tion has occurred recently within the reserve boundaries (Fig. 2), and continual clearing in the reserve has been reported (*32*). Soil no longer protected by forest is subject to rapid erosion from intense rainstorms and frequent hurricanes, and erosion rates as high as 250 tons of soil per hectare have been reported (*33*).

This study provides an example of how remote sensing data can be used to map forest extent and to monitor deforestation. Landsat images are already available for most of Earth's tropical forests. Many of these images are nearly two decades old and thus provide a remarkable but essentially unused database.

Sustainable agriculture and agroforestry to provide local inhabitants with needed food and fuel, accompanied by reduction of population growth, are among the prerequisites for effective tropical rain forest preservation. Detailed ethnographic studies addressing the social and economic needs of local peoples are needed if these efforts are to succeed.

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Code of Ant-Plant Mutualism Broken by Parasite

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Newly discovered *Phyllobaenus* beetles are parasites of a mutualism. *Piper* ant-plants in tropical forests provide lipid and protein-rich food cells and shelter for *Pheidole bicornis* ants while the ants remove small herbivores and vines from the foliage. In contrast to all other ant-plants, *Piper* ant-plants produce food bodies only when *Pheidole bicornis* is present in the plant. However, *Phyllobaenus* beetles can stimulate the plants to produce food bodies as if ants were present. The beetles then inhabit the plant, exploiting nest sites and food produced by the plants for ants. These beetles may also prey on ant brood, depriving the plants of resources and services provided by the ants.

PARASITES OF MUTUALISMS EXPLOIT the resources or services of the mutualists without providing reciprocal benefits (*1*). Previous examples of a third species that derives benefits from both interacting mutualists while benefitting neither have at least one characteristic in common: the parasitism depends on a mimetic relationship (*1*). These include palatable butterflies that resemble and associate with Mullerian mimics and nectarless flowers that receive pollinator visits because they resemble flowers that have functioning nectaries. I present evidence of a novel association lacking a mimetic relationship in which a parasite takes advantage of two interacting mutualists. A newly discovered predator of ants can stimulate a plant's cells to become engorged with lipids and proteins, thus providing food for the predator's subsistence in the absence of its prey (*2*). When ants are present, the predatory beetle eventually destroys the colony and feeds on the brood within the plant.

The plants, several species of *Piper* treelets in the understory of mature, tropical forests of Costa Rica, are inhabited by *Pheidole bicornis* ants. Ants reside initially in hollow petiole chambers. As the colony grows, the workers hollow out the stem and the entire plant becomes a domicile. Hundreds of single-celled, opalescent food bodies, rich in lipids and proteins, are produced by the plant on the adaxial surface of the petiole chambers; *P. bicornis* ants collect and consume the food bodies. The ants may provide dual benefits to the plant through nutrient provision and through plant defense from herbivores and vines (*3*).

Unlike all other known ant-plants, food production by *Piper* is induced by its ant inhabitants (*4*). The production of food bodies nearly ceases when *P. bicornis* is removed from the plant, and food body production commences again when the ants reinvade. Under natural conditions, *Piper* ant-plants rarely lack ant colonies. However, I recently discovered an unusual population of *Piper obliquum* in Carara Biological Reserve, Puntarenas, Costa Rica, in which plants with ants were rare (*5*). The other plants had no external signs of previous occupancy by *P. bicornis* ants and none had hollow stems. According to previous studies, the hollow petiole chambers on these vacant plants should not have contained food bodies.

To test this assumption, I conducted a systematic survey at Carara Biological Reserve of all of the leaves of eight plants [mean leaves per plant, 9.1 ± 7.9 (SD); range, 4–28] appearing to be unoccupied by *P. bicornis*. Only one petiole on one tree contained both *P. bicornis* ants and food bodies. Each of the remaining seven trees that lacked ants had petioles that were smooth, vacant, and contained no food bodies whereas some adjacent petioles had substantial food body production (*6*). In every case, the petioles that had produced food bodies also contained a *Phyllobaenus* sp. *a* beetle larva (fam. Cleridae) (*7*). The presence of *Phyllobaenus* in trees without ant colonies, however, was puzzling since in other localities, they are specialized ant predators. Thus, the *Piper* plants at Carara produced ant food when ants were absent, and *Phyllobaenus* predators seemed to be subsisting where there were no prey.

A closely related predator *Phyllobaenus* sp. *b* found on the Caribbean side of the country, is a common cause of colony demise in *Piper* ant-plants. Predation behavior by this species was observed by rearing larvae in excised petiole chambers in petri dishes (*9*). The larva does not feed on adult ants. Indeed, *P. bicornis* ants can kill the beetle larva if its soft body is not wedged into a protective crevice. The beetle larva typically backs into the cone-like end of the chamber with mandibles protruding. As ants approach the larva, it cracks their head capsules or crushes the pronotum and tosses the bodies aside. After all oncoming adults are killed or disabled, the beetle larva proceeds to feed on the ant brood.

