Coffee pollination in tropical fragmented landscapes

About two-thirds of crop plants cultivated globally require animal pollination. Up to one-third of the food Americans consume is derived from animal-pollinated plants. Without insects such as bees (or costly hand-pollination to replace them), we could grow almost no apples, almonds, blueberries, watermelons, sunflowers, or alfalfa, to name just a few crops. Pollination is thus a particularly clear example of the many services provided by ecosystems and their biodiversity that both sustain and enrich human life. Indeed, the economic value of animal pollination has been estimated at $200 billion per year!

For many crops, farmers have often replaced natural pollination services with managed colonies of the introduced European honeybee (*Apis mellifera*). However, the recent difficulties facing honeybee apiculture (e.g., parasites, diseases, and hybridization with Africanized “killer” bees) have sparked a renewed interest in the value of wild pollinators to crops, and in conserving the natural habitats that support these species. Like many other ecosystem services, natural crop pollination is increasingly threatened due to land use practices in agricultural areas, such as pesticides use and habitat conversion.

With other members of the CCB, I have begun a project to address these issues, focusing on coffee

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The underpinnings of human behavior: How flexible are we?

The question of what shapes human behavior—and, implicitly, how much influence we can exert over it ourselves—has intrigued people for millennia. Ancient Greeks including Homer emphasized the role of external forces, in the form of their gods, on the course of people’s everyday lives. A few centuries later, Hippocrates made a case for the internal, physiological roots of human health and malfunction. Today, scientists and laypeople alike ask how, and how much, we are shaped by our genetic heritage and by our external environments. As we work towards greater understanding, the focus of the ceaseless “nature versus nurture” debate swings from one side to the other. CCB President Paul Ehrlich has joined in the inquiry, in his recent book *Human Natures: Genes, Culture, and the Human Prospect*, and in current work with Professor Marc Feldman, Director of Stanford’s Morrison Institute for Population and Resource Studies.

In the first half of the 20th century, biological and social scientists were fascinated by the infant science of genetics. Without any scientific basis, this led to an emphasis on the “nature” side, resulting in, among other things, a racist US public policy on immigration. Then, after World War II, in reaction against Hitler’s genocidal policies, genetic determinism lost favor. Scientists turned their attention to the role that our environment plays in shaping us and our behavior. In recent decades, the pendulum seems to have swung back again toward emphasizing the importance of our genetic inheritance. The field of evolutionary psychology—based on the idea that humans have evolved for most of our history in a certain kind of environment, and that genetic programming in that see *Genetic Determinism*, page 3

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The Tuna Research and Conservation Center

Anyone who has seen a tuna swim cannot help but be impressed with their superbly streamlined body, pectoral fins shaped like airplane wings, and powerful crescent-shaped tails. Tunas also have an amazing lifestyle that has sparked the interest of many biologists. They are unique among bony fish for their endothermy (i.e., being warm-blooded) and are capable of swimming across a major ocean basin in less than 60 days. They are also renowned for their high commercial food value and are sought by fishers throughout the world. Although they constitute less than 5% of the world’s commercial catch by weight, they contribute a much larger fraction by dollar value. One species of tuna, the Atlantic bluefin, *Thunnus thynnus*, is the most valuable fish in the sea and some individuals have sold recently for more than $150,000 on the Tokyo fish market.

Tuna’s open sea lifestyle and highly migratory movements make them difficult to study. A unique collaborative effort centered at the Tuna Research and Conservation Center (TRCC) at Stanford’s Hopkins Marine Station focuses on advancing the understanding of tunas through research, conservation and education. The program combines the resources and personnel of Prof. Barbara Block’s lab at Hopkins Marine Station and the Monterey Bay Aquarium (MBA). Twenty researchers, including the co-directors (Barbara Block and Charles Farwell), veterinarian Dr. Tom Williams, Stanford University graduate and undergraduate students, post-doctoral fellows, research associates, technical staff, MBA aquarists, and visiting scholars, are involved. A large contingent of dedicated and experienced fishers, scientists and volunteers helps carry out field activities. The TRCC program provides a successful model for future partnerships between academic researchers and aquaria, zoos or museum personnel attempting to work together on science conservation and outreach.

