and non-D chromosomes (these variants make up the other members of haplogroup D).

Another signature of positive selection is extended linkage disequilibrium (LD) (*8*), which is evident in the 62.1-kb region. Indeed, the 50 haplogroup D chromosomes show nearly complete LD across the region, with only three cases of LD breakdown [haplotypes 62, 65, and 105, present in one, two, and one copy, respectively (table S2)]. In contrast, the non-D chromosomes do not show any unusual LD across the region. We investigated the decay of LD beyond the 62.1-kb region by sequencing the Coriell panel for two flanking intergenic segments of roughly 5 kb each, positioned 25 kb upstream and downstream of *ASPM*. There is notable LD breakdown in these two segments, confirming that the site of selection is most likely within *ASPM*.

Following established methodology (*7*), we estimated the coalescence age (i.e., time to the most recent common ancestor) of haplogroup D at 5800 years, with a 95% confidence interval between 500 and 14,100 years. In comparison, the coalescence age of all the chromosomes (both D and non-D) is ~800,000 years. Thus, the age of haplogroup D substantially postdates the emergence of anatomically modern humans, estimated at ~200,000 years ago (*11*). A rough calculation showed that the fitness advantage of haplogroup D is in the range of a few percent over non-D haplotypes.

By genotyping the A44871G diagnostic polymorphism described earlier, we obtained the global frequency distribution of haplogroup D chromosomes from a separate panel of 1186 individuals (*7*). Consistent with the Coriell panel, we observed much higher frequency of haplogroup D chromosomes in Europeans and Middle Easterners than in other populations (Fig. 1). The corresponding estimate of F_{ST}, a statistic of genetic differentiation, is 0.29 between Europeans/Middle Easterners and other populations and 0.31 between Europeans/Middle Easterners and sub-Saharan Africans. These values indicate considerable genetic differentiation at this locus (*12*). Several scenarios may account for such notable differentiation. One is that haplogroup D first arose somewhere in Eurasia and is still in the process of spreading to other regions. The other is that it arose in sub-Saharan Africa, but reached higher frequency outside of Africa partly because of the bottleneck during human migration out of Africa. Finally, it is possible that differential selective pressure in different geographic regions is partly responsible.

Collectively, our data offer strong evidence that haplogroup D emerged very recently and subsequently rose to high frequency under strong positive selection. The recent selective history of *ASPM* in humans thus continues the trend of positive selection that has operated at this locus for millions of years in the hominid lineage (*3–5*). Although the age of haplogroup D and its geographic distribution across Eurasia roughly coincide with two important events in the cultural evolution of Eurasia—namely, the emergence and spread of domestication from the Middle East ~10,000 years ago (*13*) and the rapid increase in population associated with the development of cities and written language 5000 to 6000 years ago around the Middle East (*14*)—the significance of this correlation is not yet clear.

References and Notes
1. J. Bond *et al.*, *Nat. Genet.* **32**, 316 (2002).
2. P. Ripoll, S. Pimpinelli, M. M. Valdivia, J. Avila, *Cell* **41**, 907 (1985).
3. J. Zhang, *Genetics* **165**, 2063 (2003).
4. P. D. Evans *et al.*, *Hum. Mol. Genet.* **13**, 489 (2004).
5. N. Kouprina *et al.*, *PLoS Biol.* **2**, E126 (2004).
6. S. L. Gilbert, W. B. Dobyns, B. T. Lahn, *Nat. Rev. Genet.* **6**, 581 (2005).
7. Materials and methods are available as supporting material on Science Online.
8. M. Bamshad, S. P. Wooding, *Nat. Rev. Genet.* **4**, 99 (2003).
9. N. A. Rosenberg *et al.*, *Science* **298**, 2381 (2002).
10. E. Zietkiewicz *et al.*, *J. Mol. Evol.* **47**, 146 (1998).
11. I. McDougall, F. H. Brown, J. G. Fleagle, *Nature* **433**, 733 (2005).
12. S. Wright, *Evolution and the Genetics of Populations* (Univ. of Chicago Press, Chicago, 1978).
13. L. L. Cavalli-Sforza, P. Menozzi, A. Piazza, *The History and Geography of Human Genes* (Princeton Univ. Press, Princeton, 1994).
14. S. D. Houston, *The First Writing: Script Invention as History and Process* (Cambridge Univ. Press, New York, 2004).
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Neutral Ecological Theory Reveals Isolation and Rapid Speciation in a Biodiversity Hot Spot

