

Drosophilid Fruit-Fly Guilds in Forest Fragments

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Habitat fragmentation and subsequent isolation of forests has received much attention in conservation research, both worldwide and in tropical forests, including the Amazon. By definition, forest fragmentation reduces the original habitat and increases the isolation of remaining forest patches. Additionally, a series of microclimatic changes increase temperature and luminosity and decrease humidity in forest remnants (Kapos 1989).

In the case of the Amazon forest, high species diversity compounds the initial effects of fragmentation. Because many plant species occur at very low densities, deforestation produces a strong sampling effect; many plant species will not be present in the forest remnants because of their low density or patchy distribution. This may have cascading effects through faunal communities.

Habitat fragmentation is accompanied by the creation of a new matrix habitat that replaces the original forest. For example, in the case of a forest transformed into pasture, this new habitat has totally different temperature, humidity, vegetation cover. Many species not present in the original forest can opportunistically use the new matrix habitat and possibly invade forest remnants

(Martins 1989; Gascon et al. 1999; Chapters 19 and 20). The contact among these distinct faunas can initially increase species richness, but with time, the occurrence of competitive interactions and changes in forest conditions could lead many native species to local extinction (Chapter 2). This effect can be more or less intense in accordance with the level of susceptibility of the species to the alterations of the habitat (humidity loss, wind increase, temperature increase, qualitative and quantitative alterations in resources, invasion by new species [Bierregaard et al. 1992]).

The drosophilid fruit-fly community associated with decomposing fruits, as a group of organisms that use the same class of resources in a similar manner, constitutes a guild as defined by Root (1967). Although this guild concept groups species with similar ecological requirements without their necessarily being taxonomically related, in the case of drosophilids, taxonomic relationships do exist. Simberloff and Dayan (1991) argued that members of a guild are potential competitors for similar resources in a dynamic equilibrium. The composition of the guild, therefore, represents functional redundancy in an ecosystem, such that the structure of the guild can be more pre-

dictable than the abundance of the individual species or the guild's specific composition. The guild can be seen in this manner as a functional category shaped by adaptation for the exploitation of the same class of resources (Hawkin and MacMahon 1989).

Wolda (1992) suggested that populations are in a dynamic balance with the resource availability, that the communities are highly organized, presenting specific composition patterns with foreseeable changes, and that the number of individuals and their biomass can suffer great variations while species richness remains similar. This suggests that changes in guild structure caused by an anthropogenic influence, for example, can reflect changes in resource availability. Such a response would serve as an indicator of habitat disturbance.

Studies have shown drosophilids to be sensitive to fragmentation effects in a relatively short time period (van der Linde 1992; Davis and Jones 1994). Drosophilids can represent a significant portion of the small insect community, which, although nearly imperceptible to the human eye, represents a significant portion of Amazonian forest species diversity. The small insect community contributes effectively to the maintenance of the forest through pollination, seed dispersal, recycling of nutrients, and energy flux.

In this chapter I study drosophilid guild structure. I investigated the response of a drosophilid guild (drosophilids linked to decomposing fruits) to two different scenarios of habitat fragmentation in two fragmented forest landscapes to determine if changes in guild structure can serve as an indication of anthropogenic disturbance. The basic questions are as follows: Does fragmentation cause alterations in the characteristics of this guild? If so, what are these alterations? In the first case, results are reported from the Biological Dynamic of For-

est Fragments Project north of Manaus (Martins 1985, 1987; see fig. 4.1). In the second case, results are reported from the extreme eastern Amazon, in the Mocambo Reserve within the Belém city limits (Martins 1996). Some other examples will be considered in less detail. In both studies, species abundance and guild composition were evaluated. A comparison of the response of the drosophilid guild in different fragmented landscapes permits us to detect common patterns that will aid in setting conservation guidelines for these invertebrates.

