

REVIEW AND SYNTHESIS

Ecological and evolutionary implications of food subsidies from humans

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Abstract

Human activities are the main current driver of global change. From hunter-gatherers through to Neolithic societies—and particularly in contemporary industrialised countries—humans have (voluntarily or involuntarily) provided other animals with food, often with a high spatio-temporal predictability. Nowadays, as much as 30–40% of all food produced in Earth is wasted. We argue here that predictable anthropogenic food subsidies (PAFS) provided historically by humans to animals has shaped many communities and ecosystems as we see them nowadays. PAFS improve individual fitness triggering population increases of opportunistic species, which may affect communities, food webs and ecosystems by altering processes such as competition, predator–prey interactions and nutrient transfer between biotopes and ecosystems. We also show that PAFS decrease temporal population variability, increase resilience of opportunistic species and reduce community diversity. Recent environmental policies, such as the regulation of dumps or the ban of fishing discards, constitute natural experiments that should improve our understanding of the role of food supply in a range of ecological and evolutionary processes at the ecosystem level. Comparison of subsidised and non-subsidised ecosystems can help predict changes in diversity and the related ecosystem services that have suffered the impact of other global change agents.

Keywords

Ecological processes, evolutionary changes, food availability, food webs, global change, predictability, resilience.

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INTRODUCTION

Modern humans have played an active role in ecosystem functioning since their appearance ca. 10 000 year ago (Douglas *et al.* 2004). Humans began as opportunistic omnivorous species but the first evidence of anthropogenic food subsidies comes from hunter-gatherer societies, in the form of food remains exploited by other scavenging opportunistic species (e.g. prey carcasses). Those subsidies have increased substantially since the appearance of Neolithic societies, as agriculture and, particularly, livestock and domesticated farm animals provided additional food to other commensal species (Chamberlain *et al.* 2005; Agudo *et al.* 2010). A prime example comes from the appearance of dogs domesticated from wild wolves, related to the exploitation of waste dumps near increasingly common human settlements (Axelsson *et al.* 2013). However, the most dramatic human-based changes in ecosystems (such as habitat transformation and its consequences) arrived with the industrial revolution, with the appearance of technology and the successful battle against infectious diseases, triggering a human population explosion across the planet. The accumulation of those changes has deeply transformed ecosystems to the point that human activities are now considered the main driver of global change. Beside direct impacts through habitat destruction, ecosystems are altered voluntarily or involuntarily by food subsidies to animals generated by human activities (Table 1). At the global level, regions with both the highest human densities and per capita food losses are those most affected by those anthro-

pogenic subsidies (Fig. 1). Furthermore, some of these regions overlap with several of the 25 identified global biodiversity hotspots (e.g. Indo-Burma, Western Ghats and Sri Lanka, Mediterranean Basin, see Fig. 1 in Myers *et al.* 2000). The relatively high predictability in space and time of subsidised food supplies make this food resource easier to access compared to natural sources (Bartumeus *et al.* 2010; Cortés-Avizanda *et al.* 2012). This decreases required foraging times, consequently improving fitness components. An abundant and predictable food resource should improve physiology (i.e. body condition and body mass) and individual breeding performance, while mortality risks such as susceptibility to pathogens (except in cases such as landfills) and vulnerability to predation should decrease. Some cosmopolitan opportunistic species (facultative scavengers), such as cockroaches, rats, foxes or gulls, provide paradigmatic examples of species that benefit from such predictable anthropogenic food subsidies (PAFS). These species exploit food from human origin, have increased their numbers and are considered 'over-abundant', and may behave as native invaders causing changes in food webs and ecosystems (see Table 1 in Carey *et al.* 2012).

Here, we will argue that the food that humans make available to animal species through anthropogenic activities, such as agriculture, livestock farming, hunting, fishing and commercial trade has shaped the architecture of many ecosystems. We focus here on food resources that are wasted or intentionally offered to animals by humans and that are predictable in space and/or in time, hereafter

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Table 1 Estimated amounts of human provided food subsidies at large and global scales

Parameter	Quantification	References
Food production	As much as 30–40% of all food produced is wasted	Parfitt <i>et al.</i> (2010)
Dumps	In Australia and the USA, ca. $3 \cdot 10^6$ tonnes and $4 \cdot 10^6$ tonnes of food waste, respectively, goes to dumps each year; edible food wasted <i>per capita</i> by consumers in Europe and North America ranges from 95 to 115 kg/year and 6–11 kg/year in sub-Saharan Africa and South/Southeast Asia	Parfitt <i>et al.</i> (2010)
Fisheries discards	Ca. 8% of all fish caught worldwide are discarded; world fisheries discard ca. 7.3 million tonnes of fish annually	Bicknell <i>et al.</i> (2013)
Crop residuals	Arable land comprises ca. 11% of the total world land surface; agriculture has replaced ca. 70, 50 and 45% of the world's grasslands, savannahs and temperate deciduous forests respectively; in the USA, ca. 315 kg/ha of chopped corn stovers are left in the fall to prevent soil water evaporation and runoffs	Foley <i>et al.</i> (2011) http://data.worldbank.org/
Bird feeders	In the USA, 4.500 million dollars spent in a single year, involving 82 million householders and over $45 \cdot 10^7$ kg of seed; 34–75% of households in the USA and UK are engaged in this practice	Robb <i>et al.</i> (2008); Jones (2011)
Middens	In Africa and Asia, ca. $3.3 \cdot 10^7$ and $7.3 \cdot 10^7$ tonnes of carcasses of slaughtered cattle are rejected each year	http://faostat3.fao.org/
Restaurants	In Spain, ca. $6.4 \cdot 10^3$ tonnes of carrion are supplied each year targeting several vulture species; restaurants are implemented in America, Asia, Europe and Africa	Own data; Donazar <i>et al.</i> (2009)
Feeding stations for game species	In the USA, ca. $2.8 \cdot 10^{12}$ tonnes of bait (e.g. shelled corn) is offered for big game each year, though this amount is reduced some years when bait ban regulations occurs	http://www.michigandnr.com/publications/pdfs/huntingwildlifehabitat/deer_99baiting.pdf ; see also reference below
Carcasses from hunting	In the USA, there are ca. $11 \cdot 10^6$ big game hunters discarding ca. $6.9 \cdot 10^5$ tonnes of carcasses (e.g. deer, elk) in the field each year	US Fish & Wildlife Service (http://wsfirprograms.fws.gov/Subpages/NationalSurvey/nat_survey2006_final.pdf)

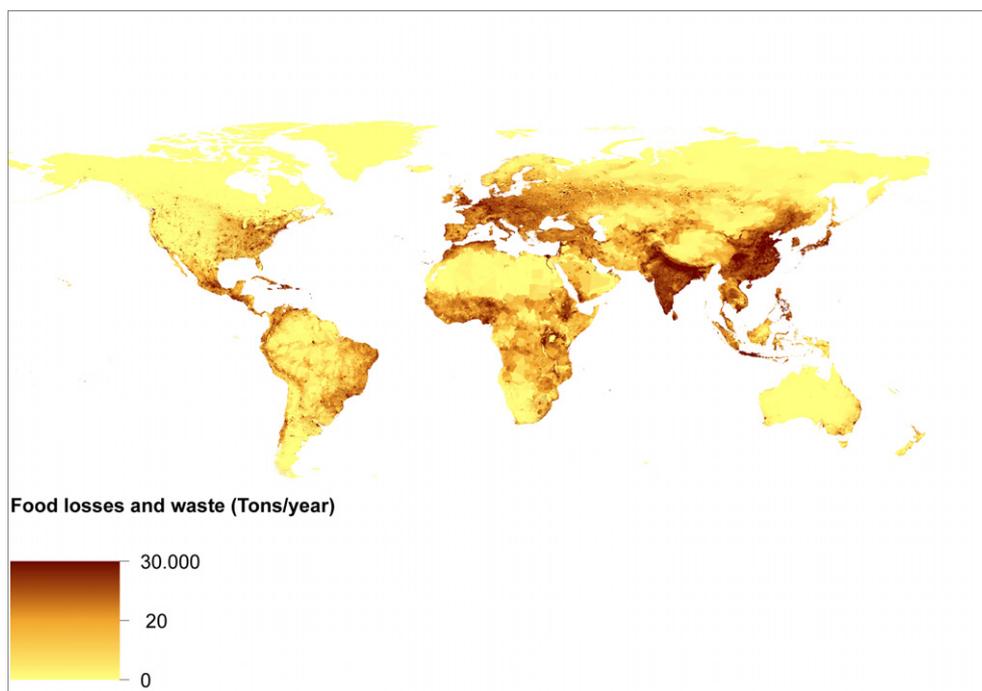


Figure 1 Food losses and waste (Tons/year on a log scale) generated from human food production. Data obtained from <http://faostat3.fao.org/> (wasted food by country) <http://sedac.ciesin.columbia.edu/data/dataset/grump-v1-population-count> (human population density in 2000 in a 30" longbow grid). Technical considerations are described in Appendix S4.

