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## Ecological and evolutionary implications of food subsidies from humans

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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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**Abstract**

Human activities are the main current driver of global change. From hunter-gatherers through to Neolithic societies – and particularly in contemporary industrialized 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 communities, 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 subsidized and non-subsidized ecosystems can help predict changes in diversity and the related ecosystem services that have suffered the impact of other global change agents.

## INTRODUCTION

Modern humans have played an active role in ecosystem functioning since their appearance ca. 10,000y ago (e.g. 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 (Roemer et al. 2002; 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 both human densities and per capita food losses are those most affected by those anthropogenic 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

1  
2  
3 time of subsidized food supplies make this food resource easier to access compared to  
4  
5 natural sources (Bartumeus et al. 2010; Cortés-Avizanda et al. 2012). This decreases  
6  
7 required foraging times, consequently improving fitness components. An abundant  
8  
9 and predictable food resource should improve physiology (i.e. body condition and  
10  
11 body mass) and individual breeding performance, while mortality risks such as  
12  
13 susceptibility to pathogens and vulnerability to predation should decrease. Some  
14  
15 cosmopolitan opportunistic species (facultative scavengers), such as rats, foxes or gulls  
16  
17 provide paradigmatic examples of species that benefit from PAFS. These species  
18  
19 exploit food from human origin, have increased their numbers and are considered  
20  
21 “over-abundant”, and may behave as native invaders causing changes in food webs  
22  
23 and ecosystems (see Table 1 in Carey et al. 2012).

24  
25  
26 Here, we will argue that the food that humans make available to animal species  
27  
28 through anthropogenic activities, such as agriculture, livestock farming, hunting,  
29  
30 fishing and commercial trade, has shaped the architecture of many ecosystems. We  
31  
32 focus here on food resources that are wasted or intentionally offered to animals by  
33  
34 humans and that are predictable in space and/or in time, hereafter referred as PAFS  
35  
36 (Predictable Anthropogenic Food Subsidies). Research oriented towards assessing the  
37  
38 effects of PAFS on species, communities and ecosystems should greatly improve our  
39  
40 understanding of the ecological and evolutionary roles of food and food webs in those  
41  
42 systems, beyond the limitations of the numerous experimental studies (Margalef  
43  
44 1997).  
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## 55 **FOOD SUBSIDIES FROM INTENSIVE HUMAN ACTIVITIES IN CONTEMPORARY TIME**

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3 The subsidizing of species by human activities and consequent effects on food webs  
4  
5 was first identified several decades ago (Margalef 1997). However, the role of humans  
6  
7 in configuring the mosaic of an ecosystem's foraging resources has only recently  
8  
9 started to be analysed (Leu et al. 2008; Robb et al. 2008). Table 1 lists situations where  
10  
11 large quantities of PAFS are made available to animal species; these include organic  
12  
13 remains from refuse dumps, discards from fisheries, livestock middens (also called  
14  
15 "restaurants" with respect to obligate scavenging birds), crop leftovers, feeding  
16  
17 stations for game species and seeds supplied in backyard bird feeders. There is  
18  
19 evidence that all PAFS generate impacts at both individual and population levels, with  
20  
21 consequences translated to ecosystem functioning (Table 2). At the same time,  
22  
23 individuals can vary in their use of PAFS, according to cultural, gender, age and  
24  
25 personality differences (Table 2, see also quantitative data in Table S1).  
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31 The three main PAFS in terms of food availability and global distribution are dump  
32  
33 sites, crop residuals and fishing discards (Table 1). Dumps have the potential to sustain  
34  
35 a large number of species and individuals (Table 3, see also Tables S1-S2); even though  
36  
37 edible food wasted *per capita* is higher in industrialized countries than in developing  
38  
39 countries (Table 1), environmental policies and regulations that have progressively  
40  
41 been applied there limit the accessibility of these resources to scavenging organisms,  
42  
43 whereas in developing countries, where high human densities are often coupled with  
44  
45 less strict environmental policies, dumps are large and numerous. On the other hand,  
46  
47 intensive plant agriculture has affected terrestrial ecosystems worldwide more than  
48  
49 any other human activity. Crops for human or livestock consumption are a valuable  
50  
51 source of food for wild animals globally. Here, we consider the leftover crops  
52  
53 remaining after harvesting to be a type of PAFS originally intended for  
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3 commercialization or consumption (Tables 1 and 2). Crop leftovers benefit herbivorous  
4  
5 and granivorous species at lower trophic levels than those, for example, foraging at  
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7 dump sites, discards or at middens (Table 3). While dumps and crops residuals affect  
8  
9 mainly terrestrial ecosystems, fisheries discards have an impact on marine ecosystems.  
10  
11 It has been estimated that 8% of all fish caught worldwide are discarded, equating to  
12  
13 >7 million tonnes of waste entering the marine ecosystems each year (Bicknell et al.  
14  
15 2013). The diversity of organisms exploiting discards is wide, from large whales to  
16  
17 invertebrates such as cephalopods, amphipods, isopods and decapods, and this PAFS  
18  
19 impacts the entire water column from surface feeders (such as seabirds) to benthic  
20  
21 organisms (see below). At least 143 (52% of global) seabird species from all 14  
22  
23 taxonomic families exploit fishing discard to different degrees worldwide, from  
24  
25 sporadic use up to 75% of their diet (Table S2).  
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30  
31 The above PAFS, together with gutpiles and carcasses from hunting are all provided  
32  
33 involuntarily. Other PAFS (e.g. restaurants, bird feeders and feeding stations for game  
34  
35 species, see Table 3) are intentionally provided, especially in industrialized countries.  
36  
37 For instance, feeding stations are used to maintain high densities of game wildlife (e.g.  
38  
39 Draycott et al. 2005)(Table S1). Restaurants are used in most industrialized countries  
40  
41 to counterbalance the effects that the regulation (including the ban) of middens and  
42  
43 livestock carcasses (traditionally abandoned in the field) have on obligate scavenging  
44  
45 birds (Margalida et al. 2010; Martínez-Abraín et al. 2012). Bird feeding is particularly  
46  
47 important in some industrialized countries (e.g. USA and the UK, see Table 1) with  
48  
49 important consequences for passerine communities and the cascading effects  
50  
51 associated (Table S1, see also Robb et al. 2008). Although these PAFS represent less  
52  
53 food for wild animals than dumps, crop residuals and fishing discards, voluntarily  
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3 supplemented food is also assumed to increase body condition, especially in winter.  
4  
5 This improves fertility, increases seasonal or annual survival and potentially reduces  
6  
7 levels of damage caused to agriculture, game and forestry (Table 2).  
8  
9