At the core of the TRCC program is a unique facility established at Hopkins Marine Station in 1994 for the maintenance of captive tunas—the first such facility in North America. It consists of three holding tanks for tunas and one for smaller fish. Each tank has its own life-support system. The tunas are held in two tanks that hold 30,000 gallons (109 m³) each and one large tank of 90,000 gallons (327 m³). All are served by pumps, high speed sand filters, aeration tower and protein fractionator tower to provide high quality sea water, a must for open sea organisms. The MBA also maintains tunas on exhibit in a one million-gallon capacity tank. The largest and oldest tunas in our collection are in the MBA facility. The TRCC played a key role in establishing MBA’s Outer Bay Window, an extraordinary exhibit which provides the North American public their first view of tunas in captivity—and inspires conservation of pelagic fish. Data on feeding, growth and behavior are also obtained from this collection.

A tuna at the TRCC with experimental tag installed. *Photo courtesy of TRCC.*

### Center Notes

#### Awards

Undergraduates David Goehring and Lisa Walling received Firestone Medals for their senior honors theses. These medals recognize the top 10% of honors theses done at Stanford each year. David’s work, with Gretchen Daily, explored the relationship between the keystone species concept and community structure as represented by species interaction strengths. Lisa’s work, with Carol Boggs, explored phylogenetic aspects of butterfly feeding habits. Congratulations to both!

CCB collaborator Jose Sarukhán received a 2001 Distinguished Service Award from the Society for Conservation Biology in the Individual in Government category. This award was given in recognition of Sarukhán’s leadership in using diverse mechanisms to coordinate and implement conservation activities and national environmental policy in Mexico. The award will be presented at the 2001 meeting of the Society for Conservation Biology in Hilo, Hawaii, later this summer.

#### Comings and Goings

CCB collaborator Jessica Hellmann will be leaving Stanford’s Institute for International Studies in the fall to begin a postdoctoral fellowship at the University of British Columbia in the Centre for Biodiversity Research. Claire Kremen, senior research scientist at the CCB, will also leave in the fall to begin a faculty position at Princeton University. Research associate Diane O’Brien will be away temporarily teaching at Swarthmore College. Erika DuRoss, a research assistant, is moving to Utah. Congratulations and best wishes to all!

We welcome Jack Liu, who will be here on sabbatical from Michigan State University; Henrique Pereira, who will begin a postdoctoral fellowship; and Jai Ranganathan, a first-year doctoral student.

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Genetic Determinism, continued from front page

ancient environment is what has shaped our behaviors even today—has garnered public interest. Ehrlich speculates that this latest “swing” may be a response to our most recent blossoming of understanding of genetic material itself.

In Human Natures, Ehrlich lays out evidence for a different approach to the debate. He acknowledges the importance of our genetic heritage in shaping us in fundamental ways. For instance, because our visual systems are our most keenly developed senses, we tend to respond most to the visual information we encounter in our environment. If our chemical sensory systems were more highly developed, and we could smell with the keenness of dogs, we might respond much more strongly to invisible changes in our chemical environment, like toxins in our air and water.

But the passion of the nature-nurture debate doesn’t stem from examples like that one. Ehrlich points out that the critical social question at hand, the reason this debate is so heated, is really this: how much of our noteworthy everyday behaviors, our personality and individual qualities, and the differences in these traits among individuals or groups, can be traced to our genes? The kinds of behaviors people really want to know about are sensitive topics such as differences in female and male mating behavior, differences in individuals’ tendency toward aggression or degree of problem-solving skill, and the like.

In Human Natures, Ehrlich questions the capacity of our genome to prescribe such details of our personalities and everyday behaviors. He sees more parsimonious ways to explain human behavior. Essentially, he concludes instead that our genetic inheritance provides us with a big brain capable of great flexibility in responding to our ever-changing environment, of assessing a wide range of situations, and of discovering how to adapt to them.

For example, evolutionary psychologists have postulated that mate preference tendencies are programmed by genetics, and further, that women and men inherit different reproductive strategies in their respective genomes. In this school of thought, women are commonly believed to have the genetically-based proclivity to seek dependable, generous, intelligent, and socially powerful mates. Ehrlich questions this. If these assumptions about what women prefer in mates are accurate, they could just as easily—and much more parsimoniously—be explained by the alternative evolutionary explanation that, as he puts it, women (and men too) “evolved big brains and aren’t stupid.” The genetic evolution of a flexible intelligence can easily explain observed patterns in human behaviors such as choice of a spouse. Also, Ehrlich notes that we have no evidence to show that gene-based differences in mate preference have ever existed among populations of women, nor that women who sought certain characteristics in mates have had greater reproductive success. Such evidence would be critical to lend credence to the less frugal of the evolutionary explanations.

