

Biological Invasions in the Amazonian Tropical Rain Forest: The Case of Drosophilidae (Insecta, Diptera) in Ecuador, South America

Andrea Acurio^{1,4}, Violeta Rafael¹, and Olivier Dangles^{1,2,3}

¹ Department of Biological Sciences, Pontificia Universidad Católica del Ecuador, Apartado 17-01-2184, Quito, Ecuador

² IRD, UR 072, LEGS, UPR 9034, CNRS 91198 Gif-sur Yvette, Cedex, France

³ Université Paris-Sud 11, 91405 Orsay, Cedex, France

ABSTRACT

There have been few reports of invasions in continental rain forests, especially for exotic animals. This study provides original data concerning the potential of exotic drosophilid species to colonize the Amazonian tropical rain forest. To investigate if the structure of drosophilid assemblages differed in response to anthropogenic disturbance, we performed a taxonomic survey at six sites within the Yasuni National Park in Ecuadorian Amazonia along a disturbance gradient from pristine to clearcut artificial forest. A total of 7425 individuals from 34 species were collected of which seven species were exotic. There was significant variation in the assemblage composition along this disturbance gradient; 31 percent of which was explained by the presence of exotic species, particularly at the most disturbed sites, through nonmetric multidimensional scaling and SIMPER analyses. These results confirm the susceptibility of continental rain forests to invasion by exotic species. There is an urgent need to develop and implement monitoring systems, for example, based on drosophilid assemblage surveys, to detect exotic invasions in continental tropical forests.

Abstract in Spanish is available at <http://www.blackwell-synergy.com/loi/btp>

Key words: community composition; disturbance gradient; monitoring systems; nonmetric multidimensional scaling; SIMPER analysis.

LIKE OTHER ECOSYSTEMS, TROPICAL RAIN FORESTS face significant threats from exotic species, especially in areas disturbed by anthropogenic activities (Rejmánek 1996, Phillips 1997). Most examples come from oceanic islands where rain forest communities have been under the pressure by a wide array of plant (Lorence & Sussman 1986, D'Antonio & Vitousek 1992, Green *et al.* 2004, Meyer & Lavergne 2004, Zimmerman *et al.* 2007) and animal invaders (Lehtonen *et al.* 2001, Kraus & Campbell 2002, Borges *et al.* 2006, Wetterer 2007, Peck *et al.* 2008). Reports of biological invasions of continental rain forest are much less common, although such invasions can be equally damaging (Fine 2002).

Early ecologists hypothesized that the high species richness of mainland rain forest made them less susceptible to invasion by exotic plants and animals (Darwin 1859, Elton 1958). However, patterns of invasibility have since proven to be complex and depend on various factors such as spatial scale, biome or species-specific responses to disturbances (Stohlgren *et al.* 1999, Fridley *et al.* 2007). This has been supported by recent studies showing that exotic organisms may also successfully invade continental rain forest (Scariot 1999, Peters 2001, Cordeiro *et al.* 2004, Murphy *et al.* 2006). Published studies, however, have mostly focused on plants, and documented invasions of continental rain forest by exotic animals are scarce (Roubik 1978, Tennant 1994, Hoffmann *et al.* 1999, Martins 2002). In this study, we investigated the structure of fly (Drosophilidae: Diptera) assemblages in Amazonian tropical forest sites differing in their level of anthropogenic disturbance. The Drosophilidae are ubiquitous and can spread and settle largely unnoticed as 'tramp' species associated with human settlements. Al-

though the colonization potential of these flies has been reported (Avondet *et al.* 2003, Ferreira & Tidon 2005), little is known about their ability to invade continental tropical rain forests.

METHODS

STUDY AREA.—The study was performed in the area surrounding the Yasuni Scientific Research Station (YSRS) of the Pontifical Catholic University of Ecuador (0°39'03" S, 76°22'42" W) located in Yasuni National Park (YNP) in the northwestern part of the Ecuadorian Amazon forest, one of the most megadiverse areas of the world. This park encompasses *ca* 1 million ha with extensive areas of primary forest. Disturbances have originated from indigenous groups clearing the forest for agriculture as well as oil companies that have constructed roads for prospecting and exploitation (Valencia *et al.* 2004). This evergreen lowland wet forest has a 15–30 m canopy, with some emergent trees reaching 50 m. The altitude of the YNP is 200–300 m asl. The vegetation belongs to the AF subtype described by Koeppen (Peel *et al.* 2007). Rainfall and temperature are aseasonal with a monthly mean precipitation of 235 mm. No months receive < 100 mm of rain. Temperatures range from 22°C to 32°C and humidity from 56 to 96 percent. Despite this lack of seasonality in climatic variables, plants show three distinct flowering periods: 'active' (high flowering, from mid-July to December), 'passive' (low flowering, from the second half of February to May) and 'intermediate' (from June to the beginning of July and from January to the first half of February) (Aguilar 2004). Such flowering periods are likely to influence drosophilid abundance (Pipkin 1953, Tidon 2006).

In 1994 a road was opened for oil extraction activities in YNP. The road is 140 km long and 20 m wide and end at the Napo River.