Central Amazon

METHODS

Studies in the central Amazon were performed at BDFFP reserves, in particular on the Esteio and Porto Alegre cattle ranches (see fig. 4.1, table 4.3). In 1980 and 1983, only two reserves were isolated (1104 and 1202, of 1 ha and 10 ha, respectively, on the Esteio ranch; see plate 1). On the Porto Alegre ranch, reserves 3114, 3209, and 3304 were not yet isolated. In 1986, a survey was conducted in the fragments of the Esteio ranch and in Reserve 3304 (by then isolated; see plate 2) on the Porto Alegre ranch. In April 1995 another survey of the area was performed with only one series of collections in 1 and 10 ha forest fragments of the Esteio ranch and in the 100 ha reserve on the Porto Alegre ranch (see Chapter 4, esp. table 4.3, for a more detailed history of the isolation of these reserves).

The climate of the region follows the "Afi" type of the Koeppen classification, having no monthly precipitation values below 40 mm and with mean temperatures between 26° and 27° C. Rains begin in January, reach their peak in March and April, and generally decrease between August and October (fig. 5.1).

In this study, adult drosophilids were collected at natural feeding and breeding sources, using local commercial fruit baits. The type of bait most commonly used was naturally fermented bananas, but surveys were also made using papaya and oranges.

Species abundance estimates were made with standardized banana baits, distributed uniformly in the habitat in 500 ml tin containers placed 10 cm above the ground. The same methods were used during the entire study period. Collections were made by netting fruit-flies over the baits twenty-four and forty-eight hours after they were set out.

The flies collected were stored in 70 percent alcohol, separated according to bait and day of collection, identified, and quantified in the laboratory. The interval between each sampling bout was one to two months.

For guild characterization, the Shannon and Fisher alpha indices and the Berger-Parker dominance (D) index were used. The similarity between habitats was estimated using the Jaccard index (see Krebs 1989).

Surveys in July 1986 were conducted during two consecutive days in each reserve (1104, 1202, and 3304) and in the secondary forest adjacent to the Esteio reserves, using naturally fermented bananas as bait placed in tin containers 50 cm from the ground.

In April 1995, only banana bait was used in the central areas of Reserves 1202, 1104, and 3304 to evaluate possible changes in the composition and relative abundance of the *Drosophila* species in these habitats. During this time, sampling was performed for three consecutive days in each reserve, using naturally fermented banana bait placed on the ground and in containers similar to those of previous surveys. Survey data for each bait station were totaled.

RESULTS

Occurrence of drosophilids on native fruits. The *willistoni* group (*Drosophila*, subgenus *sophophora*) represented 64 percent of the collections from native fruit on the forest floor. Species of this group occurred on all types of fruit and were the only taxa present on fruits of the families Guttiferae and Moraceae (*Ficus* sp.). The *tripunctata* group (*Drosophila*, subgenus *Drosophila*) represented 18 percent of collections and occurred on six of the nineteen types of sampled fruits. In the collections that were made on flowers dispersed on the forest floor, the *tripunctata* group was dominant, representing 89 percent of the individuals; it was present in all the flowers where drosophilids occurred. The abundance of the group was notable in the flowers of *Eschweilera odora* ("mata-mata"; Lecythidaceae), a species found quite frequently in the reserves. Drosophilids were found on only three types of fungi: *Auricularia delicata*, *Pleurotus* sp., and *Scuteiger brasiliensis*. These included flies of the subgenus *Hirtodrosophila* and, predominantly, of the genus *Zygothrica*.

In the 1983 surveys with different types of baits (oranges, bananas, and papaya), the *willistoni* subgroup once again dominated, representing 51 percent of the individuals, followed by *D. nebulosa* and *D. malerkotliana* with 21 percent and 12 percent of the individuals, respectively. The distribution of species occurrence did not significantly differ among bait types.

