28. D. T. Aubele, D. Wang, K. W. Post, S. Hahn, *Mol. Cell Biol.* **17**, 4842 (1997).
29. F. Wincott *et al.*, *Nucleic Acids Res.* **23**, 2677 (1995).
30. C. W. van Gelder *et al.*, *EMBO J.* **12**, 5191 (1993).

Effectiveness of Parks in Protecting Tropical Biodiversity

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We assessed the impacts of anthropogenic threats on 93 protected areas in 22 tropical countries to test the hypothesis that parks are an effective means to protect tropical biodiversity. We found that the majority of parks are successful at stopping land clearing, and to a lesser degree effective at mitigating logging, hunting, fire, and grazing. Park effectiveness correlates with basic management activities such as enforcement, boundary demarcation, and direct compensation to local communities, suggesting that even modest increases in funding would directly increase the ability of parks to protect tropical biodiversity.

Much of tropical biodiversity is unlikely to survive without effective protection (*1–3*). Conservationists have tried strategies ranging from establishing and maintaining parks and other strictly protected areas (henceforth "parks"), to promoting sustainable forest management and other integrated conservation and development projects. How well do parks measure up among these alternatives (*4*, *5*)? Critics claim that in the context of growing human pressures and development needs, parks cannot protect the biological resources within their borders (*6*), and there is a widespread sense that parks are simply not working. The accuracy of these claims is of critical importance to policy and funding decisions. If parks are failing despite best efforts, then better options should be sought. If, on the other hand, parks are performing relatively well in a context of serious threats and limited resources, or are simply performing better than the alternatives, their level of support should be increased.

Past studies of park effectiveness have focused on improving park management (*7*), improving protected area system design (*8*), and increasing local and national political support (*9*, *10*), but none has provided a quantitative assessment of effectiveness using a large sample of parks around the world (*11*, *12*).

We used a questionnaire to collect data on land-use pressure (land clearing, logging, hunting, grazing, and fire), local conditions (e.g., presence of human communities in parks and degree of access), and management activities (e.g., number of guards and level of community involvement in management) (*13*). To confine our sample to parks at risk of failure, we selected regions subject to significant human land-use pressure (*14*, *15*). From these regions, we selected only parks that have been established for at least 5 years to allow sufficient time for management activities to be reflected in park performance. We also restricted the sample to protected areas of >5000 ha in which only nonconsumptive uses were permitted (*16*, *17*). Directors of conservation organizations and protected area agencies helped identify a representative group for this study from the 535 parks that met these criteria (*18*, *19*) [additional information is available on *Science* Online (*20*)]. The sample comprised 93 parks (*21*) in 22 countries (*22*), covering 17% (18 million ha) of the parks that met our criteria (*23*).
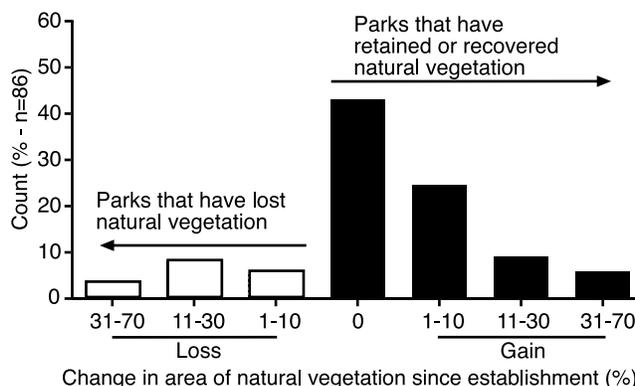
The parks in the sample varied greatly in size, primary ecosystem type, budget, management strategy, and type and degree of threats. Seventy percent had people living inside their boundaries, and 54% had residents who contested the ownership of some percentage of the

park area. Two-thirds of the parks were accessible by at least one major road or river (*24*). Median annual funding was 1.18 USD ha^{-1}, significantly less than the amount often recommended for effective management (*25*). Finally, respondents judged that many park staff were lacking in critical training and equipment.

