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Conserving tropical nature: current challenges for ecologists

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Tropical biodiversity continues to erode unabated, which calls for ecologists to address the problem directly, placing less reliance on indirect interventions, such as community-based development schemes. Ecologists must become more assertive in providing scientifically formulated and adaptively managed interventions, involving biodiversity payments, to serve local, regional and global interests in tropical nature. Priorities for tropical ecologists thus include the identification of key thresholds to ecological resilience, and the formulation of clear monitoring protocols and management strategies for implementation by local resource managers. A particular challenge is to demonstrate how nature reserves contribute to the adaptive capacity of regional land-use matrices and, hence, to the provision of sustainable benefits at multiple spatial and temporal scales.

It is widely accepted that the conservation of terrestrial biodiversity requires nature reserves, which must be protected from unsustainable human activities [1]. Although the theoretical underpinnings of reserve networks are strong [2], the problem lies in putting theory into practice. First, most biodiversity is found in the tropics, in countries where institutions are weak [3], where development policies destroy rich natural systems [4], where corruption and rent-seeking behavior go unchecked [5] and where people resort to unsustainable activities to survive [6]. Second, even if a country can reserve $\sim 15\%$ of its land area for biodiversity, with $\sim 10\%$ effectively protected [7], human activities in the remaining 85% cannot be ignored if the reserve network is to achieve its objectives.

In our quest to conserve biodiversity, there are very clear roles for sociologists, economists, political scientists and development practitioners, because considerable effort is needed to alleviate poverty and improve governance. But what is the role for ecologists? Here, we break this question into three parts and propose some answers to the following: (i) How do we work with local resource users to address the challenges of conserving tropical nature? (ii) How do we apply our ecological skills to the conservation needs of large, underfunded and weakly administered tropical nature reserves and the landscape matrices in which they occur? (iii) How can the benefits for humans of conserving wild tropical nature be evaluated for comparisons against competing land-use alternatives? Our motivation for writing this article is to provide ecologists with new ideas about how they could become involved effectively in addressing the extreme challenges of biodiversity conservation in the tropics, where biological resources are richest but the information gap between ecologists and resource managers is widest [8] (Box 1).

Getting involved: terms of engagement for ecologists working with tropical biodiversity

There is a popular perception that, if local communities are empowered to do so, they will use their local knowledge to manage their natural resources under a regime of sustainable use [9-11]. This perception of the 'ecologically noble savage' [12], coupled with the stigma of conservation imperialism, has placed scientists in a dilemma as to how to engage with the issue of declining tropical biodiversity. Over the past two decades, there was a general acceptance among conservation and development agencies that tropical ecologists should serve an advisory function for conservation projects operating under the principles of community-based natural resource management. The terms of engagement then had an emphasis on local custodianship of nature with ecologists participating indirectly by attempting to influence the behavior of resource users [13]. It has now emerged, however, that, under many circumstances, local 'custodians' do not reinvest in nature or exercise selfrestraint in the use of scarce communal resources, even when deriving immediate and tangible benefits [6,12], and

Box 1. The wider picture

- Present efforts to conserve tropical biodiversity depend largely on local-level community-based projects.
- This is not working well enough, because tropical biodiversity continues to disappear at a catastrophic rate.
- It is unrealistic to expect local villagers to pay the opportunity costs associated with conserving tropical biodiversity, which is a global responsibility.
- Large-scale global funding is required for scientifically formulated conservation interventions that focus on critical thresholds within social-ecological systems, to prevent rapid and irreversible changes in key ecosystems.
- Ecologists need to interact more effectively with economists, sociologists and political scientists to quantify the benefits of tropical biodiversity to everyone, ranging from subsistence farmers to company directors.

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Opinion

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so the underlying assumption of community-based conservation might be flawed [14,15]. Issues such as who has the right to the custody of nature are now being widely debated and the shrinking reserves of biodiversity are increasingly being viewed as global assets about which everyone has a right to be concerned [1] (Box 2). Furthermore, although it is unquestioned that local ecological knowledge is a vital store of information about the properties and uses of nature, there is mounting empirical and theoretical evidence that traditional and other local resource-use practices are not adapted to the scales and kinds of disturbance that contemporary society is exerting on natural systems [16–19]. In cases where local resource-use practices could be sustainable, such as isolated coastal fishing communities in Asia [10], the institutional framework for their effective implementation is usually tied to local mores and norms or to specific religious beliefs and practices that prevent rule breaking [20–22]. With increasing globalization and societal homogenization, however, such controls are diminishing. Effective conservation clearly requires partnerships with local resource users, but, to conserve what is left of tropical biodiversity, professional ecologists