Perhaps the beetles have evolved the ability to stimulate food body production and thus subsist directly on plant products. I tested the hypothesis that the predaceous larvae can stimulate food body production in the absence of ants with a series of transfer experiments at Carara Biological Reserve. Seven *Phyllobaenus* sp. *a* larvae were removed from their chambers and added to adjacent or nearly adjacent petioles that were smooth and empty. The appressed petiole margins were gently pried open to transfer larvae, and they overlapped again, closing the chamber. None of the trees in this experiment contained ant colonies. Eighteen days later, newly occupied chambers had hundreds of food bodies whereas the petioles from which they had been taken lacked food bodies. Thus, plant surveys showing that larval presence in petioles coincided exactly with food body production were confirmed by manipulative experiments in which larvae induced food body production in newly occupied petioles on plants with no *P. bicornis* ants. The beetle larvae seem to have exploited the mutualistic association between the ant and the plant by causing the plant to produce food for them even in the absence of ants.

I cannot say with certainty that *Phyllobaenus* sp. *b* can stimulate food body production in *Piper* ant-plants because virtually all of the plants at La Selva have ants, but my field observations suggest that it does. Of five plants recorded as lacking ant colonies, four plants were inhabited only by queen ants and *Phyllobaenus* larvae. Each of the occupied petioles on these plants contained food bodies. The single plant with dead adult ants and no brood contained a *Phyllobaenus* larva and many newly developing food bodies. Early instar *Phyllobaenus* sp. *b* larvae were found in hollow petioles with a barrier sealing the chamber closed. They may stimulate food body production for growth during the early instars and then break the barrier as a large larva to feed on ant brood. There is some evidence for this scenario from rearing *Phyllobaenus* larvae from La Selva. As small larvae, they tend to leave excised petioles with ant brood but feed voraciously in excised petioles lacking ants but containing food bodies.

The cause of the rarity of *P. bicornis* ants in *Piper* ant-plants at Carara is not known. That none of the petioles on plants containing larvae had chewed entrance holes and that adults emerged from these petioles (*7*) suggest that beetle larvae at Carara can complete their development on the protein and lipid-containing food bodies. Because captive larvae fed and developed on ant brood for periods of 6 to 8 weeks, I assume that *Phyllobaenus* sp. *a* has not lost the predatory habits of the taxon (*8*). If *Phyllobaenus* beetles do play a role as predators in maintaining low ant occupancy of the trees at Carara, then they may be indirectly affecting another aspect of the plant's productivity. In early experiments (*2*) I found that average herbivory levels of unoccupied *Piper* ant-plants were greater than those of plants containing *P. bicornis* ants. One might expect the *Piper* population at Carara Reserve, then, in which plants are likely to house predators but unlikely to contain ants, to have an unusually high natural level of herbivore damage as compared to *Piper* ant-plant populations that are nearly 100% occupied by *P. bicornis* ant colonies.

Herbivory on the Carara population of *P. obliquum* was compared (*9*) with herbivore damage at two other sites (on *P. cenocladum* at La Selva and *P. obliquum* at Cañas Gordas, Puntarenas). Although not a definitive experiment since it compares herbivory at different sites, each presumably with a different herbivore load, these data showed an extreme result. Herbivore damage to plants at Carara Reserve (mean leaf damage, 29.7% ± 15.1) was significantly greater, about four times that of plants at La Selva (mean, 7.6% ± 3.5) and Cañas Gordas (mean, 7.9% ± 5.8) (ANOVA, df = 2, $F = 12.3$, $P = 0.0004$; Tukey's mean separation test, $\alpha = 0.05$). Thus, *Phyllobaenus* predators may be considered parasites of a mutualism: they exploit both the ants and the plants as food and may secondarily reduce plant fitness by disrupting plant defense against other herbivores.

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4. A field study by S. J. Risch and F. R. Rickson [*Nature* **291**, 149 (1981)] showed that *Piper* plants produce food bodies when associated with *P. bicornis* ants but that congenerics do not stimulate food body production. In censuses of nearly a thousand plants in four *Piper* species, I have observed also many instances in which single petioles were inhabited by ants other than *P. bicornis*, but these petioles have never contained food bodies.
5. I have censused ants in *Piper* plants in nine forest sites throughout Costa Rica, including *P. cenocladum* at the La Selva Biological Station and in Gondoca de Talamanca; *P. fimbriulatum*, *P. sagittifolium*, and *P. obliquum* at Corcovado National Park (Sirena, Llorona, and Cerro de Oro), at Cañas Gordas, and at the Las Cruces Biological Station. Almost every plant with more than three full-sized leaves housed a *P. bicornis* ant colony. The few mature plants found to be vacant had obviously been inhabited in the past, as evidenced by chewed entrance holes into the sheathing leaf bases and hollow stems. Yet at Carara Biological Reserve, only 2 of 13 plants had *Pheidole bicornis* inhabitants.
6. I pried open each of the 56 petioles on the remaining seven plants enough to see its contents with a light. Twenty one chambers, distributed among all the plants, contained hundreds of food bodies whereas 35 interspersed petioles had no food body production.
7. In addition to the larvae found in the hollow chambers, nine beetle eggs were deposited one or two per petiole, and four pupae and one teneral adult were closed into the ends of hollow petioles by a partition.
8. *Phyllobaenus* and related genera are known to be predaceous as larvae and as adults. *Phyllobaenus* sp. *a* larvae collected from *Piper obliquum* at Carara were reared through the later instars on ant brood alone, and adult ants released into petioles with captive larvae were killed.
9. I reared this congeneric from *Piper cenocladum* at La Selva Biological Station, Heredia, Costa Rica. During censuses of petiole chambers over a 5-year period I have seen petiole chambers that contained a *Phyllobaenus* larva and ant carcasses at La Selva, Gondoca de Talamanca, and Cañas Gordas.
10. I estimated the leaf area missing from each leaf to obtain a mean herbivory index per plant for the four most recently produced, mature leaves. At Carara, all eight plants at the study site were used. At La Selva and Agua Buena, 8 plants were chosen randomly from a larger sample of 15 and 25 plants, respectively. The latter plants are control plants in studies of the effects of herbivory and ant occupancy on plant fitness.

