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Phenology or resources limit *Drosophila* local biodiversity in a southern Asian continental subtropical forest.

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Introduction

Biodiversity is typically greater in the tropics and semitropics than in temperate areas. The question then is, how is this greater biodiversity achieved? High diversity would result if there were more resources in low latitudes than in high with a small number of species using each resource. High diversity would also result from greater spatial or temporal (*i.e.*, phenological) variability in species identities. This mechanism also suggests that local species numbers will be small. The proportional sampling model, however, predicts high local diversity (Cornell and Lawton, 1992). This is because the proportional model holds that interspecific competition is relatively unimportant. The number of species coexisting locally is then a simple proportion of the number of species in the regional pool.

As an initial step towards examining this question in *Drosophila*, we sampled flies in a species rich semitropical forest in continental southern China.

This genus is species rich with 2874 species world-wide (Wheeler, 1981, 1986) and provides a very diverse but phylogenetically restricted fauna. The genus is better known, particularly in the tropics, than most dipteran taxa. We looked at continental eastern Asia because there are no major barriers to north-south movement of faunas at this longitude. The existing faunas are, therefore, unlikely to be affected by restricted post-glacial colonization. Major barriers do exist at other longitudes. The Himalayas and Caucuses, together with deserts, limit exchange in western Asia. The subtropical African faunas are separated from Europe by the double barrier of the Sahara desert and the Mediterranean sea. And in the Americas the relatively recent rise of the Isthmus of Panama is a similar complicating factor. Diverse drosophilid faunas are, however, found in tropical mainland Asia. In an area of only 1130 ha, our main study site in southern China has over 115 drosophilid species. Of these, 63 are currently in the genus *Drosophila* (Toda and Peng, 1989; Peng *et al.*, 1990a, 1990b). This contrasts markedly with 54 *Drosophila* species recorded for the entire British Isles. We, therefore, concentrated our study on the *Drosophila* faunas of two locations near Guangzhou, Guangdong Province, China. Local biodiversity was remarkably low. This completely contradicts the proportional sampling model. We are now investigating the contribution of spatial, temporal, and resource variability in species richness to the high biodiversity of continental southern Asia.

Methods

Dinghu Shan (DHS) (23°08' N 112°35' E) is a mountainous area of remnant forest 86 km west of Guangzhou City in the southern subtropical biogeographic zone of China. The mountain summits are 150-500 m with the highest peak at 1000.3 m. The topography is rugged and steep-sloped (Wu *et al.*, 1982). The underlying rocks are Devonian sandstones or slates and the soils are generally acidic and humus-rich (He *et al.*, 1982). The area has a subtropical monsoon climate (Huang and Shen, 1982) with tropical storms and typhoons bringing heavy rain from April to October (Huang and Fan, 1982). Annual precipitation reaches 1962.9 mm and annual insolation 10.48 Kcal cm^{-2} (Huang and Shen, 1982). The dominant vegetation type is subtropical monsoon evergreen broadleaf forest composed mainly of *Castaneopsis*, but also including *Caryota* and *Calamus* palms, screwpine *Pandanus*, and treeferns. Plant diversity is very high with 1489 species (Wang *et al.*, 1982).

We made limited additional collections on the campus of the Guangdong Institute of Entomology (GEI). This is within the urban area of Guangzhou city at 23°05" N 113°17' E. It contains research and domestic buildings, gardens, ponds, and trees. It is at the south west corner of the 117 ha Zhongshang University campus. This campus is well wooded and park-like.

Few of the tree species at DHS were fruiting, so we collected *Drosophila* by putting out fruit baits. Small pieces of banana or of pineapple were put into 1 × 3" glass vials. Twenty-four baits, 12 of each fruit, were placed in pairs at two sites and 26, 13 of each, at two other sites in unfrequented montane evergreen broadleaved forest 200-400m away from Qing Yun Si temple at DHS. These 4 sites were at least 100 m away from each other. At a fifth site 10 tubes of each bait type were exposed among scrubby undergrowth and young trees. We exposed the baits for 6 days and then collected them. A second series of baits was then set out in the same way as the same locations and these in turn were collected 6 days later. All the samples were, therefore, made within 12 days in the last 2 weeks of July.

The same procedure was followed at one site on the GEI campus. On the first occasion we set out 25 banana and 10 pineapple baits and on the second 20 of each.

After collection the baits were maintained at the GEI in an outdoor insectary (at 29 ± 2° and 80-100% RH). They received natural light but were shaded from direct sun. We identified the adults that emerged to species and recorded the numbers of each taxon.

Results

A total of 224 baits were successfully recovered. Many of the missing baits, particularly the banana baits, exposed at DHS had been removed by ants. The proportions of baits of the two types recovered from each site varied greatly (Table 1). Of the recovered baits, 15 produced no adults. We have omitted these baits, and those lost, from our analysis.

