

## Early resistance of alien and native pines against two native generalist insect herbivores: no support for the Natural Enemy Hypothesis

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The Natural Enemy Hypothesis (NEH) predicts that alien plant species might receive less pressure from natural enemies than do related coexisting native plants. However, most studies to date are based on pairs of native and alien species and the results remain inconclusive. The level of attack by native generalist herbivores can vary considerably between plant species, depending on defensive traits and strategies. Plant defenses include preformed constitutive and induced defenses that are activated as plastic responses to herbivore attack. However, the efficacy of induced defenses could be altered when alien species entering an area are exposed to native enemies.

We tested the NEH for several closely related alien and native pines to Europe by examining early anti-herbivore resistance to damage by two generalist native insect herbivores (*Hylobius abietis* and *Thaumetopoea pityocampa*); the differences in constitutive and inducible chemical defenses (i.e. non-volatile resin and total phenolics in the stem and needles); and whether consumption preferences shift after induced defenses have been triggered by real herbivory.

We did not find alien pines to be less damaged by two generalist herbivores than native pines were. The constitutive concentration of chemical defenses significantly differed among pine species. The concentration of constitutive total phenolics in the stem was greater in native than in alien pines. The opposite trend was found for constitutive total phenolics in the needles. The concentration of chemical defenses (non-volatile resin and total phenolics) in the stem significantly increased after herbivory by *H. abietis*. Moreover, the induction of total phenolics by *H. abietis* damage was significantly greater in native pine species than in alien pines. On the other hand, only concentrations of non-volatile resin in needles significantly increased after herbivory by *T. pityocampa*, but without significant differences in inducibility between alien and native pines. In cafeteria bioassays, *H. abietis* consumed the twigs from alien more than those from native species irrespective of prior exposure to the insect. Meanwhile, no differences among range origin were found in the *T. pityocampa* cafeteria bioassays.

Overall, we found no support for the NEH in alien pines to Europe. This suggests that alien pines, in regions where they coexist with native congeners, may be controlled by native generalist herbivores, this being one reason that invasion by alien pines is not frequent in Europe.