Another weakness Ehrlich points out in genetic determinism is in its proponents’ assumptions about the connection between DNA and behavior. There certainly are some examples of clear links between heritable disease and behavior disorders, such as Huntington’s disease, which causes neurological disorders that may lead to manic-depressive or schizophrenia-like illness. But at the level of personality differences among healthy individuals or groups, biologists actually know very little about exactly what a pathway might be from the base pairs in our DNA to our everyday behaviors. Just the scale of the task of guiding the fine details of our behavior makes much genetic influence improbable. While humans have on the order of 100,000 genes, our brains have over a trillion nerve cells, and about 100 to 1,000 trillion synapses among them. Since we have only three times as many genes as fruit flies, and 98% of our DNA sequence is the same as chimps, the evolutionary pressure toward enabling the environment to “program” the brain to generate adaptive behaviors becomes clear.

Of course, one could argue that our genes may simply set a chain of development in motion, which could shape behavior as surely as other such chains shape our intricate physiological development. But Ehrlich suggests that our behavioral success depends more on flexibility and plasticity in response to rapidly changing cultural, social and other environmental demands. Our genes have evolved, and operate, in terribly complex synchrony with one another; the genetic fine-tuning of a particular behavior seems inefficient, slow, and highly improbable.

Ehrlich argues that cultural evolution, on the other hand, is abundantly able to guide and shape us. The body of information that humans have gathered outside of our genes is immense. How that body of information—the cultural analog of the collective human genome—changes, and how it shapes us, is still largely uncharted territory. He suggests that if we want to know more about why we behave as we do, we will do well to start exploring.

Joan Schwan is assistant director of the CCB.

Coffee, continued from front page

crops in Costa Rica. The overall goals of the project are to determine the ecological importance of wild pollinators to coffee production, to evaluate the importance of native forest habitats as sources of these pollinators, and thus to estimate the economic value of forest fragments to coffee farmers. Two other researchers at the CCB (Claire Kremen and Margie Mayfield) are also pursuing projects on pollination services, making the Center a focal point for such work.

Coffee and its pollinators

Coffee is the world’s #2 international commodity (behind petroleum) in terms of dollar value of exports, and about 10 billion pounds of it are produced globally every year. Native to the Ethiopian highlands, Coffea arabica has been cultivated all over the world in areas with amenable climates. In Costa Rica,
13th Annual Boething Lecture

Negotiating Nature: Saving Urban Forests

King County, Washington extends from the Puget Sound east into the Cascades. It includes Seattle, the tenth fastest-growing county in the US, and yet 2/3 of the county is still covered by forest. In the 13th Annual Boething Lecture on Forests and the Human Predicament, King County Executive Ron Sims articulated a personal commitment to maintain the county’s forestland and to improve the quality of life for generations to come: ensuring clean air, clean water, and losing no plant or animal species while he is in office.

Sims and his staff consult extensively with biologists, engineers, and other scientists to inform their policy choices. One of the lessons they’ve learned from these advisors is that healthy natural systems provide essential services that the county could scarcely hope to purchase. Sims considers the 800,000 acres of parks and forestland in his county to be its “lungs,” removing air pollutants and providing carbon dioxide sinks. Those lands also provide habitat for valued (and threatened) salmon, and storm water management services (critical to a water-rich urban area like Seattle) that no human-made system could match. Healthy forestlands are important to King County in other ways too: the timber, paper, and recreation industries all have central roles there.

Sims has initiated many policies to protect forestland. “Forest production districts” have been established, a transfer of development rights program exists, and tax incentives are offered to landowners who maintain their property in forestland. An urban growth boundary is in place. The county works to restore areas where land use practices have degraded habitat quality. A biosolids program treats all of the county’s sewage and applies it as fertilizer or soil amendment to forest and cropland.

Many politicians work hard to forge what they see as positive changes for their communities, but find their work undone by the next administration. Sims feels strongly about protecting forestland “in perpetuity,” and aims to achieve this by working extensively with non-profits like the Trust for Public Land and the local Cascade Conservancy. Using a variety of arrangements, the county, non-profits, and sometimes other agencies as well cooperate to establish lasting protection for the land that won’t simply change with the whim of a new county administration.

The Boething Lecture series addresses forest resources and processes, and their relationships to human populations. The annual lecture is sponsored by the CCB with the support of John and Sue Boething.

