



# Agriculture—a key element for conservation in the developing world

Hugh L. Wright, Iain R. Lake, & Paul M. Dolman

School of Environmental Sciences, University of East Anglia, Norwich, NR4 7TJ, UK

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High nature value farming; land sparing; low-impact agriculture; rural livelihoods; seminatural habitat; traditional land management; wildlife-friendly farming.

## Correspondence

H.L. Wright or P.M. Dolman, School of Environmental Sciences, University of East Anglia, Norwich NR4 7TJ, UK. E-mail: hugh.wright@uea.ac.uk or p.dolman@uea.ac.uk

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## Abstract

Conserving biodiversity through supporting or mimicking traditional management of anthropogenic habitats is a paradigm in the developed world, particularly Europe. It is rarely applied in developing countries where forest biota are more common foci. We quantified the numbers of globally threatened bird species using anthropogenic habitats and examined scientific literature to identify those that are dependent on low-impact agriculture in the developing world. Such dependency is distinct from species using farmland to supplement or move between their remnant natural habitats. We show that low-impact agriculture is important to a number of threatened open-habitat species in a variety of farming systems. However, these systems are expected to undergo widespread transformation due to economic change. Conservation must identify valuable farmed landscapes and seek new mechanisms to maintain or mimic important land-management techniques in developing countries. A suite of policy instruments should be considered to provide incentives or development benefits that encourage farmers to manage landscapes for wildlife. The land sparing approach to balancing biodiversity conservation and agricultural production will be detrimental to those open-habitat bird species dependent on agriculture; a mix of agricultural land-use types may offer the best compromise.

## Introduction

Anthropogenic landscapes are receiving increasing attention in developing world conservation (Daily 2001; Urquiza-Haas *et al.* 2007; Gardner *et al.* 2009; Edwards *et al.* 2011). However, outside developed countries the conservation value of the agricultural matrix is usually interpreted in terms of its permeability to forest species that retain access to fragments of natural habitat (Daily *et al.* 2001; Ranganathan *et al.* 2008; Perfecto & Vandermeer 2010). Here we present evidence that anthropogenic landscapes are of primary importance to a distinct set of mainly open-habitat species. This situation most commonly arises in ancient farmed landscapes in parts of Europe, Africa, and Asia, but also in recently transformed landscapes where novel human land use has substituted for natural ecosystem processes. Forest species, the focus of countryside biogeography, use farm-

lands as a means of dispersal, a buffer to populations in core natural ecosystems or as a supplementary resource. For these, farmland is still only second best compared to intact forest. In contrast, many open-habitat species have come to fully depend on anthropogenic or seminatural landscapes where their natural habitat has been entirely lost. Examples of this dependency can now be found in the developing world, where conservation approaches emphasizing seminatural landscapes will have great relevance.

## A developed world conservation paradigm

Anthropogenic landscapes sustain much biodiversity in the developed world after the loss and conversion of natural ecosystems over recent millennia. Although progressive landscape transformation extirpated numerous

species (often filtering top predators, large herbivores, old-growth dependent and some open-habitat species), remaining taxa were able to exploit these landscapes and the low-impact practices that maintained them, resulting in dependency in the absence of their natural habitat. Open-habitat species, those once occurring naturally in nonforested habitats such as grasslands, savannas, and steppe, have developed particularly strong dependencies on anthropogenic and seminatural habitats.

Twentieth-century mechanization and market transformation brought further ecosystem change (Donald *et al.* 2001). Intensified land use resulted in temporal and spatial homogenization of habitats (Benton *et al.* 2003), whereas abandonment of marginal lands caused ecological succession and further reductions in habitat complexity (Sirami *et al.* 2008). As a result, reintroducing or mimicking low-impact practices to sustain the conservation value of seminatural habitats became a dominant paradigm in European conservation (Sutherland & Hill 1995; Bignal & McCracken 2000). Traditional management of forest, fen, anthropogenic grasslands, shrublands, and pseudo-steppe habitats has been widely applied and incorporated into legislation, such as the European Habitats Directive.

