142			62	0.025
speed of budburst	6.11	**0.014**			0.04	0.84		
distance to nearest oak	9.44	**0.002**			0.01	0.91		
speed of budburst : distance to nearest oak	8.73	**0.003**			0.07	0.79		
Phylogenetic isolation model			62	0.059			62	0.068
speed of budburst	2.44	**0.118**			1.21	0.27		
phylogenetic isolation	1.37	0.242			1.75	0.19		
speed of budburst : phylogenetic isolation	2.78	**0.095**			0.56	0.46		
Budburst consistency model			55	0.062			55	0.008
speed of budburst	2.46	**0.116**			0.05	0.82		
consistency of budburst	5.80	**0.016**			0.16	0.69		
speed of budburst : consistency of budburst	3.73	**0.053**			0.02	0.90		


Before species correction
After species correction
Distance to nearest oak
Below median
Above median
Phylogenetic isolation
Below median
Above median
Consistency of budburst
Below median
Above median
Predicted value of ln phenology matching
Speed of budburst
Distance to nearest oak model
Phylogenetic isolation model
Budburst consistency model

Chapter 3

Biogeographic rules of arthropod body-size across trees in a forest canopy

Biogeographic rules of arthropod body-size across trees in a forest canopy

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Abstract

Body size is arguably the single trait that integrates the largest amount of variation of life histories and physiologies across arthropod species. Biogeographic rules relate large body size in arthropods species to large-scale environmental gradients of decreasing temperature or increasing isolation, reflecting decreasing developmental speed and increasing need for resources to disperse. Temperature and isolation also vary at much smaller scale, such as among different tree individuals within a forest canopy, but we do not know whether larger arthropod species establish on colder and on more isolated trees. We studied moths, spiders and true bugs across oak individuals varying in thermal regime and in phylogenetic isolation from neighbouring trees. We found that in all three taxa the body size significantly relates to host-tree temperature, but strengths and even signs of the relationships shifted between taxa and within taxa between years. Shifts between years can be explained by the fact that in some years high temperature decreases host-plant quality and might thereby indirectly decrease rather than increase developmental speed. In all three taxa, body size increased with phylogenetic isolation at least in some years. In some cases, phylogenetic isolation of host trees reinforced the decline of body size with temperature. Overall, body size of arthropods relates to temperature and isolation even across the micro-archipelago of tree crowns within a forest canopy. We suggest that small and large species are sorted across trees through a mosaic of isolation and heat, and reshuffled through shifts between direct and indirect impacts of heat, ultimately contributing to the emblematic species diversity of forest canopies.

Keywords: budburst, leaf advancement, species sorting, phylogenetic isolation, plant-animal interactions, oak

Introduction

Body size is arguably the single trait that integrates the largest amount of variation of life histories and physiologies across species (Peters 1983; Chown & Gaston 2010; Shingleton 2011). Patterns of body size among populations and among communities can throw light on body-size evolution. Biogeographic rules describe patterns in the body size of species by temperature and isolation (Bergmann 1848; Foster 1964; Gaston *et al.* 2008; Lomolino *et al.* 2013). In warmer regions, populations and species tend to have smaller-body sizes (Atkinson 1994; Atkinson & Sibly 1997). On isolated islands, species often show extremely large or small body sizes (Foster 1964; Lomolino *et al.* 2013). These relationships also occur in arthropods (Kingsolver & Huey 2008; Chown & Gaston 2010; Shelomi 2012). In addition to large-scale geographic variation in temperature and isolation, arthropods also experience such variation at much smaller scales, such as among trees within a forest canopy. Temperature variation among individual trees has been observed within a forest canopy (Haesen *et al.* 2021; Zakrzewska *et al.* 2022), and such temperature variation might influence the species composition of arthropod communities in forest canopy (Rebaudo *et al.* 2016). Furthermore, individual trees within a forest canopy vary drastically in isolation from the point of arthropods. Herbivorous arthropods are usually specialised to use one or a few closely related tree species as hosts (Ehrlich & Raven 1964; Kennedy & Southwood 1984; Brändle & Brandl 2006; Seifert *et al.* 2020). Thus, host trees growing in the neighbourhood of unusable distantly related trees be isolated from the point of view of these arthropods. Such isolation of host trees can be quantified as mean phylogenetic distance from spatial neighbours (phylogenetic isolation from here on; Vialatte *et al.* 2010). Phylogenetic isolation has been shown to reduce arthropod abundance, diversity, and affect community composition on individual trees (Vialatte *et al.* 2010; Yguel *et al.* 2011; Mallick *et al.* 2022). Effects of phylogenetic isolation on specialized herbivorous insects will have knock-on effects on polyphagous herbivores and higher trophic levels such as parasitoids and predators (Yguel *et al.* 2014; Molleman *et al.* 2016). However, we do not know whether temperature and phylogenetic isolation also affect arthropod body size within a forest canopy.

Temperature of trees could affect body size of associated arthropods both directly and indirectly. Warmer temperatures usually speed up the development (transitions between stages) more than the growth, resulting in smaller adult body size (Atkinson 1994; Atkinson & Sibly 1997). Thus, warmer temperatures may decrease body size of individuals within populations, as well as sort for faster developing species of smaller body size within communities (predicted by Bergmann's Rule). Indeed, in many arthropod clades, the latitudinal cline of body size is explained by the occurrence of faster developing species at warmer regions (Kingsolver & Huey 2008; Chown & Gaston 2010; Shelomi 2012). Furthermore, warmer regions can be associated with lower-quality foods for the arthropods; for example, there can be lower amount of nitrogen in the environment, which may reflect in lower nitrogen content in host trees

(Weih & Karlsson 2001; Reich & Oleksyn 2004). Such low-quality food may restrict growth and select against large bodied species. Altogether, we predict that warmer trees sort for smaller species of arthropods into communities, in particular when that relates to reduced food quality (flowchart in Fig. 1).

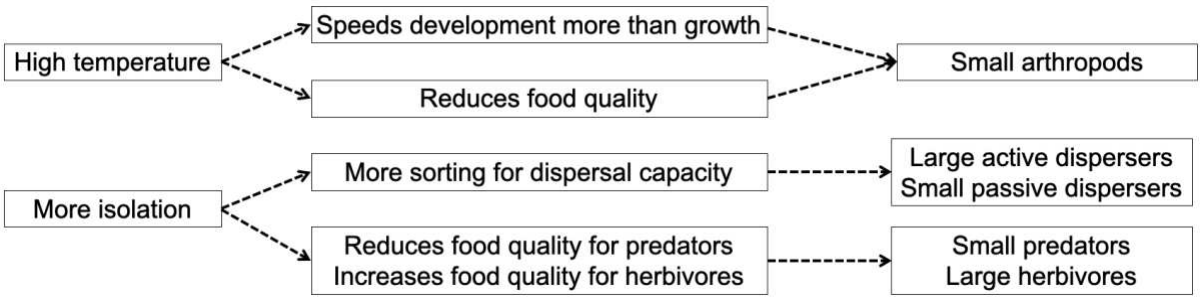

Fig.1 Effects of temperature and isolation on sorting species of arthropods based on body sizes.

Phylogenetic isolation of trees could affect body size of associated arthropods both directly and indirectly. Higher isolation usually sorts for species with higher dispersal capacity (MacArthur & Wilson 1967). Larger body can enhance or hinder dispersal capacity depending on dispersal mode. For active dispersers, larger body allows higher energy storage (fuel for flight), stronger flight muscle and better flight control (Hill *et al.* 1999; Kingsolver & Srygley 2000; Kvist *et al.* 2001; Stevens *et al.* 2014). Whereas, for passive dispersers, larger body results in more drag. Thus, active dispersers tend to disperse better when they are larger, while larger passive dispersers tend to float or drift only short distances (Jung & Croft 2001; Jenkins *et al.* 2007; Bailey *et al.* 2018). Thus, phylogenetic isolation may directly sort for larger species of active dispersers, and smaller species of passive dispersers. Furthermore, growing among phylogenetically distant neighbours can release the trees from competition with neighbours, and thus increase food quality for the herbivores (Molleman *et al.* 2016; Castagneyrol *et al.* 2018). In contrast, for predators, higher phylogenetic isolation of trees can lower food quality, such as lower abundance of prey arthropods (Vialatte *et al.* 2010; Yguel *et al.* 2011). Therefore, higher phylogenetic isolation of trees may sort for larger species of herbivores through higher food quality, and smaller species of predators through lower food quality. Altogether, we predict that phylogenetic isolation of trees sorts for larger active dispersers and herbivores, and smaller passive dispersers and predators (flowchart in Fig. 1).

Phylogenetic isolation of trees could also disrupt the temperature-size relationship of arthropod species by reducing arthropod movements between trees. As stated above, specialist arthropods find it difficult to use trees that are phylogenetically distant from their host trees. These arthropods may even repelled by the odour of such trees (Stratton *et al.* 2019). Hence, arthropods may not move between phylogenetically distant trees as much as they move between phylogenetically proximate trees. Such reduced movement when trees are phylogenetically isolated, may make it more difficult for arthropods to reach host trees with matching temperature, and thus arthropods may also be reluctant to leave mismatching host trees. Therefore,

phylogenetic isolation may weaken the temperature-size relationship of arthropod species.

To study how temperature and phylogenetic isolation of individual trees are associated with body size in arthropods, we characterized for two years arthropod communities across oak individuals varying in thermal regime and in phylogenetic isolation, and derived body-size information from the literature. For each year, we investigated the relationship of arthropod body-size to temperature, phylogenetic isolation, and their interaction. We explored three groups of arthropods – moths (Lepidoptera, herbivores), spiders (Araneae, predators) and true bugs (Heteroptera, including both herbivores and predators). We asked – (1) Are warmer trees dominated by smaller arthropod species? (2) Are more isolated trees dominated by larger active and smaller passive dispersing species? Are more isolated trees dominated by larger herbivore but smaller predator species? (3) Do the relationship between arthropod size and host-tree temperature weaken with increasing phylogenetic isolation of trees ? To explore indirect effects of temperature and phylogenetic isolation on arthropod body size via leaf quality we also investigated if there was a relationships between temperature and leaf quality, temperature and herbivore abundance, phylogenetic isolation and leaf quality, and phylogenetic isolation and herbivore abundance.

Methods

Field site

Our study was conducted in the Forest of Rennes (48° 11′ Noth, 1° 34′ West; *c.* 90 m altitude), a temperate forest in Western France. The forest has an oceanic climate with cumulative annual rainfall 836 mm and mean annual temperature 11.3°C. It is spread over 3000 hectares and divided into 202 parcels. The parcels are usually dominated by either oaks (*Q. petraea*, *Q. robur* and their hybrids) or pines (*Pinus sylvestris* L.). From these parcels triplets and pairs of oak trees were studied (fifteen triplets in 2006, eleven pairs in 2010, and twelve pairs in 2019). The triplets were composed of two trees from oak-dominated parcel and one from pine-dominated parcel. The pairs were composed of one tree from oak-dominated parcel, and the other one from pine-dominated parcel. Trees within a triplet or pair were only 30-150 meters apart, and cross-species triplets and pairs were avoided. The triplets and pairs were spread across the entire forest. The triplets were used earlier in Vialatte *et al.* (2010), and the pairs of 2010 were used earlier in Yguel *et al.* (2011). Eight out of twelve pairs of 2019 were common to that of 2010.

Phylogenetic isolation of study trees

The study trees were growing in the neighbourhood of a total 19 other species, spanning a continuous range of phylogenetic distances from oak (quantified as in

Supplementary material 1). Phylogenetic isolation of trees was measured in terms of average phylogenetic distance to the spatially proximate neighbours (detailed as in Supplementary material 1). Understory neighbours (height < 6 meters) were not considered because there is little exchange of insects between canopy and understory (Corff & Marquis 1999; Gossner *et al.* 2009).

Temperature of study trees

To measure temperature, a sensor (iButton in 2006 and 2010, Tzone in 2019) was placed at the middle of the crown of each tree. The sensors were attached to the under-side of the top-shade of a malaise trap. This avoided heating of the sensors through direct radiation of sun, and recorded temperature that represents what arthropods experiences under the shade of the crown. The iButton sensors were programmed to record measurements every 30 minutes, and the Tzone sensors to record every 10 minutes. The measurements were taken from the beginning of April to the end of June – the active period of most of the arthropod species used in this study. The measurements were averaged to calculate the mean temperature of each tree. Besides that, average of daily maximum and daily minimum temperatures of trees were tested, which lead to the same general conclusion (not shown in this chapter).

