

distributional ranges), but also more than 10% of the specimens belonging to this group were not identified below the family level. Ease of access to data on the worldwide web tends to hide the fact that some of these data are not as reliable as one would wish.

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## Reply from M. de L. Brooke

I would like to thank all three correspondents<sup>1–3</sup> who commented on my recent *TREE* News & Comment. All were concerned about making data available on the Web. Several points merit further comment.

Although it is true that some locality information on older specimen labels is not as precise as one would wish, this information can be enhanced as computerization proceeds. For example, a red-footed booby *Sula sula* labelled as collected in the channel (lower case) between London and Paris (country not given) was almost assuredly collected on the Pacific Christmas Island (= Kiritimati), and not in the English Channel between England and France. It is crucial that such enhancements are marked as such.

Both Scoble and Wirtz note what is indisputable – that specimen data on labels are sometimes wrong and are sometimes superseded by taxonomic revision. Is that an argument for not putting the data on the Web? Anyone undertaking a taxonomic analysis of a group is going to use that label data, whether it is on the Web or still attached to the specimen, as a mere first pointer to identity. That researcher will then look at the actual specimen and be thankful if the Web information has facilitated tracking it down. Alternatively, an imaginary scientist called John Smith doing, say, a hotspot analysis of Indonesian butterflies, will almost certainly be less critical. Smith's analysis will make use of the data as is, whether it is read off labels or off the Web. Yes, this means a slightly erroneous analysis will be published (not for the first time!) and, yes, the accessibility of the Web data might increase the chance that the analysis is undertaken. However, the faster availability of raw data on the Web, which is easily corrected in the light of curation and taxonomic revision, potentially increases the chance that the next researcher will return to the raw data, rather than make use of Smith's faulty compilation.

I now address Graves' concern about the cost of computerization and the risk that this will draw funds away from, for example, biodiversity surveys. If computerizing the bird

skins at New York's American Museum of Natural History costs US\$1–2million, then it is a bargain and curators should say so. That sum is <10% of the probable value of the Van Gogh self-portrait in the Metropolitan Museum across Central Park. Moreover, one of the key reasons for computerization is to make the data more accessible to those planning biodiversity surveys, allowing the surveys to be more efficiently planned and targeted.

Graves took me to task for suggesting that museums should use the prospect of improved data availability to lever more core funding. I did not suggest that all the data should be made available before the leverage process started. That would indeed be a poor bargaining tactic.

Graves is also concerned about the free transfer of data. As my original article indicated, data on endangered and/or commercially valuable species and specimens must be restricted. I accept that more than a statement of copyright might be necessary to ensure museums are recompensed for any commercial use made of data posted on the Web. However, while the Web pages are not in downloading format, it might be easier for any closet data miner to pay a modest licensing fee to the museum in order to receive the data in a manageable format, than laboriously to re-enter Web page data.

My basic position as a curator is that I have temporary charge of a treasure that belongs to the world, not to myself and my career ambitions, scarcely even to Cambridge University, UK. Similarly, when I have submitted specimens to museums, it has been in the hope that they would be of use to the community of biologists, not for the aggrandisement of the receiving museum. I believe that the mood of the curators assembled at the meeting on which I reported was in accord with this spirit of openness.

Finally, I would like to clarify a point made by Scoble. In my parlance top-down initiatives, such as GBIF and ENHSIN, involve the great and the good of the museum world planning collaborative ventures. Bottom-up initiatives involve individual curators developing systems and then inviting other curators to link in. This might be more anarchic, but it could gain strength from the fact that the people developing the links have day-to-day involvement with their databases. Thus, my distinction between top-down and bottom-up has nothing to do with taxonomic level, as Scoble implies.

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## Have we forgotten the forest because of the trees?

In their recent *TREE* Review, Brokaw and Busing argued that there is limited evidence for niche partitioning of tree species within forest gaps<sup>1</sup>. Consequently, gaps appear to play a relatively minor role in the maintenance of tree species diversity in forests via traditional resource partitioning. This conclusion is strongly supported by the existing empirical evidence, particularly for shade-tolerant tree species. However, most studies of gaps have failed to take into account plant groups other than trees<sup>2–4</sup>. Gaps might be a necessary habitat for the persistence of a large proportion of vascular plant species other than shade-tolerant trees – specifically, pioneer trees, lianas, herbs, shrubs and herbaceous vines<sup>2–8</sup>. For example, in a study on Barro Colorado Island (BCI), Panama, gaps had higher liana and pioneer tree diversity compared with the surrounding forest<sup>2,3</sup>, on both a per area and a per stem basis (thus removing the effect of density). These two plant groups alone account for approximately 43% of the woody species in this tropical forest<sup>2</sup>. There is also evidence that many forest herbs are gap dependent<sup>5,6</sup>. The role of gaps in the maintenance of shrubs is less clear, although there is some evidence that gaps promote shrub growth and reproduction<sup>7,8</sup>. Overall, when the major vascular plant groups are considered, as much as 65% of the flora of BCI might be gap dependent (Table 1). The specific mechanism that leads to the higher diversity of these groups in gaps remains unknown. Nonetheless, because these vascular plant groups represent most of the plant species in tropical forests worldwide<sup>4,9</sup>, gaps might often play a strong role in the maintenance of species diversity.