Agriculture in Europe became a particular focus of the seminatural habitats paradigm. Heterogeneous agricultural mosaics offer benefits to numerous complementing species (Fuller *et al.* 2004), whereas other taxa require extensively farmed landscapes of less structural complexity. Legislation, such as the European Common Agricultural Policy has incentivized wildlife-friendly, lower-impact farming to counter the twin threats of agricultural intensification and abandonment. However, such agri-environmental schemes sometimes achieve mixed or meager success due to broad and shallow approaches that minimize transaction costs at the risk of ignoring important ecological detail (Kleijn *et al.* 2006; Batáry *et al.* 2011).

## Conservation and agriculture in the developing world

By contrast, the seminatural habitat approach has rarely been applied in the developing world. Although this may be partly due to challenging social and political conditions that limit policy transfer, dominant schools of thought in developing world conservation also contribute. Priority is given to closed-habitat species and their frontier forest ecosystems (Bond & Parr 2010), where agricultural conversion causes considerable primary habitat and species loss (Sodhi *et al.* 2010). Policy is dominated by efforts to stem the impacts of exploitation or land-use change in

natural habitats. Agricultural landscapes, when considered, are typically assessed for their suitability in maintaining or assisting the survival of forest species, such as studies of wildlife-friendly coffee plantations (Mas & Dietsch 2004). Although in some cases agriculture is treated as an intimate component of biodiversity conservation (Perfecto & Vandermeer 2010), the focus remains on sustaining populations of declining natural habitats. Conservation approaches directed primarily at frontier ecosystems or by countryside biogeography may overlook the importance of agricultural landscapes for open-habitat species.

Global food demand is increasing due to growing human population but also greater affluence and changing consumption. Although famine and food security may best be addressed by resolving food entitlement inequalities (Sen 1981), global demand may nonetheless double by 2050, outstripping human population increase (Loh 2002). How this can be met without widespread species extinctions is of great concern, with agricultural land-use considered one of the greatest threats to global biodiversity (Sala *et al.* 2000; MEA 2005). The majority of human population and economic growth is occurring in developing countries where pressures for natural habitat conversion and agricultural intensification are greatest and expected to escalate (Cincotta *et al.* 2000; Tilman *et al.* 2001).

Species already dependent, or increasingly reliant, on farmland due to loss of natural habitats are at particular risk from agricultural change. It is important to identify and protect those seminatural habitats and agricultural landscapes of high conservation value in developing countries. Here we present evidence that agricultural landscapes support not just a filtered subset of the biota remaining in extant natural habitats, but rather a unique and dependent biodiversity. This justifies the wider application of European conservation approaches to the developing world and influences how habitats are prioritized for conservation in these countries.

## Threatened species and low-impact agriculture in the developing world

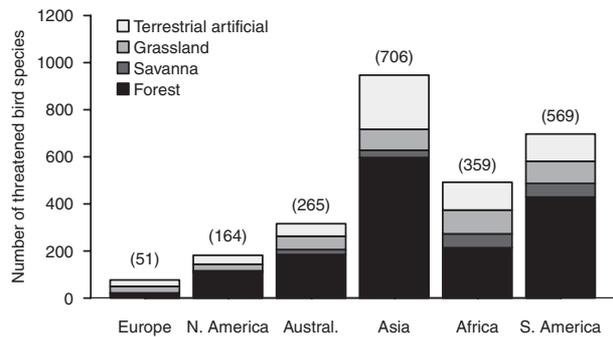
Globally threatened birds were systematically examined to quantify their associations with agricultural habitats, followed by an assessment of candidate species and their potential dependency on farming. The analysis was restricted to birds as there is little comparable autoecological data for other taxa. Nonetheless, the multitude of evidence from developed countries suggests that dependencies of nonavian wildlife on agriculture will also occur more widely. Numerous butterflies (van Swaay

*et al.* 2006), arthropods (Di Giulio *et al.* 2001), reptiles (Michael *et al.* 2011), amphibians (Hartel *et al.* 2010), bats (Boughey *et al.* 2011), and even sessile organisms such as vascular plants (Haines-Young *et al.* 2000), rely on or benefit from management of anthropogenic habitats in the developed world.

