Storm surge: A glacial flood appears to have deposited morraines to the right, threatening valley-bottom flora. (Photograph: David Knott, Edinburgh Botanic Gardens.)

6,000–7,000 species. This huge variation in altitude and environment makes it one of the most plant-rich countries in the world. By comparison the UK has 2,000 species recorded in its own flora. Knott describes the excitement at the extraordinary diversity of habitats and plants found in just one short preliminary expedition up just one mountain valley.

The project is taking place as a result of the British Government's Darwin Initiative — a scheme of grants targeted at biodiversity conservation and sustainability issues in less developed countries. The grant involves three partner institutes within Nepal: the Royal Nepal Academy of Science and Technology, the government's Department of Plant Resources, and the Department of Botany at Tribhuvan University.

The current project builds on previous grants under the Darwin Initiative that focused on Nepal's flora, a key one of which dealt with plant information and technology transfer, run by the Natural History Museum in London.

But the current project is much more ambitious. Although only funded for three years at present, the team hopes funds will be made available for the estimated 15 years it will take to complete the new project.

The Royal Botanic Gardens in Edinburgh already have a few of Nepal's most illusive plants. Collected over 100 years ago by Victorian explorers, the plants have been nurtured by generations of botanists. Back in their native homeland, some have not fared quite so well and are on the verge of extinction. The botanists hope to reintroduce Victorian and modern seedlings to Nepal from the Edinburgh gardens.

In spite of the hi-tech approach, the team will set about collecting the thousands of different plants in the same way the Victorians did — by going out and searching for them. Part of the training has involved three expeditions, with the most recent in September, going to the Sagarmatha national park in the Mount Everest region. On these expeditions, each botanist specialises in a particular plant group and gathers specimens.

But already the team are making worrying discoveries. In the picture above, a stand of gentians can be seen in the foreground but to the right, a recent deposit of morraines is visible. Knott believes these deposits are the result of a recent glacial lake outburst flood, which may have occurred because of temperature changes as a result global warming. "It looks like quite a devastating flood," he says.

With growing human pressures on native plant species too, the challenge to document Nepal's present flora is on.

Quick guide

Figs and fig wasps

James M. Cook[1] and Stuart A. West[2]

What are figs and fig wasps? Figs are plants in the genus *Ficus*, which have a unique closed inflorescence called a syconium, typically containing hundreds of flowers. We eat the ripe syconia of one species, *F. carica*, and call these 'pseudofruits' figs too. There are about 750 fig species worldwide, mostly in the tropics, where dramatic 'strangler' figs are found. These start life as epiphytes on other trees and then drop aerial roots that slowly smother and kill their host. Figs have an obligate mutualism with tiny fig-pollinating wasps (family Agaonidae). Female wasps enter receptive syconia, where they pollinate female flowers. They also lay eggs into some flowers, where their larvae induce galls. Some weeks later, the wasp offspring emerge from their galls into the syconium, just as the male flowers have matured their pollen sacs. The new generation of female wasps leave the scyonium through holes made by the males and carry pollen to receptive syconia elsewhere. This symbiosis is exploited by many species of fig-parasitic wasps. Most of them do not enter the syconium or contribute to pollination, but use long ovipositors to inject eggs through the fig wall so that their larvae can feed on either fig flowers or other wasps.

Who cares about figs and fig wasps? Monkeys, birds, bats and other animals care about figs because they eat them (Figure 1). They care a lot, because fig trees keep fruiting all year round, including times when other trees are not producing fruit. This provision of food at otherwise tricky times makes figs 'keystone' plant species, because they play a crucial role in maintaining the

Figure 1. A rainbow lorikeet enjoys a fig break. (Copyright James Cook.)

populations and diversity of rainforest animals. Evolutionary biologists also care about figs and fig wasps. Fig wasps show huge variation across species in a number of things, including the amount of violence males use when trying to get mates, the proportion of individuals that are female, and the virulence of their nematode parasites. Evolutionary theory predicts these traits should depend on the ecology of a species, especially factors like population density and the amount of inbreeding. Fig wasps make these theories easy to test because the closed world of the syconium allows the ecology of each species to be quantified fully.