Box 2. Community-based conservation must go global

Efforts to conserve tropical biodiversity in recent decades have emphasized community-based approaches, in which the community is usually defined as a local rural population that depends to some significant degree on its natural environment for subsistence. The ideal is to achieve improved livelihoods at a local level through integrated conservation and development projects, by which the sustainable use of the indigenous resources of a community provides the foundation for the social and economic development of that community. Community-based conservation is, however, fraught with problems [15,40-42], ranging from the reluctance of central governments to concede property rights to local people, such as in Indonesia [43], to the simple lack of interest among local people to participate, such as around the Selous Game Reserve, Tanzania [44]. Furthermore, human populations in many tropical countries have already outgrown their indigenous biological resources. In the remaining expanses of tropical forest in Southeast Asia, Africa and Central America, human populations now require one to two orders of magnitude more protein than can be sustained by wild meat from the forests [6]. Finally, to expect local people in the tropics to voluntarily forego modern Western living standards for the sake of nature conservation is to naively expect them to bear iniquitous opportunity costs [45,46].

Economic benefits from conserved tropical nature are greater for the global community, in the form of dispersed ecological services (such as carbon storage) and option, existence and bequest values, than they are for local communities [46]. Consequently, if the responsibility for making community-based conservation work should rest with the community that stands to benefit most from conserving tropical nature, then it is the global community that must come forward. Shouldering this responsibility will entail the sustained allocation of effort and funding on a scale previously unmatched, except perhaps during episodic military campaigns [42]. Most of this should be directed at achieving reforms at spatial scales and political levels that are far wider and higher than those of local rural communities. Nevertheless, conservation practitioners should be enabled to introduce pragmatic, scientifically formulated interventions at the local scale with the same urgency and efficacy as is expected from medical practitioners in the combat of emerging diseases. Ultimately, all people who diligently participate in conserving tropical nature at all levels should earn the income, education and status they deserve for providing their services to the global community.

must become more directly engaged in augmenting local ecological knowledge with modern science [8]. In addition, the delivery of science should be better organized to provide timely and relevant information to resource managers and other clients [23].

To foster compliance with conservation requirements, there is a mounting argument in favor of the international conservation community making direct payments to local land managers in developing countries in return for specified outcomes [15]. If the principle of direct payments gains acceptance, then ecologists will increasingly be required to identify target outcomes and intermediate indicators of success (e.g. gorillas surviving in a defined forest area, water turbidity in streams draining a degraded catchment, etc.), and prescribe protocols for local people to follow so that they can earn their rewards for achieving the contracted conservation outcomes. Although the principles and practicalities are still being debated, we expect mainstream ecologists to participate more enthusiastically in scientifically focused conservation projects involving direct interventions than in those involving indirect community-based approaches, which require sociological skills that ecologists are seldom trained in.

What to do: shifting scales from local interventions to identifying critical thresholds within social-ecological systems

Conserving nature requires money and technical expertise, both of which are demonstrably lacking in most tropical regions. Given that the average annual global expenditure on nature reserves by governments and for eign donors is presently US\$ 453 km^{-2} , but only US\$ 93 km⁻² is spent on reserves in the tropics [24], it follows that tropical ecologists must concentrate on key species and processes for focused conservation interventions, and on key ecological indicators for focused monitoring. Ecologists are also being called upon to provide local users with better means of assessing, monitoring and valuing their natural resources [25] and devising alternatives to unsustainable practices, at scales from subsistence bushmeat hunting [6] to commercial logging [26]. For ecologists to take on such responsibility requires an awareness that scientific credibility is frequently at risk, such as when 'pet' issues are promoted at the cost of real priorities [27]. In Indonesian Borneo, for example, forest ecologists persist in trying to understand the intricacies of reduced impact logging, whereas the real conservation priority is to control the rapid transformations occurring at the landscape scale [23].

Identifying the real priorities for regional biodiversity management requires ecological knowledge at multiple spatial and temporal scales that include both nature reserves and their surrounding matrices [28]. This is because nature reserves are embedded in a nested set of social-ecological systems [29], necessitating the inclusion of at least the scales above and below the scale of immediate concern [30]. A nature reserve comprises a set of interacting and interdependent subsystems, and changes at lower scales can trigger changes at the scale of the whole reserve. Most reserve managers know this, but few acknowledge the extent to which the reserve itself is a

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subsystem at regional and national scales, or how changes at these higher scales can feed back on dynamics at the reserve scale [6].

