Phylogenetic isolation of host trees affects assembly of local Heteroptera communities

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A host may be physically isolated in space and then may correspond to a geographical island, but it may also be separated from its local neighbours by hundreds of millions of years of evolutionary history, and may form in this case an evolutionarily distinct island. We test how this affects the assembly processes of the host's colonizers, this question being until now only invoked at the scale of physically distinct islands or patches. We studied the assembly of true bugs in crowns of oaks surrounded by phylogenetically more or less closely related trees. Despite the short distances (less than 150 m) between phylogenetically isolated and non-isolated trees, we found major differences between their Heteroptera faunas. We show that phylogenetically isolated trees support smaller numbers and fewer species of Heteroptera, an increasing proportion of phytophages and a decreasing proportion of omnivores, and proportionally more non-host-specialists. These differences were not due to changes in the nutritional quality of the trees, i.e. species sorting, which we accounted for. Comparison with predictions from meta-community theories suggests that the assembly of local Heteroptera communities may be strongly driven by independent metapopulation processes at the level of the individual species. We conclude that the assembly of communities on hosts separated from their neighbours by long periods of evolutionary history is qualitatively and quantitatively different from that on hosts established surrounded by closely related trees. Potentially, the biotic selection pressure on a host might thus change with the evolutionary proximity of the surrounding hosts.

Keywords: community assembly; canopy; evolutionary landscape; habitat fragmentation; metapopulation; trophic level

1. INTRODUCTION

Most habitats on Earth may correspond to living hosts, i.e. plant or animal species that are colonized by distinct communities of parasites, phytophages (in the case of plants), inquilines and their natural enemies or mutualists. These hosts may be physically isolated in space, forming geographical islands surrounded by uninhabitable matrix. Colonization processes of such hosts are relatively well understood, thanks notably to the island biogeography theory of MacArthur & Wilson (1967). But hosts can also be isolated from their local neighbours by many millions of years of evolutionary history. As a consequence, macroevolutionary isolation of a host may affect colonization processes, owing to a correlation

between phylogenetic distance and difference in niche suitability for the associated colonizer species. For example, phylogenetically isolated tree species, i.e. those which have few closely related species within a region, harbour a depauperate colonizer fauna (Kennedy & Southwood 1984; Brändle & Brandl 2006). At a regional scale, phylogenetically isolated tree species have thus been considered as 'macroevolutionary islands', with typically poor faunas. However, it remains unknown whether the occupation of a macroevolutionarily distinct island at a local scale triggers assembly processes that are similar to those at the regional scale. An individual tree, for instance, may have many closely related species across an entire region, but find itself isolated within a local canopy of distantly related species. An oak in a pine canopy is such a local evolutionarily distinct island. Species adapted to use pines as a habitat may not be able to colonize oaks (niche limitation), and those adapted to use oaks may only rarely reach an oak among pines (dispersal limitation). This leads to the question of whether the same processes occur at a local as at a regional scale, affecting the assembly of associated local communities of colonizers on macroevolutionarily distinct hosts.

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Indirect evidence comes from the agro-ecology literature about intercropping and host-diversity effects on the control of crop pathogens and pest dynamics (e.g. Garrett & Mundt 1999; Gilbert & Webb 2007). These plant/pest-based studies demonstrate that closely related hosts should be susceptible to the same plant pests, revealing a strong phylogenetic signal in host range of pests (Novotny *et al.* 2002; Parker & Gilbert 2004; Novotny & Basset 2005). However, the effect of intercropping may to a large extent reflect the dilution of suitable food sources among non-suitable food sources at a very fine scale, i.e. within the search range of a phytophage. The impact of the distribution of phylogenetically distinct hosts on the assembly of entire communities of colonizers (their local richness, abundance, trait and trophic composition) still remains unknown.

The assembly of local communities in habitat patches within a physically distinct matrix has attracted much interest in ecology, leading to the emergence of multiple 'metacommunity' paradigms (Leibold & Miller 2004). These paradigms may also be applicable to the assembly of communities on evolutionarily distinct patches. The paradigms invoke (i) local niche-based processes such as birth and death rates driven by interactions with the abiotic and biotic environment (Tilman 1982) and (ii) spatial dispersal processes such as emigration and immigration connecting local communities into a metacommunity (Wilson 1992). The main paradigms for metacommunity theory (reviewed in Leibold & Miller 2004) thus suggest a balance between local processes and those occurring at a larger scale (mediated by dispersal). In the case of evolutionarily distinct islands, these processes depend on the hostility of the matrix surrounding a patch, which varies along a continuum, and on the degree of host specialization within the colonizer communities in question affecting sharing of species between matrix and patch (Holt 1996; Tscharntke *et al.* 2005).

