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REVIEW PAPER

Supporting conservation with biodiversity research in sub-Saharan Africa's human-modified landscapes

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Abstract Protected areas (PAs) cover 12 % of terrestrial sub-Saharan Africa. However, given the inherent inadequacies of these PAs to cater for all species in conjunction with the effects of climate change and human pressures on PAs, the future of biodiversity depends heavily on the 88 % of land that is unprotected. The study of biodiversity patterns and the processes that maintain them in human-modified landscapes can provide a valuable evidence base to support science-based policy-making that seeks to make land outside of PAs as amenable as possible for biodiversity persistence. We discuss the literature on biodiversity in sub-Saharan Africa's human-modified landscapes as it relates to four broad ecosystem categorizations (i.e. rangelands, tropical forest, the Cape Floristic Region, and the urban and rural built environment) within which we expect similar patterns of biodiversity persistence in relation to specific human land uses and land management actions. Available research demonstrates the potential contribution of biodiversity conservation in human-modified landscapes within all four ecosystem types and goes some way towards providing general conclusions that could support policy-making. Nonetheless, conservation success in human-modified landscapes is hampered by constraints requiring further scientific investment, e.g. deficiencies in the available research, uncertainties regarding implementation strategies, and difficulties of coexisting with biodiversity. However, information currently available can and should support efforts at individual, community, provincial, national, and international levels to support biodiversity conservation in human-modified landscapes.

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Introduction

Conservation of biodiversity in Africa, like elsewhere, historically focused on the fortress model, whereby most protected areas (PAs) excluded people (see Carruthers 2009; Adams and Hulme 2001; Siurua 2006). Though PAs are essential for conservation success, they are insufficient (Rosenzweig 2003). For example, large mammal populations have been reduced by half in some African PAs since 1970 (Craigie et al. 2010), probably due, in part, to increasing isolation of PAs (Newmark 2008). Weak enforcement and ineffective management plague many of Africa's current PAs (Kiringe et al. 2007; Metzger et al. 2010; Pare et al. 2010), and many fail to cater to species with extensive spatial requirements, e.g. migratory animals (Holdo et al. 2010; Kirby et al. 2008; Thirgood et al. 2004; Western et al. 2009) and elephants *Loxodonta africana* (van Aarde and Jackson 2007). Even small-bodied species are not necessarily safe-guarded (Pauw 2007). Additionally, the configuration of PAs within the continent neglects key areas for biodiversity (Fjeldsa and Burgess 2008; Eardley et al. 2009; Chown et al. 2003; Fjeldsa et al. 2004; Beresford et al. 2011), a problem that may escalate if climate change makes PAs inhospitable to species they once protected (Loarie et al. 2009). If species' ranges shift with shifting climate, the areas crucial for their persistence will be transient (Hole et al. 2011). Furthermore, the scale of beta-diversity and habitat heterogeneity often extends far beyond that of individual PAs (Gardner et al. 2007), while human activities beyond PAs influence biodiversity within them (Hansen and DeFries 2007).

There are calls for an increased focus on biodiversity beyond African PAs (e.g. Eardley et al. 2009) on two fronts. First, conservation of some biodiversity elements depends on how well matrices outside of PAs cater for persistence. At the species level, for example, the Blue Crane *Anthropoides paradiseus* in South Africa (McCann et al. 2007), Ethiopia's critically endangered Sidamo lark *Heteromirafra sidamoensis* (Spottiswoode et al. 2009; Donald et al. 2010), and the last giraffes *Giraffa camelopardalis peralta* in West Africa (Ciofolo 1995) all depend on human-modified landscapes. At the ecosystem level, three biomes fall below the threshold 10 % protection status within the Afrotropic realm, i.e. tropical and subtropical dry broadleaf forests (6 %), montane grasslands and shrublands (8 %), and deserts and xeric shrublands (9 %), while several ecoregions are <5 % protected, especially when limited to IUCN categories I–IV, e.g. Southern Congolian forest-savanna mosaic (0 %) (Jenkins and Joppa 2009). Second, there are important links between biodiversity and ecosystem function, ecosystem services, and human livelihoods in working landscapes (Daily et al. 2001; Rosenzweig 2003). For example, maintaining natural habitat in and around farms can enhance pollination and, thus, has an economic value to production landscapes (Carvalheiro et al. 2010; Munyuli 2012), and natural systems in Africa provide economic and nutritional benefits to both rural and urban dwellers (Tabuti et al. 2009; Schreckenberg 1999; Vanderpost 2006).

Though, scientists have neglected the biogeography of human-modified landscapes in sub-Saharan Africa, ecologists are increasingly studying the capacity of such landscapes to support biodiversity (Trimble and van Aarde 2012). Such studies are required in order for policy-makers to make defensible decisions regarding land use in relation to biodiversity conservation goals in the face of rapid economic development that could potentially decimate biodiversity. Agriculture in Africa has been characterized by traditional, labor-intensive, smallholder enterprise; production has been low and has remained relatively stagnant (Abate et al. 2000; Deininger et al. 2011). However, economic development and population growth are driving change in African landscapes, with several nations among the world's fastest growing economies (IMF 2013). In 2009, the population reached one billion and is predicted to double by 2050 (UN-HABITAT 2010). Urbanization is a strong force; 40 % of the current African population is city-dwelling, and by 2050, 60 % will be urban (UN-HABITAT 2010). Even so, the rural population will also grow substantially, predicted to increase by nearly 50 % by mid-century (UN Population Division 2012), while growing urban centers will depend heavily on rural resources. To meet this demand and to improve food security, there are calls for both intensifying smallholder agriculture (Baiphethi and Jacobs 2009; Snapp et al. 2010; Muriuki et al. 2005; Baudron et al. 2011) and extensifying production (Muriuki et al. 2005).

Therefore, the interest in biodiversity in human-modified lands is timely. Although Africa's natural ecosystems are more intact than many other regions', a proactive approach to biodiversity conservation that strives for the most prudent management of the unprotected matrices between PAs is clearly preferable to trying to reconnect and restore already degraded ecosystems (Gardner et al. 2010). Thus, as policy-makers chart the future course of development in Africa, they should consider the effects of different choices on biodiversity in human-modified lands, what steps can be taken to prevent biodiversity loss, and the benefits and costs of biodiversity persistence to people. Failure to do so may necessitate expensive restoration and reintroduction efforts. Studies of biodiversity patterns and the processes that maintain them in human-modified landscapes provide an evidence base to support defensible management that meets the needs of people and biodiversity simultaneously. The evidence base should, furthermore, provide for relevant ecological contexts. For example, management standards for timber plantations aim to minimize impact on biodiversity in surrounding natural forests. Yet, the same standards have been applied in plantations embedded in grasslands with dubious efficacy for minimizing impacts on grassland biodiversity (Lipsey and Hockey 2010; Pryke and Samways 2003).