How do figs and wasps cope with all that intimacy? Their interaction dominates the lives of both and, as each relies on the other for reproduction, they are stuck with each other. But this does not mean that all is harmonious. Natural selection operates independently upon figs and wasps and may lead to conflicts. Female flowers illustrate the point. These can nurture a single wasp or a single seed, but not both. Figs are selected to raise some seeds (female function) and some wasps (male function as pollen vectors); however, wasps are selected to maximise their own offspring production, with no regard for seed production. This leads to coevolution of various fig and wasp traits. For example, some wasp species pollinate flowers actively, while others, like most insects, do it passively. Figs with passive pollinators make about 30% male flowers, while those with efficient active pollinators get away with just 10%. Figs and fig wasps have been coevolving for about 90 million years, and have diversified in parallel with broadly congruent (similar) phylogenies. This reflects a history involving cospeciation, with only limited shifting of wasps to different fig species.

Is there really one pollinator species for every fig species? Textbooks and many journal articles say that there is a one-to-one correspondence of fig and pollinator species. It is not true. It has long been known that the rule is sometimes broken; for example, some widespread fig species have different pollinators in different places. Recent studies further suggest that many fig species have two sympatric pollinator species, although pollinators are generally more faithful to their particular fig species. Co-pollinators of a given fig may look very similar, requiring genetic data to reveal their true identities; in other cases, the wasps are obviously different, but previous sampling was limited or biased. The existence of sympatric co-pollinators raises important questions. How did they evolve? One species may have split into two on the same host plant, or a host shift may have been involved for at least one of the wasp species. How do they coexist? And how does the fig–pollinator interaction differ between co-pollinator species?

Why are there so many female fig wasps? Many species of fig wasps produce few males, with up to 95% females. This is because in these species, only a few mothers lay eggs in each fig (Figure 2), and all the mating takes place in that same fig before the daughters fly away. This leads to males competing with their own brothers for females to mate (who may be their sisters). This competition between brothers reduces the fitness benefit of producing sons relative to daughters, and hence selects for a female-biased sex ratio. In the extreme, if only one female lays eggs in a fig, she needs very few sons to mate all of her daughters. Female fig wasps are capable of very clever sex ratio adjustment: evolutionary (mathematical) models predict the exact proportion of sons that a female should produce, depending upon how many females lay eggs in a fig, and female fig wasps follow the predictions of these models with remarkable precision.

Why do some male fig wasps have such long penises? Size matters when you are a fig-pollinating wasp. Males mature before females and crawl around searching for galls containing females. They then chew a hole into the gall, not big enough for the female to get out, but big enough for their impressive telescopic genitalia to get in, and inseminate the female within. Later, they enlarge the hole so that the female can leave the gall, and then the fig, carrying their sperm with her. The ripe syconium is a sealed unit and males must also bite exit tunnels through the fig wall, through which the winged females disperse to search for new receptive figs. Males themselves do not disperse and do not even have wings, which would hinder movement in the confines of the syconium.

Figure 2. A female pollinating wasp laying eggs inside a fig. (Copyright James Cook.)

Figure 3. A formidable *Sycoscapter* fighting male with large jaws and spiked legs. (Copyright James Cook.)

Why do male fig wasps bite each others' heads off? What male fig wasps do with their short lives in the syconium varies hugely between species. In some, males peacefully stumble around, ignoring each other and focusing their efforts on finding females to mate with. In others, males are aggressive, and spend a large proportion of their time fighting each other. In some cases, fighting involves huge mandibles that are used to chop off rivals' heads (Figure 3). What makes some fig wasps so mean to each other that they can even decapitate their own brothers? Males are most aggressive when there are not many females for them to mate: the males then fight viciously to monopolise those females — they do not have much to lose. In species where lots of females develop in each fruit, an individual female is not worth fighting over, and so a male is better off just searching peacefully for other females to mate.