Fourth Holm/Thomas Lecture

The Biodiversity and Ecosystem Functioning Debate: Insights from a Seven Year Experiment

Is a more diverse ecosystem inherently a more productive one? A more stable one? Ecologists have not yet reached consensus on the answers. Because solid evidence on these questions may have important implications for conservation planning and policy, the debate has been lively. For the Fourth Holm/Thomas Lecture, Dr. David Tilman, McKnight Presidential Professor of Ecology of the University of Minnesota, brought his own set of long-term data to bear on the matter.

Tilman and colleagues began their study in 1994 at Cedar Creek Natural History Area in Minnesota. On 20 acres of prairie, they laid out hundreds of plots. In each they established a subset of locally native perennial prairie species, then collected data on biomass productivity and other measures of ecosystem function. They found that plots with greater numbers of species tended to produce more biomass over a season than plots with fewer species.

Various mechanisms might contribute to this correlation. Perhaps greater diversity means that a system is more likely to include a particular, dominant, highly productive species. Or maybe complementary interactions among species, which are more likely to occur at higher diversity, lead to greater productivity. Early in the experiment, the first hypothesis was a reasonable fit with Tilman’s data. But after several more years of observation, Tilman grew more confident in the latter hypothesis. When plots with different numbers of species were compared, more species always meant more biomass produced, with no evident upper limit to the relationship.

In his upcoming work, Tilman will be exploring the practical application of what he’s learned: How much diversity is needed on a regional basis to maintain the ecosystem functions that people value and rely on?

The Holm/Thomas Lecture series is sponsored by the Department of Biological Sciences in honor and memory of Richard W. Holm and John H. Thomas, former professors of Biological Sciences.

Joan Schwan is assistant director of the CCB.

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Most of the program’s tunas are collected at sea 500-800 miles from Monterey. The logistics of capture and transport sea and truck transport on land. Working together, MBA and Stanford personnel have overcome many obstacles (such as how to transport tunas up the highway from Scripps to Monterey!) to bring the tunas into captivity. Among the most valuable accomplishments of the captive tuna program are a variety of new handling techniques (stretchers, vinyl slings and mats) that help reduce stress when tunas are captured for sampling. In particular, obtaining blood samples has become a routine and reliable means for assessing a variety of physiological parameters. Mortality at both facilities is less than 10%, primarily due to careful study of the diet and husbandry needs of the fish. Tunas have been at the MBA exhibit for over six years and several yellowfin and a single bluefin are now approaching the 100 kg size. Tunas in the tank have the potential to grow to over 400 kg.

The tuna populations at the TRCC serve as a focal point for research on the basic biology of this family of fishes, with an emphasis on the development of tagging technology, physiology, biomechanics and captive husbandry. The TRCC has pioneered the use of electronic tag technologies for tracking the movements, diving behavior and physiology of open sea fish. We have established an open ocean research program, called Tag-A-Giant (TAG), aimed at deploying archival tag technology on wild Atlantic bluefin tunas. The major objectives of the TAG research program are to collaboratively develop archival and satellite technologies with engineers, and to tag bluefin tuna in the wild to obtain detailed information on their migration and biology. To date over 475 electronic tags have been deployed in the open ocean. Most of our tag deployments have been implantable archival tags—miniature computers which are inserted into the fish. The tag “wakes up” every two minutes and collects data from sensors that provide information on internal body temperature, ambient temperature, depth and light intensity. From light intensity and corresponding estimates of sunrise and sunset times, it is possible to determine the geolocation of fish between the time of release and recapture. Depth and temperature data allow us to monitor behavior in relation to oceanographic conditions.

We also use a pop-up satellite tag designed to detach from the fish after recording data, then float to the surface where it transmits that information to satellites. Over 200 have been placed in bluefin tuna across the North Atlantic, and we plan to implant 200 more by the year 2003. We hope to provide international fisheries managers with a large data set on the migratory habits, breeding grounds, and mixing rates of western Atlantic bluefin tuna. Such data is crucial to making management decisions about the species that will help ensure its future survival.

Researchers are also using molecular technologies to discern biological stock structure of highly migratory species. Swordfish and bluefin are both being examined with mitochondrial DNA and microsatellite genetic markers. We think it will eventually be possible to compare estimates of gene flow and migration rate obtained from genetic analysis to those obtained from tagging data.

