in all cell types, irrespective of tissue-specific gene expression. If the asynchrony of replication of the IL-2 gene is also present in cells other than T cells, this would indicate that before T cell development, one IL-2 allele is rendered unavailable for future activation.

All other known examples of random monoallelic expression of autosomal genes (immunoglobulins, T cell receptors, olfactory receptors, and LY49 NK cell receptors) involve genes encoding diverse receptors in systems in which receptor expression is restricted so that cells have distinct specificities. In all of these cases, monoallelic expression is a fundamental aspect of the transcriptional restriction of receptor expression. Why would the cytokine IL-2, which is expressed in most activated CD4$^+$ T cells be expressed monoallelically? Interestingly, both IL-2 and the IL-2 receptor are expressed during thymocyte development around the time of establishment of allelic exclusion in T cell receptor genes. For mature T cells, the well-characterized integration of signal transduction pathways by the transcription factors could account for the observed regulation without having to invoke monoallelic expression (6). Thus, monoallelic expression may reflect a new aspect of the regulation of IL-2 gene expression, perhaps one involving an interplay between nuclear architecture and chromatin structure (10).

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ECOLOGY

Planning for Biodiversity

Stuart L. Pimm and John H. Lawton

At present, species are going extinct at a rate 100 times the natural background rates (1). The readily observable destruction of habitats such as the Amazon (2) and the now-calibrated relationship between habitat loss and species loss (3) predict that these rates will only get larger. Only ~5% of the planet's land surface is in reserves that are protected to one degree or another (4). If human activities destroy or greatly modify the remaining 95% of the land, only half the planet's species would survive in the protected 5%, the other half would go extinct. (See related commentary on page 2060.)

The most vulnerable species—those with the smallest geographical ranges—are not distributed randomly. Nature has put her eggs in a few baskets—hotspots—where these rare, endemic species are concentrated (5). By a cruel twist of fate, current rates of deforestation appear to be highest in the richest hotspots (6). If humanity placed reserves judiciously over these special places, could we save a greater fraction of species (7)? Two reports from southern Africa, one on page 2106 of this issue, and a third from North America, on page 2126, describe the challenges involved and conclude that the solution is not so simple.

Globally, reserves are allocated poorly. The reserves that are larger than 100,000 km^2 are high mountains, tundra, and the driest deserts, areas not particularly species-rich (4). Hotspots such as Madagascar and the Philippines protect less than 2% of their land (4). The same is true in the Algulhas Plain, the southern tip of Africa and one of the world's hottest spots for plants. Here, some 1500 km^2 (half the size of Rhode Island) house 1751 species; although most of the state forests and private nature reserves are coastal, most of this region's 99 endemic plants live inland.

Lombard *et al.* (8) asked: Where should new reserves be situated to protect the maximum number of species at minimum cost? One aspect of their analysis is purely a matter of biogeography. Computer algorithms select sets of cells (which represent subsections of land) according to their complementary species composition. These can be designed so that a set of cells captures either as many total species or as many rare species as possible (see the diagram) (9). Lombard *et al.* developed software similar to that widely available (9), but they included both endemic species and different kinds of classified vegetation types. Selecting complementary vegetation types is another way of setting conservation priorities.

Naïvely applied, these algorithms are not practical conservation tools. The selected sites may not be available for reserves. In addition, selection of too small a cell size can lead to the "Noah's Ark" effect. All the desired species can be captured in a collection of widely scattered, tiny cells of a small combined area, but in fact the populations protected in this seemingly efficient strategy are too small to persist. Like Noah, scattered tiny reserves protect everything in a small area, but only for a short time—and he had divine help.

Lombard *et al.* selected a grid size of 3 km by 3 km. Reserves of this size are politically feasible and represent a trade-off between efficiency and population viability. When other constraints are added to the biogeographical ones, these ecology and computer algorithms become a practical tool. Some species are already in reserves and do not need to be preserved again, and every species should be represented more than once as insurance against disasters. Some areas are unsuitable; alien weeds overrun others; and some selected sites are in mostly agricultural or urban areas. Whenever possible, algorithms should add areas adjacent to existing reserves. Combined, these constraints produce a variety of selections, but the results are broadly comparable in their priorities. As such, the methods outlined by Lombard *et al.* provide both local advice and an excellent case history that combines ecological patterns with practical and political considerations.

