

Ecosystem services provided by waterbirds

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ABSTRACT

Ecosystem services are ecosystem processes that directly or indirectly benefit human well-being. There has been much recent literature identifying different services and the communities and species that provide them. This is a vital first step towards management and maintenance of these services. In this review, we specifically address the waterbirds, which play key functional roles in many aquatic ecosystems, including as predators, herbivores and vectors of seeds, invertebrates and nutrients, although these roles have often been overlooked. Waterbirds can maintain the diversity of other organisms, control pests, be effective bioindicators of ecological conditions, and act as sentinels of potential disease outbreaks. They also provide important provisioning (meat, feathers, eggs, etc.) and cultural services to both indigenous and westernized societies. We identify key gaps in the understanding of ecosystem services provided by waterbirds and areas for future research required to clarify their functional role in ecosystems and the services they provide. We consider how the economic value of these services could be calculated, giving some examples. Such valuation will provide powerful arguments for waterbird conservation.

Key words: bioindicators, cultural services, economic value, ecosystem engineering, ecosystem services, nutrient fluxes, pest control, seed dispersal, waterfowl harvest, zoochory.

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I. INTRODUCTION

The term ‘ecosystem services’ is increasingly used to describe ecosystem resources and processes that have a benefit to human society, particularly since its popularization by the

Millennium Ecosystem Assessment (MEA) (2005). If we can identify such services and quantify their value, we can argue more effectively for the protection of ecosystems and the species within them, and so influence public opinion and policy decisions (Daily *et al.*, 2009). As recently pointed out

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by Wenny *et al.* (2011), there is an urgent need to further the understanding of what ecosystem services are provided by birds, and to establish methodologies for quantifying their value. Although these authors provide an excellent review of the different services carried out by birds and progress to date in estimating their value (see also Whelan, Wenny & Marquise, 2008), they focus on terrestrial birds. In this paper we focus exclusively on waterbirds (*sensu* Wetlands International, 2012, including all aquatic birds such as Anatidae, shorebirds, rails, wading birds, gulls and terns) and aim to complement existing work by reviewing how waterbirds provide the service categories identified by the above authors, as well as by identifying additional services. In doing so, we highlight ecosystem services that are unique for waterbirds, and which are powerful arguments for their conservation.

Ultimately, terrestrial and aquatic systems are strongly interdependent, as shown by a growing body of research (Nakano & Murakami, 2001; Burdon & Harding, 2008). Nevertheless, it is important to consider explicitly the role of waterbirds in subsidies between aquatic and terrestrial ecosystems. Furthermore, ecosystem service research is in its infancy and is largely proceeding on a case by case basis at the scale of individual sites (Luck *et al.*, 2009), making it practical to address the services provided by waterbirds in and around a specific lake or other wetland. There is obviously much to be learned and gained by considering the role of birds in freshwater and wetland habitats. In this review we make the point that there are many ways in which waterbirds provide a service, but also highlight numerous areas in which our understanding of the functional role of waterbirds remains very limited. We make proposals for further research required to clarify the importance of the services provided by waterbirds, and the role of different species, in the hope that this will stimulate others.

Ecosystem services provided by wetlands have been relatively well studied and their value has been estimated in an increasing number of cases (MWO, 2012). Wetland services include water purification, fixation of run-off nutrients, flood prevention, aquifer recharge and fishery maintenance. By contrast, the specific role of waterbirds within aquatic ecosystems has often been overlooked. In our view this is largely owing to a shortage of interdisciplinary research between ornithologists and aquatic ecologists or limnologists. Birds are surprisingly often excluded from models of aquatic food webs (Mooij *et al.*, 2007; van Nes, Rip & Scheffer, 2007), or perceived as only reacting to the 'bottom-up' influence of fish, vegetation or other organisms, without having any 'top-down' influence themselves (e.g. Janse, 1997; Scheffer *et al.*, 2006). Sometimes birds are not even mentioned in aquatic ecology textbooks (Lampert & Sommer, 2007). On the other hand, the extensive literature on North American waterfowl is focused principally on how to create suitable conditions so as to guarantee a hunting resource, with little or no attention to other ecological services provided by those populations. In this review we will cite numerous cases that testify to the unique and often central

role of waterbirds in many aquatic ecosystems and to the importance of the services they provide.

The profound impact of seabirds on island ecosystems by depositing nutrients of marine origin and *via* ecosystem engineering is now clearly recognized (Fukami *et al.*, 2006; Sekercioglu, 2006). The present review focuses on waterbirds using inland waterbodies and estuaries, and does not explicitly cover seabirds, although many bird species use both marine and inland aquatic ecosystems during different stages of the life cycle, and there is overlap in the services provided by each group. Our aim is to concentrate on the positive ecological consequences of waterbirds, rather than on the negative ones or 'ecological disservices' (Dunn, 2010). Disservices such as transmission of diseases that can potentially affect humans (Hubalek, 2004), or conflicts with fisheries (Carss & Marzano, 2005; Harris *et al.*, 2008), are dealt with adequately by existing literature and do not require further review here. However, we point out other, less well-known, disservices below without reviewing them at length. All kinds of disservices must be taken into account to evaluate the 'net contribution' of waterbirds.

Ecosystem services are generally divided into four categories (Table 1; Millennium Ecosystem Assessment, 2005). Many of the services provided by waterbirds are 'supporting services' such as propagule dispersal or nutrient cycling, which are processes vital to ecological communities and agricultural or fishery ecosystems. Others are 'regulating services' such as pest control, or 'provisioning services', which apply to resources directly exploited for food, clothing or other uses. Finally there are 'cultural services', which apply to the recreational value or spiritual value of birds. However, in the case of waterbirds this 'four-box' terminology cannot be applied in a straightforward manner, as services frequently overlap and interact among categories. For example, waterbird hunting for subsistence is a provisioning service, but at the same time in many cultures waterbird hunting is a cultural service with recreational or spiritual value (e.g. as indicated by Figs 1, 2). We therefore do not refer consistently to this categorization.

II. CULTURAL SERVICES

Anatidae and other waterbirds have a major cultural value in many parts of the world (Kear, 1990). Ducks also have important amenity values for the human population, both in rural (van Kooten, Withey & Wong, 2011) and urban landscapes. In modern times, the human interest in seeing concentrations of waterfowl on migration or at wintering sites (Fig. 3) has facilitated the protection of many of these sites and ultimately led to the initiative to establish the Ramsar Convention (Convention on Wetlands) in 1971 as well as non-governmental organizations such as The Wildfowl & Wetlands Trust (UK) and Wetlands International (originally The International Waterfowl Research Bureau). Ducks, geese, swans, flamingoes and other waterbirds are used as flagships of conservation in general; the wide public

