

1 **Seabird influence on ecological processes in coastal marine ecosystems: an**  
2 **overlooked role?**

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14 **Abstract**

15 Seabirds are vital components of coastal ecosystems and connect marine and terrestrial  
16 systems at a global scale, significantly contributing to inter-habitat connectivity and the  
17 ecological dynamics of the recipient systems. By exhibiting a wide range of ecological  
18 functions, seabirds can contribute to shape coastal ecological processes in a multitude of  
19 ways, among which directly influencing trophic status, environmental contamination,  
20 biodiversity and food webs through trophic (bottom-up or top-down) and non-trophic  
21 processes. Although the ecological and functional role of birds in terrestrial areas, islands in  
22 particular, has been deeply studied since the last century, the same does not hold true for  
23 coastal area. Since coastal areas have a crucial economic and ecological role worldwide  
24 and, at the same time, are highly vulnerable, looking into the role of seabirds in influencing  
25 the ecosystem functioning in coastal areas is needed nowadays. Here, we review the current  
26 knowledge regarding the influence of seabirds on coastal ecological processes highlighting

27 knowledge gaps, with particular emphasis on the avian ecological functions that are crucial  
28 in influencing the ecosystem processes and functioning and, therefore, their influence on  
29 the provision of ecosystem services and goods for the human well-being.

30

### 31 **Keywords**

32 Aquatic birds, waterbirds, allochthonous input, ecological functions, ecosystem services

33

### 34 **1. Introduction**

35 Seabirds live or spend part of their lives in marine coastal systems where play a wide range  
36 of ecological functions and provide a multitude of ecosystem services (Green and Elmberg,  
37 2013; Sekercioglu, 2006). Nevertheless, they are rarely perceived as real components of  
38 the ecosystems probably because they are not permanently settled in coastal systems but,  
39 instead, they move between terrestrial and coastal systems at different spatial scales, i.e.  
40 local, regional, up to inter-continental (Lundberg and Moberg, 2003). Coastal systems are  
41 preferential stop-over and nesting sites for a wide variety of migrating waterbirds, among  
42 which seabirds, with well-diversified ecological and trophic roles. Historically, research on  
43 seabirds has focused on the seabirds themselves, their physiology, reproductive and  
44 migration patterns, and was rarely ecologically-oriented. Moreover, many studies focused  
45 on seabird sensitivity to anthropic impact and seldom the perspective was opposite, that is  
46 looking at the impact of seabirds on coastal ecosystems. However, awareness is growing,  
47 today, that seabirds may influence the functioning of ecosystem processes and the provision  
48 of ecosystem services and goods, especially because of their pulsed movements through  
49 which they redistribute resources among systems.

50 Although the early ecologically-oriented studies were carried out in coastal areas (Bédard  
51 et al., 1980; Bosman et al., 1986; Bosman and Hockey, 1988, 1986; Delille, 1987; Ganning

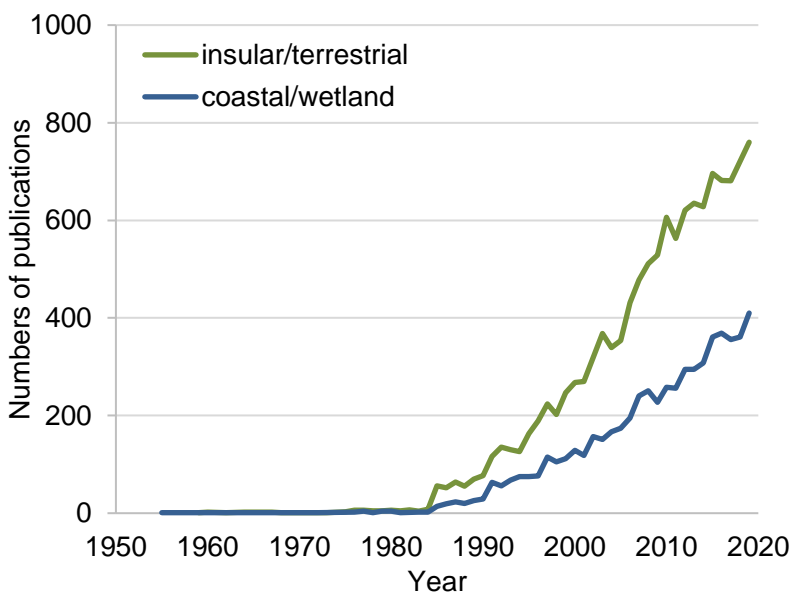
52 and Wulff, 1969; Golovkin, 1967; Golovkin and Garkavaya, 1975), the following pivotal  
53 studies of Gary A. Post and colleagues in the Gulf of California islands (Anderson and Polis,  
54 1999; Polis et al., 1996, 1997; Polis and Hurd, 1995, 1996; Sanchez-Pinero and Polis, 2000;  
55 Stapp et al., 1999) laid the basis of a wide line of research about the effects of seabirds on  
56 terrestrial island systems. As a result, much more studies have been carried out so far in  
57 insular systems than in coastal systems. A recent search in Web of Science platform using  
58 the search string “(seabird\* OR waterbird\* OR shorebird\*) coupled with another string that  
59 limited the research to terrestrial insular areas (soil\* OR land OR terrestrial OR island\* OR  
60 insular) reported 12 434 published papers from 1950 to 2019. If the same generic string was  
61 coupled, instead, with another string that limited the research to coastal areas (coast\* OR  
62 wetland\* OR estuar\* OR lagoon\* OR pond\* OR rockpool\* OR bay) the results have been  
63 halved (n: 5977). The temporal trend of both searches is overall similar and revealed a  
64 significant increase of the interest in these matter since the ‘80s but also a growing gap  
65 between terrestrial- and coastal-focused studies (Fig. 1). Green and Elmberg, (2013)  
66 reviewed the ecological functions and services provided by waterbirds in general, and a  
67 number of provisioning, supporting, regulating and cultural services were listed. However,  
68 most information is related to the effects of waterbirds on islands and, to a much lesser  
69 extent, to coastal ecosystems.