We assessed the effectiveness of these parks from three perspectives: land clearing within the boundaries of parks since establishment, current condition of parks compared with the condition of their surroundings, and factors correlated with effective park protection.

We assessed the effectiveness of parks at preventing land clearing by comparing the current extent of clearing with clearing at the time of park establishment (Fig. 1). We found that 43% of the parks have had no net clearing since establishment. In an additional 40% of parks, land formerly under cultivation was incorporated into park boundaries, and had been able to recover, leading to an actual increase in vegetative cover. Eighty-three percent of parks were therefore fully holding their borders against agricultural encroachment. Only 17% of the parks experienced net clearing since establishment. This is a substantial achievement, given that the median age of the parks in our sample is 23 years.

To test effectiveness over a wider range of threats, we compared anthropogenic impacts in the 10-km belt surrounding parks with the level of impacts within park boundaries for five different threats (Fig. 2). This comparison shows that the parks in our sample are under great pressure from clearing, hunting, and logging, and to a lesser extent, fire and grazing. A comparison of the conditions inside the parks with the surrounding area shows that for all five threats, parks were in significantly better condition than their surrounding areas (Mann-Whitney U-test, medians significantly different at

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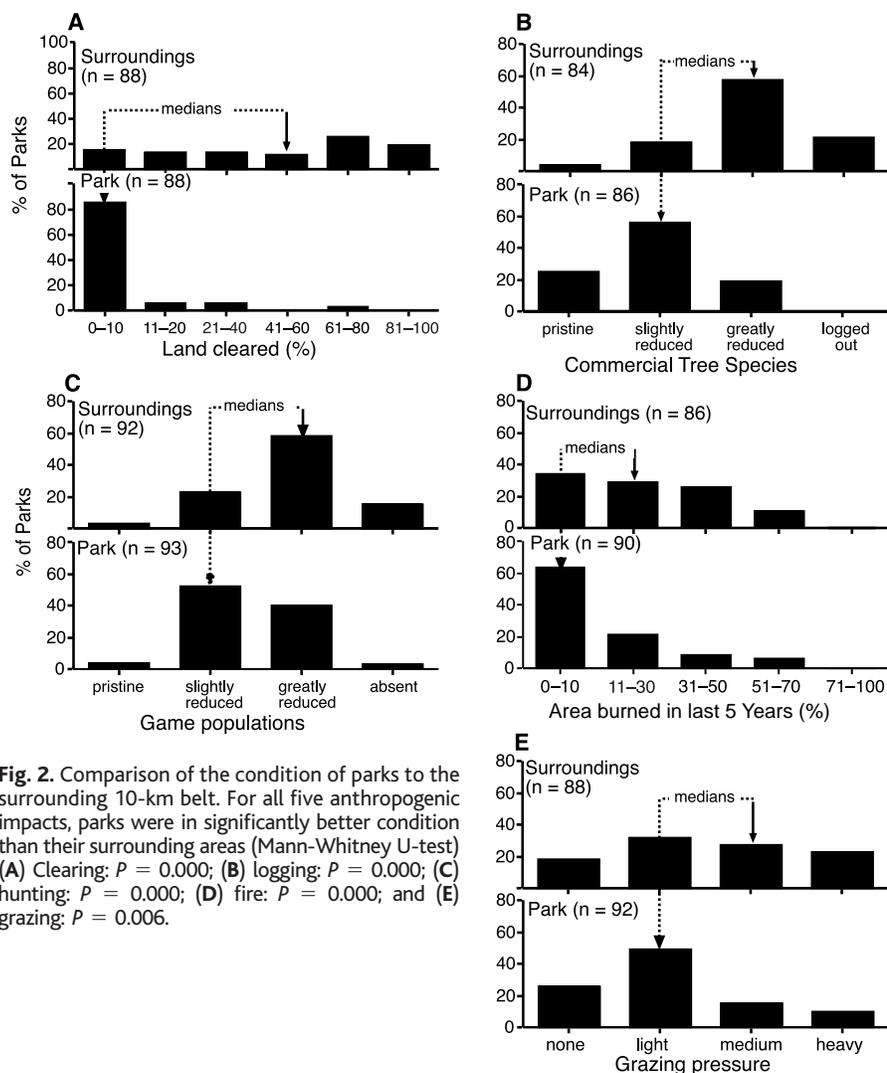
Fig. 1. Change in the area of natural vegetation since establishment for 86 tropical parks. The majority of parks have either experienced no net clearing or have actually increased natural vegetative cover. Median park age is 23 years.