Comparison of abundance between fragments and continuous forest. Comparison of the relative species abundance patterns between these two habitats showed that among the most abundant species there were no changes in species ranking even though the total number of individuals collected in the fragments was about twice as

TABLE 14.1. Abundance of *Drosophila* Taxa in Continuous Forest and Forest Fragments from a Seven-Day Survey in 1983, Three Years After Fragmentation

Taxa	Forest	Fragments		Total	Percentage
		Forest	Secondary		
Subgroup <i>willistoni</i>	1,584	3,007	39	4,700	81.5
<i>D. malerkotliana</i>	45	275	30	332	5.7
<i>D. sturtevanti</i>	18	23	1	42	0.7
group <i>tripunctata</i>	10	25	4	39	0.7
<i>D. nebulosa</i>	5	63	195	263	4.5
<i>D. cardini</i>	0	39	80	119	2.1
<i>D. latifasciaeformis</i>	0	35	236	271	4.7
TOTAL	1,662	3,519	585	5,766	

TABLE 14.2. Abundance of *Drosophila* Taxa in Forest Interior and Forest-Edge Habitats from a Five-Day Survey

Taxa	Forest interior	Forest edge	Total	Percentage
Subgroup <i>willistoni</i>	1,058	433	1,491	69.70
<i>D. malerkotliana</i>	234	149	383	17.90
<i>D. latifasciaeformis</i>	1	103	104	4.80
<i>D. cardini</i>	0	2	2	0.09
group <i>cardini</i>	0	11	11	0.50
<i>D. sturtevanti</i>	39	33	72	3.40
Group <i>saltans</i>	5	3	8	0.40
<i>D. nebulosa</i>	29	13	42	2.00
Group <i>tripunctata</i>	10	0	10	0.40
<i>D. fumipennis</i>	7	2	9	0.40
sp. 1	1	0	1	0.05
sp. 2	0	1	1	0.05
sp. 3	0	2	2	0.90
sp. 4	0	1	1	0.05
sp. 5	0	1	1	0.05
sp. 6	0	1	1	0.05
TOTAL TAXA	9	15	16	
TOTAL INDIVIDUALS	1,384	755	2,139	
Fisher's Alpha	1.2883	2.6525		
Shannon Index	1.126	1.854		
Dominance Index	0.76	0.57		

Note: Survey made in Reserve 3304 of Porto Alegre. Forest edge was one month old at time of survey.

large as in continuous forest (table 14.1). The predominant species in the second-growth forest (*D. latifasciaeformis*) was not present in continuous forest and appeared in low frequency in forest fragments. The subgroup *willistoni* was only the fourth most abundant species in second growth.

After complete isolation of one of the 100

ha reserves (3304), the comparison between forest edge and the reserve interior revealed intermediate changes in species abundance and diversity patterns in relation to the prior comparisons (table 14.2). The subgroup *willistoni* predominated in the interior as well as in the forest edge. Its abundance, however, was 2.5 times lower at the forest

TABLE 14.3. Abundance of *Drosophila* Taxa in the Different Habitats Surveyed on Esteio Ranch, 1980-83

