

Successful invasion of a floral market

An exotic Asian plant has moved in on Europe's river-banks by bribing pollinators.

Invasive plants can displace native species through competition for nutrients, water, light and space. Here we show that they may also exert indirect pressure by competing for pollinators. We use the Asian plant *Impatiens glandulifera* as an example — this aggressive invader tempts bee pollinators away from native flowers with its rich nectar, which is more rewarding than that of any known native plant in central Europe. This causes a reduction of seed set in local plants in the vicinity and enables *I. glandulifera* to take over, reducing the fitness of native flora before competition for other resources even takes effect.

In just over a century since its introduction from the Himalayas, *I. glandulifera* (Fig. 1a) has conquered more than half of the river banks in the Czech Republic¹ and is spreading at a comparable rate elsewhere in Europe² and in North America³. At over 2 metres high, it is the tallest annual in Europe, with extensive branching of the main stem ensuring monopoly of the aerial environment. It also tolerates a wide range of climates and soil types⁴, which contributes to its success as a competitor. Each plant produces about 2,500 seeds, which fall to the ground at a density of 5,000–6,000 per square metre (ref. 2).

Pollination systems may be viewed as biological markets in which animals choose between 'products' (flower species) on the basis of their quality (sugar quantity in nectar, for example) and the plants compete for 'customers' (pollinators)^{4–6}. We tested whether competition for pollinators^{4,5} could be a mechanism by which *I. glandulifera* successfully excludes other plants. We first quantified the rewards they offer to pollinators. The nectar sugar concentration of *I. glandulifera* (48%) is well within the range of bumblebee-pollinated plants⁷, but the rate of sugar production (0.47 ± 0.12 mg per flower per hour; $n=213$) is substantially higher than in the other common bumblebee-visited species that we found associated with *I. glandulifera* along river-banks near Würzburg. These include *Stachys palustris* (0.04 ± 0.02 mg per flower per hour; $n=167$), *Lythrum salicaria* (0.02 ± 0.01 mg per flower per hour; $n=85$) and *Epilobium hirsutum* (0.01 ± 0.02 mg per flower per hour; $n=40$).

The rate of sugar production by *I. glandulifera* exceeds that recorded for any other central European plant — of the nectar-rewarding plant species, none produces more than of 0.3 mg per flower per hour and most generate less than 0.1 mg per flower per hour^{7–9}. *I. glandulifera* offers an

even richer reward than some flowers pollinated by hummingbirds (up to 0.27 mg per flower per hour by *Ipomopsis aggregata*¹⁰).

Stachys palustris occurs along river-banks in 'pure' patches, as well as in patches intermingled with *I. glandulifera*, a convenient arrangement for comparing the two species. Because of its extraordinarily rewarding nectar, visitation of *I. glandulifera* by bumblebees (mostly *Bombus pascuorum*) is frequent (2.5 ± 1.5 visits per flower per 10-min interval) — roughly fourfold more often than to *S. palustris* (Fig. 1b).

We simulated invasion by *I. glandulifera* by moving ten large *I. glandulifera* plants in water buckets into previously pure *S. palustris* patches (both plant types bore at least 30 flowers each). Bees readily accepted the new plants and, although visitation (0.88 ± 0.19 visits per flower per 10 min) was less frequent than in naturally occurring *I. glandulifera* patches, it was still greater than to *S. palustris* (Fig. 1b). We monitored the visitation frequency to *S. palustris* patches for 1–2 days before and 1–3 days after introducing *I. glandulifera* (excluding the first 3 h), by recording visitation to marked flowers in 7–50 short intervals (10 min per patch) according to a random schedule. We found that the number of visits to *S. palustris* was reduced by almost 50% when *I. glandulifera* was present (t -test, $t=5.171$, $P=0.0006$).

If the presence of *I. glandulifera* alters the visitation behaviour of pollinators to other plants, the fitness of these plants may also be affected. We therefore measured seed set in 102 inflorescences (with 2,567 flowers) from 15 pure patches of *S. palustris*, which were at least 500 m from the nearest *I. glandulifera* stand. We compared this seed set with that in 102 inflorescences (with 2,541 flowers) from 11 patches in which *S. palustris* grew intermingled with *I. glandulifera*. Seed set in the mixed patches was reduced by 25% relative to pure patches (Fig. 1c). A chi-squared contingency test on the frequency of flowers with 0, 1, 2, 3 or 4 seeds yielded a highly significant result ($\chi^2=21$; d.f. = 4; $P<0.0001$).

To control for possible effects of competition for resources other than pollination, we repeated the experiment using potted *S. palustris* plants and found that, again, seed set in plants placed in *I. glandulifera* patches (mean, 2.29; s.d., ± 1.45) was significantly lower than in pure patches (mean, 3.2; s.d., ± 1.07 ; $\chi^2=16$; d.f. = 4; $P=0.003$).

Our results show that the presence of *I. glandulifera* has a strong negative effect on the fitness of native plants, simply because it attracts many more pollinators. As such 'economic' choices may be made by bees

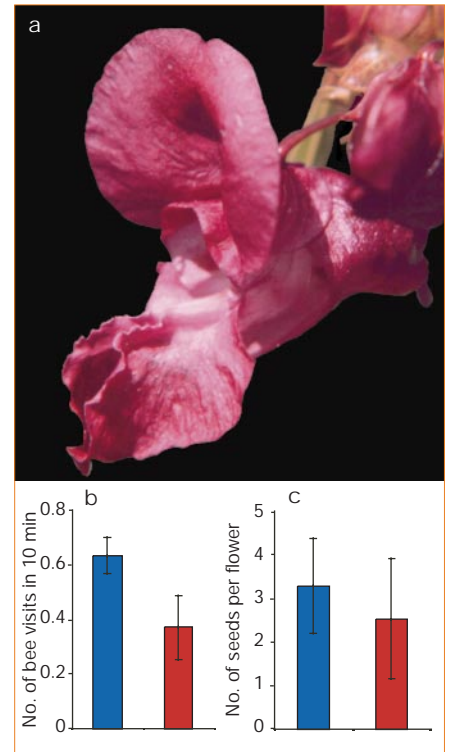


Figure 1 *Impatiens glandulifera*, an Asian beauty that has conquered Europe's river-banks. **a**, The strongly scented flowers of *I. glandulifera* are extremely rich in nectar and therefore very attractive to bumblebee pollinators. Photograph by J. Bitz. **b**, Pollinator visitation to *Stachys palustris* growing in uninterrupted patches (left) or in patches intermingled with *I. glandulifera* (right). **c**, Effect of the presence of *I. glandulifera* (right) on seed set of *S. palustris* (left, uninterrupted). *S. palustris* normally produces up to four seeds per flower. Error bars indicate standard deviation.

across large foraging ranges, competitive interactions between exotic and native plants may take place over much larger distances than previously thought. *I. glandulifera* and other exotic species may reduce the fitness of neighbouring plants even before competition for resources other than pollinators becomes an issue.

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