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Perspective

Historic livelihoods and land uses as ecological disturbances and their role in enhancing biodiversity: An example from Bhutan

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ABSTRACT

International conservation efforts have ignored the role and importance of historic disturbance regimes, both natural and anthropogenic, in creating and maintaining biodiversity. In this article we focus on historic livelihoods and land uses which we argue can and should be viewed as a type of intermediate ecological disturbance that may increase landscape heterogeneity which is correlated with biological diversity. Using historic swidden in Bhutan as an example, we illustrate how this historic livelihood and land use maintained intermediate ecological disturbances in an otherwise densely forested landscape and increased plant structural heterogeneity, the proportion of early successional plant species, and the availability of forage and browse of importance to wild ungulates and their predators (e.g., tigers). The cessation of swidden in Bhutan and elsewhere alters historic disturbance regimes with potentially profound effects on flora and fauna. We argue that biodiversity conservation requires understanding and building upon ecological disturbance regimes which should include historic livelihoods and land uses. To be realized in practice, this requires not only further ecological study, but addressing the politics of knowledge.

Contents

1. Introduction

International conservation efforts have ignored the role and importance of historic disturbance regimes, both natural and anthropogenic, in creating and maintaining biodiversity. Many biologists and conservationists consider anthropogenic activities to be unnatural and incompatible with the conservation of biological diversity, irrespective of their type, size or duration (Barlow et al., 2012; Gardner et al., 2009; Lindenmayer et al., 2006; Soule, 2013; Terborgh, 1999). Renowned conservationist Soule (2013) recently asserted that "new conservation" efforts which seek to integrate managed human uses in conservation threaten biodiversity (Soule, 2013). This perspective dismisses all human managed

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uses despite evidence that some historic practices not only used and managed, but contributed to creating biodiversity (Belair et al., 2010; Bird et al., 2008; Fowler, 2013; Sturgeon, 2005; Xu et al., 2009). While some conservation efforts include community-based natural resource management (CBNRM), many of these efforts are state or NGO inventions that reflect their understandings and interests, and introduce new practices and "model" livelihoods notably ecotourism, rather than building upon historic livelihoods and land uses (Belsky, 1999; Brosius et al., 1998; Dressler et al., 2013). Joint positive effects between livelihoods and biodiversity are not found everywhere, but are more likely where CBNRM involves user participation in resource governance and in some cases incorporated historic livelihoods (Persha et al., 2011).

We argue that conservation efforts must understand and build upon the site-specific role and importance of historic disturbance regimes, both natural and anthropogenic, in shaping and maintaining biodiversity. A critically important disturbance warranting attention is historic livelihoods, specifically the multi-generational land uses that created, maintained and managed ecological disturbances in many places.

The role and importance of historic livelihood and land uses as ecological disturbances and their effect on biodiversity warrant consideration for many reasons. First, it may facilitate moving beyond persistent culture vs. nature debates which do not speak to each other, but "pass each other like ships in the night" (Leach and Fairhead, 2000, 55) or are purposefully ignored when they challenge dominant paradigms and interests (Dove, 1983). Second, some historic land uses and associated disturbances influenced the composition, abundance and distribution of flora and fauna in places of conservation importance (Brown and Kothari, 2011; Grove and Rackham, 2001; Kerkhoff and Sharma, 2006; Willis et al., 2004). In addition, "Landscapes that have co-evolved with or have been altered by human activities often depend on the continuation of these activities to maintain the presence of certain species and ecosystem services" (Oudenhoven et al., 2010, 13). Third, attention to landscapes as socioecological systems may suggest how "new conservation" efforts could incorporate dynamic ecological knowledge and forces over large temporal and spatial scales. We are not advocating that historic land uses be maintained or recreated, which is unrealistic given highly altered contexts and concerns. However, we are suggesting that the functional links that previously existed between some historic livelihoods, land uses and biodiversity be identified and their underlying principles be used to inform future development and conservation policies and practices.

In the following sections we review relationships between ecological disturbance and biodiversity, describing the specific disturbance attributes associated with one prevalent historic livelihood and land use, swidden (or shifting cultivation) as practiced in Bhutan, and its effects on flora and fauna. We conclude that understanding the site-specific effects associated with swidden and other historic livelihoods and land uses as ecological disturbances, is essential to understanding the current composition, abundance and distribution of flora and fauna, and may contribute to the identification of policies and practices that support sustainable livelihoods, culture and biodiversity in the future. Our analysis relies primarily on published literature from Bhutan and the eastern Himalayas, supplemented by personal observations and research conducted over the past eight years in central Bhutan.