Fig. 2. Comparison of the condition of parks to the surrounding 10-km belt. For all five anthropogenic impacts, parks were in significantly better condition than their surrounding areas (Mann-Whitney U-test) (**A**) Clearing: $P = 0.000$; (**B**) logging: $P = 0.000$; (**C**) hunting: $P = 0.000$; (**D**) fire: $P = 0.000$; and (**E**) grazing: $P = 0.006$.

Table 1. Park effectiveness against anthropogenic threats. Shown for each threat is the percentage of parks surveyed that are either in better condition ("functioning") than the surrounding 10-km belt or in equal or worse condition ("not functioning"). Also shown is the percentage of parks with no presence of each threat in the surrounding area ("untested parks").

Type of impact	n	Function-ing (% of tested parks)	Not function-ing (% of tested parks)	Untested parks (% of total)
Clearing	85	97.2	2.8	16.5
Logging	84	85.2	14.8	3.6
Fire	87	81.0	19.0	27.6
Hunting	91	62.2	37.8	1.1
Grazing	88	59.7	40.3	12.5

was more than eight times higher than in the 15 least effective parks (3 guards per 100 km^2 in the 15 most effective parks compared with 0.4 guards per 100 km^2 in the least effective). However, enforcement capacity (a composite variable of training, equipment, and salary) was not found to correlate with effectiveness, suggesting that these characteristics are less important than the presence of guards.

Effectiveness was also significantly correlated with the level of deterrents to illegal activities in the park. Deterrents were measured as the product of the probability of apprehending violators when guards detected a violation (either in progress or after-the-fact) by the probability of the violator receiving a significant sanction if apprehended. Deterrents against clearing and logging correlated with park effectiveness, whereas deterrents against hunting did not.

The degree of border demarcation and the existence of direct compensation programs to local communities (Table 2) were also found to correlate significantly with management effectiveness.

Other factors potentially related to park success did not correlate significantly with effectiveness, including number of people living in the park, accessibility, local support, percentage of the park area contested, budget, number of staff working on economic development or education, and local involvement of communities in park management.

The findings of this study suggest three basic conclusions. First, the claim that the majority of parks in tropical countries are "paper parks"—i.e., parks in name only—is not substantiated. Tropical parks have been surprisingly effective at protecting the ecosystems and species within their borders in the context of chronic underfunding and significant land-use pressure. They have been especially effective in preventing land clearing, arguably the most serious threat to biodiversity. Second, despite their successes, there is a clear need to increase support for parks to improve effectiveness against all threats, perhaps especially against hunting. Finally, these

$P < 0.006$ for all five impacts). Because we used relatively few response categories to represent the entire range of outcomes (e.g., four categories were used to classify the abundance of game animals, ranging from pristine levels of abundance to absent), any differences found between the parks and their surroundings are great.

Parks are more effective at mitigating some impacts than others. Parks are in far better condition than their surroundings with respect to land clearing, with the majority of parks being intact or only slightly cleared. Parks were more heavily impacted by logging and hunting, but these impacts were still reduced considerably compared with their surroundings. Finally, although parks were still in significantly better condition than their surroundings with respect to damage from fire and grazing, the differences were less pronounced.

