CENTER FOR CONSERVATION BIOLOGY
# UPDATE
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## Where we live threatens biodiversity conservation

Human settlement and use patterns often echo the distribution of habitats with high biodiversity. Areas with moderate climate, good water supply, arable land, and forest resources often have a high level of both biodiversity and attraction for humans. For example, the highest human density occurs in Australia along the east coast - an area of complex habitat ranging from heathland to tropical rainforest that harbors many endemic and endangered native fauna.

Scientists and planners have largely overlooked the problems caused by the overlap of human use and biodiversity. Conservation efforts have often focused on "wilderness areas" such as high mountains, deserts, and arctic and antarctic habitats.

In our study, we (Taylor Ricketts, Gretchen Daily, Marc Imhoff and I) looked for ways to maximize biodiversity conservation while working with the common patterns of human development we see around us. We used as conservation goals either protecting species richness or maintaining a representative sample of each species. We determined whether these conservation goals could be met when planning is shifted to focus on areas of high species richness and lower human density.

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## Native plant persistence in countryside landscapes

A rain forest native found in a road verge in a deforested area. *Photo by Margie Mayfield.*

Approximately 4.4 million hectares were deforested in Latin America annually between 1990 and 2000, according to the Food and Agriculture Organization of the United Nations. Rather than leaving an entirely barren, sterile land surface, deforestation often results in complex landscapes that vary greatly in their ability to support biodiversity. These countryside habitats include recently cleared land, pastures, agricultural plots, gardens, and residential areas, as well as secondary re-growth and small remnants of primary forest. Fragmented countryside habitats acquire greater conservation importance as human enterprise expands throughout the tropics and preservation of large tracts of native habitat becomes more difficult.

Traditional studies of biodiversity in human-modified or countryside landscapes in both temperate and tropical regions view the world as simple combinations of habitats surrounded by a matrix of human-dominated non-habitat. Reality is less simple. For example, in southern Costa Rica, a series of research efforts by other members of the CCB and collaborators at the National Autonomous University of Mexico (UNAM) have found that for a variety of animal taxa, 50% or more of native species sampled were found in both open, deforested and forested habitats (See *Update*, Vol. 14 #2, Vol. 13, #2, Vol. 12 #2, Vol. 11 #2, Vol. 11 #1). Although these studies have provided valuable information about the conservation potential of deforested areas of the New World tropics for animals, including birds, moths, butterflies, mammals, reptiles, and amphibians, the ability of plants to survive deforestation and major landscape alteration

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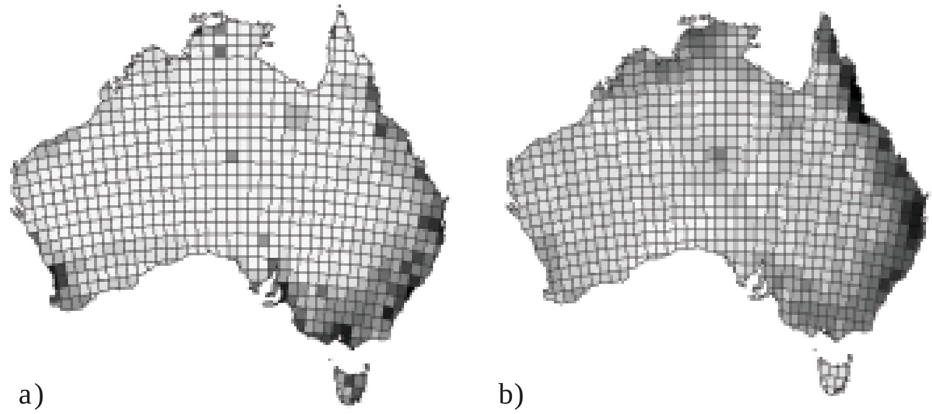


*The distribution of human population density(a) and species richness for all taxa(b) across Australia. Darker areas equal higher values.*

### *Human Density vs. Species Diversity*

In order to test the concept that careful development and conservation planning can strongly assist sustainable habitat preservation, we investigated the relationship between human population density and the species richness of birds, mammals, reptiles, amphibians, and butterflies across mainland Australia and North America.

