

Table 1. The number and percentage of species in different vascular plant groups on Barro Colorado Island, Panama^a

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	–

^aData taken from Ref. 9.

of forest diversity¹¹ 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 letter¹ helps define and extend the ideas in our recent *TREE* Review². 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 short³, 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 lianas¹, 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 considered⁴.

Schnitzer and Carson¹ 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 Sunnucks¹ 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 mammals². 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^{3–7}, 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*⁸, although a similar study (in the same laboratory and using the same method) on *Parnassius mnemosyne* (the clouded Apollo) yielded only three loci³. 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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Table 1. Number of scorable loci in various Hymenoptera and Lepidoptera species

Species	No. of scorable loci	Refs
Hymenoptera		
<i>Vespula rufa</i>	47	9
<i>Apis mellifera</i>	75	8
<i>Bombus terrestris</i>	26	8
Lepidoptera		
<i>Parnassius mnemosyne</i>	3	3
<i>Parnassius smintheus</i>	4	4
<i>Melitaea cinxia</i>	2	5
<i>Lymantria dispar</i>	4	6
<i>Bombyx mori</i>	15	7

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Reply from P. Sunnucks

Nève and Megléc¹ are quite right that performance and availability of genetic markers might vary greatly among taxonomic groups, even over and above strong biases in research effort and technical factors. In particular, they highlighted the taxonomically heterogeneous nature of microsatellites. Anyone who has cloned microsatellites from even a modest diversity of species is likely to have encountered one sort of challenge or another. Indeed, my own research has run into unusual difficulties in obtaining usable

microsatellites from the invertebrate Phylum Onychophora^{2,3}, when libraries from other invertebrates and vertebrates cloned in parallel were unproblematic. Similar comments would apply to most other genetic marker systems. Even the usually highly reliable mtDNA can throw up surprises; for example, its use in a restricted clade of *Sitobion* aphids is severely limited by the presence of multiple nuclear copies⁴.

The undoubted taxonomical variation in density, physical properties, mutation and evolutionary behaviour of microsatellites are important topics of research⁵. Accordingly, I highlighted increased knowledge of molecular evolution as one of the most important research areas in molecular population genetics. However, none of this undermines my main premise that single locus codominant markers capable of yielding allele phylogenies are worthy of the bulk of research effort, because they provide connectable data that inform us about ecology and evolution at a variety of levels in the hierarchy of life. Such markers and the data they generate (particularly as compared with multilocus

dominant markers) are of ongoing, as well as current, use in population biology and molecular evolution.

When certain taxa or questions throw up technical barriers, we need to be imaginative and resourceful in finding markers that fulfil the most important criterion – generating the type of data we have decided we need. If microsatellites are rare in a genome, we might decide to work harder at obtaining them: Nève and Megléc point out that microsatellites are five times less abundant in the genomes of plants than mammals, but that still leaves plenty of loci for everything, except perhaps gene mapping. We can also investigate the availability of other single locus, codominant, phylogeny-yielding markers, such as codominant AFLPs, SNPs or rDNA spacers.

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