Taxa	1202 center	1202 border	1202 edge	1202 total	1104	Secondary forest	Total	Percentage
<i>Group annulimana</i>								
<i>D. araicus</i>	1	0	1	2	1	0	3	0.03
<i>Group calloptera</i>								
<i>D. cannalina</i> (sp. 10)	0	1	0	1	0	0	1	0.01
<i>Group cardini</i> (sp. 7)								
<i>D. polyinorpha</i> (sp. 14)	0	0	0	0	1	0	1	0.01
sp. 5	0	0	0	0	5	0	5	0.06
<i>D. cardini</i>	1	14	60	75	11	320	406	21.09
<i>D. cardinoides</i>	0	0	0	0	1	0	1	0.01
<i>Group Dreyfusi</i> (sp. 24)								
<i>Group guarani</i>	0	3	0	3	2	0	5	0.06
<i>D. moju</i>	0	1	0	1	0	0	1	0.01
<i>D. mercatorum</i>	0	2	0	2	0	4	6	0.07
<i>D. ellisoni</i>	0	1	1	2	1	0	3	0.03
sp. 31	0	1	0	1	0	0	1	0.01
sp. 32	0	0	4	4	0	4	8	0.09
sp. 16	0	1	0	1	0	0	1	0.01
sp. 3	0	0	0	0	1	0	1	0.01
<i>Group tripunctata</i>								
<i>Hirtodrosophila</i>	0	0	0	0	2	0	2	0.02
<i>D. latifasciaeformis</i>	2	8	44	54	2	142	198	2.31
<i>D. ananassae</i>	0	0	1	1	0	2	3	0.03
<i>D. malerkotliana</i>	36	68	65	169	74	110	353	4.12
<i>D. simulans</i>	0	1	0	1	0	3	4	0.05
sp. 1 group saltans	0	0	0	0	1	0	1	0.01
<i>Subgroup sturtevanti</i>								
<i>D. prossaltans</i>	0	1	0	1	0	1	2	0.02
<i>Subgroup willistoni</i>								
<i>D. nebulosa</i>	988	2,419	299	3,706	2,676	121	6,503	75.94
<i>D. fumipennis</i>	6	38	40	84	127	59	270	3.15
<i>D. fumipennis</i>	0	0	0	0	4	1	5	0.06
sp. a	3	0	0	3	0	0	3	0.03
sp. b	0	0	0	0	0	1	1	0.01
sp. 2, n13	0	0	0	0	1	0	1	0.01
sp. 9	0	1	0	1	0	0	1	0.01
sp. 11	0	0	1	1	0	0	1	0.01
sp. 19	0	3	0	3	0	0	3	0.03
sp. 20	0	0	0	0	1	0	1	0.01
sp. 22	0	0	0	0	1	0	1	0.01
sp. 26	0	0	0	0	1	0	1	0.01
<i>D. tuchaua</i> sp. 27	0	0	0	0	1	1	2	0.02
sp. 29	0	0	0	0	0	1	1	0.01
TOTAL	1,152	2,795	572	4,519	3,211	833	8,563	
TOTAL SPECIES	11	19	12	25	24	16	40	
Fisher's Alpha	1.684	2.742	2.147	3.487	3.520	2.809	5.424	
Shannon Index	0.811	0.849	2.193	1.105	1.032	2.520	1.437	
Dominance Index	0.858	0.865	0.523	0.820	0.833	0.384	0.7594	

TABLE 14.4. Jaccard Similarity Index Values Between Habitats Surveyed on the Esteio Ranch

Habitats	1202 center	1202 border	1202 edge	1104	Secondary forest
1202 center	1.00	0.36	0.30	0.34	0.35
1202 border		1.00	0.35	0.30	0.40
1202 edge			1.00	0.33	0.50
1104				1.00	0.26
Secondary forest					1.00

edge, whereas *D. latifasciaeformis* increased in abundance more than 100 times from the interior to the edge. The number of species increased from nine to fifteen at the forest edge, and the diversity, measured by the Shannon diversity index, varied from $H = 1.126$ to $H = 1.854$. There was a slight increase in species diversity at the forest edge. The similarity between forest edge and interior as measured by the Jaccard index was $J = 0.4375$.

The evaluation of diversity of the forest fragments in the 1980s. Overall, forty taxa of Drosophilidae were encountered, including species and morpho-species (individuals apparently distinct from other species in the sample but not yet reliably identified). The number of taxa increased with increasing reserve size and with the degree of preservation of the habitat. Sixteen taxa were found in second-growth forest, twenty-four in the 1 ha reserve, and twenty-five in the 10 ha reserve. The dominance index was higher for fragments than for second-growth forest, with the *willistoni* subgroup in the forest areas reaching dominance levels above 80 percent (table 14.3). The Jaccard similarity values indicated a greater similarity between the 10 ha forest edge and the second-growth forest, and a lower similarity between the second-growth forest and Reserve 1104 (table 14.4). In general, similarity among habitats was much lower, between

0.26 and 0.50, demonstrating a high level of heterogeneity in species distribution.

Collections made in 1986. A total of 1,667 individuals, pertaining to five taxa and three unidentified individuals, were collected in continuous forest (table 14.5). Fragments revealed 3,526 drosophilids of eight taxa and nine unidentified individuals. The same eight taxa were found in the second-growth area, although the number of individuals was smaller—590 (table 14.5). Abundance patterns were similar to those of the 1981 and 1983 collections.