Arthropod sampling

Each arthropod taxon was sampled for two years –moths in 2010 and 2019, and spiders and true bugs in 2006 and 2019. To sample caterpillars of moths, branches were cut from upper and lower stratum of each tree. This was done after budburst had just completed (give approx. date as you say till late-May later)and. then three weeks after the first sampling in 2010, and twice a week until late-May in 2019. The cut branches were brought to the laboratory in plastic bags, and visually searched for caterpillars. The caterpillars were reared to adulthood in the laboratory under common conditions. To sample spiders and true bugs, malaise traps were used in 2006, and malaise-interception traps in 2019. A trap was placed at the middle of the crown of each study tree. To protect the samples from degradation, the sample containers of the traps were filled with a mix of water and copper sulfate in 2006, and with ethylene glycol in 2019. The samples were collected from the traps from late May to mid-November. The collection was done once a month in 2006, and in five events of irregular intervals in 2019.

Arthropod identification

To identify the moths, all caterpillars were photographed and assigned to morpho-species. Those that were successfully reared to adults were identified to species based on taxonomic literature. In 2010, those individuals that died before eclosion (due to parasitism or other causes) were assumed to be of the same species as those

that eclosed from the same caterpillar morpho-species. In 2019, those individuals that died before eclosion were identified by individual barcoding. To identify the spiders and true bugs, the specimens from the trap samples were first manually sorted to order level. Subsequently, spiders from 2006 were visually identified to family based on taxonomic literature. Spiders collected in 2019 were identified to species by metabarcoding. True bugs from both the years, were identified to species based on taxonomic literature (details in Vialatte *et al.* 2010).

Determining body size

Sizes of moths, spiders and true bugs were mainly determined by taxonomic literature and data bases. For moths, the species level data on wingspan were taken from Kimber (2021). For spiders in 2006, family level data on body length were taken from Stańska & Stański (2017). For spiders in 2019, the body size was interpreted as the average genetic material per individual that was detected by the metabarcoding process as 'read'. For true bugs, the species level data on body length were taken from Vialatte *et al.* (2010). Community-weighted mean of these values, i.e. sum of body sizes of all individuals divided by total number of individuals, was interpreted as the body size of a given taxon on a given tree (except for spiders in 2019 it was mean 'reads' per individual).

Determining trophic position and dispersal mode

Trophic position and dispersal mode were mainly determined based on taxa. Moth caterpillars found on oak branches are usually herbivores, and fly actively at their adult stage except for females of some winter-active species. Spiders usually predate on other arthropods, and disperse passively through ballooning. Adult true bugs are either herbivores or predators, and usually weak active-flyers. We sub-grouped the true bugs to herbivores or predators (Botting & Bantock 2022), and also calculated community-weighted mean body size separately for each subgroup.

Determining leaf quality and quantity

Leaves with higher polyphenol content tend to be harmful for herbivores (Singh *et al.* 2021). Therefore, we quantified leaf polyphenol as a measurement of leaf quality: higher polyphenol content means lower quality. For the analyses of total polyphenol, the leaves from the cut branches from the year 2006 and 2010 were frozen and lyophilised for 36h, and pooled per stratum to obtain sufficient material. Leaf polyphenol concentration was characterised at the Polyphenols Biotech lab, Bordeaux (France), by spectrometry following the Folin-Ciocalteu indices method and expressed as the percentage of dry mass gallic acid equivalent (Singleton *et al.* 1999). For the leaves from the year 2019, flavanol (which is a major group of polyphenols) was

measured using Dualex – a leafclip sensor just after cutting the branches (Goulas *et al.* 2004).

Moths are one of the major food sources for spiders and predator adult true bugs. Hence, abundance of moth caterpillar per leaf was interpreted as quantity of available food for the predators. To obtain the abundance of caterpillars per leaf, the total number of caterpillars sampled from a given tree was divided by the number of leaves those caterpillars were sampled from.

Data analyses

Multiple-linear-regression models were used to test the effects of temperature and phylogenetic isolation on the body size of a given taxa. The models explained community weighted mean body size of arthropods in a tree by mean temperature, phylogenetic isolation, and the interaction between mean temperature and phylogenetic isolation. The effects of temperature and phylogenetic isolation on body size were interpreted from their respective main effects. The interaction term addressed the effect of phylogenetic isolation on the temperature-size relationship of the taxa. When the interaction term was not significant, it was removed from the model to avoid over-parametrisation. Finally, simple linear regression models were used to test the effects of temperature or phylogenetic isolation on the leaf polyphenol or caterpillar abundance.

All statistical analyses were performed using R version 4.2.1 (R Core Team 2022). A normal error distribution was used as the residuals of the models approached normality and homoscedasticity. Influential data points were identified by the visual assessment of four plots: residuals vs fitted values, normal Q-Q, scale-location, and residuals vs leverage (with Cook's distance). At most two influential data points were removed from any analyses.

Results

Data overview

Data used in this study is given in Supplementary material 2. Phylogenetic isolation ranged between 10 to 125.67 million years. Average temperatures among all the trees were 11.64 °C in 2006, 10.44 °C in 2010 and 12.47 °C in 2019. Average temperatures of individual trees ranged from 11.22 to 12.31 °C in 2006, 9.86 to 11.13 °C in 2010 and between 12.19 to 12.80 °C in 2019. Community weighted wing span of moths ranged between 18.0 to 37.0 mm in 2010, 20.5 to 31.6 mm in 2019. Community weighted body length of spiders ranged between 6.162 to 8.810 mm in 2006, and

'read' per individual ranged between 9.5 to 1412.9 in 2019. Community weighted body length of true bugs ranged between 3.6 to 8. 1 mm in 2006, 4.1to 15.1 mm in 2019.

The community compositions of each taxa are summarised in Supplementary material 3. For moths, 220 caterpillars belonging to 34 species were collected in 2010, and 322 caterpillars belonging to 59 species in 2019. For spiders, 1144 individual belonging to 26 species were found in 2006. For true bugs, 3285 individual belonging to 73 species were found in 2006, and 89 individual belonging to 21 species were found in 2019.

Relationship of leaf polyphenol and herbivore abundance with temperature and phylogenetic isolation

Leaf polyphenol increased (i.e. quality reduced) significantly with an increase in temperature only in 2006 (Table 1). Leaf polyphenol was not predicted by phylogenetic isolation in any study year. Herbivore abundance was not predicted by temperature in any study year. Abundance of moth caterpillars decreased significantly with an increase in phylogenetic isolation in all study years (Table 1).

Table 1: Effects of temperature or phylogenetic isolation on leaf polyphenol content or herbivore abundance (i.e. number of caterpillar per leaf).

Effect on	Effects of	Year	*t*	*p*	df	R^2
Leaf polyphenol	Temperature	2006	2.363	**0.026**	25	-0.040
		2010	-0.130	0.898	18	-0.055
		2019	0.803	0.431	20	-0.017
	Phylogentic isolation	2006	0.487	0.630	25	0.630
		2010	0.434	0.669	20	-0.040
		2019	-0.198	0.845	22	-0.044
Herbivore abundance	Temperature	2010	0.719	0.482	18	-0.026
		2019	0.266	0.793	20	-0.046
	Phylogentic isolation	2010	-5.031	**<0.001**	20	0.537
		2019	-3.749	**0.001**	22	0.362

Relationship of arthropod body-size with temperature and phylogenetic isolation.

For moths, body size was not explained by temperature and phylogenetic isolation in 2010. However in 2019, body size decreased significantly with an increase in temperature, and increased significantly with an increase in phylogenetic isolation (Table 2, Fig. 2). For spiders, body size increased significantly with an increase in temperature of trees, and in phylogenetic isolation of trees (Table 2, Fig. 2). These patterns were consistent between years. Notably, in 2006, higher phylogenetic

isolation reversed the effect of temperature and caused a decrease in body-size with an increase in temperature (Table 2, Fig. 3). For all true bugs (herbivores and predators mixed), in 2006, body size was not related to temperature of the trees, but it increased significantly with an increase in phylogenetic isolation (Table 2, Fig. 2). Moreover, higher phylogenetic isolation reinforced a decrease in body size with an increase in temperature, given by a significant interaction of phylogenetic isolation and temperature (Table 2, Fig. 3). Both of these patterns (the main effect and the interaction effect of phylogenetic isolation) were seen in the sub-group of predators (Table 2, Fig. 3), but not in herbivores. For the herbivores, body size decreased significantly with an increase in temperature. In 2019, body size of all true bugs (herbivores and predators mixed) increased significantly only with an increase in temperature (Table 2, Fig. 2), but this effect was not present in any of the subgroups.

Table 2: Effect of phylogenetic isolation, temperature and their interaction on community weighted mean body sizes of three arthropod groups: moths, spiders and true bugs.

Group	Year		$t_{Temp.}$	$p_{Temp.}$	t_{PI}	p_{PI}	$t_{Int.}$	$p_{Int.}$	R^2	df
Moths	2010		-0.562	0.582	-0.573	0.575	NA	NA	-0.089	16
	2019		-2.717	**0.015**	2.914	**0.010**	NA	NA	0.451	17
Spiders	2006		3.219	**0.003**	2.341	**0.025**	-2.379	**0.023**	0.212	35
	2019		3.972	**0.001**	4.045	**0.001**	NA	NA	0.567	17
True bugs	2006	Mixed	0.290	0.774	2.567	**0.015**	-2.589	**0.014**	0.331	36
		Predators	1.417	0.165	2.762	**0.009**	-2.782	**0.009**	0.190	36
		Herbivores	-4.344	**<0.001**	-0.501	0.619	NA	NA	0.306	37
	2019	Mixed	2.747	**0.015**	-0.015	0.998	NA	NA	0.142	16
		Predators	1.258	0.228	0.177	0.862	NA	NA	-0.025	15
		Herbivores	1.949	*0.069*	0.118	0.908	NA	NA	0.094	16

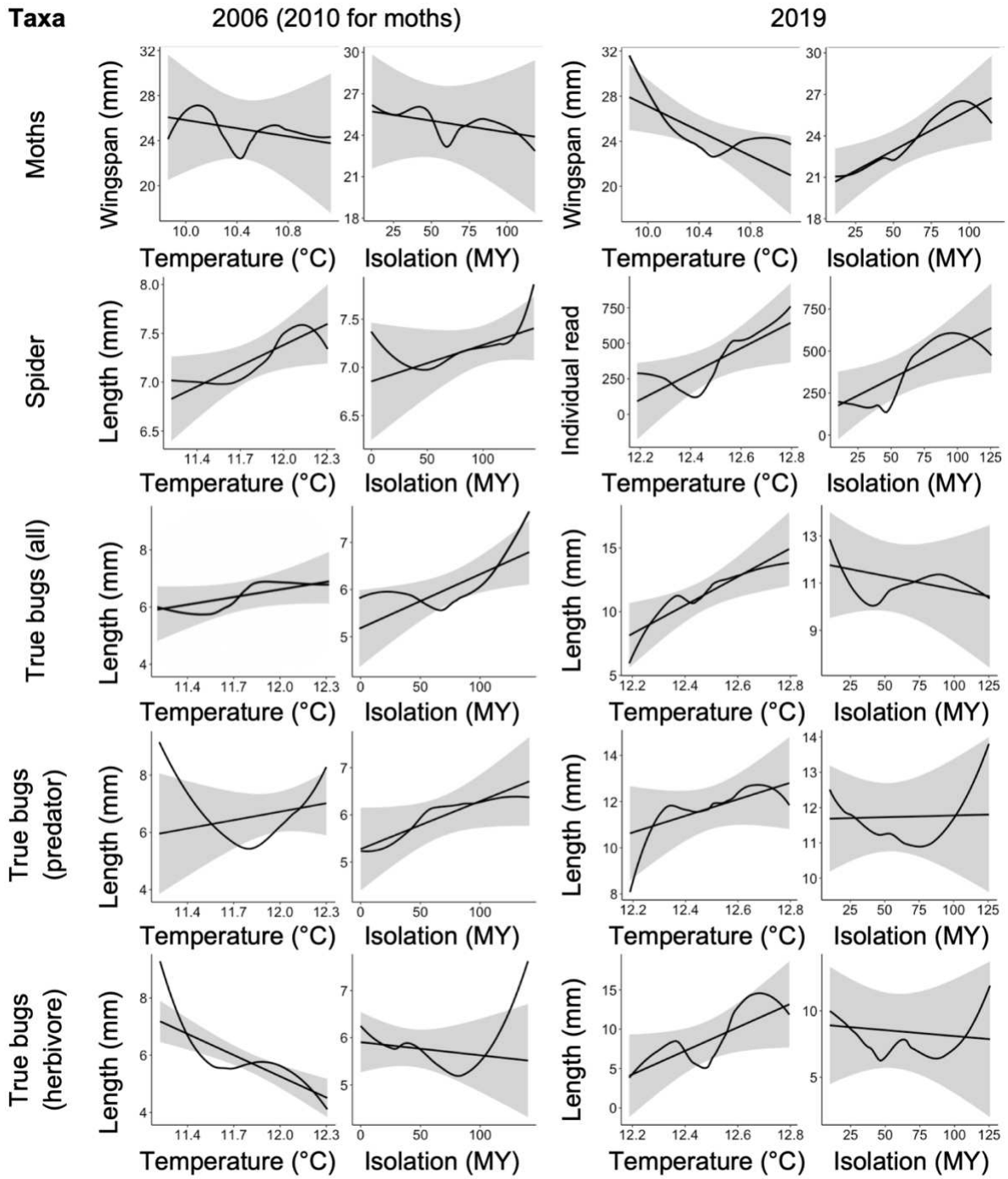

Fig. 2 Plots of main effects of phylogenetic isolation and temperature on community weighted mean body sizes of three arthropod groups: moths, spiders and true bugs. See Table 2 for statistics.

