

compartment contains a high (+N) and the other a low nitrate (-N) concentration, high nitrate is sensed and triggers repression of root nodule formation in both compartments (6). Roots exposed to +N produce a CLE (CLAVATA3/endosperm surrounding region-related) peptide that is translocated by the xylem in an arabinosylated form to the shoot (7), where it binds to the legume LRR-RK NARK [nodulation autoregulation receptor kinase, an ortholog of CLAVATA1 (CLV1)]. NARK is essential for CLE peptide-induced systemic suppression of nodulation in the roots. The nature of the shoot-derived compound suppressing lateral organ formation is not known.

It is possible that the CLE/CLV1 relay controlling nodulation has evolved from one controlling lateral root elongation. In *Arabidopsis*, overexpression of certain CLE genes inhibits lateral root growth in a CLV1-dependent manner. However, it remains to be demonstrated whether this inhibition is controlled by root- or shoot-located CLV1 (8).

There is ample evidence that the availability of multiple nutrients is assessed in plants and that their uptake systems interact with one another. Nitrate and phosphate levels can both trigger local growth responses and are subject to systemic control (9). Other important nutrients, such as potassium and sulfur, are also sensed, and this information is integrated in the overall response of the plant to nutrient status. The work of Tabata *et al.* shows that small-peptide signaling pathways play an important role in the process by which plants deal with trade-offs between nutrient demands. In addition, it suggests that plants use a general mechanism to compute multiple nutrient levels in the shoot and relay this information back to individual root tips. There, inhibition due to local nutrient deprivation might be balanced with activation signals that relay multiple global nutrient levels. Such a modular design might help to achieve optimal root foraging architecture under competing nutrient demands (see the figure, panel C). ■

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CONSERVATION

Sensing biodiversity

Sophisticated networks are required to make the best use of biodiversity data from satellites and in situ sensors

By Woody Turner

Biodiversity loss is a global change with consequences that may exceed those of climate change (1). Yet, limited data on key aspects of biodiversity continue to constrain conservation efforts. Effective biodiversity conservation will require rapidly increasing understanding of the elements of biodiversity (such as the condition of ecosystems or the number and identities of species) and how they are changing through time. Satellite and airborne remote sensing are key to this effort but will only achieve their conservation potential when networked with in situ sensors (see the figure).

Remote sensing involves a wide array of tools and techniques on orbiting satellites and flying aircraft. It enables directly observing large-scale ecosystems and large organisms, depicting the broader environmental context for biodiversity, tracking climatic and other drivers of biodiversity change (often for use in ecological models), and making consistent observations across time and space for biodiversity monitoring (2). Remote sensing is increasingly complemented by in situ sensing with cameras on stationary objects or small drones, sound recorders, cell phones, electronic tags, and fragments of genetic material sampled directly from the environment.

INDIRECT REMOTE SENSING. Some biodiversity research and conservation efforts make good use of global satellite data that are recorded (typically for climate research) at spatial scales of 1 km or more (3). Most of these efforts involve indirect remote sensing of biodiversity. In this approach, climatic parameters like temperature, integrated vegetation measures such as vegetation indices, or observations of the three-dimensional structure of vegetation serve as inputs to models. Used either with species data in ecological niche models or with information about organismal physiology and/or demography in mechanistic models, remotely sensed data allow estimation of species distributions and abundance. For example, Pearson *et al.* have used

modeled climate variables and remotely sensed land cover and land surface data in a coupled ecological niche-demographic model to estimate climate change extinction risk with a mix of spatial and demographic variables (4).



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Appropriate use of remote sensing data for species distribution modeling is challenging because it unites tools developed separately by geographers and ecologists. Doing so requires attention to sample sizes and characteristics of both remote sensing and ecological data, matching the scales of the observations and the phenomena under investigation, determining whether species absence information is needed, and defining clearly one's purpose for modeling (5).

DIRECT REMOTE SENSING. The scales of satellite data from climate research satellites are generally too coarse for direct observation of important elements of biodiversity. However, airborne instruments and a rapidly growing array of private-sector satellites, designed for online mapping, can directly sense and identify organisms, including large tree canopies and even big mammals and birds. These instruments have pixel sizes ranging from 50 cm to a few meters.

Fretwell *et al.* (6) used images from three such satellites to estimate the global population of emperor penguins. They found four new colonies and confirmed locations of three previously suspected sites while determining the total number of breeding colonies in an area of the world difficult to survey. A global population estimate for species of concern is a key conservation measure. Separating penguins, snow, shadow, and guano is unique to this and similar efforts, but the study is indicative of a growing body of work using remote sensing to distinguish organisms from their surroundings.