Table 1. Selected examples of ecosystem services provided by waterbirds

Category	Ecosystem service	Waterbird taxon	References
Provisioning	Meat	Anatidae	Krcmar <i>et al.</i> (2010)
	Down	Common eider, geese	Sveinsson 2013; and Kear (1990)
	Feathers for clothing and ornaments	Anatidae, herons, others	Green & Figuerola (2005) and Frisch <i>et al.</i> (2007)
Supporting	Grease for waterproofing	Geese	MacMillan & Leader-Williams (2008)
	Animal propagule dispersal	Anatidae, coots	Green & Figuerola (2005) and Frisch <i>et al.</i> (2007)
	Plant propagule dispersal	Anatidae, shorebirds	Green <i>et al.</i> (2002 <i>b</i>), Klein <i>et al.</i> (2008) and Brochet <i>et al.</i> (2009)
	Nutrient cycling	Geese, cormorants	(Iacobelli & Jefferies, 1991), Gauthier <i>et al.</i> (2006) and Kameda <i>et al.</i> (2006)
	Stimulating primary productivity	Geese	(Cargill & Jefferies, 1984), Bazely & Jefferies (1985) and Nolet (2004)
	Stimulating decomposition	Ducks	Bird <i>et al.</i> (2000) and van Groenigen <i>et al.</i> (2003)
	Reduction of methane production	Swans	Bodelier <i>et al.</i> (2006)
	Plant diversity	Anatidae	Maron <i>et al.</i> (2006), Jasmin <i>et al.</i> (2008) and Hidding <i>et al.</i> (2010)
	Animal diversity	Anatidae, others	Fabricius & Norgren (1987) and Georgiev <i>et al.</i> (2005, 2007)
	Protection from predators	Geese	Fabricius & Norgren (1987) and Allard & Gilchrist (2002)
	Bioindicators of plants	Anatidae, coots	Elmberg <i>et al.</i> (1993), Wicker & Endres (1995) and Green <i>et al.</i> (2002 <i>a</i>)
	Bioindicators of animals	Anatidae	Elmberg <i>et al.</i> (1993, 2010) and Gunnarsson <i>et al.</i> (2004)
	Bioindicators of nutrients/contaminants	Hérons, grebes, ducks	Fasola <i>et al.</i> (1998), Nummi <i>et al.</i> (2000) and Burger & Eichhorst (2007)
Regulating	Pest control	Ducks	Hamilton <i>et al.</i> (1994), Teo (2001) and Miles <i>et al.</i> (2002)
	Disease surveillance	Ducks	Munster <i>et al.</i> (2005), Wallensten <i>et al.</i> (2007) and Ziegler <i>et al.</i> (2010)
Cultural	Regime shifts of wetlands	Cormorants	Leah <i>et al.</i> (1980) and Dirksen <i>et al.</i> (1995)
	Recreational hunting	Anatidae	Losey & Vaughan (2006), Grado <i>et al.</i> (2011) and Withey & van Kooten (2011)
	Birdwatching	Geese	MacMillan & Leader-Williams (2008)
	Ecotourism	Geese	Edgell & Williams (1992)
	Conservation flagships	Anatidae, flamingoes	Kear (1990) and Galicia & Baldassarre (1997)
	Art	Flamingoes, others	Mas (2000) and Arnott (2007)

'Category' refers to the standard classification as outlined by the Millennium Ecosystem Assessment (2005). A maximum of three references is given per example. The waterbird taxa correspond to the studies cited, other taxa are also likely to provide the same service.

interest in them has led to a greater awareness of conservation issues and promoted action to protect populations, species and their habitats. As a small child, the first author was inspired to think about global conservation by a poster about flamingoes at Lake Nakuru on his bedroom wall. These flagships have in turn benefited other wetland species for which awareness and public support have generally been much lower. For example, most of the 2087 wetlands around the world declared as Ramsar sites (collectively protecting 204803109 ha of habitat, <http://www.ramsar.org/>) were declared using criteria based on their importance for waterbirds.

Larger waterbirds are particularly important for cultural services. Humans clearly feel a special reverence for birds such as swans, flamingos and ibises for example, as reflected through their artistic and religious importance through history (e.g. association between royalty and swans in the UK, Fig. 4, or the African sacred ibis *Threskiornis aethiopicus*

in Ancient Egypt). Greater flamingoes *Phoenicopterus roseus* are represented in Palaeolithic cave art from southern Spain (Mas, 2000). Arnott (2007) cited numerous examples of waterbirds in ancient art. Feathers from waterbirds such as herons, terns and grebes became highly prized for fashion items in the 19th century, leading to overhunting of these birds and ultimately to the birth of bird conservation organizations (Doughty, 1975). The economic benefits from cultural services are important, although they have rarely been quantified. Contingent valuation was used to estimate the extent to which the human population values goose populations in Scotland, and found that the economic benefits of goose conservation outweighed the costs resulting from agricultural conflicts (crop damage) by a factor of up to 700 (MacMillan, Hanley & Daw, 2004). Goose-related tourism has been shown to play a vital role in the local economy of the Scottish island of Islay (Edgell & Williams, 1992). However, for the purposes of this review we are



Fig. 1. One of three figures holding harvested geese on the decoration of the Tomb of Akhetep from Saqqara in ancient Egypt (fifth dynasty, c. 2400 BC), now in the Louvre in Paris (see layout of the tomb at http://www.insecula.com/oeuvre/photo_ME0000036922.html). Many other images of goose harvest are found in the Egyptian section of the Louvre. Photograph: David Stroud.



Fig. 2. Duck hunting in Sweden. Waterbirds have provided a provisioning service *via* hunting throughout history, and the modern economic benefits are a powerful force for wetland management and conservation. Photograph: Sten Christoffersson.

concerned primarily with the ecological role of birds, and we will not consider these cultural services in further detail (but see Kear, 1990).

III. HARVEST VALUE AND OTHER PROVISIONING SERVICES

Anatidae, Rallidae, shorebirds and other waterbirds are harvested for human consumption the world over (Figs 1, 2). For example, waterfowl are a major part of the diet of indigenous people at high latitudes in North

America (Krcmar, van Kooten & Chan-McLeod, 2010). The economic value of harvest has been quantified in several studies (Table 2). An estimated \$1.5 billion was spent on waterfowl hunting in the USA in 1996 alone (Losey & Vaughan, 2006). In the state of Mississippi, the total economic impact of waterfowl hunting has been valued at \$155 million (2010 USD) a year (Henderson *et al.*, 2010). Withey & van Kooten (2011) estimated the value of each duck hunted in Canada as \$26. The economic values of duck hunting are such that the economic benefits of conserving natural prairie wetlands in North and South Dakota owing to greater duck production are considered to outweigh the benefits of converting to cropland (Gascoigne *et al.*, 2011).

In the European Union, there are more than 6.7 million hunters (Mooij, 2005), which is more than the number of inhabitants in many of its member states. Together, EU hunters shoot at least 7.6 million waterfowl and 4.2 million shorebirds and gulls annually (Hirschfeld & Heyd, 2005). In parts of northern Europe (e.g. southern Sweden) arable land has been converted to wetlands for the purpose of waterfowl hunting in the last decades, because the value of waterfowl harvest and ecotourism is greater than that of traditional farming. Although the economic value of waterfowl hunting has not been quantified in many parts of Europe, visitor expenditure by goose hunters in Scotland in 1997–1998 was estimated as 40% greater than expenditure by the considerable number of birdwatchers watching geese (MacMillan & Leader-Williams, 2008).

'Harvest' represents more than just killing birds for meat consumption. Picking eggs of ducks and geese for consumption was historically commonplace in many countries, as was use of their feathers for arrow flights and their grease for waterproofing, lubrication, as ointments and as oil for lamps (MacMillan & Leader-Williams, 2008). Although eggs may still be an important source of protein in poor countries and to some indigenous peoples, this habit is nowadays much rarer or prohibited in most industrialized countries owing to the widespread availability of hens' eggs. Another important provisioning service by waterfowl is the use of down and other feathers for bedding and insulation. Today much of the latter stem from farmed geese, but historically down from wild eider ducks *Somateria mollissima* was highly prized. Nowadays, most eider down is harvested in Iceland, and the annual retail value of goods made from this down has been estimated at \$40 million (Sveinsson, 2013).

IV. SUPPORTING AND REGULATING SERVICES

(1) Biodiversity of other taxa

In multiple ways, the presence and activity of waterbirds can have profound positive effects on aquatic biodiversity. For example, they are major vectors of dispersal with a crucial role in maintaining general diversity of isolated or ephemeral wetlands by the spread of plant and animal propagules.