On both continents, we found that the majority of people live in areas that support the most species. Human population density on both continents was highest in the areas containing the greatest number of species for all animal groups combined, and for each group individually, except reptiles in Australia. The negative relationship with Australian reptiles probably occurs because many of these species occupy the sparsely populated arid and semi-arid regions in the center of the continent. Our results illustrate two crucial points. First, the most biodiverse regions of each continent are also the most threatened by human population density. Second, the level of overlap differs among animal groups, so relying on popular indicator groups (e.g., birds) to set conservation policy may be misleading.

*...The most biodiverse regions of each continent are also the most threatened by human population density.*

### *Endemic and threatened species*

Because threatened species and species with limited distributions are especially susceptible to human interference, we examined their relationships with human population density separately. In Australia, high population density coincided only with a high number of threatened reptiles and birds. In North America, human population density overlapped strongly with the location of threatened species in all animal groups. Relationships between human population density and the percentage of species with restricted geographic ranges were positive for all groups in Australia, and for each group except birds in North America.

Although the outlook is bleak for preserving species that are isolated on patches of land under high human density pressure, we found that a representative sample of almost all species could be conserved, even when avoiding areas of high human population density. Sample preservation is possible because many species occurred in sites of low as well as high human density. Therefore, conservation efforts could be focused on species populations in areas of low human density. In addition, the area required to represent most species is not substantially greater if we avoid regions of high human population density compared to situations where the selection of conservation reserves is unrestricted.

### *Land use planning*

Our results show that it may be possible to reduce conflicts between biodiversity conservation and human settlements. If factors such as population density are explicitly considered when assessing conservation options, only a small increase in the total conservation area will be required.

Two implications of our results could be used in making policy for land use planning, depending on whether the conservation objective is to unilaterally protect species richness or to conserve a representative sample of each species. If the objective is to protect sites with high species richness, then current human population distribution patterns represent a substantial barrier to success. If representation of species is the objective, then careful planning may alleviate the overlap between people and species distributions, although some direct conflict appears inevitable. Local to national governments already influence human distribution patterns at multiple levels through, for example, zoning, land tenure and immigration quotas. If we wish to conserve biodiversity, then future demographic planning must consider species location as an important constraint.

Ultimately, conserving a representative sample of each species is a poor substitute for the protection of local ecosystems and populations throughout their ranges. Local populations of species need to be distributed among these communities because they are the ecological units that confer ecosystem goods and services to humans. This point, along with predicted future population growth in Australia, North America and other regions, underscores the immediate need to develop effective conservation strategies in heavily populated landscapes. Our conservation focus should not be biased towards "wilderness" areas with few people, because these areas may contain only a small number of species (e.g., desert or arctic landscapes). Conservation must also occur where people live.

*Gary Luck was a post-doctoral fellow with the CCB. He is currently a lecturer in the School of Environmental and Information Sciences at Charles Sturt University, Australia. This article is based on work he conducted with Taylor Ricketts (formerly CCB, now at WWF-US), Gretchen Daily (CCB) and Marc Imhoff (NASA).*

CCB is pleased to announce a new publication:

***Butterflies: Ecology and Evolution Taking Flight***

Carol Boggs, Ward Watt and Paul Ehrlich
Editors

University of Chicago Press.

The book synthesizes current studies using butterflies as model systems, showing their contributions to our understanding of ecology and evolution.

## Center Notes

### Transitions

Thanks and farewell to Joan Schwan, who has left CCB to move with her husband and son to Sebastopol. Many thanks to Joan for her work at CCB.

Prof. Gerardo Ceballos has joined us on sabbatical leave from the Universdad Nacional Autonoma de Mexico. He is collaborating with Paul Ehrlich on studies of biodiversity patterns.

Welcome to Karim Al-Khafaji, who is a new graduate student at CCB. Karim plans to apply quantitative approaches to conservation problems. He attended the University of Nevada, Las Vegas where he recieved BS degrees in biological sciences and in civil engineering. Recently he has worked at the US EPA.

Paul Armsworth is a new post-doctoral researcher working with Gretchen Daily on conservation finance. He received his Ph.D. this summer from Stanford, working with Prof. Joan Roughgarden.

Kai Chan has just completed a Ph.D. at Princeton University. He is now doing post-doctoral work with Gretchen Daily on countryside biogeography.

Congratulations to Cagan Sekercioglu, who received his Ph.D. this summer. He is staying on at the CCB for another year as a post-doctoral researcher, to continue work on bird utilization of countryside landscapes.