Focusing on species of high conservation priority revealed the importance of agriculture to conservation globally. Habitat associations were collated and quantified across six regions: Europe, North America, Australasia, Asia, Africa, and South America. We searched the IUCN Red List for Birds database (BirdLife International 2011) using terms consistently used for status (critically endangered, endangered, vulnerable, or near threatened) and habitat (forest, grasslands, savannas, or terrestrial artificial landscapes—which we interpret as mainly comprising agriculture); these are elaborated in Supporting Information.

The potential agricultural dependency of candidate bird species was initially assessed using species accounts of the Red List database (BirdLife International 2011), identifying birds that make use of food resources or habitat conditions (foraging or breeding) maintained by farming practices. Where these suggested possible dependency (replacing or substituting, rather than complementing natural habitats) we sought scientific evidence from primary literature. Species were considered largely or entirely dependent on agriculture where approximately >75% of the population was reliant on an agricultural habitat or practice at one or more stages of its life history. Population data were obtained from species accounts or primary literature, but when unavailable the proportion of the species range with dependency was inferred qualitatively from distribution maps. Our assessment of agricultural dependencies will be incomplete, particularly for grassland or savanna species, where species accounts and past autoecological studies have often failed to recognize the dynamic nature of these systems and the crucial role of human land use. The true importance of agriculture to dependent species is therefore underestimated.

Although 77% of all threatened or near threatened bird species in developing countries use forest habitats, 28% use terrestrial artificial landscapes (22% in addition to forests and 6% in artificial landscapes but not forests). Thirty-three percent of threatened species in Asia use artificial habitats (Figure 1), matched by 33% of African and 20% of South American species, demonstrating that such associations are widespread in the developing world. Furthermore, 25% of all globally threatened or near threatened developing-world birds occur in grassland or savanna habitats, many of which are modified or maintained by human land-use. Grassland is especially



**Figure 1** The numbers of globally threatened or near threatened species using forest, savanna, grassland, or other artificial habitats (primarily agricultural but also including urban, rural gardens, and heavily degraded forest) by region. As individual species may use more than one habitat and more than one region, the number of species represented in each region is shown in parentheses. Australasia (Austral.) includes Australia, New Zealand, New Guinea, and Pacific Islands.

valuable in Africa, where it is used by 95 of the 144 globally threatened birds (Beresford *et al.* 2010).

Beyond the use of agricultural and potentially modified habitats presented in Figure 1, we identified nearly 30 threatened bird species for which there is strong evidence of dependence on low-impact agriculture in the developing world (Table 1). The number of examples suggests this is not a trivial pattern and many more cases would be found if appropriate data were available. We found dependence on anthropogenic landscapes and habitats across a wide range of open-habitat species and taxonomic groups, from grassland specialists such as larks and bustards, to birds of prey and waterbirds. These occurred at both breeding and nonbreeding life stages and across all six geographic regions. As in Europe, open-habitat species worldwide benefit from a variety of resources and management techniques across a range of farming systems.

In pastoral systems, domestic livestock may mimic or substitute crucial ecosystem functions once provided by wild herbivores, now extirpated or scarce. Consequently, many threatened species, such as larks and terrestrial waders, now appear reliant on livestock for maintaining habitat suitability in extensive savannas, rangelands and agro-forestry systems (Table 1). Inappropriate exclusion of livestock from wetland or grassland systems can lead to declines of dependent biodiversity as has occurred in certain Indian conservation programmes (Lewis 2003). Domestic livestock can also be a vital food source for carcass-feeders such as South Asian *Gyps* and *Sarcogyps* vultures—so long as diclofenac residue is absent (Houston 1996; Pain *et al.* 2003).