Table 1. Mean number of flies of each species per bait (and standard deviation) for each bait type at each of the two locations. The number of successful, recovered baits is given in brackets after the bait type.

Site	Bait Type	*Drosophila albomicans*	*Drosophila bochi*	*Drosophila kikkawai*	*Drosophila lini*	*Drosophila melanogaster*	*Drosophila montium*	*Drosophila punjabi*	*Drosophila suzukii*	*Drosophila takahashi*	*Drosophila tani*
Dinghu Shan	banana (59)	53.85 (47.52)	0.05 (0.22)	0.02 (0.13)	0.17 (0.70)		0.66 (2.05)	0.05 (0.39)	0.02 (0.13)	5.97 (17.39)	0.73 (1.54)
	pineapple (88)	21.10 (17.86)	0.01 (0.11)		0.14 (0.57)		0.23 (0.62)			1.36 (3.17)	1.17 (2.44)
Guangzhou	banana (40)	8.05 (12.39)	0.25 (1.28)			18.30 (21.29)	0.15 (0.66)	0.05 (0.32)	0.03 (0.16)	1.60 (2.66)	
	pineapple (22)	4.45 (6.91)	0.05 (0.21)			40.05 (41.94)			0.18 (0.85)	2.32 (3.14)	

We reared out 7194 adult flies from 10 *Drosophila* species taxa. There were 5454 *D. albomicans,* 15 *D. bochi,* just one *D. kikkawai,* 22 *D. lini* (lini-complex), 1613 *D. melanogaster,* 65 *D. montium* (montium-complex), 5 *D. punjabi,* 6 *D. suzukii,* 587 *D. takahashi,* and 146 *D. tani*.

We identified 9 species from DHS baits and 7 from those at GEI (Table 1). We reared two species, *D. lini* and *D. tani*, from DHS that were not found at GEI. *Drosophila melanogaster* emerged only from GEI baits and not at all from those at DHS. It is of interest that we reared *D. suzukii* from fruit baits exposed on the ground despite the frequent claim that this species specializes on ripe rather than decaying fruit. We also reared a very few *Asobara*-like braconids from DHS. From GEI there were a few *Leptopilina*-like eucoilids and a single braconid (not like *Asobara*). At both sites there were occasional individuals of at least 2 beetle species and a species of large, long legged acalypterate fly.

The *Drosophila* fauna we collected was dominated by very few species, *D. albomicans*, *D. takahashi* and, in GEI, *D. melanogaster* (omitting the infrequent *D. kikkawai*, *D. punjabi*, and *D. suzukii*) (Figure 1). There were significant faunistic differences between DHS and GEI ($F^{1}_{195} = 40.20$, $p < 0.001$) by permutated nested Anderson manova using Jaccard similarity. There were also significant differences between bait types within sites and locations ($F^{7}_{195} = 2.67$, $p < 0.001$). However, there were no significant differences in faunas between sites within locations ($F^{5}_{195} = 1.37$, $p < 0.079$) (see also Figure 1).