Such metacommunity processes across multiple generations lead to specific predictions regarding the spatial structuring of species assemblages (table 1). First, according to the island biogeography theory of MacArthur & Wilson (1967), community assemblages result exclusively from the stochastic processes of (rare) colonizations and extinctions that decrease and increase, respectively, with the number of species established in a patch. Isolated patches have lower species richness because, in comparison with non-isolated patches, the colonization rate is lower relative to the extinction rate. The few species on isolated patches, however, reach the same total abundance as the numerous species in non-isolated patches. Furthermore, such isolated patches are most likely to be colonized by good dispersers; local communities therefore contain fewer species but with greater dispersal capacity than non-isolated patches (in the absence of any post-colonization reduction in dispersiveness).

Second, based on the theoretical requirement for a trade-off between species traits to allow the coexistence of species with differing competitive ability, the patch-dynamic model (Levins 1969; Leibold *et al.* 2004) implies a negative correlation between competitive ability and dispersal, favouring good dispersers in isolated patches and good competitors in non-isolated patches. As a result, local species composition in strongly isolated patches is

characterized by a higher proportion of good dispersers and fewer good competitors. In intermediately isolated patches, good competitors increase in abundance without yet entirely replacing the good dispersers and species richness is thus high. In non-isolated trees, extinction risk for good dispersers is high, owing to their local exclusion by good competitors, leading to a loss of species richness. Third, the mass (rescue) effect model (Brown & Kodric-Brown 1977; Shmida & Wilson 1985) is based on a system composed of patches and matrix representing different types of habitat, which, unlike the previous models, are connected by dispersal. Dispersal leads to source-sink relations between populations of species adapted to those different habitats. This model predicts in particular massive immigration of individuals into isolated patches of one habitat type from the surrounding matrix of other habitat types, thereby sustaining local sink populations of non-specialist species, i.e. species that are only poorly adapted to the habitat type in question but are well adapted to the surrounding matrix habitat types (Pulliam 1988; Danielson 1991; Holt *et al.* 2003). Consequently, local community composition in isolated habitat patches is characterized by a large proportion of non-specialist species. In contrast, the number of species specialized on the patch habitat type will decrease with increasing isolation (owing to lower immigration). The highest species richness is then observed in intermediate isolated habitat patches, profiting from both immigration of non-specialists and local persistence of specialists (Mouquet & Loreau 2002).

Fourth, based on a species distribution closely related to local niche conditions, the species-sorting paradigm (Tilman 1982; Chase & Leibold 2003) implies an independence of both species abundance and richness from spatial positions of patches. The best adapted species are found in each habitat, whatever their dispersal abilities and the habitat connectedness. Furthermore, the more local patches are heterogeneous in some habitat factors, the higher the species richness.

Finally, the above mechanisms may be strongly modified by metapopulation processes (Gilpin & Hanski 1991). In contrast to the island biogeography theory that focuses on multi-species equilibria and rare colonization and extinction events, metapopulation theory focuses on population turnover of individual species and postulates frequent extinctions and re-establishments of each local population on an individual patch. In the case of dispersal limitation, isolated patches harbour isolated and thus small populations, in particular owing to the reduced rescue effect of immigration from nearby populations. Small local populations are more likely to go extinct than large ones, and traits reducing the size of local populations—such as being a predator, being specialized on only one habitat type or having a large body size—will further increase the frequency of local extinctions (Lawton 1995). In isolated patches where re-colonization is less frequent, species with these traits are thus likely to be lost from communities (Holt & Keitt 2000). As a consequence, metapopulation processes induce lower average abundances in isolated patches. We summarize these mechanisms and predictions in table 1. By comparing predicted to observed patterns, we can qualitatively assess the probable pertinence of the different mechanisms in nature for entire communities, even though the

Table 1. Tested theoretical models on spatial organization of population and species organized in metacommunities. Respective main mechanisms and predictions concerning abundance, species richness and species traits associated to species assemblages in isolated habitat patches are specified. Positive or negative support ((supported) versus (not supported)) for each prediction from our empirical results on Heteroptera communities are mentioned for each prediction.