### 10 11 12 **THE IMPORTANCE OF PREDICTABILITY** 13

14 The role of predictability in the exploitation and advantages of PAFS compared to  
15  
16 natural and less predictable foraging resources, has seldom been considered (Goldberg  
17  
18 et al. 2001; Shochat 2004). Margalef (1997) noted that humans have introduced new  
19  
20 temporal structures with predictable features to ecosystems, like our calendar week,  
21  
22 which have resulted in a more scheduled behaviour for some species. Many  
23  
24 anthropogenic activities are based on a weekly cycle, triggering weekly climate  
25  
26 patterns, which can also have a high degree of spatial predictability (e.g. Deygout et al.  
27  
28 2010). In contrast to the stochastic fluctuations inherent in natural systems, higher  
29  
30 predictability should translate into greater stability (e.g. affecting optimal evolutionary  
31  
32 stable strategies), but the potential consequences of the increased temporal and  
33  
34 spatial predictability of PAFS remain poorly understood, across species, community  
35  
36 and ecosystem levels.  
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42  
43 A prime example illustrating how the predictability of anthropogenic resources may  
44  
45 impact opportunistic species comes from trawling fishery discards and a  
46  
47 Mediterranean seabird community. Here, fishing vessels have a precise operating  
48  
49 timetable, which generates temporal predictability, resulting in seabirds following daily  
50  
51 and weekly cycles in foraging activity (see Table S1). Furthermore, highly productive  
52  
53 fishing grounds at the mesoscale are relatively fixed in space (e.g. fronts, eddies, fresh  
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55 water inputs, island effects) (Cama et al. 2012). This high spatio-temporal predictability  
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3 influences the foraging activity and searching process (i.e. optimal diffusivity) of  
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5 opportunistic scavenging seabirds (Bartumeus et al. 2010). Trawling moratoria in the  
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7 western Mediterranean have been used to quantify the effects of fisheries discards on  
8  
9 opportunistic seabird species. Discards have resulted in reduced foraging time, a great  
10  
11 reduction in foraging area, and in increasing fitness parameters (e.g. survival, breeding  
12  
13 performance) leading to population growth for all seabird species exploiting such  
14  
15 resources (with larger effects larger for bigger species) (Almaraz & Oro 2011)(see also  
16  
17 Table S1). The same phenomenon has been recorded for avian scavenging  
18  
19 communities. Obligate scavengers such as vultures, which evolved in unpredictable  
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21 food resource environments (i.e. scattered carcasses), have also shown the capacity to  
22  
23 change their searching strategy when predictable resources are available in the form  
24  
25 of middens and restaurants (López-López et al. 2013). The spatio-temporal  
26  
27 predictability of these PAFS alters these scavengers by modifying their nested  
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29 community structure (Selva & Fortuna 2007) and decreasing diversity (Cortés-Avizanda  
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31 et al. 2012). In this vulture community, predictability also modifies the value of social  
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33 information when searching for food (Deygout et al. 2010), increases survival  
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35 (particularly that of juvenile, inexperienced individuals, see Oro et al. 2008) and affects  
36  
37 population dynamics (Martínez-Abraín et al. 2012). Finally, gutpiles and carcasses from  
38  
39 hunting also have a larger predictability in space and time compared to natural  
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41 carcasses due to restrictions on when and where hunting is allowed, and this affects  
42  
43 the ecology of the carnivore communities exploiting these PAFS (Wilmers & Getz  
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## QUANTIFIED EFFECTS OF PAFS ON LIFE-HISTORY TRAITS

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3 In the absence of other factors (e.g. sites for reproducing, density of both predators  
4 and mates), the carrying capacity of populations is mostly limited by resource  
5 availability and density-dependence (i.e. food *per capita*), through intraspecific or  
6 inter-specific (within guild) competition. Several reviews have compiled a large number  
7 of studies that have found that food supply limits fitness components and affects  
8 population dynamics, although this influence may vary between demographic  
9 parameters, taxa and populations at different habitats (Martin 1987; Boutin 1990).  
10 Thus, even though the importance of food is rarely questioned now, the effects of  
11 PAFS on individual life-history traits (particularly on survival and dispersal, see Fig. 2)  
12 have seldom been quantified (see Table 2).  
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27       Supplementary feeding experiments have commonly been conducted to assess the  
28 importance of food in limiting populations for a variety of demographic and  
29 reproductive parameters and for studying the role of intraspecific competition in  
30 different taxa. In a random sample of papers dealing with the study of food-limitation  
31 in birds using bird feeders (N = 48), 73% of them were experimental. These  
32 experiments are challenging because the number of stochastic environmental factors  
33 affecting individuals in a population are large and difficult to control (e.g. Newey et al.  
34 2010). For instance, when natural food is abundant, supplementary experiments might  
35 not reveal differences between treatment and control groups and would erroneously  
36 conclude that food is not a limiting factor. This may explain why results from the same  
37 species might appear contradictory (e.g. Korpimäki 1989; Hörnfeldt et al. 2000).  
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3 the contrary, some particular systems have allowed researchers to quantify the effects  
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5 of the availability of PAFS at the population level or over multiple populations, allowing  
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7 consideration of spatial processes such as dispersal and differences between  
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9 population patches to be assessed. For instance, some on-going environmental policies  
10  
11 represent large-scale natural experiments that would otherwise be impossible to  
12  
13 perform using classical experimental approaches. In some industrialized countries,  
14  
15 those environmental policies include the closure of garbage dumps and the ban of  
16  
17 discarding practices (Bicknell et al. 2013). The closure of dumps in Yellowstone  
18  
19 National Park in the 1970's provided the first opportunity to test the effects of a PAFS  
20  
21 on grizzly bears (*Ursus arctos horribilis*), which fed almost exclusively on this resource.  
22  
23 Once dumps were not available, bear mortality increased rapidly with more than a  
24  
25 fivefold increase in annual home range areas (Craighead et al. 1995). Pons & Migot  
26  
27 (1995) demonstrated the effects of the closure of a dump on the reproductive  
28  
29 performance of herring gulls (*Larus argentatus*), an opportunistic species: clutch size  
30  
31 and fertility decreased by 7% and 49% respectively, whereas adult survival and the  
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33 breeding age-structure of this long-lived species remained stable.  
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40 Another insightful example of the quantification of the effects of PAFS comes from  
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42 the study of fisheries discards and a western Mediterranean seabird community. In  
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44 that region, the trawling fishing fleet discards large amount of non-commercial fish (up  
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46 to 400% of landings), and these discards can represent up to 73% by biomass of the  
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48 diet of scavenging seabirds (Table S1). The effects of discard availability were  
49  
50 quantified when a trawling moratorium allowed researchers to compare the ecology of  
51  
52 a seabird community with and without discard availability. When discards are  
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54 available, many demographic traits of the seabirds increase: laying dates advanced by  
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3 two weeks, feeding rates to chicks increased by 45%, clutch and egg sizes increased by  
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5 19% and 6% respectively, hatching and breeding success increased by 15% and 75%  
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7 respectively, yet adult survival remained stable. Behaviour is also affected: copulation  
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9 rates increased by 14% and the occurrence of interspecific kleptoparasitism decreases  
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11 when trawlers operate. At the physiological level, seabirds spare energy by reducing  
12  
13 the foraging range by 50%, and reducing the time devoted to feeding by 38% (Table  
14  
15 S1).  
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18  
19 Bino et al. (2010) were able to experimentally modify the availability of  
20  
21 anthropogenic food sources for overabundant, opportunistic foxes, and recorded  
22  
23 either an increase or shifts in home ranges and more importantly a severe (between  
24  
25 64%-100%) and rapid reduction in survival when that food was drastically reduced.  
26  
27 Finally, recently developed capture-recapture models allowed Oro et al. (2008) to  
28  
29 quantify the positive relationship between attendance at restaurants and survival in  
30  
31 bearded vultures (*Gypaetus barbatus*), illustrating how prolonging population viability  
32  
33 can allow other harmful anthropogenic actions to be mitigated.  
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#### 40 41 **EFFECTS OF PAFS AT THE POPULATION LEVEL**

