2 Relyea, R.A. (2003) Predator cues and pesticides: a double dose of danger for amphibians. *Ecol. Appl.* 13, 1515–1521
3 Kats, L.B. and Dill, L.M. (1998) The scent of death: chemosensory assessment of predation risk by prey animals. *Ecoscience* 5, 361–394
4 Lawler, J.J. *et al.* (2002) The scope and treatment of threats in endangered species recovery plans. *Ecol. Appl.* 12, 663–667
5 Linder, G. *et al.* (2003) *Amphibian Decline: an Integrated Analysis of Multiple Stressor Effects*, SETAC Press
6 Stephan, C.E. (1972) *Methods for Acute Toxicity Tests with Fish, Macroinvertebrates, and Amphibians*, U.S. Environmental Protection Agency, Ecological Research Series
7 Sih, A. *et al.* (1985) Predation, competition and prey communities: a review of field experiments. *Annu. Rev. Ecol. Syst.* 16, 269–311
8 Lima, S.L. (1998) Stress and decision-making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. *Adv. Study Behav.* 27, 215–290
9 Alford, R.A. and Richards, S.J. (1999) Global amphibian declines: a problem in applied ecology. *Annu. Rev. Ecol. Syst.* 30, 133–165
10 Davidson, C. *et al.* (2001) Declines of the California red-legged frog: climate, UV-B, habitat and pesticide hypotheses. *Ecol. Appl.* 11, 464–479
11 Davidson, C. *et al.* (2002) Spatial tests of the pesticide drift, habitat destruction, UV-B, and climate-change hypotheses for California amphibian declines. *Conserv. Biol.* 16, 1588–1601
12 Kiesecker, J.M. *et al.* (2001) Complex causes of amphibian population declines. *Nature* 410, 681–684
13 Berger, L. *et al.* (1998) Chytridiomycosis causes amphibian mortality associated with population declines in the rain forests of Australia and Central America. *Proc. Natl. Acad. Sci. U. S. A.* 95, 9031–9036
14 Daszak, P. *et al.* (1999) Emerging infectious diseases and amphibian population declines. *Emerg. Infect. Dis.* 5, 735–748
15 Rohr, J.R. *et al.* Multiple stressors and streamside salamanders: effects of the herbicide atrazine, food limitation, and drying conditions. *Ecol. Appl.* (in press)
16 Bridges, C.M. (1999) Effects of a pesticide on tadpole activity and predator avoidance behavior. *J. Herpetol.* 33, 303–306
17 Weis, J.S. *et al.* (2001) Effects of contaminants on behavior: biochemical mechanisms and ecological consequences. *Bioscience* 51, 209–217
18 Bridges, C.M. and Semlitsch, R.D. (2000) Variation in pesticide tolerance of tadpoles among and within species of Ranidae and patterns of amphibian decline. *Conserv. Biol.* 14, 1490–1499
19 Boone, M.D. and Semlitsch, R.D. (2001) Interactions of an insecticide with larval density and predation in experimental amphibian communities. *Conserv. Biol.* 15, 228–238
20 Boone, M.D. and Semlitsch, R.D. (2002) Interactions of an insecticide with competition and pond drying in amphibian communities. *Ecol. Appl.* 12, 307–316

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Sustainability in a nutshell

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Sustainable exploitation is widely advocated as a strategy for reconciling economic pressures upon natural habitats with nature conservation. Two recent papers examine different aspects of the sustainability of the nut harvest on wild populations of Brazil nut trees *Bertholletia excelsa* in Amazonia. Peres *et al.* find that many populations of the Brazil nut tree lack juvenile trees and are not regenerating. In a socioeconomic study, Escobal and Aldana find that nut-gathering provides insufficient income on its own to support nut-gatherers and that their other income-raising activities damage the forest. The existence of a market for rainforest products is, therefore, not sufficient on its own to prevent habitat destruction or the overexploitation of the resource and a more sophisticated approach to sustainability is required. Development of a market in ethically traded Brazil nuts might be one solution.