paradigms	mechanism invoked	predictions in habitat patches with increasing isolation			traits of species (proportional representation)
		total abundance	species richness		
island biogeography ^a	few species succeed in colonizing isolated patches, notably good dispersers. There is equilibrium between colonization of new species and extinction of established species	equal (not supported)	lower (supported)		more good dispersers with increasing isolation (not supported)
patch dynamics ^b (competition/ colonization trade-off)	good dispersers are poor competitors and vice versa continuum of level of isolation: strongly isolated patches are colonized mainly by good dispersers. With decreasing isolation, patches become increasingly colonized by poor dispersers and good competitors. These latter tend to exclude the good dispersers/poor competitor species in the non-isolated patches	—	relationship to isolation: hump-shaped, higher for intermediate levels of isolation lowest richness under weakest and strongest isolation (not supported)		more good dispersers with increasing isolation (not supported)
mass effect ^c	continuum of level of isolation: — strongly isolated: patches are colonized by non-specialists species from the surrounding matrix (i.e. species not specialized on the isolated type of habitat, but potentially specialized on another surrounding habitat), but only few habitat specialists succeed to colonize it. Non-specialists may form sink populations maintained by influx from surrounding matrix — patches of intermediate degree of isolation are colonized by non-specialists species from the surrounding matrix, in addition to habitat specialists — non-isolated patches are mainly colonized by specialists, few non-specialists available in the surrounding matrix	—	relationship to isolation: hump-shaped, higher for intermediate levels of isolation (not supported)		increased proportion of species not specialized on the patch type on which they occur (supported)
species sorting ^d	local patches differ in means and variance of niche attributes affecting local species interactions. Species distribution is then closely related to local conditions and largely independent of spatial effects	independent of isolation linked to niche attributes (partially supported)	independent of isolation linked to niche attributes: larger range of niche conditions, more species (partially supported)		—
metapopulation ^e	local populations are linked into a metapopulation. Frequent stochastic local extinctions are compensated by re-colonization, but on isolated patches this is slow, in particular for habitat specialists. Stochastic extinctions will in particular affect inherently rare species (large species, predators), and this, more probably on isolated patches	lower (supported)	lower (supported)		few predators and omnivores, few large species, few habitat specialists many phytophages and 'non-specialists' (partially supported)

^aMacArthur & Wilson (1967).

^bLevins (1969) and Leibold *et al.* (2004).

^cShmida & Wilson (1985) and Mouquet & Loreau (2002).

^dTilman (1982) and Chase & Leibold (2003).

^eGilpin & Hanski (1991).

direct quantitative test of these mechanisms remains usually not feasible.

The canopy of a forest is an ideal heterogeneous and patchy macroevolutionary landscape with tree crowns representing relatively large discrete habitat patches with distinct evolutionary histories (as reflected by phylogenetic positions), easily perceptible for both humans and canopy arthropods and with high documented biodiversity (e.g. Stork *et al.* 1997; Ozanne *et al.* 2000; Southwood *et al.* 2005). Among tree-crown arthropods, Heteroptera are a diverse group in terms of body size, dispersal capabilities, degree of host plant specialization and trophic level, ranging from strictly phytophagous species to predators. Furthermore, Heteroptera are relatively large and rely on active dispersal, rather than falling as a rain of aerial plankton, hence dispersal limitation should occur on a relatively small scale, and local extinction in 1 year may often persist into the following year (Lewis & Taylor 1965). Spatial patterns at one moment thus reflect a dynamic equilibrium between the frequency of prior local extinction and re-colonization events.

We used Heteroptera to test which of the metacommunity paradigms most accurately predict patterns of species richness, abundance and species traits on more or less phylogenetically isolated individual crowns within the evolutionary landscape of a forest canopy. We considered the local scale of a forest at which individual Heteroptera have a realistic chance of moving between patches within their lifetime, but at which some dispersal limitation may occur for many of them. We compared Heteroptera richness, abundance and trait composition (body size, macroptery, host specialization and trophic level) within crowns to phylogenetic isolation of crowns. To account for potential differences in niche conditions between more or less phylogenetically isolated trees (species-sorting effect, Tilman 1982), we included information on leaf chemistry in our analyses. We discuss the results in the light of metacommunity paradigms.

2. MATERIAL AND METHODS

(a) Site description and experimental design

Sampling was carried out in the Forêt de Rennes (surface area: 2000 ha, Brittany, France), a forest dating back to at least the twelfth century. As with all forests occurring in western and central Europe, this forest is under the influence of human activities, such as the wood management itself and the surrounding agricultural land use (including meadows). No entirely natural forest may serve as a source of Heteroptera in this western part of Europe. European temperate forests are typically composed of indigenous deciduous species such as oak (*Quercus* sp.), beech (*Fagus sylvatica*), hornbeam (*Carpinus betulus*), poplar (*Populus* sp.) and birch (*Betula* sp.), and also native conifers such as pine (*Pinus* sp.) and fir (*Abies* sp.), according to the region. The Rennes forest is split into parcels, and is mostly managed following the shelterwood cutting system (Borghetti & Giannini 2001). Each parcel is mainly composed either of oak (*Q. petraea* or *Q. robur*) or pine (*P. sylvestris*). The other main tree species in these parcels are holly (*Ilex aquifolium*) and beech (*F. sylvatica*). In addition, there were 19 less abundant species (see electronic supplementary material, appendix table S1). All these species are native to the

occidental European region. The planted trees are from a few years to more than 150 years old, depending on the parcels.