Abundance and diversity patterns in 1995. A total of 7,371 individuals of thirteen species were collected in 1995 (table 14.6). Nine species were collected in continuous forest, eleven in the 10 ha reserve and nine in the 1 ha; eight species were common to the three habitats. These results show only slight differences in diversity and species composition when compared to the 1983 surveys (table 14.7). Ten taxa were common to the two periods in at least one reserve. The Jaccard similarity index between 1981–83 and 1995 was 0.38 for the 1 ha reserve, 0.69 for the 10 ha reserve, and 0.60 for Reserve 3304. These results suggest a much larger change in species composition in the 1 ha reserve than in the larger reserves.

DISCUSSION

Although drosophilid fruit-flies use varied resources, species composition by resource type is fairly constant. In the forest, drosophilids associated with fruits are a distinct guild from those associated with flowers or fungi. It is expected that response patterns obtained for one of these guilds will reflect similar responses for other guilds.

Drosophilid species composition changed dramatically between the forest and the open areas. Forest fragmentation modified specific composition and abundance pat-

TABLE 14.5. Abundance of *Drosophila* Taxa in the Habitats Surveyed in 1986 Within the BDFFP Landscape

Taxa	Continuous forest	1202 center	1202 border	1104	Secondary forest	Total	Percentage
Subgroup							
<i>willistoni</i>	1,584	656	1,599	823	39	4,701	81.10
<i>D. malerkotliana</i>	45	33	128	96	30	332	5.72
<i>D. sturtevanti</i>	23	6	11	6	1	47	0.81
Group <i>tripunctata</i>	10	4	8	13	4	39	0.67
<i>D. nebulosa</i>	5	4	39	20	196	264	4.55
<i>D. cardini</i>	0	28	8	3	80	119	2.05
<i>D. latifasciaeformis</i>	0	11	11	13	236	271	4.67
<i>D. simulans</i>	0	1	5	0	4	10	0.17
Others	3	3	0	3	4	13	0.22
TOTAL	1,670	746	1,809	977	594	579	

TABLE 14.6. Abundance of *Drosophila* Taxa in Continuous Forest and Forest Fragments in April 1995

Taxa	Location					
	Continuous Forest		1202		1104	
	Abundance	Percentage	Abundance	Percentage	Abundance	Percentage
Subgroup						
<i>willistoni</i>	3,460	89.10	1,865	86.20	1,107	83.40
<i>D. malerkotliana</i>	163	4.20	39	1.80	99	7.40
<i>D. nebulosa</i>	11	0.30	14	0.60	6	0.40
<i>D. latifasciaeformis</i>	0		0		2	0.10
Group <i>tripunctata</i>	12	0.30	41	1.90	91	6.80
<i>D. annulimana</i>	4	0.10	7	0.30	1	0.07
<i>D. guarani</i>	0		1	0.04	0	
<i>D. fulvimacula</i>	13	0.30	20	0.90	1	0.07
<i>D. repleta</i>	0		21	1.00	0	
Group <i>cardini</i>	1	0.02	3	0.10	1	0.07
<i>D. camargoi</i>	0		1	0.04	0	
<i>D. fumipennis</i>	4	0.10	0		0	
<i>D. sturtevanti</i>	214	5.50	169	7.80	28	2.10
TOTAL	3,882		2,163		1,326	
TOTAL SPECIES	9		11		9	
Fisher's Alpha	1.099		1.513		1.298	
Shannon Index	0.671		0.914		0.956	
Dominance Index	0.89		0.86		0.83	

terns of the drosophilid guild. The main changes were a decrease in species richness with decreasing reserve size, producing guilds in fragments with intermediate composition between continuous forest and second-growth forest guilds.