70 Coastal systems worldwide are highly heterogeneous from a geomorphological and  
71 hydrological point of view, highly variable and unstable from a physico-chemical standpoint,  
72 and highly complex from an ecological point of view. Moreover, they are of great relevance  
73 because of their ecological role and good and services provided to humans, but, at the same  
74 time, they are highly vulnerable. In this framework, we can expect that a plethora of  
75 scenarios may take place when coastal areas are influenced by seabirds. Hence, neglecting

76 seabirds in coastal ecology reduces the understanding of numbers of processes and their  
77 spatial and temporal dynamics.

78 The main aim of this review is to summarize the current knowledge about the functional role  
79 of seabirds in coastal areas worldwide, polar, tropical and temperate, in order to provide a  
80 better understanding and foster a higher awareness, of the importance of the avian  
81 contribution to coastal system functioning and services. In more detail, we will concentrate  
82 on the studies focused on the avian ecological functions that are crucial in influencing the  
83 ecosystem processes and functioning and, therefore, their influence on the provision of  
84 ecosystem services and goods for the human well-being.

85



86

87 Fig. 1. The temporal trend in the publications existing in the literature about seabirds in  
88 terrestrial vs. coastal ecosystems. The research strings were respectively ((seabird\* OR  
89 waterbird\* OR shorebird\*) AND (soil\* OR land OR terrestrial OR island\* OR insular)) vs.  
90 ((seabird\* OR waterbird\* OR shorebird\*) AND (coast\* OR wetland\* OR estuar\* OR  
91 lagoon\* OR pond\* OR rockpool\* OR bay))

92

## 93 2. Birds as biovectors

94 Most of the effects of seabirds on coastal systems are related to their role as mobile links,  
95 namely organisms that move in the landscape and connect habitats in space and time  
96 (Lundberg and Moberg, 2003). While moving across ecosystem boundaries, seabirds act  
97 as biovectors, by redistributing abiotic (nutrients, organic matter, contaminants) and biotic  
98 (parasites, seeds, larvae and organisms) resources from marine systems to land (e.g. Ellis  
99 et al. 2006, Kolb et al. 2015, Lovas-Kiss et al. 2019). Only recently, few studies highlighted  
100 the importance of the processes driven by the movements in the opposite direction, that is  
101 from land to the coast (e.g. Signa et al. 2012, Gagnon et al. 2013, Lorrain et al. 2017,  
102 Benkwitt et al. 2019). Therefore, seabirds encompass all three major categories of mobile  
103 linkers: resource linkers, genetic linkers and process linkers (Sekercioglu, 2006), and,  
104 consequently, they trigger and shape a multitude of ecological processes (Table 1). Besides,  
105 for the first time, here we mention explicitly the role of seabirds as contaminant linkers, as  
106 their neglected role in the distribution of many pollutants worldwide.

107 Table 1. Outline of the ecological processes and related effects driven by seabirds in different coastal areas. Results are grouped per  
 108 type of seabird linkage according to Sekercioglu (2006), plus contaminant linkage. System typology where the effects have been  
 109 found, and related references, are also showed.