This scientific focus on biodiversity in human-modified landscapes is distinct from Africa's thirty-some-year experiment in community-based conservation (CBC, but also known as Integrated Conservation and Development Projects, Community-Based Natural Resource Management, and others), but these two fields can and should be amalgamated. Promoters of CBC claim that it increases the chance of conservation success and simultaneously reduces rural poverty by allowing community involvement in management and profit from natural resources, especially large mammals (see Hackel 1999). The philosophy of linking wildlife conservation and rural economic development and the practical successes and failures therein have been discussed in a large body of literature (e.g. Songorwa et al. 2000; Torquebiau and Taylor 2009; Hackel 1999) and are subjects of renewed controversy outside of Africa (see Kareiva and Marvier 2012; Doak et al. 2013). However, the discussion has focused on socioeconomics and politics with fleeting consideration for assessing actual biodiversity persistence under different CBC models, a problem pointed out by Caro (1999) and subsequently largely ignored.

In this review, our objective was to elucidate the state of knowledge regarding biodiversity in sub-Saharan Africa's human-modified landscapes to provide an overview for scientists and policy-makers. We also sought to identify constraints and opportunities for integrating biodiversity conservation with land-use management that require further attention in order to support the implementation of sensible policies.

Methods

Literature search

We searched the ISI Web of Knowledge (up to 2012) with keywords "Africa" and "biodiversity or conservation" and each of the following terms: "agricultur*", "agroforestry", "communal", "farm*", "game farm", "game ranch", "human-modified", "multiple-use management", "peri$urban", "private nature reserve", "range$land", "rural", "suburban", and "urban". We also searched for the terms "countryside biography", "reconciliation ecology", and "off-reserve conservation". Additionally, we included relevant papers found coincidentally or in reference lists.

Biodiversity in human-modified landscapes of African ecosystems

In summarizing the literature on biodiversity in Africa's human-modified landscapes, we separate our discussion into four major ecosystem types (see Fig. 1) within which we expect similar patterns to emerge. (1) Rangelands attract the bulk of our attention as Africa's biggest ecosystem type, and rangeland biodiversity is perhaps the most compatible with human land-uses, so biodiversity-conscious land-use planning in rangelands could yield huge benefits. (2) Tropical forests are discussed briefly with a focus on Central and East African forests, and we refer readers to an excellent review of the abundant literature from West Africa (Norris et al. 2010). (3) The Cape Floristic Region, though small, is extremely rich in species yet threatened by extensive commercial development, and we discuss a growing body of literature on land-use management in the region. Finally, (4) the urban and rural built environment will become an increasingly important concern for biodiversity conservation in Africa where the increase of urban land cover is predicted to be the highest in the world at nearly 600 % in the first three decades of the twenty-first century (Seto et al. 2012); proper management and infrastructure development could attenuate the consequences for biodiversity.

Rangelands

Two-thirds of sub-Saharan Africa is composed of rangelands (Fig. 1), consisting of arid and semi-arid grasslands, woodlands, savannas, shrublands, and deserts. The rural people inhabiting rangelands are typically agropastoralists, specializing in small-scale farming or livestock keeping or a combination. Some agricultural practices in rangelands may be harmful to biodiversity, e.g. overcultivation, overgrazing (Kerley et al. 1995), bush fires, cultivation of marginal and easily eroded land, and widespread use of chemicals and pesticides (Darkoh 2003). Many people in rangelands depend heavily on wild resources, e.g. via hunting and gathering or by profiting from wildlife tourism (Homewood 2004). Game ranching is an increasingly popular land-use option across African rangelands (McGranahan 2008), and so are "eco-estates" (Grey-Ross et al. 2009b), where people choose to live amongst the natural beauty of African rangelands and their considerable species diversity, especially charismatic large mammals.

The ecological mechanisms that maintain different rangeland types in different locations, e.g. grassland versus woodland, are not fully understood though interactions between soils, climate, fire, herbivory, and human disturbance are thought to be important (see Bond and Parr 2010). The biggest threats to grasslands include afforestation or bush

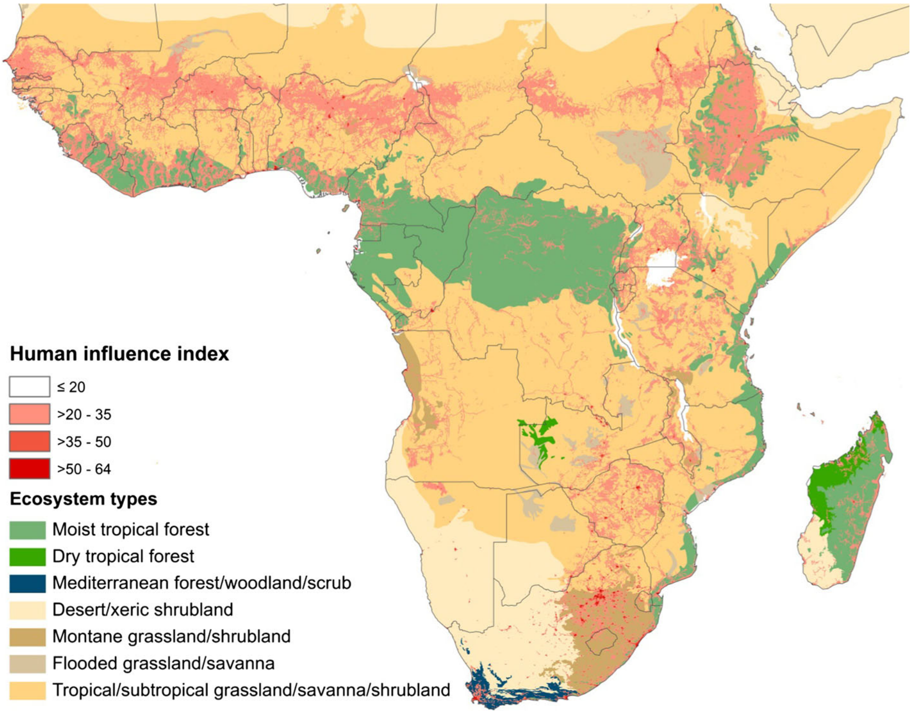

Fig. 1 Map of sub-Saharan Africa showing ecosystem types adapted from Olson et al. (2001): rangelands (desert and xeric shrubland, montane grassland/shrubland, flooded grassland/savanna, and tropical/subtropical grassland/savanna/shrubland), tropical forests (moist and dry tropical forest), the Cape Floristic Region (Mediterranean forest/woodland/scrub), and the urban and rural built environment represented by the human influence index (Wildlife Conservation Society and Center for International Earth Science Information Network 2005), a dataset comprising nine data layers incorporating population pressure (population density), human land use and infrastructure (built-up areas, nighttime lights, land use, land cover), and human access (coastlines, roads, railroads, navigable rivers)

