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Climate affects neighbour-induced changes in leaf chemical defences and tree diversity-herbivory relationships

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Associational resistance theory predicts that insect herbivory decreases with increasing tree diversity in forest ecosystems. In practice, the numerous studies on the subject have sometimes found a neutral or positive effect of tree diversity on the abundance of herbivorous insects or the level of damage they cause to trees. Recently, evidence has accumulated that the direction and strength of the relationship between tree diversity and insect herbivory could be influenced by the climatic context.

Besides, several mechanisms have been proposed and demonstrated to explain diversity-herbivory relationships (*i.e.* associational effects), but recent research on indirect trait-mediated effects is bringing new insights: tree diversity effects on insect herbivory could be indirectly mediated by interspecific neighbour-induced changes in tree chemical defences. Given the dependence of the physiology of both trees and insects on climate, this mechanism is likely to vary depending on the climatic conditions, but this remains to be clarified.

Using a unique network of tree diversity experiments, ranging from temperate to boreal biomes (TreeDivNet, https://treedivnet.ugent.be/), we investigated i) whether the effects of neighbouring tree species diversity on insect herbivory in birch, *i.e.* associational effects, were dependent on the climatic context, and ii) whether neighbour-induced changes in birch chemical defences were involved in associational resistance to insect herbivory, and under which climatic conditions. To do so, we quantified insect leaf herbivory and leaf chemical defences (phenolic compounds) in silver birch (*Betula pendula*) in plots with different tree species composition across twelve locations with different climates.

A birch leaf waiting to be devoured by the larva of a herbivore.

With this study, we showed that the effect of tree species diversity on insect herbivory on silver birch leaves was climate-dependent and, specifically, varied with temperature. Our findings also showed that tree species diversity modified chemical defence levels in birch leaves, but further suggested that such changes in leaf chemistry induced by heterospecific neighbours are complex, as they are influenced in opposite ways by the number of species and the functional dissimilarity between species. Altogether, our results showed that neighbour-induced changes in birch chemical defences were climate-dependent and that they partly explained associational resistance to herbivory. Our findings build toward a more general predictive framework of the effects of tree diversity on resistance to insect herbivores. In this sense, it could help forest managers to mitigate the risk of pest invasions that is likely to increase with the ongoing environmental changes.