referred as PAFS (Predictable Anthropogenic Food Subsidies). Our review focuses on vertebrates, given that most research addressing the effects of food from humans has focussed on this taxa (see Table S1). Research oriented towards assessing the effects of PAFS

on species, communities and ecosystems should greatly improve our understanding of the ecological and evolutionary roles of food and food webs in those systems, beyond the limitations of the numerous experimental studies (Margalef 1997).

FOOD SUBSIDIES FROM INTENSIVE HUMAN ACTIVITIES IN CONTEMPORARY TIME

The subsidising of species by human activities and consequent effects on food webs was first identified several decades ago (Margalef 1997). However, the role of humans in configuring the mosaic of an ecosystem's foraging resources has only recently started to be analysed (Leu *et al.* 2008; Robb *et al.* 2008). Table 1 lists situations where large quantities of PAFS are made available to animal species; these include organic remains from refuse dumps, discards from fisheries, livestock middens (also called 'restaurants' with respect to obligate scavenging birds), crop leftovers, feeding stations for game

species and tourism and seeds supplied in backyard bird feeders. There is evidence that all PAFS generate impacts at both individual and population levels, with consequences translated to ecosystem functioning (Table 2). At the same time, individuals can vary in their use of PAFS, according to cultural, gender, age and personality differences (Table 2, see also quantitative data in Table S1).

The three main PAFS in terms of food availability and global distribution are dump sites, crop residuals and fishing discards (Table 1). Dumps have the potential to sustain a large number of species and individuals (Table 3, see also Tables S1 and S2); even though edible food wasted *per capita* is higher in industrialised countries than in developing countries (Table 1), environmental policies

Table 2 Recorded effects of different PAFS on several individual and population level parameters. Published records of individual differences in the use of PAFS are also shown. For a list of references on each recorded effects, see Table S1

Parameter	Type of PAFS						
	Dumps	Fishing discards	Middens and restaurants	Crop residuals	Bird feeders	Feeding stations for game species and tourism	Gutpiles and carcasses from hunting
Individual level							
Body condition	X			X	X	X	
Reproductive parameters	X	X	X	X	X	X	
Spatial distribution/home range	X	X	X	X	X	X	X
Survival			X	X	X	X	
Population level							
Population size/Densities	X	X	X	X	X	X	
Dispersal		X	X				
Differences in individual use							
Sex	X	X				X	
Age	X		X				
Personality	X		X			X	

Table 3 Comparison of different types of PAFS depending on their distribution, human intentionality, amounts of food available (in relative terms, see also Table 1), predictability and biomes and trophic levels affected. The percentage of taxonomic Orders of birds (29 Orders) and mammals (21 Orders) exploiting each PAFS is also shown (for details see Table S2)

Type of PAFS	Distribution	Relative amounts of food	Human intentionality	Predictability	Biomes	Trophic levels	% taxa (birds–mammals)
Dumps	Worldwide	Very high	No	Spatial and temporal	Terrestrial; nutrient transfer to coastal	From producers to top predators	21–29%
Fishing discards	Worldwide	High	No	Spatial and temporal	Marine; nutrient transfer to coastal	From producers to top predators	14–5%
Middens and restaurants	Worldwide and mainly in industrialised countries respectively	Locally medium	Only for restaurants (avian scavengers)	Mainly spatial	Terrestrial	Producers, secondary consumers and top predators	10–19%
Crop residuals	Mainly in industrialised countries	High	No	Spatial and temporal	Terrestrial	Mainly herbivores	21–38%
Bird feeders	Industrialised countries	Low and local	Yes	Spatial and temporal	Terrestrial	Herbivores	3–0%
Feeding stations for game species and tourism	Mainly in industrialised countries	Locally high	Yes	Spatial and temporal	Terrestrial and marine	Mainly herbivores	10–24%
Gut piles and carcasses from hunting	Where large wild game is practised	Locally high	No	Spatial	Terrestrial	Producers, secondary consumers and top predators	10–19%

and regulations that have progressively been applied there limit the accessibility of these resources to scavenging organisms, whereas in developing countries, where high human densities are often coupled with less strict environmental policies, dumps are large and numerous. On the other hand, intensive plant agriculture has affected terrestrial ecosystems worldwide more than any other human activity. Crops for human or livestock consumption are a valuable source of food for wild animals globally. Here, we consider the leftover crops remaining after harvesting to be a type of PAFS originally intended for commercialisation or consumption (Tables 1 and 2). Crop leftovers benefit herbivorous and granivorous species at lower trophic levels than those, e.g. foraging at dump sites, discards or at middens (Table 3). While dumps and crops residuals affect mainly terrestrial ecosystems, fisheries discards have an impact on marine ecosystems. It has been estimated that 8% of all fish caught worldwide are discarded, equating to > 7 million tonnes of waste entering the marine ecosystems each year (Bicknell *et al.* 2013). The diversity of organisms exploiting discards is wide, from large whales to invertebrates such as cephalopods, amphipods, isopods and decapods, and this PAFS impacts the entire water column from surface feeders (such as seabirds) to benthic organisms (see below). At least 143 (52% of global) seabird species from all 14 taxonomic families exploit fishing discard to different degrees worldwide, from sporadic use up to 75% of their diet (Table S2).

The above PAFS, together with gutpiles and carcasses from hunting are all provided involuntarily. Other PAFS (e.g. restaurants, bird feeders and feeding stations for game species and tourism, see Table 3) are intentionally provided, especially in industrialised countries. For instance, feeding stations are used to maintain high densities of game wildlife (e.g. Draycott *et al.* 2005)(Table S1). The feeding of wildlife has become a widespread means by which tourists and tourism operators can facilitate interaction with wildlife in the wild (Orams 2002; Vignon *et al.* 2010). Restaurants are used in most industrialised countries to counterbalance the effects that the regulation (including the ban) of middens and livestock carcasses (traditionally abandoned in the field) have on obligate scavenging birds (Margalida *et al.* 2010; Martínez-Abraín *et al.* 2012). Bird feeding is particularly important in some industrialised countries (e.g. the USA and the UK, see Table 1) with important consequences for passerine communities and the cascading effects associated (Table S1, see also Robb *et al.* 2008). Although these PAFS represent less food for wild animals than dumps, crop residuals and fishing discards, voluntarily supplemented food is also assumed to increase body condition, especially in winter. This improves fertility, increases seasonal or annual survival and potentially reduces levels of damage caused, to agriculture, game and forestry (Table 2).

THE IMPORTANCE OF PREDICTABILITY

The role of predictability in the exploitation and advantages of PAFS compared to natural and less predictable foraging resources has seldom been considered (Goldberg *et al.* 2001). Margalef (1997) noted that humans have introduced new temporal structures with predictable features to ecosystems, like our calendar week, which have resulted in a more scheduled behaviour for some species. Many anthropogenic activities are based on a weekly cycle, triggering weekly climate patterns, which can also have a high degree of spatial predictability (e.g. Deygout *et al.* 2010). In contrast to the

stochastic fluctuations inherent in natural systems, higher predictability should translate into greater stability (e.g. affecting optimal evolutionary stable strategies). Nevertheless, the potential consequences of the increased temporal and spatial predictability of PAFS compared to the relative unpredictability of natural food sources remain poorly understood, across species, community and ecosystem levels. Furthermore, predictability of several PAFS, such as dumps and fishing discards, may change with social, cultural and economic trends to a degree comparable with natural variation in resource availability.