<b>ecological process a) resource linkage</b>	<b>main effect</b>	<b>system typology</b>	<b>reference</b>
nutrient input	increase in nutrient load	coastal ponds, estuaries	Portnoy 1990; Bildstein et al. 1992
	changes in nutrient cycling	rocky shores	Ganning and Wulff 1969; Golovkin and Garkavaya 1975
	change in water and sediment chemistry (high pH, chlorophyll-a and nutrient concentrations)	coastal ponds coral reefs	Weber et al. 2006; Keatley et al. 2009; Signa et al. 2012; Duda et al. 2018 Honig and Mahoney 2016; Lorrain et al. 2017
bottom-up control on primary producers	increase in phytoplankton production	tidepools, coastal ponds	Methratta 2004, Signa et al. 2012, Shatova et al. 2016, Petkuvienė et al. 2019
	change in macroalgae community composition (shift from perennial to opportunistic species)	rocky shores	Bosman and Hockey 1986; Wootton 1991; Kolb et al. 2010; Gagnon et al. 2016
	species shift and increase in macrophyte biomass	estuaries	Powell et al. 1991; Herbert and Fourqurean 2008; Benkwitt et al. 2019
bottom-up control on consumers	limited or no effects	coastal waters	Berchenko et al. 2017; Zmudczyńska-Skarbek et al. 2015; Bouchard Marmen et al. 2017
	higher biomass of larger-bodied opportunistic benthic taxa	rocky shores	Kolb et al. 2010
	increased density of omnivorous invasive species decrease in biomass and dominance of opportunistic/generalist consumers	coastal ponds	Gagnon et al. 2016 Palomo et al. 1999; Signa et al. 2015
bottom-up control on trophic webs	subsidised phytodetritus is the main OM source of the whole food web	coastal ponds	Treasure et al. 2015; Vizzini et al. 2016

	subsidised phytoplankton fuels secondary production		coastal waters	McCauley et al. 2012; Zmudczyńska-Skarbek and Balazy 2017; Graham et al. 2018, Savage 2019
	subsidised zooplankton attracts zooplanktivorous predators			McCauley et al. 2012
<b><i>b) contaminant linkage</i></b>				
contaminant input	High sediment concentration of inorganic (As, Cd, Hg, Zn) and organic contaminants (HCB, DDT; PCB)		freshwater coastal ponds	Brimble et al. 2009; Blais et al. 2005; Michelutti et al. 2009, Foster et al. 2011
	High sediment concentration of inorganic (As, Cd, Hg, Pb) and organic contaminants (POPs; PCB)		ornithogenic sediments	Sun and Xie 2001, Roosens et al. 2007; Nie et al. 2012, Lou et al. 2015, 2016
	High sediment concentration of inorganic elements (Zn, Cu, Cd, THg and MeHg)		sandy shores	Liu et al. 2006; Chen et al. 2012
	High sediment concentration of inorganic elements (As, Cd, Cr, Cu, Ni, Pb, THg, V, Zn)		coastal ponds	Signa et al. 2013b
contaminant transfer to organisms	high As, Cd, Pb and THg concentration in particulate organic matter and macrophytes; THg biomagnification		coastal ponds	Signa et al. 2013a
<b><i>c) genetic linkage</i></b>				
seed dispersal (endozoochory/ectozoochory)	plant (including alien species) colonization of remote areas		oceanic islands	Nogales et al. 2001; Burger 2005; Calvino-Cancela 2011; Aoyama et al. 2012; Green 2016
dispersal of plants, algae, invertebrates and eggs	maintenance of biodiversity at regional scale		lagoons, ponds and salt pans	Green et al. 2002; Brochet et al. 2010; Charalambidou and Santamaría 2005; Martínez-Garrido et al. 2017; Moreno et al. 2019
	invasion of brine shrimp <i>Artemia</i> spp.			Muñoz et al. 2014
dispersal of disease agents	Long-distance dissemination of Lyme disease agent (through tick dispersal)		worldwide	Dietrich et al. 2011
	dissemination of avian influenza viruses			Olsen et al. 2006
<b><i>d) Process linkage - trophic (top-down control)</i></b>				
feeding pressure of primary consumers	community stabilization due to compensatory effects		todepools, mudflats, rocky shores	Methratta 2004; Hamilton et al. 2006; Cheverie et al. 2014; Gagnon et al. 2016

predatory pressure of cormorants	potential conflicts with human fishing activities limited conflicts with human fishing activities due to niche and size segregation of fish stock	lagoons and fish ponds	Leopold et al. 1998, Hobson 2009, Vetemaa et al. 2010, Steffens 2011 Žydelis and Kontautas 2008; Doucette et al. 2011; Troynikov et al. 2013
predatory pressure of penguins and petrels	"wasp-waist" food web structure	pelagic water	Ainley et al. 2015
<b><i>e) Process linkage - non trophic (ecosystem engineers)</i></b>			
grazing activities (mute-swans)	destruction of submerged macrophyte beds limit opportunistic macroalgae	estuaries, lagoons, coastal ponds and salt pans	Tatu et al. 2007 Gayet et al. 2012
trampling (flamingoes)	uprooting seagrass beds, bioturbation of sediment		Widdicombe et al. 2000; Rodríguez-Pérez and Green 2006; Green and Elmberg 2013
feeding on invertebrates (shorebirds)	increase of sediment stability through cascading effects	mudflats	Daborn et al. 1993; Hamilton et al. 2006