The previous comparison treats the sample of parks as a group. We also compared individual parks with their own surroundings to determine what percentage of individual parks are functioning (Table 1). Virtually all parks in our

sample are under pressure from clearing, grazing, fire, hunting, and logging, and the majority of parks are effective at least to some degree in mitigating these threats. More than 80% of the individual parks were in better condition than their surroundings for clearing, logging, and fire, including 97% for clearing. About 60% of the parks were in better condition than land outside their borders with respect to hunting and grazing.

We also investigated which management activities and local conditions correlated with effectiveness, which we defined as the difference between illegal impacts inside the park and the surrounding 10-km belt. Because units and scales differed among the threats, we rescaled each threat to a value ranging from 1 to 4, and then averaged the effectiveness among the five threats. Average effectiveness was then tested for correlation with management activities and local conditions by means of a nonparametric test (26).

Park effectiveness correlated most strongly with density of guards (Table 2). The median density of guards in the 15 most effective parks

Table 2. Spearman rank correlations of variables with park effectiveness. Variables that are significantly correlated with effectiveness are shown in bold in the upper portion of the table. Where sample size and type of data permitted, the ratio of the 15 most effective to 15 least effective parks is included to illustrate the difference in magnitude.

Variable	Correlation with park effectiveness			Median	Minimum	Maximum	Ratio of 15 most to 15 least effective
	r_s	n	p				
Guards (no. per 100 km²)	**0.270**	**85**	**0.008**	**1.7**	**0**	**200**	**8.1**
Logging deterrent (see text)	**0.242**	**54**	**0.038**	**0.094**	**0.016**	**0.563**	**3.0**
Clearing deterrent (see text)	**0.267**	**45**	**0.038**	**0.016**	**0.016**	**0.563**	**2.0**
Demarcation of park border in areas under pressure (%)	**0.208**	**82**	**0.038**	**5%**	**5%**	**95%**	**1.2**
Compensation to locals for damage (yes or no)	**0.203**	**78**	**0.038**	**No**	**No**	**Yes**	**—**
Size of park (hectares)	0.015	86	—	79,073	5,300	1,532,806	—
Population density in park (no. per 100 km²)	0.145	61	—	8.9	0	5718	—
Distance of park to major access point (km)	0.050	86	—	0–3 km	0–3 km	>15 km	—
Local support for park (from strong support to strong opposition)	−0.037	83	—	Some support	Strong opposition	Strong support	—
Local participation in management (none, some, high)	0.026	84	—	Some	None	High	—
Percentage of park area contested	−0.149	79	—	10%	None	90%	—
Budget (USD per hectare)	−0.014	46	—	$1.34	$0.00	$49.98	—
Change in budget over last 5 years (much lower to much greater)	−0.001	73	—	Stable	Currently much lower	Currently much greater	—
Economic and education staff (no. per 100 km²)	0.084	59	—	0. 6	0	14.8	—
Composite variable of enforcement capacity (scale of 1 –to 13)	−0.056	79	—	8	4	11	—
Hunting deterrent (see text)	0.191	66	—	0.047	0.016	0.563	—

findings suggest that parks should remain a central component of conservation strategies. Both creating new parks and addressing the tractable problem of making existing parks perform better will make a significant contribution to long-term biodiversity conservation in the tropics.