### Awards

Congratulations to Gretchen C. Daily for her election to the American Academy of Arts and Sciences.

Gretchen Daily has also been named a David H. Smith Senior Scholar by The Nature Conservancy. She is using the award to launch a study on innovative approaches to conservation finance in collaboration with other researchers from Stanford and The Nature Conservancy. As a first step, she and Paul Armsworth convened an international workshop on conservation finance at Stanford. Their overarching aim is to enhance the flow of resources to conservation and to allocate that flow more efficiently. They plan to sustain a major research and outreach effort, involving a symposium in a year's time and a suite of products.

Congratulations to Paul Ehrlich, who was awarded the Fellows' Medal by the California Academy of Sciences, in recognition of his many contributions to systematic and evolutionary biology.

Cagan Sekercioglu received the Environmental and Moral Leadership Award from the Junior Chamber International in recognition of his research activities. The association recognizes ten individuals between the ages of 18 and 40 who exemplify the best attributes of the world's young people.

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is still poorly understood.

Plants, unlike animals, cannot escape deleterious impacts of habitat modification by moving among habitats on a daily or seasonal basis. Immobility has an important implication: fewer native forest plant species than animal species may persist in deforested habitats. Study of herbaceous and shrubby plants offers insight into the capacity of countryside landscapes to support plant species for their entire life cycles and generations to come, and hence may indicate the long-term conservation value of countryside for both the entire flora and the animals that depend on it.

Forest edge habitat close to Las Cruces. *Photo by Margie Mayfield.*

My doctoral work examines the differences and similarities in plant diversity between forested and deforested plant communities in three tropical countryside landscapes. Specifically, I have been studying the diversity and composition of herbaceous and shrubby plant communities in six forested and deforested habitats in three areas of southern Costa Rica. Over the course of two field seasons, one in the summer of 2001, the second in the winter of 2003, my field assistants, Martha Roberts, Daisy Pistey-Lyhne, Elizabeth Wilder, Andrew Prag, Ethan Scott, Berry Brosi, and I sampled 85 sites in six major habitat types. Our site types included three deforested and three forested habitat types. The deforested sites types were pasture, road verges and riverbanks running through pasture. Forested sites were forest understory, tree-fall gaps and riverbanks in primary forest. All site types were sampled three times (except forest river banks which we sampled twice per study area) in three study areas. The three study areas were the Organization for Tropical Studies Las Cruces Biological Station (LC), and around the towns of Pt. Jimenez (PJ) and La Palma (LP) on the Osa Peninsula.

At each site, my field assistants and I recorded the number and abundance of each non-tree plant species in 20 1 x 1 $m^2$ quadrats in an 80 $m^2$ area. We included all non-tree, non-grass flowering plants. In total, we sampled 772 plant species from 83 families, which is approximately 40% of the non-tree plant diversity of this region of Costa Rica. Ron Liesner, Micheal Grayum, Barry Hammel, and numerous other botanists at the Missouri Botanical Garden, the California Academy of Sciences, and INBIO in Costa Rica helped me identify my plant species.

*Between 16 and 20% of species were found growing in both forested and deforested habitats. Thus, the majority of individual native forest species are unable to survive outside of the forest.*

*Species patterns*

I found no significant difference in the average number of plant species per site in deforested and forested sites. However, when we estimated total species richness across all deforested and forested sites, we did find that forested sites as a group were significantly more species rich than all deforested sites. Thus, herbaceous and shrubby species richness within individual locations is not lower in human-deforested areas of these countryside landscapes but may be across the entire landscape. In all three study areas, pasture and understory sites were consistently the most species-poor and tree-fall gaps and road verges near forest were consistently the most species-rich habitats. Species composition showed very low overlap between any of the sites, especially between deforested and forested habitats. Between 16 and 20% of species were found growing in both forested and deforested habitats. Thus, the majority of individual native forest species are unable to survive outside of the forest.

*Explanations for patterns*

Despite the dramatic shift in species composition between forested and deforested habitats, the majority of species in deforested habitats were native species (90% native to Costa Rica). One cause for this pattern might be that the native species in deforested habitats originate from natural ecosystems that we did not sample. However, using Landsat TM satellite images, we evaluated the land use in our LC study area. The majority of non-forest or pasture land was urban area and coffee plantation; habitats that are not likely to have contributed many native species to our plant communities.