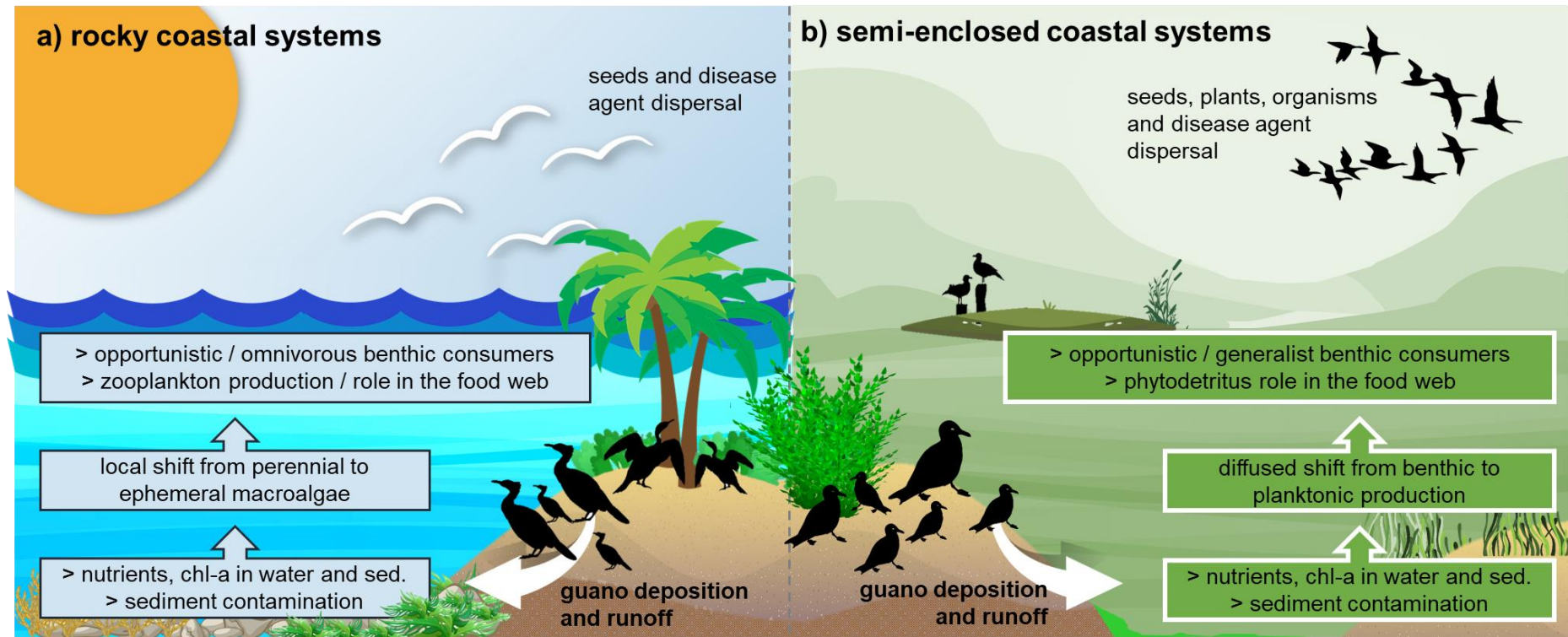


## 111        **2.1. Resource linkage**

112        The role of seabirds as nutrient subsidizer is maybe the most acknowledged and  
113        documented in coastal areas. Bird excrements, generically called “guano”, have been  
114        always recognized as a powerful fertilizer due to the high nutrient concentration, especially  
115        nitrogen and phosphorus (Otero et al., 2018). Fertilization effects induced by guano supply,  
116        also called guanotrophication (since Leentvaar 1967), have been observed in coastal waters  
117        since the last century when Ganning and Wulff (1969) and Golovkin and Garkavaya (1975)  
118        found significant changes in the nutrient cycling patterns along the coasts of northern  
119        Europe. Since the first attempts to quantify the nutrient load induced by guano release, it  
120        turned out that phosphorus and nitrogen load in estuaries and ponds may be substantial  
121        when compared to other potential sources, such as atmospheric deposition or land drainage  
122        (Bildstein et al., 1992; Portnoy, 1990), highlighting the need to include the bird contribution  
123        into nutrient budget models of semi-enclosed coastal areas. Afterwards, more recent studies  
124        reported an overall change in water and sediment chemistry in seabird-impacted areas: high  
125        pH, chlorophyll-a and dissolved and sediment nutrient concentrations were distinctive of  
126        polar (Duda et al., 2018; Keatley et al., 2009), Atlantic (Weber et al., 2006) and  
127        Mediterranean ponds (Signa et al., 2012), as well as of Pacific coral reefs (Honig and  
128        Mahoney, 2016; Lorrain et al., 2017) adjacent to big and small seabird colonies. Rainfall and  
129        tidal oscillation are the main mechanisms responsible for the nutrient runoff from the guano  
130        deposited in the areas surrounding the colonies to the adjacent coastal waters, together with  
131        the direct release of guano by overflying birds (Signa et al., 2012; Staunton Smith and  
132        Johnson, 1995). Nevertheless, the N input through runoff is reduced by the rapid  
133        volatilization of ammonia ( $\text{NH}_3$ ) that forms from microbial degradation of uric acid, which is  
134        the most abundant N form in fresh guano (Blackall et al., 2007; Lindeboom, 1984), and the  
135        remaining part is converted into nitrate and nitrite by nitrifying bacteria (Bosman and Hockey,

