

positive covariation is strong and significant even after taking into account factors such as body size and elevation. Furthermore, the variation is a geographic mosaic rather than being clinal. The fly and the scroph together have undergone extreme divergence among populations within their respective species.

'The cool thing about P. ganglbaueri and its flowers is that tongue and tube lengths are jazzing around within species, among populations, across their geographic ranges, not subsequent to the establishment of a phylogenetic scaffold.'

Striking example of avatars evolving together among local communities

An 'avatar' is a local population of a species in a local community; it is the local embodiment of the group – the tangible representative that interacts with avatars of other species (Damuth, 1985). In this issue of *New Phytologist*, Anderson & Johnson (pp. 533–540) report on a striking story of avatars evolving under the influence of one another in diverging communities. Previously, Anderson & Johnson (2008) reported on a species of long-tongued fly, *Prosoeca ganglbaueri*, which seems to have co-evolved locally with a species of Scrophulariaceae, *Zalusianskya microsiphon*. In the area studied, the fly gets much of its nectar from this one plant; the scroph is even more specialized in being pollinated almost exclusively by this one fly. The fly's average tongue length varies among sites from 20 to 50 mm, and the scroph's average floral tube length covaries from 19 to 55 mm. The

The story is wondrously more complicated than just these two species. A third species is an orchid named *Disa nivea* that offers no nectar reward (Anderson *et al.*, 2005). It depends exclusively on *P. ganglbaueri* for pollination. It is the same color as the scroph, and its avatars have diverged among sites, along with the scroph, in floral tube length and in flower width. The orchid is a Batesian mimic, and the scroph is its rewarding model. Experiments confirm that the mimic suffers reduced pollination success when it is placed in a high-density patch without many inflorescences of the model compared with when the rewarding scroph is present at high density (Anderson & Johnson, 2006). In the current paper, a reciprocal transfer experiment was carried out in which orchids with long and short tubes were moved between communities that had long vs short tongues and tubes.

- For pollinaria removed (a measure of male function), there was an interaction in which the long-tubed orchids had more pollinaria removed at a site where tongue lengths and floral tubes were long, whereas short-tubed orchids had more pollinaria removed at a site where tongues and tubes were short.
- For receipt of pollen (a measure of female function), there was no interaction, just large parallel main effects in which the long-tubed orchids were better pollinated at both sites, and flowers were better pollinated at the site where everything was long.

All this is consistent with a scenario in which the avatars of the orchid have been evolutionarily tracking the divergence among local populations in the tongue length of the flies, perhaps with the selection being sexual selection on the efficiency of pollen transfer.

However, there are not just these three species involved. Anderson & Johnson also found *Gladiolus oppositiflorus* at a number of the sites studied, and its flower depth correlated tightly with fly tongue length. In fact, there are *c.* 20 species

of flowers that are pollinated by *P. ganglbaueri*. Most of them are rare and probably have relatively little effect on the fly's evolution compared with the effect of the common scroph. However, the fly seems to have driven the divergence of floral tube lengths among populations of the rare species. For each of the rare species found at more than one site, the functional tube length varied significantly, and often in the direction of being longer when the fly's tongue was longer. Not all of these flowers are specialists on only *P. ganglbaueri*, and one would expect that the way in which populations diverge ought to be a complicated response to the interactions with all their pollinators. Nevertheless, placing all the species together on one scatterplot reveals a general correspondence between fly tongue length and the depth of floral tubes among populations.

Pay attention for a moment to the scroph–fly mutualism. What exactly are the selection mechanics that drive their organs to become so long, and the length to become so varied, among populations? The explanation dating back to Darwin (1862) hinges on assuming that flowers that are just a little bit longer than the going-rate for fly tongues have enhanced pollen transfer – the longer tube would force pollinators to make closer or more precise contact with the sex organs of the flower as they sip nectar from the depths of the corolla tube. This would constitute selection for ever-longer scroph tubes. Because the fly relies specifically on the scrophs of the local population for much of its food, there would also be selection for tongues to be longer rather than shorter. The two partners would always be engaged in a runaway process (Wallace, 1867; Nilsson, 1998; cf. Wasserthal, 1997). That process might be held in check by just how costly it is to the fly to have such a long tongue protruding from its face and/or the cost of growing such a long nectar tube, or the degree to which populations are pollinator limited. The costs might vary from site to site, depending on environmental conditions, such as how windy the site is. Also, populations might have been stalled in the runaway process at varying stages by the lack of new mutations that lengthen the organisms' organs.

The runaway process would not be so coupled if both scroph and fly were less specialized; also, if they did not depend specifically on one another, their geographic patchiness would not coincide, which might fail to foster so much local divergence. The degree of specialization is unusual for systems of flowers and flower foragers. More often either the flower, or the forager, would be a generalist (Waser & Ollerton, 2006). Thus, we should not use *P. ganglbaueri* and its flowers to exemplify pollination mutualisms. Rather, the system is placed towards one extreme. As yet we have no details on how the system came to be so specialized, although southern Africa seems to have more than its share of specialized pollination systems that have evolved in-place with relatively little community reassembly (Johnson & Steiner, 2000). Even though the story of *P. ganglbaueri* and its flowers must be understood in the context of the principal actors being specialists, the phenomenon of local adaptation to pollinators causing a geographic

mosaic in flowers does not depend on extreme specialization (Thompson, 2005). Generalist flowers experiencing a varying mosaic of pollinator communities presumably adapt to the local pollinator mixes they experience (Dilley *et al.*, 2000), but the story of generalists wandering evolutionarily seems harder to document as the history seems harder to infer.

Because of the specialization involved, one is tempted to draw a parallel between the phenomenon of local pollination ecotypes radiating evolutionarily and another phenomenon much discussed in pollination biology, namely that of shifts between pollination syndromes. Think of bee-pollinated flowers giving rise to hummingbird-pollinated flowers. Indeed, Anderson & Johnson introduce their paper by citing work on pollination syndromes. As they imply, the two phenomena are related, but I would point out that there could also be a marked difference. *P. ganglbaueri* and its flowers exemplify differences in organ length arising among many populations within species, organ length being a character that is evidently free-to-vary in flies and in flowers of several species. But shifts between pollinators probably occur late in the process of species divergence, as a matter of multitrait co-adaptation in just one of the lineages emerging from cladogenesis, and shifts seem to be relatively rare events on flower phylogenies (Whittall & Hodges, 2007; Thomson & Wilson, 2008). It may well be true that all-adaptation-is-local, but it is certainly not the case that all differences arise at the cutting edge of divergence. Two incipient species may come to be adapted to different elevations first, and then because of an unusual ecological community, one of the lineages may shift to a new pollinator and away from its ancestral adaptive norm. The cool thing about *P. ganglbaueri* and its flowers is that tongue and tube lengths are jazzing around within species, among populations, across their geographic ranges, not subsequent to the establishment of a phylogenetic scaffold. In each very local community, the several avatars have been evolving, quite possibly co-evolving.

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