Another, more likely, hypothesis about the source of native species in deforested habitats is that the natives are actually ancient exotic species that moved in thousands of years ago and became naturalized to the area. Recent studies of pollen deposits in the LC area have found evidence for human-caused deforestation *ca*. 3000 years ago. Many of the species we now call "native" to Costa Rica could have come from other parts of Central and South America with the first agricultural humans, and remained as fugitive species until the current round of deforestation.

*...[H}abitat heterogeneity in deforested landscapes is important for maximizing the diversity of herbaceous and shrubby plant species.*

A third, non-exclusive hypothesis regarding the origins of native species found in deforested habitats argues that these species come from habitats with long-term natural disturbances. Indeed, most of the native species found in both forested and deforested habitats are forest riverbank species. This result is consistent with studies of the origin of old-field plants in temperate regions. Peter Marks, working in the northeastern USA, found that most native forest species living outside of the local forests originated from permanent marginal forest habitats, such as persistent landslide edges and riverbanks. Unlike plants from tree-fall gaps and other short-term disturbances, species from long-term disturbances are accustomed to high light intensities for extended periods of time, more wind exposure and continuously disturbed soil conditions. Thus, plants from these long-term natural disturbances may be better adapted to life in human-created fields and pastures.

*Implications for the future*

The results from our study agree with the predictions we made about the ability of native forest plant species to survive outside of their original habitats. Only 16% of forest plant species are also found living in deforested habitats. This species proportion is much smaller than was found for birds, butterflies, moths, mammals, amphibians, or reptiles. However, deforested habitats do not appear to be devoid of plant life. In fact, road verge vegetation was one of the most diverse habitat types sampled in my study. One of the most important findings of this study is that each of the surveyed habitats had very different plant species living in them. This observation suggests that habitat heterogeneity in deforested landscapes is important for maximizing the diversity of herbaceous and shrubby plant species.

From a conservation perspective, my study suggests that as many as 80% of specific forest herbaceous and shrubby plant species will be lost if all the tropical forest in Southern Costa Rica is cut. However, the total number of species held in the landscape will not be as dramatically affected. This finding is promising for the conservation of ecological interactions and ecosystem services, which may rely more heavily on functional traits (i.e. pollination resources, edible fruits) than specific plant species. Additionally, patterns at the plant family level suggest that as long as a complex deforested landscape is retained, few families will be lost. This result suggests that despite major changes in species composition these landscapes will retain a phylogenetically deep pool of species for evolutionary processes to work on in the future.

Pasture habitat closly abutting primary rainforest on the Osa Peninsula. *Photo by Margie Mayfield.*

*Margaret Mayfield is a doctoral student in the CCB.*

# Whittled away? Woodcarving, forests, and craft certification

The small shops dotting the stone streets of the city of Oaxaca, Mexico are home to some of the most memorable handicrafts in the world. Inside the shops, travelers can see stacks of exquisitely patterned weavings, burnished black pottery, and, jammed together in a riot of color, pattern, and form, brightly painted woodcarvings called *alebrijes*. The little figures are intoxicating: porcupines armored in a sheaf of multicolored quills, a fanciful dragon in swirls and shimmering dots of color breathing tongues of painted wooden fire, a polka-dotted mermaid playing a purple guitar. Mesmerized by the whimsical carvings, many tourists bring them home by the armload.

*The down-side of local crafts*

Buying local handicrafts as souvenirs makes sense to many travelers; they find a handmade memento of their trip while providing much-needed income to local people. Unfortunately, many buyers are unaware of the secrets that a piece of local art can hide. If a tourist group were to drive out to the villages where *alebrijes* are made, most of the travelers probably would not notice anything unusual. However, the landscape around the villages looks different now than it did only ten or twelve years ago. Although the terrain still holds forestlands, they seem sparse or even bare to people familiar with other Oaxacan dry forests.

The artisans living in these pueblos value the wood of the copal tree, *Bursera glabrifolia* (Burseraceae), for the making of *alebrijes*. The wood carves easily when green but dries hard and very light. It was once an abundant raw material, as copal trees were a dominant part of the diverse dry forests in the hills surrounding these towns. After *alebrijes* exploded onto the international crafts market, artisans changed their method of wood harvest from selectively removing branches to cutting down entire trees. With this change, and the steadily increasing numbers of woodcarvers, the number of copal trees has dropped precipitously. Now copal, once a vital part of the threatened dry forest ecosystem surrounding these villages, is gone.