A new initiative called the Tagging of Pacific Pelagics (TOPP) is currently being organized with the leadership of the TRCC staff and collaborators from surrounding institutions (National Marine Fisheries Service, UC Santa Cruz). A pilot project of the Census of Marine Life (sponsored by the Sloan Foundation), TOPP will provide the opportunity to examine multiple species in the North Pacific. Researchers will use electronic tags to study the distribution and behavior of marine vertebrates and large squid relative to the ocean environment. The project will use the tagging-bearing animals as “ocean profilers” to define the oceanographic regions of critical interest, providing an organism-eye view of several interactive oceanic regimes. We aim to generate a detailed understanding of how marine animals from several trophic levels use distinct oceanic regions: the Continental Shelf System stretching from Baja California to the Aleutians; the pelagic realm of the Subarctic and the Subtropical Transition Zones and Central and Alaska Gyres; and complex current systems including the California Current and the Alaska Coastal Current. TRCC researchers will be examining the movements of Pacific bluefin tuna, white sharks and salmon sharks as part of this new initiative.

Support for the research program conducted at the TRCC has been garnered from federal funding agencies (NSF, NIH, NOAA, NMFS, California Sea Grant) as well as private foundations and societies (Packard, Pew, MacArthur, Prothro Foundations, Disney, National Geographic Society). Both the Monterey Bay Aquarium Foundation and Stanford University contribute generously to the operation and support of the facility and researchers.

Prof. Barbara Block is co-director of the Tuna Research and Conservation Center at Stanford University’s Hopkins Marine Station. To learn more about the TRCC, see: http://www.tunaresearch.org/
Local adaptation in butterflies along an elevational gradient: A source of biodiversity

Global warming threatens many of our ecosystems, but among the most vulnerable are montane habitats. An increase in temperature may lead to the movement of climatic zones upwards in elevation, with an inevitable loss of the highest habitats and their inhabitants. Since mountains are a rich source of endemic species, it is important to understand and preserve these hotspots. Although efforts are underway to protect many montane species, that alone may not be enough. We should not only be concerned about maintaining existing species, but also make an effort to protect the processes underlying biodiversity.

The species richness of montane habitats is thought to have two main causes. Many species living at high elevation are relics from the last Ice Age. When the ice caps retreated, and the land started to warm up, mountaintops provided isolated refugia for cold-adapted species. It was this isolation that led to the abundance of endemics we see today, as lack of gene flow between mountaintops caused populations to slowly drift apart into separate species. For those species we need species protection programs, as we obviously cannot duplicate the evolutionary process that led to their existence.

The second reason why montane habitats are rich in biodiversity is their large variety of niches on a relatively small geographic scale. Elevational gradients create a wide range of environmental conditions over short distances. Species occurring over such a range often develop into different ecotypes (or forms), each adapted to their own subset of environmental conditions.

Beyond being a source of current biodiversity, intra-specific genetic variation may also provide the raw material for speciation, and hence contribute to the long-term maintenance of biodiversity. This process is the topic of much discussion among evolutionary ecologists, because there is no direct evidence yet that speciation is actually taking place along continuous ecological gradients.

My research addresses local adaptation and the process of divergence across an elevational gradient in clouded sulphur butterflies (Colias philodice eriphyle) in the Colorado Rocky Mountains. Although the clouded sulphur itself is a very common species, insights into its ecology and evolution could help us understand how to protect threatened species and evolutionary processes taking place along ecological gradients.

In the Rocky Mountains, C. p. eriphyle occur from 5000 ft to 9300 ft and experience a wide range of environmental conditions, including ambient temperature. Earlier work by Ward Watt and co-workers in Stanford's Biology Department showed that, in Colias, temperature is a major factor in successful reproduction because many activities such as mating, oviposition and nectaring are achieved only at a high and narrow range of body temperatures. To raise their body temperature, Colias bask in the sun with their wings closed, relying on their wings to absorb the solar energy. Butterfly wings consist of a fine mosaic of tiny scales, which in Colias can be yellow or black (melanized). A higher number of melanized scales allows more sunlight to be absorbed and therefore a greater increase in body temperature.

The first part of my research focuses on whether there is heritable variation in wing color, which may help those populations adapt to changing climate conditions, and would supply the raw material for the formation of new species. By measuring the degree of wing melanization of individuals across the whole gradient, I was able to show that there is a steep cline in wing melanization across elevations. High elevation populations are much darker than their low elevation counterparts. From breeding experiments, we know that this difference is in large part determined by genetic variation. Hence, there is significant intra-specific genetic variation in C. p. eriphyle, which is maintained by local adaptation across the elevational gradient.

However, dispersal of individuals across elevations may counteract further divergence if dispersing individuals are able to spread their genes through mating or egg laying at different elevations. For speciation to occur, reproductive isolation between high and low elevation populations would be required. Therefore, I also study the effect of wing color on mating success. I created paper decoy female butterflies with different degrees of wing melanization, and exposed them to wild males at different elevations. If some degree of reproductive isolation across elevations had already evolved, I would expect to see assortative mating; i.e., male preference for those decoy females that most resembled resident females.