2. Ecological disturbance

2.1. Ecological disturbances and biodiversity

Ecological disturbances were defined by White and Pickett (1985) as relatively discrete events that alter ecosystems, communities or population structure, and that result in changes in resources, substrates or the physical environment. Forests, grasslands, deserts and other ecosystems, they argue, can be characterized by individual, site-specific events that not only shape, but are essential to maintaining species composition, community structure (e.g., vegetation structural complexity and distribution across the landscape) and ecosystem functions. This suggests that understanding how disturbances affect biodiversity requires: (1) identifying and characterizing disturbance attributes and their direct and indirect effects; (2) ascertaining how disturbances interact spatially and over time; (3) recognizing that disturbances are site-specific; and (4) documenting the role, if any, that historic livelihoods and land uses may have played in the development and maintenance of disturbance regimes.

Disturbances can be characterized on the basis of specific attributes, the most important of which include their type, spatial features, temporal characteristics, specificity, intensity and resulting synergisms (Mori, 2011). Effects resulting from disturbances vary with soil, topography and climatic conditions. In forests, three disturbance parameters are thought to be particularly important: (1) the return interval (i.e., the time between disturbances); (2) the severity (i.e., amount of vegetation killed and the type and amount of space available for new plant growth); and (3) the resulting landscape-level spatial patterns created (Seymour and Hunter, 1999).

Ecological theory and empirical studies have suggested that biological diversity is greatest in environments subject to intermediate levels of disturbance (Connell, 1978). In the context of forests, frequent or intense disturbances exclude species that require structurally diverse, closed canopy conditions, while in the absence of disturbance, shade-tolerant plants characteristic of mature forests will exclude species that require more sun (Rees et al., 2001). The spatial and temporal heterogeneity of biological and physical conditions resulting from disturbances increase functional heterogeneity, which in turn increases opportunities for coexistence among species assemblages and is correlated with biodiversity (Odion and Sarr, 2007). Thus, if disturbances are excessively frequent or intense, or not frequent or intense enough, communities tend to become less diverse.

Since the intermediate disturbance hypothesis was popularized by Connell (1978) almost forty years ago, hundreds of studies have explored its theoretical basis, empirical reliability, and potential explanatory mechanisms. Support of the hypothesis has been reported for tropical rain forests (Molino and Sabatier, 2001; Steege and Hammond, 2001), tall grass prairies (Collins, 1987), rangelands (Sasaki et al., 2009) and marine environments (Svensson et al., 2007). In contrast, other studies find little empirical evidence or theoretical basis for it. In a review of over one hundred studies, Mackey and Currie (2001) found evidence of diversity peaks at intermediate disturbance levels in less than 20% of cases, while Fox (2013) recently argued that the hypothesis should be abandoned on both empirical and theoretical grounds.

This debate reflects, in part, differences in spatial and temporal scales. At the level of individual forest stands, evidence in support of intermediate disturbance-diversity relationships is weak. However, if one considers large spatial scales, long time periods and the effects of multiple disturbances at landscape levels, support for intermediate disturbance-diversity relationships appears more persuasive. Even in environments where one type of disturbance dominates, such as treefalls in tropical forests, the shape, orientation, aspect and time of gap creation, plant location within gaps, soil conditions and other factors, collectively influence subsequent seed dispersal, survival, germination and growth (Sheil and Burslem, 2003). The result, at large spatial scales and long time periods, is increased heterogeneity. Furthermore, disturbance–diversity relationships are influenced by the composition of the assemblage and the cumulative, interactive effects of different disturbances over time (Svensson et al., 2010). Thus, in landscapes subject to a variety of disturbances, functional heterogeneity, opportunities for coexistence among species assemblages, and overall biodiversity may increase.

Ecosystems are considered to be in states of non-equilibrium due to the unpredictable and stochastic nature of disturbance regimes (Gardner et al., 2009; Mori, 2011). The fact that disturbances are hierarchical (i.e., a variety of disturbances occur and interact over space and time) and leave complex legacies, implies that post-disturbance pathways will be diverse and unpredictable as well. That is, the flora and fauna that establish following a disturbance develop in different and unpredictable directions (Botkin, 1990; Mori, 2011). In this way, disturbances create a range of environmental conditions and seral stages which increase habitat and potentially species diversity at landscape levels.

