

2006. The number of grains will be limited (~100 interstellar and ~1000 cometary grains), but but determination of cosmic ray exposure ages of interstellar dust, cometary GEMS/IDPs, and crystalline silicates will be very revealing.

Techniques are also being developed to identify, in samples collected in Earth orbit, those grains that are true interstellar dust grains among IDPs that may have been processed in the solar system (14). Collectors in Earth orbit using such techniques would provide a relatively cheap way to collect large samples of “fresh” interstellar dust. Moreover, this would yield IDPs that have not been exposed and al-

tered by the heating events associated with their entry into Earth’s atmosphere.

Studies of captured IDPs and “interstellar” dust will help to address the issue of the presolar nature of GEMS and the origin of comets and will be an important step toward putting the planetary formation jigsaw puzzle together on a “grain-by-grain” basis.

#### References

1. J. S. Mathis, *Annu. Rev. Astron. Astrophys.* **28**, 37 (1990).
2. S. Messenger, L. P. Keller, F. J. Stadermann, R. M. Walker, E. Zinner, *Science* **300**, 105 (2003); published online 27 February 2003 (10.1126/science.1080576).
3. R. S. Lewis, M. Tang, J. F. Wacker, E. Anders, E. Steel, *Nature* **326**, 160 (1987).

4. J. P. Bradley, *Science* **265**, 925 (1994).
5. V. Smith, D. Lambert, *Astrophys. J. Suppl. Ser.* **72**, 387 (1990).
6. A. I. Boothroyd, I.-J. Sackmann, *Astrophys. J.* **510**, 232 (1999).
7. B. S. Meyer, T. A. Weaver, S. E. Woosley, *Meteoritics* **30**, 325 (1995).
8. S. Amari, E. Zinner, R. S. Lewis, *Astrophys. J.* **447**, L147 (1995).
9. J. Crovisier *et al.*, *Science* **275**, 1904 (1997).
10. M. Hanner, *Space Sci. Rev.* **90**, 99 (1999).
11. K. Malfait *et al.*, *Astron. Astrophys.* **332**, L25 (1998).
12. D. Bockelée-Morvan *et al.*, *Astron. Astrophys.* **384**, 1107 (2002).
13. B. Reipurth, J. Bally, *Annu. Rev. Astron. Astrophys.* **39**, 403 (2001).
14. G. Dominguez, A. J. Westphal, M. L. F. Phillips, S. M. Jones, in preparation.
15. F. H. Shu, H. Shang, T. Lee, *Science* **271**, 1545 (1996).

#### ECOLOGY

## Refuting Refugia?

Sandra Knapp and James Mallet

**A**ccording to Charles Darwin, the origin of species was “the mystery of mysteries” (1). If so, then the Neotropical (Central and South American) forests, which harbor more plant species than the tropics of Asia and Africa combined (2), are the most mysterious of all. On page 122 of this issue, Wilf *et al.* (3) show that this massive diversification was active by the early Eocene, 52 million years ago. High plant species diversity in the Neotropics is clearly ancient.

Many biologists in the mid-20th century assumed that speciation occurred only in geographically separated populations. South America, with its continuous belt of rainforest and superfluity of species, might seem to contradict the idea of such “allopatric” speciation. In the 1960s, biologists applied the temperate-zone model of ice-age refugia to explain this enigma, rather than reevaluating the central role of allopatry in speciation theory (4).

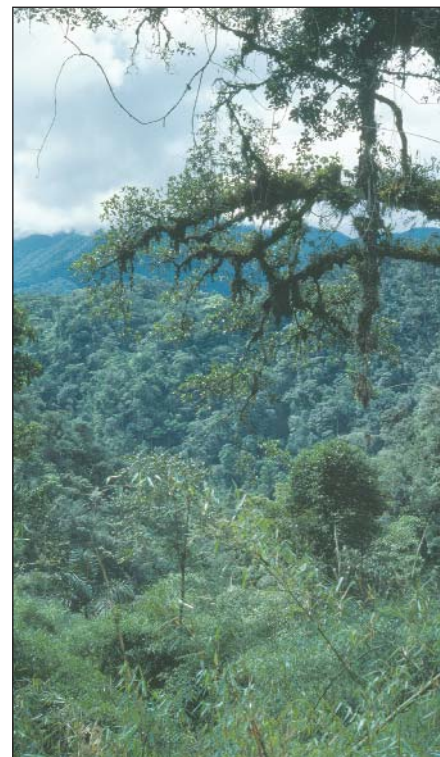
It had long been recognized that animal and plant ranges must have contracted while ice-sheets spread over the Northern Hemisphere. General cooling, sea-level reductions, and the locking up of much of the planet’s water in greatly extended polar ice caps are thought to have caused extensive aridity worldwide. Fossil sand dunes, pollen samples from sediment in high-elevation lake-beds, and “stone lines” (strata suggesting periods of high erosion expected during arid periods) all suggested that