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South Africa's Mediterranean-climate fynbos shrubland is a hot spot of species diversity, but its diversity patterns contrast strongly with other high-diversity areas, including the Amazon rain forest. With its extremely high levels of endemism and species turnover, fynbos is made up of dissimilar local communities that are species-rich but relatively poor in rare species. Using neutral ecological theory, we show that the relative species-abundance distributions in fynbos can be explained by migration rates that are two orders of magnitude lower than they are in tropical rain forests. Speciation rates, which are indexed by the "biodiversity parameter" Θ, are estimated to be higher than they are in any previously examined plant system.

Regions with many endemic resident species are typically grouped together as biodiversity "hot spots," but this label obscures fundamental differences among high-diversity systems in species-diversity patterns and in the processes that generate them. The fynbos shrubland of South Africa's Cape Floristic Region (CFR) presents a particularly strong contrast with other diverse systems such as the Amazon rain forest. Amazon rain forest tree communities are dominated by species with large ranges, most of which are locally rare (*1, 2*), whereas most fynbos shrub species are narrow endemics, and many can be locally abundant (*1, 3*). Neutral ecological theory (*4*) enables the quantification of diversity in these contrasting systems in terms of the mechanisms that generate and partition it: rates of speciation and rates of migration.

The CFR contains over 8,000 plant species, of which a majority (69%) are endemic to the region (*2*). Mediterranean-climate regions are among the most diverse systems outside the tropics, and among these, the CFR has the most species in the smallest area (*5*). Molecular phylogenetic studies have estimated that speciation rates in some lineages in the

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CFR are exceptionally high (*1*, *3*). Moreover, CFR plants are thought to have very low migration rates (*6*). High levels of endemism among CFR species are associated with low observed seed-dispersal distances and short-distance dispersal modes (ant and passive dispersal) (*7*). Even among Mediterranean-climate regions, the CFR has very high rates of species turnover along habitat and geographic gradients, i.e., high β and γ diversities, respectively (*8*), which is a spatial pattern that suggests low migration rates (*5*). Amazon rain forest, in contrast, occupies a much larger area, and can contain as many as 300 tree species in a sample of 600 individuals (extremely high local, or α, diversity) (*9*). Relatively few Amazon tree species appear to be locally endemic, because even rare species have generally broad distributions, producing comparatively lower β and γ diversities (*10*, *11*). Studies of tropical rain forest trees have shown them to be generally well dispersed, with long mean-dispersal distances and frequent long-distance dispersal events (*12*, *13*).

Hubbell's neutral theory of biodiversity and biogeography ("neutral theory") provides mechanistic insight into the processes driving these two types of high-diversity systems (*4*). Neutral theory extends previous ecological work on quantifying and comparing diversity patterns by grounding its descriptions in interpretable ecological processes; its two core parameters represent the processes of speciation and migration (*14*). The "biodiversity parameter," Θ, represents the process of speciation within a "metacommunity," which is a very large collection of similar organisms found across a biogeographic region (*4*). This parameter is twice the product of the size of the metacommunity J_m (a very large number) and the speciation rate υ, which is the number of new species arising per birth (a very small number). Thus, Θ is proportional to the expected number of new species per generation across the metacommunity and can be used to quantify the diversity-generating capacity of a system. In terrestrial plant systems, Θ has been shown to range from ~1 in boreal forest to ~200 in tropical rain forests (*4*). Within the metacommunity are "local communities," which are groups of organisms at a particular locality that are linked to the metacommunity by migration. The migration parameter *m* is the proportion of individuals per generation in each local community that come from elsewhere in the metacommunity (*4*). Given values for *m*, Θ, and the size of the local community (*J*), neutral theory produces an expected relative species abundance distribution, called the zero-sum multinomial (ZSM) (*15*, *16*), which can be fitted to sample inventory data.