2.2. Anthropogenic disturbances and biodiversity

This discussion has so far considered only "natural" disturbances, however, humans have hunted, gathered, cut and planted trees, and burned landscapes for 10,000–12,000 years throughout much of the New World (Anderson, 2013; Arno and Fiedler, 2005; Vale, 2002), 50,000 years in Australia (Bird et al., 2008), and perhaps longer in Africa (Fairhead and Leach, 1996). Some landscapes and their biotic assemblages, including those of significant conservation importance, developed in conjunction with or as a consequence of past human activity (Brown and Kothari, 2011; Grove and Rackham, 2001; Willis et al., 2004).

Debates continue regarding the extent and ecological significance of historic anthropogenic land uses, and the degree to which they influence contemporary species compositions, abundances and distributions (Barlow et al., 2012; Bush and Sherman, 2007; Gillson and Willis, 2004; Willis et al., 2004). That human activities and land uses can adversely affect biological diversity is not in doubt. Both scientific and popular literatures have catalogued the environmental destruction and biodiversity losses inflicted by contemporary and prehistoric societies throughout the world (Diamond, 2005; Gardner et al., 2009; Terborgh, 1999). The scale and persistence of anthropogenic disturbances can also be profound. Steege et al. (2013) recently reported that the tree flora of the Amazon Basin exhibits extreme hyper-dominance (i.e., 1.4% of tree species account for over half of all trees) which they hypothesize may reflect widespread cultivation prior to 1492. Similarly, as much as 15% of Amazonian soils contain charcoal reflecting prehistoric cultivation practices (Denevan, 2004). Recently, Hunt and Rabett (2013) argue that many Southeast Asian forests are cultural artifacts that reflect anthropogenic use and management since the early to mid-Holocene.

Even more contentious is the proposition that some historic livelihoods and land uses, including agriculture, grazing and forest management, may enhance biological diversity. For example, the Mediterranean Basin contains the world's greatest diversity of plant species outside of the upper Amazon Basin and Southeast Asia (Brooks et al., 2006), yet few places on the planet have a longer and more intense history of human use and disturbance. In an exhaustive study, Grove and Rackham (2001) document that the Mediterranean flora is adapted to and maintained by disturbances associated with historic livestock grazing and agricultural practices. Similarly, Bird et al. (2008) describe how managed burning by aboriginal women in Australia increased and maintained habitat diversity and small mammal populations valued as a food for thousands of years. In nearby Indonesia, the Kodi employed fire to shape the structure and function of their environment for 14,000 years in what has been described as a close interlocking of social relations and ecological disturbances (Fowler, 2013). The above practices were not haphazard, but controlled and regulated by local rules, customs and institutions. Nevertheless, that socio-ecological systems involving intermediate land use disturbances might enhance biodiversity is not widely accepted. In fact, only recently has it been recognized by some conservation scientists that some protected areas are rich in biology diversity not in spite of, but because of people and their historic land uses (Brown and Kothari, 2011).

Conserving biodiversity in any particular locale requires discerning the effects of previous human activities or disturbances and the implications associated with altering historic disturbance regimes. In a synthesis of ecological legacies, Foster et al. (2003) concluded that: (1) at regional scales both current and historical human impacts inevitably exist; (2) most "natural areas" have more human history than previously thought; (3) land use legacies are remarkably persistent, and (4) history contributes valuable explanatory power to understanding current ecosystem composition, structure and function. This suggests that if historic anthropogenic disturbance regimes change, ecological conditions and biodiversity may change as well. Importantly, interpreting "the past" demands critical attention to the dominant values and politics that exist at a given time and why some practices and theories are celebrated, while others are ignored or occluded from official views and policies (Dove, 1983; Botkin, 1990; Leach and Fairhead, 2000).