With economic forces driving deforestation in the Amazon basin at an accelerating rate [1], the strategy of 'use it or lose it' has been promoted as one of the few realistic ways in which large areas of rainforest might be protected. Since 1989, when a study published in *Nature* [2] showed that the monetary value of tropical forest timber was less than the potential value per unit area of other rainforest products, such as fruits, every plea and campaign for rainforest preservation has emphasized the opportunity cost of each hectare felled. The problem is how to turn notional, paper values of what would be lost when a forest is felled into a real income for local people. If forest dwellers can earn an income from sustainably harvesting forest products, so the theory goes, they will protect the source of their livelihood and, therefore, the rainforest will be preserved. Anything more than limited timber extraction would clearly be self-defeating to such an enterprise and so the emphasis has been on so-called 'non-timber forest products' (NTFPs), which include saleable plants, fruits and animals. Top of the list of these is the Brazil nut (Figure 1). However, two recent studies [3,4] suggest that their exploitation is not currently sustainable.

Sustainability of the Brazil nut harvest

Many familiar commodities, from avocados and chewing gum to rubber and vanilla, originated in tropical forest, but the Brazil nut (from the tree *Bertholletia excelsa*) is the only one that is widely traded and still harvested from the wild rather than from plantations. Brazil alone exports 45 000 tons of nuts a year that are worth (US$33 million. Because of the importance of the Brazil nut to the economy of Amazonia, the ecology and socioeconomics of the harvest have been reasonably well studied. Zuidema and Boot [5] reported matrix projection models parameterized for two populations of *B. excelsa* in the Bolivian Amazon. The models showed that the structure of the two populations was stable and, thus, that the nut harvest was not damaging the ability of the tree populations to renew

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Figure 1. Fruit of the Brazil nut tree *Bertholletia excelsa,* with one cut open to reveal the nuts. Reproduced with permission from Carlos Peres.

themselves, indicating that the harvest was sustainable. However, Carlos Peres and 16 others, including Zuidema, now report on a wider study that includes some populations that have a longer history of exploitation. The authors show that the two Bolivian populations were atypical and that the Brazil nut harvest is not sustainable in many parts of Amazonia.

In a sample of 23 populations of *B. excelsa* from across the Brazilian, Peruvian and Bolivian Amazon, juvenile trees <60 cm diameter at breast height were missing from populations where nuts had been persistently harvested. This finding is important, not just because of the threat that it has uncovered to the Brazil nut itself, but also because the Brazil nut is a touchstone for the sustainable exploitation of rainforest. If the Brazil nut harvest has chronically damaged its source populations, then what hope is there for the sustainable exploitation of NTFPs more generally? There is an established market for wild-collected Brazil nuts and it is therefore seen as a model of how trade in other NTFPs could be developed, but could it also be a warning of the dangers inherent in the strategy of utilization as a means of conservation?

The Brazil nut tree is a canopy dominant that can grow to 40 m in height. In natural populations, it might not reach reproductive maturity until it is over a century old, although plantation trees can reach maturity very much earlier. Unusually for a tree that can live for 350 years or more, it depends upon forest gaps for regeneration, and seedling growth in these conditions can be rapid [6]. Fortunately, the long lifespan of the Brazil nut tree should allow time for the damage caused by the nut harvest to be repaired, either by planting seedlings or by regulating the harvest so that natural regeneration can occur. However, as Peres *et al.* [3] themselves explicitly recognize, the sustainability of the Brazil nut harvest is not just a matter of managing the demographics of tree populations.