Very high spatial resolution sensors typically trade higher spatial resolution for much narrower coverage of Earth's surface, making it challenging to assemble global or even wide-area data sets. Also, the cost

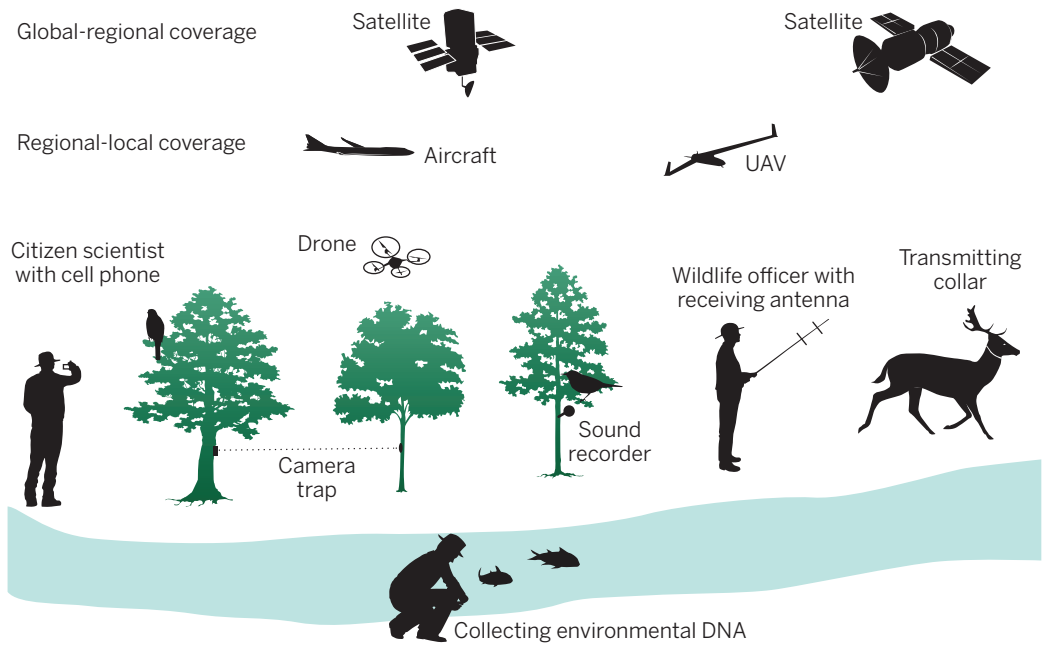
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of these commercial data sets may stretch limited conservation budgets.

Imaging spectrometers or hyperspectral sensors provide very high spectral (as opposed to spatial) resolution. They generate essentially continuous spectra from visible to short-wave infrared wavelengths and have mostly flown aboard government or commercial aircraft. The spectra reflect the unique chemistries of canopy vegetation and marine phytoplankton at resolutions of meters to tens of meters. In the resulting compiled imagery, scientists can discriminate between ecological guilds and even genera and species on the ground and in the water (7, 8), allowing these groups to be mapped and the composition and functioning of associated ecosystems to be delineated.

Recent combinations of imaging spectrometers and lidars or radars aboard aircraft have enabled simultaneous detection of vegetation biochemistry and its three-dimensional structure. Such combinations are powerful tools for discriminating species and ecosystem types and condition (9). Radar microwaves can travel through clouds, which often prohibit other forms of remote sensing in the biodiversity-rich humid tropics. At coasts, spectrometers and bathymetric lidars, incorporating water-penetrating green lasers, enable direct characterization of sea grasses, coral reefs, and other shallow benthic habitats (10). These airborne spectrometer-lidar/radar combinations may serve as precursors for orbiting biodiversity satellites that could offer detailed views of the composition, structure, and functioning of ecosystems.

IN SITU SENSING OF BIODIVERSITY. In parallel to advances in airborne and space-based sensing, developments in situ have also been dramatic. Transmission tags on terrestrial and aquatic animals, camera traps, sound recording devices, remotely piloted drones, and collections of environmental DNA in fresh and salt waters and soils are directly observing organisms, even the microbial components of biodiversity (11, 12). These approaches also provide information on animal behavior, abundance, and community organization (13). The small size of these sensors, reflecting rapidly expanding computer and battery power, offers the potential for near-ubiquitous sensing of Earth's land- and seascapes. Citizen science



Sensor power. Networking satellite and airborne remote sensing with in situ sensing will allow changes in many elements of biodiversity to be tracked over time.

further contributes to the growth in fine-scale biodiversity observations.

These in situ data provide insight at the levels of genes, species, and some ecosystems that remain hidden to remote sensing. In situ sensing thus brings critical fine-scale biodiversity information for use with the wider context and measures of environmental drivers obtained from remote sensing. It can also generate urgently needed time series of biodiversity observations, complementing remote-sensing time series of measures such as land cover and sea surface temperature that now span several decades.

NETWORKING NEEDS. The data from satellites, aircraft, and in situ sensors cover a vast range of spatial scales. Use of these sensing data in concert requires sophisticated networking and geostatistical analysis to fill gaps between fine-scale organismal or genetic observations and ecosystem-scale observations. Similar networks are necessary to tie biodiversity observations to data on broader environmental drivers of change.

Scale is not the only issue. The multitude of sensor types used to measure elements of biodiversity even at the same spatial scale further complicates networking, as does the integration of information from models. All observations and models come with their individual uncertainties, which must be addressed by any networking framework.

The first programmatic networks of this kind are now being created. In the United States, the National Ecological Observatory Network (NEON) proposes linking in situ

sampling at sites around the country with airborne and satellite remote sensing, although the satellite component still needs to be designed. The international Group on Earth Observations (GEO) partnership, particularly its global Biodiversity Observation Network (GEO BON), is a first attempt by national governments to jointly coordinate satellite, airborne, and in situ observations across biodiversity elements through genes, species, and ecosystems (14). This effort is crucial for meeting governments' obligations to assess national biodiversity under the Convention on Biological Diversity and the Intergovernmental Platform on Biodiversity and Ecosystem Services. ■

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