136 1988). Methane, ammonia and nitrogen dioxide emission from seabird colonies may be  
137 also impressive, especially when colony density is high (Blackall et al., 2007; Riddick et al.,  
138 2012; Schmale et al., 2013; Schmidt et al., 2010; Zhu et al., 2008), and may contribute to  
139 nitrogen enrichment of adjacent coastal systems driven by wind and rains (Blackall et al.,  
140 2008). Mizutani and Wada (1988) found also that this process has another important  
141 ecological implication: after deposition on the rookeries, ornithogenic nitrogen undergoes  
142 isotopic fractionation due to ammonia volatilization, which implies a high  $^{15}\text{N}$  enrichment of  
143 the nitrogen residual pool, hence showing distinctive high  $\delta^{15}\text{N}$  values. For this reason,  $\delta^{15}\text{N}$   
144 is successfully used as a proxy for ornithogenic influence on natural ecosystems and food  
145 webs, with higher values in subsidized organisms and spatial/temporal isotopic gradients  
146 according to seabird density and/or impact intensity gradients (e.g. Mizutani and Wada  
147 1988, Wainright et al. 1998, Keatley et al. 2009, Signa et al. 2012, Lorrain et al. 2017).  
148 Indeed, there is no correlation between seabird density and impact intensity, as  
149 geomorphological and hydrological drivers play a marked role in dampening (open  
150 seas/shores) or magnifying (semi-enclosed coastal areas) the effects of seabird subsidies,  
151 regardless of colony size (Signa et al., 2012; Wainright et al., 1998) (Fig. 2).

152



153

154 Fig. 2. Outline of the main known ecological processes driven by seabirds as resource, contaminant and genetic linkage, in open (a)  
 155 and semi-enclosed (b) coastal systems. The underlying process is the guano release and runoff from seabird colonies into both types  
 156 of coastal areas. Arrows indicate the effects on i) nutrient cycling, water and sediment chemistry and contamination level; ii) bottom-  
 157 up effects on primary producers and iii) on consumers and food web dynamics. The thickness of the arrows indicates the strength of  
 158 the processes.

159        **2.1.1 Bottom-up effects**

160 As previously outlined, nutrient cycling is one of the most important avian ecological  
161 functions and is also an important supporting service provided by seabirds, crucial for the  
162 functioning of ecosystems at different levels (Green and Elmberg, 2013). Indeed, as most  
163 of the excreted nitrogen and phosphorus is in a highly bioavailable form (Otero et al., 2018),  
164 guantrophication may boost primary production, that, in turns, may trigger bottom-up  
165 effects on primary and secondary consumers (Fig. 2).

166 P and N are the major limiting nutrients for primary production in most aquatic ecosystems  
167 (Smith, 2006), hence the increase of ornithogenic nutrients can lead to important shifts in  
168 primary production patterns in the recipient area, generally fostering phytoplankton growth  
169 (Methratta, 2004; Petkuvienė et al., 2019; Shatova et al., 2016; Signa et al., 2012). In  
170 particular, a shift from oligotrophic to eutrophic state and from benthic to planktonic  
171 production has been observed in temperate coastal ponds subject to guano runoff, due to  
172 the rapid phytoplankton nutrient uptake and bloom followed by decreased light availability  
173 for benthic macrophytes and further reduced benthic production (Signa et al., 2012).  
174 Similarly, change in macroalgae community composition, diversity and zonation, with  
175 ephemeral foliose, filamentous and epiphytic species dominating over perennial habitat-  
176 structuring species, was observed in seabird-impacted rocky shores, compared to seabird-  
177 free areas (Bosman and Hockey, 1986; Gagnon et al., 2016; Kolb et al., 2010; Wootton,  
178 1991). In tropical and subtropical areas, different species composition and long-term  
179 increase in seagrass (Herbert and Fourqurean, 2008; Powell et al., 1991) and crustose  
180 coralline algae biomass (Benkwitt et al., 2019), as well as support to mangrove expansion  
181 through higher soil fertility, were found (Adame et al., 2015).

182 Shift of benthonic toward planktonic production and change in species composition and  
183 diversity may have far-reaching consequences on community structure and diversity of

184 higher trophic levels, as well as on change of trophic pathways. Although the community  
185 response to seabird-induced bottom-up forces can be generalized in terms of decreased  
186 habitat complexity, lower biodiversity and simplified community structure, multiple abiotic  
187 and biotic factors may act contextually to shape the ecosystem response. Literature review  
188 reveals two main scenarios about how communities respond to seabird subsidy, mostly  
189 driven by the typology of the coastal water bodies (that mirrors differing geomorphological  
190 and hydrological constraints) coupled with the frequency and amount of ornithogenic  
191 nutrients and the interaction with top-down forces.