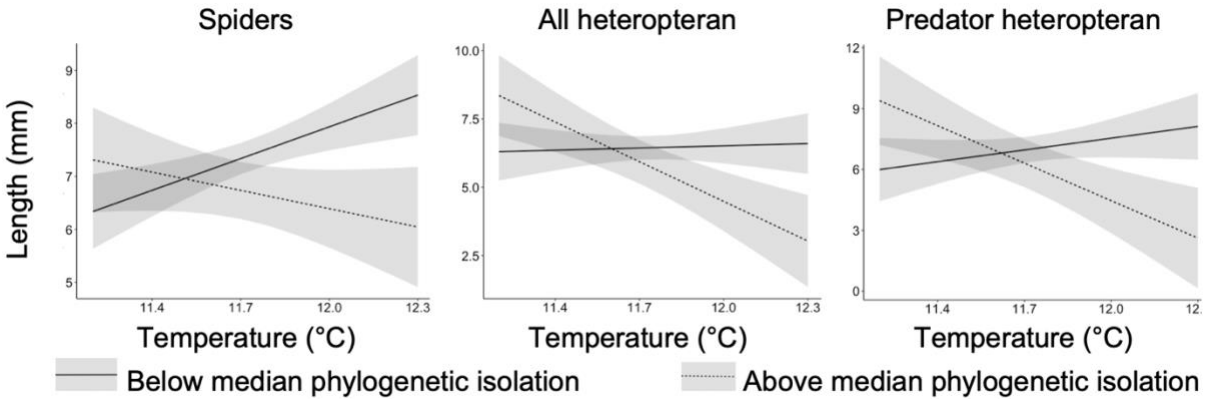

Fig. 3 Plots of interaction effects of phylogenetic isolation and temperature on community weighted mean body sizes of spiders and true bugs. These effects were seen only in 2006. See Table 2 for statistics.

Discussion

Results overview

We found that in all three taxa the body size significantly relates to host-tree temperature, but strengths and even signs of the relationships shifted between taxa and within taxa between years. In all three taxa, body size increased with phylogenetic isolation at least in some years. In some cases, phylogenetic isolation of host trees reinforced the decline of body size with temperature.

Limitations

We studied the patterns of matching of body size to temperature and to phylogenetic isolation, not the likely processes that cause it; development, growth, dispersal capacity, competition, predation and movement. Therefore, any inferences on processes are speculative. Furthermore, the difference in average temperatures among trees within a study year was little over 1°C. Even such little difference in average temperature over a time period can be crucial as it can result in a difference in terms of dree days sufficiently large to favour different arthropod species (Chen *et al.* 2015; Pincebourde & Casas 2019).

Explanations

For the herbivores (moths and subgroup of true bugs), all the significant relationships meant presence of smaller-bodied species on warmer trees. The negative temperature-size relationship of herbivores may have resulted from higher temperatures causing faster development in arthropods, thus selecting for smaller body size (Atkinson 1994; Gilbert & Raworth 1996; Atkinson & Sibly 1997). However, smaller herbivores occupied warmer trees only in some years. Smaller species of

moths were found on warmer trees in 2019, but not in 2010, the coldest year, possibly because sorting of moth species by temperature may not be significant such cold year. Smaller species of herbivorous true bugs were found on warmer trees in 2006 the year when higher temperature reduced leaf quality, but not in 2019 the year when higher temperature did not reduce leaf quality, suggesting that the effect of temperature operated through food quality (Bauerfeind & Fischer 2013).

Among the predators, true bugs showed no relationship of body size to temperature, and spiders, all the significant relationships meant presence of larger-bodied species on warmer trees. The finding that predators tended to be of larger on warmer trees is opposite to what we would expect based on the effect of temperature on developmental speed. Arguably, temperature might possibly be less limiting for metabolic rate in spiders than in insects given the lower metabolic rate of spiders (Anderson 1970). And food quality may even increase with temperature. Flying insects may be more active at higher temperatures (Mellanby & Gardiner 1939; Deutsch *et al.* 2018), and thus spiders that hunt using webs might catch more prey on warmer tree, again suggesting effect of temperature operating through food quality. Increased prey activity might also explain equally positive temperature body size relationships observed across continental scale by Entling *et al.* (2010).

Higher phylogenetic isolation of trees sorted for larger species of arthropods in all three taxa. As hypothesised, larger active dispersers disperse better (Hill *et al.* 1999; Kingsolver & Srygley 2000; Kvist *et al.* 2001; Stevens *et al.* 2014), and thus more isolated trees may sort larger species of actively dispersing moths and true bugs. To our surprise we also found this pattern in spiders, which are passive dispersers that usually drift less when large. Spiders usually disperse after hatching from eggs when they are small (Coyle 1983). Thus, large adult size may not influence the dispersal. Moreover, larger species of spiders that could disperse to isolated trees may have advantage over the smaller species: larger spiders can be better capable of handling lager prey herbivores (Read *et al.* 1987; Lang 1996), which are sorted by more isolated trees. This might allow the larger species of spiders to persist on more isolated trees. Overall, more isolated trees might have sorted for larger active- and passive-dispersers, respectively due to their higher dispersal capacity and higher capability of profiting from available food.

The reinforcement of negative temperature-size relationships on more isolated trees may have resulted from more effective sorting. As explained in the introduction, the rate of arthropod movement between trees is probably lower when the host trees grows among distantly related trees. Under such reduced movement, there would be less influx of species of poorer fitting body size and thus a stronger signal of sorting of arthropods by temperature based on their local performance on the tree. This is similar to the argument that local adaptation within species maybe be negated by influx of non-adapted individuals on non-isolated trees (Tack & Roslin 2010).

Implications

An important mechanism for species coexistence is variation in space and time in relative performance of species (Holt 2001; Chesson 2018). Therefore, the *sorting* of smaller and larger arthropods on individual trees in a forest through a *mosaic* of trees that vary in temperature and phylogenetic isolation may contribute to the emblematic species diversity of forest arthropods. Sorting of arthropod species among trees in a forest is thought to be mainly in response to host-tree species (Seifert *et al.* 2020) or genotype (Wimp *et al.* 2005; Bangert *et al.* 2006; Whitham *et al.* 2006; Tack & Roslin 2011; Barker *et al.* 2018; Faticov *et al.* 2020). In addition, host-tree phylogenetic isolation may also sort for particular arthropod traits (Vialatte *et al.* 2010). We found that more isolated trees tend to sort for larger-bodied arthropods. We also found effects of temperature on arthropod species sorting related to body size. Such sorting promotes different species along the gradient of both temperature and phylogenetic isolation, so that more species have the opportunity to perform well somewhere in the forest than if both temperature and phylogenetic isolation were homogenous. The arthropod diversity can further increase if the species promoted along the gradient of temperature differs with the level of phylogenetic isolation. We indeed found such mosaic of heat and phylogenetic isolation to sort arthropod species based on body sizes – at higher level of phylogenetic isolation temperature-size relationship was stronger in some cases. Moreover, it seems temperature sometimes directly sort for arthropods species, and sometimes through its effect on food quality. Such changes in mechanism of sorting can reshuffle the arthropod species on individual trees between years. Such variation in both space and time can potentially result in a higher overall arthropod diversity. All these processes together may contribute to the emblematic species diversity of forest canopies.

Hosting larger herbivores imposes more risk of excessive herbivory because larger herbivores consume more. To reduce such risk, trees should sort out larger species of herbivores. Trees might do so by increasing the microclimatic temperature or by reducing the phylogenetic isolation. Trees could increase their temperature by reducing transpiration by, for example, opening fewer stomata or keeping stomata open for shorter duration. Such increased microclimatic temperature may sort for smaller herbivore species, and help the trees to avoid excessive herbivory. However, this may be detrimental to photosynthesis and growth (Hew *et al.* 1969; Moore *et al.* 2021). Throughout evolution, trees could reduce phylogenetic isolation by staying in similar environments as their relatives so that they more rarely find themselves surrounded by distantly related tree species. Therefore, selection to avoid phylogenetic isolation is selection against niche shifts. However, while such reduction in phylogenetic isolation may sort for smaller herbivore species, it tends to be associated with increased herbivore abundance and overall herbivory (Yguel *et al.*

2011). Possibly, transpiring less to increase microclimatic temperature might be the relatively effective strategy for trees to avoid excessive herbivory.

Conclusions

We for the first time showed that the community weighted body-sizes of three arthropod taxa relate to the temperature of their host trees. We also showed that higher phylogenetic isolation of trees can sort for larger species of arthropods. Furthermore, higher phylogenetic isolation of trees seem to strengthen the sorting of arthropods by the temperature of the trees. Moreover, the temperature of trees seems to sometimes directly sort for arthropods species of fast or slow metabolism, and sometimes through its effect on food quality. Overall, it seems arthropod species are sorted through a mosaic of temperature and phylogenetic isolation of host trees, where the temperature sometimes seems to operate directly and sometimes through food quality. Such variation in space and time at the scale of individual trees to sort arthropod species may ultimately contribute to the emblematic species diversity of forest arthropods.

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Supplementary materials

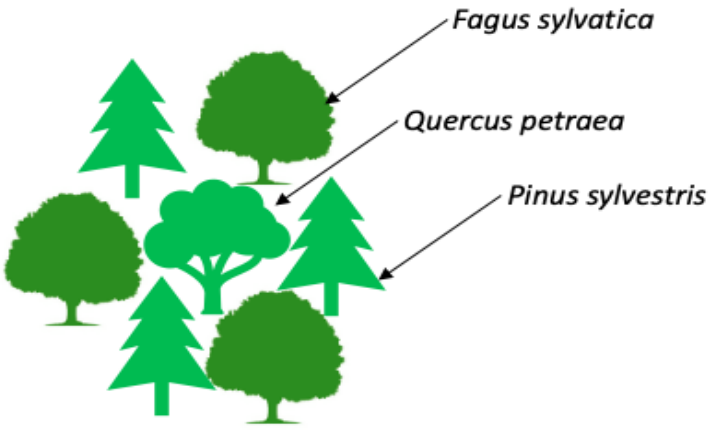
Supplementary material 1. Phylogenetic distances and calculation of phylogenetic isolation

Phylogenetic distance between two tree species is the estimated time (in MYBP) since the evolutionary establishment of the clades of a given neighbouring tree species and of oaks. These phylogenetic distances were taken from Vialatte et al. (2010) and Yguel et al. (2011), based on Magallon et al., 1999, Manos et al., 1999, Wikström et al., 2001, Poinar et al., 2007. Note that this is not the most recent common ancestor, as this would give gymnosperms such as pines an extreme weight (Savard et al., 1994), and would essentially render our parameter a simple percentage of pines in the surroundings of the oaks. Rather, this is the age when both sister clades had established their particular characteristics as hosts for insects (i.e. phylogenetic crown-age of the younger of the two lineages and not stem age). Thus, phylogenetic distance corresponds to the smaller of the two crown ages of the two lineages involved (i.e. of oak and of the other tree species) at the corresponding phylogenetic rank (ranks within Angiosperms inferred from APG 2003, 2009, and checked against 2016).