How many fig wasps are there? We do not have a really good estimate (a common problem with insects), but can make an informed guess. There are about 750 fig species: if each has its own pollinator species, shared with no other fig, that makes 750 pollinators, but up to half of fig species have two or more pollinators, so call it 1200. Including a rough estimate for the fig-parasitic wasps, from several different taxonomic groups, makes 8700 species, a number that goes up if there are (inevitably) cryptic parasite species and down if some parasites are less host-specific than we think. Basically, there are probably about as many fig wasp species as bird species (~10,000).

Do we eat fig wasps? Figs taste great, but do you get a mouthful of dead wasps every time you eat one? Not really, as long as you eat the right figs. About half of all fig species, including the edible fig, are functionally dioecious (individual trees produce either seeds or pollen). This involves having male trees with wasp and pollen-producing syconia and female trees with seed-producing syconia. We only eat the seed-producing figs, but where are the wasps? A few foundresses enter each seed fig and pollinate the flowers, but they die frustrated as they are unable to lay eggs successfully in these female flowers, which differ from the wasp-friendly ones found in gall syconia. In this case, the fig seems to have solved the problem of flower use by separating its wasp and seed-rearing tasks on different trees. And some cultivated fig varieties produce ripe syconia without the need for pollination or wasps at all. This is convenient, but a bit mundane in comparison with the natural history of figs and fig wasps!

Where can I find out more?

Figs and fig wasps website: http://www.figweb.org/index.htm

Cook, J.M., and Rasplus, J.Y. (2003). Mutualists with attitude: coevolving fig wasps and figs. Trends Ecol. Evol. *18*, 241–248.

Herre, E.A. (1996). An overview of studies on a community of Panamanian figs. J. Biogeogr. *23*, 593–607.

Jousselin, E., Rasplus, J.Y., and Kjellberg, F. (2003). Convergence and coevolution in a mutualism: Evidence from a molecular phylogeny of *Ficus.* Evolution Int. J. Org. Evolution *57*, 1255–1269.

Molbo, D., Machado, C.A., Sevenster, J.G., Keller, L., and Herre, E.A. (2003). Cryptic species of fig-pollinating wasps: Implications for the evolution of the fig-wasp mutualism, sex allocation, and precision of adaptation. Proc. Natl. Acad. Sci. USA *100*, 5867–5872.

West, S.A., Murray, M.G., Machado, C., Griffin, A.S., and Herre, E.A. (2001). Testing Hamilton's rule with competition between relatives. Nature *409*, 510–513.

[1]Division of Biology, Imperial College London, Silwood Park Campus, Ascot, Berkshire SL5 7PY, UK. [2]Institute of Evolutionary Biology, School of Biological Sciences, University of Edinburgh, West Mains Road, Edinburgh EH9 3JT, UK.

Primer

Schizophrenia

Paul D. Morrison and Robin M. Murray

Schizophrenia is a frightening illness in which intrusive 'voices' (auditory hallucinations) torment the sufferer with abusive or derogatory comments, and ideas weave together to form false beliefs (delusions), which colonise the mind. The sufferer may become convinced he is under surveillance or enmeshed in a conspiracy of huge religious or political importance. He may believe that his thoughts are no longer private or that they are controlled by an external — usually malevolent — will. The experiences feel real; the new version of reality and the sufferer's place in it resist correction by reason. Occasionally, patients act on their delusions with disastrous results. Most people recover from their first schizophrenic episode within a few weeks of receiving antipsychotic drugs, but with each succeeding episode the hallucinations and delusions — termed 'positive symptoms' — become more resistant to treatment, and negative symptoms, such as loss of motivation, poverty of thought, and emotional blunting, gradually accumulate. Negative symptoms are often accompanied by cognitive impairment, especially executive (frontal lobe) and memory (temporal lobe) deficits.

Dopamine as the 'wind of psychotic fire'

Arvid Carlsson, who won the Nobel Prize for his work on neurotransmitters, suggested four decades ago that an excess in brain dopamine levels underlies schizophrenic symptoms. However, it was only directly demonstrated in 1996 that acutely psychotic patients release excessive striatal dopamine in response to an amphetamine challenge. Furthermore, the degree of dopamine release