Because the forests surrounding carving villages were never surveyed ecologically before the exploitation that occurred with the carving boom, it is unknown exactly how many trees were destroyed. However, informal interviews with residents of carving villages have revealed that the trees had been there in profusion, and copal trees are known to be common to Oaxacan dry forests.

According to Dr. Michael Chibnik, a professor of

An array of *alebrijes*—Oaxacan wood carvings—in a village gallery. *Photo by Berry Brosi*

economic anthropology at the University of Iowa who has studied the intricacies of supply and demand for *alebrijes* for more than half a decade, most artisans are now reliant on small-scale copal vendors for their raw materials. As stocks of copal near carving villages have dwindled, suppliers have moved farther away to cut their wood. Most copal vendors run fly-by-night operations, illegally cutting a few pickup truckloads of copal on communal forestlands and quitting before local authorities confront them. Since copal suppliers struggle to stay in business, and copal is becoming rarer, the quality of the wood is lower. Much of it is knotty, too dry, the wrong size, or sometimes not even copal, and artisans won't buy it. Copal vendors may be cutting down hundreds of trees or more every year for nothing. But because copal vendors are breaking the law, exact data on this underground economy are hard to come by.

*Solutions to forest exploitation*

Dr. Silvia Purata of the Instituto de Ecología, a Mexican non-profit organization, started to study *alebrijes* and their effect on the native forest resources. Weighing different alternatives to improve the management of copal, Dr. Purata looked into a process called forest certification. To certify a forest, experts from a third party group like Smartwood (www.smartwood.com), a branch of the Rainforest Alliance, exhaustively look into all aspects of its management. If the forest is found to be managed well using a variety of ecological and social criteria, it can be certified. The timber coming from the forest will then be labeled, alerting consumers that it was produced in an ecologically and socially beneficial manner.

Dr. Purata realized that rural artisans probably could not afford to pay more for certified wood, so she developed a different angle on the same premise: to certify the crafts rather than the wood. If an artisan participated in the certification program, he or she would pay a slightly higher price for certified wood, but would more than make up the extra cost with a price benefit on the finished carvings. As Dr. Purata explains, "Soon tourists and collectors will be able to make a choice and buy *alebrijes* from well-managed wood and thus make a contribution to both the preservation of dry forests and the improvement of people's livelihoods." The plan to certify *alebrijes* includes creating a cooperative network of wood-producing villages to supply artisans with copal. This cooperative will spread out the currently localized geographic impacts on copal and ensure that communities receive a fair price for the wood they sell to artisans. The assurance of reasonable prices for copal would extend the economic benefits of certification to more people while providing a strong incentive to manage copal sustainably.

Mature copal trees in the Oaxacan dry forest (above); a truckload of cut copal being taken to the wood carving villages (left). *Photos by Berry Brosi*

### *Working toward sustainability*

Craft certification does not yet exist, but steps have been taken to sustainably manage the populations of *Bursera glabrifolia* in Oaxacan dry forests. As part of my Master's thesis at Yale University's School of Forestry and Environmental Studies, I worked with Chuck Peters of The New York Botanical Garden and Silvia Purata to produce a management plan for copal in the village of San Juan Bautista Jayacatlán, about 40km north of the city of Oaxaca. The management plan was based on a thorough forest inventory and study of the growth and population dynamics of *B. glabrifolia*, and was designed and implemented with input, field assistance, and oversight by the village. The village contains several thousand hectares of dry forest, and the management plan calls for taking only about one copal tree per hectare per year. The trees will be transported from the felling site to existing roads with burros—meaning no logging roads will be built. This scientifically based, community-considerate strategy garnered the plan approval from SEMARNAT, the Mexican Secretariat of the Environment and Natural Resources. It remains the first and only dry forest management plan to be legally approved in Mexico.

As a result of the forest management plan, Jayacatlán has stopped illegal extraction of copal on their lands and has placed a moratorium on the clearing of dry forest land for agriculture—which is the single largest threat to this endangered ecosystem in Mexico and elsewhere. They are also making an honest profit on the sales of wood, which benefit communal coffers for their school, roads, and other programs. Woodcarvers from the village of Arrazola are happy as well: shipments of wood are high quality and come on a predictable schedule with a reasonable cost.

