

debt-ridden nations to increase government revenues via natural resource exploitation, foreign investment and exports, while simultaneously cutting government spending. Far too often, a dramatic influx of foreign capital for logging has not been balanced by an improved capacity to regulate loggers; this is a formula for disaster.

The bottom line, however, is that logging is usually the fastest way for corporations and investors to make lots of money quickly in the tropics. Although the Asian timber corporations are greatly vilified these days, it is important to remember that many European and North American companies have also had poor environmental records in the developing world. At present there seem to be two main hopes for promoting sustainable logging. The first is that, through education, the public will increasingly demand and buy only FSC-approved timber products. The second is that international aid and lending programs⁴, and carbon-offset funds^{7,8}, could be used much more effectively to promote forest conservation and sustainable development in tropical regions. In addition, a promising new initiative called 'conservation concessions', in which environmental organizations buy timber leases to preclude logging and then fund sustainable development activities, might appeal to some developing countries (R.E. Rice, pers. commun.).

The stakes are high. In developing nations, forest tracts currently allocated for logging are at least 8–10 times larger than the limited areas set aside as parks and reserves⁹. The management or

mismanagement of these vast lands will have a profound influence on nature conservation in the tropics.

Acknowledgements

I thank R. Rice, M. Cochrane, C. Kremen, E. Yensen and S. Laurance for reviewing this article. The NASA–LBA program and the Smithsonian Institution provided support. The logging report can be downloaded at http://panda.org/news/download/tnc_report.pdf or a free hardcopy can be obtained by e-mail request (tropicalforest@wwf.be). This is publication number 315 in the BDFFP technical series.

William F. Laurance

Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Republic of Panamá, and Biological Dynamics of Forest Fragments Project, National Institute for Amazonian Research (INPA), CP 478, Manaus, AM 69011-970, Brazil (wfl@inpa.gov.br)

References

- 1 Bowles, I.A. *et al.* (1998) *Natural Resource Extraction in the Latin American Tropics: A Recent Wave of Investment Poses New Challenges for Biodiversity Conservation*, Conservation International
- 2 Epstein, J. and Moore, L. (1997) Far East goes deep South. *Latin Trade* July, pp. 61–66
- 3 Simonetti, E. (1999) Wall Street reina: os benefícios e os riscos que a globalização impõe aos emergentes. *Veja (Brazil)* 10 March, pp. 46–48
- 4 Sizer, N. and Plouvier, D. (2000) *Increased Investment and Trade by Transnational Logging Companies in Africa, the Caribbean and the Pacific*, Joint report of World Wide Fund for Nature–Belgium, World Resources Institute and WWF–International
- 5 Brown, P. (2000) Forest corruption report covered up. *The Guardian* 29 May
- 6 Kirby, A. (2000) Forest report 'sanitized by WWF'. *BBC News Online* 29 May
- 7 Kremen, C. *et al.* (2000) Economic incentives for rain forest conservation across scales. *Science* 288, 1828–1832
- 8 Fearnside, P.M. (1997) Monitoring needs to transform Amazonian forest maintenance into a global warming–mitigation option. *Mitigation Adapt. Strat. Glob. Change* 2, 285–302
- 9 Johns, A.G. (1997) *Timber Production and Biodiversity Conservation in Tropical Rain Forests*, Cambridge University Press
- 10 Whitmore, T.C. (1997) Tropical forest disturbance, disappearance, and species loss. In *Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities* (Laurance, W.F. and Bierregaard, R.O., eds), pp. 3–12, University of Chicago Press
- 11 Uhl, C. *et al.* (1991) Social, economic, and ecological consequences of selective logging in an Amazonian frontier: the case of Tailândia. *For. Ecol. Manage.* 46, 243–273
- 12 Verissimo, A. *et al.* (1992) Logging impacts and prospects for sustainable forest management in an old Amazonian frontier: the case of Paragominas. *For. Ecol. Manage.* 55, 169–199
- 13 Uhl, C. *et al.* (1997) Natural resource management in the Brazilian Amazon. *Bioscience* 47, 160–168
- 14 Wilkie, D.S. *et al.* (1992) Mechanized logging, market hunting, and a bank loan in Congo. *Conserv. Biol.* 6, 570–580
- 15 Brown, N. (1998) Out of control: fires and forestry in Indonesia. *Trends Ecol. Evol.* 13, 41
- 16 Laurance, W.F. (1998) A crisis in the making: responses of Amazonian forests to land use and climate change. *Trends Ecol. Evol.* 13, 411–415
- 17 Crome, F.H.J. *et al.* (1992) A study of logging damage in upland rainforest in north Queensland. *For. Ecol. Manage.* 49, 1–29