Neutral dynamics can generate two extreme types of species-rich systems, depending on the amount of migration. A high-migration system

(*m* > 0.1) has species-rich local communities with high evenness in relative abundances. A low-migration system (*m* < 0.01) is a spatially structured collection of dissimilar local communities that are less species-rich because of local extinction of rare species through stochastic drift and because of correspondingly higher dominance by a few species in each local community. For the same value of Θ, a high-migration system will have higher local diversity, whereas a low-migration system will have proportionally higher species turnover among localities.

An advantage of neutral theory over alternative descriptors of biodiversity patterns is that its parameters represent easily interpreted ecological processes. However, little work has been done to produce parameter estimates for a range of systems and to assess what insight they provide about ecological dynamics. Because most previous applications of neutral theory to plant communities have used tropical rain forest data sets (*12*, *13*, *15*, *17*), the application of the theory to real-world patterns has been confined to only a few geographic regions and a small portion of parameter space. Here we contrast the Amazon rain forest system with the CFR, which may be the clearest example of a species-rich low-migration system.

The CFR data come from three sites spanning the region—the Cederberg mountains in

the northwest, Cape Hangklip in the southwest, and the Zuurberg mountains at the eastern edge. Each of the sites in our data set is an identifiable subregion of the CFR, which consists of a range of hills or mountains and adjacent lowlands (*18*). For each site, we obtained existing floristic survey data, including hundreds of 5-m by 10-m plots, in which all vascular plants had been identified to species (Table 1) (*19–22*). From these data, we obtained the abundances of all woody plant species for each site (subshrubs, shrubs, and trees) (*23*). For the comparison to tropical rain forests, we used tree-count data from networks of large plots in the Manu National Park in Peru and Yasuní National Park in Ecuador (*10*, *11*). Estimates for Barro Colorado Island (BCI) in Panama, using tree count data from the 50-ha plot there, were also included as a well-studied baseline (*13*).

Observed patterns of diversity and abundance in the CFR are very different from those documented for tropical rain forests (*2*, *24*). Figure 1, which displays species relative abundances at a CFR site (the Cederberg) and an Amazon forest site (Manu National Park), shows that the CFR site has higher dominance by common species, with fewer rare species. Each CFR site contains fewer species than do typical tropical rain forest localities containing equivalent numbers of individuals, but local

Fig. 1. Rank-abundance plots for the Cederberg (CFR) and Manu (Amazon) sites. The triangles (Cederberg, red lines) and circles (Manu, blue lines) show abundance of the ranked species for each site, normalized by total abundance and log transformed. Solid lines show rank abundances predicted by neutral theory for each site, using maximum likelihood parameter estimates. Dashed lines indicate bootstrapped 95% confidence intervals around the predicted rank abundances, quantifying sampling error expected when drawing from a neutral community with known parameters.
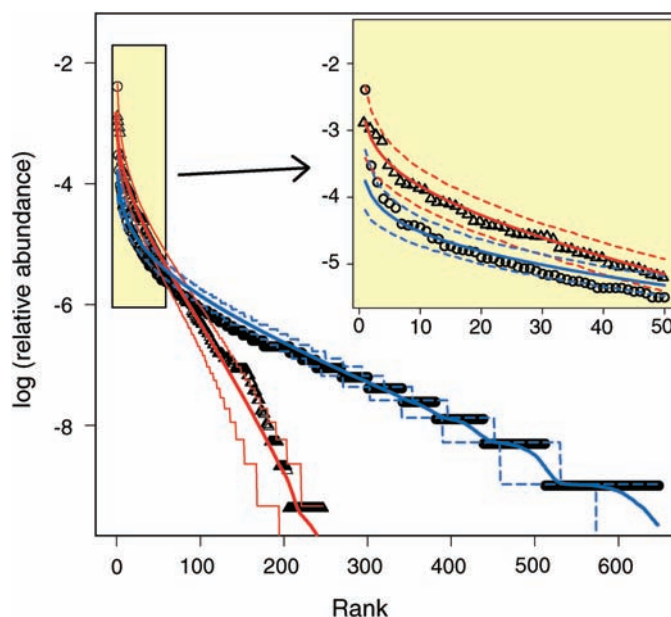
Table 1. Data sets.