References and Notes
1. N. Myers, R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, J. Kent, *Nature* **403**, 853 (2000).
2. S. L. Pimm, G. J. Russell, J. L. Gittleman, T. M. Brooks, *Science* **269**, 347 (1995).
3. J. Baillie, B. Groombridge, Eds., *1996 IUCN Red List of Threatened Animals* [IUCN (World Conservation Union)/Species Survival Commission, Gland, Switzerland, 1996].
4. IUCN, UNEP (United Nations Environment Programme), WWF (World Wide Fund for Nature), *Caring for the Earth: A Strategy for Sustainable Living* (IUCN/UNEP/WWF, Gland, Switzerland, 1991).
5. K. Redford, K. Brandon, S. E. Sanderson, in *Parks in Peril: People, Politics, and Protected Areas*, K. Brandon, K. H. Redford, S. E. Sanderson, Eds. (Nature Conservancy/Island Press, Washington, DC, 1998), pp. 455–464.
6. K. B . Ghimire, M. P. Pimbert, Eds., *Social Change and Conservation: Environmental Politics and Impacts of National Parks and Protected Areas* (Earthscan, London, 1997).
7. M. Hocking, S. Stolton, N. Dudley, *Evaluating Effectiveness: A Framework for Assessing Management of Protected Areas* [IUCN, Gland, Switzerland, and Cambridge, UK, 2000]; available at http://wcpa.iucn.org/pubs/pdfs/Evaluating_Effect.pdf.
8. M. J. B. Green, M. G. Murray, G. C. Bunting, J. R. Paine, *Priorities for Biodiversity Conservation in the Tropics* [WCMC (World Conservation Monitoring Centre) Biodiversity Bulletin No. 1, Cambridge, UK, 1996].
9. J. A. McNeely, Ed., *Expanding Partnerships in Conservation* (Island Press, Washington, DC, 1995).
10. L. V. Ferreira *et al.*, Áreas Protegidas ou Espaços Ameaçados? Relatório do WWF sobre o Grau de Implementação e Vulnerabilidade das Unidades de Conservação Federais Brasileiras de Uso Indireto (WWF, Brasilia, Brazia, 1999).
11. But see IUCN, "Threats to Forest Protected Areas: A survey of 10 countries carried out in association with the World Commission on Protected Areas" [Research Report from IUCN–The World Conservation Union for The WWF/World Bank Alliance for Conservation and Sustainable Use (1999)]; available at www-esd.worldbank.org/wwf/paperreport.pdf.
12. See also S. Singh, "Assessing Management Effectiveness of Wildlife Protected Areas in India" (Indian Institute of Public Administration, New Delhi, India, 1999); available at www.iucn.org/themes/forests/protectedareas/India.PDF.
13. Park managers or park staff constituted 56% of respondents; nongovernmental organizations (NGOs) and researchers constituted 30%; and central protected area agencies constituted 14%.
14. L. Hannah, D. Lohse, C. Hutchinson, J. Carr, A. Lankerani, *AMBIO* **23**, 246 (1994).
15. We used the "global natural areas map" created by Hannah *et al.* (*14*) to select parks in areas of anthropogenic threat. The map divided the world into three categories: natural, partly natural, and human dominated. We chose parks in "partly natural" and "human dominated" areas. One hundred and eighty-one parks, covering 49,854,888 ha, met our other criteria (see text) but were excluded because they are located in "natural" areas and are therefore likely protected by isolation.
16. IUCN Categories I and II. Category I protected areas are defined as Strict Nature Reserve/Wilderness Area—protected area managed mainly for science or wilderness protection. Category II areas are National Parks—protected area managed mainly for ecosystem protection and recreation.
17. Source: IUCN, CNPPA (Commission on National Parks and Protected Areas), WCMC, *Guidelines for Protected Area Management Categories* (IUCN, Gland, Switzerland, 1994).
18. Five hundred and twenty parks met our criteria.
19. We did not attempt to draw a statistically random sample because this would have been impractical given the difficulty of gathering data. Instead, we consulted in-country specialists to help us choose a representative sample of parks. The resulting sample was generally similar to the universe of parks with respect to age (universe median = 22 years, sample median = 23 years, 0.25 > P > 0.1; χ² = 9.8, df = 7), geographical distribution (universe: Africa 27%, Americas 32%, Asia 41%; sample: Africa 34%, Americas 37%, Asia 29%, 0.1 > P > 0.05; χ² = 5.5, df = 2), and IUCN Category (universe: Category I = 15%, Category II = 85%; sample: Category I = 14%, Category II = 85%, P > 0.25, χ² = 0.7, df = 1). However, the parks in our sample were significantly larger than the group as a whole (universe median = 50,000 ha; sample median = 80,000 ha, 0.025 < P < 0.05, χ² = 17.1, df = 8). Conservation International is active to varying degrees in 10 of the 93 parks that were selected for study. See supplementary data (*20*) for a detailed comparison of these sample and universe characteristics.