The decrease in species richness was

caused by the disappearance of rare, native, and characteristic forest species. Furthermore, patterns of dominance among the most common species were also altered. Species richness, however, showed a slight increase at the landscape level, probably resulting from a decrease in relative abun-

TABLE 14.7. Relative Abundance of *Drosophila* spp. Present in Each of Three Sampling Periods in at Least One Forest Fragment on Esteio Ranch

Taxa	1202 Center			1104		
	81-83	July '86	April '95	81-83	July '86	April '95
Subgroup <i>willistoni</i>	85.7	87.9	86.2	83.3	84.2	83.4
<i>D. malerkotliana</i>	3.1	0.04	1.8	2.3	9.8	7.4
<i>D. nebulosa</i>	3.3	0.5	0.6	3.9	2.0	0.4
<i>D. latifasciaeformis</i>	0.2	1.4	0	0.06	1.9	0.1
Group <i>tripunctata</i>	0.2	0.5	1.9	1.7	1.3	6.8
Group <i>cardini</i>	0	3.7	0.1	0.6	0.3	0.07
<i>D. sturtevanti</i>	9.4	0.8	7.8	7.4	0.6	2.1
TOTAL INDIVIDUALS	1,152	746	2,163	3,211	977	1,326

dance of the originally dominant group in second-growth forest and the appearance of exotic opportunistic species, such as *D. malerkotliana*.

Fragment size also influenced species composition, as shown by the highest dissimilarity levels between the smaller fragment and continuous forest. Observed species losses, in this case, were of species most sensitive to changes in habitat quality, such as *D. camargoi*, *D. tuchaua*, and various species of the *repleta* and *tripunctata* groups.

The invasion of *D. malerkotliana* is well known, as well as its expansion rate in the Neotropics in the past twenty years (Sene and Val 1977; Martins 1989; Martins 1990; Sevenster 1992). Between the early 1980s and 1995 the abundance of this species grew modestly in continuous forest, but relatively more in the central area of the 10 ha reserve and in the smaller 1 ha reserve.

Results from Belém, Pará, and other eastern Amazonian sites can help one understand the invasion of *D. malerkotliana* and other impacts on species composition of the drosophilid guild in forest fragments.

Eastern Amazon

METHODS

Since 1986, drosophilid guilds have been surveyed in the Mocambo Reserve, a 5 ha terra firme forest fragment near the city of Belém on the delta of the Amazon River. The reserve is almost completely surrounded by streams, which expand and contract with the rising and falling of the Rio Guamá. A small section of the edge of the reserve abuts pasture.

Banana baits were used to estimate relative abundance of the drosophilid species in the area (for detailed methods, see Martins and Fonseca 1988; L. Oliveira 1993). I also identified the resources most frequently used by the drosophilids (Martins and Santos 1988) and evaluated the strategies of native fruit use by these species, focusing on the guild associated with the *Parahancornia amapa* fruit scattered over the ground as a model (Martins 1996).

RESULTS

As for the Manaus site, the *willistoni* subgroup was the dominant taxa among the emergent species from fruits, and many of the same species found in Manaus were also encountered among the emergent fruit species in the Mocambo Reserve.

TABLE 14.8. Relative Abundance (Percentage of Sample) of Drosophilids of the *willistoni* Subgroup and of *D. malerkotliana* in Different Studies in the Mocambo Reserve in Belém Brazil

Period	Type of sampling	<i>D. malerkotliana</i>	Subgroup <i>willistoni</i>	Number of individuals
1948–1952 ¹	bait	0	84.88	28,452
May–June 1987 ²	bait	8.3	39.30	4,946
March 86–Dec. 87 ³	fruits	34.83	59.10	2,179
Jan.–Apr. 1990 ⁴	fruits	19.84	61.10	8,602
Jan.–Apr. 1991 ⁵	fruits	33.53	48.23	5,917
Jan.–Apr. 1992 ⁵	fruits	47.78	44.96	5,500
May 1992–Apr. 1993 ⁵	bait	22.92	71.84	6,017

Notes: ¹Pavan 1959. ²Fonseca and Martins 1988. ³Martins and Santos 1988. ⁴Martins 1996. ⁵L. Oliveira 1993.