No question: seed dispersal matters

Every now and then, an insight changes a field. It happened 30 years ago when Janzen¹ and Connell² revolutionized ecological ideas of seed dispersal and its effects, with what became known as the Janzen–Connell hypothesis (hereafter, 'the hypothesis'). Seed dispersal has long been associated with invasion of open habitats (where species are absent), as occurs in range extensions³ or ecological succession⁴. The hypothesis postulated that a major advantage to local seed dispersal is the removal of seeds and seedlings from density-dependent mortality from pathogens or seed predators near parent trees. Such mortality near parent trees opens up the habitat for recruitment of other species that would otherwise be

excluded by intense competition from the offspring of nearby trees. The hypothesis simultaneously offered: (1) a powerful selective advantage for an immense array of adaptations for local seed dispersal by wind, water, ballistic explosion, ants, bats, birds, monkeys or other agents; and (2) a plausible mechanism for the maintenance of species diversity in tropical rain forests. In the most significant field study on this issue in 30 years, Kyle Harms *et al.*⁵ have unequivocally demonstrated both density-dependent mortality and its effects on seedling diversity in dozens of Panamanian tree species. A chapter in dispersal ecology has closed, but inviting new ones beckon.

Speculation and partial tests

Janzen and Connell's insight had an immense catalytic effect on studies of seed dispersal. A powerful selective rationale for structure and function launched speculative discussions of the roles played by different kinds of animals in seed dispersal⁶, and the hypothesis quickly entered prominent discussions of plant diversity^{7,8}. The power of a plausible argument allowed the hypothesis to enter ecology textbooks long before its predictions were confirmed or rejected. Right or wrong, the hypothesis highlighted the importance, mechanisms and consequences of seed dispersal.

On a practical level, the idea of local advantages to seed dispersal forced ecologists to think about the reasons why seedlings located under parents almost always die, whereas those carried some distance away might not. These reasons include: (1) escape from density-dependent

mortality near parents (the escape hypothesis), (2) colonization of open habitats (range extension and succession) and (3) directed dispersal to microsites crucial for establishment⁹. Partial tests have confirmed the role of seed escape from parents in both temperate and tropical habitats^{10,11}. However, these tests cannot unequivocally identify density-dependent mortality as the cause because seed and seedling densities under parental crowns, and historical effects of insect or pathogen infestations, cannot be replicated away from fruiting trees¹². Succession remains a crucial issue for seed dissemination and directed dispersal is rare but real¹³. Although qualitative in its formulation, the Janzen–Connell hypothesis shifted thinking from a binomial view of dispersal – species present or absent – to the probabilistic view that rates of dispersal and establishment mediate plant recruitment and interaction, thus integrating the dispersal of seeds with more general discussions of ecological dispersal. At the population level, the hypothesis generated a broad spectrum of thought and partial confirmation.

Community implications of the Janzen–Connell effect have not been as easily demonstrated. Stephen Hubbell¹⁴ countered that the hypothesis could not be important for tropical diversity because anything, except total seed or seedling mortality near parents, would allow fruiting trees to occupy their immediate surroundings with their own offspring. This would overwhelm anything but the most severe density-dependent mortality, thus precluding recruitment of other species under or near their crowns. Confirmation of the compensatory effect of density-dependent mortality exists for a few species in low-diversity Australian forest, thus indicating that seed or seedling mortality near parents is sometimes severe enough to admit other species¹⁵. But, definitive confirmation has been elusive. On a community level, the hypothesis has remained a plausible abstraction.

Trapped seeds and seedling neighbors

Harms *et al.*⁵ have now changed the debate. Natural fall of 386 027 seeds into 200 traps scattered through the forest on Barro Colorado Island, Panama provided local densities of the seeds of 53 species of trees. These seed densities could be compared with the densities of 13 068 seedlings germinating nearby. Density-dependent mortality proved pervasive, even when corrected for germination rates, variation in species-specific seed mortality and high levels of seed-fall near

fruiting trees. For all 53 tree species, regression slopes of seedlings near seed traps, compared with conspecific seeds landing in adjacent traps, were <1 and many slopes were $\ll 1$ (the mean was 0.23). If seed distributions of a species are templates for future population growth¹⁶, multispecies seed distributions are community templates for whatever follows in a dynamic forest. Harms *et al.* have shown that in the key transition from seed to established seedling, this template shifts, as predicted by Janzen and Connell, towards greater richness and diversity. Density-dependent mortality of common species allows rare species to appear. The severity and spatial arrangement of such mortality varies among species, but the quantitative effect is pervasive.