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43 Although a direct relationship between the availability of PAFS and population growth  
44  
45 rate is difficult to establish, several studies demonstrate that PAFS may increase  
46  
47 population density and size. For example, the density of wild canids such as coyotes  
48  
49 (*Canis latrans*) and jackals (*C. aureus*) is higher in human populated areas where food  
50  
51 from dumps is available (Fedriani et al. 2001); spatial confinement induces a reduction  
52  
53 of home range for individuals foraging at these PAFS. The population growth rates of  
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55 yellow-legged gull and rook (*Corvus frugilegus*) colonies are positively associated with  
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3 the increase in the total annual tonnage of the nearest dumps (Duhem et al. 2008;  
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5 Olea & Baglione 2008) (Fig. 3). The availability of middens and restaurants also explains  
6  
7 part of the variance recorded in the growth rate of populations of griffon vultures *Gyps*  
8  
9 *fulvus* (Parra & Tellería 2004) (Fig. 3). Lim et al. (2003) reported that anthropogenic  
10  
11 food was the cause of the dramatic (>30-fold) increase of the non-native house crow *C.*  
12  
13 *splendens* in Singapore over the previous 16 years (see further examples in Table S1).  
14  
15 Food experimentally supplied to pheasants (*Phasianus colchicus*) released for hunting  
16  
17 increases their densities, with different effects for males and females (53% and 67%  
18  
19 increase respectively) (Draycott et al. 2005). To test the effects of PAFS availability on  
20  
21 population size we combined the findings from independent studies on several species  
22  
23 of birds exploiting different PAFS to perform a random-effects meta-analysis (see Table  
24  
25 S3). We used the available information (10 studies) to extract or calculate coefficients  
26  
27 of determination ( $r^2$ ) between different indexes of population size (density, population  
28  
29 growth rate, abundance) and availability of PAFS (Table S3). Overall correlation  
30  
31 coefficient was 0.66 (95% CI: 0.53 - 0.76), indicating a strong association between  
32  
33 population size variation and availability of different PAFS (dumps, fishing discards,  
34  
35 crop residuals, carcasses from hunting, gutpiles, middens and restaurants), with a  
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37 small degree of uncertainty.  
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45 Some evidence indicates that the effects of PAFS on population dynamics of  
46  
47 opportunistic species can be especially large when habitat quality is poor and/or in  
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49 years with harsh environmental conditions (Peterson & Messmer 2011; Ruffino et al.  
50  
51 2012; Monsarrat et al. 2013). In highly productive ecosystems, it seems that PAFS are  
52  
53 mostly used by sub-optimal individuals (e.g., younger and inexperienced, in bad  
54  
55 physical condition), or by most individuals, but only in periods of relative food  
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3 shortage. Contrarily, the availability of large quantities of PAFS can have a negative  
4  
5 effect on population growth rates when ecological traps are created. For instance,  
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7 Morris (2005) showed that, paradoxically, experimental feeding stations aimed at  
8  
9 small rodents did not improve their demographic parameters and population growth  
10  
11 rates, because they faced increased predation risk from opportunistic carnivores,  
12  
13 which were also attracted to the feeding station.  
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15

16  
17 The supply of large amounts of food with high spatio-temporal predictability can  
18  
19 have strong effects on population structure and functioning. A regime shift to a new  
20  
21 equilibrium, with a higher carrying capacity, may result from an abrupt change in food  
22  
23 supply (Brook et al. 2013). Nevertheless very little data exist on regime shifts after the  
24  
25 appearance or loss of PAFS. Increased populations of migrating snow geese subsidized  
26  
27 by agricultural PAFS have caused abrupt changes in Arctic ecosystem structure and  
28  
29 biogeochemical cycling (Jefferies et al. 2006). The population dynamics of a colony of  
30  
31 yellow-legged gull exploiting PAFS from dumps showed three marked population  
32  
33 regimes: steady population growth (average 7.4% annual growth rate) over two  
34  
35 decades (1970's and 80's) occurring with an increase in the number of dumps,  
36  
37 followed by a stable phase (average 1.0% annual growth rate) around carrying capacity  
38  
39 since the early 1990's and a dramatic decrease following the closure of most dumps  
40  
41 (2006-2011, average 12.0% decline in annual growth rate)(Pérez et al. 2012).  
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47  
48 Understanding the resilience of populations to perturbations is a scientific challenge  
49  
50 attracting research interest, especially as anthropogenic perturbations are larger and  
51  
52 more frequent in recent centuries, adding to- or interacting with non-anthropogenic  
53  
54 sources of environmental stress. Some evidence supports the idea that subsidised food  
55  
56 increases population resilience against environmental perturbation and catastrophes.  
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3 Under adverse and harsh environments, individuals able to exploit PAFS can still  
4  
5 reproduce and survive with success (Martínez-Abraín et al. 2012). Ruffino et al. (2012)  
6  
7 found that population growth rates of black rats (*Rattus rattus*) inhabiting non-  
8  
9 subsidized habitats varied with environmental fluctuation, whereas rats in habitats  
10  
11 with PAFS maintained high growth rates during both good and harsh years.  
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14 Experimental approaches providing food on a relatively long-term basis found  
15  
16 increasing population numbers, as benefits mainly occur during bad seasons or years,  
17  
18 when densities should otherwise decrease (Taitt & Krebs 1981; Krebs et al. 1986; Robb  
19  
20 et al. 2008). Thus, the availability of PAFS might reduce the variance of demographic  
21  
22 parameters. If PAFS buffer the influence of environmental stochasticity (Bartumeus et  
23  
24 al. 2010; Cortés-Avizanda et al. 2012; López-López et al. 2013) this should have an  
25  
26 effect on extinction dynamics by increasing extinction time in closed populations  
27  
28 otherwise under the same conditions. This may be especially true in isolated patches  
29  
30 containing small populations relying mostly on PAFS, in which dispersal processes  
31  
32 between populations and rescue effects from sources are obstructed by landscapes  
33  
34 artificially fragmented by anthropogenic activities (Doherty & Grubb 2002). Therefore,  
35  
36 high availability of PAFS should decrease the variability of any biological or population  
37  
38 parameter (see Fraterrigo & Rusak 2008).  
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45 To test this hypothesis we analysed the association between a population variability  
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47 index (*PV*) and an index of discard availability around each patch (which depends on  
48  
49 the size and power of the trawling fleet within the foraging radii of each species) from  
50  
51 two opportunistic seabird species in the western Mediterranean (Audouin's *L.*  
52  
53 *audouinii* and yellow-legged gulls). A detrended *PV* value was calculated for 17 time  
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55 series (371 annual censuses corresponding to 13 sites) as:  
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$$PV = \log[\sigma(\text{residuals}\{\text{time vs } \ln\left(\frac{N_{t+1}}{N_t}\right)\})]$$

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 & Neatherlin 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 predator-prey interactions (Polis et al. 1997)(Fig. 2). Predation rates on 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 destabilizing or disrupting feedback should occur between predators sharing the same prey (Sanders et al. 2013).

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



1  
2  
3 instance, some populations of the same species exploit PAFS whereas other do not,  
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5 due to differences in habitat, or cultural and behavioural traditions that may generate  
6  
7 inter-population differences in social structure (Ramsay et al. 1997; Chilvers &  
8  
9 Corkeron 2001). Yet, individuals of the same population can show two distinct foraging  
10  
11 strategies, one opportunistic (exploiting mostly PAFS due to their abundance and  
12  
13 predictability) and one specialist (exploiting natural prey due to their higher energetic  
14  
15 composition)(Annett & Pierotti 1999). For example, some species considered  
16  
17 specialists have shown a great capacity to exploit PAFS. The Audouin's gull was  
18  
19 considered a specialist until two decades ago, even though it belongs to a taxonomic  
20  
21 group of opportunistic species, because 80% of its diet was composed of small pelagic  
22  
23 fish. Its "specialization" is constrained by having nocturnal vision, a particular  
24  
25 physiological ability owned by very few other seabirds. Nocturnal foraging activity was  
26  
27 linked to a temporal refuge from competition with the dominant, diurnal and  
28  
29 sympatric yellow-legged gull (Almaraz & Oro 2011). Nevertheless, Audouin's gulls have  
30  
31 learnt to exploit discards from the diurnal trawling fleet, from which they can obtain  
32  
33 up to 70% of its diet. During winter, birds have also been observed foraging at dumps,  
34  
35 a behaviour never recorded prior to two decades ago (Table S1).  
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43 Recent studies on invasive species arriving in a novel environment and exploiting  
44  
45 new foraging resources (included PAFS) are good examples of behavioural plasticity  
46  
47 (Lim et al. 2003), especially those species that have life-history strategies prioritising  
48  
49 future rather than current reproduction (Sol et al. 2011). The range of personalities  
50  
51 across individuals and species that take advantage of PAFS may be greater than  
52  
53 originally thought. Behavioural plasticity may be sped up by cultural innovation  
54  
55 performed by individuals shifting to opportunistic behaviour, followed by  
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3 improvements in foraging efficiency and breeding performance (Price et al. 2003). For  
4  
5 instance, Annett & Pierotti (1999) found that lifetime reproductive success of  
6  
7 opportunistic western gulls (*L. occidentalis*) was positively correlated with individuals  
8  
9 foraging on fish in contrast to individuals mostly foraging on dumps, and that diet  
10  
11 choice is passed between generations by learning or cultural transmission.  
12  
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14       Apart from species-specific ability at exploiting PAFS, another source of variability  
15  
16 may occur at the spatial scale. Within the distribution range of a species, population  
17  
18 heterogeneity on the availability of PAFS and their exploitation (values ranging  
19  
20 between 0-80% of the diet depending on the population, see Table S1) may alter  
21  
22 metapopulation functioning (see Fig. 2). Patches with large PAFS increase their carrying  
23  
24 capacity and this may reduce emigration and promote immigration from non-  
25  
26 subsidized patches, especially in social species (Carrete et al. 2006; Martínez-Abraín et  
27  
28 al. 2012; Monsarrat et al. 2013). Inter-population differences generate variation in  
29  
30 body size and weights, demographic parameters and differences in density-dependent  
31  
32 population dynamics (Table S1). Dumps can modify the spatial distribution of  
33  
34 scavenging birds and carnivores by clustering their breeding territories around dump  
35  
36 sites (Kristan & Boarman 2007; Bino et al. 2010)(Table S1). Although little is known  
37  
38 about how species may compete when selecting breeding habitat close to PAFS,  
39  
40 competition for breeding habitat can also be dominated by larger and predatory  
41  
42 species, with highly developed agonistic behaviours, forcing subordinate species to  
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44 increase time switching between breeding and foraging patches.  
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#### 55 **INFLUENCE OF PAFS ON COMMUNITIES AND ACROSS ECOSYSTEMS**