Abundance and species richness patterns observed in Manaus were much more accentuated at this site. *D. malerkotliana* showed a huge increase in frequency in this area. In the 1950s, before the introduction of *D. malerkotliana*, twenty-five species of *Drosophila* were collected with banana bait (Pavan 1959) in this area. From 1987 to 1993, the number of taxa observed in the area was forty-two. However, for any given sample, a gradually smaller number of taxa was recorded. In 1986, abundance of *D. malerkotliana* and *willistoni* subgroup was 8.3 percent and 39.3 percent, respectively. In the 1992–93 survey, *D. malerkotliana* represented almost 23 percent of the samples, whereas the *willistoni* subgroup represented 70 percent. The remaining species accounted for a total of 7 percent, while in 1987 they represented about 50 percent in the surveys. Observations from the native fruits show the same pattern (table 14.8).

Between 1992 and 1993, the abundance of *Drosophila* species was estimated in a series of habitats representing a gradient of perturbation, including the Mocambo Reserve and its surroundings (L. Oliveira 1993). Perturbation levels were defined by the size of deforested area, the size of the remaining forested areas, and the proximity to human-occupied areas. Four areas in a 20 km radius were compared: one 23 ha *várzea* (flooded)

forest reserve; the Mocambo Reserve; the Ceasa forest—a 0.7 ha wooded area near a commercial farm; and a pasture adjacent to the Mocambo Reserve. Results showed a clear separation between the species composition of the pasture areas and the forested areas, similar to those observed for the western Amazon. These results also showed a reduction in species richness and a gradual decline in abundance of the *willistoni* subgroup as perturbation increased. *D. malerkotliana*, however, increased in abundance with increasing perturbation. Both taxa, however, were extremely rare or absent in the pasture area. The tendency of *D. malerkotliana* to become dominant in the more perturbed forest areas seems to represent a general trend, as it was also observed in the BDFFP area of central Amazon in the early 1980s, as well as in other forest fragments in the eastern Amazon, including Carajás, a continuous forest area; the margins of the Caruaca River, which are intensively explored for timber extraction; Paragominas, a series of forest fragments within an extensive area of pasture; Belém-Mocambo and Belém-Ceasa, fragments in close proximity with different levels of disturbance (table 14.9).

I can offer three explanations for these trends: fragmentation effects; the intensity of anthropogenic pressure on the fragments;

TABLE 14.9. Relative Abundance (Percentage of Sample), Total Number of Individuals, and Number of Taxa of the *willistoni* Subgroup and of *D. malerkotliana* in Different Localities and Years in the State of Pará

Locality and years	<i>D. malerkotliana</i>	Subgroup <i>willistoni</i>	Total Drosophilidae	Number of taxa
Carajás, 1986	0.46	82.32	1,941	25
Margins of Caruaca River, Marajó Island, Aug. 1988	59.28	31.68	1,250	8
Paragominas, Jan. 1992	68.44	27.40	4,430	9
Belém-Mocambo, 1992-93	22.92	71.84	6,017	—
Belém-Ceasa, 1992-93	74.71	14.88	5,800	—

and the biological characteristics of the species. The first and last factors may best explain the results observed in the BDFFP reserves, because they are experimental fragments with minimal human impacts. All other areas have suffered from fragmentation impacts as well as from intense human pressure through hunting, timber extraction, and being in close proximity to rural or urban areas and to centers of exotic fruit commerce.

The biology of these drosophilid species was studied by Martins and Klaczko (unpublished data) and can be summarized in the following manner: *D. malerkotliana* showed demographic characteristics similar to those of the dominant native species, but it is more aggressive in the use of resources. This species possesses the shortest life cycle, consistently occupies resources at least 24 hours before all other species, concentrates its reproductive efforts in the initial phase of life, and prefers fruit in the early phase of decomposition. These characteristics confer a competitive advantage to this species, an advantage that could in part explain the success of its invasion (Shorrocks and Bingley 1994). This priority effect may result from the strong association of the species with the yeast *Kloerklera apiculata*, which is a pioneer among the yeast in decomposing fruit and is consumed in large quantities by this *Drosophila* species (Moraes,

Martins, and Hagler 1995; Martins and Klaczko, unpublished data). The emergence of adults also starts early from the newest fruits, whereas the development period, longevity, and period of oviposition do not substantially differ from species of the *willistoni* subgroup, and in fact fecundity is slightly inferior (Martins and Klaczko, unpublished data). Because of its relatively recent introduction, lower rates of predation and parasitism may occur on this species, but this remains to be documented.

