attractive to female scientists. Discussions covered formalized mentoring at all levels of science education, parental leave policies, affordability and availability of high-quality day-care, identification of systemic factors that impede female career advancement in the sciences, and the installation of deliberate remediation programs to increase the number of women at higher levels of authority in university science and science administration.

The conference itself addressed several of the issues it raised – in particular, increasing the visibility of women in evolutionary biology, the need for female role models in the field, and the importance of forming professional networks. A central result of this highly successful meeting was that it clearly demonstrated the value of discussing these issues, and an atmosphere of cautious optimism developed during the course of the conference. Most importantly, the meeting fostered communication among women and men about the causes of women's underrepresentation in evolutionary biology. As certain issues such as the availability of day care and the significance of role models repeatedly rose to the surface, it became clear that some of

the most important strategies for supporting women scientists are easy to identify and should be straightforward to implement: now we need to put them into action.

Identification of gender-specific inequities is only a first step toward improving female representation in the sciences, and it will take more than a meeting of this sort to resolve the more complex issues raised. However, as we come to understand and appreciate the diverse ways in which science is accomplished, we may eventually lose the impetus for a conference of this type. As we work to create a climate in which more female scientists can flourish, and take steps to address the needs of other underrepresented groups, we will be able to focus more exclusively on scientific research, assured that all talented people have an equal opportunity to participate.

Readers interested in obtaining more information about issues facing women in science are directed to:
http://www.artsci.wustl.edu/~wie/

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Estimating impacts of a dominant detritivore in a neotropical stream

E cologists increasingly have a more than academic motivation to learn how species affect ecosystems. We often find ourselves in a race with time to find out how species interact with their environment while these environments are still relatively intact. Research in more natural habitats has two practical justifications. First, fundamental natural processes are often clearer in places that have not been destabilized by multiple anthropogenic disturbances. Second, understanding and documentation of the functioning of natural ecosystems may provide an essential guide if we have future opportunities to restore damaged environments.

The fresh waters of South America face massive, profound and imminent human impacts. Rivers and their floodplains are altered abruptly, over huge spatial scales, by damming and dredging. On a continental scale, plans in South America for interbasin navigational waterways linking historically isolated drainages from the Caribbean to the Rio de la Plata have been entertained for at least two centuries[1]. Imminent construction of the Paraguay-Paraná Hidrovia (a 3400 km navigational

canal) will link the headwaters of the Paraguay River near Caceres to the port of Nueva Palmira, near Buenos Aires. This project will drain much of the Pantanal, the largest and biologically richest floodplain wetlands remaining on the earth[2,3].

On a more local scale, dredging is in progress in the Apure and Orinoco rivers to extend the distance ocean-going ships can travel up the Orinoco[4]. Simultaneously, increased human fishing pressure throughout tropical South America is shifting the composition of the catch from larger, long-lived species to high-yield, faster-growing fishes such as *Prochilodus*[4,5]. Against this backdrop, Flecker[6] has investigated community and ecosystem influences of *Prochilodus mariae*, a dominant detritivorous fish that migrates seasonally into Andean piedmont streams from lower reaches of the Rio Apure drainage of the Rio Orinoco.

There are good reasons, as Flecker points out, to suspect that this species is a strong interactor, *sensu* Paine[7]. First, *Prochilodus* species are extremely successful in South American rivers, often dominating the biomass of fish assemblages[6,8]. Second, detritus is a nutritionally poor food

source, so detritivores must process large volumes. Hence, in addition to being abundant, *Prochilodus* probably have high per capita effects.

Flecker manipulated *Prochilodus* abundance to study their effects on sediment accrual and the composition and abundances of benthic algae and invertebrates in an Andean piedmont stream. In cages excluding *Prochilodus*, more sediment built up, more invertebrates accumulated and diatoms increased. Where *Prochilodus* were enclosed, and in semi-open cage controls accessible to the entire natural fish assemblage, the bluegreen *Calothrix* dominated periphyton. The relatively large mesh (25 mm) and size (4 m^2) of cages and the low suspended sediment load of the stream during this dry-season study suggest that cage effects on sediment outfall, which frequently plague experimental manipulations in streams, were probably minimal. Treatment effects attributed to *Prochilodus*, however, were often stronger in cage controls that admitted the entire fish assemblage, than in *Prochilodus* enclosures. This result leaves open the question as to how effects of enclosed *Prochilodus* compare with those of the entire, free-swimming assemblage of fishes. Were *Prochilodus*, which dominated this natural assemblage, more effective when free-ranging, or were other fishes such as the larger loricariid catfish also contributing to the effects?