Brokaw and Busing also argued that gaps might maintain diversity via the density effect<sup>10</sup>; specifically, that gaps will have a higher diversity of trees solely because they have a higher density of trees compared with the surrounding forest. However, tree density in gaps declines (thins) with age and thus the density effect could maintain diversity in the mature forest primarily in two ways. First, if individuals in gaps reach reproductive age before thinning, then they could potentially colonize new gaps; however, data are lacking on whether trees reach reproductive age sooner (i.e. smaller size or age class) in gaps than in non-gap sites. Second, there must be niche partitioning. Without niche partitioning, thinning of individuals occurs randomly and the initial increase in diversity would be merely a transitory result of the short-term increase in plant density<sup>2,11</sup>. Consequently, given the scanty evidence for niche partitioning and accelerated reproduction in gaps, the evidence for the density effect as a viable mechanism to explain the maintenance of diversity in forests is equivocal at best.

We argue that papers sounding the death knell for the role of gaps in the maintenance

**Table 1. The number and percentage of species in different vascular plant groups on Barro Colorado Island, Panama<sup>a</sup>**

| Plant group          | No. of species | % of species | % of woody species |
|----------------------|----------------|--------------|--------------------|
| Shade tolerant trees | 267            | 34           | 43                 |
| Pioneer trees        | 89             | 11           | 14                 |
| Lianas (woody vines) | 171            | 22           | 28                 |
| Shrubs               | 93             | 12           | 15                 |
| Forest herbs         | 75             | 10           | –                  |
| Herbaceous vines     | 83             | 11           | –                  |

<sup>a</sup>Data taken from Ref. 9.

of forest diversity<sup>11</sup> might be premature. The focus of previous research on the ability of tree species to partition resources in gaps might have caused us to overlook the importance of gaps for many other groups of vascular plants (Table 1). Future research is necessary to quantify further the proportion of species in these groups (and others, such as epiphytes) that require gaps for persistence in the community.

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## Reply from N. Brokaw and R.T. Busing

Schnitzer and Carson's valuable letter<sup>1</sup> helps define and extend the ideas in our recent *TREE* Review<sup>2</sup>. They clarify that it is pioneer tree species, rather than shade-tolerant tree species, that account for the degree of niche partitioning observed within treefall gaps. This makes sense. Pioneer species depend more on gap conditions than do shade-tolerant species, in terms of germination, establishment, growth and survival. With all these behaviors more fully responding to gap conditions, there is more potential for gap partitioning among pioneers. Also, the gap phase in the forest growth cycle can be short<sup>3</sup>, and we would expect species with rapid life cycles, such as many pioneers, to be the species most closely adapted to it.

The apparent gap partitioning among pioneer species and among lianas<sup>1</sup>, as opposed to shade-tolerant species, suggests that the extent to which niche versus chance controls community structure can depend on life-history strategy and growth form of the group considered. It will also depend on such environmental features as disturbance regime and seasonality, and on the spatial and temporal scales considered<sup>4</sup>.

Schnitzer and Carson<sup>1</sup> point out that the density effect is transient on a site-by-site basis. By definition, once trees in a gap site thin to background forest density the site's tree species richness should equal background richness on an area basis. However, over the forest as a whole, gaps are continually appearing, thus the density effect is permanent at that scale. The density effect is simply a manifestation of the high immigration rate to the seedling–sapling pool, which is promoted by treefall disturbance and helps sustain stand-scale tree diversity.

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## Microsatellite frequencies in different taxa

A recent *TREE* Review by Sunnucks<sup>1</sup> on molecular markers for population biology took for granted that, in principle, all markers could be used for all taxa. He made the point that the choice of markers depends primarily on the goals of the study, discussing the availability of markers in any particular taxon as a practical consideration. However, it seems that different taxa are not equivalent for the different possible methods of investigation. Microsatellites are five times less abundant in the genomes of plants than in mammals<sup>2</sup>. Furthermore, within a given class, abundance and distribution of microsatellites vary greatly, such as between Lepidoptera and Hymenoptera. For example, there have only been five studies published on Lepidoptera<sup>3–7</sup>, whereas 47 were published on Hymenoptera during the same period (1997–1999).

The bias towards certain taxa in microsatellite studies seems to lie, at least in part, in their frequency within the genome of the respective study species, and in the structure of the microsatellites and their flanking regions. Both factors are probably important to explain why about 75 microsatellite loci are available for population studies for the honey-bee *Apis mellifera*<sup>8</sup>, although a similar study (in the same laboratory and using the same method) on *Parnassius mnemosyne* (the clouded Apollo) yielded only three loci<sup>3</sup>. Apart from the silkworm moth (*Bombyx mori*), for which 15 microsatellites have been studied, no more than four scorable microsatellite loci have ever been used for population studies in Lepidoptera species, in contrast with high numbers found in the Hymenoptera (Table 1).

The more we know about the organization of the genome in different organisms, the more complex their differences are. This should lead to different molecular markers being appropriate in different taxa to tackle a given biological question.

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