Fig. 3. Ducks wintering in the Albufera de Valencia, eastern Spain. Such wintering concentrations can provide a spectacle for the public (i.e. a cultural service), an opportunity for controlled harvest (a provisioning service) and strong nutrient cycling (supporting service). Photograph: Carlos Oltra.



Fig. 4. An example of a cultural service. Two mute swans *Cygnus olor* are accompanied by 1 of 60 swan sculptures made in Wells, England to commemorate the Queen's jubilee in 2012. People have a particular affection for swans and other large waterbirds. Photograph: Andy J. Green.

This is a multiscale service, upholding biodiversity locally, regionally and even at continental scales (see Section IV.8).

Geese can play a vital role in maintaining grasslands in a natural state of high diversity, notably by promoting coexistence of different plant species by regulating interspecific competition (Jasmin, Rochefort & Gauthier, 2008), and by stimulating primary production (Cargill & Jefferies, 1984; Bazely & Jefferies, 1985). The elimination of the Aleutian cackling goose *Branta hutchinsii leucopareia* by introduced foxes is thought to have contributed to the low

diversity of plants in the Aleutian Islands (Maron *et al.*, 2006), owing to release from grazing pressure. Grazing by waterfowl can also increase the diversity of submerged macrophytes (Hidding *et al.*, 2010), as well as their productivity (Nolet, 2004). Grazing on seagrasses by geese and wigeon *Anas penelope* can have a positive long-term effect on seagrass beds due to reduced mud accretion in grazed beds (Nacken & Reise, 2000). Similarly, grazing by swans on water crowfoot *Ranunculus penicillatus pseudofluitans* in chalk streams may potentially increase the survival of this plant over winter, since grazing reduces resistance to high winter flows that cause uprooting (Wood *et al.*, 2012). However, excessive grazing by geese can lead to soil erosion, soil salinization, loss of soil nitrogen retention, and other negative effects (Iacobelli & Jefferies, 1991; Gauthier, Giroux & Locheffort, 2006; Buckeridge & Jefferies, 2007). For example, the recovery of Aleutian cackling geese is thought to have led to soil erosion and burrow collapse in a seabird colony in California, where the geese stage in spring (Mini *et al.*, 2011). Furthermore, feral geese populations can favour the spread of alien grasses, even when they selectively graze on those same grasses (Best & Arcese, 2009; Isaac-Renton *et al.*, 2010).

Waterbirds can provide protection from predators for other taxa. For example, Canada geese *Branta canadensis* defend their nests strongly against potential predators, and other birds nesting in their vicinity enjoy a higher breeding success (Allard & Gilchrist, 2002). This defence effect may also carry over to the community level; in some Swedish archipelagoes species richness of nesting birds is higher on islets with nesting Canada geese than on neighbouring islets without (Fabricius & Norgren, 1987). Mann, Proctor & Taylor (1999) suggested that predation of herbivorous

Table 2. Examples of valuation of provisioning and cultural services by waterbirds

Taxon	Valuation	Method	References
Migratory birds	\$1.5 billion spent in the US on hunting in 1996	Actual expenditure	Losey & Vaughan (2006)
Whooping crane <i>Grus americana</i>	Each US household willing to pay \$56 (2006) per year to save the species	Contingent valuation	Richardson & Loomis (2009)
Ducks	\$320 million (2008) spent hunting per year in USA, \$26 per duck harvested	Actual expenditure	Withey & van Kooten (2011)
Ducks and geese	\$763 (1991) mean expenditure per year by Louisiana hunters	Actual expenditure	Gan & Luzar (1993)
Ducks and geese	\$155 million (2010) generated by hunting in Mississippi, including 1898 jobs created	Total economic impact	Henderson <i>et al.</i> (2010)
Geese	£1.5 million (1998) per year spent on goose watching and £2.1 million on hunting in Scotland	Actual expenditure	MacMillan & Leader-Williams (2008)
Greenland white-fronted <i>Anser albifrons</i> and barnacle geese <i>Branta leucopsis</i>	Scottish population willing to pay £35 million to secure a 10% rise in goose numbers	Contingent valuation	MacMillan <i>et al.</i> (2004)
Eider <i>Somateria mollissima</i>	Annual down harvest in Iceland used to produce \$40 million worth of retail goods	Unknown	Sveinsson (2013)

invertebrates in shallow ponds by shorebirds allows the persistence of charophyte species (e.g. *Tolypella glomerata*) that lack resistance to herbivory.

Waterbirds themselves can be considered as “ecosystems” in that they act as hosts for a wide variety of parasites and commensalists, often specific to a small number of bird species, including an unknown number of parasite species yet to be described. In some cases, the presence of these parasites makes a major contribution to the total biodiversity in aquatic ecosystems, as illustrated by endoparasites with complex life cycles that use invertebrates or fish as intermediate hosts. For example, hypersaline salt ponds and lakes have unusually low invertebrate species richness and are often dominated by brine shrimp *Artemia* spp. as the main macroinvertebrate (Sánchez, Green & Castellanos, 2006). However, a diverse community of waterbirds preying on the shrimps maintains up to 15 species of cestodes within the *Artemia* population, each using a specific waterbird group as final hosts (Georgiev *et al.*, 2005, 2007). Thus, these cestodes constitute an important fraction of the total invertebrate diversity in these systems.

(2) Bioindicators

When species act as bioindicators of the general ecological status of an ecosystem, they can provide a low-cost shortcut for monitoring, for example in sparsely populated regions and in protected areas where monitoring is a priority but funds are limited. Waterbirds have the advantage that they are easy to count and attractive to large parts of the human population, such that long-term datasets on waterbird communities often exist in the absence of historical data on other aquatic organisms (e.g. Rendón *et al.*, 2008). Some waterbirds can serve as good indicators of aquatic biodiversity (Amat &

Green, 2010). For example, fluctuations in abundance of ducks and coot can accurately indicate changes in the abundance of submerged macrophytes (Wicker & Endres, 1995), which themselves have a highly positive influence on aquatic diversity (Carpenter & Lodge, 1986). The crested coot *Fulica cristata* can be a good indicator of high species richness of aquatic plants (Green *et al.*, 2002a).

At a wetland level, the number of species of breeding dabbling ducks can be a good indicator of the structural diversity of aquatic vegetation [based on a principal components analysis (PCA) of the cover, height and heterogeneity of emergent vegetation and the extent of floating vegetation] as well as of overall abundance of benthic and emerging invertebrates (Elmberg *et al.*, 1993). Even the behaviour of waterfowl can serve as a bioindicator; the degree of pair formation by adults early in the breeding season as well as foraging behaviour in ducklings later in the season correlate with nutrient status (total P) in boreal lakes (Nummi *et al.*, 2000; Pöysä *et al.*, 2001). At the other extreme, the absence of breeding common species (e.g. mallard *Anas platyrhynchos* and Eurasian teal *Anas crecca*) from seemingly suitable wetlands in Scandinavia indicates very low abundance of invertebrates (Gunnarsson *et al.*, 2004), but not necessarily low primary productivity.

Waterbirds can also be used to assess crudely the fish community of lakes and wetlands in a manner that saves time and money. For example, over large areas red-throated diver *Gavia stellata* and Slavonian grebe *Podiceps auritus* almost never nest in lakes holding fish, and there is a strong negative correlation between overall species richness of breeding ducks and occurrence of fish in boreal lakes (e.g. Elmberg, Dessborn & Englund, 2010; Dessborn, Elmberg & Englund, 2011b). The distribution of breeding great northern divers *G. immer* is strongly related to a combination of the size of lakes and their

fish production (Kerekes, 2008). Despite the ease with which waterbirds can be used to obtain important information about wetland ecosystems, their possible role as early warning indicators for regime shifts *sensu* Carpenter *et al.* (2011) remains an area for future research. Waterbird feathers and other tissues can also be very useful as biomonitors of heavy metals and other contaminants (Fasola, Movalli & Gandini, 1998; Taggart *et al.*, 2006; Burger & Eichhorst, 2007).