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3 Increasing population densities in species exploiting PAFS alter ecosystems in different  
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5 ways (Fig. 2), as reciprocal interactions (e.g. competition, predation) are inevitably  
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7 modified (see Fig. 6). These changes can result in cascading effects across non-adjacent  
8  
9 trophic levels, pervading whole ecosystems, with potential impacts on stability,  
10  
11 flexibility and persistence (Fig. 2). For instance, the snow goose (*Chen caerulescens*)  
12  
13 exploits crop leftovers in North America and has become an “over-abundant” species.  
14  
15 As a result, geese have altered the structure and species composition of plant  
16  
17 communities in both the wintering and the breeding grounds, and they transfer large  
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19 amounts of nutrients from agro-ecosystems to natural systems (e.g. Jefferies et al.  
20  
21 2004, see also Table S1). Subsidized ungulate populations can also trigger cascade  
22  
23 effects on a range of organisms through food-webs (Table S1). Supplementary food  
24  
25 increases ungulate populations, altering their browsing impact on vegetation, affecting  
26  
27 plant species richness and composition, primary productivity, habitat structure and  
28  
29 nutrient cycling. These changes cascade through bird, mammal and insect  
30  
31 communities (Table S1), although effects also vary between habitats and  
32  
33 environmental conditions (Parsons et al. 2013). Subsidized moose (*Alces alces*)  
34  
35 populations had both positive and negative effects on different functional groups of  
36  
37 birds, with zero net effect on their species richness and abundance; insect richness  
38  
39 increased with increased moose densities (see Mathisen 2011 and references therein).  
40  
41 At the same time, subsidized ungulates can also propagate disease and parasites  
42  
43 between conspecific populations or to domestic livestock. Increasing ungulate  
44  
45 populations may attract predators (i.e. carnivores) and boost their densities,  
46  
47 consequently depressing alternative prey abundance (such as reptile and avian  
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49 species, see e.g. Janzen 1976; Cooper & Ginnett 2000), a phenomenon known as  
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3 hyperpredation. Hyperpredation also occurs when PAFS are exploited directly by  
4  
5 predators modifying predator-prey relationships. The increase of yellow-legged gull  
6  
7 populations subsidized by dumps and fishing discards increases predation rates on  
8  
9 sympatric Audouin's gulls and European storm petrels (*Hydrobates pelagicus*), among  
10  
11 many other vulnerable waterbirds (see Table S1). Similar examples are subsidized killer  
12  
13 whales (*Orcinus orca*), ravens (*Corvus corax*) and mesocarnivores, and their higher  
14  
15 predation rates on Steller sea lions (*Eumetopias jubatus*), desert tortoise (*Gopherus*  
16  
17 *agassizii*) and capercaillie (*Tetrao urogallus*) respectively (Table S1). Invasive predators  
18  
19 increase predation rates on native taxa through hyperpredation, e.g., rats and  
20  
21 mongoose preying on seabird and turtle nests respectively (Table S1).  
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27 Fishing discards also illustrate how PAFS influence communities and ecosystems, by  
28  
29 affecting a range of ecological processes, trophic levels and even different ecosystems  
30  
31 (Fig. 5). Discards are exploited by a large number of organisms, from top predators  
32  
33 (such as cetaceans, sharks, sea turtles and albatrosses) to invertebrates (such as crabs,  
34  
35 crustaceans, amphipods and isopods)(see Table S1) and covering different zones or  
36  
37 habitats (e.g. sea surface, pelagic and benthic). "Horizontal" interactions (i.e.  
38  
39 competition and predation within guilds or trophic levels) are often as important as  
40  
41 "vertical" (i.e. between trophic levels) interactions (Fig. 5). In the benthic layer  
42  
43 different forms of competition (both resource and interference) and predator-prey  
44  
45 relationships are exacerbated within and between invertebrate and fish communities  
46  
47 exploiting discards arriving at the sea bottom. Complexity increases as some of these  
48  
49 species are unselectively targeted by the same trawling fleet that generates the  
50  
51 discards. Competition and predation may also occur within communities of subsidized  
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53 pelagic and aerial predators (see previous section), as well as hyperpredation on  
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3 pelagic prey (e.g. clupeids, squid) and on obligate piscivorous seabirds (Fig. 5). Among  
4  
5 opportunistic predators, seabirds have particular impacts on food webs and ecosystem  
6  
7 functioning, including the transport of nutrients between biomes (Fig. 5). Seabirds are  
8  
9 very mobile and switch between marine foraging and terrestrial breeding habitats.  
10  
11 Many seabird species exploit discards from fisheries and this has been one of the main  
12  
13 causes of the high population growth rates experienced over recent decades (e.g.  
14  
15 Votier et al. 2004). Such population growth has increased the movement of nutrients,  
16  
17 detritus and pollutants between marine and terrestrial biotopes, altering both  
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19 ecosystems (Polis et al. 1997; Caut et al. 2012), even affecting remote and relatively  
20  
21 pristine habitats (Blais et al. 2005). Seabird movement has led to increases in ammonia  
22  
23 emissions (Wilson et al. 2004) and transference of heavy metals and other pollutants  
24  
25 such as DDT (Blais et al. 2005). Impacts can also occur in the marine zones  
26  
27 surroundings seabird colonies by changing species composition and the growth of  
28  
29 keystone species such as seagrasses, with consequences for fish, invertebrates and the  
30  
31 entire marine community structure (Powell et al. 1991)(Fig. 5). Seabirds can also  
32  
33 increase nitrogen inputs in relatively simple food webs, such as islands, triggering  
34  
35 cascading effects: initially altering vegetation structure and plant species turnover at  
36  
37 the expense of native taxa (Vidal et al. 2000; van der Wal et al. 2008; Baumberger et al.  
38  
39 2012), in turn affecting beetle and vertebrate communities by favouring certain  
40  
41 assemblages (Orgeas et al. 2003; Schmitz 2003; Caut et al. 2012). Some opportunistic  
42  
43 seabirds (e.g. gulls) can act as seed dispersers from autochthonous as well as invasive  
44  
45 plants (see Table S1), although the impact of this process on plant communities is little  
46  
47 known. Finally, the changes in vegetation structure and density caused by increased  
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49 nutrient inputs from subsidized seabirds may alter their own breeding habitat,  
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3 favouring some species over others and generating differential dispersal processes at  
4  
5 intra- and inter-specific levels.  
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7 The wide range of ecosystem consequences from fisheries discards highlights the  
8  
9 influence of PAFS on community and food-web organization. Omnivores (species  
10  
11 feeding on more than one trophic level) have the potential to directly exploit most  
12  
13 types of PAFS as well as predating on lower trophic-level species that also exploit these  
14  
15 PAFS (Fig. 5). Omnivores can therefore exert a larger influence on ecosystem control  
16  
17 than specialist and lower trophic-level foragers (Morris 2005). Thus, top-down control  
18  
19 can increase at the expense of bottom-up regulations in ecosystems subsidized by  
20  
21 PAFS, yet the potential consequences for the stability and functioning of these  
22  
23 ecosystems remain poorly understood (Ostfeld & Keesing 2000).  
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28 What are the potential effects of PAFS on diversity? An increase of food supply  
29  
30 should decrease competition (scramble and interference) allowing the incorporation of  
31  
32 new species to, or persistence of existing species in the ecosystem. However, an  
33  
34 increase of food availability (through PAFS) does not always increase species richness:  
35  
36 when interference competition at PAFS is light, because it occurs in relatively low  
37  
38 trophic levels (e.g. small passerines), richness remains stable and only population  
39  
40 densities increase (Fuller et al. 2008). When interference competition occurs with  
41  
42 dominant species monopolizing PAFS (within and between guilds), species diversity at  
43  
44 local patches decreases by promoting displacement, dispersal and extinction of  
45  
46 subordinate species (Cortés-Avizanda et al. 2012). As highlighted above, the cascading  
47  
48 effects recorded in simple ecosystems (such as small islands) driven by subsidized gull  
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50 populations also suggest that PAFS can drive ecosystem simplification, reducing plant,  
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52 beetle and mammal community diversity in breeding grounds.  
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## 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. Individual response to predictable and abundant food supplies can be fast (Badyaev 1998). Substantial changes in home-range, density and survival probability in carnivores visiting dumps, for example, can occur in a matter of months (Beckmann & Berger 2003; Bino et al. 2010). Over longer time-scales, carnivores can increase their body size by exploiting new types of PAFS, and such increase is larger 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 colonized 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 colonize a previously inhospitable environment. These birds have genetically diverged from the Iberian donor population, a process that took place rapidly (less than 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