encroachment and clearing for agriculture (Bond and Parr 2010), while threats to the woodlands include woodcutting, clearing for agriculture, and over-use (Tabuti 2007; Schreckenberg 1999). Many perceive that biodiversity is declining in rangeland systems; they blame poor agricultural practices, land conversion, and over-utilization of wild resources by rural people and worry that these patterns will increase with population growth (e.g. Darkoh 2003; Thiollay 2006). However, documented evidence of biodiversity loss in rural rangelands is sparse. Many areas have likely lost some species, but surprisingly, long-inhabited regions lacking formal PAs, e.g. Kenya's Laikipia district, maintain abundant wildlife including large carnivores and elephants (Gadd 2005; Kinnaird and O'Brien 2012) that might seem at odds with human occupation (Woodroffe et al. 2007). Rangeland systems are characterized by disturbances such as fire, unpredictable rainfall, grazing and browsing pressure, and physical disturbance. Therefore, rangeland biodiversity may be relatively resilient to anthropogenic disturbance due to the ability to disperse, colonize, and persist in patchy, fluctuating environments (Homewood 2004). Thus, human-modified landscapes have the potential to maintain a relatively large portion of rangeland biodiversity.

Nonetheless, conservation in rangelands has traditionally excluded people from designated PAs. In South Africa, for example, conservation planning often dichotomizes 'human land-use' and 'conservation' with little consideration for different land-use options that may be variably amenable to biodiversity (e.g. Wessels et al. 2003; Chown et al. 2003). On the other hand, some authors have called to "mainstream" conservation into human-modified lands (e.g. Soderstrom et al. 2003; Pote et al. 2006). O'Connor and Kuyler (2009) used expert opinion to rank the impact of land uses in moist grasslands on overall biodiversity integrity (from least to most impact: conservation, game farming, livestock, tourism, crops, rural, dairy, timber, and urban). Empirical studies are amassing to assess such assertions, which could support land-use planning for conservation. Here we discuss emerging research on biodiversity in several of the most common rangeland land uses.

Grazing

Grazing is important to the maintenance of grassland and savanna habitats, economic development, and management for biodiversity. However, plant responses to grazing are idiosyncratic and incompletely understood (see Watkinson and Ormerod 2001; Rutherford et al. 2012). Overgrazing can lead to degradation and bush encroachment (the proliferation of woody plants at the expense of grasses), while too little grazing can result in succession to woodland (Watkinson and Ormerod 2001). Of course, grazing effects on vegetation can affect higher trophic levels as well, so it is important to understand vegetation responses to grazing, not only for livestock production, but also because vegetation dynamics affect many other species. However, not all grazing landscapes are alike; unique vegetation dynamics in different ecosystems mean that landscapes can respond disparately to grazing pressure (Todd and Hoffman 2009).

Research is emerging that investigates aspects of grazing management and biodiversity in Africa; we summarize 30 such studies in Online Resource Table 1. Generally, these studies look at grazing intensity, or proxies such as bush encroachment, and show that many wild species may be maintained depending on management and location. For example, traditional pastoral practices, i.e. burning and boma creation, may even be necessary to maintain avian diversity in some East African savanna areas (Gregory et al. 2010). Contrastingly, bush encroachment due to overgrazing in Ethiopia may provoke Africa's first avian extinction (Donald et al. 2010; Spottiswoode et al. 2009).

Online Resource Table 1 shows that only about a third of studies compared biodiversity of livestock grazing landscapes to controls with indigenous grazers such as PAs. Most studies came from South Africa (67 %), and most assessed grazing effects on plants (43 %) or insects (27 %). Many areas of investigation remain open, such as the role of vegetation structure including keystone, isolated trees in maintaining biodiversity in human land-use areas; such trees are important for maintaining diversity in natural systems (Dean et al. 1999). A common conclusion with regards to plant diversity is that spatial heterogeneity in grazing management that includes PAs will enhance gamma diversity because different species thrive at different grazing intensities (e.g. Fabricius et al. 2003).

Agricultural mosaic

While extensive grazing is common in arid-savannas and xeric shrublands, a land-use mosaic of grazing and cropping interspersed with settlements is common in more mesic savannas and grasslands. This mosaic effect may have important consequences for the maintenance of biodiversity, and studies of biodiversity in agricultural mosaics (24 studies summarized in Online Resource Table 2) identify some common themes. Compared to strict PAs, agricultural mosaics may actually be beneficial to some species groups. For example, Caro (2001) illustrated greater diversity and abundance of the small mammal assemblage in the agricultural matrix outside Katavi National Park, Tanzania than inside, a pattern also found for Niokolo Koba National Park, Senegal (Konecny et al. 2010). Richness of birds, amphibians, small mammals, butterflies, and trees is similar at 41 sites across a land-use gradient from Katavi National Park to non-intensive agricultural land; however, composition changes along the gradient, and although the PA holds some unique species, some species found outside the PA are absent within (Gardner et al. 2007). Thus, agricultural mosaics may contribute to greater gamma diversity at the landscape scale; nonetheless understanding the conservation implications of higher gamma diversity may require a regional or global perspective on species rarity and commonness.

It is a common finding that agricultural intensification (e.g. mechanization, shortening fallows, destruction of remnant habitat patches, and introduction of cash crops) can have detrimental effects on the biodiversity value of agricultural mosaics. The mosaic effect of traditionally managed farms in KwaZulu-Natal, South Africa may support, and even enhance, bird diversity (Ratcliffe and Crowe 2001), but intensification results in species declines due to loss of ‘edge’ habitats. In Burkina Faso, common butterfly species occur in cultivated areas, while specialists are more common in old fallows and grazed areas, probably because grazing maintains host plants and, thus, diversity (Gardiner et al. 2005). In this case, an agricultural mosaic of shifting fallows could support butterfly meta-populations that allow species persistence, while intensification could be detrimental (Gardiner et al. 2005). In Ethiopian grasslands, low-intensity agriculture supports moderate plant diversity, while larger-scale, mechanized farms reduce tree cover and diversity (Reid et al. 1997). Similarly, In the Serengeti-Mara ecosystem, commercial mechanized agriculture is associated with declining wildlife populations (Homewood et al. 2001; Homewood 2004).