However, despite the above examples, waterbirds are not always effective bioindicators. At least in Mediterranean systems, waterbirds sometimes perform poorly as bioindicators compared with taxa more directly affected by water quality, such as submerged vegetation or aquatic invertebrates. Many ducks seem to be sufficiently plastic in their habitat requirements to maintain wintering populations despite ecological change in wetlands (Tamisier & Grillas, 1994). In contrast to negative correlations found for mammal and fish species richness, Ghermandi *et al.* (2008) showed in a meta-analysis that wetland degradation had no significant impact on waterbird species richness. Similarly, waterbirds have increased in abundance in many Mediterranean wetlands since 1970 despite wetland degradation that has caused declines in amphibians, reptiles, mammals and fish (MWO, 2012). These positive trends for birds seem to be related to a reduction in hunting pressure, the decreasing impacts of DDT and other banned pesticides, and the ability of many waterbirds to exploit artificial habitats such as ricefields or fish farms that have replaced more natural wetlands (Rendón *et al.*, 2008). Overall, more research is needed to clarify under what circumstances waterbirds are reliable bioindicators, and how this relates to trophic status of the wetlands, to latitude or to different stages of the annual cycle (e.g. are breeding birds better bioindicators than wintering communities?).

(3) Disease surveillance

Waterbirds are hosts and vectors for a wide range of pathogens, those endemic for birds as well as zoonotic types potentially affecting humans (e.g. Wobeser, 1997; Hubalek, 2004). These negative effects are described well elsewhere and not the subject of our review, but on the flip side the same host-pathogen systems can be used to help monitor pathogens, and waterbirds thereby aid in disease control. Wild migratory ducks have been used successfully to monitor temporal variation in prevalence of subtypes of avian influenza virus (AIV) (Wallensten *et al.*, 2007), which is a useful tool to predict risk of outbreaks of highly pathogenic (HPAIV) variants with the potential to cause huge economic loss to the poultry industry and also epidemics or pandemics in humans (Munster *et al.*, 2005). For example, the HPAIV strain that killed a large number of poultry and even led to a human death in the Netherlands in 2003 was detected in wild mallards shortly before at an upstream site in the same flyway. Moreover, a recent study shows that wild ducks can be used to address spatial patterns of pathogens and infections; by combining AIV screening with ringing recoveries and isotope analysis of feathers grown in natal areas, Gunnarsson *et al.*

(2012) found evidence that wild transient migrant mallards carry different subtypes of the virus from different source areas. This provides evidence that wild waterbirds can be used to make inferences about the geographical source of disease outbreaks, a research field likely to develop strongly in the near future (Le Comber & Stevenson, 2012). Finally, captive or non-migratory wild ducks that are allowed to come into contact with wild waterbirds can be used as sentinels and early warning systems to monitor local infection dynamics of a wide range of pathogens (e.g. Ziegler *et al.*, 2010; Farnsworth *et al.*, 2012; Rollo *et al.*, 2012).

(4) Scavengers

In historical times when they were more abundant, greater adjutant storks *Leptoptilos dubius* (now globally threatened) used to dispose of human corpses in India (del Hoyo, Elliot & Christie, 1992). However, with the possible exception of this species and the congeneric marabou stork *L. crumeniferus* (Kahl, 1966; del Hoyo *et al.*, 1992), the waterbirds do not include obligate scavengers comparable to vultures. Many other waterbirds are facultative scavengers, and gulls, storks and ibises form large concentrations at rubbish dumps where they scavenge from human waste. Although there may be important negative consequences of this activity (Whelan *et al.*, 2008), it can provide local benefits for neighbouring human populations since it is likely to reduce the smell associated with decomposition of waste by bacteria in the absence of consumption by birds. In addition, birds are likely to remove nutrients from highly impacted sites like dumps and sewage-treatment plants by defecating elsewhere, for example at night roosts. The ecological and sociological consequences of such nutrient movement deserve more research.

(5) Nutrient and biogeochemical cycling

The great historical economic significance of seabird guano as a source of fertilizer was reviewed by Hutchinson (1950) and Whelan *et al.* (2008). When moving and forming aggregations, waterbirds automatically influence nutrient fluxes (Figs 3, 5). When forming concentrations at roosting sites or in breeding colonies, waterbirds can import enough nutrients to cause major shifts in the trophic status of wetlands. In arctic and other natural landscapes, nutrients are often limiting and guanotrophication can have positive effects on diversity and productivity (Van Geest *et al.*, 2007; Michelutti *et al.*, 2009). Wetland productivity and fish production are likely to be enhanced by the input of nutrients to oligotrophic systems by colonial waterbirds, in a manner similar to the proposed role of hippopotamuses *Hippopotamus amphibius* in promoting productivity in the Okavango, where they feed on land and then defecate in the water (Mosepele *et al.*, 2009). In Hungarian soda pans the external nutrient loading by geese and other waterbirds provides 50% of carbon, 70% of phosphorus and the basis for high production of fairy shrimps and other crustaceans (Boros *et al.*, 2008a, b). However, as eutrophication due to modern agricultural or urban activities in a catchment frequently leads to an excess

of nutrients in human-modified landscapes, these inputs from birds now often have negative effects in lakes, such as a shift from a clear-water macrophyte state to a turbid, phytoplankton-dominated state (Moss & Leah, 1982).

Waterbirds such as gulls, storks, geese, swans, and some shorebirds typically feed in both aquatic and terrestrial systems, e.g. at different times of the day or year. They are thus frequently involved in cross-habitat subsidies of energy and nutrients between strictly aquatic and terrestrial systems. Waterbird breeding colonies in forests provide major subsidies through their faeces (Kameda *et al.*, 2006). Such reciprocal subsidies are as yet poorly understood and are currently subject to growing research (Baxter *et al.*, 2004; Burdon & Harding, 2008).

Apart from simply moving nutrients around as faeces, waterbirds have more subtle and unexpected influences on nutrient and other biogeochemical cycles. Breeding colonies can have a major influence on soil chemistry and cycling of nitrogen and other elements (Ligeza & Smal, 2003). Goose grazing can promote nitrogen cycling in saltmarshes (Cargill & Jefferies, 1984; Ruess, Hik & Jefferies, 1989). Trampling by ducks foraging in ricefields after harvest can increase decomposition of residual surface straw by up to 78%, providing a clear benefit to farmers who otherwise spend up to \$125 ha⁻¹ in chopping, ploughing or disking residual rice straw (Bird, Pettygrove & Eadie, 2000; van Groenigen *et al.*, 2003). Bioturbation by swans feeding on submerged macrophytes can reduce production of methane, a powerful greenhouse gas, owing to increased oxidation of sediments (Bodelier *et al.*, 2006). However, the opposite occurs when waterbirds feed on helophytes (emergent plants) (Dingemans, Bakker & Bodelier, 2011).

(6) Pest control

Waterbirds are major predators of aquatic insect larvae and can cause reductions in the abundance of larvae of Chironomidae (non-biting midges) (Sánchez, Green & Alejandre, 2006; Rodriguez-Perez, Green & Figuerola, 2007). Chironomids can be economic pests in ricefields, waste-treatment wetlands and elsewhere (Ali, 1996). Waterbirds may also have a role in controlling mosquitoes which are well known as major pests and vectors of disease. Mosquito larvae can comprise a large part of the diet of ducklings (Miles *et al.*, 2002), and are also consumed by terns and shorebirds (Tucakov & Puzovic, 2006; Fonteneau *et al.*, 2009). However, we are not aware of any studies quantifying the influence that waterbirds have on the abundance of these or other biting dipterans. We suspect this may be substantial, especially in shallow habitats lacking fish but frequented by birds.