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3 to differentiation, even for species with long generation time. Recently Axelsson et al.  
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5 (2013) found evidence that domestic dogs differentiated from the wolf due to their  
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7 increasing commensalism with humans. For subsidized polygamous ungulates, key  
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9 elements in sexual selection, such as female aggregation and mean harem size, can be  
10  
11 affected by PAFS with potential consequences at evolutionary level (Table S1). In these  
12  
13 species, PAFS can also reduce selection pressure in the first year of life (Schmidt & Hoi  
14  
15 2002). PAFS provided to ungulates to increase hunting rates moved wild evolutionary  
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17 traits closer to those associated to a semi-domestic state affecting both natural and  
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19 sexual selection (Myrsterud 2010).  
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24 PAFS can also improve the survival prospects of individuals in poor condition (either  
25  
26 by genetic weakness or physiological constraints) and relax selection pressures  
27  
28 (Carrete et al. 2009; Genovart et al. 2010) with consequences at the population level:  
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30 increases in population size can happen at the cost of an average drop in phenotypic  
31  
32 and genetic quality (Parvinen 2005). Furthermore, the poor food quality and the  
33  
34 pollutants and pathogens associated with some PAFS, such as those obtained from  
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36 dumps, bird feeders or from certain fishery discards (Österblom et al. 2008; Carrete et  
37  
38 al. 2009) can cause the appearance of sick and obese individuals, with reduced abilities  
39  
40 to escape from predators (Carrete et al. 2009; Genovart et al. 2010). The low quality of  
41  
42 some food obtained from PAFS can generate additional fitness costs, such as lower  
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44 lifetime reproductive success (e.g. Annett & Pierotti 1999).  
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## 52 **CONCLUSIONS AND FUTURE DIRECTIONS**