Cropping

Cropping is perhaps more at odds with biodiversity than grazing is because cropping involves the direct removal of indigenous vegetation and planting of, generally, non-indigenous species. Nonetheless, crops can support wild species, and conservation value may depend on the crops planted, the farming methods employed, and the arrangement of fields with respect to natural habitat. Relatively few studies assessed biodiversity solely in cultivated areas (10 studies summarized in Online Resource Table 3), as opposed to agricultural mosaics (Online Resource Table 2). This perhaps reflects the current state of African agriculture, where most farms are smallholder or subsistence based rather than expansive, commercial cultivation. Although there are exceptions, average farm size is just 2–3 ha (Deininger et al. 2011). Where commercial cultivation does occur, loss of biodiversity may be seen as a foregone conclusion not worth investigating (see Thiollay 2006). Many studies of biodiversity in cultivation were concerned primarily with the benefits of that diversity for production via pest control, fertility enhancement, or pollination services, rather than for its value to conservation (e.g. Carvalheiro et al. 2010; Midega et al. 2008; Tchabi et al. 2008).

Agroforestry

Agroforestry, the integration of trees into agriculturally productive landscapes, has garnered much attention in the global conservation community because it has been shown to provide habitat for relatively high levels of forest species diversity (see Bhagwat et al. 2008). In African rangelands, agroforestry can be divided into two types: technological and traditional. Technological agroforestry deals with the expertise to plant and maintain tree species that increase productivity in agricultural production systems. Kenyan farmers, for example, plant crops of fodder trees, which raise milk yields of cows and goats (Pye-Smith 2010a). Government programs in Niger, Zambia, Malawi, and Burkina Faso support large-scale 'evergreen agriculture' projects to plant indigenous trees such as *Faidherbia albida* among crops, which maintain green cover year-round, increase yields by improving soil fertility, and provide fodder and firewood (Garrity et al. 2010). Evergreen agriculture and other technological agroforestry projects are touted as having greater biodiversity value than do monoculture crops (see Pye-Smith 2010a, b; Kalaba et al. 2010; Garrity et al. 2010). Yet, evidence to support these claims remains mostly anecdotal, warranting further research because plans are underway to expand technological agroforestry projects throughout Africa (Garrity et al. 2010).

Traditional agroforestry, on the other hand, is a millennia-old practice, particularly evident in the parkland savannas of West Africa, of people maintaining savanna tree species in pastures, fields, and villages. These trees provide shade, food, wood, and even cash when commercially traded (e.g. shea, baobab), and traditional agroforestry may contribute to the maintenance of tree species in addition to species for which trees provide habitat. Many studies have enumerated tree diversity in farmlands (Online Resource Table 4). Even so, the conservation value of agroforestry varies. Augusseau et al. (2006) report that in Burkina Faso, few indigenous species are important to farmers and none are planted. Even where tree richness is maintained at a relatively high level, the persistence of trees in traditional agroforestry can be compromised if the economic value of totally clearing the land, e.g. for mechanized agriculture or firewood, outpaces the value of non-timber products (Tabuti et al. 2009). Additionally, based on demographic profiles of tree species, tree regeneration appears problematic in many human-modified landscapes (e.g. Fandohan et al. 2010; Schumann et al. 2010; Venter and Witkowski 2010). For example, a study in Benin shows that the largest shea trees are often in villages or fields, but seedling survival is low compared to nearby PAs (Djossa et al. 2008). Regeneration potential can also be diminished when harvesting tree products affects recruitment, as is the case for *Khaya senegalensis* in Benin (Gaoue and Ticktin 2008). Where natural regeneration potential is compromised, intervention may be required to ensure rejuvenation (Kindt et al. 2008; Ouinsavi and Sokpon 2008), especially if farmers abandon traditional rotational land-use systems such as long fallow, where trees are often most capable of regenerating (Raebild et al. 2007; Schreckenberg 1999).

Fortunately, agroforestry management in rangeland ecosystems is an active area of research with regards to developing strategies to encourage tree persistence (Kindt et al. 2008; Tabuti et al. 2009; Augusseau et al. 2006). Yet, there is a surprising lack of research to assess the value of savanna agroforests for faunal diversity or even non-tree plant diversity (Online Resource Table 4), aspects that have been more thoroughly studied in the tropical forest context (Bhagwat et al. 2008), and this dearth should be remedied.

Game ranching and private nature reserves

The wildlife industry, including game ranching, game farming, and private nature reserves, has become big business, especially in southern and East African rangelands. These land-use options involve profiting from consumptive (e.g. trophy hunting, live animal sales, meat) or non-consumptive (e.g. tourism, aesthetic value) use of wildlife on communal or private land. South Africa alone has an estimated 9,000 private game ranches, covering 20.5 million ha, many of which were converted from traditional livestock ranches (NAMC 2006). Ranching game rather than domestic livestock may ameliorate effects of over-grazing because indigenous species have coevolved with indigenous vegetation (Kerley et al. 1995), and indigenous browsers may control bush encroachment (McGranahan 2008; Taylor and Walker 1978). Thus, the wildlife industry may be a boon to biodiversity conservation; however, very few studies have actually assessed impacts on biodiversity, which may be positive or negative and likely depend on management actions (Cousins et al. 2008).

Occurrence and abundance of mammal species on private land has increased due to game ranching (Lindsey et al. 2009). Nonetheless, some aspects of the wildlife industry are worrying. Privatization of wildlife (and sometimes legislative requirements) begets ubiquitous game fencing (McGranahan 2008; Lindsey et al. 2009) with substantial ecological consequences including the interruption of natural movements, inbreeding, and over-stocking (Lindsey et al. 2009; Hayward and Kerley 2009). Ranches are often quite small (South African provincial averages range from 8.2 to 49.2 km^2), and smaller ranches necessitate more intensive management interventions (Lindsey et al. 2009; Bothma 2002). Additionally, the industry's focus on trophies may skew natural communities in favor of valuable species and induce semi-domestication (Mysterud 2010), and it has resulted in extra-limital introductions, questionable breeding practices, and persecution of predators (Lindsey et al. 2009). Even within the mammal community, generally the focus of game ranching, the full complement of species of a given ecosystem may not be maintained on ranches despite deliberate re-introductions (Grey-Ross et al. 2009a).