Some issues do remain. High seedfall near parent trees overwhelms such mortality, to the extent that more seedlings are found near parents than further away, as predicted by Hubbell¹⁴. But, per capita mortality remains much higher under adults than further away from adults, thus suggesting that it costs up to several times more to produce a seedling under, rather than away from, parental crowns. A skeptic could argue that too few traps were located directly under fruiting trees to exclude Hubbell's idea that conspecifics replace themselves. But, randomly placed traps, monitored for the input of hundreds of thousands of seeds, and tested against distributions of thousands of seedlings, go as far as anyone is likely to go in testing John Harper's maxim that, in plant ecology, the action is in the transition of seeds to seedlings¹⁷. What comes later is history.

Useful resolutions and unresolved issues

The Harms paper closes one major chapter and opens new chapters. In tropical ecology, phenomenology will always be important; for instance, at some point one needs to demonstrate that directed dispersal actually exists¹³. But, with the publication of the Harms' results, phenomenology need no longer be the central theme. The stage is now set for the study of processes, alone and in interaction with each other. In short, the field can shift from piecemeal attempts to demonstrate a local advantage of dispersal, to applications of what is now axiomatic.

Nagging questions will be recast. Instead of asking whether an escape advantage exists, the question will be the degree to which it is important for different species, whether an escape advantage is synergistic with colonization, or why seed and seedling distributions correspond or fail to correspond¹⁸. Instead

of wondering whether a global advantage exists for local dispersal of a given tree, the basis now exists for asking whether variations in dispersal success require management in pristine, degraded, fragmented or revegetated habitats. These are questions with histories – until now largely unresolved because the fundamental tenets of the Janzen–Connell hypothesis have been in doubt.

There are other new issues to be discussed. Harms *et al.* pinpoint the demographic transition of seed to seedling. Analyses of such transitions reveal the relative contributions of life history stages to population growth or decline, and indicate which transitions do not contribute. Such an analysis can be partitioned in space: does a seedling near a parent contribute as much to population growth (a surrogate for fitness) as a seedling further away? If one projected population growth of dispersed seedlings, as compared with those under adults, would the separately calculated rates of population growth (λ) differ?

An example, far from the rain forest, illustrates the power of a partitioned demographic analysis in the bur sage, *Ambrosia dumosa* (Asteraceae), a dominant shrub of California deserts¹⁹ (M.N. Miriti, PhD thesis, University of Illinois at Chicago, 1999). Overall, in this population of long-lived shrubs, the transition from seedling to established juvenile contributes almost nothing to population growth, λ . In general, annual variation in seedling establishment varies by orders of magnitude without affecting population growth (M.N. Miriti, PhD thesis, University of Illinois at Chicago, 1999). Because some adult plants facilitate germination and early seedling survival, plants that nurse and are nursed are often seen as key to species dynamics in desert communities. Partitioned demographic projections indicate otherwise. Seedlings that establish in the open contribute substantially more to differential population growth than those that establish under the protection of adult nurse shrubs or than the adult shrubs that provide the protection. One wonders whether population projections applied to seedlings and saplings near parents, as compared with those further away, would tell the same story in the 53 species studied by Harms *et al.*⁵

In short, Janzen and Connell provided a compelling intuitive insight 30 years ago, and Harms *et al.* have now provided overwhelming empirical confirmation. Historical questions, and new and unexpected phenomena, will remain but as epilogues. The principal questions of the future will address effects of seed dispersal on spatial demography,

on spatially defined interactions among species of dispersed and undispersed cohorts, and on the application of the new axiom to the comparative studies of species with differing expressions of the hypothesis. Practical applications will abound in forest management, in promoting revegetation of tropical landscapes and in understanding effects of fragmented dispersal assemblages. The hypothesis is now more than interesting – it is useful.

Acknowledgements

We thank the Geographic Society, the National Science Foundation of the USA, The Nature Conservancy and the University of Illinois for support of research that inspired this article.

Henry F. Howe

Dept of Biological Sciences (M/C 066), University of Illinois at Chicago, 845 W. Taylor Street, Chicago, IL 60607, USA (hhowe@uic.edu)

Maria N. Miriti

Dept of Ecology and Evolution, State University of New York, Stony Brook, NY 11794-5245, USA (maria@life.bio.sunysb.edu)