However, my results were not as expected. Males preferentially mated less melanized, yellower females at all elevations, even in the highest population where resident males and females were heavily melanized. This means that low elevation

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Pollination services in California: Native bee communities can do the job!

Native bee pollinators provide essential pollination services for both native plant species and for agricultural crops. They promote the reproduction and long-term survival of native plant populations, and increase yields of fruit, vegetable and seed crops. Native bee species often depend on natural habitat for food and nesting resources, and may migrate between natural areas and agricultural areas seasonally. Thus they provide a link between natural and agricultural landscapes, and are indeed essential for the sustenance of both systems.

Until recently, the critical services provided by native bees have been largely ignored. Currently, however, the principal pollinator managed for agriculture in the United States, the European honeybee, is under threat from diseases, loss of the apiiculture subsidy, and the inexorable northward spread of the Africanized honeybee. The Africanized honeybee is an aggressive honeybee strain that hybridizes readily with managed colonies, conferring its aggressive traits. Its arrival in an area potentially spells the end of apiiculture in the region. Thus native bees, which are not affected by the Africanized bee, are likely to become increasingly important for providing pollination services to agriculture.

However, at the same time, humans may be jeopardizing native bees’ ability to provide pollination services in both agricultural and native systems by destroying or damaging their habitat. Habitat destruction leads to the isolation of small patches of natural habitat in a potentially unfriendly matrix of agricultural, urban and industrial land uses. These patches often do not provide enough undisturbed habitat for nesting, roosting and foraging of bees, or the full complement of plants that flower sequentially and provide food for bees across the season. Bee populations may decline as a result. Further declines may occur when bees venture out to seek additional resources in neighboring agricultural areas – where they may be blasted with toxic chemicals used to control crop pests.

Recognizing the value of native bees as pollinators of our food could provide new incentives for conserving natural areas as habitat for bees, and for reducing the use of toxic chemicals in agricultural production. With these aims in mind, for the past three years I have been studying the role of native bees in crop pollination in California, one of the most productive agricultural regions in the world.

With several collaborators at the University of California at Davis (Drs. Robbin Thorp and Bob Bugg), I have identified a complex of approximately 30 native bee species that visit a wide variety of crops in Yolo and Solano Counties of northern California, including watermelon, muskmelon, strawberry, eggplant, tomato and sunflower. In some species, visits by native bees make up 90% or more of the insect visits to the crop, even when managed honeybee colonies are nearby! Using various trapping methods, we have found that most of these native bee crop visitors also occur in natural habitats – riparian forests, chaparral and oak woodland mosaics, or both. The potential therefore exists for natural habitats to provide critical resources allowing the survival of these native bees and supporting them as potential crop pollinators.

Watermelon as a pollination services “indicator”

To examine how natural habitat influences pollination services on crops, I focused on one crop, watermelon, that attracts over 25 of the 30 species of native bees that we observed on crops. Most of these bees also visit other crops. Watermelon depends entirely on insect pollinators for reproduction, unlike some other plants that are partially or fully self-fertile. Watermelon has separate male and female flowers, and large, sticky pollen grains that cannot be transported by wind. They are adapted to cling to the body of an insect, which transports them to the stigma of the female flower. This stigma is also sticky, and most visits will result in transfer from the bee’s body to the stigma.

Watermelon has heavy pollination requirements – it needs approximately 1,000 grains of pollen delivered in order to produce a marketable fruit! As you know from summer picnics, watermelon contains many seeds. Each of these seeds is the product of the successful fertilization of a single ovum by a single pollen grain. Additional pollen grains are needed, however, above and beyond the number of ova, because each pollen grain landing on the stigma helps to stimulate the growth of the pollen tubes down to the ova that allow fertilization to occur. If only a few pollen grains land on the stigma, then either the fruit will abort, or it will grow into a small, misshapen fruit (see page 9) – and not a very tasty one either! The see Bees, page 8
Coffee, continued from page 3

Coffee blooms in the dry season (January-April), typically in a series of synchronized “tours” that turn the landscape into a sea of fragrant white flowers. Coffee flowers are actually autogamous, meaning they can fertilize themselves with their own pollen. Several studies have shown, however, that insect pollination results in significantly higher yields, both in terms of fruit set and seed (“bean”) weight.