Hopefully, the finished products made from this wood, *alebrijes*, will one day be certified as sustainable. If the program of *alebrije* certification works, it could be expanded to cover other folk arts made from a variety of forest products—not just timber—all over the world. Handicraft certification means that someday tourists will be able to bring home a cheerful, whimsical *alebrije* or other beautiful handmade craft and feel comfortable that their purchase contributed to the sound management of the world's forests.

*Berry Brosi is a doctoral student at the CCB studying the spatial distribution of pollination services in the human-modified tropical landscape of southern Costa Rica. He worked on a copal management plan during his master's thesis at Yale.*

# Managing Forests for Ecological Sustainability

In 1997, a Committee of Scientists (COS) was appointed by the Secretary of Agriculture to review the scientific basis of management of our National Forests. The Committee was asked to recommend changes to existing laws governing public lands management in order to "...achieve ecological, economic, and social sustainability within a multiple use framework." The Committee responded that ecological sustainability is the foundation on which all other elements rest.

A member of that Committee, Barry Noon, Professor of Wildlife Ecology at Colorado State University, delivered the 15th Annual Boething Lecture on Forests and the Human Predicament in May, 2003 at Stanford. Noon's own research includes work on the population dynamics of the spotted owl and on the sustainable management of Pacific Northwest forests in general. In his lecture, Noon described his view of sustainability, its value as a goal for public lands management, and what will be required to achieve it.

*[Noon] challenged the philosophy that we can simultaneously manage public lands for use, extraction, and conservation. Emphasis must be placed now on intergenerational responsibilities and the importance of equity.*

*Ecological and economic sustainability*

From Noon's perspective, economic sustainability means maintaining at least a subsistence standard for all and at best, an equitable standard of living. He defines social sustainability as the capacity to solve social problems and to maintain an equitable quality of life. Ecological sustainability entails protecting at least the "life support systems" that nature provides us and ideally, some additional measure of environmental quality.

In order to maintain that life support system, Noon further defined ecological sustainability as a state that maintains the characteristic composition, structure, and processes of ecosystems with their historic range of variability. Sustainable ecosystems must also provide healthy habitat for native species and host viable populations of native species abundantly distributed throughout their historic range. A final characteristic important to ecological sustainability is the preservation of the adaptation potential of species and ecosystems.

Because we are depleting natural resources overall well beyond their rate of renewal and rapidly losing essential environmental services, Noon argued that the National Forests should be managed with sustainability as a top priority, providing a refuge for the functioning ecosystems that can continue to supply these services and goods into the future. The Committee of Scientists agreed that the multiple use paradigm has not been effective in sustaining natural resources. For example, Noon described dramatic declines in trees of the largest size classes in U.S. forests just since 1952, since the inception of large-scale timber extraction.

What will it take to improve forest management? Noon suggests that stakeholders—natural resource managers, policy makers, the public that nominally owns these public lands, and everyone who uses their goods and services—need a better understanding of ecology. Some important but long-overlooked or misunderstood elements of natural, ecological systems include the dynamic nature of ecosystems and the importance of natural disturbance processes such as fire. Also, ecosystems are inherently variable and studies of them contain fairly high levels of uncertainty. Finally, Noon stressed the importance of understanding cumulative effects, which may be synergistic and non-linear, and of preserving options for accommodating future changes.

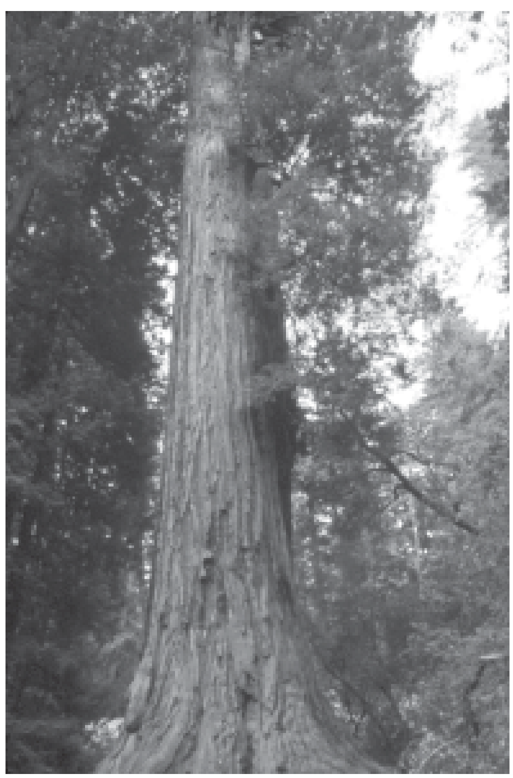


Photo by Cagan Sekercioglu.