However, because protected areas in Laos [National Biodiversity Conservation Areas (NBCAs)] cannot be accurately described by an IUCN category, they were initially excluded. On the recommendation of experts, we included 15 parks from Laos in the group of parks from which we selected our sample. Five NBCAs were ultimately included in the study. See supplementary data (*20*) for a list of parks included in this study and their characteristics.
20. Supplementary data are available on *Science* Online at www.sciencemag.org/cgi/content/full/291/5501/125/DC1.
21. Six of the 93 parks included in this study were not from the universe of parks: 2 from Colombia were in "natural" areas, 1 from the Philippines was created in 1997, and 3 from Ghana were not in the initial database from which the universe was selected.
22. Belize, Brazil, Cambodia, Colombia, Cote d'Ivoire, Ecuador, Ghana, Honduras, Indonesia, Laos, Liberia, Madagascar, Mexico, Paraguay, Peru, Philippines, Senegal, Tanzania, Thailand, Togo, Uganda, and Vietnam. See supplementary data (*20*) for names and descriptions of parks.

23. Original questionnaire data are available from authors upon request.
24. Although the lowest response category for this question was 0 to 3 km, where respondents marked this category and indicated in other responses that there were major access points to the park, we assumed that there was a major road or river at or within the border (0 km).
25. A. N. James, M. J. B. Green, J. R. Paine, *Global Review of Protected Area Budgets and Staff* (WCMC, Cambridge, UK, 1999).
26. A principle components analysis on the correlation matrix of the factors showed little underlying structure among the attributes tested. The first axis accounted for only 19% of the variation in the data set, and the second axis for only 11%. The following variables were significantly correlated with the first component: total density of people in the park, total funding per hectare, number of guards per hectare, and total economic and development staff. Only one of these variables—number of guards per hectare—correlated with park effectiveness.
27. We thank the many people who contributed the information used in this report, those individuals from both government agencies and NGOs who coordinated responses for entire countries, and the Conservation International staff who managed this project in the field. We also thank P. Benson, T. Brooks, S. Edwards, C. Gascon, J. Ginsberg, J. Hardner, D. Repasky, A. Rylands, C. Short, and J. Waugh for valuable comments and discussions.

28 July 2000; accepted 20 November 2000

Chromosomal Effects of Rapid Gene Evolution in *Drosophila melanogaster*

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Rapid adaptive fixation of a new favorable mutation is expected to affect neighboring genes along the chromosome. Evolutionary theory predicts that the chromosomal region would show a reduced level of genetic variation and an excess of rare alleles. We have confirmed these predictions in a region of the X chromosome of *Drosophila melanogaster* that contains a newly evolved gene for a component of the sperm axoneme. In *D. simulans*, where the novel gene does not exist, the pattern of genetic variation is consistent with selection against recurrent deleterious mutations. These findings imply that the pattern of genetic variation along a chromosome may be useful for inferring its evolutionary history and for revealing regions in which recent adaptive fixations have taken place.