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Despite the challenges of completely resolving the effects of individual species, which remain in many field experiments[9,10], these experiments make significant new contributions to our knowledge of species effects on ecosystems. As Flecker points out, field manipulations of detritivores are rare relative to studies of herbivores and predators. His demonstration that these detritivorous fish exert community-level impacts is quite valuable in this context. He applies the recently coined term 'ecological engineering'[11] to the indirect effects of *Prochilodus* on invertebrates and algae via their removal of sediment from stones. I would prefer the use of a more value-neutral term like 'habitat modification'[12] for such an effect, which is likely to be incidental to feeding, reserving 'ecological engineering' for special cases of habitat modification that lie further down the axis of purposeful intent (e.g. construction of dams by beavers). Semantic quibbles over buzzwords, however, are less important than addressing the issue of how, or if, we can extrapolate from field experiments like Flecker's *Prochilodus* study to anticipate larger-scale consequences of changes in their abundances or performances that might, for example, result from the human 'ecological engineering' described above.

Flecker found that sediment standing crops were reduced in cages over periods of several days to weeks in the presence of *Prochilodus*. The net effect of *Prochilodus* on sediment standing crops over even slightly larger spatial scales (tens of metres) might be small if feeding fish simply wafted unconsolidated sediments downstream, or if they ingested sediment but rapidly passed feces that were loose and quick to disintegrate and resuspend. To investigate the consequences of *Prochilodus* sediment ingestion or displacement on the next larger scale, we might need to find out how long they keep sediments 'out of circulation', stored either in their guts, or while packaged in feces. Data on gut passage rates, sedimentation rates of feces and the durability of their peritrophic membranes, would be useful in addressing sediment storage issues.

Why do effects on sediment standing crops matter? *Prochilodus*, by clearing the sediments mantling stream substrates, may affect primary and secondary productivity in streams. Algal productivity and standing crops increased with sediment removal by loricariid catfish in a Panamanian stream[13]. Whether this result would hold in the Andean piedmont stream studied by Flecker may depend on the productivity of silt-dwelling diatoms versus epilithic *Calothrix*. Is this effect important on an annual timescale? Sediments would be scoured from streambeds seasonally, even without *Prochilodus*, but during these high-flow periods, primary production would be limited by water column turbidity in white-water rivers like those of the Apure system[4]. Therefore, sediment clearing by *Prochilodus* during the low-flow, clear-water season may well enhance annual primary production.

These arguments assume that rock-bound algae are limited by light. Are primary producers also nutrient limited during their productive season? *Calothrix*, a nitrogen fixer, may contribute limiting nutrients, supplementing the influence of *Prochilodus* on primary production. This effect, however, would probably be small relative to translocation of nutrients from the lower Orinoco basin into piedmont streams during massive *Prochilodus* migrations, a role that Fittkau[14] suggested for caiman (*Caiman crocodilus, Paleosuchus palpebrosus, P. trigonatus*) commuting between nutrient-rich white waters and nutrient-poor black waters of the Amazon drainage.

To estimate the relative importance of these potential large-scale *Prochilodus* effects, mass balance models of fluxes and energy flow could be calibrated with rates such as those Flecker measured experimentally, with an attempt to account for seasonal variation in environmental factors and *Prochilodus* densities and activities. 'Scaling-up' exercises like the one sketched above also, dauntingly, require knowledge of how process rates mediated by *Prochilodus* scale with their size, density or other factors. It would be useful to quantify for 'habitat modifiers' or 'ecological engineers' the same functional and numerical responses that have proven so useful in analyzing the impacts and dynamics of predators, herbivores, parasitoids and parasites. Functional responses of *Prochilodus* might be measured as the rate of consumption (mass t^{-1}) or clearance (area t^{-1}) of sediment by a single *Prochilodus* as a function of sediment standing crop (mass $area^{-1}$). This functional response is likely to depend on *Prochilodus* size. Can larger *Prochilodus* clear deeper sediments, as is the case for loricariid catfish[15]? Do impacts of schools of *Prochilodus* on sediment standing crops or primary production differ from those predicted from additive per capita effects? Knowledge of their functional and numerical reposes to stream resources and conditions may allow us to estimate how *Prochilodus* production, and their influence on streams, will change with human fishing that alters their abundance or population size structure, and in the face of human engineering that increases or decreases sediment loading to their habitats (e.g. upstream dredging or impoundment, respectively).

These estimates will clearly be fraught with uncertainty, as many key parameters and functional relationships will be difficult to assess. The best test, of course, would be a large-scale *Prochilodus* removal, and this 'natural experiment' has in fact occurred. For the past two years, *Prochilodus* have failed to arrive at Flecker's study stream. The causes are unknown, but may involve downstream fishing pressure and/or low river flow (A. Flecker, pers. commun.). If there is a silver lining to the pace and amplitude of environmental change, it could be that we actually might get opportunities to test scaled up ecological models against some of the predicted scenarios.

Should anyone besides obsessive academics care about interactions among *Prochilodus*, sediment, and stream algae and insects? Interactions that involve the ecologically dominant and individually active *Prochilodus* may well determine much about how energy flows through neotropical streams. Ecological interactions that retain and recycle nutrients in river ecosystems tend to support higher trophic levels, including species valued by traditional and commercial fisheries. If such interactions are disrupted, nutrients in river runoff can fuel algal blooms in coastal waters with serious impacts on human health, including red tides and the stimulation of plankton blooms that support *Cholera vibrio*[16]. Clearly, such potential consequences are of more than academic interest.