Zebra mussels *Dreissena polymorpha* are highly invasive and have a great economic and ecological impact on invaded lakes and reservoirs in Europe and the Americas. In the USA alone, the damages and associated control costs were estimated at \$1 billion/year (Pimentel, Zuniga & Morrison, 2005). Enclosure experiments have shown that diving ducks often greatly reduce the abundance of these bivalves in

shallow areas (Hamilton, Ankney & Bailey, 1994; Werner *et al.*, 2005). Eurasian coots *Fulica atra* also feed actively on the mussels and seem to prevent greater colonization of boats, associated infrastructure and floating vegetation in shallow invaded systems, all of which are likely to reduce the economic costs of the invasion (G. van der Velde, personal communication).

Waterbirds are also valuable for biological control of snails that eat rice plants (Yusa, Sugiura & Wada, 2006). Teo (2001) found that a density of 5–10 domestic ducks per hectare reduced the density of golden apple snail *Pomacea canaliculata*, a major rice pest, by more than 80%. In northern Europe, domestic and wild ducks are seen as an effective means of reducing numbers of slugs, including the highly invasive Spanish slug *Arion vulgaris* (Grimm, Paill & Kaiser, 2000; Speiser *et al.*, 2001).

Many waterbirds such as storks, ibises, egrets and gulls forage extensively in both aquatic and terrestrial habitats and are likely to be important as control agents of agricultural pests. Red-swamp crayfish *Procambarus clarkii* are a widespread exotic species and major pest in ricefields in California and the Iberian Peninsula, causing significant damage to the seeds and seedlings (Anastacio, Parente & Correia, 2005) as well as to dykes by digging burrows. Wading birds such as storks, herons and ibises are important predators of these crayfish (Negro *et al.*, 2000; Tablado *et al.*, 2010). Similarly, tadpole shrimps *Triops* spp. are pests of rice and are depredated by herons (Hafner & Britton, 1983).

Fish have been widely introduced into waterbodies where they are not native, and their activity can often have a strong negative effect on water quality, e.g. by destroying macrophytes, increasing phosphorous load, or depredating larger zooplankton that are particularly efficient at feeding on phytoplankton (Starling *et al.*, 2002; Søndergaard *et al.*, 2008; Weber & Brown, 2009). Waterbirds can often be effective predators on fish populations, especially in relatively shallow waterbodies (Britton & Moser, 1982; Winfield, 1990; Gawlik, 2002; Steinmetz, Kohler & Soluk, 2003). Owing to the fear of predation, the presence of fish-eating birds can also have indirect effects that can be more important than their direct effects (Fig. 5). Perceived risk of predation affects fish behaviour and growth rates (Allouche & Gaudin, 2001; Wacht-Katz *et al.*, 2010), and leads them to avoid surface layers and shallow littoral zones during the daytime where they would be visually exposed to piscivorous birds (Gliwicz & Jachner, 1992; Lewin, Okun & Mehner, 2004; Mehner, Kasprzak & Holker, 2007). Thus, the fear of predation by birds can have dramatic cascade effects on food webs in aquatic ecosystems. Although there has been little research on this to date, an outstanding example is the bands of algae in the shallows of tropical streams that result from reduced grazing by catfish seeking to avoid herons and kingfishers (Power, Dudley & Cooper, 1989).

Massive fish mortalities are often recorded in association with heat waves, droughts and pollution events, and have a highly negative effect on water quality in the areas affected (Kushlan, 1974; Hoyer *et al.*, 2009). However,



Fig. 5. American white pelicans *Pelecanus erythrorhynchos* in Prince Albert National Park, Canada. Piscivorous waterbirds can reduce the impact of fish on the diversity of invertebrates by reducing fish activity owing to the fear of predation. They can also control the populations of undesirable, alien fish. Colonial waterbirds such as pelicans also provide important subsidies of nutrients to terrestrial areas where they breed. Photograph: Andy J. Green.

such events might be more frequent were it not for the influence of piscivorous birds. For example, herons, storks, ibises and other wading birds are able to significantly reduce fish populations from waterbodies as water levels decrease during dry periods (Kushlan, 1976; Gawlik, 2002), thus avoiding synchronous fish mortalities and effectively removing nutrients *en masse* from those wetlands. This in turn may help to reduce outbreaks of toxic cyanobacteria associated with hypertrophy, as well as the anoxia events and disease outbreaks that result from large quantities of fish decomposing. In experimental ponds in the Everglades, after 12 days birds had removed all fish in ponds of 10 cm depth, and over 50% of fish in ponds of 28 cm depth (Gawlik, 2002).

Bio-manipulation projects are often launched to improve water quality by controlling fish populations, e.g. by removing cyprinids and introducing piscivorous fish (Jeppesen *et al.*, 2007). It is possible that many shallow lakes do not reach a critical condition where such expensive remediation is necessary because of the direct and indirect influence of waterbirds on fish activity. For example, there is evidence that cormorants increase water transparency owing to their control of benthivorous fish (Leah, Moss & Forest, 1980; Dirksen *et al.*, 1995). However, effects of birds on fish have rarely been quantified in detail, even in the case of perceived conflicts between birds and economically valuable fish stocks, owing especially to lack of information as to whether or not predation by birds is additive to other sources of mortality in fish populations (Harris *et al.*,

2008). In one relatively detailed study in a Scottish fishery, cormorants were estimated to remove 40% of the rainbow trout *Oncorhynchus mykiss* catch, and 16 times the brown trout *Salmo trutta* catch (Stewart *et al.*, 2005).

Anatidae are major consumers of seeds of weeds in ricefields, and may provide a significant economic benefit by reducing the abundance of such seeds. The wintering of ducks in flooded ricefields can reduce the biomass of weeds in the following growing season by more than 50% (van Groenigen *et al.*, 2003). Wintering Anatidae typically frequent ricefields after the rice harvest, and thus do not entail an economic cost owing to loss of rice grain before harvest. On the other hand, as they are good vectors of dispersal, ducks can also promote the spread of weeds (Brochet *et al.*, 2009). Future research should examine and evaluate the costs and benefits of granivory by waterbirds in ricefields and other agricultural systems.

As well as controlling pests directly by predation, waterbirds can also do so indirectly by spreading parasites that infect pests and reduce their abundance. For example, terns are final hosts for trematode parasites that use mosquitoes as intermediate hosts (Fonteneau *et al.*, 2009). Cestodes that use piscivorous birds as final hosts can reduce the abundance of introduced cyprinids (Kennedy, Shears & Shears, 2001). Since the life cycle of most helminth parasites remains unknown (Lefebvre *et al.*, 2009) (see also <https://web2.uconn.edu/tapeworm/index.php>), birds are likely to carry many more parasites of pests than is currently known.