Thus, much more research is needed on the biodiversity value of the wildlife industry and what measures, e.g. promoting conservancies over single game ranches (Lindsey et al. 2009), can improve this value. Best-practice management in terms of grazing pressure, fire regimes, bush encroachment, wildlife ownership policies, and fencing needs more attention (McGranahan 2008). Furthermore, surprisingly little is known about the impacts of game ranching on species other than large mammals. Even so, game ranches are likely more amenable to most indigenous biodiversity than are many other commercial land-use options. For example, large eagles in South Africa's Karoo shrublands are much more common in areas stocking indigenous mammals than in areas with domestic livestock and cultivation (Machange et al. 2005).

Tropical forests

Though rangelands cover the majority of Africa, tropical forests also make up a considerable portion [$\sim$20 % (Brink and Eva 2009), Fig. 1], particularly rich in biodiversity. Research on biodiversity in human-modified landscapes is biased towards tropical forests (Trimble and van Aarde 2012). Nonetheless, biodiversity in human-modified tropical forest landscapes in Africa has received much less scientific attention than in other regions, especially South and Central America (Gardner et al. 2010). African tropical forests tend to be in less conflict with high human population densities than elsewhere (e.g. Southeast Asia and Brazilian Atlantic forests) (Gardner et al. 2010), although in West Africa 80 % of the original forest extent is now an agricultural-forest mosaic home to 200 million people (Norris et al. 2010).

We do not attempt a comprehensive review of African tropical forest biodiversity in human-modified landscapes and refer readers to Norris et al. (2010) for an excellent treatment of the West African scenario. They lament the lack of data regarding biodiversity in African agricultural-forest mosaics but are able to reach some general conclusions. Land uses that maintain tree cover are more amendable to forest biodiversity than those that do not. Species richness increases in some modified habitats, such as logged and secondary forest, for some species groups, but endemic forest species are often lost. Additionally, relatively high species richness in modified habitats comprises, in part, species not present in the baseline forest comparison, so species richness alone likely overestimates the value of modified habitats for forest species. Furthermore, habitat modification seems to affect richness of forest plant species more negatively than of some animal groups.

Although logically, it seems more difficult to encourage the persistence of biodiversity in human-modified landscapes embedded in tropical forests than in rangelands, research can indicate best practices for land-use planning. In contrast to West Africa, Central Africa still maintains large tracts of relatively undisturbed forest that are becoming increasingly threatened by development, and lessons from studying African forest biodiversity in human-modified landscapes should be incorporated into development policy for the region (Norris et al. 2010).

The tropical forest biome extends to East and southern Africa where forests are less extensive, confined largely to high altitudes inland and a linear belt along the coast. These geographic constraints present unique challenges for conservation and heighten the importance of maintaining endemic species and retaining connectivity in fragmented forests. Fewer studies consider East and southern African tropical forests than West African forests, but work is emerging to support land-use planning in the region, and results largely conform to those found for West Africa. Agroforestry in Ethiopian and Tanzania supports less diversity than forests but more than other land uses (Gove et al. 2008; Hemp 2006; Hall et al. 2011; Negash et al. 2012). While Schmitt et al. (2010) found higher overall plant richness in Ethiopian coffee agroforests than natural forests, richness of typical forest species was lower. In Kenya, connectivity of coastal forest fragments for primates may be influenced by matrix structure (Anderson et al. 2007). Farmland outside tropical forest remnants, especially structurally complex subsistence farms, support higher bird richness than forests; however, many forest species are lost, highlighting the importance of maintaining the forest remnants but also supporting traditional farming techniques over commercial monocultures (Laube et al. 2008; Mulwa et al. 2012). Furthermore, structurally diverse farmland surrounding forest remnants may enhance forest pollinator communities (Hagen and Kraemer 2010). Similarly, South African forest remnants embedded in various matrix types have similar bird species richness, but abundance is highest in fragments in agricultural matrices due to the presence of forest generalists and open-habitat species, while forest specialists are rare (Neuschulz et al. 2011). Additionally, herpetofaunal richness does not decline monotonically along a land-use gradient from forest to cultivation, while richness of functional groups erodes along the gradient due to sensitivity of some specialist groups (Trimble and van Aarde 2014). Forest fragments and grasslands in the agricultural mosaic outside a PA in southern Mozambique have more beetle species and higher abundance, while endemic beetle species are better represented inside the PA (Jacobs et al. 2010).

Cape Floristic Region

While small in area (approximately 90,000 km^2, see Fig. 1), the Cape Floristic Region (CFR) of South Africa is a biodiversity hotspot of global significance (Myers et al. 2000) consisting of a Mediterranean-type ecosystem with high species turnover across the landscape and high endemicity. Systematic conservation planning has been conducted for the region but focused on pristine habitat that could be formally protected (see Cowling and Pressey 2003). Because spatial turnover of species is so high, however, successful conservation will depend heavily on efforts in human-modified landscapes beyond PAs (Cox and Underwood 2011). Based on species-area curves for plants and vertebrates in the CFR, practicing biodiversity friendly management on just 25 % of the land that is beyond PAs, but still in a natural or semi-natural state, might add an additional 541 species to the 7,340 estimated to occur in PAs (Cox and Underwood 2011).

However, in contrast to many areas of Africa dominated by subsistence agriculture, the CFR is characterized by large areas of intensively managed agricultural monocultures with low biodiversity value (Giliomee 2006). Overall, only 26 % of the CFR has been transformed, but the CFR is made up of different habitat types, and some, especially in the fertile lowlands, have lost much more of their area to cultivation, urbanization, and heavy invasion of exotic plants; for example, coast renosterveld is more than 80 % transformed (Rouget et al. 2003a). Transformation threatens not only the CFR's plants but also endemic and vulnerable animals such as the Black Harrier *Circus Maurus*, which has been displaced from the inland plains by cereal agriculture and now breeds, less successfully, in the coastal strip and inland mountain habitats (Curtis et al. 2004). Though the Black Harrier can forage in cultivated areas, it relies on intact vegetation to breed (Curtis et al. 2004).