Site	Plots	Species	Individuals
Cederberg (*20*)	191	247	11,765
Cape Hangklip (*19*)	251	247	24,003
Zuurberg (*21*)	69	114	8,916
Manu National Park, Peru (*10*, *11*)	15	648	8,055
Yasuní National Park, Ecuador (*10*, *11*)	14	546	7,613
BCI, Panama (*13*)	1	225	21,457

endemism in the CFR is extremely high, resulting in very high species turnover among sites (*18*, *25*). The mean adjusted Jaccard's Index [a measure of taxonomic similarity between sites that adjusts for sampling effects (*26*)] for the three CFR sites studied here is 0.024, compared with 0.47 for the two Amazon sites, despite the shorter distances among the CFR sites (~150 to 400 km versus ~1500 km).

We used Bayesian and maximum-likelihood methods to fit the ZSM to species-abundance data from each site (*23*). Parameter estimates were obtained by using a likelihood derived from the closed-form expression for the ZSM given in Volkov *et al.* (*15*), which provides the predicted distribution of abundances for a sample of species from a neutral community. To obtain Bayesian parameter estimates, uninformative priors were placed on the parameters (*23*).

Bayesian estimates of *m* for the CFR ranged from 0.0018 to 0.045, which is about two orders of magnitude lower than the estimates for the rain forest sites (0.54 for Yasuní, 0.55 for Manu, and 0.1 for BCI) (Fig. 2 and Table 2). The maximum likelihood estimates for the parameters were consistent with the Bayesian results (Table 2). None of the credible intervals of the CFR estimates of *m* overlapped those of the Amazon estimates. Within the CFR, the lowest migration estimate is for Cape Hangklip, which is one of the most diverse areas of the CFR (*2*, *25*). Zuurberg, at the eastern edge of the CFR, had much higher estimates of *m*, approaching those of BCI in Panama.

Estimates of Θ for the CFR were very high, peaking in the southwest (Cape Hangklip) at Θ = 530, which is more than twice the highest value yet estimated for any rain forest (~200) (*4*). Because the posterior distribution for Θ in low-migration communities is right-skewed (Fig. 2D), we present the posterior mode rather than the posterior mean as a conservative estimate (Table 2). The credible interval for Θ for Cape Hangklip does not overlap the interval for Manu, the richer of the two Amazon communities, and this value is the highest estimate of Θ for any plant system yet examined. As with *m*, there is a longitudinal trend in Θ within the CFR: the highest Θ values coincide with the lowest migration rates in the southwest.

The eastern part of the CFR, including the Zuurberg site, has more-even seasonal rainfall patterns than does the southwestern CFR, and the vegetation contains a higher proportion of widely distributed, well-dispersed forest and thicket species (*27*). The lowest migration rates are thus associated with the highly seasonal winter rainfall conditions in the southwest, as well as with the highest levels of endemism and species turnover (*28*). The southwestern site (Cape Hangklip) is also geographically central, whereas the eastern site (Zuurberg) is the most peripheral, suggesting that edge effects may be reducing species diversity at the periphery of the region.