*Recommendations*

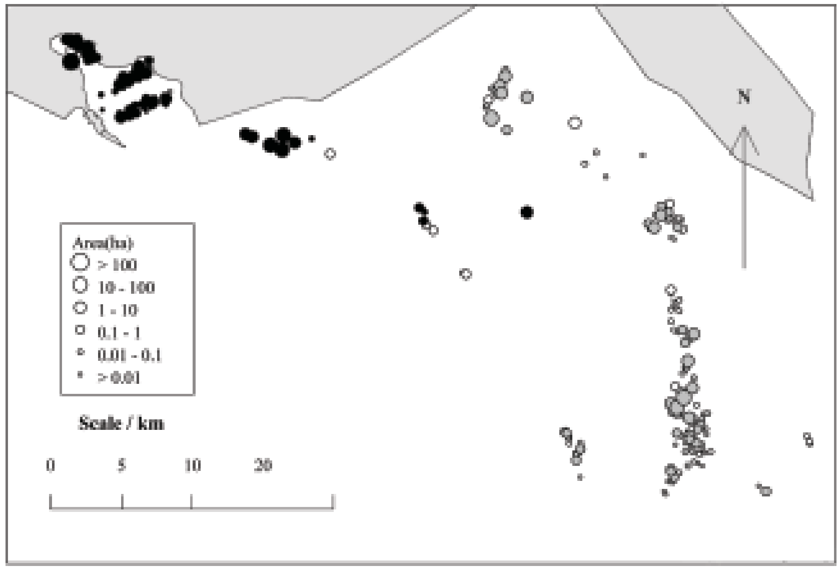
Noon recommended that

see **Boething**, pg. 10

# Conserving genetic diversity: The brown argus butterfly

Conservationists and planners traditionally focus on species preservation, because species have legal status under environmental law. Species preservation, in turn, requires the preservation of the underlying population and genetic diversity (see *Update* vol. 10 #2).

How is genetic diversity lost? One way is through genetic drift, which is defined as changes in the frequency of different variants, or alleles, of a particular gene through time, due to chance events. In a small population, fewer copies of rare variants exist, and a rare variant is more likely to be lost due to chance. Conservation efforts may focus on maintaining populations that are sufficiently large that genetic drift is negligible, or may involve preserving connectedness between populations. As individuals move between populations, carrying their genes with them, they counterbalance the effects of genetic drift by replacing lost alleles through gene flow.




Distribution of *Aricia augustus* habitat in mainland northern Wales. The black dots represent habitats with bivoltine populations and the grey dots represent habitat with univoltine populations. The white dots show locations of unoccupied habitat. *Map by Steve Burke.*

*Two strategies for gene conservation*

It may seem that populations should always be managed to prevent genetic drift by promoting inter-population migration, and therefore gene flow. However, when the genetic make-up of populations differs in a way that is adapted to their local environment, migration may actually reduce the viability of populations through the introduction of variants that are not locally adapted. In such instances, populations may benefit from being managed as independent entities.

The trade-off between the maintenance of diverse genetic variation that provides evolutionary flexibility and the maintenance of specific variants that increase the fitness of individuals in a local environment must inevitably be considered in management decisions. So when should locally adapted populations be managed independently of each other?

*By observing natural experiments taking place in heterogeneous environments, we can understand the population scale necessary for successful gene conservation.*

By observing natural experiments taking place in heterogeneous environments, we can understand the scale necessary for successful gene conservation. My previous butterfly research with colleagues at universities in Birmingham, Leeds, and London in the UK provides a good example of how population structure can affect the distribution of locally adapted traits and genetic diversity.

*The case of the brown argus butterfly*

The brown argus butterfly, *Aricia agestis*, produces two discrete generations each year (bivoltine) throughout most of its range in Europe. Since the butterflies' development must be synchronized with seasonal changes in the environment, the shorter growing season at the very northern edge of its range in northern England and Wales forces the butterflies into a life cycle of one generation a year (univoltine).