Table S1: Phylogenetic distance between oaks and other trees in our data set based on crown ages (taken from Vialatte et al. 2010 and Yguel et al. 2011).

Species	Phylogenetic rank of separation with oak						Distance (MY)
Chamaecyparis sp.	Spermatophytes	-	-	-	-	-	140
Pinus sylvestris	Spermatophytes	-	-	-	-	-	140
Abies sp.	Spermatophytes	-	-	-	-	-	140
Ilex sp.	Angiosperms	Asterids	-	-	-	-	128
Tilia sp.	Angiosperms	Rosids	Malvids	-	-	-	89.5
Salix caprea	Angiosperms	Rosids	Fabids	Malpighiales	-	-	68
Populus tremula	Angiosperms	Rosids	Fabids	Malpighiales	-	-	68
Rhamnus sp.	Angiosperms	Rosids	Fabids	Rosales	-	-	58.5
Prunus sp.	Angiosperms	Rosids	Fabids	Rosales	-	-	58.5
Sorbus sp	Angiosperms	Rosids	Fabids	Rosales	-	-	58.5
Pyrus sp.	Angiosperms	Rosids	Fabids	Rosales	-	-	58.5
Malus sp.	Angiosperms	Rosids	Fabids	Rosales	-	-	58.5
Ulmus minor	Angiosperms	Rosids	Fabids	Rosales	-	-	58.5
Alnus glutinosa	Angiosperms	Rosids	Fabids	Fagales	Betulaceae	-	54
Corylus avellana	Angiosperms	Rosids	Fabids	Fagales	Betulaceae	-	54
Betula sp.	Angiosperms	Rosids	Fabids	Fagales	Betulaceae	-	54
Carpinus betulus	Angiosperms	Rosids	Fabids	Fagales	Betulaceae	-	54
Fagus sylvatica	Angiosperms	Rosids	Fabids	Fagales	Fagaceae	Fagus	40
Castanea sativa	Angiosperms	Rosids	Fabids	Fagales	Fagaceae	Castanea	40

Degree of phylogenetic isolation of a tree was calculated as mean phylogenetic distances to the trees with which its crown was in contact (or the projections of crowns of trees on the ground were in contact). Hence, the formula to calculate the phylogenetic isolation of an oak is $Phylogenetic\ isolation = \frac{\sum_{i=1}^{n} Phylogenetic\ distance}{n}$; where n is the number of trees in crown-contact of that oak. As an example, the case given in the figure below is a *Quercus petraea* surrounded by 3 *Pinus sylvestris* and 3 *Fagus sylvatica*. So, the total number of trees in crown contact with the oak is 6. Phylogenetic distance between a *Quercus petraea* and a *Pinus sylvestris* is 140 MY, and between a *Quercus petraea* and a *Fagus sylvatica* is 40 MY. Hence, the phylogenetic isolation of this oak will be $\frac{140+140+140+40+40+40}{6} = 90\ MY$.



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Supplementary material 2: Data used
2006

Tree	Distance to nearest oak (m)	Phylogenetic isolation (MY)	Average temperature (°C)	Spider length (mm)	True bug length (mm)	Predator true bug length (mm)	Prey true bug length (mm)	Polyphenol
B11QPJAPC	3.75	26.67	11.956	7.774	6.000	6.860	5.386	3.584
B11QPJSPC	18.90	60.00	12.170	7.461	5.775	6.500	5.257	5.456
B11QPVAPC	3.50	0.00	11.846	6.173	6.800	7.289	6.462	8.296
B31QRJAPC	6.90	20.00	11.624	6.327	5.544	6.500	4.146	6.440
B31QRJSPC	14.10	78.00	11.850	6.163	3.640	3.300	4.150	4.665
B31QRVAPC	6.60	30.00	11.944	6.750	5.238	5.459	4.750	3.630
C11QRJAPC	6.00	27.70	11.390	7.606	5.783	5.356	7.067	NA
C11QRJSPC	13.60	140.00	11.361	7.428	7.850	8.162	7.482	NA
C11QRVAPC	4.65	47.00	NA	7.432	5.067	5.314	4.720	NA
C21QRJAPC	5.30	26.67	11.288	6.625	7.525	6.967	8.243	NA
C21QRJSPC	6.70	94.80	11.459	6.447	7.580	8.891	5.978	NA
C21QRVAPC	NA	NA	11.629	6.782	4.662	4.933	4.429	NA
C22QRJAPC	5.10	0.00	11.804	8.151	7.409	8.767	5.780	NA
C22QRJSPC	2.15	118.50	NA	7.346	8.082	7.806	9.020	NA
C22QRVAPC	10.40	0.00	NA	8.355	5.864	7.843	4.940	NA
D11QPJAPC	NA	13.33	11.898	7.971	5.357	6.038	4.767	NA
D11QPJSPC	3.60	32.00	12.077	8.810	5.600	5.660	5.300	NA
D11QPVAPC	10.30	13.33	NA	8.476	3.567	3.456	3.900	NA
D31QPJAPC	7.25	10.00	11.642	6.995	5.132	4.561	5.645	7.946
D31QPJSPC	14.80	82.67	11.788	6.872	5.680	7.167	5.043	3.037
D31QPVAPC	3.00	20.00	11.835	7.184	6.656	7.270	5.888	4.318
D32QPJAPC	5.50	10.00	12.001	7.941	7.279	7.118	7.527	6.026
D32QPJSPC	15.10	85.60	12.181	7.392	4.700	5.600	4.100	9.430
D32QPVAPC	3.60	22.22	12.225	8.572	5.195	6.186	4.662	10.479
D41QPJAPC	8.65	43.50	12.202	7.449	4.300	4.980	3.922	7.341
D41QPJSPC	10.90	65.00	12.306	7.256	6.040	7.333	4.100	7.437
D41QPVAPC	13.00	29.40	11.582	6.775	5.322	5.613	5.090	7.873
E21QPJAPC	2.70	15.00	11.758	7.953	6.975	8.443	5.833	NA
E21QPJSPC	18.90	60.00	12.033	6.506	5.200	4.850	5.667	NA
E21QPVAPC	6.70	15.00	11.752	6.661	6.088	6.873	5.394	NA
E41QPJAPC	2.50	29.60	11.555	7.247	6.589	7.756	5.422	4.832
E41QPJSPC	6.50	105.00	11.345	7.265	6.756	7.970	5.238	5.249
E41QPVAPC	7.67	35.85	11.472	6.207	7.638	8.817	6.930	5.442
F21QRJAPC	4.60	55.50	11.221	6.862	7.391	6.659	9.880	3.204
F21QRJSPC	4.40	27.00	11.816	6.740	7.333	7.367	7.233	5.540
F21QRVAPC	9.10	64.67	11.997	7.882	5.127	5.680	4.667	4.712
G11QPJAPC	1.25	21.79	11.746	7.324	6.900	8.167	5.864	NA
G11QPJSPC	9.75	83.42	12.044	7.827	5.980	7.233	5.443	NA
G11QPVAPC	2.70	8.00	11.997	7.030	7.967	9.900	7.000	NA
G21QPJAPC	1.40	5.71	11.469	7.691	5.914	6.217	5.688	6.251
G21QPJSPC	17.40	106.67	11.836	6.750	5.980	5.667	6.450	9.254
G21QPVAPC	4.60	17.14	11.659	6.674	6.671	7.617	5.963	4.774
H21QRJAPC	5.60	16.00	11.477	7.061	6.513	6.253	6.741	5.757
H21QRJSPC	11.90	92.67	12.240	6.650	4.900	4.411	5.529	10.010
H21QRVAPC	9.40	34.29	11.659	7.629	6.113	6.667	5.744	6.673

2010

Tree	Distance to nearest oak (m)	Phylogenetic isolation (MY)	Average temperature (°C)	Moth wingspan (mm)	Polyphenol	Moth abundance
2.1	7.10	23.50	10.320	21.700	21.014	0.034
2.2	4.00	92.67	10.186	37.000	31.097	0.010
4.1	5.70	19.14	10.632	27.050	12.182	0.050
4.2	4.60	107.71	10.295	19.000	18.969	0.016
5.1	1.20	22.33	11.135	25.938	21.732	0.038
5.2	8.30	47.50	11.019	22.000	28.468	0.021
6.1	2.90	38.80	10.454	29.667	13.793	0.023
6.2	8.10	125.67	NA	20.500	19.864	0.007
7.1	1.70	10.80	10.730	24.750	28.237	0.029
7.2	2.00	59.56	10.194	23.833	20.414	0.025
8.1	1.10	54.56	10.091	26.600	26.691	0.018
8.2	9.40	118.50	10.114	26.667	18.157	0.010
9.1	0.70	19.64	10.292	33.500	20.299	0.032
9.2	6.10	67.56	10.352	NA	36.055	0.014
10.1	2.70	11.43	10.563	27.643	16.811	0.072
10.2	4.20	85.67	10.269	19.250	16.456	0.004
13.1	4.90	10.00	NA	25.714	23.094	0.024
13.2	7.00	81.56	10.740	30.955	26.779	0.033
14.1	6.00	23.27	10.512	18.000	14.806	0.044
14.2	6.80	106.05	10.785	18.500	21.332	0.006
X.1	4.90	20.00	9.860	23.857	26.682	0.047
X.2	3.60	70.00	10.437	19.000	28.345	0.007

2019

Tree	Distance to nearest oak (m)	Phylogenetic isolation (MY)	Average temperature (°C)	Moth wingspan (mm)	Spider read per individual	True bug length (mm)	Predator true bug length (mm)	Prey true bug length (mm)	Polyphenol	Moth abundance
2.1	7.30	23.50	NA	23.161	600.2	8.790	7.838	12.600	1.205	0.034
2.2	4.00	92.67	12.289	NA	446.9	12.200	12.200	0.000	0.986	0.001
5.1	1.20	22.33	12.796	21.727	501.1	13.750	13.500	13.833	1.244	0.029
5.2	7.90	47.50	12.488	23.038	179.9	11.367	11.367	0.000	1.296	0.016
6.1	1.90	38.80	12.503	24.308	254.3	13.500	13.500	13.500	1.239	0.014
6.2	6.00	125.67	12.363	26.214	358.4	13.500	13.500	13.500	1.323	0.005
7.1	1.70	10.80	12.589	22.864	197.2	13.314	13.500	13.283	1.199	0.010
7.2	7.10	59.56	12.272	23.444	NA	NA	NA	NA	0.875	0.011
8.1	1.20	54.56	12.188	23.778	185.6	7.263	7.845	5.980	1.498	0.007
8.2	9.20	118.50	12.251	29.000	442.2	4.100	0.000	4.100	1.401	0.007
9.1	1.30	19.64	12.552	23.300	454.1	9.733	9.045	10.814	1.502	0.013
9.2	6.10	67.56	12.519	23.045	629.7	NA	NA	NA	1.225	0.011
10.1	3.00	11.43	12.435	25.900	61.7	13.167	13.000	13.500	1.105	0.059
10.2	4.30	85.67	12.435	25.200	218.8	9.700	9.700	0.000	0.965	0.008
13.1	4.90	10.00	12.495	22.343	145.1	12.500	12.500	0.000	1.267	0.037
13.2	6.10	81.56	12.264	28.643	1412.9	NA	NA	NA	1.185	0.011
15.1	2.40	16.00	12.318	27.880	9.5	11.067	11.100	11.000	1.120	0.067
15.2	7.40	92.00	NA	29.000	400.7	15.140	11.580	18.700	1.437	0.012
16.1	2.10	27.56	12.451	31.500	171.4	9.000	10.633	4.100	1.137	0.005
16.2	7.60	97.43	12.619	31.600	471.5	10.013	10.200	9.700	1.384	0.004
17.1	5.00	45.00	12.397	23.810	52.3	8.318	11.267	7.213	1.254	0.021
17.2	13.70	109.23	12.574	24.333	1125.7	15.125	13.500	16.100	0.785	0.008
18.1	16.80	68.50	12.796	22.222	1059.7	10.050	10.067	10.000	1.578	0.020
18.2	14.20	65.00	12.650	20.500	278.6	14.700	14.700	14.700	1.113	0.014