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Differential Phosphorylation of c-Abl in Cell Cycle Determined by *cdc2* Kinase and Phosphatase Activity

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The product of the *c-abl* proto-oncogene (c-Abl) is phosphorylated on three sites during interphase and seven additional sites during mitosis. Two interphase and all mitotic c-Abl sites are phosphorylated by *cdc2* kinase isolated from either interphase or mitotic cells, with the mitotic *cdc2* having an 11-fold higher activity. Inhibition of phosphatases with okadaic acid in interphase cells leads to the phosphorylation of c-Abl mitotic sites, indicating that those sites are preferentially dephosphorylated during interphase. The differential phosphorylation of c-Abl in the cell cycle is therefore determined by an equilibrium between *cdc2* kinase and protein phosphatase activities. Treatment of interphase cells with okadaic acid leads to a rounded morphology similar to that observed during mitosis.

THE *cdc2* SERINE/THREONINE KINASE is required for both the G_1-S and the G_2-M transitions in the cell cycle of the fission yeast *Schizosaccharomyces pombe* (*1*). All eukaryotic cells examined contain a protein homologous to the *cdc2* kinase (*2–7*). In higher eukaryotes, *cdc2* has been shown to be required for entry into mitosis (*3, 4*). The protein kinase activity of *cdc2* is essential for its cell cycle function (*8*). At least two substrates are known to be phosphorylated by *cdc2* kinase during mitosis: histone H1 (*5*) and $p60^{c\text{-}src}$, a nonreceptor tyrosine kinase (*9, 10*). Mitotic phosphorylation of histone H1 is thought to cause chromatin condensation (*11*). Increased tyrosine kinase activity of $p60^{c\text{-}src}$ has been observed during mitosis, and the activation of $p60^{c\text{-}src}$ may be involved in the event of nuclear envelope breakdown (*9*). Further identification of the substrates phosphorylated by *cdc2* will help to show how *cdc2* controls cell cycle progression.

The c-*abl* proto-oncogene encodes a nonreceptor tyrosine kinase. There are two forms of c-*abl* protein, type I and IV: they share 1097 common amino acids, but differ at their NH_2-terminals (*12*). Both c-*abl* proteins (c-Abl) are expressed in all tissues and cell lines examined (*13*). The ubiquitous expression suggests the possibility of a fundamental function for c-Abl tyrosine kinase in cell physiology.

Immunoblots of lysates from mitotic and interphase NIH 3T3 cells revealed that c-Abl from mitotic cells had a retarded mobility in SDS-polyacrylamide gel electrophoresis (SDS-PAGE) (Fig. 1A). This was observed whether mitotic cells were obtained by metaphase arrest with nocodazole (*14*) or by mechanical shake-off in the absence of nocodazole. The Abelson murine leukemia virus protein $p160^{gag/v\text{-}abl}$ (Fig. 1A) and a Bcr/Abl fusion protein (*15*) also had a retarded mobility in mitotic cells. More than 95% of Abl exhibited a retarded mobility during mitosis, whereas 60% of the c-*src* protein was modified during mitosis (*9*).

The altered mobility of Abl is due to phosphorylation. Treatment of mitotic Abl in vitro with potato acid phosphatase caused it to comigrate with interphase Abl. The change in the phosphorylation state of c-Abl during interphase and mitosis was determined by two-dimensional phosphotryptic peptide maps. The c-Abl from interphase cells had three major spots: a, b, and c (Fig. 1B); c-Abl from mitotic cells had the same 3 spots and 12 additional spots (Fig. 1B). The numbered spots were reproducibly observed in multiple independent analyses.

A potential kinase for the mitotic hyperphosphorylation of Abl is the *cdc2* kinase, which is activated in mitotic cells (*6, 7*). To test whether *cdc2* kinase phosphorylates c-Abl, a coimmunoprecipitation kinase reaction was used. Antibody to *cdc2* (anti-*cdc2*) and anti-Abl were added to cell lysates, and their respective antigen-antibody complexes were precipitated on the same protein A–

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