Coffee flowers are visited mostly by bees, both feral honeybees (i.e., those living in the wild, not in managed hives) and about 10 native species in the family Meliponinae. All of these bees are thought to nest primarily in tree cavities, and all of them are social, meaning they maintain hives that are active year-round. These bees, therefore, are likely to depend on forest habitats, both as a source of nest sites and as a year-round source of nectar and pollen. At one time, beekeepers managed *Apis mellifera* for honey production in this region of Costa Rica. Now, however, we could find no local honeybee keepers, mainly due to the low prices for honey, the increased difficulty and expense of keeping hives free of parasites and other disease, and the dangers of managing Africanized bees.

Our project

To investigate the importance of pollinators (and thus natural habitats) to coffee production, we want to know two things. First, are visits by bees more frequent in coffee fields near forests than in those further away? If bees nest in forest and forage within a limited radius, we would expect higher visitation rates near forests. Second, do coffee yields also decline with distance from forest? In other words, if coffee fields close to forest enjoy higher visitation rates by bees, does that translate into higher yields as well?

To address these two questions, we are comparing plots of coffee that lie different distances, up to 2 km, away from forest patches. We began by simply observing bee visits to coffee flowers and found that the diversity, abundance, and visitation rate of bees was significantly higher in plots near forest (<100 m) than further away (>1 km). In addition, we are currently counting pollen grains on flowers collected from each plot to determine whether pollen deposition is also higher in near plots (any sharp-eyed and patient volunteers?).

To examine the impact of these geographic patterns on coffee yields, we have established pollination experiments in each plot. We cover some branches with mesh bags to exclude bee visits, pollinate others by hand to ensure fully adequate pollination, and leave a third group open to ambient pollination levels. By comparing the yields of open branches to those of hand-pollinated branches, for example, we can determine the effectiveness of wild pollinators. By then comparing sites along our distance gradient, we can see whether the higher bee visitation rates near the forest result in more adequate pollination and therefore higher coffee yields, compared to plants more distant from forest. Unfortunately, the answer to this will have to wait until we can harvest our coffee in November.

Our long-term goals

We have two long-term goals in this project. First, we hope to illuminate the ecological interactions between native and agricultural habitats in fragmented landscapes. These interactions are ultimately what will determine the ability of these lands to both support native biodiversity and sustain human economies. This holistic view is crucial because the futures of perhaps the majority of earth's species lie in landscapes dominated by the activities of *Homo sapiens*.

Second, we plan to use our ecological findings, in collaboration with economists, to estimate the value of native forests as sources of pollination services to coffee crops. This would be a first step toward valuing tropical forests for the ecosystem services they confer, and may provide a powerful argument, based in the welfare of local people, for forest conservation.

Finally, depending on the results of our integrated ecological and economic analyses, we plan to work with land management agencies and regional coffee co-ops to develop recommendations that will help ensure adequate pollination services across the landscape. We hope this project will launch a longer-term collaboration with farmers, local agencies, ecologists, and economists to develop land-use strategies that will both protect native biodiversity and safeguard ecosystem services on which local people depend.

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Taylor Ricketts is a postdoctoral fellow at the CCB.

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plant allocates the bulk of its photosynthetic resources to the fruits most likely to produce lots of seeds. A nice, large, sweet fruit will attract birds and mammals that can serve as dispersers of its abundant seeds.

Because of its heavy pollination requirements and large diversity of native bee visitors, watermelon is a good “indicator” for pollination services. If the bee community is healthy enough to provide for the pollination requirements of

see Bees, page 9
Bees, continued from page 8

watermelon, chances are it is healthy enough to provide for the pollination needs of other, less demanding crops.

By looking at visitation rates by native bees across 38 farms – some organic farms located within a natural area matrix, some organic farms located with an agricultural matrix, and some conventional farms that use a variety of pesticides – we were able to see that farms located within a natural area matrix receive significantly more bees than farms located within an agricultural matrix. In addition, organic farms receive significantly more native bee visits than conventional farms.

How do these differences in visitation translate into pollination? To understand the relationship between bee visitation rates and pollination, we conducted detailed experiments to quantify the average number of pollen grains left on female stigmas after a single visit from bees of different species. To do this, we prevented any visitation to female flowers by placing an exclusion bag made of bridal veil over the unopened female flowers. Once the flowers had opened, we put a small cage around the flower, unbagged it, and introduced a bee that we had collected within the previous 15 minutes foraging on another watermelon flower. Once the bee had visited the caged flower, we collected the stigma, stained it for pollen grains, squashed it and “read” the slide (counting every pollen grain) under a microscope.