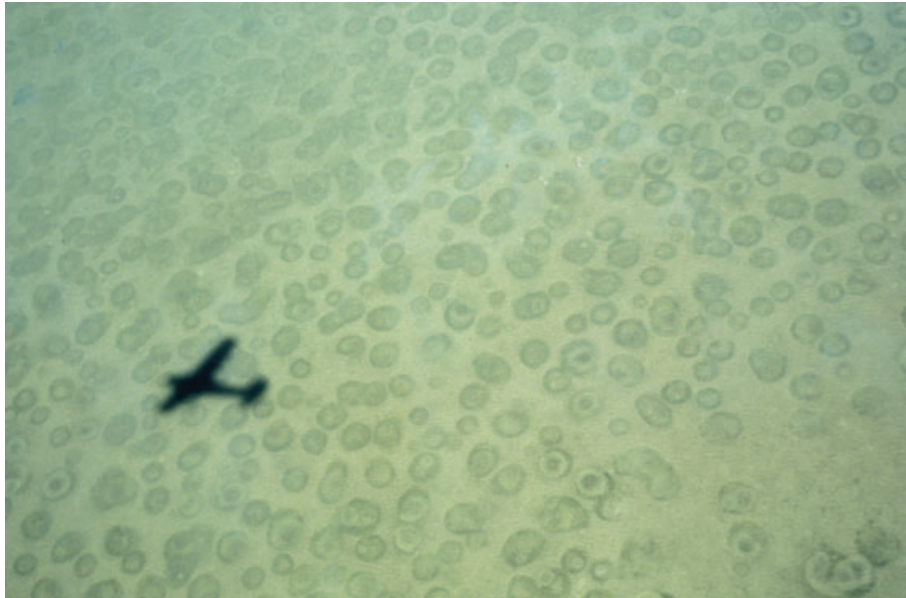


Fig. 6. Craters in soft sediments created by a flock of feeding greater flamingoes flushed by a plane used to count waterbirds in south-west Spain, illustrating the capacity of large waterbirds to act as ecological engineers. Photograph: Hector Garrido.

(7) Ecosystem engineering

To date the role of waterbirds as ecosystem engineers has largely been ignored and is in need of more research effort. Large birds such as swans or flamingoes have major bioturbation effects when feeding, and can radically change the distribution of sediments (Glassom & Branch, 1997; Rodríguez-Pérez & Green, 2006; Sandsten & Klaassen, 2008; Scott, Renaut & Owen, 2012; Fig. 6). This may have negative effects on some submerged macrophytes (Sandsten & Klaassen, 2008), but by increasing spatial heterogeneity this may have as yet unstudied benefits for annelids, dipteran larvae or other organisms exploiting the benthic environment (see Reise, 2002, for such bioturbation benefits in the marine environment). Bioturbation of this kind can also influence aquatic plant communities in subtle ways, and grazing by swans on tubers can promote spatial complexity and species diversity in such communities (Sandsten & Klaassen, 2008). It has been proposed that shorebirds increase the stability of sediments in the tidal zone, through their predation of amphipods which in turn feed on diatoms that produce carbohydrates that induce sediment cohesion (Daborn *et al.*, 1993). However, experimental evidence for such a cascading effect on mudflat stability is lacking (Hamilton, Diamond & Wells, 2006).

Colonial waterbirds can have profound effects on the vegetation where their colonies are situated (Telfair & Bister, 2004; Kolb, Jerling & Hambäck, 2010), and in dense woodland or reedbeds they open up spaces that increase spatial diversity and provide microhabitats suitable for other species. In many cases, openings in reedbeds are vital for aquatic invertebrates, other aquatic plants, fish and other waterbirds (Murkin, Kaminski & Titman, 1982; Wagner & Hansson, 1988; Murkin, Murkin & Ball, 1997).

(8) Dispersal of seeds, invertebrates and non-pathogenic microbes

Seed dispersal has been considered as the most important avian ecosystem service provided by terrestrial birds (Sekercioglu, 2006). The great majority of seed dispersal literature focuses on dispersal of plants with fleshy fruits by terrestrial birds, and much less attention has been paid to dispersal of other plants by aquatic birds. Around 36% of 135 extant families of terrestrial birds are partly or predominantly frugivorous (Herrera, 2002), but this does not include the Anatidae, rails, shorebirds or other aquatic birds as dispersers of seeds from plants lacking fleshy fruits (Green, Figuerola & Sánchez, 2002*b*). Likewise, when Wenny *et al.* (2011) stated that nearly 33% of bird species disperse seed through fruit consumption and scatter-hoarding of nuts and conifer seed crops, they did not include the dispersal of other seeds by waterbirds. Indeed, one of the conclusions of their review was that (in the context of ecosystem services) ‘dispersal of aquatic plants by waterfowl has not been addressed’. In fact, considerable progress has been made in our understanding of seed dispersal by waterbirds over the past decade, but the number of studies is still limited. For example, we are not aware of a single non-anecdotal study of dispersal of seeds or invertebrates by waterbirds in Africa or Asia (but see Aoyama, Kawakami & Chiba, 2012, for seabirds).

Whereas terrestrial birds are not generally known to act as vectors for invertebrates other than their own parasites and commensalists (but see Wada, Kawakami & Chiba, 2012, for snails), waterbirds are now known to be vectors of a whole range of aquatic invertebrates, including crustaceans, bryozoans, dipterans, molluscs, rotifers and annelids (Green & Figuerola, 2005; Frisch, Green & Figuerola, 2007). Many of these organisms are incapable

of moving between lakes or river catchments of their own accord, and are too large to disperse effectively by wind, making waterbirds the most important vectors that ensure maintenance of metacommunities and gene flow among populations (Figuerola, Green & Michot, 2005). Like seeds, invertebrates are dispersed both within the digestive tract of waterbirds and by sticking to feathers, feet and bills, although the former means is most common (Brochet *et al.*, 2010; Sánchez *et al.*, 2012). In addition, waterbirds act as vectors for microbes such as phytoplankton, diatoms, ciliates and the spores of bacteria, archaea and fungi (Schlichting, 1960; Thornton, 1971; Figuerola & Green, 2002; Green *et al.*, 2008; Brito-Echeverria *et al.*, 2009), although our current understanding of the importance of their role compared to other dispersal modes such as wind is extremely limited (Wilkinson *et al.*, 2012). Furthermore, waterbirds can disperse parasites of other organisms which lack their own means of moving between catchments (Green *et al.*, 2013).

In many cases, keystone species in aquatic systems are themselves dependent on birds for their dispersal. Besides macrophytes, these include crustaceans such as *Daphnia* spp. or *Artemia* spp. (Frisch *et al.*, 2007; Sánchez *et al.*, 2007) that are dominant zooplankters regulating phytoplankton abundance and maintaining ecosystems in a clear-water, high-biodiversity state (Wurtsbaugh, 1992; Scheffer, 2001) more likely to provide services for humans compared to a turbid, low-biodiversity state. Indeed, *Artemia* spp. are considered essential to ensure high-quality brine for salt production (Amat *et al.*, 2005). On the other hand, waterbirds are also vectors for invasive species of invertebrates, promoting their expansion within the introduced range (Green & Figuerola, 2005; Green *et al.*, 2005).

By acting as vectors of passive dispersal, waterbirds play a vital role in maintaining connectivity among communities in isolated aquatic systems, and thus in maintaining species and genetic diversity (Amezaga, Santamaria & Green, 2002). Janzen (1984) proposed that waterfowl are now the principal vectors for marshland plants originally dispersed by large, migratory mammals that are now extinct. They also enable rapid migrations of plants and invertebrates required to compensate for climate change (Brochet *et al.*, 2009). The latter is already affecting migratory behaviour of waterbirds (Sauter, Korner-Nievergelt & Jenni, 2010), thus changing their role as propagule dispersers and, for example, enabling colonization of polar regions by new plant species (Klein *et al.*, 2008).

Anatidae and other waterbirds play a vital role in the colonization and regeneration of new and restored wetlands by aquatic flora and fauna. Tens of thousands of plant and invertebrate species are likely to benefit from dispersal *via* waterbirds for colonization of new habitats, directed dispersal to suitable sites, gene flow, enhanced germination and escape from areas of high mortality e.g. owing to predation (Bilton, Freeland & Okamura, 2001; Frisch *et al.*, 2007; Brochet *et al.*, 2009). Nevertheless, owing to a lack of basic research in this subject to date, it is currently impossible to estimate accurately how many plant and invertebrate species are dispersed by waterbirds and how many waterbird species are

effective dispersers for each taxonomic group of propagules. What is clear is that waterbirds disperse many plants that are not strictly aquatic, and that have previously been assumed to disperse by other means (Green *et al.*, 2008; Bruun, Lundgren & Philipp, 2008; Brochet *et al.*, 2009, 2010). Moreover, the possible role of waterbirds as dispersers of fish and amphibians, e.g. by adhesion of eggs or their survival of gut passage as proposed by Wallace (1876), still remains unexplored.