Value for money motivates Ando *et al.* (10). Dobson *et al.* (11) documented the distribution of endangered species in the United States, county by county, thus identifying the minimum number of counties needed to achieve a given coverage of endangered species. Were land prices broadly similar everywhere, the approach would be relatively straightforward. Unfortunately, areas with many endemic species include the counties encompassing San Diego, Santa Cruz, and San Francisco in California, Honolulu in Hawai'i, and counties in Florida, all of which contain some of the highest priced land in the United States. Ando and her colleagues modified this approach in two ways. The first seeks to minimize costs by taking into account land prices while including a fixed number of species; the second maximizes the number of species protected for a given cost.

Their results include a striking feature: The average cost per hectare fluctuates widely as more species are protected. The ef-

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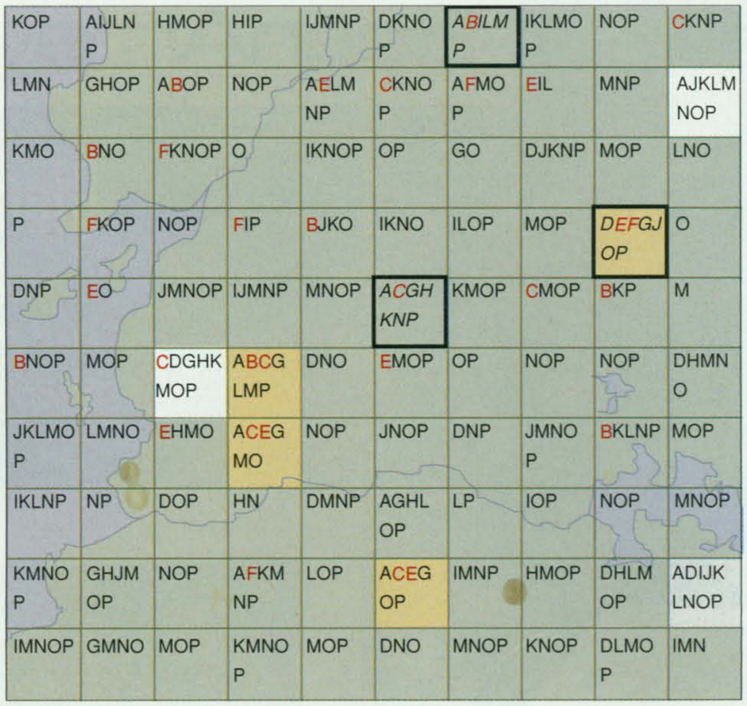
fect is driven by the patterns of complementarity (see diagram). For instance, a single site that contains the largest number of species need not be in the set of two sites that contain the largest number of species. In one example, land in San Francisco County is an order of magnitude more expensive than land elsewhere. This county is progressively added to and dropped from complementary sets of increasing total numbers of species, driving the cost fluctuations. Even without this extreme value, Ando *et al.* show the considerable savings that accrue from selecting larger, more complementary areas.



KOP	AIJLNP	HMOP	HIP	IJMNP	DKNOP	*ABILMP*	IKLMOP	NOP	CKNP
LMN	GHOP	ABOP	NOP	AELMNP	CKNOP	AFMOP	EIL	MNP	AJKLMNOP
KMO	BNO	FKNOP	O	IKNOP	OP	GO	DJKNP	MOP	LNO
P	FKOP	NOP	FIP	BJKO	IKNO	ILOP	MOP	*DEFGJOP*	O
DNP	EO	JMNOP	IJMNP	MNOP	*ACGHKNP*	KMOP	CMOP	BKP	M
BNOP	MOP	CDGHKMOP	ABCGLMP	DNO	EMOP	OP	NOP	NOP	DHMNO
JKLMOP	LMNO	EHMO	ACEGMO	NOP	JNOP	DNP	JMNOP	BKLNP	MOP
IKLNP	NP	DOP	HN	DMNP	AGHLOP	LP	IOP	NOP	MNOP
KMNOP	GHJMOP	NOP	AFKMNP	LOP	ACEGOP	IMNP	HMOP	DHLMOP	ADIJKLNOP
IMNOP	GMNO	MOP	KMNOP	MOP	DNO	MNOP	KNOP	DLMOP	IMN