Arable systems can provide abundant invertebrate prey, cereal grains, and weed seeds, particularly in

**Table 1** Threatened and near threatened open-habitat species dependent on low-impact agriculture in the developing world, by farming system and in taxonomic order

| Farming system            | Species                  | Resource <sup>a</sup>            | Status <sup>b</sup>    | Region <sup>c</sup> |  |
|---------------------------|--------------------------|----------------------------------|------------------------|---------------------|--|
| Extensive pastoral        | Jerdon's courser         | <i>Rhinoptilus bitorquatus</i>   | FH                     | CR                  | South Asia                             |
|                           | Liben lark               | <i>Heteromirafra sidamoensis</i> | NH, FH                 | CR                  | East Africa                            |
|                           | Rudd's lark              | <i>Heteromirafra ruddi</i>       | NH, FH                 | VU                  | Southern Africa                        |
|                           | Sharpe's longclaw        | <i>Macronyx sharpei</i>          | NH, FH                 | EN                  | East Africa                            |
|                           | Sierra Madre sparrow     | <i>Xenospiza baileyi</i>         | NH, FH                 | EN                  | Central America                        |
| Pastoral                  | Indian vulture           | <i>Gyps indicus</i>              | Ca                     | CR                  | South Asia                             |
|                           | Slender-billed vulture   | <i>Gyps tenuirostris</i>         | Ca                     | CR                  | South and South-East Asia              |
|                           | White-rumped vulture     | <i>Gyps bengalensis</i>          | Ca                     | CR                  | South and South-East Asia              |
|                           | Red-headed vulture       | <i>Sarcogyps calvus</i>          | Ca                     | CR                  | South and South-East Asia              |
|                           | St Helena plover         | <i>Charadrius sanctaehelenae</i> | NH, FH                 | CR                  | South Atlantic islands                 |
|                           | Sociable lapwing         | <i>Vanellus gregarius</i>        | NH, FH                 | CR                  | Central Asia                           |
|                           | Buff-breasted sandpiper  | <i>Tryngites subruficollis</i>   | FH <sub>NB</sub>       | NT                  | South America                          |
|                           | Botha's lark             | <i>Spizocorys fringillaris</i>   | NH, FH                 | EN                  | Southern Africa                        |
|                           | Pale-headed brush-finch  | <i>Atlapetes pallidiceps</i>     | FH                     | EN                  | South America                          |
|                           | Arable and rice          | Asian crested ibis               | <i>Nipponia nippon</i> | FH                  | EN                                     |
| Black-necked crane        |                          | <i>Grus nigricollis</i>          | FH, Gr <sub>NB</sub>   | VU                  | Central Asia                           |
| Hooded crane              |                          | <i>Grus monacha</i>              | FH, Gr <sub>NB</sub>   | VU                  | East Asia <sup>d</sup>                 |
| Yellow-breasted bunting   |                          | <i>Emberiza aureola</i>          | FH, Gr <sub>NB</sub>   | VU                  | Asia                                   |
| Mixed pastoral and arable | Northern bald ibis       | <i>Geronticus eremita</i>        | FH                     | CR                  | North Africa, Middle East              |
|                           | Southern bald ibis       | <i>Geronticus calvus</i>         | FH                     | VU                  | Southern Africa                        |
|                           | White-shouldered ibis    | <i>Pseudibis davisoni</i>        | FH                     | CR                  | South-East Asia                        |
|                           | Blue crane               | <i>Grus paradisea</i>            | NH, FH, Gr             | VU                  | Southern Africa                        |
|                           | Grey crowned-crane       | <i>Balearica regulorum</i>       | FH, Gr                 | VU                  | South and East Africa                  |
|                           | Bengal florican          | <i>Houbaropsis bengalensis</i>   | NH, FH                 | CR                  | South and South-East Asia              |
|                           | Blue bustard             | <i>Eupodotis caerulescens</i>    | NH, FH                 | NT                  | Southern Africa                        |
|                           | Great bustard            | <i>Otis tarda</i>                | NH, FH                 | VU                  | Middle East, Central Asia <sup>d</sup> |
|                           | Great Indian bustard     | <i>Ardeotis nigriceps</i>        | NH, FH                 | CR                  | South Asia                             |
|                           | Dupont's lark            | <i>Chersophilus duponti</i>      | NH, FH                 | NT                  | North Africa                           |
| Saffron-cowled blackbird  | <i>Xanthopsar flavus</i> | NH, FH                           | VU                     | South America       |  |

Sources are given in Supporting Information, Appendix S2.