As temporal heterogeneity in oviposition opportunities decreases and becomes more predictable, rapid life-cycle species will out-compete others and become dominant in more disturbed habitats (Sevenster and van Alphen 1993a, 1993b). For the species investigated in this study, this might occur because of an increase in available resources for some species (in this case fruit that falls and is not consumed because the usual frugivores are scarce in the disturbed area).

This three-factor model, suggested above, of ecological impacts of landscape change on the drosophilid guild seems to explain the observed responses both in the Mocambo Reserve and in the BDFFP areas. Both areas have been severely fragmented; human impact is almost absent at BDFFP, whereas it has been severe at Mocambo. The Mocambo Reserve has been exposed to intense hunting and harvesting of plant prod-

ucts for subsistence or commerce and changes in the intensity and period of stream inundation. This type of interference leads to the biological impoverishment of the forest and can alter its dynamics. One clear result has been the disappearance of a large fraction of the small mammals that consumed the fruit scattered on the ground. As a consequence, there is a greater availability of recently fallen fruit, which probably favored the increase in abundance of the rapid life cycle *Drosophila* species. This scenario may well explain the observed explosive population expansion of *D. malerkotliana*, with a consequent decrease in the total diversity and the loss of dominance of the subgroup *willistoni*, which used to be dominant in the Amazon forest (Dobzhansky and Pavan 1950; Pavan 1959). In the case of the BDFFP reserves, the process is similar, but the expansion of *D. malerkotliana* is much slower, and the reduction of diversity is manifested mainly through the disappearance of rare species and species more sensitive to microclimatic changes associated with fragmentation. Although geographic differences between eastern and central Amazonia may confound some of these results, there is little doubt that habitat fragmentation and anthropogenic impacts significantly alter the structure of drosophilid guilds. Many ecological processes in forest fragments, such as pollination, seed dispersal, and decomposition, will also be seriously affected as a result.

Conclusions

Evaluating the impact of forest fragmentation on faunal communities in tropical systems is difficult and requires the selection of indicator groups. One important recommendation is that the indicator groups be functional and representative within the

ecosystem. The drosophilid guilds have been proposed as good indicators (Parsons 1991; van der Linde 1992; Davis and Jones 1994; Martins 1996), principally owing to the following attributes: they possess short life cycles in such a way that the effects, at the habitat level, can be observed independently of the historical effects; they are sufficiently mobile, so that the absence of one species may be attributed not to its inability to colonize, but rather to the adversity of the habitat for that species; and drosophilids are sufficiently numerous to detect possible differences among habitats (Davis and Jones 1994). Drosophilids are representative of a fauna of small insects associated with decomposing organic material; this guild can represent a reasonable fraction of the total diversity. If drosophilid guilds are good indicators of changes in natural landscapes, then these results point to important effects caused by fragmentation—for example, the importance of edge effects, the facility of exotic species introduction, the decrease in relative abundance of native species and in total species richness.

Conservation Lessons

1. Drosophilid species are sufficiently sensitive to alterations at the habitat level and, therefore, can serve as good indicators of habitat perturbation.
2. Forest fragmentation incurs the loss of drosophilid species. However, the magnitude of this loss is difficult to assess because the most sensitive species are naturally rare in the habitat and their loss can go unobserved.
3. Fragmentation and human impact change abundance patterns of species, favoring opportunistic species with rapid life cycles.

4. Landscape changes facilitate the introduction and expansion of exotic species in the Amazon forest, as is the case for *D. malerkotliana*.
5. The introduction of an exotic species can accelerate the process of species loss in a fragment.
6. The differing rates of expansion of *D. malerkotliana* in central Amazonian forest fragments and in the reserve in Belém suggest that the effects of human impacts are synergistic (or additive) to those of forest fragmentation. Human access to forest fragments can therefore hasten the negative effects of fragmentation.
7. Edge effects are very important in altering faunal composition in fragments, but the size of the reserve will determine the rate of species loss in these habitats.