Combining the data from the subregions within each region (CFR and Amazon) produces a proxy for samples from the two metacommunities. By using the composite data, we can assess the importance of migration limitation by comparing the fits of models with and without a migration parameter (*16*). Estimates of Θ for the metacommunity neutral model with no migration limitation were performed by maximizing the likelihood of the metacommunity sampling distribution (*16*). The assumption of unlimited migration drastically lowers the estimate of Θ for the CFR (from 697 to 88.9), whereas Θ for the Amazon is only moderately reduced (251 to 219). The reduction in the CFR estimate is not surprising, because if migration limitation is ignored, the lower species richness can be accommodated only by lower values of Θ. The assumption of unlimited migration is clearly
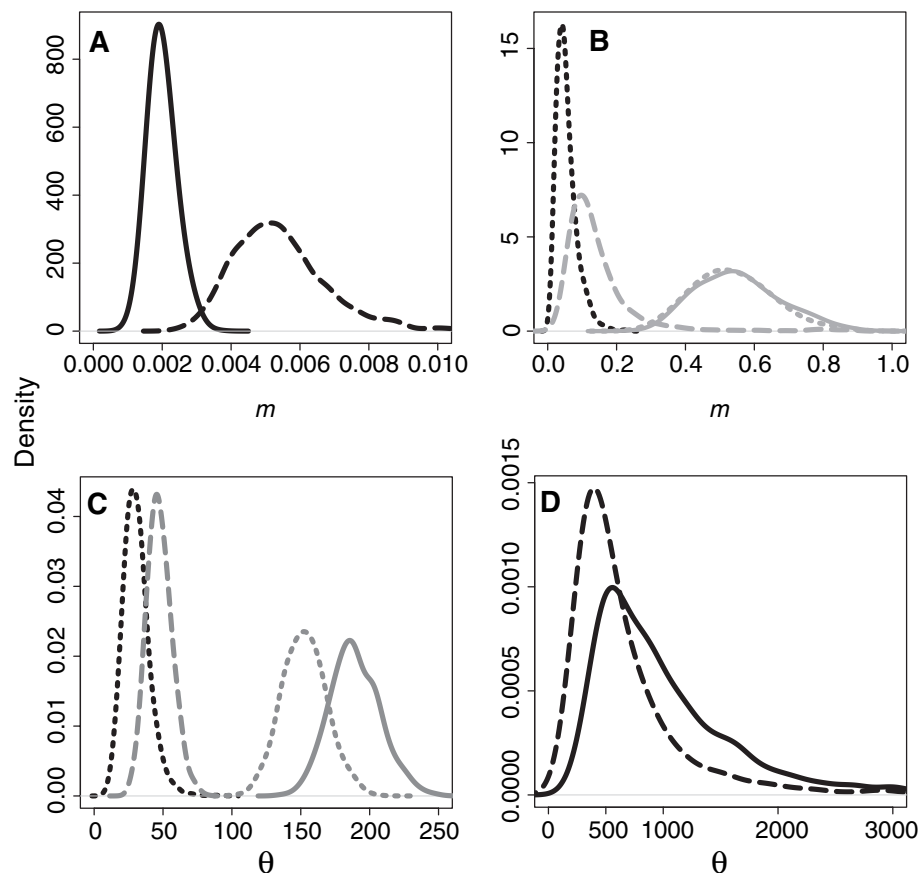
Fig. 2. Bayesian estimates of the ZSM parameters *m* (upper two panels) and Θ (lower two panels). Posterior densities for tropical rain forest sites are shown in gray and CFR sites are shown in black. (**A**) The low-*m* sites: Cape Hangklip (solid black line) and Cederberg (dashed black). (**B**) The higher-*m* sites: Zuurberg (dotted black), Barro Colorado Island (dashed gray), Yasuní (dotted gray), and Manu (solid gray). (**C**) Zuurberg (dotted black line), BCI (dashed gray line), Yasuní (dotted gray), and Manu (solid gray). (**D**) Cederberg (dashed black) and Cape Hangklip (solid black).

Table 2. Parameter estimates under neutral theory ZSM distribution. Estimates for neutral theory parameters Θ and *m* are shown. Both maximum likelihood estimates (MLE) and Bayesian estimates [posterior (Post.) mode] are presented; the 0.025 and 0.975 quantiles for the Bayesian estimates quantify the uncertainty associated with the estimates.