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54 Humans waste enormous amount of food (see Table 1 and Fig. 1) that are available to  
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56 and exploited by a large number of organisms across ecosystems, from decomposers  
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3 (e.g., bacteria and fungi) to herbivores and tertiary consumers (e.g., whales, top  
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5 predators such as wolves). In some cases, food is voluntarily provided to improve  
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7 individual survival and increase populations of endangered species; of common but  
8  
9 emblematic species (e.g. urban passerines in industrialized countries); and of game  
10  
11 species (mainly wild ungulates)(see Table S1). Since different species can benefit from  
12  
13 different PAFS, and those PAFS offer differential amounts of food (Tables 1 and 3), the  
14  
15 consequences at community and ecosystem levels may differ among PAFS. Dumps,  
16  
17 where millions of tones of food are wasted worldwide and represent the major global  
18  
19 source of PAFS (see Table 1), are exploited by ca. 20% and 30% of Orders of birds and  
20  
21 mammals respectively (Table 3), providing a rough idea of the importance of PAFS on  
22  
23 ecosystems. Dumps are mainly exploited by secondary (especially meso-carnivores and  
24  
25 omnivores) and tertiary consumers (especially top predator carnivores), so their main  
26  
27 effects are likely hyperpredation rates on herbivores and a consequent release of  
28  
29 primary consumption on plants. Such unbalancing of the food chains can be especially  
30  
31 relevant when PAFS have a worldwide distribution and provide large quantities of  
32  
33 food, as is the case also for fishing discards and for crop residuals in marine and  
34  
35 terrestrial ecosystems respectively (Table 3). However, the net balance of PAFS on  
36  
37 ecosystems is far from being understood, especially as some PAFS simultaneously  
38  
39 benefit many trophic levels (Fig. 5) and also because some PAFS, coincident in space  
40  
41 and time, benefit different food chain consumers (e.g., dumps for carnivores and crop  
42  
43 residuals for herbivores). At the same time, human harvesting (e.g., hunting, fishing,  
44  
45 whaling) has reduced large apex predator populations in food webs. The balance of  
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47 human activities at different trophic levels (including mutualists and parasites)  
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49 constitutes a challenge for future research.  
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3 We have focused here on the most conspicuous forms of food subsidies from  
4 humans. PAFS influence animal ecology at individual, population and ecosystem levels,  
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6  
7 with indirect effects on plant communities and their functioning, although the  
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9  
10 complexity of natural systems hinders understanding of the exact nature of these  
11  
12 changes. Even though PAFS may have opposing effects (e.g., an increase in survival and  
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14 breeding performance and an associated increase in pathogen spread), the  
15  
16 demographic balance at the population level is an increase in population size and the  
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18 ecological consequences at community and ecosystem levels (e.g., hyperpredation,  
19  
20 alteration of consumer-resource relationships and food webs).  
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24 Apart from the PAFS described here, there are a range of other food sources deriving  
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26 from anthropogenic activities, such as invasive and translocated species becoming prey  
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28 for native predators (e.g. Tablado et al. 2010), animal and vegetal remains wasted in  
29  
30 fish- and agricultural farms and campgrounds (Marzluff & Neatherlin 2006; Margalida  
31  
32 et al. 2010), wildlife casualties from roads and windfarms, the feeding of feral cats and  
33  
34 dogs or nutrients from sewage, all of which also alter ecosystem functioning. Some of  
35  
36 these alterations can affect human welfare, such as the increased risk of rabies spread  
37  
38 associated with the increase in vampire bats following the dramatic growth of livestock  
39  
40 farming in the Americas (Jones et al. 2013).  
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45 Given the rapid and strong ecosystem impact of PAFS, they also have potential as a  
46  
47 powerful management tool in conservation and social issues. Subsidised food can be  
48  
49 used to redistribute species, diminishing human-wildlife conflicts (Sahlsten et al. 2010;  
50  
51 Kaplan et al. 2011; Martínez-Abraín et al. 2012). PAFS can limit population declines of  
52  
53 endangered species, especially when natural food sources are diminished due to other  
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55 anthropogenic causes (e.g. the Iberian lynx *Lynx pardinus* and rabbits, the California  
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3 condor *Gymnogyps californianus*) (Table S1). PAFS can also decrease the negative  
4  
5 impacts of other human activities, for instance by delaying or compensating the  
6  
7 negative effects of anthropogenic mortality (e.g. poison, windfarm collisions, fisheries  
8  
9 bycatch mortality) (Oro et al. 2008; Laneri et al. 2010; Martínez-Abraín et al. 2012).  
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11 Despite this potential for conservation, PAFS arguably reduce natural sources of  
12  
13 selection pressure by reducing intra-specific competition, which may dilute traits that  
14  
15 are important for the persistence and resilience of small populations.  
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19 Future research directions include the study of common life-history characteristics or  
20  
21 cultural features of species or populations exploiting PAFS, to increase our ability to  
22  
23 predict changes in ecosystems due to the appearance or loss of PAFS. Oro et al. (2008)  
24  
25 forecast population extinction probabilities for the bearded vulture in the event that  
26  
27 food originating from humans was no longer available; a situation that could arise  
28  
29 following the application of environmental policies following the 'mad-cow' BSE crisis  
30  
31 in Europe (Margalida et al. 2010; Martínez-Abraín et al. 2012). Some large-scale studies  
32  
33 covering the effects of different availability of PAFS on population growth rate also  
34  
35 allow population prediction in the absence of these PAFS (Fig. 3). Forecasting can be  
36  
37 important when species exploiting PAFS are considered pests or endangered species.  
38  
39 In industrialized countries, some PAFS (e.g. dumps, fishing discards, restaurants) can  
40  
41 be curtailed by environmental regulations. Beyond the population decline for directly  
42  
43 affected pest and vulnerable species, alterations in food webs and ecosystems are to  
44  
45 be expected (Bicknell et al. 2013). More precisely, environmental policies now regulate  
46  
47 many human activities, aiming to prevent overharvesting and encourage the recycling  
48  
49 of waste food. Such regulations constitute natural experiments with food availability to  
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51 study its importance on ecological processes at population and ecosystem levels, such  
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3 as resilience, extinction thresholds, competition and extinction cascades, by comparing  
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5 subsidized and non-subsidized systems or systems before and after being subsidized.  
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7 To our knowledge, little theoretical work has specifically explored the impact of PAFS  
8  
9 on population and ecosystem stability. One related study illustrates that the addition  
10  
11 of biomass to a target species through artificial stocking can destabilise model  
12  
13 communities, in some cases leading to the extinction of non-target species (Enberg et  
14  
15 al. 2006).  
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19 How will those populations heavily exploiting PAFS behave, once they are no longer  
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21 available? We predict there is a serious risk that those populations will decline to even  
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23 smaller sizes than before the appearance of PAFS, at least until stability around a new  
24  
25 dynamic equilibrium occurs. Transient dynamics between two distinct equilibrium  
26  
27 population states (with and without availability of PAFS) should be rapid because the  
28  
29 two equilibrium points represent two different 'environments' and also because the  
30  
31 perturbation of ending PAFS will likely be of considerable magnitude. The role of those  
32  
33 transient dynamics on the ability of species, communities and ecosystems to buffer  
34  
35 against perturbations requires further investigation. Margalef (1997) suggested that  
36  
37 the demographic transition in human populations shows a decreasing trend in the  $P/B$   
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39 ratio (primary production/biomass) as we have increased our ability to buffer against  
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41 unpredictable perturbations. This may lead (by cultural means) to a pattern of control  
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43 of reproduction similar to that shaped by evolution in eusocial insects (e.g., behavioral  
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45 sterility of larvae and workers). The evidence we have presented highlighting the  
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47 capacity of PAFS to decrease population variability over time (e.g., Fig. 4), suggests that  
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49 this pattern should be further explored especially in species that have a long history of  
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51 exploiting PAFS. Comparison of subsidized and non-subsidized ecosystems can help  
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3 predict changes in diversity and ecosystem services on top of the impact of other  
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5 agents of global change. The recent appearance of scientific journals dealing with  
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7 human activities and their effects on the functioning of ecosystems, such as *Urban*  
8  
9 *Ecology* or *Human Dimensions of Wildlife*, suggest an increasing awareness of the  
10  
11 importance of these relationships. PAFS have altered many species' dynamics,  
12  
13 cascading across multiple levels of organisation, from individuals to communities and  
14  
15 ecosystems. As humans now start to alter and restrict the availability of a range of  
16  
17 PAFS, we must be prepared to mitigate against unwanted impacts on species of  
18  
19 economic and conservation importance.  
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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 et al. 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 95–115 kg/year and 6–11 kg/year in sub-Saharan Africa and South/Southeast Asia	Parfitt et al. 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 U.S.A., ca. 315kg/ha of chopped corn stovers are left in the fall to prevent soil water evaporation and runoffs	Foley <i>et al.</i> 2011 <a href="http://data.worldbank.org">http://data.worldbank.org</a>
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 2008
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	<a href="http://faostat3.fao.org/">http://faostat3.fao.org/</a>
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 et al. 2008
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	<a href="http://www.michigandnr.com/pdfs/huntingwildlifehabits.pdf">http://www.michigandnr.com/pdfs/huntingwildlifehabits.pdf</a> ; see also reference
Carcasses from	In the USA, there are ca. $11 \cdot 10^6$ big game hunters discarding ca. $6,9 \cdot 10^5$ tonnes of carcasses	U.S. Fish & Wildlife Service 2008

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tonnes of carcasses (e.g., deer, elk) in the field each year

([http://wsfrprograms.fws.gov/nationalSurvey/nat\\_survey/](http://wsfrprograms.fws.gov/nationalSurvey/nat_survey/))

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**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.

Type of PAFS	Parameter recorded		Differences in individual use
	Individual level	Population level	
Dumps	Body condition	Population size/	Sex
	Reproductive parameters	Densities	Age
	Spatial distribution/home range		Personality
Fishing discards	Reproductive parameters	Population size/	Sex
	Spatial distribution/home range	Densities	
		Dispersal	
Middens and restaurants	Survival	Population size/	Age
	Reproductive parameters	Densities	Personality
	Spatial distribution/home range	Dispersal	
Crop residuals	Body condition	Population size/	
	Survival	Densities	
	Reproductive parameters		
	Spatial distribution/home range		

Bird feeders	Body condition	Population size/	
	Survival	Densities	
	Reproductive parameters		
	Spatial distribution/home		
	range		
Feeding stations	Body condition	Population size/	Sex
for game species	Survival	Densities	Personality
	Reproductive parameters		
	Spatial distribution/home		
	range		
Gutpiles and	Spatial distribution/home		
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**Table 3** Comparison of different types of PAFS depending on their distribution, human intentionality, amounts of food (in terms, see also Table 1), predictability and biomes and trophic levels affected. The percentage of taxonomic Orders of birds 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
Dumps	Worldwide	Very high	No	Spatial and temporal	Terrestrial; nutrient transfer to coastal	From top predators
Fishing discards	Worldwide	High	No	Spatial and temporal	Marine; nutrient transfer to coastal	From top predators

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Middens and restaurants	Worldwide and mainly in industrialized countries, respectively	Locally medium	Only for restaurants (avian scavengers)	Mainly spatial	Terrestrial	Produ secon consu and to preda
Crop residuals	Mainly in industrialized countries	High	No	Spatial and temporal	Terrestrial	Mainl herbiv
Bird feeders	Industrialized countries	Low and local	Yes	Spatial and temporal	Terrestrial	Herbi
Feeding stations for game species	Mainly in industrialized countries	Locally high	Yes	Spatial and temporal	Terrestrial	Mainl herbiv
Gutpiles and	Where large wild	Locally high	No	Spatial	Terrestrial	Produ