<sup>a</sup>System resource of importance to threatened species: NH = nesting habitat, FH = foraging habitat, Gr = rice/cereal grain and Ca = animal carcasses. NB indicates that the dependence occurs in the nonbreeding season only.

<sup>b</sup>Threatened status: CR = critically endangered, EN = endangered, VU = vulnerable and NT = near threatened.

<sup>c</sup>Extent of species' ranges, in the developing world only.

<sup>d</sup>Species also occurs in developed countries.

low-input cereal and rice farming. Species such as Asian crested ibis (*Nipponia nippon*) have benefited from long historical associations with traditional arable agriculture. Numerous crane species forage on agricultural land benefiting from spilt cereal grains (Table 1), similar to the use of farmland by common crane (*Grus grus*) in Europe (Franco *et al.* 2000). In Asia, remaining areas of low-to-medium intensity rice cultivation provide stubbles that support wintering granivorous passerines, such as yellow-breasted bunting (*Emberiza aureola*). Such production systems are now increasingly rare and threatened (Gray *et al.* 2007).

Mixed farming, combining pastoral and arable land-use within a landscape, is particularly important with its heterogeneity and small-scale complexity providing var-

ied foraging resources and nest sites (van der Weijden *et al.* 2010). In Morocco, the critically endangered northern bald ibis (*Geronticus eremita*) feeds in a mosaic of extensively grazed semi-arid littoral steppe and low-intensity, traditionally-cultivated barley *fields and fallows* (Bowden *et al.* 2008). Small-scale cultivation occurs close to, or amongst, littoral steppe habitat kept open by goats and sheep. This combination of pastoralism and crops creates habitat conditions with a high density of invertebrate and lizard prey accessible to the ibis. Agricultural intensification associated with human population growth is threatening the long-term viability of this mixed farming system.

Numerous examples come from ancient, traditional farming systems, where species such as Asian crested



**Figure 2** The critically endangered sociable lapwing (*Vanellus gregarius*) (A) which depends on grazed steppic grasslands (B) during the breeding season. Photographs courtesy of Maxim Koshkin.

ibis and Bengal florican (*Houbaropsis bengalensis*) could shift to agricultural land uses over centuries or millennia, developing increasing dependency on these systems as their natural habitats were lost. Other cases have arisen much more recently where new land-use practices have replaced the key ecosystem processes that open-habitat species require. The sociable lapwing (*Vanellus gregarius*; Figure 2) became reliant on agriculture in the twentieth century as the declining influence of native ungulates coincided with the creation of new rural livelihoods and novel farmed landscapes (Kamp *et al.* 2009). A large number of our cases of agricultural dependency come from Asia and Africa. This is perhaps related both to the ancient history of pastoralism and cereal agriculture in these regions, and to ecosystem functions now being carried out by livestock following recent extirpations of native ungulates.

These developing-world cases provide wider relevance for the seminatural habitats paradigm. New and stronger dependencies are likely as agriculture continues to replace habitats and ecosystem processes in these countries.

Developing-world farming systems may support a growing set of distinct taxa, although open-habitat species may still be lost where they occupy an ecological niche not substituted by human land-use, or where agricultural change is particularly severe. Further research is needed into the value of low-impact agriculture in the developing world, particularly for nonavian taxa, so that agriculture's importance is better understood and valuable landscapes are identified.

## Prospects for low-impact agriculture and associated biodiversity

Low-impact agriculture benefits a suite of threatened species in the developing world but is under threat from economic change. Escalating food prices create incentives for agricultural investment by new, external actors (Godfray *et al.* 2010) bringing infrastructure and high-input production methods that cause rapid land-use transition. The consequences of industrialized agriculture for greenhouse gas emissions and environmental problems (such as salinization, aquifer depletion, and soil erosion), combined with increasing costs of inorganic fertilizers, may challenge the long-term viability of industrial agriculture (MEA 2005). However, economic drivers and the current failure of markets to capture externalities will probably sustain these models in the short to medium term. This represents an immediate threat to low-impact agriculture and could bring losses to open-habitat biodiversity.