A prime example illustrating how the predictability of anthropogenic resources may impact opportunistic species comes from trawling fishery discards and a Mediterranean seabird community. Here, fishing vessels have a precise operating timetable, which generates temporal predictability, resulting in seabirds following daily and weekly cycles in foraging activity (see Table S1). Furthermore, highly productive fishing grounds at the mesoscale are relatively fixed in space (e.g. fronts, eddies, fresh water inputs, island effects). This high spatio-temporal predictability influences the foraging activity and searching process (i.e. optimal diffusivity) of opportunistic scavenging seabirds (Bartumeus *et al.* 2010). Trawling moratoria in the western Mediterranean have been used to quantify the effects of fisheries discards on opportunistic seabird species. Discards have resulted in reduced foraging time, a great reduction in foraging area, and in increasing fitness parameters (e.g. survival, breeding performance) leading to population growth for all seabird species exploiting such resources (with larger effects larger for bigger species) (Almaraz & Oro 2011)(see also Table S1). The same phenomenon has been recorded for other avian scavenging communities. Obligate scavengers such as vultures, which evolved in unpredictable food resource environments (i.e. scattered carcasses), have also shown the capacity to change their searching strategy when predictable resources are available in the form of middens and restaurants (López-López *et al.* 2013; Monsarrat *et al.* 2013). The spatio-temporal predictability of these PAFS alters these scavengers by modifying their nested community structure (Selva & Fortuna 2007) and decreasing community diversity (Cortés-Avizanda *et al.* 2012). In this vulture community, predictability also modifies the value of social information when searching for food (Deygout *et al.* 2010), increases survival (particularly that of juvenile, inexperienced individuals, see Oro *et al.* 2008), may trigger the appearance of new foraging behaviour when predictable food becomes scarce (Margalida *et al.* 2011) and affects population dynamics (Martínez-Abraín *et al.* 2012). Finally, gutpiles and carcasses from hunting also have a larger predictability in space and time compared to natural carcasses due to restrictions on when and where hunting is allowed, and this affects the ecology of the carnivore communities exploiting these PAFS (Wilmers & Getz 2004).

QUANTIFIED EFFECTS OF PAFS ON LIFE-HISTORY TRAITS

In the absence of other factors (e.g. sites for reproducing, density of both predators and mates), the carrying capacity of populations is mostly limited by resource availability and density-dependence (i.e. food *per capita*), through intraspecific or interspecific (within guild) competition. Several reviews have compiled a large number of studies that have found that food supply limits fitness components and affects population dynamics, although this influence may vary between demographic parameters, taxa and populations at dif-

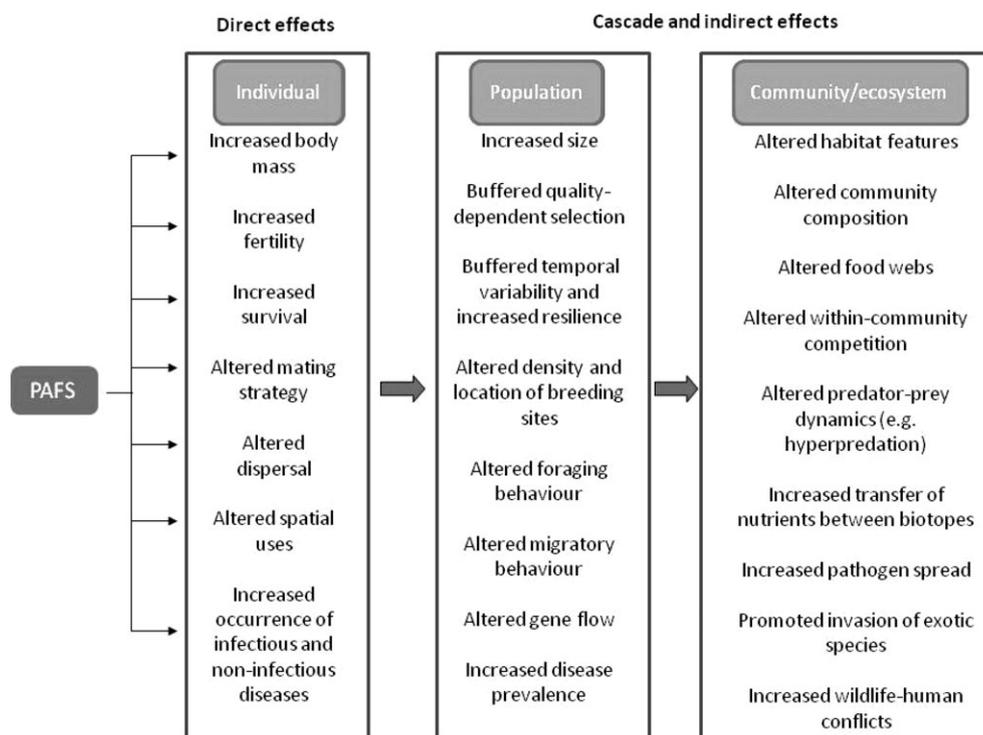


Figure 2 Effects of PAFS at individual, population, community and ecosystem levels. For a list of references and quantitative details on each of these effects, see Table S1.

ferent habitats (Martin 1987). Thus, even though the importance of food is rarely questioned now, the effects of PAFS on individual life-history traits (particularly on survival and dispersal, see Fig. 2) have seldom been quantified (see Table 2).

Supplementary feeding experiments have commonly been conducted to assess the importance of food in limiting populations for a variety of demographic and reproductive parameters and for studying the role of intraspecific competition in different taxa. In a random sample of papers dealing with the study of food-limitation in birds using bird feeders ($N = 48$), 73% of them were experimental. These experiments are challenging because the number of stochastic environmental factors affecting individuals in a population are large and difficult to control (e.g. Newey *et al.* 2010). For instance, when natural food is abundant, supplementary experiments might not reveal differences between treatment and control groups and would erroneously conclude that food is not a limiting factor. This may explain why results from the same species might appear contradictory (e.g. Korpimäki 1989; Hörnfeldt *et al.* 2000). Another factor potentially biasing experimental studies is the failure to control for individual quality (Wirsing & Murray 2007). Experiments involve a subsample of individuals and are commonly performed at small spatial scales (i.e. in a single site). On the contrary, some particular systems have allowed researchers to quantify the effects of the availability of PAFS at the population level or over multiple populations, allowing consideration of spatial processes such as dispersal and differences between population patches to be assessed. For instance, some ongoing environmental policies represent large-scale natural experiments that would otherwise be impossible to perform using classical experimental approaches. In some industrialised countries, those environmental policies include the closure of garbage dumps and the ban of discarding practices (Bicknell *et al.* 2013). The closure of dumps in

Yellowstone National Park in the 1970s provided the first opportunity to test the effects of a PAFS on grizzly bears (*Ursus arctos horribilis*), which fed almost exclusively on this resource. Once dumps were not available, bear mortality increased rapidly with more than a fivefold increase in annual home range areas (Craighead *et al.* 1995). Pons & Migot (1995) demonstrated the effects of the closure of a dump on the reproductive performance of herring gulls (*Larus argentatus*), an opportunistic species: clutch size and fertility decreased by 7 and 49%, respectively, whereas adult survival and the breeding age-structure of this long-lived species remained stable.