Site	Θ				*m*			
	MLE	Post. mode	0.025 quantile	0.975 quantile	MLE	Post. Mode	0.025 quantile	0.975 quantile
Cederberg	394.6	370	198.9	2350.5	0.0055	0.0053	0.0032	0.0090
Hangklip	640.3	530	328.3	3033.7	0.0020	0.0018	0.0014	0.0029
Zuurberg	30.2	29	15.3	52.5	0.037	0.045	0.015	0.13
Manu	187.4	183	154.9	228.3	0.53	0.55	0.34	0.81
Yasuní	152.8	153	121.9	188.6	0.50	0.50	0.34	0.80
BCI	47.7	45	31.3	67.0	0.093	0.10	0.048	0.44

unsatisfactory for both systems, because a likelihood ratio test strongly favors the model with migration limitation in both cases [for Amazon: $\chi^2 = 24.6$, 1 degree of freedom (d.f.), $P < 0.001$; for CFR: $\chi^2 = 19.4$, 1 d.f., $P < 0.001$].

Estimates of Θ can be converted to estimates of per capita speciation rate if it is possible to estimate the number of individuals in the metacommunity. With a much larger area, the Amazon rain forest metacommunity almost certainly contains at least as many individuals as does fynbos, which covers <50,000 km². The high estimates for Θ thus imply a substantially higher per capita speciation rate in the CFR. These results are consistent with the prevailing view that the western CFR is an extremely migration-limited system with extraordinarily high speciation rates. Each of the local communities in our data set is an identifiable subregion of the CFR that consists of a range of hills or mountains and adjacent lowlands. Thus, the CFR metacommunity is topographically fragmented, which predicts low migration rates, consistent with our results. With these low migration rates, it is likely that local communities will be sufficiently isolated to allow ecological drift to cause divergence among communities, because few individuals per generation will be exchanged (19). Further, populations of individual species will be genetically isolated, so that genetic drift will tend to cause divergence and the formation of

new species. Thus, our results support the view that the fynbos metacommunity consists of topographical islands isolated not by water but by drier lowlands. This pattern contrasts sharply with that found in tropical rain forests, which exhibit high connectivity over long distances. Within the CFR, the association of the highest values of Θ, and thus speciation rates, with lowest migration rates supports the view that isolation over short spatial scales (1 to 100 km) has played a role in generating, as well as structuring, the high diversity of the CFR.