As it turns out, bees don’t behave naturally in confined conditions, and thus we spent months to collect a tiny data set. Nonetheless, what we found is that tiny to small bees deposit minute quantities of pollen – around 10 grains per visit – while medium to large bees may deposit hundreds of grains in a single visit. When combined with our visitation data, we could then determine not only which species contributed the most to watermelon pollination, but also how many pollen grains any female flower would be likely to receive during her entire lifetime in a given farm situation.

What we found is that the native bee community on organic farms in the natural area matrix can deliver 1000 or more pollen grains to each female flower, enough to produce a marketable fruit. However, native bees were neither abundant nor diverse enough on organic farms within the agricultural matrix or on conventional farms to provide sufficient pollination. These farms are only successful in producing watermelon currently because they import managed honeybees to support the pollination needs of the crop. If honeybees were to become scarce, these farmers would no longer be able to grow crops such as watermelon that require bee pollinators. Certain crops would then become scarce, prices would increase, and consumers would lose their “consumer surplus” – i.e., the advantage consumers enjoy when prices are low compared to what they are willing to pay.

Maintaining native bee populations

Given these results, it would be prudent to take steps to maintain our native bee communities across wild and agricultural landscapes. These creatures provide an important “insurance policy,” providing pollination services if managed pollination should fail. Although we are still working out the details, we already know a lot about how to protect these important animals:

- Protect source areas (areas of natural habitat where native bees can thrive).
- Buffer these important areas from the negative effects of pesticides by locating organic, rather than conventional, farms adjacent to them.
- Maintain the diversity of floral resources in the agricultural landscape by maintaining weedy borders, planting mixed crops, cover-cropping, and planting hedgerows and gardens that attract beneficial insects.
- Reduce the use of pesticides in the environment.

These tenets are none other than principles of good agricultural management – and they provide many benefits beyond pollination. I hope that these results will help encourage farmers to grow crops in a more sustainable fashion, one that recognizes the many benefits available from the natural world and that attempts to preserve a harmony between agriculture and nature.

Claire Kremen is a senior research scientist with the CCB.

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females that migrate upward should have increased mating success compared to the resident females and thus be able to spread their genes in high elevation populations. As a consequence, the potential for speciation to occur in this Colias system at this moment is fairly small. A change in male mate preference would be necessary for reproductive isolation to evolve.

Research on species distributions and adaptation processes across elevational gradients is not only important for current species conservation, but also illustrates the role of montane habitats as a source of genetic variation and biodiversity in the future. Beyond individual species-conservation programs, our best shot at preserving long-term biodiversity in montane regions is to protect genetic diversity over the whole elevational range, not only in the most limited habitats at the mountaintop.

Jainiba Eppers is a postdoctoral fellow at the CCB.


Report on conservation activities associated with the San Francisquito and Matadero watersheds. Holtgrieve, G. and AE Launer. 2000. (Initially distributed to Stanford University, the US Fish and Wildlife Service, California Department of Fish and Game, and Santa Clara County.)


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The Center for Conservation Biology (CCB) was established in the Department of Biological Sciences at Stanford University in 1984. Its mission is to promote human well-being by developing scientific basis for managing Earth’s life-support systems and helping arrest environmental deterioration. In so doing it fosters wide collaboration with other scientists, social scientists, journalists, and representatives of NGOs, Federal and State agencies, and the business community. It disseminates its findings widely. In pursuit of this mission, the CCB conducts scientific and policy research to build a sound basis for the conservation, management, and restoration of Earth’s biotic resources, to evaluate factors that are leading to the “human predicament” (declining environmental security, increasing inequity) and to find practical solutions to that predicament. Its research integrates biological with economic, anthropological, legal, and other social science perspectives.

The CCB publishes its Update bi-annually and Ecofables/Ecoscience occasionally on the Web. The CCB maintains a Connections website http://ccb.stanford.edu/connections/ designed to aid journalists in their coverage of environmental issues.

Do you know of a teacher looking for relevant, engaging biology or environmental science materials? We have extra back copies of some CCB publications: the Update, Ecotono (the Spanish-language newsletter of our tropical education program), and Ecofables/Ecoscience (an occasional publication exploring, and countering, the distortion of environmental science). They all include brief, accessible, relevant articles that could be great assets in a high school science classroom or in a community environmental resource center. If you know of any worthy groups that might make good use of some of these publications in quantities large or small, please contact Joan Schwan (650-723-3237).

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