In terrestrial systems, the distances that seeds are dispersed by frugivores are now relatively well studied, but typically are of the order of a few hundred meters (Jordano *et al.*, 2007; Hernández, 2011). For example, Levey, Tewksbury & Bolker (2008) consider 'long-distance dispersal' by terrestrial birds to be that over 150 m. By contrast, distances that seeds and eggs are moved by aquatic birds remain unclear and poorly studied, but generally much greater distances can be expected, with maxima of hundreds of kilometers likely for many migratory species (Green *et al.*, 2002b; Figuerola *et al.*, 2010; Sánchez *et al.*, 2012; Viana *et al.*, 2013). However, there is an urgent need to integrate new studies of bird movements using the latest global positioning system (GPS) technologies with studies of seed dispersal, to produce accurate seed shadows.

V. GENERAL DISCUSSION

We believe this review serves as a valuable first step towards a clearer understanding of the ecosystem services provided by waterbirds. Many of the services identified above (see also Table 1) were reviewed by Wenny *et al.* (2011) and Whelan *et al.* (2008) for terrestrial birds. On the other hand, other services considered here (e.g. provisioning services, dispersal of invertebrates, disease surveillance, influence on methane production) were not considered in these previous reviews. In cases where terrestrial birds and waterbirds provide similar services, they are generally in different habitats, so that 'which group is most important?' is not a relevant question. For example, terrestrial birds obviously provide more services in forests, and waterbirds unique services in wetlands.

Working with waterbirds in this field has some major advantages. Researchers have been urged to 'identify and count the organisms and their characteristics that provide services, and determine how changes in these organisms affect service provision' (Luck *et al.*, 2009, p. 225). Waterbirds are much easier to quantify than the vast majority of organisms, and are generally easier than terrestrial birds as they often occur in open, clearly defined spaces. For that reason, and because they are attractive to people, long-term extensive datasets of waterbird counts and trend analyses of individual populations already exist for many parts of the developed world (e.g. U.S. Fish and Wildlife Service, 2012; Wetlands International, 2012). The fact that the study boundary can often be clearly defined at a relatively local scale (e.g. a particular lake) is another advantage. The demand for, and supply of, ecosystem services is most easily quantified at a local scale (Luck *et al.*, 2009). There is also a great deal of existing literature on waterbirds (e.g. on the ecology of

Holarctic Anatidae), which provides a solid basis for further research and has been very influential in our review. It has been widely recognized that quantifying the contributions of individual species to a service is challenging compared to working with functional guilds (Luck *et al.*, 2009). However, in the case of waterbirds the ease of quantification makes it more practical. We are fortunate in that a great deal is known about the habitat requirements of many waterbird species. This knowledge can enable managers to attract desirable service providers to wetlands, e.g. pest-controlling species to ricefields or dispersers to newly created wetlands.

However, we often lack essential information about the levels of interactions between waterbirds and other aspects of ecosystems, which currently prevents us from formulating both ecological and economic models. One major impediment for service valuation is undoubtedly the high intrinsic temporal and spatial variability in many of the processes that can be considered as an ecosystem service. Even a single waterbird species can feed and behave in very different ways in different ecosystems, changing its interactions such as prey control or propagule dispersal [see e.g. the spatial variation in diet for ducks (Kear, 2005; Dessborn *et al.*, 2011a)]. Understanding such variability in time and space is vital to the proper accounting of any ecosystem service (Millennium Ecosystem Assessment, 2005). The division of ecological activity of waterbirds into specific services is itself complicated, as many of them are closely interlinked. For example, birds removing alien fish are providing both pest control and biodiversity support. When dispersing seeds, waterbirds are also moving nutrients and parasites with complex life cycles. However, we should not be intimidated by the complexities of these relationships, as in practical terms it is sufficient to identify the service which is of most interest in a particular landscape (e.g. owing to an obvious economic benefit), and to know how to ensure the persistence of the birds providing that service (Luck *et al.*, 2009).

The value of waterbirds for harvest is an example of a direct service. However, the services provided by birds within an aquatic ecosystem are often indirect and exist because bird activities provide links within and among ecosystems and can have large effects on other species. For this reason, birds and their services are usually excluded from economic models that value ecosystems (Wenny *et al.*, 2011). However, accurate valuation of bird services will improve the corresponding models of ecosystem valuation, as well as strengthening bird conservation and ultimately offering benefits to human society. Furthermore, attempts to value waterbird services will further research on many fundamental questions in ecology regarding the functional role of waterbirds in aquatic ecosystems.

A benefit accruing under natural conditions from waterbird activity might become a cost under modern conditions in transformed habitats, e.g. the supply of nutrients to wetlands by waterbirds is less likely to be beneficial in areas with a large human population, owing to widespread anthropogenic eutrophication. Similarly, colonial waterbirds might kill the only remaining trees in highly fragmented

forest habitats (Garcia *et al.*, 2011), and in highly invaded ecosystems, the dispersal of alien plants by waterbirds may be of greater significance than the dispersal of native ones. Hence, the same activity by waterbirds (e.g. herbivory or seed dispersal) can provide a beneficial service in some ecosystems but have deleterious effects in others, and it is likely that research is required in a given system to establish whether or not the costs outweigh the benefits.

Both the current ecological and economic crises make it more important for us to identify and quantify the services provided by waterbirds. This can help us to understand how effectively to conserve, manage, restore, and utilize aquatic biodiversity, and how to make a solid economic case to counter proposals for economic development with a harmful impact on ecosystems. Nevertheless, an ecosystem service approach should be used in combination with traditional conservation strategies, as it does not necessarily advocate for the conservation of endangered species or high species richness, and may positively value exotic species (Luck *et al.*, 2009). For example, alien aquatic plants dispersed by waterbirds can also provide services such as improving water quality and clarity.

It is likely that ecosystem services as a concept will become progressively more influential in decision-making in politics as well as in the management of natural and semi-natural landscapes. The concept of 'ecosystem services' has been adopted by many environmentalists (e.g. Juniper, 2013) who see it as a powerful means to get the attention of economists and others who have previously failed to recognize the value of 'nature' or seen it as an impediment to economic growth. However, some environmentalists have objected to the very principle of 'putting a price on nature' (Monbiot, 2012), and there may be a risk that the 'ecosystem service' concept could be misused or hijacked in a manner resembling the misuse of the 'sustainability' concept.

In order to manage the ecosystem services waterbirds provide, we need to develop a better understanding of their underlying functional ecology. We still lack much basic information on the role that waterbirds have in many ecosystem services, but hope to have made important progress by identifying major gaps for future research, e.g. regarding trophic cascades initiated by piscivorous birds or the importance of waterbirds as vectors of non-pathogenic microbes.

More research is required into the functional responses of waterbirds, as it is extremely useful for prediction, e.g. of how pest control or seed dispersal is influenced by changing abundance of pests or seeds. For example, existing work already gives some idea of how ducks should respond to changing densities of weed seeds in ricefields (Arzel *et al.*, 2007; Greer *et al.*, 2009), or how shorebirds should respond to changing densities of invertebrate pests (Goss-Custard *et al.*, 2006). These functional responses can also be applied within individual-based models that could be developed to allow prediction of when birds switch habitats (Stillman & Goss-Custard, 2010), e.g. when they forage in habitats where a service such as pest control is desirable.