In order to understand how the butterflies are adapted to their local environment, we examined populations along an environmental gradient in North Wales. In the western part of this region, low elevation, coastal habitat supports populations that are bivoltine. The eastern landscape is cooler, higher elevation, and farther from the coast; this habitat hosts populations that produce only one generation each year.

We found that the butterflies regulate their development in two ways. First, larvae from bivoltine populations grow faster and pupate earlier than do larvae from univoltine populations, even when reared

see **Gene conservation**, page 10

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in a common environment in the laboratory. Second, univoltine and bivoltine larvae enter diapause (over-wintering suspension of development) at different times of year, using day-length as a cue to the changing seasons. Univoltine larvae from the cooler areas enter diapause earlier in the year than do bivoltine larvae, for which the growing season is a little longer. By delaying diapause and growing faster, bivoltine butterflies are able to take advantage of the longer growing season and produce a second generation every year.

In order to understand the relationship between the local thermal environment and the distribution of these two voltinism types, we modeled the mean daily temperature of each suitable habitat patch in North Wales. Using temperature and larval development rate curves that we established in the lab, we asked which voltinism each population would follow based on our thermal model. The model successfully predicted the voltinism of a population in 138 out of 155 cases.

The remaining 17 misclassified populations shared the same voltinism as surrounding patches, even though their own thermal environment was more suitable for the 'other' voltinism type. High rates of gene flow from nearby populations prevented local adaptation taking place in these misfit populations despite strong selection pressure. Additionally, when these populations go extinct (as they readily do because they are not locally adapted), recolonization comes from these same nearby populations with "maladaptive" voltinism. Thus, individuals within the populations are adapted to the dominant thermal regime in the region rather than being adapted to their own local climate.

*Lessons learned*

Conserving populations that are anomalies within their regions may be seen as futile, but conserving the marginal habitat in which they exist may benefit other populations in the region by providing stepping stones for gene flow. Conservation efforts should be focused at the larger, metapopulation scale of connected populations in order to promote gene flow within each voltinism type and maintain intrapopulation diversity. Sets of populations of each voltinism type should be managed as separate units to conserve locally adapted traits

A clear understanding of the level at which a species interacts with the landscape can provide conservation practitioners with valuable information on how to manage populations and genetic diversity. It is important to balance the need to keep populations diverse while supporting the connections between populations in order to prevent genetic biodiversity loss. Too little connection between populations will lead to genetic drift and extinctions under stress. Too much dispersal between populations can cause homogenization of the gene pool and loss of the benefits that variability provides. Our study of *A. agestis* illustrated that an in-depth knowledge of how genes flow through a species is crucial to understanding the scale necessary to design effective reserves.

*Steve Burke is a post-doctoral fellow at the Center for Conservation Biology. His current research focuses on the interactions among butterfly host-plant use, thermal environment and population structure, and on the genetics of small populations.*

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policy makers should explicitly account for human-nature relations in conservation solutions, and change laws that encourage over-exploitation of natural resources. He also challenged the philosophy that we can simultaneously manage public lands for use, extraction, and conservation. Emphasis must now be placed on intergenerational responsibilities and the importance of equity. Despite the clear mandate of the COS report, the response of the US Forest Service and its future directions are still unsettled. Much depends on the current political climate; substantial legislative changes toward sustainability have yet to be taken. Environmental scientists can help lead the way toward better policy, Noon said, by conducting research relevant to key policy questions, communicating the implications of research to the public and politicians, and making data freely available.

*The Boething Lecture series addresses forest resources and processes, and their relationships to human populations. The annual lecture is sponsored by the Center for Conservation Biology, thanks to the generous support of John and Susan Boething.*

## The Center for Conservation Biology

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The Center for Conservation Biology (CCB) was established in the Department of Biological Sciences at Stanford University in 1984. Our mission is to promote human well-being by developing a scientific basis for managing Earth's life-support systems and for helping arrest environmental deterioration.

In pursuit of this mission, CCB staff conduct scientific and policy research to evaluate factors contributing to the "human predicament"—declining environmental security and increasing inequity—and to find practical solutions to that predicament. Our research integrates biological with economic, anthropological, legal, and other social science perspectives.

Collaboration with others and communication of our findings are important aspects of our work. Our partners include other scientists, social scientists, journalists, conservation practitioners, and members of the business community. Through printed publications and Internet sites, we disseminate our results in these realms and to the public at large.

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