Received 15 April 2009; revision accepted 3 December 2009.

⁴Corresponding author; e-mail: andreaacurio@yahoo.com

© 2010 The Author(s)

Journal compilation © 2010 by The Association for Tropical Biology and Conservation

Before road construction, the forest was considered a primary forest, except for some local disturbances originating from indigenous groups who clear the forest for agriculture. As the road is the main source of disturbance in this area, we used the distance of each sampling site to the road as a proxy of disturbance level (Table 1).

SAMPLING DESIGN.—Drosophilid assemblages were studied in six distinct sites in YNP spanning a range of anthropogenic disturbance from pristine to high disturbance (clearcut forest). We used a nested sampling design in which each of the three low-disturbance sites were nested to a site with a different level of disturbance: medium, high and pristine. These three pairs of sites were located along a road for oil extraction activities at 5, 7 and 15 km, respectively.

All sites were ranked according to their category of disturbance, estimated by proximity to the petroleum road and evidence of forestry practices (Table 1). The six sites were divided into four categories of disturbance: (1) pristine: site located 100 km away from the petroleum road, rivers or small villages; (2) low disturbance: sites located few hundred meters away from road for oil extraction activities; (3) medium disturbance: site that was logged and cleared 20 yr ago to build a helicopter landing platform; and (4) high disturbance: cleared site located close to the YSRS and the access petroleum road. To describe relative levels of invasions in each of the sites, we calculated the proportion of exotic species to native species during three flowering periods (Table 2).

Drosophilid collections were made on three occasions (December 2005, March and July 2006) to include active, passive and intermediate flowering periods. For each sampling session, daily collections were made over 15 d. At each site, we sampled six plots separated by a minimum of 30 m. Drosophilid traps, 25 × 5 cm (see more details in Rafael *et al.* 2000), were filled with ca 110 mL of a 3:1 mixture of banana (*Musa paradisiaca*) and Baker's yeast (*Saccharomyces cerevisiae*), and were hung in trees ca 15 cm above-ground level.

Because *Drosophila* communities are known to be vertically segregated (Tidon-Sklorz & Sene 1992), our sampling procedure was unlikely to capture all possible species. Instead our design focused on effectively sampling the understory community where most early establishing exotic invasive species are found (Huebner 2007).

Baits were replaced daily after collection of the trapped insects. Trapped male drosophilids were identified by their terminalia and other morphologic characters (Vilela & Bächli 1990). Single inseminated females collected from the wild were allowed to oviposit and the larvae were reared to adults to analyze the terminalia of offspring males for species determination. For sibling species in the *melanogaster* species group and the *willistoni* species subgroup, we used morphologic characters proposed by Bächli *et al.* (2004), Burla *et al.* (1949), Malogolowkin (1952) and Shorrocks (1972). Based on available literature (Vilela & Bächli 1990, Tidon 2006), species were classified into three categories: new species (previously undescribed), endemic species and exotic species to the Neotropical region.

DATA ANALYSIS.—We quantitatively compared the differences in assemblage structure of drosophilids among the six sites using ranked species abundance (RSA) plots (Magurran 2004). Data from the three trapping periods were pooled to calculate the cumulative relative abundance (logarithmic scale) of each species against its rank in sequence from most to least abundant. RSA data were fitted to the exponential model ($y = 100e^{-ax}$). Differences among sites were evaluated by comparing the value of the exponential factor a ; higher a values indicate greater dominance within the assemblage.

Secondly, we used nonmetric multidimensional scaling (NMDS) analysis to examine the patterns of biological similarity of the drosophilid assemblages among sites. This technique represents samples as points in an ordination space, such that the relative distances between points reflects the relative similarities of the samples with respect to both abundance and composition (van der Gucht *et al.* 2005). Abundance data were $\log(x+1)$ transformed to reduce the importance of extremely high values and the Bray–Curtis method was used as a measure of similarity. Plots of the same level of disturbance were grouped within convex hulls, which are the boundaries of the minimal convex set containing the set of sampling points in the plane. The NMDS goodness of fit was estimated with a stress function (which ranges from 0 to 1) with values close to zero indicating a good fit.

Differences in composition of the fly assemblage among the four levels of disturbance were tested using an analysis of similarities (ANOSIM). ANOSIM generates a statistical parameter R which is indicative of the degree of separation between groups; a score of 1 indicates complete separation, and a score of 0 indicates no

TABLE 1. Disturbance level (pristine, low, medium and high) of the six sites where drosophilid assemblages were sampled. The distance to the road is used as a proxy of disturbance (sites close to the road have higher probability to be colonized by exotic species). The first column shows the three pairs of sites tested (A, B and C).

Site	Disturbance level	Pairs tested	Forest clearcut	Proximity to the road	Dominant tree species (family)
1	Pristine	A	Never	100 km	<i>Memora cladotrichia</i> (Bignoniaceae)
2	Low A		Never	300 m	<i>Matisia oblongifolia</i> (Bombacaceae)
3	Low B		Never	200 m	<i>Matisia oblongifolia</i> (Bombacaceae)
5	Medium	B	1980	350 m	<i>Cecropia sciadophylla</i> (Cecropiaceae)
4	Low C		Never	100 m	<i>Rinorea lindeniana</i> (Fabaceae)
6	High		2007	5 m	Surrounded by <i>Cecropia sciadophylla</i>

TABLE 2. Percentage of invasive species in the drosophilid assemblage at four levels of disturbance. Data from December 2005, and March and July 2006 have been pooled.