PAs within the CFR are concentrated in areas of low agricultural value (e.g. mountains and coastlines), so biodiversity in fertile areas depends on conservation on privately owned land (Giliomee 2006; Rouget et al. 2003b). To increase the biodiversity value of agricultural areas, the primary focus should be on conserving remnants of natural vegetation on farms (Giliomee 2006). This is being attempted through incentive-driven stewardship agreements that protected almost 70,000 ha of vegetation on private land between 2003 and 2007 (Von Hase et al. 2010). Additionally, farm management practices may be variably amenable to biodiversity. For example, though vineyards have very different arthropod communities than those in natural vegetation, organic vineyards support greater diversity than do more intensively managed vineyards (Gaigher and Samways 2010). However, these effects may be taxon dependent; for instance, organic vineyard management benefits richness of monkey beetles (crucial pollinators), but not bees (Kehinde and Samways 2012). Similarly, apple orchards support less arthropod diversity than natural vegetation does, but orchards that are not sprayed with pesticides have a higher diversity than sprayed sites (Witt and Samways 2004). On the other hand, farms with a mixture of different crops and remnants of natural vegetation maintain most fynbos bird species and attract several additional species, while single crop sites without remnant vegetation have much less bird diversity and lose many fynbos species (Mangnall and Crowe 2003). Clearly, maintaining remnant vegetation and connectivity in agricultural areas of the CFR is crucial, but more research is needed to tailor agricultural practices to better conserve CFR species in production landscapes.

Urban and rural built environment

Plant and vertebrate species richness and endemism are correlated with human population density and human infrastructure in sub-Saharan Africa (Burgess et al. 2007; Fjeldsa and Burgess 2008; Balmford et al. 2001), which is substantial in many regions (see Fig. 1). That the pattern endures in relatively developed South Africa means either that species persist to some degree with humans in disturbed habitats at current levels, that human-disturbed habitats actually attract more species, or that a major extinction debt is yet to be paid (Fairbanks 2004; Chown et al. 2003). Regardless, areas with high human density [predicted to increase dramatically in Africa, outpacing growth in all other regions in the coming decades (Seto et al. 2012)] require appropriate regulations to ensure they remain as amenable as possible to biodiversity conservation. This will be especially important in Africa's most biologically rich yet rapidly urbanizing regions; by 2030 for example, the urban area within the Eastern Afromontane and Guinean Forests of West Africa hotspots is forecasted to be 1,900 and 920 % of 2,000 levels respectively (Seto et al. 2012).

Some obvious steps include discouraging urban sprawl; providing appropriate housing for low income populations while controlling illegal settlements in biodiversity sensitive areas; designing relevant green spaces that include aquatic habitats and indigenous plants; and managing invasive species, waste, and pollutants (Puppim de Oliveira et al. 2011; Muriuki et al. 2011). Research on managing Africa's urban and rural built environments for biodiversity is in its infancy and is mostly constrained to South Africa. Clearly, more research is needed, yet several studies provide pertinent information for planners.

While urban environments might not seem particularly hospitable to biodiversity, even small home gardens in African cities can harbor a remarkable number of species, especially in the tropics, both intentionally cultivated and otherwise (Cumming and Wesolowska 2004; Lubbe et al. 2010; Bigirimana et al. 2012). In South Africa, socioeconomics, urbanicity, and ecological factors influence plant diversity and the proportion of invasive species in home gardens (Lubbe et al. 2010; Molebatsi et al. 2010). Gardens with a high number of non-indigenous species contribute to biotic homogenization and pose the risk of new introductions that could prove detrimental to indigenous ecosystems. Therefore, invasive species in the urban landscape need to be controlled through regulation and removal, especially in threatened and fragile ecosystems (Alston and Richardson 2006; Dures and Cumming 2010; Cilliers et al. 2008; Bigirimana et al. 2012).

Green spaces such as city parks, tree-lined streets, and even golf courses in urban environments can support certain species. Dures and Cumming (2010) show that habitat quality, rather than patch metrics such as area, have the greatest influence on bird diversity in fynbos in an urban gradient in Cape Town. Thus, controlling invasive species even in high-density housing areas may be more beneficial for birds than expanding the low quality network of urban reserves. Alien pine tree removal helps restore invertebrate species diversity in Cape Town, and fragments of natural vegetation and gardens with indigenous plants help maintain it (Pryke and Samways 2009). In the Durban Metropolitan Open Space System, complex habitats (i.e. with trees and shrubs) support higher invertebrate diversity than simplified habitats (i.e. mown lawns); however, simple habitats might cater for certain rare species (Whitmore et al. 2002). Green spaces in urban Pretoria contribute to butterfly and moth diversity (McGeoch and Chown 1997) and also support indigenous birds (van Rensburg et al. 2009), while maintaining urban riparian vegetation is necessary for dragonfly conservation in Pietermaritzburg (Samways and Steytler 1996). Better ecological planning for developments such as golf courses could increase the likelihood for biodiversity persistence and minimize negative consequences, even in the CFR (Fox and Hockey 2007). Additionally, habitat engineering, e.g. creating biotopes for dragonflies (Steytler and Samways 1995), might be a useful tool in the urban context to promote biodiversity, although continual management of these habitats may be necessary to ensure species persistence (Suh and Samways 2005).

When species are range-restricted such that a single metropolitan area may affect most of their range, special attention is required. For example, two small forest parks in Durban suburbs are home to the last remnant populations of the rare tree *Oxyanthus pyriformis* whose specialist pollinators, the long-tongued hawkmoths, appear unable to tolerate suburban living. Hand pollination and planting of seedlings will be necessary to maintain the species (Johnson et al. 2004). Similarly, conservation of plants in Cape Town is hampered by apparent sensitivity of specialist pollinator birds to urbanization, which is concerning given the increasing urbanization in the CFR (Seto et al. 2012). Durban covers a large portion of the range of the black-headed dwarf chameleon *Bradypodion melanocephalum,* and translocations from sites demarcated for development to sites reserved for conservation have proven somewhat successful, dependent on adequate alien-plant-control and habitat restoration (Armstrong 2008). Unique landscape features within urban areas may also require special attention. For example, Table Mountain in Cape Town harbors endemic species whose conservation depends not only on the PA of Table Mountain but also on management of lower elevation suburban woodlands (Pryke and Samways 2010).

On the rural end of the settlement spectrum, less attention has been given to biodiversity persistence. Some agricultural mosaic studies consider rural settlements, but a few studies treat it explicitly. For example, similar to shifting cultivation, some cultures practice shifting settlement, and abandoned settlements have been shown to provide valuable seasonal resources, e.g. fruit trees, to chimpanzees *Pan troglodytes* in Mali (Duvall 2008). Even road verges may provide for some types of biodiversity. For example, verges in the Karoo support some plant species not found in adjacent grazing lands, though many species from pastures are not found in verges (O'Farrell and Milton 2006). Verges also support invertebrates and could prove valuable to conservation because verges are public spaces that can be managed for biodiversity (Tshiguvho et al. 1999).