Socioeconomics of Brazil nuts

A glimpse of the wider, socioeconomic context of the Brazil nut harvest is afforded by another recent study by Javier Escobal and Ursula Aldana in the Peruvian Amazon [4]. One thousand families in the study region were directly involved in harvesting Brazil nuts and many more ((20% of the population) were involved directly or indirectly. Measured by Peruvian standards, (75% of the nut gatherers were poor, compared with just over half of the population of Peru as a whole. Brazil nut gathering is seasonal and contributed about half the income of gatherers, which they supplemented with agriculture, timber extraction, fishing, hunting and sometimes paid work. The poorest of the nut gatherers were the ones that were most likely to be engaged in agriculture, although earning very little from it. Richer gatherers favoured timber extraction over agriculture and earned nearly as much from this as they did from nut gathering. In economic terms, it therefore appears that Brazil nut gathering, although important, does not provide a living on its own and cannot provide an escape from poverty. As a result, Brazil nut gatherers depend upon other activities, such as timber extraction and agriculture, to supplement their income. These other activities, particularly agriculture, are damaging to the forest. Escobal and Aldana [6] found that nearly half of the Brazil nut groves were damaged to such an extent that they had lost (20% of their forest cover. Most worrying was the finding that the larger the number of nut trees a household had in their concession, the more likely they were to be involved in timber harvesting. Apparently, a good Brazil nut concession provides the working capital required to buy a chain saw.

Future directions

The studies of the Brazil nut by Peres *et al.* [3] and Escobal and Aldana [4] are both reminders of just how hard it is to exploit natural ecosystems sustainably. The first step must be to recognize the complexity of the system. The Brazil nut tree exists within a web of ecological interactions that includes not only agoutis (*Dasyprocta* spp.) that devour as well as disperse its seeds, but also people who gather nuts and hunt agoutis. The Brazil nut is protected from these rodents by armour so strong that it challenges the strongest nutcracker in the kitchen drawer, but, if an agouti does not gnaw at the fruit case that holds the nuts, the seed will never germinate in the forest [7]. This ambivalent relationship of depredation and dependence is a metaphor for the idea that rainforests must also pay a price through exploitation if they are to survive the attentions of humans. It might even be called the 'Brazil nut principle'.

The amount that consumers in first world countries are prepared to pay for Brazil nuts is perhaps the key to making the harvest economically as well as ecologically sustainable. One economic problem is that any one of 14 other nuts, including hazel, almond and peanut, can be substituted for the Brazil nut in most of its uses [8]. However, if the harvest could be made sustainable, Brazil nuts would have the unique selling point for ethical consumers that their purchase can aid the preservation of rainforest. The market in fair-traded food is a burgeoning

one [9], although making it work for Brazil nuts might not be easy [10]. As the case of the Brazil nut shows, the socioeconomics of managing NTFPs sustainably is going to be the hardest nut to crack (http://www.demonsineden.com).

References

1 Laurance, W.F. *et al.* (2001) Is deforestation accelerating in the Brazilian Amazon? *Environ. Conserv.* 28, 305–311
2 Peters, C.M. *et al.* (1989) Valuation of an Amazonian rainforest. *Nature* 339, 655–656
3 Peres, C.A. *et al.* (2003) Demographic threats to the sustainability of Brazil nut exploitation. *Science* 302, 2112–2114
4 Escobal, J. and Aldana, U. (2003) Are nontimber forest products the antidote to rainforest degradation? Brazil nut extraction in Madre De Dios, Peru. *World Dev.* 31, 1873–1887
5 Zuidema, P.A. and Boot, R.G.A. (2002) Demography of the Brazil nut tree (*Bertholletia excelsa*) in the Bolivian Amazon: impact of seed extraction on recruitment and population dynamics. *J. Trop. Ecol.* 18, 1–31
6 Zuidema, P.A. (2003) *Ecology and Management of the Brazil Nut Tree* (Bertholletia excelsa), PROMAB Scientific Series 6. http://www.promab.org/pieter_zuidema/pdfs_pss6_eng/00_hfdst.pdf
7 Peres, C.A. and Baider, C. (1997) Seed dispersal, spatial distribution and size structure of Brazil-nut trees (*Bertholletia excelsa*, Lecythidaceae) at an unharvested stand of eastern Amazonia. *J. Trop. Ecol.* 12, 595–616
8 Collinson, C. *et al.* (2000) *Economic Viability of Brazil Nut Trading in Peru*. Natural Resources Institute, Report 2520 http://www.nri.org/NRET/brazilnuts.pdf
9 Vidal, J. (2004) Fairtrade sales hit £100m a year. *The Guardian* http://www.guardian.co.uk/fairtrade
10 Nelson, V. *et al.* (2002) Assessing the benefits of ethical trade schemes in cocoa (Ecuador) and Brazil nuts (Peru) for forest-dependent people and their livelihoods. *Int. For. Rev.* 4, 99–109