Resilience is the ability of a social-ecological system to continue functioning in the same way following big shocks and disturbances [31,32], and a large nature reserve contributes to regional resilience. It serves as a continuing source of replenishment for species occurring in unstable populations outside the park (maintaining functional diversity), as a refuge for such populations in bad times and as a back-up supply of harvestable goods. The reserve also contributes to regional adaptive capacity, which is the ability of people in the surrounding land matrix to come up with new ways of doing things and of adapting to changed external conditions. It maintains options for the future that are not yet recognized (Box 3). Seen in this way, the reserve influences adaptive cycles at higher (regional and national) scales, and the question then is what sort of management regime and, therefore, what sorts of state are appropriate for the reserve to serve this function.

There are thresholds to resilience, however [31]. Social-ecological systems exhibit many nonlinear effects and excessive anthropogenic disturbances to an ecosystem can be expected to drive an array of ecological response variables into irreversible trajectories through time. There is an increasing number of examples of how nonlinear ecological responses lead to human-induced flips into unwanted ecosystem states [33] (see also the thresholds data base in http://www.resalliance.org), in ecosystems ranging from shallow lakes to semi-arid rangelands [32], and driven by human processes ranging from the clearing of savanna elephant habitat (Box 4) to the disturbance of closed-canopy forests (Box 5). Current approaches to conserving tropical ecosystems are thus directed at understanding how people and nature interact within complex adaptive systems [34] so that thresholds of potential concern can be identified and managed for a key set of ecological response variables. To determine the thresholds requires the understanding of causal links, after which adaptive management strategies should be devised for the drivers, such as wild meat consumption [6], instead of wasting funds and effort on the palliative care of responders, such as the population levels of numerous animal species that are overhunted in tropical forests.

Justifying the commitment: placing values on conserved areas

Any sustainable conservation initiatives must be buffered against corrupt practices and must provide tangible benefits to rural people and national treasuries that are equal to or greater than the perceived benefits of alternative land-use options (e.g. logging, mining, agropastoralism, commercial bushmeat hunting, etc). However, standardized procedures for identifying the goods and services provided by nature have only recently entered the formal repertoire of conservation practitioners [35] and the comparative benefits of keeping wild ecosystems or substituting them with alternatives have been poorly evaluated [36]. Recent analyses [24,37] suggest that, although developing countries cannot be expected to foot the bill, direct compensation for opportunity costs could be

Box 3. Tropical nature reserves as sources of regional ecological resilience

Regional social-ecological systems behave as complex adaptive systems, one of the key characteristics of which is a constant source of novelty. The richness and type of novelty will determine the possible new trajectories that the social-ecological system can follow. Novelty comes from two sources: human ingenuity (expressed as technology) and the basic biological materials (food, drugs, wood, and so on) that go into our production and support systems. Nature reserves are vital sources of undiscovered or untested biological novelty. They also act as sources of replenishment in the surrounding regions for species that have been made locally extinct or rare. A particular aspect of this concerns species that promote ecosystem resilience.

The goal of sustainable development places an emphasis on resilience rather than maximum production, and resilience is achieved through maintaining the diversity of species response types within essential functional types [47,48]. This is a new way of looking at species, requiring knowledge of their functional attributes. Rather than knowing the phylogenetic relationships of plants in an ecosystem, it is more important to know which of them fix nitrogen, have deep or shallow roots, have high or low water use efficiencies, and so on. In the absence of adequate knowledge about functional attributes, it is difficult to identify particular species that are crucial to the resilience of ecosystem function, which highlights a functional role for nature reserves. In an Australian rangeland example, some of the dominant grass species had several functional analogues that could respond differently to external disturbances, such as grazing pressure (thus conferring resilience on that functional type), whereas others had none [47]. The functional analogues of these latter species might have been eliminated soon after livestock grazing was introduced and before botanical monitoring was initiated [49]. Replenishment of transformed landscapes with such species will be an increasingly important function of nature reserves, with the process involving either passive diffusion or targeted collection and active re-introduction.