Month	Levels of disturbance (%)			
	1 Pristine	2 Low	3 Medium	4 High
March	0	0	0.2	50
July	0	0.1	0.3	45
December	0	0.1	0.1	50

separation (van der Gucht *et al.* 2005). Monte-Carlo randomization of the group labels was used to generate null distributions to test the hypothesis that within-group similarities were higher than would be expected by chance. A one-way ANOSIM was performed with 10,000 permutations using a Bray–Curtis distance measure. Pairwise ANOSIMs between all pairs of groups were provided as a *post-hoc* test. *P*-values were adjusted using the Bonferroni correction. Finally, we determined which species (*e.g.*, native or exotic) were most responsible for differentiating sites with different levels of disturbance by performing a SIMPER analysis on density log-transformed data for all drosophilid taxa. The contribution of exotic species was calculated by summing the contribution of each exotic species over the average dissimilarity of all the exotic species (Clarke 1993). The contribution of each species to the ordination is shown in Table S1. All analyses were performed using PAST (Paleontological statistics, version 1.90; Hammer *et al.* 2001).

RESULTS

A total of 7425 individuals of 34 species belonging to four genera of Drosophilidae (*Drosophila* Fallen 1823, *Scaptodrosophila* Duda

1924, *Neotanygastrella* Duda 1925 and *Zaprionus* Coquillett 1901) were captured (Table S1). There was significant variation in the assemblage structure of drosophilids in each sampled site with an increased abundance of invasive exotic species at sites showing higher disturbance intensity as illustrated by RSA curves (Fig. 1). Species richness in the high-disturbance site was greater than that of the other sites (19 species). In the medium-disturbance site, 13 species were recorded and the pristine site had eight species. The high-disturbance site also had the highest number of exotic species (seven species). In pristine-, low- and medium-disturbance sites, the three neotropical species *Drosophila willistoni*, *Drosophila paulistorum* and *Drosophila sturtevantii* were the most abundant, accounting for 44 percent (site 5) to 97 percent (site 2) of total individuals. The most abundant species in the high-disturbance site was a native species (20%) but the next four most abundant species (*Drosophila melanogaster*, *Drosophila simulans*, *Drosophila malerkotliana* and *Zaprionus indianus*) were exotic. We found an increase in the exponential *a* coefficient from pristine- to medium-disturbed sites when RSA data were fitted to exponential models; pristine $a = 0.51$, low disturbance (A, B and C) $a = 0.55$, 0.58 and 0.59 , respectively, and medium disturbance $a = 1.06$. This indicates that the drosophilid community at the medium-disturbance site was dominated by a few species. Surprisingly, the high-disturbance site had a low *a* value (0.27) suggesting a more uniform distribution of species. There was a similar positive relationship between the raw proportion of exotic species in the drosophilid communities and the levels of disturbance pooled over the three sample periods (Table 2).

There were clear differences in the composition of drosophilid assemblages relative to degree of disturbance in NMDS analysis. The pristine-, low- and medium-disturbance sites were distinctly separated from the high-disturbance site in the two-dimensional space defined by the first two coordinates (Fig. 2). The NMDS showed that assemblage composition in the low- and medium-disturbance sites (1–4) was influenced more by collection month than

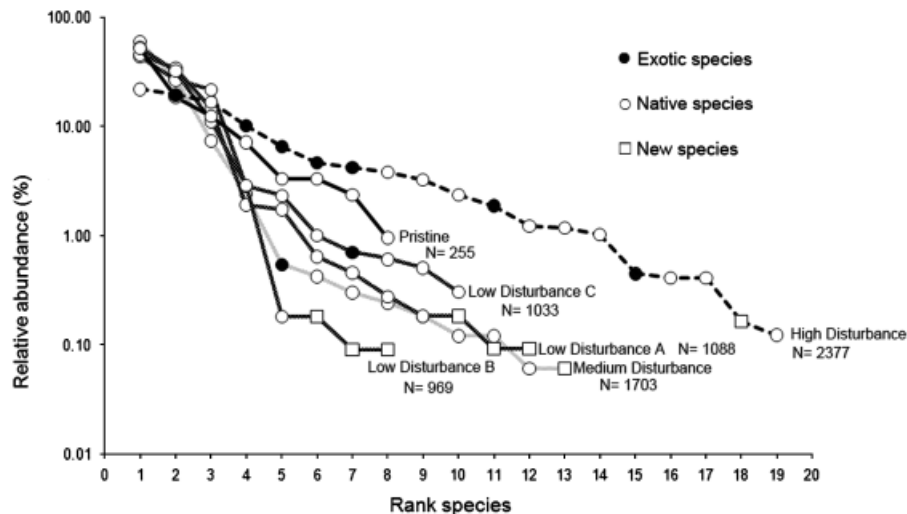


FIGURE 1. Species rank abundance (RSA) distribution plot of the drosophilid assemblages in the six study sites. Data from the different collection periods (December 2005, March and July 2006) have been pooled. All abundance curves have been fit to an exponential model. *N*, total abundance.