Another insightful example of the quantification of the effects of PAFS comes from the study of fisheries discards and a western Mediterranean seabird community. In that region, the trawling fishing fleet discards large amount of non-commercial fish (up to 400% of landings), and these discards can represent up to 73% by biomass of the diet of scavenging seabirds (Table S1). The effects of discard availability were quantified when a trawling moratorium allowed researchers to compare the ecology of a seabird community with and without discard availability. When discards are available, many demographic traits of the seabirds increase: laying dates advanced by 2 weeks, daily feeding rates to chicks increased by 45%, clutch and egg sizes increased by 19 and 6%, respectively, hatching and breeding success increased by 15 and 75%, respectively, yet adult survival remained stable. Behaviour is also affected: successful copulation rates increased by 14% and the occurrence of interspecific kleptoparasitism decreases when trawlers operate (Table S1). At the physiological level, seabirds spare energy by reducing the foraging range by 50%, and reducing the time devoted to feeding by 38% (Table S1).

Bino *et al.* (2010) were able to experimentally modify the availability of anthropogenic food sources for overabundant, opportunistic foxes, and recorded either an increase or shifts in home ranges and

more importantly a severe (between 64 and 100%) and rapid reduction in survival when that food was drastically reduced. A recent example about the shortage of PAFS related to policy decisions (health regulations) suggests detrimental effects on breeding performance, survival, foraging and behaviour in an avian obligate scavenger community. The effects were asymmetrical, affecting mainly meat-consumers such as griffon vultures (*Gyps fulvus*) rather than species with greater diet plasticity such as Egyptian or bearded vultures (*Neophron percnopterus* and *Gypaetus barbatus* respectively) (Margalida & Colomer 2012). Finally, recently developed capture–recapture models allowed Oro *et al.* (2008) to quantify the positive relationship between attendance at restaurants and survival in bearded vultures, illustrating how prolonging population viability can allow harmful anthropogenic actions (e.g. poison mortality) to be mitigated.

EFFECTS OF PAFS AT THE POPULATION LEVEL

Although a direct relationship between the availability of PAFS and population growth rate is difficult to establish, several studies demonstrate that PAFS may increase population density and size. For example, the density of wild canids such as coyotes (*Canis latrans*) and jackals (*C. aureus*) is higher in human populated areas where food from dumps is available (Fedriani *et al.* 2001); spatial confinement induces a reduction of home range for individuals foraging at these PAFS. The population growth rates of yellow-legged gull and rook (*Corvus frugilegus*) colonies are positively associated with the increase in the total annual tonnage of the nearest dumps (Duhem *et al.* 2008; Olea & Baglione 2008) (Fig. 3). The availability of middens and restaurants also explains part of the variance recorded in the growth rate of populations of griffon vultures (Parra & Tellería 2004) (Fig. 3). Lim *et al.* (2003) reported that anthropogenic food was the cause of the dramatic (> 30-fold) increase of the non-native house crow *C. splendens* in Singapore over the previous 16 years (see further examples in Table S1). Food experimentally supplied to pheasants (*Phasianus colchicus*) released for hunting increases their densities, with different effects for males and females (53 and 67% increase respectively) (Draycott *et al.* 2005). To test the effects of PAFS availability on population size, we combined the findings from independent studies on several species of birds exploiting different PAFS to perform a random-effects meta-analysis (see Table S3). We used the available information (10 studies) to extract or calculate coefficients of determination (R^2) between different detrended indices of population size (density, population growth rate, abundance) and availability of PAFS (Table S3). Detrending series decreases the chance of finding spurious correlations (due to e.g. factors independent of PAFS that may also have increased over time). The mean effect size was 0.67 (95% CI: 0.53–0.75), indicating a strong association between population size variation and availability of different PAFS (dumps, fishing discards, crop residuals, carcasses from hunting, gutpiles, middens and restaurants), with a small degree of uncertainty.

Some evidence indicates that the effects of PAFS on population dynamics of opportunistic species can be especially large when habitat quality is poor and/or in years with harsh environmental conditions (Peterson & Messmer 2011; Ruffino *et al.* 2012; Monsarrat *et al.* 2013). In highly productive ecosystems, it seems that PAFS are mostly used by suboptimal individuals (e.g. younger and inexperienced, in bad physical condition), or by most individuals, but only in periods of relative food shortage (Leu *et al.* 2008; Tew Kai *et al.*

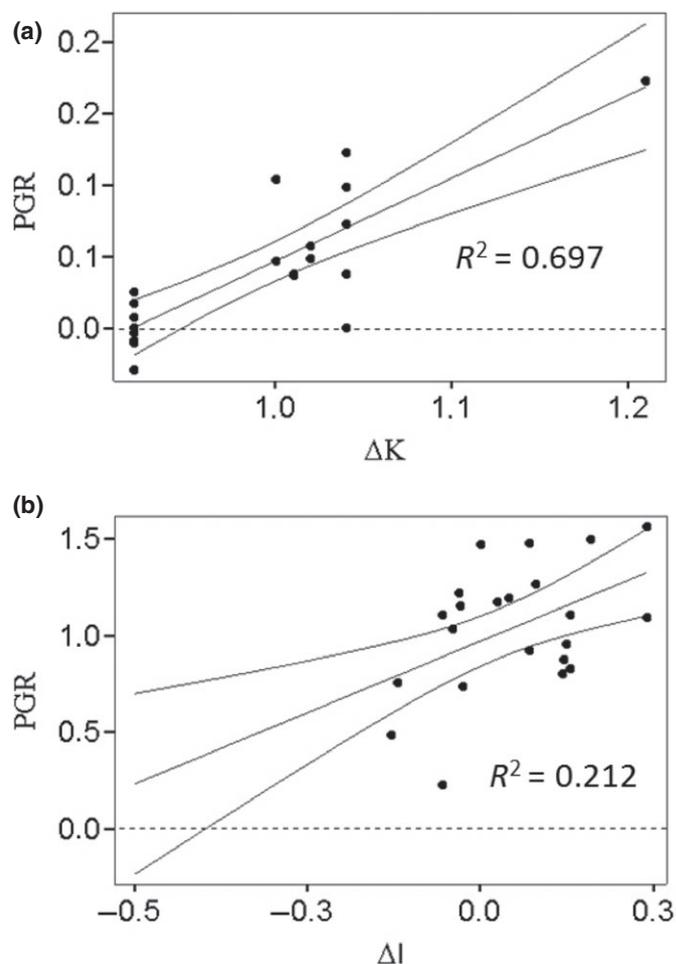


Figure 3 Association between PAFS availability and population growth rate (PGR, expressed as $\ln(N_{t+1}/N_t)$) in: (a) yellow-legged gull colonies in southern France and an index of dump availability (ΔK , calculated as the ratio between the annual tonnage of the nearest dump and its distance to each colony) between 1982 and 2000; and (b) Spanish populations of griffon vultures and the variation of livestock biomass (ΔI , as a proxy of PAFS availability in the form of middens and restaurants) between 1989 and 1999. Data in panels (a) and (b) are adapted from Duhem *et al.* (2008) and Parra & Tellería (2004) respectively. Regression lines (and their 95% CI) are shown. Dashed lines indicate a stable population equilibrium (i.e. PGR = 0) and arrows point to the level of PAFS at which populations should stop growing or declining.

2013). Contrarily, the availability of large quantities of PAFS can have a negative effect on population growth rates when ecological traps are created. For instance, Morris (2005) showed that, paradoxically, experimental feeding stations aimed at small rodents did not improve their demographic parameters and population growth rates, because they faced increased predation risk from opportunistic carnivores, which were also attracted to the feeding station.

The supply of large amounts of food with high spatio-temporal predictability can have strong effects on population structure and dynamics. A regime shift to a new equilibrium, with a higher carrying capacity, may result from an abrupt change in food supply (Brook *et al.* 2013). Nevertheless, very little data exist on regime shifts after the appearance or loss of PAFS. Increased populations of migrating snow geese subsidised by agricultural PAFS have caused abrupt changes in Arctic ecosystem structure and biogeochemical cycling (Jefferies *et al.* 2006). The population dynamics of

a colony of yellow-legged gull exploiting PAFS from dumps showed three marked population regimes: steady population growth (average 7.4% annual growth rate) over two decades (1970s and 1980s) occurring with an increase in the number of dumps, followed by a stable phase (average 1.0% annual growth rate) around carrying capacity since the early-1990s and a dramatic decrease following the closure of most dumps (2006–2011, average 12.0% decline in annual growth rate; Table S1).