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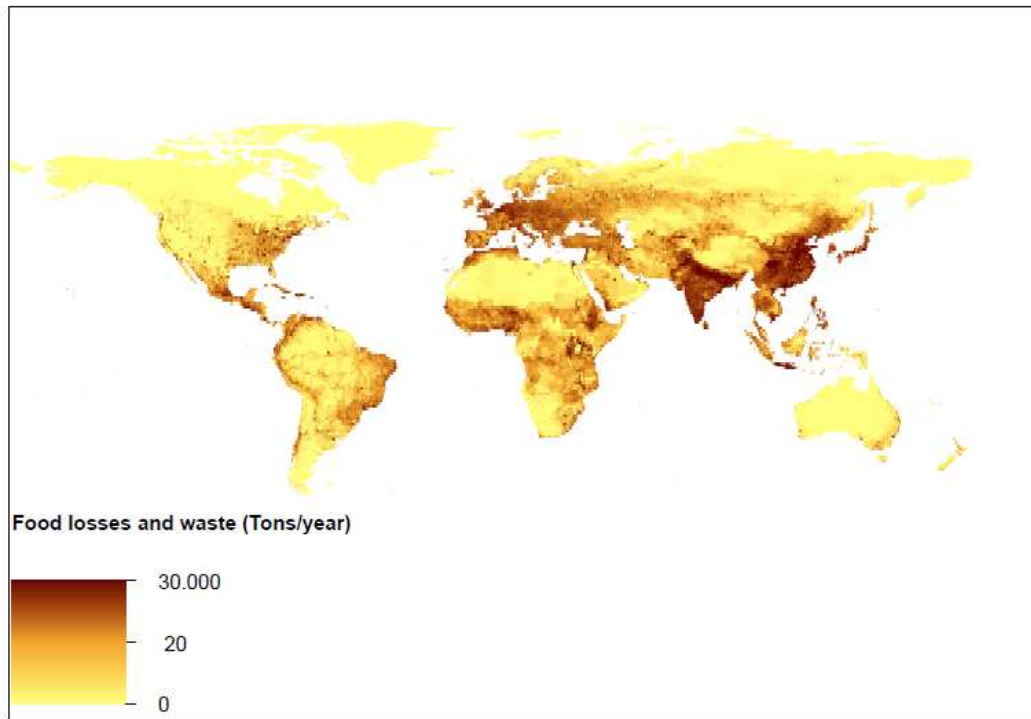
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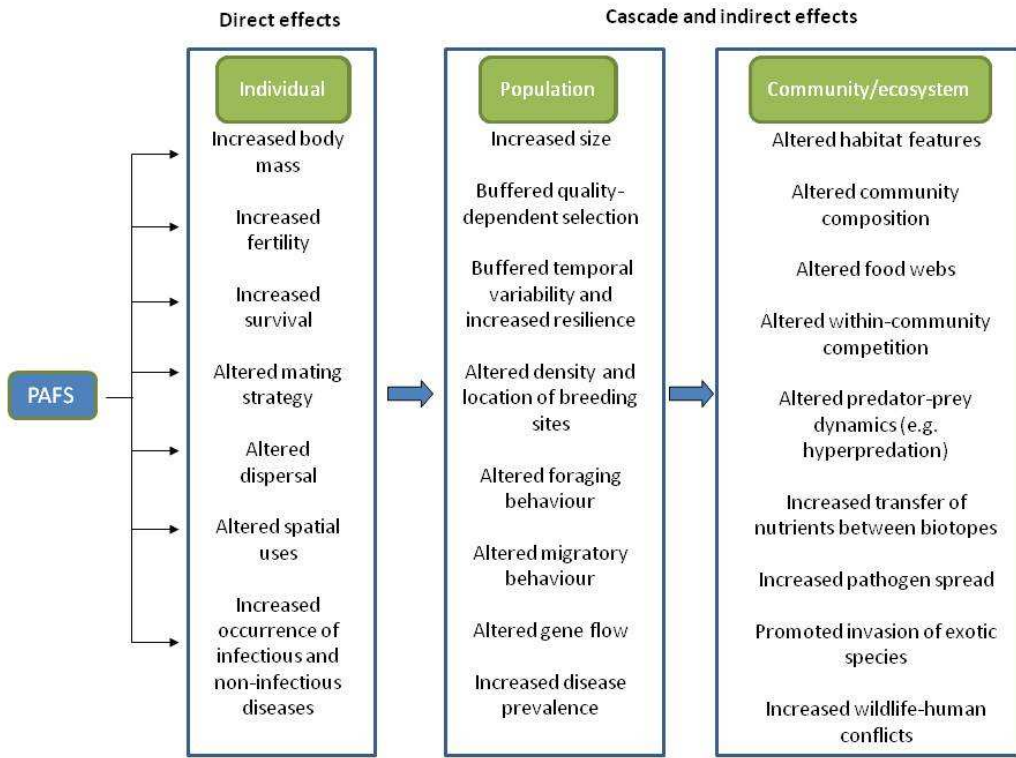


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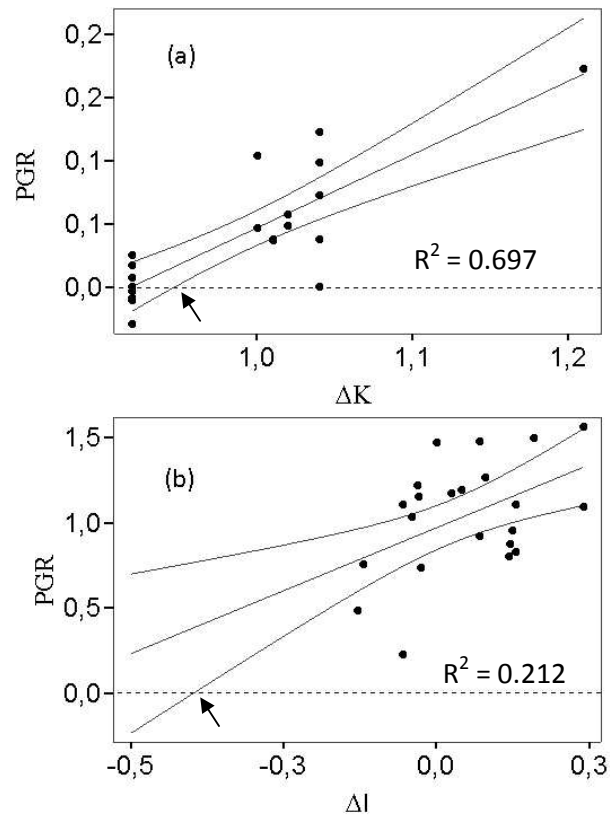
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Figure 2