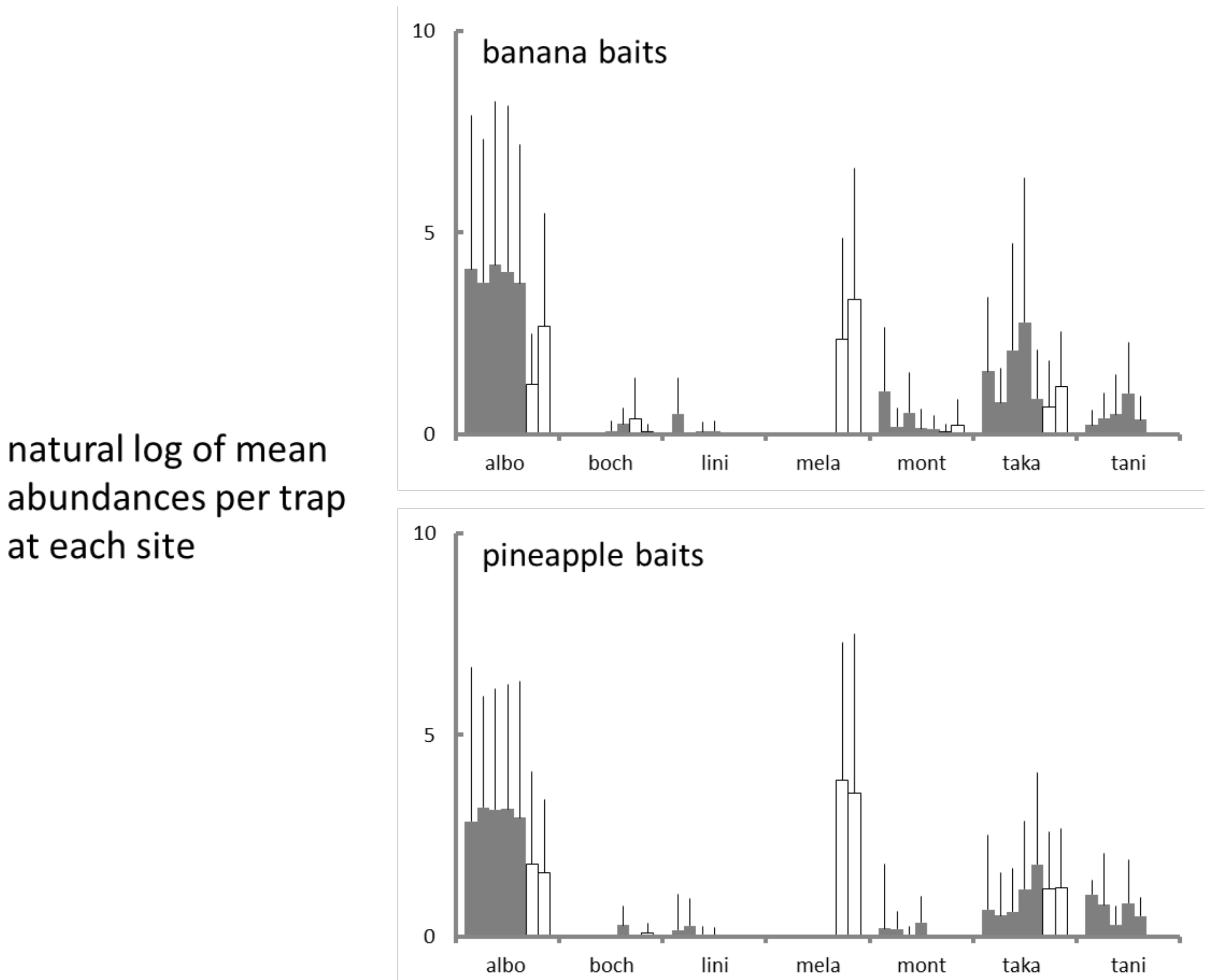

Figure 1. Average numbers of adults (as natural logs of abundance) at 5 sites in DHS (gray) and 2 in GEI (white) emerging from the 2 different bait types. The error bars are the natural log of 1 standard deviation of the corresponding mean.

Discussion

The small number of species from DHS and GEI contradicts the proportional sampling model (Cornell and Lawton, 1992), because more would be expected under this model given the 63 *Drosophila* species recoded from the area. That we only reared 10 species, only 7 in any numbers, is not the result of using banana and pineapple as baits. It is true that neither is present in DHS. However, banana has been present in eastern Asia for millennia and so is likely to have accumulated a *Drosophila* fauna. Banana, furthermore, is attractive to many *Drosophila* species, particularly those breeding on fruit, even species that never breed on banana naturally. Therefore, the banana baits probably attracted all the fruit breeding *Drosophila* species active in the trapping area during late July. The similar number of species reared from pineapple suggests that this fruit is also a broadly attractive bait.

We would have reared such a small number of species despite a recorded fauna of at least 63 species if the majority of the 63 were not fruit breeders. This is not the case as the faunal list for DHS is derived from static retention trapping using fruit bait (Peng *et al.*, 1990b). Most of the *Drosophila* listed usually or often breed on fruit.

Other mechanisms must, therefore, produce the high species diversity of DHS and of semitropical continental east Asia generally. One mechanism is a high turnover in species present with distance, *i.e.*, spatial variation in species. There were differences in the species found in DHS and in GEI, particularly the occurrence of *D. melanogaster* at GEI. However, there were no significant differences between sites within DHS or within GEI suggesting that spatial variation in species, if it occurs, does so on a scale greater than 100-500 m, the distances between traps. Another possible mechanism is variation in species between different breeding resources. The operation of this mechanism is suggested by the significant differences in the faunas reported from banana and pineapple in both DHS and GEI. Collections of *Drosophila* species from a wider range of fruits is needed to substantiate this mechanism. However, the differences in faunas between banana and pineapple are not very great. A further mechanism is variation in species over time as a result of different species phenologies. There are, indeed, considerable differences in phenology among the species occurring in DHS (Peng *et al.*, 1990a). This mechanism thus probably contributes greatly to the high total diversity of *Drosophila* species in semitropical east Asia and is a prime target for future research. The local diversity, however, is limited to a few species by phenology as our study occurred within 2 weeks and resources as we used only 2 bait types.

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