arid climates may have prevailed in the Neotropics during much of the Pleistocene (1.64 million to 10,000 years ago).

Modern geographic patterns of differentiation and speciation across the Neotropical forest also hinted at past allopatry. If, during dry periods, rainforest became restricted to refuges scattered across tropical America, the allopatry deemed necessary for speciation could have occurred in waves throughout the Pleistocene. This

“refugium theory” was proposed to explain both geographic variation within species and overall high species diversity (4).

From the 1970s, the Neotropical refugium model accumulated many critics. If natural selection drives speciation, then gene flow will not affect diversification in areas that are much larger than the per-generation dispersal range of individuals; thus, “parapatric” speciation (geographic speciation while populations remain in contact, or “isolation by distance”) is as plausible as allopatric speciation (5). Furthermore, the geographic ranges of Amazonian birds may require no historical refugium explanation because random placement produces similar distributions (6). An analysis



**Where do all the species come from?** The diversity of the vast Neotropical rainforests has spawned numerous theories of origin, mostly based on climate change during the Pleistocene.

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of hypothesized plant “refugia” showed that they corresponded closely with maxima of collecting activity (7), rather than representing a historical signal.

Today, the refugium hypothesis has been considerably modified (8) in the face of data on distributions, ages, and phylogenetic relationships of Neotropical taxa, and of recent paleoecological findings. There is little biological evidence for a set of forest refuges common to all organisms; in fact, the number and sizes of hypothesized refugia for any particular group appear to depend strongly on the dispersal abilities of the taxa examined (9).

Molecular evidence also suggests that divergence of many sister taxa preceded the Pleistocene (10), even though recent explosive speciation has been found in several Neotropical groups. Butterflies show evidence of species divergences at about 1 to 2 million years ago (11), and in some species-rich genera of flowering plants speciation occurred mostly in the last few million years (12). New alternative theories for speciation have been proposed. For example, Fjelds  (13) has argued that the Andes, after their formation during the Tertiary (65 million to 1.64 million years ago), became the species pump for the entire region, and that lowland forest acts merely as a “museum” for the diversity created in the highlands.

The geological evidence for periods of extreme aridity in the Neotropical rainforest is also now under attack (14). There is strong evidence for cyclical climatic change due to orbital forcing; what is less clear is whether “refugia,” islands of wet forest separated by dry savanna or semidesert, ever existed. According to Hooghiemstra, “the available evidence is far too inadequate to make any well-documented decision” about the existence of Pleistocene refugia (15).

Neotropical diversity clearly does depend on much more than the Amazon basin, although most debate about the exceptional plant species diversity of the Neotropics has centered on these seemingly continuous forests. The Andes, the most extensive mountain range in the world’s tropics, were certainly a factor promoting Neotropical species richness, and many plant species today are found only in the Andes. The late A. L. Gentry (16) pointed out two decades ago that families diverse in the Andes are not the same as those diverse in the Amazon; these patterns are rarely taken into account by those attempting to explain the excess of species-level diversity in the Neotropics.

Wilf *et al.* (3) show that high plant species diversity in the Neotropics was already present during the early Eocene. The Amazon at this time was almost certainly

as warm and as wet as it is today. The extremely high diversity of the Laguna del Hunco site in Patagonia, Argentina, apparently existed long before the main phase of Andean uplift (contradicting Fjelds ’s “museum” hypothesis), and long before the cooler and more turbulent climates of the Pleistocene.