This concept can be broadened to include a wide range of species, from soil organisms to large vertebrates. Under the management paradigm of optimizing short-term production, elimination of apparently redundant ('unnecessary') species is considered a good thing. But in an era of sustainable development objectives, nature reserves assume high importance for their role as refugia for, and sources of, all the locally adapted species in the region that can contribute to the emergence of resilient production systems. This role is particularly significant in the tropics, where examples of the unsustainability of simplified agro-ecosystems abound and where knowledge of local species lags far behind that in the developed, less speciose, temperate world.

provided from global funds. According to one estimate [24], the cost would be a fraction of what governments currently spend on perverse subsidies, which are subsidies that ultimately undermine both biodiversity and the economy [38]. The challenge is to assess the benefits to humans of conserved areas at spatial scales ranging from the rural household to the continent to the planet - a task requiring multiple inputs, including those from ecologists, who need to document the biophysical flows of goods and services to improve the economic analyses. In turn, ecologists and economists need to interface better with sociologists and political scientists to sharpen their arguments. For example, in the Zambezi Valley, settlers are converting natural woodland to cotton fields on soils that can sustain high production levels for <5 years. As much as fieldworkers from conservation NGOs might attempt to dissuade them, the settlers are understandably attracted by

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Box 4. Thresholds to ecosystem resilience: elephants and people

It is tempting to interpret a linear relationship within a scatter of data points showing a responder variable (e.g. the diversity of some taxonomic or functional group) declining as a driver variable (e.g. human density) increases its effect within an ecological interaction. Linear relationships are alluring in being statistically tractable and implicitly assuming both predictive power and reversibility (i.e. the responder will settle back into a former state if the effects of the driver are reduced). Although such assumptions might be, at least partially, upheld at a macro (continental) scale, there is a real danger that the illusion of gradualism is derived from a series of irreversible step-changes at the ecosystem scale, as resilience thresholds are exceeded in one locality after another.

An example is the interaction between human and elephant densities in African savannas. In the 1990s, it was almost axiomatic in the conservation literature, based on macro-scale evidence, that elephant densities decline in linear response to increasing human densities [50-52]. A detailed study in northwestern Zimbabwe, however, using census units of ~500 km², indicates that maximum elephant density (Figure I; solid line) remains unchanged at \sim 1 elephant km⁻² when human density (depicted here on a log₁₀ scale) is increasing from low levels, but, at a threshold of \sim 16 people km⁻¹ the elephants suddenly disappear [53]. Scattered human settlements in expanses of elephant habitat have no effect on the elephant population but, as the cultivated area expands, the elephant habitat becomes fragmented. When a habitat patch becomes too small to include the home range of an elephant breeding group, the elephants move away and compress into the nearest wildlife reserves. At this point, the system flips from a state in which human settlement occurs within an elephant-occupied matrix to a state in which elephants are absent from a human-dominated matrix. A statistically significant linear relationship can be fitted to the data (Figure I; dashed line; $r^2 = 0.446$, p < 0.001), but this has no relevance to the main finding, which is that the capacity of this region to support elephants diminishes quickly and irreversibly when a threshold level of human settlement is exceeded.

Understanding where the threshold lies should enable local resource managers to plan ahead for wildlife-rich areas where human density is low but increasing [19]. Pre-emptive planning to retain elephants, and thereby conserve the adaptive capacity of the social-ecological system, should include consideration of the positions and configurations of wildlife reserves in relation to human development within the regional land-use matrix.



the immediate cash value of cotton and have no basis for evaluating it against the long-term benefits of sustainable wildlife harvesting [19]. At a larger scale, the obvious merits of diverting funds from perverse subsidies to conservation payments [24,36] will remain unrealized unless sociopolitical reforms can curb the powers of corrupt actors in tropical countries and remove the entrenched reasons for why national governments use subsidies.

The cost of maintaining regional/national resilience and adaptive capacity is the foregone discounted stream of future benefits that could accrue from other potential uses of the nature reserve, and these costs have to be taken into account over long time periods. For a large reserve, a pertinent question is: how would the region in which the reserve is situated progress through the next 20, 50, 100 years with, and without, the reserve? Putting aside the aesthetic, nonutilitarian benefits for now, there are two utilitarian ways in which the reserve influences the region. First, it provides short-term benefits in the form of ecosystem goods and services, such as tourism revenue, local harvesting, clean water, and so on. Second, it contributes to the resilience and adaptive capacity of the region as a whole. A challenge now facing those whose work entails placing values on conserved nature is to incorporate values related to the maintenance of adaptive capacity. Furthermore, such values must be quantified with an inside-out perspective [29], in that all of the benefits that flow in all directions are relevant, not just those that are presently or potentially enjoyed by residents of the region, or even the country, in which a nature reserve occurs. For example, the Kruger National Park extends over 20 000 km² and acts as a waste disposal/ purification system and flood regulator for rivers that arise in the industrialized South African highveld and provide water to the most densely settled region of Mozambique [39]. An economic argument for retaining Kruger as a wildlife reserve instead of turning it over to agropastoralism and coal mining (which have been lobbied for) must include the value of this subsidy to the weak economy of Mozambique.