References

- 1 Janzen, D.H. (1970) Herbivores and the number of tree species in tropical forests. *Am. Nat.* 104, 501–528
- 2 Connell, J.H. (1971) On the role of natural enemies in preventing competitive exclusion isome marine mammals and in rain forest trees. In *Dynamics of Populations* (Boer, P.J. and Gradwell, G., eds), pp. 298–310, PUDOC
- 3 Ridley, H.N. (1930) *The Dispersal of Plants throughout the World*, Ashford
- 4 Gleason, H.A. (1926) The individualistic concept of the plant association. *Bull. Torrey Bot. Club* 53, 7–26
- 5 Harms, K.E. *et al.* (2000) Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature* 404, 493–495
- 6 McKey, D. (1975) The ecology of coevolved seed dispersal systems. In *Coevolution of Animals and Plants* (Gilbert, L.E., ed.), pp. 159–191, University of Texas Press
- 7 May, R.M. (1972) *Model Ecosystems*, Princeton University Press
- 8 Tilman, D. (1988) *Dynamics and Structure of Plant Communities*, Princeton University Press
- 9 Howe, H.F. and Smallwood, J. (1982) Ecology of seed dispersal. *Annu. Rev. Ecol. Syst.* 13, 201–228
- 10 Clark, D.A. and Clark, D.B. (1984) Spacing dynamics of a tropical rain forest tree: evaluation of the Janzen–Connell model. *Am. Nat.* 124, 769–788
- 11 Packer, A. and Clay, K. (2000) Soil pathogens and spatial patterns of seedling mortality in a temperate tree. *Nature* 404, 278–281
- 12 Howe, H.F. (1993) Aspects of variation in a neotropical seed dispersal system. *Vegetatio* 107/108, 149–162
- 13 Wenny, D.G. and Levey, D.J. (1998) Directed seed dispersal by bellbirds in a tropical cloud forest. *Proc. Natl. Acad. Sci. U. S. A.* 95, 6204–6207
- 14 Hubbell, S.P. (1980) Seed predation and the coexistence of tree species in tropical forests. *Oikos* 35, 214–229
- 15 Penfold, G.C. and Lamb, D. (1999) Species co-existence in an Australian subtropical rain forest: evidence for compensatory mortality. *J. Ecol.* 87, 316–329
- 16 Schupp, E.W. and Fuentes, M. (1995) Spatial patterns of seed dispersal and the unification of plant population ecology. *Ecoscience* 2, 267–275
- 17 Harper, J.L. (1977) *The Population Biology of Plants*, Academic Press
- 18 Nathan, R. and Muller-Landau, H. (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends Ecol. Evol.* 15, 278–285
- 19 Miriti, M.N. *et al.* (1998) Spatial patterns of mortality in a Colorado Desert plant community. *Plant Ecol.* 136, 41–51

Female secondary sexual characteristics: appearances might be deceptive

The function of exaggerated secondary sexual characteristics (SSCs) has been the focus of extensive research¹. Theory emphasizes that exaggeration can be difficult to fake and can occur if the signals need to represent reliable indicators of the quality of potential mating partners. Now, Funk and Tallamy² have shown that exaggerated sexually dimorphic traits, in a sex role-reversed species of dance fly (*Rhamphomyia* spp.), might have evolved to provide misleading sexual signals to males. Females have bizarre abdominal extensions that might deceive males by incorrectly indicating the size and, particularly, the maturational state of their eggs. If correct, this is an extraordinary example of a mating signal evolving through a dishonest intra-specific signalling function.

Sex roles depend on the relative investment of the sexes, the operational

sex ratio or the variance in mating partner quality^{3,4}. In conventional mating systems, females are more choosy because their investment in reproduction greatly exceeds that of males. However, in species where males provide nuptial gifts or paternal care, it is often the males that choose females⁵. Sex role reversal can be facultative; for example, a male nuptial gift can lead to role reversal if food availability is scarce⁶. In other mating systems (for example, when males always care for offspring), male investment can always exceed that of the females, therefore males are always the choosy sex.

Many species within the Dipteran subfamily Empidinae display consistent sex role reversal. These are predatory species, although many females do not hunt and only feed on pollen. In such species, males capture arthropod prey and enter a swarm of lekking females. Males choose a female, transfer the

nuptial gift and then they fly off in tandem to copulate (Fig. 1). Females feed upon the nuptial gift during sperm transfer. In many species, this is the only opportunity that females have to feed on such proteinaceous food because they have lost the ability to hunt. Females probably require this gift of insect prey to complete egg development. Nuptial gifts in such species are therefore likely to represent an important food resource to females⁷.

As expected for species in which males are consistently the choosy sex, females of many empidine species show SSCs, such as enlarged wings, pinnate leg scales and eversible abdominal sacs⁸. These traits influence male choice⁹, probably because males prefer larger females¹⁰. However, the precise function of the SSCs remains unclear. The abdominal sacs are particularly bizarre – they are pleural membranes into which the female forces her gut, haemolymph, ovaries, malpighian tubules and so on, by swallowing air into her midgut. The effect is to produce a dramatically laterally enlarged appearance (Fig. 2). Funk and Tallamy² used ingenious experimental methods to examine the function of abdominal sacs and leg scales in the sex role-reversed species *Rhamphomyia longicauda*. They complemented this study by comparing male mate choice in