Although large-scale industrial agriculture can benefit national economies and increase food production, it often threatens the livelihoods and social stability of rural communities (MEA 2005; Cook 2009). Corrupt institutions lacking transparency and accountability, weak land tenure, and marginalized status can leave rural communities vulnerable to land concessions, land grabbing, and mass-privatization of common resources (Cotula *et al.* 2009). These factors threaten wildlife-compatible pastoral economies in seminatural grassland and savanna ecosystems causing conversion to ranching or cereal agriculture (Norton-Griffiths 1995). For example, land conversion in the Tonle Sap floodplain of Cambodia is eroding customary land rights and replacing pastoralism and traditional rice farming with intensive, irrigated rice cultivation, putting Bengal florican at serious risk of extirpation (Gray *et al.* 2007).

Where high-input agriculture threatens both people and wildlife, conservation could attempt to halt, or at least delay, land-use transition by empowering rural communities. In such cases, supporting social justice and local land-use entitlement could provide a win-win scenario that advances the mutualistic goals of biodiversity

and livelihood protection, enabling low-impact agriculture to persist, at least in the short term. Conservation goals may be particularly closely aligned with livelihoods when other opportunities are limited, such as in infertile marginal lands or hostile environments. However, economic changes and greater access to technology and markets will still encourage transition to more profitable, higher-yielding practices (Lambin *et al.* 2001), even where the impacts of external actors can be alleviated.

Small-scale farming is being championed as an alternative to industrial models. Characterized by low mechanical or chemical inputs with high crop complexity and high labor intensity, this form of agriculture could deliver greater productivity in relation to land area and provide a more sustainable means of future food supply (Perfecto & Vandermeer 2010). New models from both the development and conservation agendas propose that small-scale agriculture could achieve greater food production, food security, ecological and social resilience, and poverty reduction (FAO 2007; IAASTD 2009), as well as promoting biodiversity conservation (Knoke *et al.* 2009; Perfecto & Vandermeer 2010). Nevertheless, achieving these socio-economic goals will require that existing small-scale farming systems are developed (Hazell *et al.* 2007), making the prospects for wildlife dependent on low-impact agriculture unclear. Intensification of production may prove detrimental to species dependent on extensive techniques, and with nearly one-third of the human population living on small farms (Hazell *et al.* 2007) the impacts of agricultural development could be considerable.

### **The conservation response: applying the seminatural habitats approach**

The widespread transformation of low-impact agriculture appears likely, whether through extrinsic actors or internal agricultural development. Where threatened biodiversity is dependent on agriculture, minimizing the threat of rapid industrialization is a crucial first step. However, merely defending community entitlements to resist land grabbing by external actors may not guarantee the status quo in the face of economic pressures and technological opportunities. Conservation should prepare for intervention, developing, and adopting a range of policy mechanisms with the aim of maintaining, supporting, or mimicking beneficial land management; thereby transferring the seminatural habitats paradigm to the developing world. Effective interventions must be harmonized with socio-economic policies to ensure social development is not prevented (Adams *et al.* 2004). Curtailing economic

growth or constraining livelihood opportunities could result in stakeholder discontent or threaten a policy's long-term viability.

Various policy measures offer economic opportunities, incentives or development benefits to stakeholders, including: market enhancements such as certification schemes; community-based ecotourism; payments for environmental services; direct payments for conservation and conservation concessions (Bennett 2000; Ferraro & Kiss 2002). Such instruments could reward farmers for the take-up or continuation of valuable agricultural practices sustaining open-habitat species. Education to raise awareness of sustainable land management and resource use combined with disincentives for bad practice, such as enforcement of wildlife protection legislation and compulsory public disclosure of practices will also be important (Bruner *et al.* 2001). In many cases, policy measures would support rather than replace existing livelihoods, although compensation may be required for lost opportunities of developing higher-yielding, higher-impact agriculture. The need to quantify the costs of wildlife-friendly farming is recognized in the developed world (House *et al.* 2008), but elsewhere these costs and the necessary levels of compensation or incentive deserve further research.