Eighteen *ca* 80-year-old oaks were chosen for the study, with age estimated by tree circumference at breast height (total mean equal to 93.2 cm (s.d. = 22.4)) combined with information from foresters. We chose pairs of trees in close proximity to one another (around 30–150 m apart), one in a canopy of mainly oak and beech and the other in a canopy of mainly pine. Such an approach of ‘blocking’ has been recommended to partial out spatially varying environmental impacts (Legendre *et al.* 2004).

Heteroptera species were sampled monthly from late May to mid-November 2006, with insect flight interception traps (one per tree) placed in crowns at a mean height of 13 m above the ground (s.d. = 4.1). These traps are well established as a means of studying faunal composition of actively or passively flying insects in tree crowns. Specifically, we opted for flight interception traps because they permit an overview of the entire season, hence covering the large temporal species turnover observed in many insect taxa. Owing to the long sampling period, these traps are not biased by similar but temporally offset faunas on different trees, as would be the case with methods that take a snapshot at a given moment. The collecting bottle at the base of the trap was filled one-third full with 30 per cent copper sulphate solution to kill the insects, and a few drops of detergent were added to cause them to drop into the liquid. A total of four to five samples were taken per tree, with a gap of two to seven weeks (normally four) between each sampling, all trees from all pairs being sampled at all dates. Specimens were manually sorted and identified to species based on taxonomic literature (Stichel 1956; Wagner & Weber 1964; Pericart 1972, 1987, 1998) and several species-level publications (e.g. Wagner 1975). For all analyses, we pooled the samples from a given tree to calculate total Heteroptera richness and abundance.

(b) Estimation of the phylogenetic isolation of focal oaks

In order to have a quantitative and continuous variable to estimate focal tree isolation according to the proximal environment, we used a ‘phylogenetic isolation’ index, which measures the mean phylogenetic distance between the focal oak and the surrounding tree species directly in contact with its crown. This phylogenetic index is calculated as follows, with distance weights corresponding to the phylogenetic time separating oak from surrounding tree species:

$$I_{\text{phylogenetic isolation}} = \frac{\sum (N_{\text{tree sp.}} \times t_{\text{tree sp.}})}{N_{\text{total trees}}},$$

where $N_{\text{tree sp.}}$ is the number of trees of a given species surrounding the focal oak, and $t_{\text{tree sp.}}$ is the estimated time (in MYBP) since the evolutionary establishment of the clades of that tree species and of oaks as distinct hosts (Magallon *et al.* 1999; Manos *et al.* 1999; Wikström *et al.* 2001; APG 2003; Poinar *et al.* 2007). Note that this is not the most recent common ancestor as this would give pines an extreme weight, given the large age of gymnosperms (probably more 160 million years older than angiosperms as we know them today), and would essentially render our parameter a simple percentage of pines in the surrounding of the oaks. Rather, this is the age when both sister clades had established their particular characteristics as hosts for

insects. The distance weights are listed in electronic supplementary material, appendix table S1. Overall, this index ranged from 5.71 (non-isolated oaks) to 106.67 (strong phylogenetic isolation), covering the continuum of oak isolation.

An alternative scale of phylogenetic isolation was also tested, corresponding to a 'distant phylogenetic isolation' index, which measures the mean phylogenetic distance between the focal oak and the surrounding tree species situated at the four cardinal points at 20 m distance from the focal oak. This index leads to the same results as the above based on crowns in direct contact with the focal crown (results not shown), which means that the canopy composition in contact with the tree is representative of the general canopy composition in a radius of 20 m. We note that phylogenetic isolation of trees did not correlate to crown size (i.e. distance from lowest to the highest live branch, $r = -0.008$, $p = 0.97$). We also note that the understory is not included into the estimation of phylogenetic isolation index, as Goßner *et al.* (2009) have shown that angiosperm understory is not a major source of colonizers of angiosperm canopy. More importantly, the number of non-oak specialists (inferred from host-plant associations of European Heteroptera given in Wagner & Weber (1964) and Wachmann *et al.* (2004) did not differ between isolated and non-isolated trees in present study. The contributions of the different probable host origins of the Heteroptera colonizing oaks are given in electronic supplementary material, appendix table S2.