The total number of waterbirds on Earth is in decline, and many waterbird species are threatened with extinction,

although these declines are more acute in some parts of the world than others (Wetlands International, 2012). This translates into a loss of their positive ecological functions, such that the declining status of waterbirds is likely to have important negative consequences for aquatic ecosystems (Sekercioglu, Daily & Erlich, 2004). Wetland birds are projected to have higher rates of extinction this century than those frequenting terrestrial habitats (Sekercioglu *et al.*, 2004). This increases the urgency of identifying and quantifying the services that declining waterbird populations provide.

Given that many waterbird species are undergoing rapid declines, it is important to establish how a service such as seed dispersal is affected by the loss or decline of individual species. At the moment it is unclear to what extent different waterbird species overlap in their roles as vectors and how robust this service is to changes in the waterbird community. Thus, a key question for research is how much functional redundancy there is in the provision of services by different species (Kremen, 2005). In general, if different waterbird species provide similar services over space and time, this reduces the impact of disturbance on the service (Winfree & Kremen, 2009). It is therefore vital to establish whether individual species dominate in a given service. If so, these species can be considered as key service providers, somewhat analogous to keystone species (Luck *et al.*, 2009). Management for service provision must then focus on this species, whose provisioning may be highly sensitive to disturbance.

Thus, to manage ecosystem services, we need to understand how changes in waterbird communities affect the magnitude and stability of services provided, i.e. the extent of resilience to changes in community composition. We might expect that the provision of services is not usually strongly dependent on single species, since waterbird communities typically have clearly defined guilds with several species in each one, with considerable 'within-group redundancy' owing to similar provisioning of services. In such a case, the characterization of ecosystem services is facilitated by the division of the community into functionally similar guilds, which are made up of redundant species but show functional complementarity between guilds (Kremen & Ostfeld, 2005). For example, herons and dabbling ducks are two guilds likely to provide very different services. But different species in each of these guilds often overlap considerably in foraging ecology, behaviour and hence service provision. Work so far suggests considerable redundancy in seed dispersal by individual dabbling duck species (Green *et al.*, 2002*b*; Figuerola, Green & Santamaria, 2003).

VI. TOWARDS A VALUATION OF WATERBIRD SERVICES

There is an urgent need to quantify the economic value of the ecosystem services provided by birds (Wenny *et al.*, 2011). Progress has already been made for cultural and provisioning services (Table 2). Although we now know in general the kinds of ecosystem services provided by waterbirds, in many

cases we are currently a long way from having enough understanding of their behaviour and ecology to formulate models of ecosystem valuation that allow us to estimate the economic importance of such services. Prior detailed research is essential in these cases before quantifying the values of these ecosystem services becomes possible. In some other cases, we already have much of the ecological knowledge that could readily be applied to a specific case study. In these cases, the valuation itself is the remaining task. However, rather than measure the absolute value of a service, it is only necessary to compare different situations (typically with or without a service) by marginalist valuation (Salles, 2011). Once the value of a service provided by a waterbird species has been calculated for one study area, 'benefit transfer' can allow the application of the results to other areas (Plummer, 2009).

In case studies for pest control or seed dispersal, economic valuation of services provided by terrestrial birds has been successfully carried out (Wenny *et al.*, 2011). By contrast, to our knowledge, there has to date been no ecosystem-services valuation research on such supporting services by waterbirds. In some cases it is easy to imagine how this could be done. The studies of waterfowl in California ricefields (Bird *et al.*, 2000; van Groenigen *et al.*, 2003) are the closest to date, since they quantify the removal of rice straw and weeds by ducks, but do not include a precise economic valuation. As in this case, enclosure experiments might be used to quantify the benefits of the pest-control service provided by waterbirds in other landscapes, just as they have been used to quantify the crop damage caused by some waterfowl (Parrott & McKay, 2001; Borman *et al.*, 2002). One way of valuing part of the dispersal service by waterbirds would be to calculate the replacement costs of planting manually the aquatic vegetation, or introducing the zooplankton and other invertebrates which actually become established in created or restored wetlands owing to their arrival *via* birds. Equally, the costs of replacing dykes that are vital in preventing floods or in containing water in fish ponds and are protected from wave erosion by vegetation brought by birds could readily be estimated. The high quality of waterbird census data can sometimes greatly facilitate quantification of ecosystem services or disservices. In particular, the models of Hahn, Bauer & Klaassen (2007, 2008) provide an excellent tool for straightforward quantification of the amounts of nutrients moved by different waterbird species found in northern Europe based on waterbird counts. These models could be readily adapted for species in other areas, applying the same assumptions.

As explained above, there has been particular progress in the valuation of provisioning services such as waterfowl harvest value (Table 2). Nevertheless, there is a surprising lack of information on the harvest value of waterbirds in Europe, and in principle progress could readily be made in quantifying the benefits of waterbirds as quarry to hunters in many European countries.

Collaboration between ecologists and economists is required so that progress can be made in valuing the services identified above. Other types of transdisciplinary scientific

approaches are also sorely needed; management policies used for carnivores, ungulates, and wintering geese in northern Europe during the last decades all show that social sciences must have a key role in the process of valuation of ecosystem services, especially to understand stakeholder acceptance and success of management implementation. Recent progress in accounting for services provided by migratory species (Semmens *et al.*, 2011) is important, since many migratory waterbirds crossing natural boundaries are providing services such as propagule dispersal or pest control. For example, ducks controlling pests or removing straw in ricefields in the USA or Japan breed mainly in Canada or Russia, respectively.

VII. CONCLUSIONS

(1) Wildfowl, shorebirds, gulls, rails, flamingoes and other waterbirds are major players in the theatre of aquatic ecosystems, and provide a range of important ecosystem services (Table 1). ‘Cultural services’ such as value for human recreation, and ‘provisioning services’ such as harvest for meat or feathers, have been evident throughout history and continue to be important. Less attention has been paid to ‘regulating services’ such as pest control, and ‘supporting services’ such as maintaining connectivity for plants and invertebrates in isolated wetlands by acting as vectors for dispersal, but these are growth areas for recent research.

(2) Owing to their interactions with other organisms, waterbirds can provide clear indirect benefits for human populations, e.g. by consuming invertebrate pests such as golden apple snails or zebra mussels, facilitating the colonization of new or restored wetlands by plants and invertebrates, promoting decomposition of waste rice straw, reducing the incidence of fish die-offs, or providing a cheap and practical means of monitoring the conservation status of different sites.

(3) Waterbirds often have a positive effect on biodiversity in general, e.g. by regulating competition through grazing, by controlling fish populations, by acting as hosts for unique parasites, by cycling nutrients, and by dispersing seeds, invertebrates and microbes. Other ecosystem services waterbirds provide have only recently become apparent (e.g. disease surveillance) or may be unexpected or easily overlooked (e.g. reduced production of the greenhouse gas methane when swans feed on submerged plants).

(4) Economic valuation of ecosystem services by birds is an emerging research field, but is currently in its infancy. There are relatively advanced studies of the income associated with the hunting of ducks and geese, as well as the recreational value of these groups and the value of harvesting their down (Table 2). To date, studies of the extent to which ducks remove weed seeds and invertebrate pests, and accelerate the breakdown of straw in ricefields, come closest to providing a net economic value of the services that waterbirds provide through their general ecological activity.

(5) An ecosystem service approach has great potential as a positive force for management and conservation of waterbirds, especially in areas of high human density and development pressure. Waterbird and wetland ecologists should demand the resources necessary to investigate the ecosystem services provided by waterbirds in more detail, and use the results to inform decision-makers, the general public and wetland managers. Key questions remain, such as the extent to which services are species-specific or provided in a similar way by closely related species in the same guild.

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