Understanding more about urban settlement and biodiversity may even benefit conservation in once remote PAs where rural sprawl and infrastructure for wildlife tourism can be dramatic (Wittemyer et al. 2008). For example, recent decades have seen substantial increases in rural sprawl along with the construction of 60 tourist lodges, 1,200 boreholes, and 540 km of roads in the Okavango Delta, one of Botswana's premiere conservation areas (Vanderpost 2006).

Constraints and opportunities

The scope of this review was broad, covering four major ecosystem types within sub-Saharan Africa. Specific conclusions are difficult because species' responses to land use are clearly idiosyncratic and dependent on local factors. Nonetheless, we have identified some general conclusions and constraints summarized in Table 1 and discussed below.

The science of biodiversity in human-modified landscapes

As others have pointed out, understanding the value of human-modified landscapes for biodiversity, especially in Africa, is hampered by data constraints (Norris et al. 2010; Pettorelli et al. 2010; Waltert et al. 2011; Trimble and van Aarde 2012). Many studies are limited in temporal and spatial scale, and poor study design may result in insufficient sampling of habitats. The focus on species richness of certain habitat types while failing to account for the importance of species from other habitats in assigning conservation value to different land-use options may neglect the bigger picture; Bond and Parr (2010), for example, call for more collaboration between forest conservationists and others. More consideration for the value of different species in terms of commonness and rarity also needs to be developed because human-modified landscapes often fail to cater for endemic and specialist species (Waltert et al. 2011), and a better understanding of beta and gamma diversity at a landscape scale is necessary.

Table 1 General conclusions regarding practices that support biodiversity in human-modified landscapes and scientific and implementation concerns requiring further investigation

Practices that tend to support species diversity and richness in human-modified landscapes
Prefer diversity in selection of crops grown (i.e. polyculture) and land use (i.e. land-use mosaics, over homogenous monocultures)
Encourage traditional agricultural practices over large-scale, mechanized farming
Leave as much remnant natural vegetation as possible and monitor or assist maintenance of keystone structures or species, e.g. large trees
Ensure strict protection for specialist and endemic species and expand PA coverage focused on these groups
Encourage appreciation and understanding of conservation goals among land users
Discourage urban sprawl and maintain and manage urban green spaces
Favor use of native species in gardens and cultivation
Avenues for further investigation into scientific uncertainties and implementation practices
Researching poorly documented combinations of species group, ecosystem type, and land use, e.g. mammals in rangeland agroforests
Moving beyond occurrence data to likelihood of persistence, e.g. how dependent are species in human-modified landscapes on nearby PAs or remnant habitat?
Investigating the value of reintroduction or rewilding in human-modified landscapes
Going beyond the species level of biodiversity to integrate genetic and ecosystem concepts
Supporting technological and traditional knowledge for cultivating useful native species and investigating the effects of these practices on other taxa
Creating frameworks for valuing importance of different species in different landscapes at a local level within a global context, e.g. commonness versus rarity and specialist versus generalist
Developing policies that integrate and account for local, regional, and global conservation needs and land use systems

Additionally, further investigation into the relationship between occurrence and persistence is required, as are more studies that delve beyond species richness into the processes that support the observed patterns of biodiversity. For example, studies of demographic processes (e.g. Venter and Witkowski 2010; Djossa et al. 2008; Schumann et al. 2010) and population trends (e.g. Trimble and van Aarde 2011; Stoner et al. 2007) for species inhabiting human-modified landscapes can provide insight beyond mere patterns of occurrence. Furthermore, as elsewhere (Gardner et al. 2010), studies of biodiversity in African human-modified landscapes is biased towards certain taxa—and the patterns exhibited by these species might not apply to others (Caro 2001). Also, genetic diversity, has not generally been considered though may be important in terms of traits valuable to humans and for conservation (Ashley et al. 2006). Conservation in human-modified landscapes may be particularly important in conserving genetic diversity because the traditional fortress PA model may encompass relatively little, especially for plants (Atta-Krah et al. 2004).

Many authors lament erosion of ecological knowledge to maintain species, especially trees, medicinal plants, and wild food plants, and urge more effort towards domestication, cultivation, and marketing to provide farmers with the means to conserve species while easing pressure on wild stock and improving food security and economic stability (Kindt et al. 2008; Ntupanyama et al. 2008; Tabuti et al. 2009; Leakey and Tchoundjeu 2001; Dold and Cocks 2002; Dovie et al. 2007; Khumalo et al. 2012). However, care must be taken to ensure that genetic diversity is maintained in the process (Lengkeek et al. 2006;

Muchugi et al. 2008). Development of domestication and cultivation methods could promote the use of native species in human-dominated lands, and these native plants may contribute to conservation of other taxa (Dovie et al. 2007), but more research is clearly required.

Implementing policies

Given the limitations of the available science, it is difficult to develop strategies to encourage land uses that are of the highest conservation value. The effect of policy on biodiversity conservation in human-modified landscapes under different land tenure systems and different settlement patterns needs more research because decisions are largely opinion driven and not evidence based (Homewood 2004; Duvall 2008). Perhaps the community-based conservation literature, which has focused heavily on implementation and policy, could lend some insight. A review of this literature stresses that better implementation results are achieved when there is quality governance, resilient local institutions with local power and accountability, consideration for local context, integration across social and ecological systems, and mutual learning involving communities and other involved parties, e.g. outside experts (Balint and Mashinya 2008). NGO's and foreign aid are more likely to encourage successful conservation when projects are flexible, small-scale, and targeted at local interests, and when they prioritize innovation, learning, and experimentation (Nelson 2009). Conservationists must also take cognizance of perspectives and needs of local communities in both rural and urban settings in order to better engage them in conservation management (Ferketic et al. 2010). CBC projects that are independent of PAs are excellent opportunities to maintain biodiversity on human-modified land of marginal use for agriculture; and expert opinion, monitoring, and ecological modeling tools can help communities manage their natural resources (Du Toit 2002).

We have indicated several gaps in the literature on biodiversity in African human-modified landscapes, and while much more work is required to create sensible policies that meet conservation needs and those of governments and people (Ashley et al. 2006), as it stands, current research can go some way towards supporting policy-making. Studies of biodiversity persistence in different land-use options for a given region can be incorporated into scenario modeling for future development. For example, Turpie et al. (2007) amalgamated studies of plants, invertebrates, birds, and mammals in human-modified landscapes to predict how varying levels of afforestation or dairy production in the Drakensberg grasslands of South Africa would influence alpha diversity.