A similarly rich flora at another Eocene Neotropical site (3) suggests large areas of forested habitat. There is fossil evidence for plant families that are now extinct (Casuarinaceae) or less diverse (Proteaceae) in the Neotropics, indicating that extinction and taxonomic turnover must be taken into account when trying to explain the species richness of the Neotropics. With high species diversity evident in the early Eocene, later climate change is neither sufficient nor necessary to explain Neotropical diversity.

Those who still believe that some form of allopatry was required for the current species diversity in the Neotropical rainforest may have to go back about 60 million years to find the requisite refugia. The debate over more recent Neotropical refugia may be irrelevant. A viable alternative to the refugium model is that a vast, relatively unbroken continental region will have sufficient genetic variation, ecological diversity, and isolation by distance to drive the evolution of the outstanding Neotropical diversity we see today.

Does all this matter? If we are to formulate strategies to nurture future evolutionary potential as well as conserve extant species, understanding the origins of

diversity is of the utmost urgency. Darwin was doubtless thinking of the diverse forests of South America when he wrote (1): “Although I do not doubt that [geographic] isolation is of considerable importance in the production of new species, on the whole I am inclined to believe that largeness of area is of more importance... not only will there be a better chance of favourable variations arising from the large number of individuals of the same species there supported, but the conditions of life are infinitely complex from the large number of already existing species” (p. 105). After three decades of debate about Pleistocene refugia, the findings of Wilf *et al.* (3) suggest that Darwin’s ideas may just turn out to be nearer the mark.

#### References

1. C. Darwin, *The Origin of Species* (John Murray and Sons, London, 1859).
2. W. W. Thomas, *Biodivers. Conserv.* **8**, 1007 (1999).
3. P. Wilf *et al.* *Science* **300**, 122 (2002).
4. J. Haffer, *Science* **165**, 131 (1969).
5. J. A. Endler, *Geographic Variation, Speciation and Clines* (Princeton Univ. Press, Princeton, NJ, 1977).
6. S. Beven *et al.*, *J. Biogeogr.* **11**, 383 (1984).
7. B. W. Nelson *et al.*, *Nature* **345**, 714 (1993).
8. J. Haffer, G. T. Prance, *Amazoniana* **16**, 579 (2001).
9. J. Mallet, in *Hybrid Zones and the Evolutionary Process* (Oxford Univ. Press, New York, 1993), pp. 226–260.
10. C. Moritz *et al.*, *Ann. Rev. Ecol. Syst.* **31**, 533 (2000).
11. A. V. Z. Brower, M. G. Egan, *Proc. R. Soc. London Ser. B* **264**, 969 (1997).
12. J. E. Richardson *et al.*, *Science* **293**, 2242 (2001).
13. J. Fjelds , *Biodivers. Conserv.* **3**, 207 (1994).
14. P. A. Colinvaux *et al.*, *Amazoniana* **16**, 609 (2001).
15. H. Hooghiemstra, *Amazoniana* **16**, 653 (2001).
16. A. H. Gentry, *Ann. Mo. Bot. Gard.* **69**, 557 (1982).

#### STRUCTURAL BIOLOGY

## A Glimpse into tmRNA-Mediated Ribosome Rescue

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**T**he basic mechanism of protein synthesis is conserved in all organisms. In reactions orchestrated by the ribosome and charged transfer RNAs (tRNAs), the genetic information in a messenger RNA (mRNA) is decoded into a protein sequence (1). However, occasionally the ribosomal machine stalls on an mRNA before polypeptide synthesis is complete. To rescue stalled ribosomes, eubacteria employ a molecule, called tmRNA, which functions both as a tRNA (2) and a mRNA

(3). It restarts protein synthesis and adds a peptide tag to the incomplete protein to target it for destruction by cellular proteases (see the figure) (4). On page 127 in this issue, Valle and colleagues report the cryo-electron microscopy (cryo-EM) structure of tmRNA in complex with the ribosome (5). The images of this rescue complex provide important new insights into tmRNA function.

During protein synthesis, a charged tRNA is delivered to the A site of the ribosome by EF-Tu, a guanosine triphosphatase (GTPase) that increases translational fidelity (1). EF-Tu senses proper matching of the tRNA anticodon and mRNA codon, trig-

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