(c) Niche attributes and diversity of individual oak canopies

The species diversity of the surrounding canopy of the focal oak crowns was measured using the natural logarithm of Simpson's diversity index (Rosenzweig 1995) of tree species in contact with each focal crown.

In order to characterize the nutritional living conditions in tree crowns, we studied mean per cent dry matter content, per cent phenolic compounds and carbon/nitrogen ratio of the leaves (Roslin *et al.* 2006). Variances (i.e. standard deviations) of these niche variables were also calculated in order to account for intra-patch heterogeneity. On the 18 trees, 30 leaves were sampled per crown from 16 August 2006 to 27 September 2006, 10 from the top stratum (the highest quarter of the tree, in proximity to the trunk), 10 from the exposed stratum (in the outer canopy, with no branches above preventing sun exposure) and 10 from a sheltered stratum (typically lower in the canopy, always with branches above reducing sun exposure). Each leaf was cut longitudinally into two pieces: the one carrying the main central vein was reserved for polyphenol analyses, while the smaller was used to measure dry matter content and C/N ratio. Measures of dry matter content were made according to Cornelissen *et al.* (2003). Measures of C/N were conducted at University of Bodenkultur, Vienna. For total phenolics analyses, the 10 leaves of the same stratum were pooled, frozen and lyophilized (36 h) altogether, in order to obtain sufficient biological material. Total phenolic compound measurements were conducted at the Polyphenol 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).

(d) Traits of Heteroptera

Based on a literature review (Stichel 1956; Wagner & Weber 1964; Pericart 1972, 1987, 1998; Wagner 1975; Wachmann *et al.* 2004), we assigned each Heteroptera species to (i) trophic level (predator = 1, omnivore (i.e. eating both plant and prey) = 2, phytophagous = 3), (ii) level of oak specialization (oak specialist = 1 versus non-specialist = 0; none of the species is a true generalist using equally oaks and pines), (iii) mean adult body size in centimetres (in case of multiple values given in the literature we took the mean), and (iv) as an indicator of the dispersal capacity the degree of macroptery (0 was theoretically assigned to exclusively brachypterous species (no species was exclusively brachypterous), 1 was assigned to macropterous species and an intermediate value of 0.67 was given to species that, across both sexes, are mainly macropterous and 0.33 to species that are mainly brachypterous). For five species (all rare: one to three individuals), information on biological traits was not available and these were excluded from the analyses (cf. electronic supplementary material, appendix table S3).

(e) Data analyses

Phylogenetic isolation of a tree in a canopy may be correlated to the tree-species diversity of that canopy. We hence tested by linear regression the relationship between the phylogenetic isolation and Simpson's index of species diversity of the canopy. Phylogenetic isolation of crowns may also have some impact on niche attributes (per cent phenolic compounds, per cent dry matter, C/N and their variance) as the light intensity or sun exposure, for example, may vary according to the surrounding canopy (Niinemets 1997; Wieser *et al.* 2003). We thus tested the effect of phylogenetic isolation on niche attributes using linear regressions.

To evaluate how species richness and abundance of Heteroptera vary according to isolation of the tree host (cf. predictions in table 1), we conducted multiple regressions with species richness or abundance as dependant variables, and phylogenetic isolation index, Simpson's index and means and standard deviations of leaf chemistry variables as predictive variables. Tree pair (the pair of trees present in the same forest parcel) was used as a blocking factor to account for spatial effects. This proved to be significant (§3) and was hence retained in the model. The best-fitting models were determined using the Akaike Information Criterion (AIC) (Johnson & Omland 2004) and employing 'all subsets regression', which calculates AIC for every possible combination of explanatory variables, allowing the best-fitting models to be identified. Our aim was to examine specifically the relationship between tree phylogenetic isolation and Heteroptera abundance and richness, while accounting for potential confounding effects of niche attributes. We did not intend to examine the effects of these covariables, although we note that some of these niche variables which were retained in the final model (together with phylogenetic isolation) provides support for the species sorting paradigm. We therefore present, for each of richness and abundance, only the model with the best AIC and note that the relationship between phylogenetic isolation and either response variable was little affected by the presence or absence of the covariables. Both richness and abundance are count data, and hence a generalized linear model with Poisson errors and log link was used in both cases, and the dispersion parameter was estimated rather than fixed at 1. Additionally, simple regressions were performed to illustrate

Table 2. Results of the best-fitting (AIC criterion) regressions explaining the species richness and abundance of Heteroptera by the environmental attributes showing significant ($p < 0.05$) correlations. Other tested environmental attributes (Simpson's index, mean per cent dry matter and mean C/N ratio) were not significant ($p > 0.05$) in these models.