192 Along the high Arctic sea coasts, fertilization of water through bird guano did not exert any  
193 effects on planktonic (Berchenko et al., 2017) and benthic communities (Zmudczyńska-  
194 Skarbek et al., 2015), unless a few limited, and maybe indirect, negative effects on deep  
195 benthic fauna (Bouchard Marmen et al., 2017). Dilution effect driven by currents and  
196 excessive depth and distance from the coasts were identified as the main factors  
197 contributing to this lack of effects. Along the coasts of the semi-enclosed Baltic Sea, an  
198 evident benthic response followed the regime shift occurred from perennial to ephemeral  
199 algae, in term of higher biomass of larger-bodied opportunistic benthic taxa (Kolb et al.,  
200 2010) and increased density of omnivorous invasive species (Gagnon et al., 2016). The  
201 community response of benthic fauna to guano fertilization appears even more pronounced  
202 in subsidized coastal ponds and lagoon (Palomo et al., 1999; Signa et al., 2015) and showed  
203 a pattern which reminds the classical Pearson and Rosenberg (1978) model in eutrophic  
204 systems. In brief, at intermediate fertilization level, both biomass and taxonomic/functional  
205 abundance tend to decrease followed by a complete decline of benthic fauna at extreme  
206 fertilization conditions. Accordingly, the influence of seabird-nutrient subsidies on food web  
207 dynamics varies along with ecosystem properties, more than with seabird density. Isotopic  
208 tracers and food web models were used to investigate if and how trophic relationships, food

209 web dynamics and structure may change in recipient systems as a final effect of the seabird-  
210 induced bottom-up forces: in phytoplankton-dominated coastal systems, bento-pelagic  
211 coupling resulted the main process favoring the subsidization of benthic food web, due to  
212 the sinking of large amounts of phytodetritus which enter and flows over the whole food web  
213 (Treasure et al., 2015; Vizzini et al., 2016). Therefore, an erosion of the benthic pathway in  
214 favor of the planktonic one and dominance of opportunistic/generalist consumers is the main  
215 expected food web response in this context. Other studies revealed a marked incorporation  
216 of ornithogenic nutrients in zooplankton (McCauley et al., 2012; Zmudczyńska-Skarbek and  
217 Balazy, 2017) and corals (Graham et al., 2018; Savage, 2019), and a marked positive effect  
218 on higher trophic levels: in the remote tropical atoll of Palmyra, the higher planktonic  
219 abundance and size attracted many zooplanktivorous manta ray specimens further  
220 contributing to the ecological connectivity through the export offshore of ornithogenic  
221 nutrients (McCauley et al., 2012).

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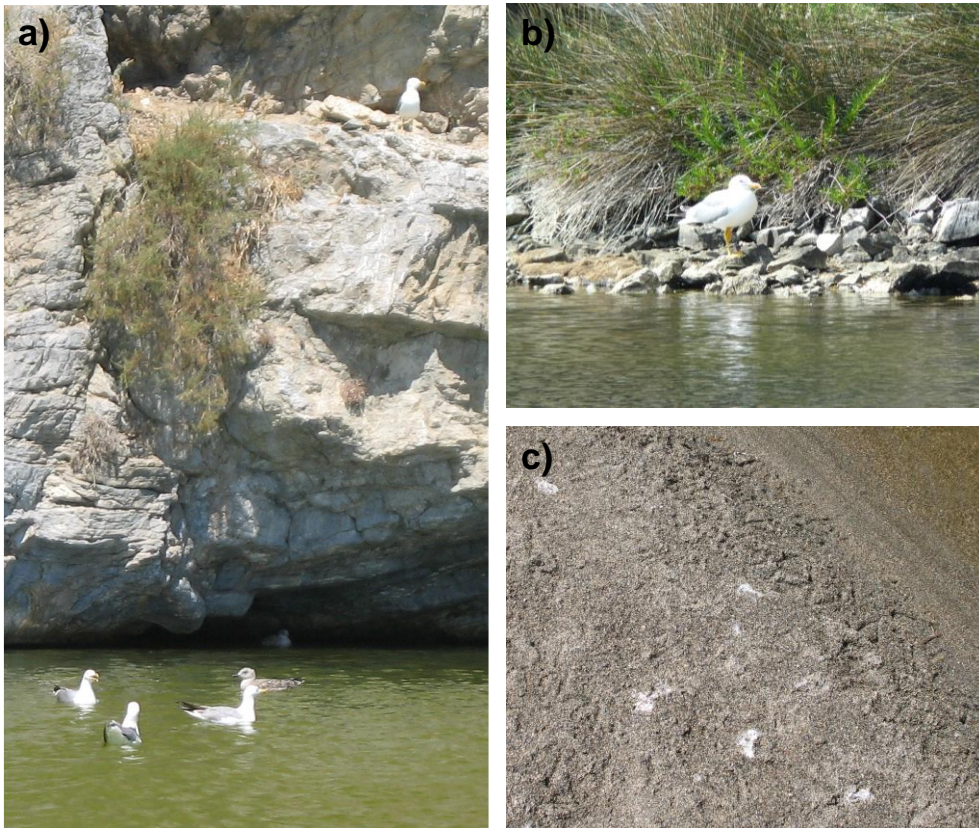
## 223 **2.2. Contaminant linkage**