Understanding the resilience of populations to perturbations is a scientific challenge attracting research interest, especially as anthropogenic perturbations are larger and more frequent in recent centuries, adding to- or interacting with non-anthropogenic sources of environmental stress. Some evidence supports the idea that subsidised food increases population resilience against environmental perturbation and catastrophes. Under adverse and harsh environments, individuals able to exploit PAFS can still reproduce and survive with success (Martínez-Abraín *et al.* 2012). Ruffino *et al.* (2012) found that population growth rates of black rats (*Rattus rattus*) inhabiting non-subsidised habitats varied with environmental fluctuation, whereas rats in habitats with PAFS maintained high growth rates during both good and harsh years. Experimental approaches providing food on a relatively long-term basis found increasing population numbers, as benefits mainly occur during bad seasons or years, when densities should otherwise decrease (Taitt & Krebs 1981; Krebs *et al.* 1986; Robb *et al.* 2008). Thus, the availability of PAFS might reduce the variance of demographic parameters. If PAFS buffer the influence of environmental stochasticity (Cortés-Avizanda *et al.* 2012; López-López *et al.* 2013) this should have an effect on extinction dynamics by increasing extinction time in closed populations which otherwise experience the same conditions. This may be especially true in isolated patches containing small populations relying mostly on PAFS, in which dispersal processes between populations and rescue effects from sources are obstructed by landscapes artificially fragmented by anthropogenic activities. Therefore, high availability of PAFS should decrease the variability of any biological or population parameter (see Fraterrigo & Rusak 2008).

To test this hypothesis, we analysed the association between a population variability index (*PV*) and an index of discard availability around each patch (which depends on the size and power of the trawling fleet within the foraging radii of each species) from two opportunistic seabird species in the western Mediterranean (Audouin's *L. audouinii* and yellow-legged gulls). A detrended *PV* value was calculated for 17 time series (371 annual censuses corresponding to 13 sites) as:

$$PV = \log[\sigma(\text{residualtime} \ln(\frac{N_{t+1}}{N_t}))],$$

where σ is the standard deviation and N is the population size. Discard availability has a significant, negative effect on the variability of *PV*: a higher mean availability of discards stabilises population fluctuations (Fig. 4).

Some species, populations or even individuals are expected to exploit PAFS more than others. In general, large outcompete smaller species within guilds. Several examples of species differences exploiting PAFS come from obligate avian scavengers or carnivores, e.g. corvids and seabirds (Marzluff & Natherlin 2006; Vanak & Gompper 2009; Cortés-Avizanda *et al.* 2012). Exploiting PAFS may affect communities by altering interference competition mediated by density (Vanak & Gompper 2009; Almaraz & Oro 2011) and preda-

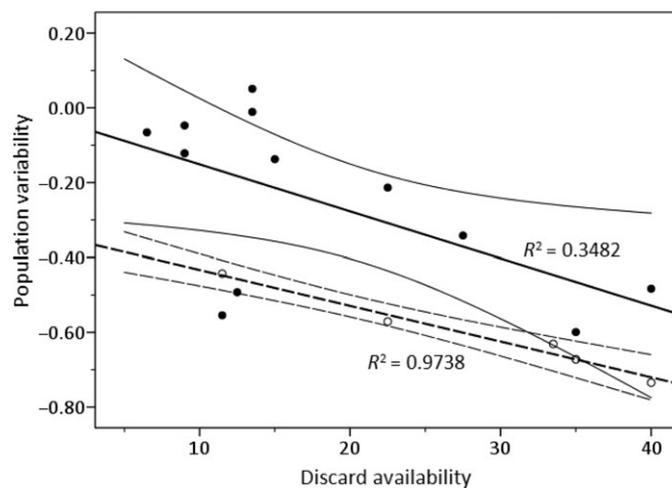


Figure 4 Discard availability has a significant, negative effect on the variability of detrended per capita growth rates in Audouin's (solid circles, line; $P = 0.0434$) and yellow-legged gulls (open circles, dashed line; $P = 0.0018$). Regression lines (and their 95% CI) are shown: solid for Audouin's gulls and dashed for yellow-legged gulls. A higher mean availability of discards stabilises population fluctuations.

tor–prey interactions (Polis *et al.* 1997)(Fig. 2). Predation rates and the fertility and recruitment of smaller species can be affected by differential changes in density across each species in a community (e.g. Votier *et al.* 2004); this interference may influence population growth of small, subordinate species by inverse density-dependence, increasing their extinction probabilities (Linnell & Strand 2000). In fact, increased extinction probabilities are predicted by simple theoretical models based on Lotka-Volterra equations, in which a destabilising or disrupting feedback should occur between predators sharing the same prey (Sanders *et al.* 2013).

At the spatial scale, not all the populations may show the same ability at exploiting PAFS. Within the distribution range of a species, populations may differ in the local availability of PAFS (values ranging between 0 and 80% of the diet depending on the population, see Table S1), which may alter meta-population functioning (see Fig. 2). Patches with large PAFS increase their carrying capacity and this may reduce emigration and promote immigration from non-subsidised patches, especially in social species (Carrete *et al.* 2006; Martínez-Abraín *et al.* 2012; Monsarrat *et al.* 2013) and reduce geographical expansion and foraging movements in solitary species (Table S1). Interpopulation differences generate variation in body size and weights, demographic parameters and differences in density-dependent population dynamics (Table S1). Dumps can modify the spatial distribution of scavenging birds and carnivores by clustering their breeding territories around dump sites (Kristan & Boarman 2007; Bino *et al.* 2010)(Table S1). Although little is known about how species may compete when selecting breeding habitat close to PAFS, competition for breeding habitat can also be dominated by larger and predatory species, with highly developed agonistic behaviours, forcing subordinate species to increase time switching between breeding and foraging patches.

EFFECTS OF PAFS AT BEHAVIOURAL LEVEL

Why do some species and populations exploit PAFS better than others? Species using PAFS are labelled 'opportunistic' (a category

of omnivorous species) and are considered to have the skills to exploit a wide variety of food types including those appearing from human activities. However, this definition is tautological, implicitly assuming that species not using PAFS (e.g. 'specialists') are not able to do so. For instance, some populations of the same species exploit PAFS whereas other do not, due to differences in habitat, or cultural and behavioural traditions that may generate interpopulation differences in social structure (Ramsay *et al.* 1997; Chilvers & Corkeron 2001). Yet, individuals of the same population can show two distinct foraging strategies, one opportunistic (exploiting mostly PAFS due to their abundance and predictability) and one specialist (exploiting natural prey due to their higher energetic composition) (Annett & Pierotti 1999; Gremillet *et al.* 2008). For example, some species considered specialists have shown a great capacity to exploit PAFS. The Audouin's gull was considered a specialist until two decades ago, even though it belongs to a taxonomic group of opportunistic species, because 80% of its diet was composed of small pelagic fish. Its 'specialisation' is constrained by having nocturnal vision, a particular physiological ability owned by very few other seabirds. Nocturnal foraging activity was linked to a temporal refuge from competition with the dominant, diurnal and sympatric yellow-legged gull (Almaraz & Oro 2011). Nevertheless, Audouin's gulls have learnt to exploit discards from the diurnal trawling fleet, from which they can obtain up to 70% of its diet. During winter, birds have also been observed foraging at dumps, a behaviour never recorded prior to two decades ago (Table S1).

Recent studies on invasive species arriving in a novel environment and exploiting new foraging resources (included PAFS) are good examples of behavioural plasticity (Lim *et al.* 2003), especially those species that have life-history strategies prioritising future rather than current reproduction (Sol *et al.* 2011). The range of personalities across individuals and species that take advantage of PAFS may be greater than originally thought. Behavioural plasticity may be sped up by cultural innovation performed by individuals shifting to opportunistic behaviour, followed by improvements in foraging efficiency and breeding performance (Price *et al.* 2003). For instance, Annett & Pierotti (1999) found that lifetime reproductive success of opportunistic western gulls (*L. occidentalis*) was positively correlated with individuals foraging on fish in contrast to individuals mostly foraging on dumps, and that diet choice is passed between generations by learning or cultural transmission. In summary, PAFS can cause several behavioural changes such as dietary shifts, changes in home ranges and foraging techniques and changes in social systems to find food (see also section 'Implications for evolutionary processes' below).