	d.f.	null deviance	residual deviance	r^2	F	t -stat.	p
species richness	11,6	17.8	0.5	97.2	19.5		<0.001
phylogenetic isolation						-9.6	<0.001
s.d. C/N						-6.25	<0.001
s.d. %polyphenols						5.31	<0.01
tree pairs						—	<0.01 (overall)
constant						15.5	<0.001
species abundance	12,5	31.1	0.4	98.7	34.23		<0.001
phylogenetic isolation						-15.6	<0.001
s.d. C/N						-11.5	<0.001
mean % polyphenols						9.2	<0.001
s.d. % dry matter						2.94	<0.05
tree pairs						—	<0.01 (overall)
constant						14.45	<0.001

how the species richness of Heteroptera depended on only phylogenetic isolation of trees. Analyses were conducted using GENSTAT v. 10 (VSN International, Ltd).

To evaluate how the biological characteristics of Heteroptera species are affected by host tree phylogenetic isolation (cf. predictions in table 1), we used the '4th Corner method' (Legendre *et al.* 1997, free-access 'R' software available at http://www.bio.umontreal.ca/casgrain/en/labo/4th_corner.html). This method uses three matrices (matrix 1: species distribution i.e. sites versus species; matrix 2: species traits i.e. species versus traits; matrix 3: environmental characteristics i.e. sites versus environment and habitat attributes) to develop a fourth matrix that links the distinct kinds of habitat to biological traits (matrix 4: environment and habitat attributes versus species traits). In our case, such analysis allows evaluation of associations between traits of Heteroptera species and phylogenetic isolation of host oaks. Again, including variables of leaf chemistry in addition to phylogenetic isolation allows niche effects to be controlled for in tests of host isolation. In this study, matrix 1 contained the abundance of Heteroptera species in each crown over the entire sampling season (sites versus taxa: 18×51). The trait matrix, matrix 2, contained the trait categories, corresponding to two binary variables (trophic level and oak specialization) and two quantitative variable (body size and macroptery) for each species (trait categories versus taxa: 4×51). The environmental matrix, matrix 3, contained the eight environmental and habitat attributes (phylogenetic isolation, Simpson's species diversity and the means and variances of the three leaf chemistry variables) of each tree crown (sites versus environmental and habitat attributes: 18×8). To obtain a global measure of association between trait variables and habitat variables, an analysis of variance (yielding an F -statistic) was conducted for each trait variable. When the F -value is significant, this indicates that the proportional representation of at least one category of that trait is significantly correlated with the considered habitat variable. A Pearson product-moment correlation coefficient r is then calculated between each trait category and each habitat variable to estimate the strength of the association. Both the F -statistics and the correlation statistics are tested using random permutation (999 runs) according to the Model-1 (environmental control over individual species) proposed in the 4th Corner Method (Legendre *et al.* 1997).

3. RESULTS

(a) Relationship between phylogenetic isolation of crowns and niche conditions

There was no significant relationship between phylogenetic isolation and Simpson's species diversity of the canopy ($r = 0.24$, $t = 1.28$, d.f. = 1,16, $p = 0.22$).

The phylogenetic isolation had no significant effect on the mean or variance of per cent polyphenols (respectively, $r = 0.2$, $t = 0.83$, d.f. = 1,16, $p = 0.42$ and $r = -0.01$, $t = 0.04$, d.f. = 1,16, $p = 0.97$), or mean and variance per cent dry matter (respectively, $r = -0.23$, $t = -0.93$, d.f. = 1,16, $p = 0.37$ and $r = -0.13$, $t = -0.52$, d.f. = 1,16, $p = 0.61$), and had a marginally significant influence on mean and variance C/N ratio (respectively, $r = -0.41$, $t = -0.78$, d.f. = 1,16, $p = 0.09$ and $r = -0.46$, $t = -2.06$, d.f. = 1,16, $p = 0.06$; table 2).

(b) Relationship between phylogenetic isolation of crowns and abundance and diversity of heteroptera

A total of 302 Heteroptera individuals comprising 50 species and six smallest identifiable units were recorded (electronic supplementary material, appendix table S3), with 1–31 individuals per species and a mean of 5.4 (s.d. = 4.9). Seventeen species were found only on isolated oaks (those in pine parcels), all in very low numbers (generally only one individual in total, mean = 1.35, s.d. = 0.8), while 26 species were found only on non-isolated oaks, also in very low numbers (mean = 1.57, s.d. = 1.17). All the species found only on isolated trees were non-oak specialists.