3. Biodiversity, historic livelihoods and land uses, and ecological change in Bhutan

To ground the discussion of historic livelihoods and land uses as ecological disturbances and their role in biodiversity, we focus on one example from Bhutan. The Himalayan country of Bhutan (38,394 km^2) ranges from lowland subtropical forests, through warm and cool temperate broadleaf and coniferous forests, to alpine environments, and contains exceptional biological diversity. Bhutan is a particularly appropriate place for evaluating the biodiversity significance of swidden because it was widely practiced until the 1990s. In addition, unlike other areas where swidden transitioned to permanent annual crops or perennial plantations (Cramb et al., 2009; Mertz et al., 2009a), most former swiddens in Bhutan transitioned to forests (NSSC, PPD, 2011; Siebert et al., 2014) where human activities and disturbances have declined or ceased. Lastly, the eastern Himalaya, including Bhutan, is considered a global biodiversity hotspot, that is a region with high biodiversity under imminent anthropogenic threat (Brooks et al., 2006). However, historic anthropogenic lands uses and their associated disturbances are declining throughout much of Bhutan. Thus, Bhutan provides the opportunity to evaluate the implications of reduced human use and disturbance on biodiversity.

Bhutan's biodiversity reflects a number of factors, including its location in a convergence zone of several biogeographic realms, extreme altitudinal gradient, pronounced climatic variability, and natural and anthropogenic disturbances that have interacted in complex, hierarchical ways over large spatial scales for centuries. Historic natural disturbances in Bhutan include: (1) earthquakes, mass wasting, landslides and erosion associated with steep, unstable mountain slopes and heavy, monsoon-related precipitation and (2) individual tree mortality due to insects, diseases and wind throw. These disturbances differ in important ways. The former are relatively large (i.e., 10s–100s ha) and entail primary plant succession from bare soil or bedrock. In contrast, individual tree deaths tend to be small (less than 0.25 ha), maintain ground cover and result in rapid secondary plant succession (per. obs).

The Government of Bhutan is committed to biodiversity conservation and has established protected areas and biological corridors that encompass over half of the country. While established human communities are permitted to remain within parks, historic livelihoods and land uses have been prohibited or restricted both in and outside protected areas and no longer operate as they did in the past. The ecological function of historic livelihoods and land uses as disturbances and their effects on biodiversity have not been examined in Bhutan. Utilizing swidden as an example, we ask: (1) what role might this historic land use have played in fostering and maintaining biological diversity in particular locales? And (2) what insights and principles can understanding this socio-ecological system offer biodiversity conservation and rural livelihood efforts in the future?

3.1. Swidden as an historic intermediate ecological disturbance

Swidden, or shifting cultivation, was important and widely practiced in Bhutan and elsewhere around the world for centuries (Brookfield, 2014; Cairns, 2007; Fox et al., 2009; Padoch and Pinedo-Vasquez, 2010). Despite suppression by colonial regimes and post-independent governments (Dove, 1983; Mertz et al., 2009a), estimates suggest 10 million hectares remain in some form of forest farming (Kerkhoff and Sharma, 2006) and that there are 50–200 million swidden farmers in the eastern Himalayas alone (Mertz et al., 2009b; Ziegler et al., 2009).

The extent of swidden in Bhutan prior to its political and economic opening to the outside world in the mid-20th Century is unknown. The Government of Bhutan began to curtail swidden with passage of the Bhutan Forestry Act in 1969, which reflected the common view among international agencies, government officials and scientists at the time that swidden is backward, unproductive and destructive (Padoch and Pinedo-Vasquez, 2010; Rerkasem et al., 2009). Approximately 200,000 ha (5.2% of the country's land area) were estimated to have been swidden fields or fallows in 1988 (Roder et al., 1992). The area under swidden declined to 71,250 ha in 1995, the same year the National Assembly adopted a nation-wide ban, and by 1997 swidden had ceased in most of the country (Dukpa et al., 2007). Two types of swidden were historically practiced in Bhutan: (1) *tseri*, a bush fallow system in which trees and shrubs comprised the fallow, and (2) *pangshing*, a grass fallow system. *Tseri* was particularly widespread in eastern and central Bhutan between 300 and 2500 m elevations where maize, millet, rice and vegetables were commonly grown, while *pangshing* was used at high elevations (2500–3500 m), especially in central Bhutan, and wheat, buckwheat, barley and greens were cultivated (Roder et al., 1992).

The size of historic swidden fields in Bhutan is unknown, but recent field sizes in central Bhutan ranged from 1 to 3 ha with some as large as 5+ ha where plots were adjacent to one another (Siebert et al., 2014). In nearby NE India, swiddens ranged from 1 to 2.5 ha in size (Ramakrishan, 1992). Thus, swiddens were much larger than natural canopy gaps caused by wind, insects and disease-associated tree mortality.