Conclusions

Declining tropical biodiversity is placing mounting pressure on ecologists to frame their arguments for protecting nature reserves in terms that are locally plausible. The danger in opening up the possibility of restricted multiple uses of such areas is rampant corruption leading to ecosystem degradation. But the danger of not doing so is a decline in the actual and perceived utility of a reserve, to the point where it is overturned and replaced by other land uses, such as small-scale agriculture. It is not a new observation that the future of these areas depends more on getting the institutional arrangements right than on devising better systems of environmental management. Getting the institutions right is a slow political process that probably requires major, continued, international involvement until the institutions, and the regional adaptive cycles in which they are embedded, are self-organizing. In the meantime, as windows of opportunity close on the conservation of tropical nature, ecologists must become more directly engaged in formulating targeted conservation interventions. We argue that such interventions should depend less on teasing conservation gains out of local resource-use practices and more on bringing

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Box 5. Forest fires in tropical forest areas: shifting past the threshold?

Forest fires, which occur naturally in undisturbed closed canopy tropical forests, usually have return intervals of hundreds of years and are of low intensity, but forest fires in Amazonia and Southeast Asia are now increasing, in both extent and frequency [54,55]. The 1997–1998 fires in Indonesia illustrated the effect that such fires can have by causing a smog blanket over 3 million km², affecting the health of 75 million people in six countries, and inflicting economic losses of ~US\$ 4.5 billion [55].

There are several main factors that are driving the escalation of tropical forest fires [56] (Figure I). Road building directly affects transportation costs and economic accessibility, promoting in-migration and increased logging (arrows a and b), which, in turn, attract further post-logging in-migration (arrow c). In-migration and logging both result in deforestation (arrows d and e) through creating roads and log landings, whilst intense logging can completely transform forest structure, as evidenced by many of the new district-level concessions in Indonesian Borneo. A predisposing factor to deforestation is if the area is suitable for agriculture (arrow f); for example, areas suitable for oil palm



Figure I.

modern science to bear against the dire threats facing tropical ecosystems. Short-term benefits of local participation in scientifically formulated conservation interventions will have to include direct payments made as rewards for the achievement of prescribed conservation goals, with funding derived from external sources. Longterm benefits should be derived (institutional structures and governance systems permitting) from the wider range of opportunities for sustainable endeavors that are afforded to local communities in regions where ecological resilience is conserved within nature reserves and surrounding land-use matrices.

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plantation in Indonesia are being more rapidly deforested than are other areas [55]. Deforestation causes fragmentation of the remaining forest (arrow g), thus increasing both edge effects [57], and the occurrence of fires (arrow h), because forest edges undergo biomass diebacks and microclimatic changes that increase their fire susceptibility [58]. Deforestation for croplands and burning for pastures result in many accidental forest fires (arrow i), whilst logging degrades forests (arrow j) and promotes conditions for fire [59]. An overriding factor is climate (arrow k), with high-intensity fires being more likely in drier vears [55]. However, a feedback loop does begin to establish (arrow I) whereby repeated forest fires lead to unintentional deforestation and, indirectly, further fragmentation, which result in more fires [54]. In addition, research at an Amazonian site [54] has shown that the probability of fire is greater after a first burn because diebacks and regrowth cause fuel loads to increase (Figure II); therefore subsequent fires burn with even greater intensity. All evidence thus indicates that, when a closed-canopy tropical forest is pushed beyond some threshold level of canopy opening, the landscape undergoes rapid fire-driven change towards a new equilibrium, with the original forest all but disappearing.



Figure II. Fuel and fire characteristics in four forest types, each with different fire histories, in the Brazilian Amazon. Fuel height (green bars) and maximum fireline intensity (red bars) are presented together, using the same scale. Based on data from [54].

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