Supplementary material 3: Community composition of spiders, moths and true bugs

Moths 2010

Tree	*Acrobasis consociella*	*Acrobasis repandana*	*Aglia tau*	*Agriopis aurantaria*	*Aleimma loeflingiana*	*Archips Podana*	*Biston strataria*	*Carcina quercana*	*Catocala promissa*	*Catocala sponsa*	*Cyclophora linearia*	*Ennomos quercinaria*	*Epirrita autumnata*	*Erannis defoliaria*	*Eupithecia abbreviata*	*Eupsilia transversa*	*Hedya nubifera*	*Lymantria dispar*	*Lymantria monacha*	*Operophtera brumata*	*Orgyia antiqua*	*Orthosia cerasi*	*Orthosia incerta*	*Orthosia munda*	*Pammene argyrana*	*Phycita roborella*	*Poecilocampa populi*	*Polyploca ridens*	*Spilonota ocellana*	*Tortrix viridana*	*Ypsolopha parenthesella*	*Ypsolopha ustella*	*Zeiraphera isertana*	Undetermined
2.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	4	1	0	2	5
2.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
4.1	0	0	0	1	0	0	0	2	0	0	0	0	0	1	0	1	1	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	1	5
4.2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	6
5.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	0	0	0	0	0	0	2	1	1	1	8
5.2	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	1	0	3	1	0	0	1
6.1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	3	0	0	0	0	0	0	0	0	1	0	0	3
6.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1
7.1	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	8
7.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	5
8.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	2	0	0	0	4
8.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
9.1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	11
9.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6
10.1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	1	1	0	0	15
10.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
13.1	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	2	0	0	0	0	3	0	0	0	1	0	0	1	4	0	0	1	1
13.2	0	1	0	2	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	3	0	0	0	0	0	0	0	2	0	0	0	6
14.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	6
14.2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
X.1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	1	0	0	0	0	0	0	0	6	0	0	1	2
X.2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

Moths 2019

Tree	*Acrobasis consociella*	*Acrobasis repandana*	*Acrobasis tumidana*	*Agriopis marginaria*	*Agrochola macilenta*	*Aleimma loeflingiana*	*Alsophila aescularia*	*Amphipyra pyramidea*	*Ancylolomia tentaculella*	*Anorthoa munda*	*Archips crataegana*	*Archips podana*	*Archips xylosteana*	*Carcina quercana*	*Catocala sponsa*	*Choristoneura hebenstreitella*	*Chrysoteuchia culmella*	*Coleophora flavipennella*	*Conistra erythrocephala*	*Conistra vaccinii*	*Cosmia trapezina*	*Cymatophorina diluta*	*Ditula angustiorana*	*Diumea fagella*	*Diumea lipsiella*	*Eilema depressa*	*Epirrita dilutata*	*Erannis defoliaria*	*Eudemis porphyrana*	*Eudemis profundana*
2.1	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	3	2	0	0	0	0	0	0	0	0	2
5.1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
5.2	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
6.1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	1
6.2	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
7.1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	3	1	0	0	0	0	1	1
7.2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1
8.1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
8.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
9.1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9.2	2	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
10.1	1	1	0	3	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	2
10.2	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0
13.1	0	3	0	2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1
13.2	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
15.1	0	0	0	0	0	0	0	2	0	0	1	0	0	0	1	0	0	0	0	4	1	0	0	0	1	0	0	1	0	2
15.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0
16.1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	2	0	0	0	0	0	0	0	0	0
16.2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0
17.1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	2
17.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0
18.1	4	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
18.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1

Tree	*Eupithecia abbreviata*	*Euproctis chrysorrhoea*	*Eupsilia transversa*	*Favonius quercus*	*Griposia aprilina*	*Gypsonoma dealbana*	*Hemithea aestivaria*	*Lymantria dispar*	*Lymantria monacha*	*Malacosoma neustria*	*Operophtera brumata*	*Orthosia cerasi*	*Orthosia cruda*	*Pandemis cerasana*	*Pandemis corylana*	*Phycita roborella*	*Poecilocampa populi*	*Polyploca ridens*	*Psoricoptera gibbosella*	*Ptycholoma lecheana*	*Spilonota ocellana*	*Teleiopsis diffinis*	*Tortricodes altemella*	*Tortrix viridana*	*Ypsolopha alpella*	*Ypsolopha parenthesella*	*Ypsolopha ustella*	*Zeiraphera isertana*	*Undetermined*
2.1	0	0	0	0	0	1	0	0	0	0	9	0	0	0	0	1	0	0	0	1	1	1	2	0	1	1	0	1	2
5.1	0	0	0	0	0	1	0	0	0	0	3	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	3	2
5.2	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	1	3	2
6.1	0	0	1	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0
6.2	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7.1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
7.2	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
8.1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	1
8.2	0	0	0	0	0	1	0	0	1	0	2	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
9.1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1
9.2	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	2	1
10.1	0	1	0	1	0	0	0	0	0	0	19	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	3
10.2	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0
13.1	0	0	0	0	0	1	1	0	0	0	10	0	0	0	0	1	0	0	1	0	0	0	4	0	0	2	0	6	1
13.2	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
15.1	1	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	3
15.2	0	0	0	1	1	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
16.1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
16.2	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
17.1	2	0	0	0	0	0	0	0	0	0	8	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	4	1
17.2	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	1	0	1
18.1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
18.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

Spiders 2006

Tree	*Achaearanea simulans*	*Amaurobus similis*	*Anelosimus vitatus*	*Anyphaena accentuata*	*Araneus diadematus*	*Araniella opisthographa*	*Ballus chabyleius*	*Bathyphantes gracilis*	*Centromerus serratus*	*Cetonana laticeps*	*Clubiona brevipes*	*Clubiona corticalis*	*Clubiona terrestris*	*Cyclosa conica*	*Diaea dorsata*	*Enoplognatha ovata*	*Episinus maculipes*	*Erigone atra*	*Ero aphana*	*Ero tuberculata*	*Gibbaranea gibbosa*	*Harpactea hombergi*	*Hypomma cornutum*	*Lathys humilis*	*Lepthyphantes minutus*	*Linyphia triangularis*
B11QPJAPC	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	1	0	0
B11QPJSPC	0	0	0	6	0	0	2	0	0	1	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0
B11QPVAPC	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0
B31QRJAPC	0	0	0	5	0	0	2	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
B31QRJSPC	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B31QRVAPC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
C11QRJSPC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C11QRVAPC	0	0	0	5	0	0	1	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
C21QRJAPC	1	0	0	3	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
C21QRJSPC	1	0	0	7	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C21QRVAPC	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
C22QRJAPC	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C22QRJSPC	0	0	0	3	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C22QRVAPC	0	0	0	2	0	0	3	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
D11QPJAPC	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
D11QPJSPC	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
D11QPVAPC	0	0	0	2	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
D31QPJAPC	0	0	0	3	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
D31QPJSPC	0	0	0	1	0	0	0	0	0	3	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
D31QPVAPC	0	0	1	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
D32QPJAPC	0	1	0	2	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0
D32QPJSPC	0	0	0	1	0	0	3	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
D32QPVAPC	0	0	0	4	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0
D41QPJAPC	0	0	0	7	0	0	6	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
D41QPJSPC	0	0	0	7	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
D41QPVAPC	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E21QPJAPC	0	0	0	3	1	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E21QPJSPC	0	0	0	1	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
E21QPVAPC	2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
E41QPJAPC	0	0	0	9	0	0	4	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
E41QPJSPC	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
E41QPVAPC	0	0	0	8	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	2	0	0	0	1	0	0
F21QPJAPC	0	0	0	3	0	0	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
F21QPJSPC	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
F21QPVAPC	0	0	1	5	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
G11QPJAPC	0	0	0	5	0	0	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0
G11QPJSPC	0	0	0	2	0	0	2	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
G11QPVAPC	0	0	0	3	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0
G21QPJAPC	0	0	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
G21QPJSPC	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
G21QPVAPC	0	0	0	2	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
H21QRJAPC	0	0	0	3	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
H21QRJSPC	0	0	0	4	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
H21QRVAPC	0	0	0	2	1	1	2	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0

(Continued)

Tree	*Misumena vatia*	*Nuctenea umbratica*	*Paidiscura pallens*	*Parasteatoda simulans*	*Philodromus aureolus*	*Philodromus collinus*	*Philodromus dispar*	*Philodromus longipalpis*	*Philodromus praedatus*	*Philodromus rufus*	*Pocadicnemis juncea*	*Salticus zebraneus*	*Scotina celans*	*Synaema globosum*	*Tenuiphantes flavipes*	*Tenuiphantes mengei*	*Tenuiphantes tenuis*	*Tetragnatha obtusa*	*Theridion mystaceum*	*Theridion pinastri*	*Theridion tinctum*	*Theridion varians*	*Xysticus cristatus*	*Xysticus lanio*	*Zygiella atrica*	Undetermined
B11QPJAPC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2	0	0	0	0	40
B11QPJSPC	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	1	0	0	0	0	0	0	24
B11QPVAPC	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	26
B31QRJAPC	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	58
B31QRJSPC	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	5
B31QRVAPC	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	9
C11QRJSPC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	19
C11QRVAPC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	57
C21QRJAPC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0	0	0	0	25
C21QRJSPC	0	0	2	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	18
C21QRVAPC	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	41
C22QRJAPC	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	10
C22QRJSPC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	42
C22QRVAPC	0	0	1	0	0	0	0	0	3	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	27
D11QPJAPC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	30
D11QPJSPC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5
D11QPVAPC	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	11
D31QPJAPC	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	52
D31QPJSPC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13
D31QPVAPC	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0	0	0	0	40
D32QPJAPC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	18
D32QPJSPC	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	23
D32QPVAPC	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	42
D41QPJAPC	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	37
D41QPJSPC	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	23
D41QPVAPC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	33
E21QPJAPC	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	35
E21QPJSPC	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9
E21QPVAPC	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	1	0	15
E41QPJAPC	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	34
E41QPJSPC	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	22
E41QPVAPC	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	43
F21QPJAPC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	30
F21QPJSPC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	15
F21QPVAPC	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	31
G11QPJAPC	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	45
G11QPJSPC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	23
G11QPVAPC	0	0	0	0	0	0	0	0	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	56
G21QPJAPC	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20
G21QPJSPC	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	18
G21QPVAPC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	39
H21QRJAPC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	41
H21QRJSPC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	31
H21QRVAPC	0	0	1	0	1	0	0	1	2	1	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	36

Spiders 2019

Tree	*Anyphaena accentuata*	*Cetonana laticeps*	*Clubiona brevipes*	*Clubiona corticalis*	*Clubiona corticalis*	*Clubiona pallidula*	*Clubiona terrestris*	*Enoplognatha sp*	*Lathys humilis*	*Misumena sp*	*Nuctenea umbratica*	*Paidiscura pallens*	*Parasteatoda lunata*	*Philodromus albidus*	*Philodromus aureolus*	*Philodromus aureolus*	*Philodromus margaritatus*	*Pistius sp*	*Platnickina tincta*	*Theridion melanurum*	*Xysticus sp*	Undetermined
2.1	7299	0	0	0	0	0	0	0	0	0	0	0	0	0	7105	0	0	0	0	0	0	0
2.2	6361	39	0	9092	1924	0	0	0	0	0	0	0	0	0	3068	0	0	0	0	0	0	73
5.1	12005	0	0	0	0	5	0	0	219	0	81	0	0	0	0	95	0	0	0	16	0	1109
5.2	125	0	0	1019	1367	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0
6.1	1526	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6.2	1946	0	0	943	1021	0	0	0	0	0	32	0	0	0	0	0	0	0	0	0	0	0
7.1	3828	0	0	0	0	0	0	0	0	0	86	0	0	3	0	0	0	0	0	0	0	26
7.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8.1	14	51	0	0	0	0	0	40	0	0	4534	0	0	0	0	0	0	0	0	0	0	0
8.2	202	4	129	0	9	0	0	0	68	0	5393	0	0	0	0	2931	101	0	0	0	0	6
9.1	393	0	34	4951	0	0	0	0	0	0	163	0	0	0	0	0	335	0	0	0	0	27
9.2	4973	0	0	0	0	0	0	0	173	0	521	0	0	0	0	0	0	0	0	0	0	0
10.1	298	0	0	0	0	0	100	0	0	0	237	0	0	0	0	0	0	50	406	0	82	0
10.2	0	0	34	2567	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14	0	10	0
13.1	898	0	0	231	300	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	22
13.2	12581	0	0	7200	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15.1	0	0	0	0	0	0	0	0	19	0	0	0	0	0	0	0	0	0	0	0	0	0
15.2	2	0	0	648	986	0	0	0	0	0	0	0	0	0	0	4702	0	0	0	0	0	73
16.1	19	0	0	332	486	0	0	0	0	0	0	0	0	0	0	1418	0	0	0	0	0	145
16.2	8334	0	0	1257	771	0	0	0	0	0	0	12	0	0	0	0	0	0	0	0	0	0
17.1	57	0	0	0	0	0	0	0	0	0	0	0	68	28	0	0	0	0	0	0	9	152
17.2	0	0	0	598	875	0	0	0	0	143	0	0	0	0	0	0	0	0	7	0	0	1754
18.1	845	0	0	1071	1251	0	0	0	0	0	0	0	0	0	0	8	0	0	2	0	0	2
18.2	11	0	0	1246	1417	0	0	5	4	0	0	0	0	96	0	0	0	0	0	7	0	0