Bhutanese farmers did not convert all forests to swiddens. Due to slope, access, soils, as well as religious and cultural reasons, many areas were not utilized for farming, livestock grazing or forest product collecting. Customary rules and governance institutions, building upon local as well as Buddhist beliefs, guided resource access, use and management. For example, Upadhyay (1988) reported that swidden farmers in Zhemgang often worked in groups of 3–5 households who collectively determined if a site had fallowed sufficiently long to be cultivated again and demarcated plot boundaries. More recently, farmers in one Zhemgang village stated that village elders determined access to swiddens and the location and size of fields (pers. com., 2011). There are also numerous sacred sites throughout Bhutan where 'defiling' utilitarian uses and killing animals are prohibited (Dorji et al., 2006; Kuyakanon Knapp, 2012).

The intensity of swidden-related disturbances is a function, most notably, of the temperature, duration and frequency of fires and cultivation. A moderate swidden burn creates temperatures of around 400 C. at the soil surface and 100 C. at 2 cm depth (Zinke et al., 1978). The result is widespread deposition of ash, well-suited to uptake by annual crops, but not too hot to volatilize nutrients or reduce coppicing by fallow species.

Planting and weeding crops are potentially significant disturbances. In *tseri*, soil disturbance is minimal because the ground is rarely plowed and weeding and harvesting are performed by hand. The soil organic layer and associated flora and fauna are not physically altered in most tree-based swidden practices, consequently nutrients losses are minimal and secondary vegetation regrowth is rapid (Conklin, 1957; Nye and Greenland, 1960). In contrast, grass fallow systems cause significant disturbance. In *pangshing*, top soil is cut to a depth of 5–7 cm, dried for several months, piled into mounds and burned at temperatures up to 500 C (Roder et al., 1992). The ash is then spread across the field and the ground plowed using draft animals. These practices eliminate perennial vegetation as well as most soil fauna, and increase runoff and erosion risks.

The duration and frequency, or return interval, of swidden cultivation is expressed as the cultivation: fallow ratio. In Bhutanese *tseri*, fields were historically cultivated for 1–2 years and fallowed for 2–8+ years, while *pangshing* were cropped for 2–3 years and fallowed for 6–20 years (Roder et al., 1992). These disturbances and fallows lengths clearly differ from natural disturbances and are too short to support forest-dependent plant or animal species.

3.2. Swidden effects on flora

Historic swidden practices in Bhutan generally increased the number and size of open areas (i.e., canopy gaps) in comparison to natural treefalls, and maintained complex mosaics of early successional species at various stages of development. The composition, diversity and richness of swidden fallow vegetation have not been well studied in Bhutan. However, research in other areas of the eastern Himalayas provides insights into their potential biodiversity importance. For example, Rerkasem et al. (2009) recorded 370 plant species around one swidden village and greater plant diversity and richness in swidden fallows than in adjacent mature forest plots in both northern Thailand and West Kalimantan, Indonesia. Similarly, Sturgeon (2005) found greater plant species richness in Ahka swiddens than in nearby forest plots in southern China. It is important to note that in the above cases the flora in swidden fallows differed from that in adjacent forest plots (i.e., there was little species overlap). Thus, where 'undisturbed' forests are retained, swiddens may increase floristic diversity at large spatial scales.

Swidden practices in Bhutan differ somewhat from those described above. Karen farmers in northern Thailand reportedly retained large, relict forest trees in their swiddens and observed long (17 years) fallows (Schmidt-Vogt, 1998). In contrast, Bhutanese farmers rarely retain forest relicts and fallows are typically shorter. Nevertheless, Bhutanese fallows can contain a rich diversity of tree species. For example, we observed locally valued *Exbucklandia populnea, Ficus roxburghii, Ficus semicordata*, *Malus* sp., *Quercus griffithii*, and three species of *Castanopsis*, along with other unutilized trees, in one swidden fallow in a temperate broadleaf forest in central Bhutan. Farmers in this area stated that they particularly favor *Ficus* spp. as livestock fodder, bedding and fuelwood, and transplant wild seedlings into their swiddens (pers. com., 2011).

intermediate (i.e., swidden) to low (i.e., natural treefall) disturbance size, frequencies and intensities, and will alter floristic diversity, heterogeneity and structural complexity at landscape levels.