It remains the job of ecologists to sift through the myriad of details that characterize interactions of organisms with environments, struggling to winnow the crucial and the general from the trivial and the idiosyncratic. Experiments like Flecker's usually give the clearest insights about local processes. Increasingly, ecologists are attempting to combine experiments with observations and modeling, expanding the temporal and spatial scales of their inferences to address questions relevant to the long-term sustainability of large ecosystems.

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Building phylogenies: are the big easy?

Just as nothing in biology makes sense except in the light of evolution, so evolution is hard to interpret without the light shed by phylogeny. Phylogenies underpin inferences about character evolution, speciation and extinction[1] – unsurprising, then, that trying to reconstruct the tree of life is such big business. Unfortunately, it isn't always easy. One problem is that, as the number of taxa increases, the number of possible phylogenies grows very fast: for three species there are three choices, but for 10 there are over 34 million, and for 20 there are over 8.2×10^{21}. Tree-building methods that have an optimality criterion, like parsimony (see Box 1) or maximum likelihood, have to search through these trees to find the best one and, with more than about 20 taxa, life is too short to guarantee finding the optimal solution.

To keep trees manageable, researchers investigating higher relationships often include only a few species from each taxon. But even small trees can pose problems: in simulations, many tree-building methods often fail to find the right tree for only four species[2]. With even such small trees likely to be wrong, it seemed that building trees large enough to be interesting was bound to fail. However, simulations reported recently in *Nature* by David Hillis[3] suggest that, bizarrely, big phylogenies might be the easiest of all to get right.

Hillis simulated DNA sequence evolution along a tree with 228 species. He forced rates of change to vary among nucleotides (using a gamma distribution[4] with half the changes concentrated in about one-eighth of the sites) and among branches of the tree, and transitions were twice as frequent as transversions. He then applied three tree-building methods – unweighted parsimony, neighbour-joining, and UPGMA (Box 1) – reconstructing the tree from the virtual sequences.

UPGMA did badly, as expected (see Box 1): however long the sequences, it never got more than 40% of the tree right. Neighbour-joining did very well, getting more than 99% of the branches right when sequences were 5000 bases long – but this is a best-case result (see Box 1).

Unweighted parsimony might have been expected to do badly, for two reasons. First, it allows for none of the complexities of the model used to generate the sequences. The second reason reflects the vast number of possible trees for large numbers of taxa. In tree-building, taxa are first joined together in a process called stepwise addition, with each in turn added to the growing tree at the point where it fits best. This stage is quick, but early incorrect placements cannot be reversed, so inevitably lead to the wrong tree. Therefore, stepwise addition is usually followed by a protracted bout of branch-swapping, with boughs of the tree pruned and regrafted elsewhere in an attempt to find more parsimonious solutions. But stepwise addition alone found as good a tree as neighbour-joining from the full sequences, and did better when both used shorter sequences. And when Hillis allowed parsimony to swap branches, it actually found the right tree – from over 10^{500} possibilities!

So how come big trees are easy for parsimony when small ones are nigh impossible? What matters isn't the size of the tree *per se*, but the lengths of its branches, or more precisely, how many times each character changes along them. If no character changes more than once on the true tree, similarities among sequences arise only through shared inheritance (homology), and phylogeny reconstruction becomes a trivial problem. But Hillis's data include many rapidly evolving sites changing up to about 15 times across the tree. Such parallel changes, reversals and convergences are called homoplasy. Homoplastic similarity misleads parsimony, because parsimony cannot distinguish it from homologies. Parsimony will still work provided that the signal of true homology outweighs the noise of homoplasy, allowing sequence evolution to be reconstructed accurately. As branches get longer and homoplasy increases, however, something horrible happens: homoplasy makes the sequences at the end of long branches converge so much that the noise overwhelms the signal, and parsimony favours trees in which such sequences are closest relatives[5,6]. We are entering the so-called 'Felsenstein Zone', where long branches stick together and where adding more data makes it ever more certain that we will choose the wrong tree. This convergence upon an incorrect solution is termed inconsistency.

There are essentially two ways to avoid inconsistency. The first, which has attracted most attention recently, is to use more complicated algorithms that accommodate homoplastic changes according to some model of sequence evolution (see Ref. 7 for many possible models). Unfortunately, we don't know how real sequences evolve, so our models are always over simple and could be plain wrong, with inevitable consequences[4,8]. Furthermore, many models are so computationally intensive that they can be applied only to very small trees[7].

The second, and conceptually simpler, solution is the one Hillis has followed: shorten the branches. By including so many taxa, what would have been long branches become chopped into shorter sections. Thus it will be less common that any character changes more than once along a single branch – good news for parsimony. And characters that are globally homoplastic can now become locally informative. With the signal-to-noise ratio thus improved, an accurate tree can be

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