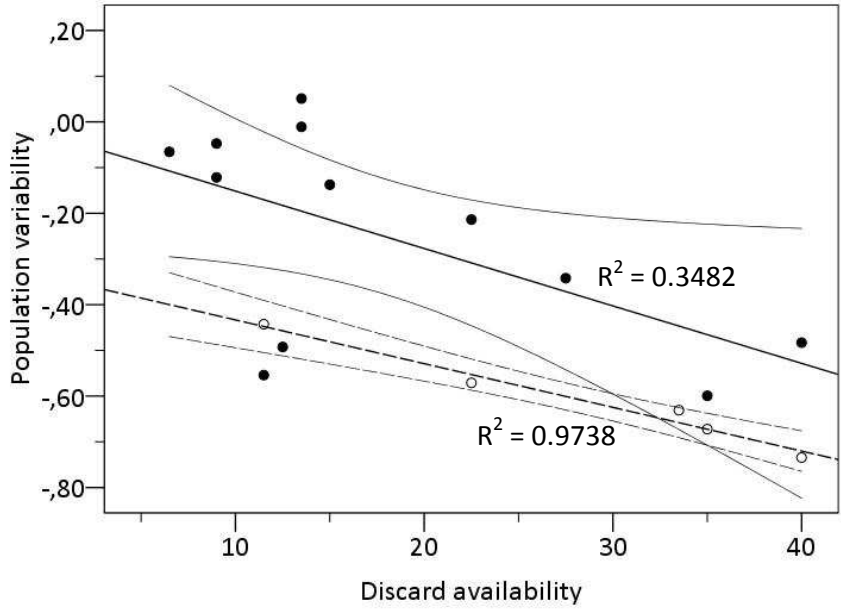
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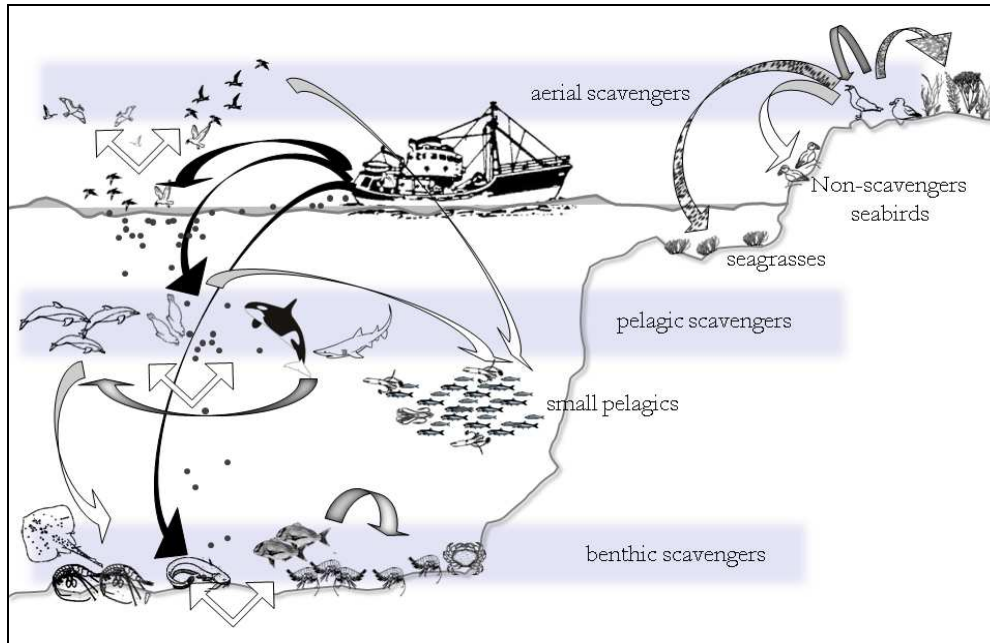
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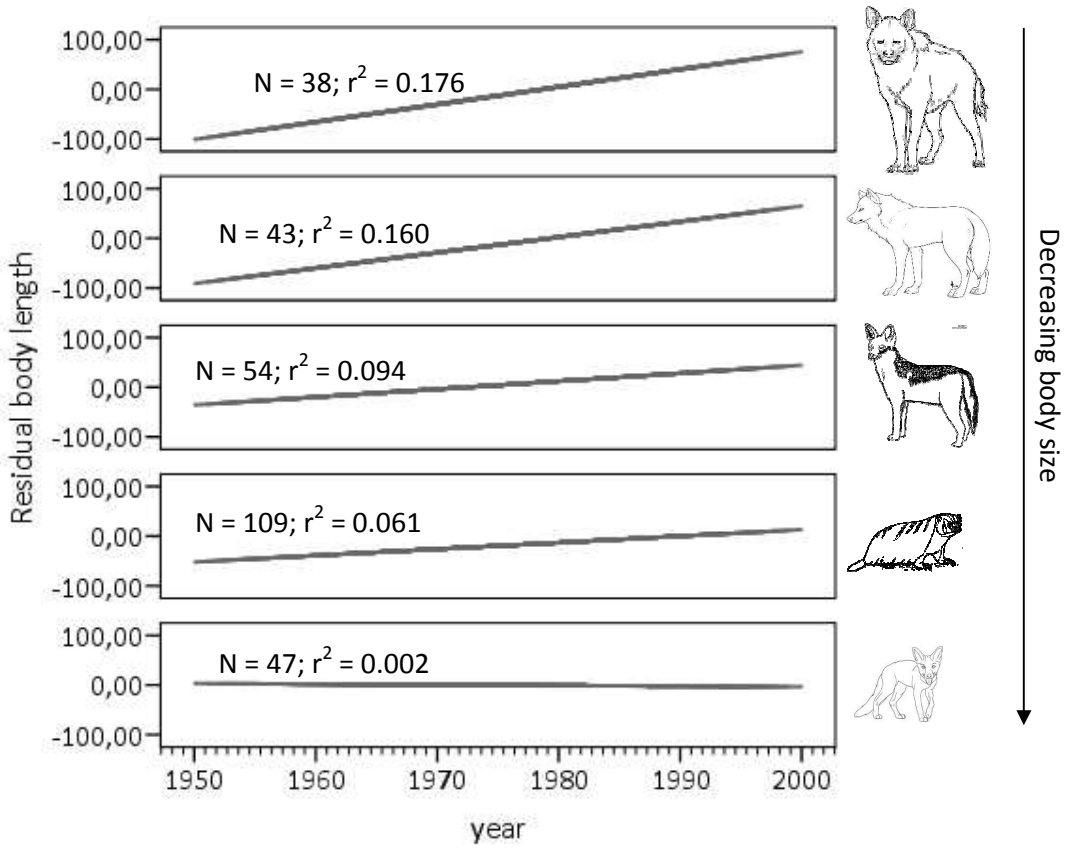


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Figure 6



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4 **Figure 1** Food losses and waste (Tons/year on a log scale) from human food  
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6 production. Data obtained from <http://faostat3.fao.org/> (wasted food by country)  
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8 <http://sedac.ciesin.columbia.edu/data/dataset/grump-v1-population-count> (human  
9  
10 population density in 2000 in a 30" longbow grid). Technical considerations are  
11  
12 described in Appendix S4.  
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16 **Figure 2** Effects of PAFS at individual, population, community and ecosystem levels. For  
17  
18 a list of references and quantitative details on each of these effects, see Table S1.  
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21 **Figure 3** Association between PAFS availability and population growth rate (PGR,  
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23 expressed as  $\ln(N_{t+1}/N_t)$  in: a) yellow-legged gull colonies in southern France and an  
24  
25 index of dump availability ( $\Delta K$ , calculated as the ratio between the annual tonnage of  
26  
27 the nearest dump and its distance to each colony) between 1982 and 2000; and b)  
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29 Spanish populations of griffon vultures and the variation of livestock biomass ( $\Delta I$ , as a  
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31 proxy of PAFS availability in the form of middens and restaurants) between 1989 and  
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33 1999. Data in panels a) and b) are adapted from Duhem et al. (2008) and Parra &  
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35 Tellería (2004) respectively. Regression lines (and their 95% CI) are shown. Dashed  
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37 lines indicate a stable population equilibrium (i.e. PGR = 0) and arrows point to the  
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39 level of PAFS at which populations should stop growing or declining.  
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45 **Figure 4** Discard availability has a significant, negative effect on the variability of  
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47 detrended per-capita growth rates in Audouin's (solid circles, line;  $P = 0.0434$ ) and  
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49 yellow-legged gulls (open circles, dashed line;  $P = 0.0018$ ). Regression lines (and their  
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51 95% CI) are shown: solid for Audouin's gulls and dashed for yellow-legged gulls. A  
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53 higher mean availability of discards stabilises population fluctuations.  
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3 **Figure 5** Conceptual model of a range of effects of PAFS at population, community and  
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5 ecosystem levels using fisheries discards as an example. Five types of ecological  
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7 processes are represented: 1) foraging exploitation of discards by the three main  
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9 communities of scavenging organisms (shown by black arrows); 2) predation within  
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11 communities (shadow grey arrows); 3) competition (both resource and interference)  
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13 within communities (double white arrows); 4) hyperpredation (white arrows), and 5)  
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15 transfer of nutrients (stained arrows). Species illustrations are not drawn to scale.  
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19 **Figure 6** Temporal trend (only fitted regression lines are shown) in residual body length  
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21 in five species of carnivores commensal with humans in Israel following an increase in  
22  
23 the availability of PAFS (garbage dumps, livestock carcasses in middens, crop residuals)  
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25 during 1950-2000. Species are sorted by body size from top to down: spotted hyena,  
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27 wolf, golden jackal, European badger and fox. Note that correlation coefficients  
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29 decrease with body size and are all statistically significant except for the fox. Adapted  
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31 from Yom-Tov (2003).  
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