We have previously described the de novo evolution of a gene in the lineage of *D. melanogaster* (*1*). This gene, denoted *Sdic*, encodes a novel intermediate chain in a sperm-specific axonemal dynein. Changes that led to the creation of *Sdic* during the short evolutionary history of *D. melanogaster* [about 3 million years (*2*)] exhibit evidence for adaptive evolution. The gene was created from duplicated—and hence dispensable—copies of the genes for annexin X (*AnnX*) and the cytoplasmic dynein intermediate chain (*Cdic*). Three large deletions led to the fusion of the duplicated genes, whereupon a series of smaller deletions and nucleotide substitutions fashioned a new amino end of the Sdic polypeptide and created motifs characteristic of known axonemal dynein intermediate chains. The regulatory region of *Sdic*, including a spermatocyte-specific promoter element, also evolved from *AnnX* and *Cdic* sequences (*1*).

In principle, the evolutionary changes in *Sdic* could have taken place relatively rapidly during and immediately following speciation (*3*). In this case, current selection pressure on *Sdic* should be mainly to eliminate deleterious mutations. However, *Sdic* still appears to be evolving rapidly, as evidenced by the fact that the ratio of replacement to synonymous polymorphisms is in excess of 2:1 [(*1*) and additional data shown below].

The evidence for ongoing positive selection of *Sdic* prompted us to examine genetic variation in the surrounding genomic region to determine whether the theoretically predicted consequences of a rapid adaptive fixation (selective sweep) could be detected. The key issue is whether selection has been sufficiently recent and strong enough to yield a statistically significant deviation from the pattern of genetic variation that would be expected from nearly neutral polymorphisms affected only by random genetic drift, as well as selection against linked deleterious mutations ["background selection" (*4*, *5*)]. Strong positive selection increases the frequency of a new favorable mutation and displaces linked nucleotide polymorphisms in the process (*6*). Theory predicts that a recent selective sweep should create a characteristic "trough" in the level of polymorphism in a region that includes the selected gene (*7*), as well as an excess of "singleton" polymorphisms (those present in only one sequence in the sample). On the other hand, theory also indicates that levels of polymorphism should be restored relatively rapidly after a selective sweep. The time required for effective recovery of Tajima's *D* (*8*) is approximately 2*N* generations, where *N* is the effective population number; in *D. melanogaster* 2*N* generations are about 80,000 years. Tajima's *D* (*9*) is a conventional measure that compares the nucleotide diversity (pairwise differences) in a sample with the proportion of polymorphic sites, and it is negative when there is an excess of low-frequency polymorphisms, such as singletons.

To look for evidence of a selective sweep, we examined the spatial distribution of polymorphisms in the region at the base of the X chromosome that includes *Sdic* in *D. melanogaster*. The same analysis was carried out in the homologous region of the sibling species *D. simulans*, which lacks the *Sdic* gene. The pattern of polymorphism in *D. simulans* serves as a control, since there is no a priori reason to expect a recent selective sweep.

We sampled genes from polytene chromosome bands 18E1 to 20D. Messenger RNAs from 11 genes in *D. melanogaster* and 10 genes in *D. simulans* were reverse-transcribed, and the products were amplified by the polymerase chain reaction (PCR) and sequenced. Our analysis is based on an average of 903 base pairs per gene in each of 15 strains of *D. melanogaster* and 834 base pairs per gene in each of 7 strains of *D. simulans* (*10*). The analysis was confined to synonymous polymorphisms to eliminate possible artifacts due to different selective constraints or rates of amino acid replacement among the proteins.

To analyze the distribution of polymorphism along the chromosome, we used logistic regression. For each gene, let $W(x)$ be the number of segregating synonymous sites and $L(x)$ be the total number of synonymous sites in the sample. In these functions, x corresponds to the relative position of the gene in the chromosome. Under a simple model of background selection, the fraction of segregating sites, $S(x) = W(x)/L(x)$, should decrease monotonically as x moves from the euchromatin of the X chromosome toward and into the pericentromeric heterochromatin, owing to the progressive decrease in the rate of recombination and effective population size (*11*). The logistic regression model is used rather than an ordinary linear regression of S on x, because S is necessarily bounded on (0, 1). This feature favors anal-

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