Some generalities emerge from the literature that may be helpful in working towards sensible policies. Generally, diversifying human-modified landscapes at all levels, e.g. polyculture cropping, diverse agroforestry, and maintaining farmlands with high heterogeneity in terms of both crops and vegetation structure, is likely to support more species than do more homogenous land uses, while potentially also providing economic stability, given fluctuating markets for specific crops (Franzen and Mulder 2007). Endemic and specialist species tend not to persist in human-modified landscapes; thus, PAs continue to be crucial to conservation efforts, and expanding PA coverage within areas rich in such species is important (Jenkins et al. 2013). Furthermore, a regional approach to management of these sensitive species is necessary. Past and present implementation strategies are beyond the scope of this review, yet there is literature dealing with such strategies in Africa that may be of use, e.g. certification of sustainable and biodiversity friendly products (Lilieholm and Weatherly 2010).

Living with nature

Maintaining biodiversity in landscapes where humans live, work, and extract resources implies that humans will have to coexist with other species. While the consequences of living without nature may be worse than the difficulties of living with it, certain issues present considerable, though not unmanageable, obstacles for promoting conservation beyond PAs. Many, and perhaps most, species are easily compatible with human livelihoods and may have a positive impact via aesthetic or functional value, but some, especially large mammals, can be problematic in human-dominated landscapes, e.g. carnivores threaten livelihoods by predating livestock and, occasionally, people. Nonetheless, specific and practical actions can greatly reduce the probability of carnivore attacks. For example, in Kenyan communal lands, having a domestic dog accompany herds reduces risk of a carnivore attack by 63 %; conversely each additional boma gate increases risk of attack by 40 % (Woodroffe et al. 2007). However, carnivores are not the only concern. Other animals, such as baboons and bush pigs, can damage structures and destroy crops while larger herbivores, such as elephants, also threaten human lives. Knowledge of attitudes of people employing different land uses can help land-use planners develop strategies to reduce conflict and negative attitudes towards conservation. For example, crop agriculture should not be encouraged in predominantly pastoral areas where elephants and people coexist relatively peacefully (Gadd 2005). Furthermore, land-use planning that incorporates knowledge of which crops are most likely to generate conflict could allow creation of buffer zones in areas with high conflict potential (Hockings and McLennan 2012).

The risk of disease transmission poses an additional difficulty. Diseases of domestic animals threaten wildlife. For example, domestic dogs are carriers of canid diseases transmissible to wild carnivores (Butler et al. 2004) and were partly responsible for extinction of the African wild dog *Lycaon pictus* and decimation of lions *Panthera leo* in areas of the Serengeti (see Woodroffe 1999). Additionally, livestock can transmit animal diseases (e.g. bovine tuberculosis) to wildlife with negative conservation outcomes, while wildlife can also transmit diseases (e.g. foot and mouth) to livestock with immense economic consequences (Michel et al. 2006; Thomson 2009).

Fencing has been heavily used in Africa to assist people in their ability to coexist with nature—to reduce direct conflict and disease transmission. Laws regarding fencing differ by country; for example, Zambia requires game fences while Namibia encourages large-scale cooperation between game-farmers to discourage fencing (McGranahan 2008). Obviously, fencing has serious ecological consequences (Trimble and van Aarde 2010; Hayward and Kerley 2009) and is anathema in many ways to the goals of conservation, especially conservation beyond PAs (Trimble and van Aarde 2010; Woodroffe et al. 2014). However, non-traditional fencing technologies (see Hayward and Kerley 2009), such as fences targeted at particular problem species (e.g. elephant fences that allow other species to pass), virtual barriers, or fencing wildlife out of villages and fields instead of into PAs, may be acceptable compromises. The effect of fences on the persistence of species in human-modified landscapes certainly deserves more investigation.

Economically, wild animals provide an important resource for many people in Africa (Bharucha and Pretty 2010), which may threaten species persistence. ‘Sustainable use’ is frequently discussed with relation to bushmeat hunting, but food scarcity and population growth dictate that it will likely be impossible to enforce rules for sustainable use unless food security issues are addressed (Fa et al. 2003). Sustainable harvesting is also an issue for plants (Sambou et al. 2002). Community forests must be carefully managed, e.g. by restricting harvesting of pole-sized stems to certain species, to ensure that species are not used to extinction (Obiri et al. 2002). Additionally, rules must be assessed to ensure that they achieve the desired goals; for example, in the Republic of Guinea, tax to the forestry administration for harvesting palm wine counterproductively encourages harvesters to employ lethal yet profitable methods of harvesting to compensate for the initial investment (Sambou et al. 2002).

Conclusion

There is clearly both necessity and great potential for human-modified land in sub-Saharan Africa to contribute to the conservation of the continent's biodiversity. While PAs will remain essential, and are especially important for protecting species sensitive to human disturbance (Devineau et al. 2009), a greater focus on biodiversity conservation beyond their boundaries could be complementary to overall conservation goals. The information gleaned from studies of biodiversity in human-modified landscapes in Africa discussed in this review goes some way toward providing policy-makers with evidence to support defensible decisions for land-use planning and conservation management beyond PAs (see Table 1). Improving the amenity of human-modified landscapes for biodiversity can be encouraged at all levels from individuals' choices to plant indigenous home gardens, to grass roots endeavors to manage communal resources, to communities deciding to share their land with wildlife, to commercial farms going organic and maintaining patches of natural habitat. Governmental intervention at the level of the city (e.g. green space planning), region (e.g. extension agencies demonstrating biodiversity friendly agricultural practices), nation (e.g. policy-setting for control of invasive species, pesticide or poison usage, and land-use zoning), or even internationally (e.g. cooperative removal of boundary fences) are also warranted.

Although several factors including lack of knowledge, implementation challenges, and problems of coexistence with wildlife may constrain successful implementation of biodiversity conservation in human-modified landscapes, given each constraint, opportunity exists for progress. On the bright side, scientific interest in the topic is increasing (Trimble and van Aarde 2012), and as research accumulates, it will allow for systematic reviews useful for policy decisions. Additionally, many issues associated with human-wildlife coexistence are primarily related to large mammals and efforts to solve these problems should continue. Meanwhile, the barriers to implementing strategies to conserve other species groups in human-modified landscapes are far from insurmountable and such strategies should be prioritized.

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