INFLUENCE OF PAFS ON COMMUNITIES AND ACROSS ECOSYSTEMS

Increasing population densities in species exploiting PAFS alter ecosystems in different ways (Fig. 2), as reciprocal interactions (e.g. competition, predation) are inevitably modified (see Fig. 6). These changes in population densities can result in cascading effects across non-adjacent trophic levels, pervading whole ecosystems, with potential impacts on stability, flexibility and persistence (Fig. 2). For instance, the snow goose (*Chen caerulescens*) exploits crop leftovers in North America and has become an 'over-abundant' species. As a result, geese have altered the structure and species composition of plant communities in both the wintering and the breeding grounds,

and they transfer large amounts of nutrients from agro-ecosystems to natural systems (e.g. Jefferies *et al.* 2004; see also Table S1). Subsidised ungulate populations can also trigger cascade effects on a range of organisms through food-webs (Table S1). Supplementary food increases ungulate populations, altering their browsing impact on vegetation, affecting plant species richness and composition, primary productivity, habitat structure and nutrient cycling. These changes cascade through bird, mammal and insect communities (Table S1), although the magnitude of the effects on those communities can also vary between habitats and environmental conditions (Parsons *et al.* 2013). At the same time, subsidised ungulates can also propagate disease and parasites between conspecific populations or to domestic livestock. Increasing ungulate populations may attract predators (i.e. carnivores) and boost their densities, consequently depressing alternative prey abundance (such as reptile and avian species, Cooper & Ginnett 2000; Cortés-Avizanda *et al.* 2009), a phenomenon known as hyperpredation. Hyperpredation also occurs when PAFS are exploited directly by predators modifying predator-prey relationships. The increase of yellow-legged gull populations subsidised by dumps and fishing discards increases predation rates on sympatric Audouin's gulls and European storm petrels (*Hydrobates pelagicus*), among many other vulnerable seabirds and waterbirds (see Table S1). Similar examples are subsidised killer whales (*Orcinus orca*), ravens (*Corvus corax*) and mesocarnivores, and their higher predation rates on Steller sea lions (*Eumetopias jubatus*), desert tortoise (*Gopherus agassizii*) and capercaillie (*Tetrao urogallus*) respectively (Table S1). Invasive predators increase predation rates on native taxa through hyperpredation, e.g. rats and mongoose preying on seabird and turtle nests respectively (Table S1).

Fishing discards also illustrate how PAFS influence communities and ecosystems, by affecting a range of ecological processes, trophic levels and even different ecosystems (Fig. 5). Discards are exploited by a large number of organisms, from top predators (such as cetaceans, sharks, sea turtles and seabirds) to invertebrates (such as crabs, crustaceans, amphipods and isopods) (see Table S1) and covering different zones or habitats (e.g. sea surface, pelagic and benthic). 'Horizontal' interactions (i.e. competition and predation within guilds or trophic levels) are often as important as 'vertical' (i.e. between trophic levels) interactions (Fig. 5). In the benthic layer different forms of competition (both resource and interference) and predator-prey relationships are exacerbated within and between invertebrate and fish communities exploiting discards arriving at the sea bottom. Complexity increases as some of these species are unselectively targeted by the same trawling fleet that generates the discards. Competition and predation may also occur within communities of subsidised pelagic and aerial predators (see previous section), as well as hyperpredation on pelagic prey (e.g. clupeids, squid) and on obligate piscivorous seabirds by subsidised top predators such as seabirds and marine mammals (Fig. 5). Among opportunistic predators, seabirds have particular impacts on food-webs and ecosystem functioning, including the transport of nutrients between biomes (Fig. 5). Seabirds are very mobile and switch between marine foraging and terrestrial breeding habitats. Population growth experienced by many subsidised seabird species has increased ammonia emissions (excreted by seabirds) and increased the movement of nutrients, detritus and pollutants (heavy metals and other pollutants such as DDT) between marine and terrestrial biotopes, altering both ecosystems (Polis *et al.* 1997; Caut *et al.* 2012), even affecting remote and relatively pristine habitats (Blais *et al.* 2005) (see also Table S1). Impacts can also occur in the marine zones

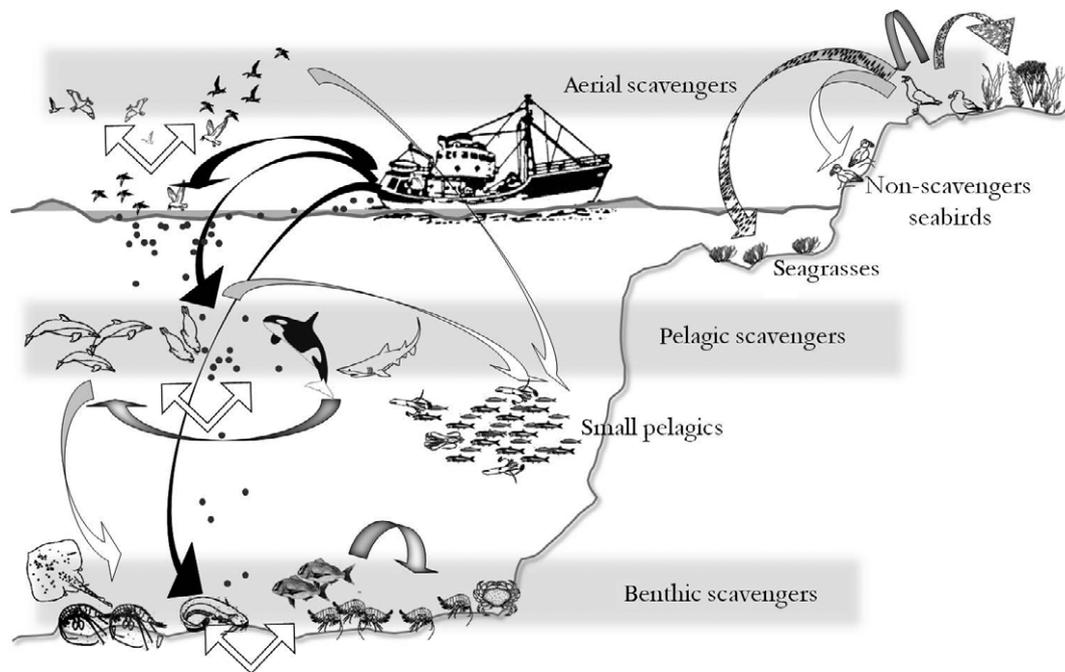


Figure 5 Conceptual model of a range of effects of PAFS at population, community and ecosystem levels using fisheries discards as an example. Five types of ecological processes are represented: (1) foraging exploitation of discards by the three main communities of scavenging organisms (shown by black arrows), (2) predation within communities (shadow grey arrows), (3) competition (both resource and interference) within communities (double white arrows), (4) hyperpredation (white arrows), and (5) transfer of nutrients (stained arrows). Species illustrations are not drawn to scale.

surroundings seabird colonies by changing species composition and the growth of keystone species such as seagrasses, with consequences for fish, invertebrates and the entire marine community structure (Powell *et al.* 1991)(Fig. 5). Seabirds can also increase nitrogen inputs in relatively simple food webs, such as islands, triggering cascading effects: initially altering vegetation structure and plant species turnover at the expense of native taxa (Vidal *et al.* 2000; Van der Wal *et al.* 2008; Baumberger *et al.* 2012), in turn affecting beetle and vertebrate communities by favouring certain assemblages (Orgeas *et al.* 2003; Schmitz 2003; Caut *et al.* 2012). Some opportunistic seabirds (e.g. gulls) can act as seed dispersers from autochthonous as well as invasive plants (see Table S1), although the impact of this process on plant communities is little known. Finally, the changes in vegetation structure and density caused by increased nutrient inputs from subsidised seabirds may alter their own breeding habitat, favouring some species over others and generating differential dispersal processes at intra- and interspecific levels.