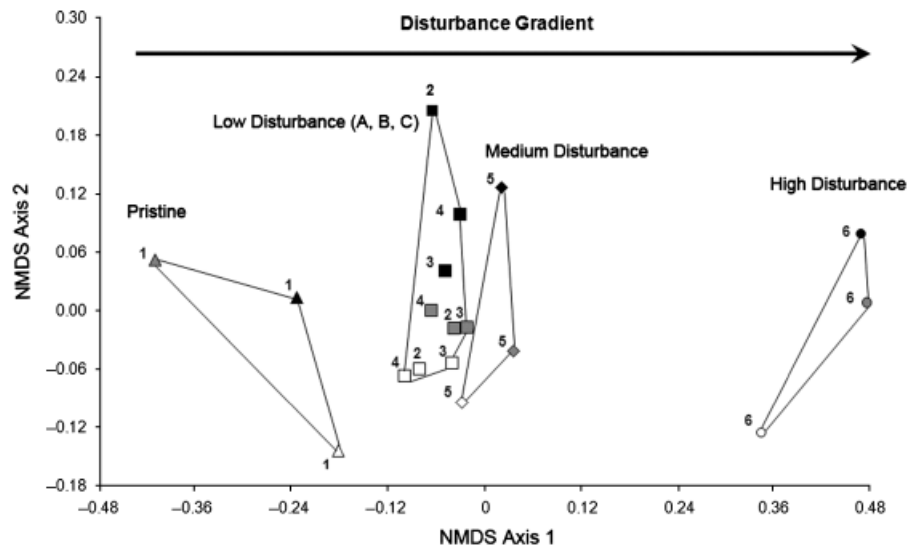


FIGURE 2. Nonmetric multidimensional scaling (NMDS) analysis of drosophilid assemblages in six study sites. Site numbers are given in Table 1. Collection month is denoted by empty symbols (December), gray symbols (March) and black symbols (July). Numbers indicate the disturbance category for each site. NMDS Stress = 0.01. The lines connecting points denote the convex hull (see Methods).

location, indicating there were similarities in drosophilid composition within flowering periods. The ANOSIM global test confirmed the statistical separation in ordination space of the sites presented in the NMDS into four groups relative to the category of disturbance ($R = 0.72$, $P < 0.001$; Fig. 2). In pairwise tests, the differences were significant in two pairs (A and C), each involving a high- and a low-disturbance site (ANOSIM, pairwise test, $P < 0.01$ and $P < 0.02$, respectively), but not in the third pair (B) comprising a low- and a medium-disturbance site ($P = 0.232$). The latter two sites also plotted closely to each other but separated from pristine- and high-disturbance sites in the NMDS graph.

Seven exotic species contribute 31 percent to the ordination. Irrespective of site, the exotic discriminating species were *D. melanogaster*, *D. simulans*, *D. ananassae*, *D. malerkotliana*, *Z. indianus* and *Scaptodrosophila latifasciiformis*. These species were recorded only in the high-disturbance site with exception of *D. ananassae* that was also recorded in the medium-disturbance site.

DISCUSSION

This study is the first to document a change in the structure of drosophilid assemblages along a disturbance gradient in the Amazon forest. There are very few reports of invasions by exotic species in continental tropical rain forest, suggesting that species-rich rain forests, particularly continental ones, are relatively resistant to invasions (Laurance & Bierregaard 1997, Laurance *et al.* 2002, Sax *et al.* 2005). However, we found that tropical rain forests subjected to severe anthropogenic disturbance can be susceptible to invasion by exotic drosophilid species. Thereby supporting the view of Davis (2005) that even environments with rich regional species pools like tropical rain forests are susceptible to exotic species invasions.

There is little information about when these exotic species, native to oriental and afrotropical regions (David & Tsacas 1981), arrived in YNP. They were probably introduced accidentally, mostly by the first settlements related to petroleum exploration in the 1980s. After these introductions, the establishment of the YSRS in 1994 and the lack of quarantine controls have likely created an environment favorable to colonization by exotic species such as *D. melanogaster*. This latter species was the most abundant in our survey, and is the most invasive species of *Drosophila* globally, being present on all vegetated continents (Huey *et al.* 2005). Another exotic species found in the most disturbed site was *Z. indianus*. This species prefers open and disturbed habitats (Tidon *et al.* 2003), demonstrating that anthropogenic disturbance can facilitate invasions of exotic species into species-rich communities of tropical rain forests.

From four categories of disturbance sampled in YNP, the pristine site recorded the lowest number of individuals collected. This could be a result of sampling bias in our collection. Our results (34 species from 7425 individuals), however, are within the range of fly abundance and species richness collected in other studies within the region (Tidon-Sklorz & Sene 1995, Torres & Madi-Ravazzi 2006).