224 High contaminant accumulation and biomagnification have been observed in many  
225 seabirds, due to the high position in the food webs and the wide foraging range (Michelutti  
226 et al., 2010). For this reason, birds are commonly used as bioindicators of pollution in coastal  
227 and marine systems (Burger and Gochfeld, 2004). So far, existing literature paid great  
228 attention to the impact of the anthropic release of contaminants on bird health, but the  
229 reverse process has been unfairly underestimated.

230 Along with nutrients, seabirds release a plethora of contaminants into the environment  
231 through feathers, eggs, guano, and carrions. Poles are certainly the most studied areas in  
232 regards to contaminant transport, concentration and deposition driven by seabirds because  
233 many resident and migrating species concentrate in very large breeding colonies (up to

234 thousands of pairs) offering a good opportunity for studying these processes. Again, seabird-  
235 driven contamination in coastal areas has been markedly overlooked compared with  
236 terrestrial ones. The most studied case of ornithogenic contamination is represented by the  
237 Arctic coastal freshwater ponds at Cape Vera (Devon Island, Arctic Canada) where toxic  
238 levels of inorganic elements (Brimble et al. 2009: As, Cd, Zn; Blais et al. 2005: Hg) and  
239 organic pollutants (Blais et al. 2005: HCB, DDT; Michelutti et al. 2009: PCBs; Foster et al.  
240 2011: PCBs, DDT) in sediments were recorded and related to the adjacent big colony (~  
241 10 000 pairs) of northern fulmar (*Fulmarus glacialis*). In Antarctica, penguin guano  
242 historically contributed to the formations of ornithogenic sediments, whose paleoecological  
243 study provided insights about the potential threat of trace elements (As, Cd, Hg, Pb; Sun  
244 and Xie 2001, Nie et al. 2012, Lou et al. 2015, 2016) and also POPs and PCB (Roosens et  
245 al., 2007) in the surrounding coastal systems. Also a few studies from southern China  
246 tropical islands and Mediterranean coastal ponds close to colonies of red-footed booby (*Sula*  
247 *sula*) and yellow-legged gull (*Larus michahellis*) were limited to the assessment of the  
248 contamination levels in the surrounding sediment (Liu et al. 2006, Chen et al. 2012: Zn, Cu,  
249 Cd, THg and MeHg; Signa et al. 2013b: As, Cd, Cr, Cu, Ni, Pb, THg, V, Zn) confirming the  
250 role of seabirds as trace element biovector able to focus pollutants at toxic levels even when  
251 they group in small colonies. Similarly, to our knowledge only one study followed the fate of  
252 seabird-driven contaminants in coastal organisms and food webs (Signa et al. 2013a) and  
253 found high As, Cd, Pb and THg concentration in subsidized particulate organic matter and  
254 macrophytes of one of the coastal ponds from a Mediterranean Nature Reserve (Laghetti di  
255 Marinello, South Italy) where a small colony (~ 100 individuals) of yellow-legged gull resides  
256 (Fig. 3). Moreover, regression analysis between trace elements and  $\delta^{15}\text{N}$  revealed that  
257 significant ornithogenic trophic transfer and biomagnification take place only for THg and  
258 leads to high concentration also in benthic invertebrates and fish (Signa et al., 2013b).

259 These results highlight the need to change perspective, paying more attention to the  
260 potential of seabirds to convey large quantities of contaminants to coastal systems, with  
261 associated potential risks to organisms, as they are one of the dominant wildlife group along  
262 coastlines worldwide.  
263



264  
265 Fig. 3. Scenes from the coastal pond Verde (= Green) in the Nature Reserve Laghetti di  
266 Marinello (Sicily, Italy) where a small colony of yellow-legged gull (*Larus michahellis*)  
267 resides. To be noticed the greenish colour of seawater (a) due to the gulls bathing, nesting  
268 (b) roosting, (c) defecating and walking around the shores.