Recipe for preservation. Sixteen hypothetical species (A through P) are distributed across a landscape divided into 100 cells. How can all 16 species be preserved in a small (thus cost-efficient) set of cells? Three cells have the greatest number of species (white). However, these cells combined have only one of the four rarest species (B, C, E, F, in red). Four cells each have two of these rarest species (yellow). The best solution is three cells (outlined in black), which together contain all 16 species, but this set does not include any of the three cells with the largest number of species and only one of the four cells with the largest number of the four rarest species.

Used wisely in these ways, complementarity algorithms open up new, cost-effective possibilities for setting conservation priorities for a particular group of endangered species. Could these approaches be extended to encompass both species richness and rarity, and more than one taxon? In the past, ecologists naïvely preserved those areas with the greatest number of species. However, contrary to expectations, these areas often do not contain the geographically rarest species (*12*) (see diagram). So what about multiple taxa? The hope was that reserves optimally selected on the basis of information from a well-studied "indicator taxon" (higher plants, birds, or butterflies are typical examples) might also provide protection for more poorly studied groups. The data squelch this hope. Areas rich in species of one taxon, say butterflies, often do not overlap with areas rich in another, like birds. Nor, generally, do the areas with the rarest species of both groups overlap (*12*). These results, from Britain, might stem from that country's dense human population and highly fragmented habitats. Yet the same message is repeated in similar analyses of much larger areas in Australia and North America, and for smaller areas in tropical African forest (*11*, *13*).

One possibility remains: Might sets of complementary sites for different taxa coincide? This is the question van Jaarsveld *et al.* asked for 300,000 km^2 of the Transvaal, an area in southern Africa roughly the size of the United Kingdom (*14*). Data from more than 9000 species of well-studied birds, butterflies, mammals, and vascular plants and from less well-known termites, antlions, and two kinds of beetles were mapped onto 25 km by 25 km grids.

As in previous studies, the most species-rich cells and those with the rarest species do not tend to coincide. However, complementary sets could still coincide, despite these mismatches, if the majority of organisms in a region shared common biogeographical patterns. Numerous species in every taxon could be confined to northern areas and others to southern areas, for example.

Contrary to this hope, pairwise comparisons of complementary sets revealed a mean overlap of only 10% of cells, with a maximum of 21%. No cell fell into the set selected for every taxon. Just six cells from 474 were in the same set for six of the eight taxa. Such feeble coincidence provides no basis for an effective conservation strategy embracing a variety of organisms.

Perhaps species are the wrong units to study. Would complementarity be better if genera or families were analyzed? The answer is again no. Simply, different areas are required to conserve different taxa, and conserving areas by using genus or family data does not result in efficient species conservation. This still leaves open the possibility that in parts of the world more strongly and consistently biogeographically zoned than the Transvaal, complementarity across taxa may offer a route to efficient reserve selection. But without doing the surveys to check such zoning, how could we be sure they were zoned ?

These practical issues aside, we still do not have a theoretical understanding of why the geographical patterns of hotspots, rarity, and complementarity are so different among taxa. Although at very large scales distinct biogeographic realms are apparent, within these, nature apparently plays dice with distributions.

In a world in which conservation biologists struggle against the odds, these are depressing conclusions. They also convey a much deeper message. In a current advertisement, the statement "Dr. X spends his life doing boring work on the bioluminescence of coelenterates" is contrasted with the company's exciting molecular biological techniques. The message is that taxonomy is boring, but molecular biology is sexy. We admire the advances of molecular biology. But if each biologist wishes to maintain a rich and interesting world to study (*15*), we cannot afford the luxury of ignoring those most basic of all biological skills—taxonomy and the knowledge of which species live where. Without this knowledge, conservation efforts are seriously impaired, and 100 years from now the world will be a biologically less interesting place.

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