True buds 2006

Tree	*Aelia acuminata*	*Alloeotomus gothicus*	*Aphanus rolandri*	*Aradus cinnamomeus*	*Arma custos*	*Atractotomus magnicornis*	*Cardiastethus fasciiventris*	*Ceraleptus lividus*	*Chlorochroa pinicola*	*Cyllecoris histrionius*	*Deraeocoris lutescens*	*Deraeocoris trifasciatus*	*Derephysia foliacea*	*Dolycoris baccarum*	*Drymus sylvaticus*	*Drymus sylvaticus*	*Elasmostethus interstinctus*	*Elasmucha fieberi*	*Emblethis denticollis*	*Eurygaster austriaca*	*Eysarcoris ventralis*	*Gastrodes grossipes*	*Geotomus punctulatus*	*Harpocera thoracica*
B11_J_APC	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
B11_J_SPC	0	0	0	0	0	0	0	0	0	1	4	0	0	0	0	0	1	0	0	0	0	0	0	2
B11_V_APC	0	0	0	0	0	0	0	0	0	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0
B31_J_APC	0	0	0	1	0	0	1	0	0	0	3	0	0	1	0	0	0	0	0	0	0	0	0	0
B31_J_SPC	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
B31_V_APC	1	0	1	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
C11_J_APC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C11_J_SPC	1	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0
C11_V_APC	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	2	0	1	0	0	0
C21_J_APC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C21_J_SPC	1	0	0	1	0	0	0	0	1	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0
C21_V_APC	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
C22_J_APC	2	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
C22_J_SPC	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0
C22_V_APC	0	1	0	0	0	0	0	0	0	0	3	0	0	1	0	0	0	0	0	0	0	0	0	0
D11_J_APC	0	0	0	0	0	0	1	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0
D11_J_SPC	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
D11_V_APC	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0
D31_J_APC	0	0	0	0	0	0	0	0	0	0	3	1	0	0	0	0	0	0	0	0	0	0	0	0
D31_J_SPC	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	1	0
D31_V_APC	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0
D32_J_APC	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
D32_J_SPC	1	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0
D32_V_APC	0	0	0	0	0	0	0	1	0	1	5	0	0	0	0	0	0	0	1	0	0	0	0	0
D41_J_APC	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	1
D41_J_SPC	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
D41_V_APC	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0
E21_J_APC	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
E21_J_SPC	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
E21_V_APC	0	0	0	0	0	0	1	0	0	1	2	0	0	0	0	0	0	0	0	1	0	0	0	0
E41_J_APC	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0
E41_J_SPC	1	0	0	0	0	0	0	0	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0	1
E41_V_APC	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
F21_J_APC	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
F21_J_SPC	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0
F21_V_APC	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	1
G11_J_APC	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0
G11_J_SPC	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	1	0	0	0	0	0	0	0	0
G11_V_APC	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
G21_J_APC	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
G21_J_SPC	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
G21_V_APC	0	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	1	0	0	0	0	0
H21_J_APC	1	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0
H21_J_SPC	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
H21_V_APC	0	0	0	0	0	0	1	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0

(Continued)

Tree	*Himacerus apterus*	*Holcogaster fibulata*	*Holcostethus strictus*	*Isometopus intrusus*	*Isometopus mirificus*	*Kleidocerys resedae*	*Loricula elegantula*	*Lygus pratensis*	*Lygus rugulipennis*	*Megacoelum beckeri*	*Megalonotus chiragra*	*Megalonotus emarginatus*	*Megalonotus sabulicola*	*Miris striatus*	*Nabis ferus*	*Neolygus contaminatus*	*Notonecta glauca*	*Nysius thymi*	*Orius majusculus*	*Orius minutus*	*Orius niger*	*Palomena prasina*	*Pantilius tunicatus*	*Pentatoma rufipes*
B11_J_APC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
B11_J_SPC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
B11_V_APC	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	2
B31_J_APC	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	1	1	1	0	1
B31_J_SPC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B31_V_APC	0	0	0	1	0	0	2	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1
C11_J_APC	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
C11_J_SPC	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
C11_V_APC	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
C21_J_APC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
C21_J_SPC	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
C21_V_APC	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
C22_J_APC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	2
C22_J_SPC	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
C22_V_APC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
D11_J_APC	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	2
D11_J_SPC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
D11_V_APC	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
D31_J_APC	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
D31_J_SPC	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
D31_V_APC	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
D32_J_APC	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	3
D32_J_SPC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
D32_V_APC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1
D41_J_APC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
D41_J_SPC	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
D41_V_APC	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
E21_J_APC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2
E21_J_SPC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
E21_V_APC	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
E41_J_APC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
E41_J_SPC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
E41_V_APC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
F21_J_APC	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1
F21_J_SPC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
F21_V_APC	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
G11_J_APC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
G11_J_SPC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
G11_V_APC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
G21_J_APC	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
G21_J_SPC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
G21_V_APC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
H21_J_APC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	2
H21_J_SPC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
H21_V_APC	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2

(Continued)

Tree	*Peritrechus geniculatus*	*Peritrechus gracilicornis*	*Phoenicocoris modestus*	*Phoenicocoris obscurellus*	*Phylus melanocephalus*	*Phytocoris dimidiatus*	*Piesma maculatum*	*Piezodorus lituratus*	*Pinthaeus sanguinipes*	*Psallus albicinctus*	*Psallus confusus*	*Psallus mollis*	*Psallus wagnerii*	*Psallus variabilis*	*Psallus varians*	*Rhabdomiris striatellus*	*Rhaphigaster nebulosa*	*Saldula saltatoria*	*Scolopostethus decoratus*	*Stygnocoris fuligineus*	*Temnostethus gracilis*	*Temnostethus pusillus*	*Troilus luridus*	*Xanthochilus quadratus*	Undetermined
B11_J_APC	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	1
B11_J_SPC	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1
B11_V_APC	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1
B31_J_APC	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1
B31_J_SPC	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
B31_V_APC	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	2	0
C11_J_APC	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0
C11_J_SPC	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	1	1	0
C11_V_APC	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0
C21_J_APC	0	0	0	0	0	0	1	0	1	0	0	0	0	0	2	0	0	1	0	0	0	0	0	1	1
C21_J_SPC	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5
C21_V_APC	0	0	0	0	1	1	0	0	0	1	0	0	2	0	2	0	0	0	0	0	1	1	0	0	1
C22_J_APC	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0
C22_J_SPC	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
C22_V_APC	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0
D11_J_APC	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	2	2
D11_J_SPC	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
D11_V_APC	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1
D31_J_APC	0	0	0	0	2	0	2	0	0	2	0	1	2	0	1	3	0	0	0	0	0	0	0	0	2
D31_J_SPC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
D31_V_APC	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	2
D32_J_APC	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	2	0
D32_J_SPC	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
D32_V_APC	0	0	0	0	1	1	1	0	0	0	0	1	1	0	2	0	0	0	0	0	0	2	0	0	1
D41_J_APC	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0
D41_J_SPC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
D41_V_APC	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	1	0	0	0
E21_J_APC	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	1
E21_J_SPC	0	0	1	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
E21_V_APC	0	1	0	0	1	1	0	0	0	0	0	2	0	0	1	0	1	0	0	0	0	1	0	0	0
E41_J_APC	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	1	0	0	0	0	0	0	0	0	0
E41_J_SPC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	2
E41_V_APC	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0
F21_J_APC	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	1
F21_J_SPC	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
F21_V_APC	0	0	0	0	0	0	0	0	0	1	0	0	2	0	1	0	0	0	0	0	0	1	0	0	1
G11_J_APC	0	0	0	0	2	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	1
G11_J_SPC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
G11_V_APC	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
G21_J_APC	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0
G21_J_SPC	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	2
G21_V_APC	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	1	1	0	0	0	1	1	0	1	0
H21_J_APC	0	0	0	0	1	0	0	0	0	1	1	0	3	0	0	0	0	0	0	0	0	0	0	1	0
H21_J_SPC	0	0	0	2	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
H21_V_APC	0	0	0	0	1	0	0	0	0	1	0	0	1	0	2	1	1	0	0	0	0	1	0	0	2

True bugs 2019

Tree	*Aphanus rolandri*	*Arma custos*	*Ceraleptus lividus*	*Chlorochroa pinicola*	*Coreus marginatus*	*Deraeocoris lutescens*	*Drymus sylvaticus*	*Elasmostethus interstinctus*	*Gonocerus acuteangulatus*	*Himacerus apterus*	*Holcogaster fibulata*	*Kleidocerys resedae*	*Leptoglossus occidentalis*	*Lygus pratensis*	*Palomena prasina*	*Palomena viridissima*	*Pentatoma rufipes*	*Peribalus strictus*	*Peritrechus gracilicornis*	*Pinthaeus sanguinipes*	*Rhaphigaster nebulosa*
2.1	0	1	1	0	0	0	0	0	0	0	0	5	0	0	1	0	2	0	0	0	0
2.2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
5.2	0	0	0	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
6.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
6.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
7.1	0	0	0	0	2	0	0	0	0	0	0	0	3	0	0	0	2	0	0	0	0
8.1	0	0	0	0	0	2	0	2	0	0	1	2	0	0	0	0	1	0	0	0	0
8.2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9.1	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	5	0	1	0	0
10.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0	0	0	0
10.2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
13.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
15.1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0
15.2	0	0	0	0	0	0	0	1	0	0	0	0	2	0	1	0	1	0	0	0	0
16.1	0	0	0	0	0	1	0	2	0	0	0	0	0	0	1	0	0	0	0	0	0
16.2	0	0	0	0	0	1	0	2	2	0	1	0	0	0	2	0	0	0	0	0	0
17.1	1	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	4	1	0	0	0
17.2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	3	0	0	0	0
18.1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	2	0	0	0	0	0	0
18.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

Discussion

Discussion

In the three main chapters, I presented the role of phylogenetic isolation of trees in a forest in determining the level of matching of communities of arthropods to the characteristics of individual host trees – leaf size, phenology and temperature. In these chapters, I also discussed what I think are the most likely mechanisms behind the specific patterns that I found, along with some implications. Here, as a general discussion, I present the overall patterns, and their mechanisms and implications from the perspectives of the arthropods and of the trees, and the future research perspectives that these patterns and mechanisms open up. I also discuss the contribution of the thesis to advance the concept of phylogenetic isolation for understanding the ecology and evolution of forest arthropods and trees.

The arthropod perspective

Forest arthropods find it difficult to match the characteristics of phylogenetically isolated host trees.

The reduction of matching of host-tree characteristics by the arthropod abundance and leaf damage is usually explained by higher competition among arthropods and higher enemy pressure on arthropods on the trees that offer better resources to herbivores (as described in the introduction). The results of my thesis suggest that the phylogenetic isolation of host trees can also cause reduced matching: when trees are surrounded by distantly related neighbours, arthropods may have difficulty using the more profitable trees more. This may be the case because the distantly related neighbours of the focal tree have dissimilar characteristics (Prinzing et al. 2001; Chazdon et al. 2003; Losos 2008), and thus harbour dissimilar arthropods (as most of the arthropods are usually specialist to one or a few closely related trees, Novotny and Basset 2005; Grandez-Rios et al. 2015; Seifert et al. 2020). Hence, there will be little exchange of arthropods between the focal tree and its phylogenetically distantly related neighbours (Vialatte et al. 2010). Furthermore, the distantly related neighbours may reduce the physical and chemical apparency of the focal tree (Castagneyrol et al. 2013; Binyameen et al. 2013). As a result, for the arthropods that are in search of a suitable host tree, it is then difficult to assess the characteristics of the focal tree and make an informed decision (Jactel et al. 2001, 2011; Salazar et al. 2016). Together, such reduced movement and reduced availability of information may make it difficult for arthropods to find the most profitable host trees in a forest. Indeed, I found that on phylogenetically isolated trees, the consumption of leaf surface area does not increase with an increase in leaf size as much as it does on phylogenetically non-isolated trees. Moreover, phylogenetic isolation does not only affect overall arthropod abundance, but also the matching of certain arthropod traits with tree traits. Specifically, I found that herbivores from phylogenetically isolated trees cannot match the timing of budburst more when the trees burst buds rapidly and thus offer the highest

concentration of freshly emerged leaves. As a result, arthropods are not able to take full advantage of rapid bud burst when trees are phylogenetically isolated. I also found that the relationship of arthropod body size with temperature often changes with the phylogenetic isolation of the host trees, indicating that phylogenetic isolation reduces matching of body size with microclimate. Overall, my results suggest that arthropods cannot profit from matching the favourable host-tree characteristics when the trees are phylogenetically isolated not only in terms of abundance but also in terms of species or genotypes that are better able to consume the leaves.