The similarity between the low disturbance A and medium-disturbance site in the RSA plot (Fig. 1) could be explained by the geographic proximity of these two localities. This is consistent with the well-documented distance-decay of similarity relationship among communities (Morlon *et al.* 2008). Geographically, these two sites are in the closest proximity to each other and are located at kilometer 5 on the road. This close proximity may have resulted in an artificial similarity in the drosophilid fauna.

The trends observed in the RSA analysis indicate that exotics species responded positively to disturbances by increasing their abundance in disturbed sites. The exotics were the dominant species in the high-disturbance site thereby decreasing the proportion of the fauna contributed by native species. The establishment of exotic

species in disturbed sites may promote changes in the structure and dynamics of resident assemblages (Fig. 1).

Disturbance in Amazonian rain forest fragments has been shown to promote invasion by exotic species, as documented for plants (Scariot 1999), insects (Klein 1989, Brown & Hutchings 1997, Dick 2001, Martins 2002), frogs (Tocher *et al.* 1997) and bats (Kalko 1998). Aside from disturbance, we think that other factors that could have aided in the successful establishment of exotic drosophilid species including ability to tolerate change in microclimatic conditions, efficient life history strategies (Parsons & Stanley 1981) and repetitive introductions of new individuals of exotic species via decaying vegetables and fruit used as food at the YSRS. We cannot conclude definitively if the absence of invasive flies at the pristine site was related to a resistance of this site to invasions or if it was simply too far from a source of invasion, impeding colonization by exotics.

Our results are in general agreement with Martins (2002), who reported that forest fragmentation modified the species composition and relative abundance patterns of drosophilid guilds. However, we found a rather equitable distribution of species at the high-disturbance site, probably due to the loss of rare species. This contrasts with the general view that highly disturbed areas exhibit a greater degree of dominance of a few species (Tilman & Lehman 2001, Sanchez-Moyano *et al.* 2002, Seabloom *et al.* 2003). This may be a compensatory response of the drosophilid assemblage due to both the arrival of exotic species and the absence of 15 native species in the high-disturbance site. This suggests an ongoing, continual process of colonization by exotics. Although the competitive relationships between exotics and native species are unknown, similar patterns of reduction in abundance of native species concurrent with the co-occurrence of exotic species have been reported for drosophilid assemblages (Parsons 1983, Huey *et al.* 2005, Tidon 2006).

CONCLUSION

This study provides evidence that, in the presence of disturbance, even species-rich tropical rain forests are susceptible to exotic species invasions. Resource exploitation by humans in this habitat is increasing and causing loss of species diversity. Detection of the early establishment of exotics species using long-term monitoring is essential to understand invasion patterns and impacts on associated native species. Effective evaluation and management of the impacts of anthropogenic disturbance in tropical rain forests requires appropriate assessment and monitoring tools to detect and monitor exotic invasive species. Drosophilids may represent useful indicators as they are short-lived, mobile, abundant organisms and inexpensive to collect (Powell 1997, van der Linde 1997). However, there are still few studies using this group to monitor environmental disturbance in tropical rain forests (Parsons 1991, Davis & Jones 1993, van der Linde & Sevenster 2002, Mata *et al.* 2008). Our results suggest that the response of drosophilid assemblages to forest disturbance could be a fruitful avenue to develop as a useful indicator of invasion risk by exotics in continental rain forests.

ACKNOWLEDGMENTS

Our thanks to T. Markow, K. Franklin, C. Keil and two anonymous reviewers for critical feedback and suggestions that greatly improved an earlier version of this manuscript. We are also grateful to L. Arcos Terán, to Pontificia Universidad Católica del Ecuador (PUCE) for its financial support and field materials donated by Idea Wild Organization.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *List of the Drosophilid species found in the six study sites during the three sampling periods (December 2005, March and July 2006) in the Yasuni National Park.*

Please note: Wiley-Blackwell is not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.