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Limpets break Dollo's Law

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A new molecular phylogeny of the limpet molluscs (Calyptraeidae) reveals that coiled shells have independently re-evolved at least once in this family, which is a violation of Dollo's Law that complex ancestral states, once lost, are never reacquired. Reacquisition of the coiled ancestral state is remarkable in that uncoiled shells have been the most recent ancestral state for 20 million–100 million years. Adult coiling might have re-evolved by the mechanism of prolonging the period during which genes for coiling are expressed in larvae. This and other developmental mechanisms could provide general routes for maintaining the potential to produce traits lost in distant ancestors.

In 1893, the Belgian palaeontologist Louis Dollo (1857–1931) proposed an idea that Stephen Gould [1] would later canonize as 'Dollo's Law', that complex organs or structures, once lost through evolution, cannot re-evolve. Dollo arrived at his views from the study of trends in the fossil record. But modern phylogenetic–comparative studies are beginning to overturn the domination of fossils in our understanding of the historical course of evolution. The recent discovery of the re-evolution of coiled shells in gastropods [2] shows one reason why: phylogenetic studies can link contemporary species to unexpected ancestors.

Rachel Collin and Roberto Cipriani analyzed shell coiling in the calyptraeid gastropods [2], which comprise 200 species of sedentary filter feeders known as slipper limpets. Whereas most gastropod molluscs have coiled shells, most limpets have uncoiled or only slightly coiled shells. Ten–twelve calyptraeid species in the genera *Trochita*, *Sigapatella* and *Zegalerus* are exceptional in having coiled shells. These genera are conventionally placed at the base of the calyptraeid phylogeny, such that the remaining uncoiled species represent derived evolutionary losses of coiling. Uncoiled shells are thought to be an evolutionary dead-end because, once in the uncoiled state, there are fewer ways to produce genuine evolutionary novelty in the design of the shell.

Collin and Cipriani collected DNA sequence data from the mitochondrial cytochrome oxidase I gene (involved in respiration) and the 16S and 28S nuclear ribosomal segments to infer the phylogeny of the calyptraeids. The faster evolving mitochondrial DNA is useful for specifying close relationships, whereas the slower evolving ribosomal segments can identify deeper relationships in the tree. Their tree placed the coiled *Sigapatella* and the *Zegalerus* near the base as expected, but its placement of the *Trochita* was a surprise. This genus of coiled species, which is thought to be ancestral to the calyptraeids, turned out to be a comparatively recent derived form, firmly nested within a clade of species known as the *Crepidula*. The new phylogenetic position of *Trochita* is striking in that none of the *Crepidula* has a coiled shell (Figure 1). Combine this with independent fossil and morphological evidence [3] that gastropods are ancestrally coiled and Collin and Cipriani's tree suggests that the *Trochita* have reacquired coiled shells.

Evaluating the phylogenetic tree

Can the tree be trusted? The clade of *Crepidula* species, and the placement of *Trochita* in it, were both found in >95% of the trees in a Bayesian sample of trees that the authors derived from their combined data set. Bayesian methods for inferring phylogenies provide a statistical

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