Forest arthropods have to match life history to both speed of budburst and leaf development of their host trees.

Arthropod life history is usually thought to be determined by factors like food quality, biotic interactions, and microclimate (Boggs 2009; Price 2011). For herbivores feeding on deciduous trees, host-tree phenology also seems to play an important role by selecting for certain genotypes (Feeny 1970; Watt and McFarlane 1991; Buse and Good 1996; Forkner et al. 2004). In particular, early-bursting host trees may sort for early-developing arthropods and *vice versa*. While this adaptation to tree phenology has been demonstrated for egg-hatching within arthropod species both among tree species (Posledovich et al. 2015, 2018), and within tree species (Buse and Good 1996; Van Dongen et al. 1997), I for the first time show that budburst phenology sorts for matching arthropod species within tree species, thus affecting community composition on individual trees. Moreover, this effect is not limited to species that rely on matching egg-hatching, but also includes species that match tree phenology in other ways (e.g. female moths eclosing during the time of budburst in spring). In addition to matching to budburst timing, I found that host trees with rapidly-developing leaves sort for rapidly-developing arthropod species. On such trees, the slowly-developing arthropods may not be able to complete their development before the leaves become too hard to chew and too chemically defended to digest (Feeny 1968, 1970; Hunter and Lechowicz 1992). Therefore, the speed of leaf development can be a strong selective or sorting agent for the life history of associated arthropods. My analyses discovered the importance of arthropod species sorting, both in terms of matching the timing of budburst and in terms of matching the speed of leaf development. Specifically, early and late budburst were associated with particular caterpillar community composition, and on trees with faster leaf development, caterpilars tended to be of species that pupated earlier. When this sorting is hampered by phylogenetic isolation, the reduced match between arthropod and tree traits leads to a reduced rate of herbivory. Therefore, arthropod life history can be determined by both speed of budburst and leaf development.

Forest arthropods might respond to unpredictable timing of budburst by adopting bet-hatching strategies.

Arthropods may respond to among-year fluctuation in timing of budburst of their host trees relative to other trees by adopting a bet-hatching strategy. I found that under high fluctuation in the timing of budburst, herbivores cannot match the timing of budburst more when the trees burst buds rapidly and thus offer a higher concentration of freshly emerged leaves. This is probably because it creates fluctuating selection and species sorting so that arthropod species cannot adapt and arthropod communities cannot become sorted for a particular budburst phenology (Kisdi 2002; Blanquart and Gandon 2011). Under such fluctuation in timing of budburst, the herbivores may evolve to spread the risk of mismatching the host-tree phenology (a.k.a bet-hedging strategies Slatkin 1974; Seger et al. 1987). In particular, by having a wide range of hatching dates in a single brood, at least some eggs will hatch while matching the date of budburst. When the timing of budburst is unpredictable, such a strategy may result in maximum fitness for arthropods (Evans and Dennehy 2005). Therefore, future studies should e.g. not only record the date of the first hatchling of a female's egg batch, but also record the variation in egg-hatching date within egg batches.

Arthropods within a forest follow biogeographic rules of body size: microclimate meets phylogenetic isolation.

Body size is arguably the single trait that integrates the largest amount of variation in life histories across arthropod species (Peters 1983; Chown and Gaston 2010; Shingleton 2011). Body size rules describe the patterns of animal body size over a large biogeographic area. For example, Bergmann's rule predicts that within a given taxonomic clade the smaller bodied populations and species usually occupy the warmer biogeographic regions (Bergmann 1848; Shelomi 2012), and island biogeography predicts colonization biased towards better dispersers and evolution of extreme body sizes on islands (Foster 1964; Lomolino et al. 2013). These body-size rules are usually thought to operate only at larger spatial scales. However, the mechanisms behind such rules may also operate at smaller scales such as among trees within a forest. I found that within a forest, the host trees with warmer microclimate sort for either smaller or larger species of arthropods, depending on the group. I further found that the phylogenetically isolated host trees sort for larger species of flying insects, consistent with isolation sorting for species with higher dispersal ability (Hanski and Mononen 2011; Bouget et al. 2015). Also, in few cases, the sorting of smaller species by warmer trees was reinforced by the phylogenetic isolation of trees. Furthermore, Molleman et al. (2016) found that within species of click beetles, herbivores tend to be larger and predators smaller on phylogenetically isolated trees, similar to the evolution of extreme body sizes found in species on islands. The fact that the arthropods follow body size rules for temperature and isolation at the scale of individual trees in a forest suggests that individual trees within

a forest can function as micro-archipelagos for the arthropods in which trees vary in both temperature and degree of isolation.

Arthropod diversity within a forest can be enhanced by the sorting of arthropods through a mosaic of leaf size, leaf developmental phenology, temperature, and phylogenetic isolation of the host trees.

A potentially important mechanism that promotes the continued coexistence of many species within an ecosystem is niche segregation where the relative competitive ability of species varies in space and time (Becerra 2015). Arthropods in forests can coexist in part because they are specialized on different tree species, so that tree species diversity is seen as the main driver of arthropod diversity (Becerra 2015; O'Brien et al. 2017). However, there are also many species of arthropod coexisting on a single tree species and this suggest multiple niches within trees (Whitham 1981). Partly, these can be feeding guilds such as free-feeding leaf chewers, semi-concealed feeders and leaf miners, leaf suckers and omnivores among the herbivores. These groups respond differently to tree characteristics such as leaf size and tree neighborhood: leaf chewers (termed as ectophages in Chapter 1) gathered in large numbers on large-leaved trees as long as the trees were surrounded by phylogenetically non-isolated trees, and such effect was absent in leaf gallers and in leaf miners. I also found other aspects of niche space that operate within feeding guilds within tree species. Early bursting trees sort for early developing caterpillars (free-living larvae of Lepidoptera), and early leaf maturing trees sort for early pupating caterpillars. I also found that forest trees sort for smaller and larger arthropods along the gradient of temperature. Furthermore, I found that forest trees sort for larger arthropods along the gradient of phylogenetic isolation. Moreover, I found that in some cases, the same value of temperature can sort for different arthropod body size at different levels of phylogenetic isolation. Such mosaic of temperature and isolation to sort arthropod species can further enhance the coexistence of diverse species of arthropods in forests. Altogether, I found evidence for multiple important niche dimensions that could contribute to maintaining the diversity of arthropods in forests that have hardly been considered before.

The tree perspective

Tree populations in which individuals are often phylogenetically isolated may evolve to have larger leaves and faster budburst.

Phylogenetically isolated trees may be able to afford being profitable for herbivores because the herbivores have trouble profiting from them. Phylogenetically isolated trees have been shown to benefit from a lower abundance of herbivores, and lower rates of herbivory (Vialatte et al. 2010; Yguel et al. 2011). I showed that in addition, phylogenetically isolated trees might benefit from having traits that may be beneficial for their growth but may make them attractive to herbivores that then can negate these

benefits. Larger leaves may be beneficial to trees as they can reduce water loss (Wang et al. 2016), but this benefit may be negated when it attracts more herbivory. Indeed, when trees grow amongst closely related individuals they suffer more herbivory when their leaves are larger. When host trees are phylogenetically isolated however, herbivory does not increase proportionally with leaf size as much as it does when the host trees are phylogenetically non-isolated. This implies that having larger leaves may benefit trees that are phylogenetically isolated more than those that are not. In a further example, rapid budburst (all leaf buds bursting within a short time in spring) may be beneficial for trees as it permits better use of the growing season, but this benefit may be negated if rapid budburst leads to higher rates of herbivory. While rapid budburst is associated with better matching arthropods and more leaf damage in non-isolated trees, when host trees are phylogenetically isolated, rapid budburst does not increase the level of phenology matching by herbivores. This implies that having rapid budburst may benefit the phylogenetically isolated trees more than those that are non-isolated. Hence, I predict that tree populations in which individuals are often phylogenetically isolated may evolve to have larger leaves and faster budburst. Similarly, Pihain et al. (2019) found that descendants of trees from phylogenetically distant neighbourhoods have evolved to have softer leaves with lower concentrations of flavonol and anthocyanin, which are more profitable for the herbivores.

Tree populations in which individuals are often phylogenetically non-isolated may evolve to increasingly depend on constitutive defences.

It is costly for the trees to accrue defences against herbivores (Baldwin and Hamilton 2000; Koricheva 2002; Moore et al. 2003; Stamp 2003; Preisser et al. 2007; Siemens et al. 2009; Cipollini et al. 2017), and thus the trees need to balance these costs with the expected benefits in order to maximize fitness (Vos et al. 2013; Huot et al. 2014; Karasov et al. 2017). The costs of constitutive defences are likely to be paid even in the absence of herbivore attack (Loehle 1988; Sampedro 2014; Galmán et al. 2021). Thus, optimal defence theory (as stated in McKey 1974, 1979; Rhoades 1979) predicts that the constitutive defences should be favoured in environments where herbivory is predictably high (Zangerl and Rutledge 1996; Bixenmann et al. 2016). Yguel et al. (2011) found that herbivore pressure is higher on phylogenetically non-isolated trees. Besides that, I found that for phylogenetically non-isolated trees, the herbivore pressure tends to be predictable: increase of herbivore pressure with an increase in leaf size and in budburst speed. Hence, phylogenetically non-isolated trees with large leaves (or rapid budburst) are more likely to suffer high herbivory constantly. Therefore, such trees may evolve to rely more on constitutive defences. In contrast, phylogenetically non-isolated trees may rely more on herbivore induced defences irrespective of leaf size (or speed of budburst). Such trees are expected to usually suffer from only little herbivore pressure, but might occasionally experience higher herbivore pressure. Hence, for such trees, investment in constitutive defence may be a waste of energy that could have been used for growth or reproduction, and they are better off relying more on induced defences. However, being phylogenetically isolated

may also mean that calling for the help of natural enemies such as parasitoids may be less effective (Jactel et al. 2011; Yguel et al. 2014), so this type of induced defence may not be selected for in populations in which individuals are often phylogenetically isolated. Overall, tree populations in which individuals are often phylogenetically non-isolated are expected to increasingly depend on constitutive defences, in particular when the leaves are larger (or budburst is rapid).

Phylogenetic isolation of trees seems to confer associational resistance, which can theoretically disappear with tree age.

It is not fully clear why certain associations confer resistance to trees from damage caused by herbivores while certain associations confer susceptibility, as described in the introduction. A meta-analysis of studies from last five decades suggested that the effects of tree diversity on insect herbivory depends on herbivore diet breadth and phylogenetic distance between a focal tree and its neighbours (Jactel et al. 2021). In particular, they found that association of gymnosperms with angiosperms can reduce damage caused by specialist herbivores. In addition, Yguel et al. (2011) showed that rate of herbivory reduces with increasing phylogenetic isolation of trees. Furthermore, my findings suggest that association with phylogenetically distant tree species may also benefit the trees by reducing the matching of tree characteristics by specialist herbivores. My study trees were dominated by specialist herbivores, and when the oaks were phylogenetically isolated, the herbivores could not benefit from matching profitable tree characteristics such as large leaves or rapid budburst. This might have permitted the phylogenetically isolated trees to benefit from large leaves or rapid budburst. Therefore, it seems that trees benefit from phylogenetic isolation. However, in particular situations, phylogenetic isolation of host trees may be detrimental for the trees. For example, oak seedlings suffer higher mollusc attack and higher mortality when surrounded by phylogenetically distantly related neighbours (Deniau et al. 2017, 2018, 2021). Besides that, I found that phylogenetic isolation of host trees reduces support from the parasitoids of herbivores. The number of parasitized caterpillars increased only little with an increase in number of available caterpillars on phylogenetically isolated trees. Furthermore, Yguel et al. (2014) found a lower rate of parasitisation on phylogenetically isolated trees. Release from parasitoid pressure on phylogenetically isolated trees may result in higher demographic growth of herbivore populations (Anderson 1978; Møller 2005). Thus, over many generations of herbivores, herbivore abundance could be similar on phylogenetically isolated and non-isolated trees, and it could even be higher on phylogenetically isolated trees. Molleman et al. (2022) is the first to find higher abundance of herbivores on phylogenetically isolated host trees. Among other differences, Molleman's trees were much older than those used in my analyses (includes trees of studies by Vialatte, Yguel, and colleagues). For such larger (and older) trees, the higher abundance of herbivores on phylogenetically isolated trees might have resulted from many generations of higher demographic growth of herbivores due to release from parasitoid

pressure. Therefore, the benefit of phylogenetic isolation for the trees may reduce with an increase in age.