References and Notes

1. H. P. Linder, C. R. Hardy, *Philos. Trans. R. Soc. London Ser. B* **359**, 1623 (2004).
2. P. Goldblatt, J. Manning, *Cape Plants: A Conspectus of the Cape Flora of South Africa* (National Botanical Institute of South Africa, Cape Town, 2000).
3. J. E. Richardson et al., *Nature* **412**, 181 (2001).
4. S. P. Hubbell, *The Unified Neutral Theory of Biodiversity and Biogeography* (Princeton Univ. Press, Princeton, 2001).
5. R. M. Cowling, P. W. Rundel, B. B. Lamont, M. K. Arroyo, M. Arianoutsou, *Trends Ecol. Evol.* **11**, 362 (1996).
6. P. Slingsby, W. J. Bond, *S. Afr. J. Bot.* **51**, 30 (1985).
7. D. J. McDonald, J. M. Juritz, R. M. Cowling, W. J. Knottenbelt, *Plant Syst. Evol.* **195**, 137 (1995).
8. R. H. Whittaker, *Taxon* **21**, 213 (1972).
9. H. ter Steege et al., *Biodivers Conserv.* **12**, 2255 (2003).
10. N. C. A. Pitman, J. W. Terborgh, M. R. Silman, P. V. Nuñez, *Ecology* **80**, 2651 (1999).
11. N. C. A. Pitman et al., *Ecology* **82**, 2101 (2001).
12. O. J. Hardy, B. Sonké, *For. Ecol. Manage.* **197**, 191 (2004).
13. R. Condit et al., *Science* **295**, 666 (2002).
14. J. Chave, *Ecol. Lett.* **7**, 241 (2004).
15. I. Volkov, J. R. Banavar, S. P. Hubbell, A. Maritan, *Nature* **424**, 1035 (2003).
16. D. Alonso, A. J. McKane, *Ecol. Lett.* **7**, 901 (2004).
17. B. J. McGill, *Nature* **422**, 881 (2003).
18. R. M. Cowling, Ed., *The Ecology of Fynbos: Nutrients, Fire and Diversity* (Oxford Univ. Press, Cape Town, 1992).
19. C. Boucher, *Bothalia* **12**, 455 (1978).
20. H. C. Taylor, *Cederberg Vegetation and Flora* (National Botanical Institute, Cape Town, 1996).
21. B. E. Van Wyk, P. A. Novellie, C. M. Van Wyk, *Bothalia* **18**, 211 (1988).
22. M. J. A. Werger, *Bothalia* **11**, 309 (1974).
23. Materials and methods are available as supporting material on *Science* Online.
24. R. M. Cowling, B. B. Lamont, *Aust. J. Bot.* **46**, 335 (1998).
25. R. M. Cowling, P. M. Holmes, *Biol. J. Linn. Soc.* **47**, 367 (1992).
26. A. Chao, R. L. Chazdon, R. K. Colwell, T.-J. Shen, *Ecol. Lett.* **8**, 148 (2005).
27. R. M. Cowling, S. Proches, in *Plant Diversity and Complexity Patterns. Local, Regional and Global Dimensions*, H. Balslev, Ed. (The Royal Danish Academy of Sciences and Letters, Copenhagen, 2005), vol. 55, pp. 273–288.
28. R. M. Cowling, A. T. Lombard, *Diversity Distr.* **8**, 163 (2002).
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Generating Electricity While Walking with Loads

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We have developed the suspended-load backpack, which converts mechanical energy from the vertical movement of carried loads (weighing 20 to 38 kilograms) to electricity during normal walking [generating up to 7.4 watts, or a 300-fold increase over previous shoe devices (20 milliwatts)]. Unexpectedly, little extra metabolic energy (as compared to that expended carrying a rigid backpack) is required during electricity generation. This is probably due to a compensatory change in gait or loading regime, which reduces the metabolic power required for walking. This electricity generation can help give field scientists, explorers, and disaster-relief workers freedom from the heavy weight of replacement batteries and thereby extend their ability to operate in remote areas.

Over the past century, humans have become increasingly dependent on technology, particularly electronic devices. During the past decade, electronic devices have become more mobile, enabling people to use medical, communication, and Global Positioning System (GPS) devices as they move around cities or in the wilderness. At present, all of these devices are powered by batteries, which have a limited energy storage capacity and add considerable weight. Although substantial progress has been made in reducing the power requirements of devices and increasing the power densities of batteries, there has not been a breakthrough in the parallel development of a portable and renewable human-driven energy source (1, 2).

The combination of limited energy and the large weight of batteries poses the most critical problem for individuals having high electricity demands in remote areas and who are already carrying heavy loads (such as field scientists or explorers on prolonged expeditions). At present, replacement batteries may make up a substantial proportion (as much as 25%) of the very heavy packs (>36 kg or 80 lbs) that such users must carry (3). To help solve this problem, we developed a passive device, the suspended-load backpack, which extracts mechanical energy from the vertical movement of the load during walking and converts it to electricity for powering portable devices.

During terrestrial locomotion, the environment does no work on the body (except for the small force of aerodynamic drag) and conversely, humans do no work on the environment. Rather, almost all of the mechanical work is generated and dissipated inside the body (4, 5). This makes it exceedingly difficult to capture mechanical energy to drive an electrical energy conversion apparatus, because the device would need to be either surgically placed within the body or attached to the outside of the body (such as an exoskeleton), which would affect the person's maneuverability and comfort. Therefore, researchers in the field have focused on putting devices in the only acces-

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