The opportunity to identify and describe historic land uses and disturbance regimes persists in Bhutan and other areas, and should be undertaken while physical evidence and human memory of them remain. As noted previously, this is not to attempt to reinstate them, but because site-specific understanding of historically significant ecological disturbance attributes and their effects could inform future land use policies and practices. For example, harvesting trees for fuelwood in 1–5 ha blocks followed by low-intensity burning to reduce slash, could create secondary vegetation mosaics of different age and size classes. This would replicate historic swidden disturbances while sustaining use of a widely used and readily available renewable energy resource. Another historic practice or disturbance is periodic burning of lemongrass (*Cymbopogon* spp.) in pine stands to stimulate valuable resin production. The development of species diverse forest gardens and improved fallow management for both domestic consumption and market have been advocated elsewhere as potential ways to build upon swidden systems (Cairns, 2007; Padoch and Pinedo-Vasquez, 2010; Xu et al., 2009).

Appreciating the conservation value of historic livelihoods and their associated land uses, and actually building upon them will be challenging in Bhutan and elsewhere. It requires not only further ecological analyses, but explicit recognition of the politics of knowledge, notably ideologies which continue to portray forests and other human-modified landscapes as natural despite empirical evidence to the contrary and decades of attention to this debate (Escobar, 1999; Dove et al., 2011). Historic practices are changing throughout the region in response to government laws and policies, expanded economic opportunities, demographic transitions, and the loss of traditional ecological knowledge and customary governance institutions (Kerkhoff and Sharma, 2006; Mertz et al., 2009a; Wangchuk and Siebert, 2013). Swidden was outlawed in Bhutan and by colonial regimes and independent nation-states elsewhere, a policy supported by international agencies (e.g., UNFAO) despite evidence of their productivity, sustainability and adaptation to local soil, climate and cultural conditions (Conklin, 1957; Nye and Greenland, 1960). Over thirty years ago, Dove (1983) aptly characterized the refusal to recognize the benefits of swidden as a "political economy of ignorance". That is, states and powerful economic interests purposefully ignored or misrepresented swidden as a means to secure control over lands and other resources, and to justify their conversion to what those in power presented as more "productive", specifically logging and export cash crops, from which they often benefited (see also Fox et al., 2009; Mertz et al., 2009a; Sturgeon, 2005).

In recent years, the value and effects of swidden are being reconsidered. ICIMOD, an international organization focused on Himalayan mountain ecosystems, has stated that some swidden systems were productive, sustainable, and even preferable to the agricultural practices that replaced them in the eastern Himalayas (Kerkhoff and Sharma, 2006). The governments of Bangladesh, Bhutan, China, India, Myanmar and Nepal formally acknowledged in 2005 that "shifting cultivation must be recognized as an agricultural and an adaptive forest management practice which is based on scientific and sound ecological principles" (as cited in Kerkhoff and Sharma, 2006). These views suggest new possibilities for recognizing and building upon swidden and other historic practices in future policies and programs.

5. Conclusion

For centuries, swidden and other historic livelihoods and land uses exerted profound ecological effects throughout the world, while supporting local economies and communities. In Bhutan, swidden likely maintained intermediate ecological disturbances, complex mosaics of early seral vegetation, and open and disturbed habitats over large areas for centuries. At the same time, many areas were not used due to steep slopes, poor soils, difficult access, religious beliefs and local customs which maintained habitat for forest-dependent flora and fauna. At the landscape level, the overall effect was increased plant species richness and structural heterogeneity, and more open and disturbed habitats of value to ungulates, tigers and other species.

As Bhutan and other regions of the world change, historic livelihoods, land uses and disturbance regimes change as well. Swidden and other ecologically important intermediate livelihoods and land uses no longer exist or provide the ecological (and economic) functions they did in the past. Nevertheless, ecological and cultural legacies of swidden persist in Bhutanese landscapes. Understanding the site-specific effects that historic livelihoods and land uses exerted on the composition, abundance and distribution of plants and animals, and how societies contributed to creating and managing them, represents an opportunity for biodiversity conservation. The principles underlying historic livelihoods and land uses as ecological disturbances in social–ecological systems should inform conservation policies and practices and could facilitate building much needed bridges between conservation and particular types and scales of development.

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