LITERATURE CITED

- AGUILAR, Z. 2004. Flowering on community level in a terra firme forest in Ecuadorian Amazon. *Lyonia* 7: 115–123.
- AVONDET, J. L., R. B. BLAIR, D. J. BERG, AND M. A. EBBERT. 2003. *Drosophila* (Diptera: Drosophilidae) response to changes in ecological parameters across an urban gradient. *Environ. Entomol.* 32: 347–358.
- BÄCHLI, G., C. R. VILELA, S. ANDERSSON ESCHER, AND A. SAURA. 2004. The Drosophilidae (Diptera) of Fennoscandia and Denmark. *Fauna Entomologica Scandinavica*. Brill, Leiden, The Netherlands.
- BORGES, P. A. V., J. M. LOBO, A. B. DE AZEVEDO, C. S. DE GASPAR, C. MELO, AND L. V. NUÑES. 2006. Invasibility and species richness of island endemic arthropods: A general model of endemic vs. exotic species. *J. Biogeogr.* 33: 169–187.
- BROWN, K. S. JR., AND R. W. HUTCHINGS. 1997. Disturbance, fragmentation, and the dynamics of diversity in Amazonian forest butterflies. In W. F. Laurence and R. O. Bierregaard Jr. (Eds.). *Tropical forest remnants: Ecology, management, and conservation of fragmented communities*, pp. 91–110. University of Chicago Press, Chicago, Illinois.
- BURLA, H., A. B. DA CUNHA, A. R. CORDEIRO, T. H. DOBZHANSKY, C. MALOGOLOWKIN, AND C. PAVAN. 1949. The *willistoni* group of sibling species of *Drosophila*. *Evolution* 3: 300–314.
- CLARKE, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. *Aust. J. Ecol.* 18: 117–143.
- CORDEIRO, N. J., D. PATRICK, B. MUNISI, AND V. GUPTA. 2004. Role of dispersal in the invasion of an exotic tree in an East African submontane forest. *J. Trop. Ecol.* 20: 449–457.
- D'ANTONIO, C. M., AND P. M. VITOUSEK. 1992. Biological invasions by exotic grasses, the grass/fire cycle and global change. *Annu. Rev. Ecol. Syst.* 23: 63–87.
- DARWIN, C. 1859. *The origin of species*. Reprinted by Penguin Books, London, UK.
- DAVID, J. R., AND L. TSACAS. 1981. Cosmopolitan, subcosmopolitan and wide-spread species: Different strategies within the drosophilid family (Diptera). *C. R. Soc. Biogeog.* 57: 11–26.
- DAVIS, M. A. 2005. Invasibility: The local mechanism driving community assembly and species diversity. *Ecography* 28: 696–704.