The wide range of ecosystem consequences from fisheries discards highlights the influence of PAFS on community and food-web organisation. Omnivores (species feeding on more than one trophic level) have the potential to directly exploit most types of PAFS as well as predated on lower trophic level species that also exploit these PAFS (Fig. 5). Omnivores can therefore exert a larger influence on ecosystem control than specialist and lower trophic level foragers (Morris 2005). Thus, top-down control can increase at the expense of bottom-up regulations in ecosystems subsidised by PAFS, yet the potential consequences for the stability and functioning of these ecosystems remain poorly understood (Ostfeld & Keesing 2000).

What are the potential effects of PAFS on species diversity? An increase of food supply should decrease competition (scramble and

interference) allowing the incorporation of new species to, or persistence of existing species in the ecosystem. However, an increase of food availability (through PAFS) does not always increase species richness: when interference competition at PAFS is light, because it occurs in relatively low trophic levels (e.g. small passerines), richness remains stable and only population densities increase (Fuller *et al.* 2008). When interference competition occurs with dominant species monopolising PAFS (within and between guilds), species diversity at local patches decreases by promoting displacement, dispersal and extinction of subordinate species (Cortés-Avizanda *et al.* 2012). As highlighted above, the cascading effects recorded in simple ecosystems (such as small islands) driven by subsidised gull populations also suggest that PAFS can drive ecosystem simplification, reducing species diversity within communities of plants, beetles and mammals in breeding grounds.

IMPLICATIONS FOR EVOLUTIONARY PROCESSES

The main prerequisite for natural selection to operate is competition for scarce resources. Studies on Darwin's finches (e.g. Grant & Grant 2011) have confirmed the importance of food variability in shaping micro-evolutionary changes (see also previous section on Effects of PAFS at behavioural level). Individual responses to predictable and abundant food supplies can be fast (Badyaev 1998). Substantial changes in home-range (increased), density and survival probability (reduced) in carnivores visiting dumps, for example, can occur in a matter of months (Bino *et al.* 2010). There is also evidence of interindividual differences in body condition linked with differences in the use of fishing discards (Votier *et al.* 2010) as well as heterogeneity in survival probability linked with attraction to feed on these PAFS (Barbraud *et al.* 2013). Over longer time-scales (e.g.

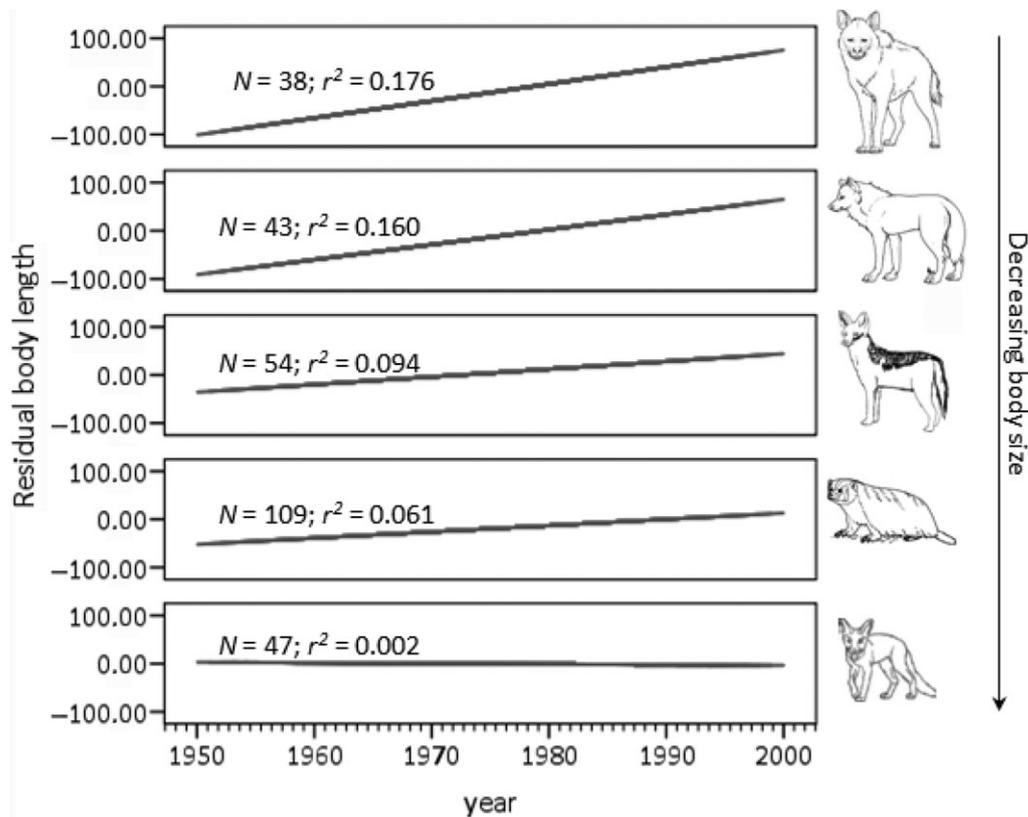


Figure 6 Temporal trend (only fitted regression lines are shown) in residual body length in five species of carnivores commensal with humans in Israel following an increase in the availability of PAFS (garbage dumps, livestock carcasses in middens, crop residuals) during 1950–2000. Species are sorted by body size from top to down: spotted hyena, wolf, golden jackal, European badger and fox. Note that correlation coefficients decrease with body size and are all statistically significant except for the fox. Adapted from Yom-Tov (2003).

generations or decades), carnivores can increase their body size by exploiting new types of PAFS, with greater increases for large species dominating interference competition within the community (Fig. 6). This can lead to behavioural and morphological differences across populations which may, in turn, lead to changes in gene frequency (Yom-Tov 2003; Cohen *et al.* 2013). For instance, the Canary Islands were colonised 2500 years ago by Berber people from northern Africa who imported goats (*Capra aegagrus*). This new and abundant food source is hypothesised to have allowed Egyptian vultures (*Neophron percnopterus*) to colonise a previously inhospitable environment. These birds have genetically diverged from the Iberian donor population, a speciation process that took place rapidly (< 200 generations) (Agudo *et al.* 2010). Following the closure of dumps in Yellowstone, Badyaev (1998) found that fluctuating asymmetry of grizzly bear canines, which are under directional sexual selection in males, was more affected by the abrupt decrease of food availability compared to that of female dentition, and that only a small number of males were able to achieve both large size and symmetrical development of these teeth. These phenotypic changes suggest that a shift to anthropogenic food might lead to differentiation, even for species with long generation time. Recently Axelsson *et al.* (2013) found evidence that domestic dogs differentiated from the wolf due to their increasing commensalism with humans. For subsidised polygamous ungulates, key elements in sexual selection, such as female aggregation and mean harem size, can be affected by PAFS with potential consequences at evolutionary level (Table S1).

In these species, PAFS can also reduce selection pressure in the first year of life (Schmidt & Hoi 2002). PAFS provided to ungulates to increase hunting rates moved wild evolutionary traits closer to those associated to a semi-domestic state affecting both natural and sexual selection (Mysterud 2010).

PAFS can also improve the survival prospects of individuals in poor condition (either by genetic weakness or physiological constraints) and relax selection pressures (Carrete *et al.* 2009; Genovart *et al.* 2010) with consequences at the population level: increases in population size can happen at the cost of an average drop in phenotypic and genetic quality (Parvinen 2005). Furthermore, the poor food quality and the pollutants and pathogens associated with some PAFS, such as those obtained from dumps, bird feeders or from certain fishery discards (the so-called ‘junk food hypothesis’ see Gremillet *et al.* 2008) can modify selection pressures by causing the appearance of sick and obese individuals, with reduced abilities to escape from predators (Carrete *et al.* 2009; Genovart *et al.* 2010). The low quality of some food obtained from PAFS can generate additional fitness costs, such as lower lifetime reproductive success (e.g. Annett & Pierotti 1999; Gremillet *et al.* 2008).