Trees may fluctuate their timing of budburst among-years to defend against herbivores.

I found that trees can defend themselves against herbivores by varying the timing of budburst among years (relative to other trees). Variation in relative timing of budburst might result in fluctuating selection pressures for local adaptation and species sorting of arthropods. Hence, the arthropods associated with the tree may not become adapted to the timing of budburst. Thus, variation in relative timing of budburst can be expected to reduce the matching of timing of budburst by the arthropods. This pattern is what I found: When trees show much variation in among-year relative timing of budburst, the matching of timing of budburst by herbivores does not increase with an increase in speed of budburst. Hence, such fluctuation in relative timing of budburst prevents herbivores from profiting from the highest concentration of freshly emerged leaves offered by rapid budburst. Therefore, trees may profit from varying their budburst among years, especially when herbivory is extensive. Trees may thus also be selected to respond to intense herbivory by changing the timing of budburst to exclude populations of herbivores that were sorted or selected to match the budburst of the tree based on budburst during previous years.

Trees may sort against larger herbivores to defend themselves.

In general, larger herbivores will individually feed more than the smaller ones (Theunissen et al. 1985), in particular when herbivores are locally adapted (although in my study larger wingspan was not related to higher herbivory, possibly because of lower local adaptation of herbivores due to low average tree age of c.a. 80 years). Hence, under similar abundance of herbivores, trees with larger herbivores may suffer more herbivory than trees with smaller herbivores. Therefore, to reduce the damage caused by herbivores, trees may also sort against larger-bodied species. I found that higher microclimatic temperature of the host trees sorts against larger species of herbivores. To maintain higher microclimatic temperature, trees may reduce water transpiration (Lin et al. 2017; Gupta et al. 2018). This strategy can further help trees to avoid water loss, and to overcome environmental stress such as drought (David et al. 2007; Grossiord et al. 2014). Therefore, higher herbivory could be a cue for the trees to transpire less and maintain a higher microclimatic temperature to reduce the abundance of larger herbivores.

Trees are highly apparent hosts but can nevertheless hide from their enemies.

Plants defend themselves among others by being unapparent to the herbivores (Feeny 1976). The unapparent plants are usually short-lived, and refuge geologically (grow on cliff ledges and plateaus), or spatially (grow near the ground and remain

hidden under other plants). Whereas, the apparent plants are usually long-lived such as trees. Castagneyrol et al. (2013) showed that an apparent tree species like oak can remain visually concealed while it is young due to the presence of taller neighbours. Studying adult oaks, I found that arthropods poorly match the tree characteristics when the trees are phylogenetically isolated. As explained in the introduction, phylogenetically distant neighbours can mask the olfactory and visual search cues for the arthropods (Jactel et al. 2001, 2011). This suggests that trees also can be hidden from herbivores by growing in the neighbourhood of phylogenetically distant trees. The mixture of phylogenetically distant tree species might allow the world to be green, an aspect scientists are trying to explain since decades ('why the world is green'? Sherratt and Wilkinson 2009). So far, the main two lines of arguments are top-down and bottom-up controls of herbivores (Hunter and Price 1992; Castagneyrol et al. 2017). Top-down means that predators control herbivores, allowing plants to flourish. Bottom-up means that plants themselves limit the effectiveness of herbivores. These processes also interact as plants can increase effectiveness of natural enemies by slowing the growth of their herbivores and by making them more apparent by emitting herbivore-induced volatiles or changing leaf color where herbivores are active (Amo et al. 2013; Wilkinson and Sherratt 2016). Bottom-up control may be increased by plants by causing the herbivores to not match the plant characteristics, allowing plants to flourish. Therefore, my results suggest that 'the world is green' partly because often the herbivores have trouble matching the tree characteristics as the trees are hidden among phylogenetically distant neighbours.

Phylogenetic isolation: patterns and processes

Patterns observed among phylogenetically isolated trees can be explained by deterministic processes.

Phylogenetic isolation produces patterns similar to classical biogeographical isolation. Classical biogeographic isolation is known to reduce species richness on islands (MacArthur and Wilson 2001). Furthermore, abundant resources are left unused on islands as specialized consumers are often lacking (Lomolino et al. 2006). Moreover, species experience enemy release on islands as natural enemies are often lacking (Lomolino et al. 2006). Similarly, phylogenetic isolation of trees has been shown to reduce the richness of arthropods (Vialatte et al. 2010). Furthermore, resources are found to be left unused more on phylogenetically isolated trees (Yguel et al. 2011). Moreover, phylogenetic isolation of trees also released the herbivores from enemy pressure in terms of lower parasitisation rate (Yguel et al. 2014). These patterns on phylogenetically isolated trees are thus similar to the patterns on islands resulting from classical biogeographical isolation. Hence, in terms of patterns, the phylogenetically isolated trees resemble a micro-archipelago within a forest. The patterns of oceanic archipelagos can to a large extent be explained by stochastic immigration and stochastic extinction (equilibrium theory of island biogeography, Hubbell 2001;

MacArthur and Wilson 2001). Similarly, earlier studies on phylogenetic isolation of trees explained the patterns by stochastic immigration and stochastic extinction (Vialatte et al. 2010; Yguel et al. 2011, 2014), where the arthropod trait 'degree of specialization' was regarded as affecting the degree of isolation. However, my results show that those patterns can also be explained by deterministic processes. All three chapters of this thesis show that the phylogenetic isolation of host trees reduces matching of arthropod traits to the host-tree characteristics. The reduced match between herbivores and tree traits such as leaf size and leaf development phenology can lead to overall reduced herbivore abundance and reduced rate of herbivory on more phylogenetically isolated trees. Furthermore, the reduced match between parasitoids and herbivore abundance can lead to overall reduced rate of parasitisation on more phylogenetically isolated trees. This shows that arthropod species traits are important, and thus that deterministic processes operate.

Conclusions

I found that phylogenetic isolation prevents arthropods from effectively choosing trees with abundant resources, matching phenology, and matching microclimate. This reduction in matching of arthropod abundance and traits with tree traits resulted in a reduction in herbivory. Thus, this reduced matching appears to help trees avoid excessive herbivory when they grow far from phylogenetically closely related species. This would contribute to selection to leave the ancestral niche to then co-occur with more distantly related tree species. Furthermore, as herbivores find it difficult to profit from favourable tree-traits when trees grow far from phylogenetically closely related species, such trees may be able to benefit from having traits that are favourable for herbivores such as large leaves and rapid budburst. Thus, the phylogenetic neighbourhood can also affect trait evolution in tree populations. Specifically, phylogenetic isolation would allow the evolution of larger leaves, more respiration (and thus a cooler canopy), and faster and predictable budburst. The low but unpredictable herbivore pressure may further select for induced defences in phylogenetically isolated trees, while trees with closely related neighbours may benefit more from constitutive defences as they face predicable and high herbivore pressure. Trees can also avoid excessive herbivory by fluctuating budburst so that herbivore communities and species have trouble adapting to the unpredictable budburst phenology. Taken together, I found evidence for multiple important niche dimensions that could contribute to maintaining the diversity of arthropods in forests that have hardly been considered before; leaf size, speed of budburst, predictability of budburst, and crown temperature, and these all interact with phylogenetic neighborhood in determining arthropod community composition and traits, with consequences for leaf damage. Overall, this thesis contributes to demonstrating the utility of the concept of phylogenetic isolation of trees for understanding interactions between forest arthropods and trees that could contribute to arthropod diversity in forests and trait evolution in both arthropods and trees.

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UNIVERSITÉ DE RENNES 1

Titre : Des voisins phylogénétiquement éloignés peuvent empêcher les arthropodes de concorder aux caractéristiques d'un arbre hôte : une histoire de phénotypes d'arthropodes et de dommages foliaires sur des chênes

Mots clés: arthropodes, herbivores, microclimat, phénologie, isolement phylogénétique, ressource

Résumé : Beaucoup arthropodes se nourrissant des arbres. Pour réussir, ces arthropodes doivent concorder aux caractéristiques des arbres. Nous avons émis l'hypothèse que les arthropodes concordent mal lorsque les arbres sont entourés de voisins phylogénétiquement éloignés, en raison de la réduction des échange d'arthropodes entre les arbres voisins. Plus précisément, l'isolement phylogénétique empêche les arthropodes de profiter (i) des arbres riches en ressources, (ii) des arbres qui débourrent rapidement, et (iii) des arbres avec un microclimat chaud. Nous avons étudié si : (i) il y a plus d'herbivorie sur les arbres avec des feuilles plus grandes et de meilleure qualité (utilisation proportionnelle des ressources), (ii) les chenilles sont plus grandes sur les arbres avec des bourgeons qui éclatent plus tôt, et se nymphosent plus tôt sur les arbres avec des feuilles qui mûrissent plus tôt (concordance phénologique), et (iii) les arthropodes de petite taille dominent sur les arbres avec un microclimat chaud permettant d'atteindre la maturité à une petite taille (règle température/taille). Nous avons prédit que ces relations disparaissent parmi les arbres phylogénétiquement isolés. Nous nous sommes concentrés sur l'espèce d'arbre la plus diversifiée en arthropodes d'Europe occidentale, *Quercus petraea* (hybridé avec *Q. robur*), dans une forêt de l'ouest de la France. Nous avons constaté que lorsque les arbres hôtes étaient phylogénétiquement isolés (i) l'herbivorie n'augmentait plus proportionnellement à la taille des feuilles, (ii) la concordance phénologique diminuait, en particulier sur les arbres à éclatement rapide, et (iii) la relation température/taille changeait. Nous suggérons que l'isolement phylogénétique empêche les arthropodes de choisir efficacement les arbres avec des ressources abondantes, une phénologie et un microclimat approprié. Nos résultats suggèrent donc que pour éviter une herbivorie excessive, les arbres devraient pousser loin des espèces phylogénétiquement proches (ou alternativement débourrer lentement).

Title : Distantly related neighbours of host trees can prevent arthropods from matching tree characteristics: a story of arthropod phenotypes and leaf damage on oak trees

Keywords : arthropods, herbivores, microclimate, phenology, phylogenetic isolation, resource.

Abstract : The success of tree-feeding arthropods depends on how well they match tree characteristics. We hypothesised that arthropods match poorly when trees are surrounded by phylogenetically distant neighbours, due to the reduced exchange of arthropods between neighbouring trees. Specifically, phylogenetic isolation prevents arthropods from profiting from (i) resource-rich trees, (ii) trees that burst buds rapidly, and (iii) trees with warm microclimate. We studied whether: (i) there is more herbivory on trees with larger and higher-quality leaves (proportional use of resources), (ii) caterpillars are larger on trees with earlier bursting buds, and pupate earlier on trees with earlier maturing leaves (phenology matching), and (iii) arthropods of small body size dominate on trees with warm microclimate permitting to reach maturity at small size (temperature/size rule). We predicted these relationships to disappear among phylogenetically isolated trees. We focused on the most arthropod-diverse tree species of western Europe, *Quercus petraea* (hybridised with *Q. robur*), in a forest in western France. We found that when host trees were phylogenetically isolated (i) herbivory no longer increased proportionally with leaf size, (ii) phenology matching declined in particular on rapidly bursting trees, and (iii) temperature/size relationships shifted. We suggest that phylogenetic isolation prevents arthropods from effectively choosing trees with abundant resources, from matching phenology and from matching microclimate. Our results thus suggest that to avoid excessive herbivory, trees should grow far from phylogenetically closely related species (or alternatively budburst slowly).