- DAVIS, A. J., AND K. E. JONES. 1993. *Drosophila* as indicators of habitat type and habitat disturbance in tropical forest, Central Borneo. *Dros. Inf. Serv.* 75: 150–151.
- DICK, C. 2001. Habitat change, African honeybees, and fecundity in the Amazonian tree, *Dinizia excelsa* (Fabaceae). In O. Bierregaard Jr., C. Gascon, and T. E. Lovejoy (Eds.). *Lessons from Amazonia: Ecology and conservation of a fragmented forest*, pp. 146–157. Yale University Press, New Haven, Connecticut.
- ELTON, C. S. 1958. *The ecology of invasions by animals and plants*. Methuen, London, UK.
- FERREIRA, L. B., AND R. TIDON. 2005. Colonizing potential of Drosophilidae (Insecta, Diptera) in environments with different grades of urbanization. *Biodiversity Conserv.* 14: 1809–1821.
- FINE, P. V. A. 2002. The invasibility of tropical forests by exotic plants. *J. Trop. Ecol.* 18: 687–705.
- FRIDLEY, J. D., J. J. STACHOWICZ, S. NAEEM, E. W. SAX, M. D. SEABLOOM, T. J. STOHLGREN, D. TILMAN, AND B. VON HOLLE. 2007. The invasion paradox: Reconciling pattern and process in species invasions. *Ecology* 88: 3–17.
- GREEN, P. T., P. S. LAKE, AND D. J. O'DOWD. 2004. Resistance of island rain forest to invasion by alien plants: Influence of microhabitat and herbivory on seedling performance. *Biol. Invasions* 6: 1–9.
- HAMMER, Ø., D. A. T. HARPER, AND P. D. RYAN. 2001. PAST: Paleontological statistics software package for education and data analysis. *Palaeontol. Electronica* 4: 4–9.
- HOFFMANN, B. D., A. N. ANDERSEN, AND G. J. E. HILL. 1999. Impact of an introduced ant on native rain forest invertebrates: *Pheidole megacephala* in monsoonal Australia. *Oecologia* 120: 595–604.
- HUEBNER, C. D. 2007. Detection and monitoring of invasive exotic plants: A comparison of four sampling methods. *Northeast Nat.* 14: 183–206.
- HUEY, R. B., G. W. GILCHRIST, AND A. P. HENDRY. 2005. Using invasive species to study evolution. In D. F. Sax, S. D. Gaines, and J. J. Stachowicz (Eds.). *Species invasions: Insights to ecology, evolution and biogeography*, pp. 139–164. Sinauer Associates, Sunderland, Massachusetts.
- KALKO, E. K. V. 1998. Organisation and diversity of tropical bat communities through space and time. *Zoology* 101: 281–297.
- KLEIN, B. C. 1989. Effects of forest fragmentation on dung and carrion beetle communities in central Amazonia. *Ecology* 70: 1715–1725.
- KRAUS, F., AND E. W. CAMPBELL. 2002. Human-mediated escalation of a formerly eradicable problem: The invasion of Caribbean frogs in the Hawaiian Islands. *Biol. Invasions* 4: 327–332.
- LAURANCE, W. F., AND R. O. JR. BIERREGAARD. 1997. *Tropical forest remnants: Ecology, management, and conservation of fragmented communities*. University of Chicago Press, Chicago, Illinois.
- LAURANCE, W. F., T. E. LOVEJOY, H. L. VASCONSELOS, E. M. BRUNA, R. K. DIDHAM, P. C. STOFFER, C. GASCON, R. O. BIERREGAARD, S. G. LAURANCE, AND E. SAMPAIO. 2002. Ecosystem decay of Amazonian forest fragments: A 22-year investigation. *Conserv. Biol.* 16: 605–618.
- LEHTONEN, J. T., O. MUSTONEN, H. RAMIARINJANAHARY, J. NIEMELÄ, AND H. RITA. 2001. Habitat use by endemic and introduced rodents along a gradient of forest disturbance in Madagascar. *Biodiversity Conserv.* 10: 1185–1202.
- LORENCE, D. H., AND R. W. SUSSMAN. 1986. Exotic species invasion into Mauritius wet forest remnants. *J. Trop. Ecol.* 2: 147–162.
- MAGURRAN, A. E. 2004. *Measuring biological diversity*. Blackwell Publishing, Oxford, UK.
- MALOGOLOWKIN, C. 1952. Sobre a genitalia dos Drosophilidae (Diptera). III. Grupo *willistoni* do gênero *Drosophila*. *Revta. Bras. Biol.* 12: 79–96.
- MARTINS, M. B. 2002. Drosophilid fruit-fly guilds in forest fragments. In R. Bierregaard, C. Gascon, and T. E. Lovejoy (Eds.). *Lessons from Amazonia: The ecology and conservation of a fragmented forest*, pp. 175–186. Yale University Press, New Haven, Connecticut.
- MATA, R. A., M. MCGEOCH, AND R. TIDON. 2008. Drosophilid assemblages as a bioindicator system of human disturbance in the Brazilian savanna. *Biodiversity Conserv.* 17: 2899–2916.
- MEYER, J. Y., AND C. LAVERGNE. 2004. Beautés fatales: Acanthaceae species as invasive alien plants on tropical Indo-Pacific Islands. *Diversity Distrib.* 10: 333–347.
- MORLON, H., G. CHUYONG, R. CONDIT, S. HUBBELL, D. KENFACK, D. THOMAS, R. VALENCIA, AND J. L. GREEN. 2008. A general framework for the distance–decay of similarity in ecological communities. *Ecol. Lett.* 11: 904–917.
- MURPHY, H. T., D. A. WESTCOTT, AND D. J. METCALFE. 2006. Functional diversity of native and invasive plant species in tropical rain forests. In C. Preston, J. H. Watts, and N. D. Crossman (Eds.). *Proceedings of the 15th Australian Weeds Conference*, pp. 199–202. Weed Management Society, Adelaide, Australia.
- PARSONS, P. A. 1983. Ecobehavioral genetics: Habitats and colonist. *Annu. Rev. Ecol. Syst.* 14: 35–55.
- PARSONS, P. A. 1991. Biodiversity conservation under global climatic change, the insect *Drosophila* as a biological indicator. *Global Ecol. Biogeogr.* 1: 77–83.
- PARSONS, P. A., AND S. M. STANLEY. 1981. Domesticated and widespread species. In M. Ashburner, H. L. Carson, and J. N. Thompson (Eds.). *The genetics and biology of Drosophila*, pp. 349–393. Academic Press, Cambridge, UK.
- PECK, R. W., P. BANKO, M. SCHWARZFELD, M. EUAPARADORN, AND W. K. BRINCK. 2008. Alien dominance of the parasitoid wasp community along an elevation gradient on Hawaii Island. *Biol. Invasions* 10: 1441–1455.
- PEEL, M. C., B. L. FINLAYSON, AND T. A. MCMAHON. 2007. Updated world map of the Köppen–Geiger climate classification. *Hydrol. Earth Syst. Sci.* 1: 1633–1644.
- PETERS, H. A. 2001. *Clidemia hirta* invasion at the Pasoh Forest Reserve: An unexpected plant invasion in an undisturbed tropical forest. *Biotropica* 33: 60–68.
- PHILLIPS, O. L. 1997. The changing ecology of tropical forests. *Biodiversity Conserv.* 6: 291–311.
- PIPKIN, S. B. 1953. Fluctuations in *Drosophila* populations in a tropical area. *Am. Nat.* 87: 317–322.
- POWELL, J. R. 1997. *Progress and prospects in evolutionary biology. The Drosophila model*. Oxford University Press, Oxford, UK.
- RAFAEL, V., G. ARCOS, AND L. ARCOS. 2000. Ecología y distribución del género *Drosophila* en Guayllabamba y el Quinche, provincia de Pichincha-Ecuador. *Rev. Pont. Univ. Cat.* 65: 130–155.
- REJMÁNEK, M. 1996. Species richness and resistance to invasions. In G. Orians, R. Dirzo, and J. H. Cushman (Eds.). *Biodiversity and ecosystem processes in tropical forests*, pp. 153–172. Springer-Verlag, New York, New York.
- ROUBIK, D. W. 1978. Competitive interactions between neotropical pollinators and africanized honey bees. *Science* 201: 1030–1032.
- SANCHEZ-MOYANO, J. E., E. M. GARCIA-ADIEGO, F. ESTACIO, AND J. C. GARCIA-GOMEZ. 2002. Effect of environmental factors on the spatial variation epifaunal polychaetes of the alga *Halopteris scoparia* in Algeciras Bay (Strait of Gibraltar). *Hydrobiologia* 470: 133–148.
- SAX, D. F., J. J. STACHOWICZ, AND S. D. GAINES. 2005. *Species invasions: Insights into ecology, evolution and biogeography*. Sinauer Associates, Sunderland, Massachusetts.
- SCARIOT, A. 1999. Forest fragmentation effects on palm diversity in central Amazonia. *J. Ecol.* 87: 66–76.
- SEABLOOM, E. W., S. W. HARPOLE, O. J. REICHMAN, AND D. TILMAN. 2003. Invasion, competitive dominance, and resource use by exotic and native California grassland species. *Proc. Natl. Acad. Sci.* 100: 13384–13389.
- SHORROCKS, B. 1972. *Invertebrate types: Drosophila*. Ginn & Company, London, UK.
- STOHLGREN, T. J., D. BINKLEY, AND G. W. CHON. 1999. Exotic plant species invade hot spots of native plant diversity. *Ecol. Monogr.* 69: 25–46.
- TENNANT, L. E. 1994. The ecology of *Wasmannia auropunctata* in primary tropical rain forest in Costa Rica and Panama. In D. F. Williams (Ed.). *Exotic ants: Biology, impact, and control of introduced species*, pp. 80–90. Westview Press, Boulder, Colorado.