In the best model (AIC) retained among the multiple regressions analysing the effect of the eight independent variables (phylogenetic and Simpson indices and the six leaf chemistry variables) on Heteroptera richness, only phylogenetic isolation, s.d. of per cent polyphenols and s.d. of C/N ratio remained significant (table 2). In particular, richness decreased with increasing isolation. The univariate regression illustrating the link between species richness and phylogenetic isolation index was significant ($r = -0.54$, $t = -2.59$, d.f. = 1;16, $p = 0.02$; figure 1a).

Similarly, phylogenetic isolation index, s.d. of per cent dry matter, mean polyphenol content and s.d. of C/N

Figure 1. Relationship between tree phylogenetic isolation index (isolation increasing to the right) and (a) the species richness of Heteroptera ($r = -0.54$, $t = -2.59$, d.f. = 1,16, $p = 0.02$) and (b) the species abundance of Heteroptera ($r = -0.53$, $t = -2.62$, d.f. = 1,16, $p < 0.02$). These results are for univariate analyses, while results of multivariate analyses (showing stronger effects) are presented in the text.

ratio were significant in the best model (AIC) explaining the total Heteroptera abundance (table 2). Abundance was lower on more isolated trees. The univariate regression illustrating the link between Heteroptera abundance and phylogenetic isolation index was significant ($r = -0.53$, $t = -2.62$, d.f. = 1;16, $p < 0.02$; figure 1b).

(c) Relationship between phylogenetic isolation of crowns and traits of Heteroptera species

Results from the 4th Corner analyses showed that all the niche characteristics were (much) less correlated with species traits than was phylogenetic isolation, and there was no significant correlation between traits and Simpson's index (table 3). The trait 'macroptery' was not correlated with tree phylogenetic isolation (see F - and r -values in table 3). The proportions of phytophages and of non-oak specialists were significantly higher on more isolated trees, while omnivores and oak specialists were significantly less frequent on more isolated trees. There was no effect of phylogenetic isolation on the representation of predators or on body size.

4. DISCUSSION

Theoretical metacommunity and metapopulation models make specific assumptions about dispersal processes and the ecological traits of the species involved in community

functioning, leading to a unique combination of predictions of species and community traits in isolated habitat patches for each model (MacArthur & Wilson 1967; Levins 1969; Shmida & Wilson 1985; Gilpin & Hanski 1991; table 1). Our empirical results allow testing of the concordance of these theoretical models with the observed Heteroptera communities on more or less phylogenetically isolated oaks. Furthermore, they permit us to address two important points. First, our results are robust to the precise distance across which isolation was measured (trees in contact with the focal tree versus trees at 20 m distance; §2). Second, the absence of a correlation between Simpson's species diversity (contrary to strong effects of phylogenetic isolation) and Heteroptera assemblages provides no support for an effect of canopy species diversity on Heteroptera assemblages on oak.

None of the five main metacommunity and metapopulation paradigms can be universally supported by our results. However, two of them make the most predictions and are most consistently supported: the species sorting and the metapopulation paradigms. Species abundance and richness are linked to some niche attributes, as predicted by the species-sorting paradigm. But this paradigm also strongly assumes that the species distributions are largely independent of unrelated purely spatial effects (Leibold *et al.* 2004), which is not the case in our results with the Heteroptera community being strongly influenced by the phylogenetic isolation of a tree from its neighbours (while controlling for niche attributes). The results are much more consistent with the metapopulation hypothesis. The decreasing abundance and the consequently decreasing species richness, both associated with increasing tree isolation, suggest that the influence of stochastic extinction events is higher on more isolated trees as local extinctions will only rarely be prevented by rescue effects. Moreover, the impact of stochastic extinction in isolated patches should be higher for higher trophic levels (§1); this is indeed observed in the Heteroptera communities in isolated oaks, which contain proportionally more phytophages and fewer omnivores, although the prediction of fewer predators is not supported. Metapopulation models also predict a greater spill-over of non-oak specialists from the surrounding matrix habitat as patch isolation increases (Holt 1997), and this prediction is well supported.

Hence, although the future production of more sophisticated metacommunity models may lead to a closer match to our results, based on existing knowledge we conclude that independent metapopulation dynamics cannot be ruled out. Regarding the other theories, most predictions are not supported by this analysis: the mass effect model is supported only by the greater proportion of non-oak specialists with increasing isolation, while the accompanying linear decrease in richness along the continuum of tree relatedness does not match with the hump-shaped local species richness predictions associated to mass effect models (Mouquet & Loreau 2002). The island biogeography model is supported only by lower species richness, and the patch dynamics model is not well supported at all.