CONCLUSIONS AND FUTURE DIRECTIONS

Humans waste enormous amount of food (see Table 1 and Fig. 1) that are available to and exploited by a large number of organisms across ecosystems, from decomposers (e.g. bacteria and fungi) to

herbivores and tertiary consumers (e.g. whales, top predators such as wolves). In some cases, food is voluntarily provided to improve individual survival and increase populations of endangered species; of common but emblematic species (e.g. urban passerines in industrialised countries); and of game species (mainly wild ungulates) (see Table S1). Since different species can benefit from different PAFS, and those PAFS offer differential amounts of food (Tables 1 and 3), the consequences at community and ecosystem levels may differ among PAFS. Dumps, where millions of tonnes of food are wasted worldwide and represent the major global source of PAFS (see Table 1), are exploited by ca. 20 and 30% of Orders of birds and mammals, respectively (Table 3), providing a rough idea of the importance of PAFS on ecosystems. Dumps are mainly exploited by secondary (especially meso-carnivores and omnivores) and tertiary consumers (especially top predator carnivores), so their main effects are likely hyperpredation rates on herbivores and a consequent release of primary consumption on plants. Such unbalancing of the food chains can be especially relevant when PAFS have a worldwide distribution and provide large quantities of food, as is the case also for fishing discards and for crop residuals in marine and terrestrial ecosystems respectively (Table 3). However, the net balance of PAFS on ecosystems is far from being understood, especially as some PAFS simultaneously benefit many trophic levels (Fig. 5) and also because some PAFS, coincident in space and time, benefit different food chain consumers (e.g. dumps for carnivores and crop residuals for herbivores). At the same time, human harvesting (e.g. hunting, fishing, and whaling) has reduced large apex predator populations in food webs. Understanding and managing the net balance of the effects of human activities (positive and negative, including overharvesting, habitat loss and transformation and other perturbations) at different trophic levels of the ecosystems (including mutualistic and parasitic relationships) constitutes a challenge for future research.

We have focused here on the most conspicuous forms of food subsidies from humans. PAFS influence animal ecology at individual, population and ecosystem levels, with indirect effects on plant communities and their functioning, although the complexity of natural systems hinders understanding of the exact nature of these changes. Even though PAFS may have opposing effects (e.g. an increase in survival and breeding performance and an associated increase in pathogen spread), the demographic balance at the population level is an increase in population size and the ecological consequences at community and ecosystem levels (e.g. hyperpredation, alteration of consumer-resource relationships and food webs).

Apart from the PAFS described here, there are a range of other food sources deriving from anthropogenic activities, such as invasive and translocated species becoming prey for native predators (e.g. Tablado *et al.* 2010), animal and vegetal remains wasted in fish- and agricultural farms and campgrounds (Marzluff & Neatherlin 2006; Margalida *et al.* 2010), wildlife casualties from roads and wind farms, the feeding of feral cats and dogs or nutrients from sewage, all of which also alter ecosystem functioning. Some of these alterations can affect human welfare, such as the increased risk of rabies spread associated with the increase in vampire bats following the dramatic growth of livestock farming in the Americas (Jones *et al.* 2013).

Given the rapid and strong ecosystem impact of PAFS, they also have potential as a powerful management tool in conservation and social issues. Subsidised food can be used to redistribute species, diminishing human-wildlife conflicts (Sahlsten *et al.* 2010; Kaplan *et al.* 2011) (see also Table S1). PAFS can limit population declines

of endangered species, especially when natural food sources are diminished due to other anthropogenic causes (e.g. the Iberian lynx *Lynx pardinus* and rabbits, the California condor *Gymnogyps californianus*) (Table S1). PAFS can also decrease the negative impacts of other human activities, for instance by delaying or compensating the negative effects of anthropogenic mortality (e.g. poison, wind-farm collisions, fisheries bycatch mortality) (Oro *et al.* 2008; Laneri *et al.* 2010; Martínez-Abraín *et al.* 2012). Despite this potential for conservation, PAFS arguably reduce natural sources of selection pressure by reducing intraspecific competition, although in some localised instances, because of the clumped nature of some PAFS, there may be higher levels of competition especially if resources may be quickly lost (i.e. waste covered by heavy machinery at landfill sites and discards sinking through the water column). When PAFS reduce selection pressures this may dilute traits that are important for the persistence and resilience of small populations. The potential negative effects of PAFS (as junk food and source of pollutants) also have to be integrated in the balance of PAFS effects on species and ecosystems.

Future research directions include the study of common life-history characteristics or cultural features of species or populations exploiting PAFS, to increase our ability to predict changes in ecosystems due to the appearance or loss of PAFS. Oro *et al.* (2008) forecast population extinction probabilities for the bearded vulture in the event that food originating from humans was no longer available; a situation that could arise following the application of environmental policies following the 'mad-cow' BSE crisis in Europe (Margalida *et al.* 2010; Margalida & Colomer 2012; Martínez-Abraín *et al.* 2012). Some large-scale studies covering the effects of different availability of PAFS on population growth rate also allow population prediction in the absence of these PAFS (Fig. 3). Forecasting can be important when species exploiting PAFS are considered pests or endangered species. In industrialised countries, some PAFS (e.g. dumps, fishing discards, restaurants) can be curtailed by environmental regulations. Beyond the population decline for directly affected pest and vulnerable species, alterations in food webs and ecosystems are to be expected (Bicknell *et al.* 2013). More precisely, environmental policies now regulate many human activities, aiming to prevent overharvesting and encourage the recycling of waste food. Such regulations constitute natural experiments to study the effects of PAFS on ecological processes at population and ecosystem levels, such as resilience, extinction thresholds, competition and extinction cascades, by comparing subsidised and non-subsidised systems or systems before and after being subsidised. To our knowledge, little theoretical work has specifically explored the impact of PAFS on population and ecosystem stability. One related study illustrates that the addition of biomass to a target species through artificial stocking can destabilise model communities, in some cases leading to the extinction of non-target species (Enberg *et al.* 2006). Other recent work demonstrates qualitative shifts in extinction risk for different species across food webs driven by changes in the symmetry of competition (Fowler 2013), which could arise through differences in the exploitation of PAFS across species.

How will populations heavily exploiting PAFS behave, when those PAFS are no longer available? We predict there is a serious risk that those populations will decline to even smaller sizes than before the appearance of PAFS, at least until stability around a new dynamic equilibrium occurs. Transient dynamics between two distinct equilibrium population states (e.g. higher or lower carrying capacities

in the same locality, with and without availability of PAFS) should be rapid because the two equilibrium points represent two very different environmental situations and also because the perturbation of ending PAFS will likely be of considerable magnitude. The role of those transient dynamics on the ability of species, communities and ecosystems to buffer against perturbations requires further investigation. Margalef (1997) suggested that the demographic transition in human populations shows a decreasing trend in the *P/B* ratio (primary production/biomass) as we have increased our ability to buffer against unpredictable perturbations. This may lead (by cultural means) to a pattern of control of reproduction similar to that shaped by evolution in eusocial insects (e.g. behavioural sterility of larvae and workers). The evidence we have presented highlighting the capacity of PAFS to decrease population size variability over time (e.g. Fig. 4), suggests that this pattern should be further explored especially in species that have a long history of exploiting PAFS. Comparison of subsidised and non-subsidised ecosystems can help predict changes in species diversity and ecosystem services on top of the impact of other agents of global change. The appearance of scientific journals dealing with human activities and their effects on the functioning of ecosystems, such as *Urban Ecosystems*, *Human and Ecological Risk Assessment* or *Human Dimensions of Wildlife*, suggest an increasing awareness of the importance of these relationships. PAFS have altered many species' dynamics, cascading across multiple levels of organisation, from individuals to communities and ecosystems. As humans now start to restrict the availability of a range of PAFS, we must be prepared to mitigate against unwanted impacts on species of economic and conservation importance.

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AUTHORSHIP

DO conceived the study; DO, MG, GT and MSF carried out analyses; DO wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

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