- TIDON, R. 2006. Relationships between Drosophilids (Diptera, Drosophilidae) and the environment in two contrasting tropical vegetations. *Biol. J. Linn. Soc.* 87: 233–247.
- TIDON, R., D. F. LEITE, AND B. F. D. LEO. 2003. Impact of the colonisation of *Zaprionus* (Diptera, Drosophilidae) in different ecosystems of the neotropical region two years after the invasion. *Biol. Conserv.* 112: 299–305.
- TIDON-SKLORZ, R., AND F. M. SENE. 1992. Vertical and temporal distribution of *Drosophila* (Diptera, Drosophilidae) species in wooded area in the state of São Paulo, Brazil. *Rev. Bras. Biol.* 52: 311–317.
- TIDON-SKLORZ, R., AND F. M. SENE. 1995. Fauna of *Drosophila* (Diptera, Drosophilidae) in the northern area of the 'Cadeia do Espinhaco', States of Minas Gerais and Bahia, Brazil; biogeographical and ecological aspects. *Iheringia, Sér. Zool.* 78: 85–94.
- TILMAN, D., AND C. LEHMAN. 2001. Human-caused environmental change: Impacts on plant diversity and evolution. *Proc. Natl. Acad. Sci.* 98: 5433–5440.
- TOCHER, M., C. GASCON, AND B. L. ZIMMERMAN. 1997. Fragmentation effects on a central Amazonian frog community: A ten-year study. *In* W. F. Laurance and R. O. Bierregaard Jr. (Eds.). *Tropical forest remnants: Ecology, management, and conservation of fragmented communities*, pp. 124–137. University of Chicago Press, Chicago, Illinois.
- TORRES, F. R., AND L. MADI-RAVAZZI. 2006. Seasonal variation in natural populations of *Drosophila* spp. (Diptera) in two woodlands in the State of São Paulo, Brazil. *Iheringia, Sér. Zool.* 96: 437–444.
- VALENCIA, R., R. B. FOSTER, G. VILLA, R. CONDIT, J. C. SVENNING, C. HERMANDEZ, K. ROMOLEROUX, E. LOSOS, E. MARGARD, AND H. BALSLEV. 2004. Tree species distributions and local habitat variation in the Amazon: Large forest plot in eastern Ecuador. *J. Ecol.* 92: 214–229.
- VAN DER GUCHT, K., T. VANDEKERCKHOVE, N. VLOEMANS, S. COUSIN, K. MUYLAERT, K. SABBE, M. GILLIS, S. DECLERK, L. DE MEESTER, AND W. VYVERMAN. 2005. Characterization of bacterial communities in four freshwater lakes differing in nutrient load and food web structure. *Microbiol. Ecol.* 53: 205–220.
- VAN DER LINDE, K. 1997. Exploring the use of the *Drosophila* genus as biodiversity indicator. *In* R. S. Guzman and W. T. de Groot (Eds.). *Research for the Sierra Madre Forest*. CVPED, Cabagan, Philippines.
- VAN DER LINDE, K., AND J. G. SEVENSTER. 2002. *Drosophila* diversity over a disturbance gradient. *Proc. Sec. Exp. Appl. Ent. Soc.* 13: 51–56.
- VILELA, C. R., AND G. BÄCHLI. 1990. Taxonomic studies on neotropical species of seven genera of Drosophilidae (Diptera). *Mitt. Schweiz. Entomol. Ges.* 63: 1–332.
- WETTERER, J. K. 2007. Biology and impacts of Pacific Island invasive species. The African big-headed ant, *Pheidole megacephala* (Hymenoptera: Formicidae). *Pac. Sci.* 61: 437–456.
- ZIMMERMAN, N., R. F. HUGHES, S. CORDELL, P. HART, H. KALEI CHANG, D. PEREZ, R. KAIPALOHAAKALA LIKE, AND R. OSTERTAG. 2007. Patterns of primary succession on native and introduced plants in lowland wet forest in eastern Hawaii. *Biotropica* 40: 277–284.