The absence of an effect of tree isolation on Heteroptera size or on the prevalence of predators highlights a major challenge in comparing these paradigms

Table 3. Relationships between canopy attributes and Heteroptera traits. For continuous traits the table reports *r*-values and significances (n.s., *p* > 0.05, **p* < 0.05, ***p* < 0.01, ****p* < 0.001.). For categorical traits, the table reports the global tests of significant (*F*) and their probabilities significances obtained by permutations (999 runs) following Model 1 of the 4th Corner method (Legendre *et al.* 1997). The *r*-values of individual states of a categorical trait from the correlation traits–habitat matrix are given in case of significant global test of variance, and also tested by permutations.

Heteroptera traits	canopy attributes		local patch conditions					
	surrounding canopy							
	contact phylogenetic isolation	Simpson index	mean C/N	% dry matter	% phenolic compounds	s.d. C/N	s.d. dry matter	s.d. phenolic compounds
continuous variable								
body size	<i>r</i> = 0.03 n.s.	<i>r</i> = -0.02 n.s.	<i>r</i> = -0.11 n.s.	<i>r</i> = 0.09 n.s.	<i>r</i> = -0.07 n.s.	<i>r</i> = -0.03 n.s.	<i>r</i> = 0.02 n.s.	<i>r</i> = -0.06 n.s.
categorical variables								
wing size	<i>F</i> = 1.21 n.s.	<i>F</i> = 1.91 n.s.	<i>F</i> = 0.31 n.s.	<i>F</i> = 0.62 n.s.	<i>F</i> = 1.15 n.s.	<i>F</i> = 3.36 n.s.	<i>F</i> = 0.10 n.s.	<i>F</i> = 1.74 n.s.
strict macropterous								
semi- and strict								
brachypterous								
trophic level	<i>F</i> = 5.58***	<i>F</i> = 1.61 n.s.	<i>F</i> = 0.89 n.s.	<i>F</i> = 1.92 n.s.	<i>F</i> = 1.09 n.s.	<i>F</i> = 3.85*	<i>F</i> = 1.53 n.s.	<i>F</i> = 0.38 n.s.
phytophagous	<i>r</i> = 0.14*					<i>r</i> = -0.16*		
omnivorous	<i>r</i> = -0.25***					<i>r</i> = 0.19**		
predator	<i>r</i> = 0.10 n.s.					<i>r</i> = -0.02 n.s.		
oak specialization	<i>F</i> = 9.13**	<i>F</i> = 1.46 n.s.	<i>F</i> = 0.12 n.s.	<i>F</i> = 1.18 n.s.	<i>F</i> = 0.41 n.s.	<i>F</i> = 4.48*	<i>F</i> = 1.18 n.s.	<i>F</i> = 0.41 n.s.
specialist	<i>r</i> = -0.22**					<i>r</i> = 0.16*		

empirically: landscape structure, matrix hostility and the isolation of individual patches differ between species depending on their degree of habitat specialization, indicating different 'functional spatial scales' among species (Holt 1996; Roland & Taylor 1997; Ritchie & Olff 1999; Tscharntke *et al.* 2005; Hirao *et al.* 2008). For example, the lack of impact of crown isolation on predators may simply be because predatory Heteroptera are less dependent on host plant physiology than either phytophages or omnivores, and hence are less host-plant specific. From a predator's perspective, the phylogenetic isolation may therefore be less representative of patch isolation than for phytophages or omnivores because the canopy is perceived as more homogeneous.

5. CONCLUSION

Our results indicate that (i) species and population dynamics of forest insects in a patchy environment occur at a very small scale; (ii) phylogenetically isolated trees have Heteroptera communities with fewer specialists, more phytophages and fewer omnivores, lower abundance, and lower species richness; (iii) these observations lend some support to certain theoretical models of community assembly, but are in contrast to others. The dynamics of communities and food webs are undoubtedly influenced by patterns of species interactions and multispecies equilibria (Holt 2000). But we demonstrated that within each trophic level, the assembly of local species communities on a phylogenetically isolated host (evolutionarily distinct island) may possibly be driven rather by metapopulation processes at the level of the individual species. Further work focusing on the influence of local species interactions on species distributions will make more refined comparisons of the respective roles of metacommunity and metapopulation processes possible.

Overall, our results show the importance of evolutionary landscapes for community assembly: the common ancestor of a host tree and its neighbouring trees may have lived between some centuries and more than hundred million years ago, and this influences today's assembly of insects on this host tree. Trees may often immigrate into a matrix of non-related trees, during ecological succession, during biogeographical expansion (human assisted or not), or during the macroevolutionary origin of novel lineages. Our results suggest that these immigrating trees, or any other kinds of immigrating hosts, may be exposed to a fauna that is qualitatively and quantitatively different from that on trees established in a matrix of closely related trees. The biotic selection pressure on a host may thus change with the evolutionary proximity of the surrounding hosts.

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