Conservation of the endangered Sharpe's longclaw (*Macronyx sharpei*) in Kenya is beginning to adopt the seminatural habitat approach. The species requires short-sward grassland maintained by livestock, a habitat being lost to both agro-business- and smallholder-scale arable cultivation (Muchai *et al.* 2002). Land purchases are alleviating the threat of habitat conversion and grazing lets, administered by the community, provide income while creating suitable habitat conditions. At a larger scale, sheep-rearing is being advocated to provide a livelihood alternative and deliver habitat management for conservation (P. Matiku personal communication). Training and marketing is provided to encourage uptake of sheep-farming, supplemented by bee-keeping and an emerging eco-tourism scheme to provide further livelihood development.

Appropriate policy instruments will be highly context dependent. The pace of economic development, land entitlement of farmers, political transparency, complexity of stakeholder relations, strength of institutions, and empowerment of local people are all important considerations (Salafsky *et al.* 2001). European policies such as agri-environmental schemes may be relevant in some instances, particularly where institutions are well developed and legitimate. However, geographical transfer of policy measures will require assessments of their suitability under different social, political and economic conditions. The ability to undertake conservation of

open-habitat species in agricultural landscapes will also depend on finding sustainable sources of funding—a challenge to be addressed for species conservation in general. Where financial resources are scarce and priorities have to be drawn, the decision on whether to conserve biodiversity in natural versus anthropogenic landscapes should be based on evidence regarding relative threat, conservation value, cost, and likelihood of success.

## Reconciling conservation and global food production

Protecting biodiversity in the face of projected rises in food demand is a challenge. To reconcile the aims of conservation and agricultural development, conservation has proposed a trade-off between two approaches: wildlife-friendly farming and land sparing (Green *et al.* 2005; Ewers *et al.* 2009; Phalan *et al.* 2011). The former attempts to conserve species on farmland but with costs to yield, therefore requiring more land in cultivation. The latter would intensify agriculture to increase yields, reducing the need to convert further natural habitat to agriculture (Balmford *et al.* 2005). This trade-off can potentially be resolved using a model examining the response of species population density to agricultural yield. Where increases in yield cause steep (concave) declines in population density, land sparing through intensification is most appropriate as it gives greater regional species abundance for a given level of agricultural yield (Green *et al.* 2005; Phalan *et al.* 2011).

However, this model assumes population density is always maximal in an existing and available natural habitat, with lower densities in all forms of agriculture and a monotonic decline with increasing yield. This does not apply to those open-habitat species now dependent on agriculture, for which natural habitats or processes are absent and maximal density occurs along the gradient of human land-use and agricultural yield. Although agricultural intensification, offset by land sparing, may be an appropriate strategy in frontier ecosystems (Sodhi *et al.* 2010), elsewhere it may heighten the risk of extinction for biota reliant on low-impact agriculture. This form of agriculture is the only option for such species, at least in the absence of large-scale restoration of natural habitats and ecosystem function. A further limitation is the model's assumption that meeting human need depends solely on the volume of agricultural production. Although markets may drive increased production, human welfare is often better served by resilient livelihoods, social security, and adequate entitlements, all of which can be threatened by intensified industrial agriculture.

Conservation strategies that provide not just for forest species, but also agriculture-dependent species, will require a mixture of intensification, land sparing, and extensive low-impact agriculture that should be optimized for any particular region (Fischer *et al.* 2008). Agriculture's paradoxical nature, as both a great threat to biodiversity and a valuable land-use that sustains open-habitat species (van der Weijden *et al.* 2010), would be better represented by such a compromise. We have shown that agricultural dependency is widespread across the developing world; however, uncertainty remains as to its relative frequency and regional variability. An urgent task for conservation is to identify the land-use practices and anthropogenic landscapes important to biodiversity and to develop the mechanisms to maintain them before they are lost through land-use change.

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## Supporting Information

The following supporting information is available for this article:

**Appendix S1.** Details of search terms for the analysis of bird species habitat associations using the IUCN Red List for Birds database.

**Appendix S2.** Primary literature sources for species demonstrating a dependency on low-impact agriculture in the developing world (Table 1 of the main text), listed by species in alphabetical order by common name.

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