269

### 270 **2.3. Genetic linkage (dispersal role)**

271 Birds carry and spread genetic material between habitats through their short- and long-  
272 distance movements, promoting the colonization of new sites and the recolonization of  
273 disturbed sites, and ensuring the maintenance of metacommunities and gene flow among



274 populations at a landscape, and sometimes continental, scale (Viana et al., 2013), with far-  
275 reaching effects on ecosystem processes and services (Green and Elmberg, 2013;  
276 Sekercioglu, 2006; Whelan et al., 2008). Unlike the wealth of studies on the dispersal role  
277 of aquatic birds in freshwater habitats (recently reviewed by Reynolds et al. 2015), current  
278 knowledge of the dispersal potential of seabirds in coastal systems is more limited. For  
279 instance, only a few studies documented the role of seabirds as seed dispersers in coastal  
280 habitats and revealed that gulls are highly effective long-distance seed dispersers along the  
281 coastal strips of several islands, through faeces and regurgitation (i.e. endozoochory), due  
282 to their generalist feeding habit and long-gut retention times (Calvino-Cancela, 2011;  
283 Nogales et al., 2001). Other seabirds, such as noddies, terns, shearwaters (Burger, 2005),  
284 and also albatrosses, petrels and boobies (Aoyama et al., 2012) act as seed-dispersal  
285 agents of aquatic and terrestrial plant species which have adapted for adhesive dispersal  
286 by sticking seeds to feathers (i.e. ectozoochory). Both processes play a key role in plant  
287 colonization of remote oceanic islands, favouring also the spread of alien species (Aoyama  
288 et al., 2012; Calvino-Cancela, 2011; Green, 2016).

289 Waterbirds, such as migratory ducks, swans, geese and coots, and shorebirds, such as  
290 oystercatchers, sandpipers, herons and storks, are acknowledged dispersal vectors of  
291 aquatic organisms (plants, algae, invertebrates and eggs) between coastal wetlands, such  
292 as lagoons, brackish ponds and saltpans (Brochet et al., 2010; Clausen et al., 2002; Frisch  
293 et al., 2007; Green et al., 2002; Van Leeuwen et al., 2012). Although their high dispersal  
294 potential over long distances (up to hundreds of kilometres), other factors, among which gut  
295 retention time, seed characteristics and propagule viability, together with local inhibitory  
296 effects, act as powerful buffer to prevent successful establishments (Charalambidou et al.,  
297 2003; Charalambidou and Santamaría, 2002; Espinar et al., 2004). However, the incredibly  
298 high abundance (e.g. up to millions of individuals) that waterbirds may reach in some regions

299 [e.g. Mediterranean wetlands of the Camargue (France) and Doñana ponds (Spain)]  
300 ensures that birds act anyway as ecological links contributing to the maintenance of  
301 biodiversity at a regional scale (Charalambidou and Santamaría, 2005; Martínez-Garrido et  
302 al., 2017; Moreno et al., 2019). In contrast, long-distance flamingo migrations are thought  
303 as the way through which natural dispersion of the invasive brine shrimp *Artemia* spp.  
304 occurred in Mediterranean wetlands (Muñoz et al., 2014).

305 Seabirds also host and move a wide array of microorganisms, mainly viruses and spores of  
306 bacteria and fungi, both directly than within parasitic secondary vectors, with implications in  
307 spatial ecology, evolution, and epidemiology of infectious diseases (Boulinier et al., 2016).  
308 Long-distance migrations and inter-colony movements, together with long-life, site fidelity  
309 and high density of breeding aggregations made seabirds ideal models for studying the  
310 processes of dissemination of disease agents. Ticks are among the most abundant and  
311 diverse seabird parasites, and they host, in turn, a number of viruses and bacteria, including  
312 the complex *Borrelia burgdorferi sensu lato*, which is the agent responsible for the Lyme  
313 disease (Dietrich et al., 2011). Likewise, seabirds and waterbirds can harbour and spread a  
314 large variety of avian influenza viruses through their global movements (Olsen et al., 2006).  
315 Many other non-pathogenic parasites, with complex life cycles and various aquatic  
316 intermediate hosts, are harboured and dispersed by waterbirds with profound positive  
317 effects on wetland biodiversity (Green and Elmberg, 2013).

318

## 319 **2.4. Process linkage**

### 320 **2.4.1 Trophic linkage (top-down control)**

321 Together with bottom-up control, coastal communities are structured by top-down (predator-  
322 mediated) forces, which may be particularly important in coastal systems, where grazers  
323 influence macrophyte cover and diversity and predators may alter prey abundance, and both

324 processes may interact and trigger trophic cascades (Pace et al., 1999; Power, 1992).  
325 Although it is acknowledged that bottom-up and top-down forces are not mutually exclusive  
326 and may lead to synergistic or antagonistic effects on coastal communities (Atalah and  
327 Crowe, 2010; Cheverie et al., 2014), only a few studies have taken into account the  
328 interactive effects of both forces in coastal systems subsidized by seabirds (Cheverie et al.,  
329 2014; Gagnon et al., 2013, 2016; Hamilton et al., 2006; Methratta, 2004; Palomo et al.,  
330 1999). A common pattern characterizes both subsidized intertidal mudflat and rocky shores,  
331 and namely that bottom-up forces tend to overwhelm top-down control, consistent with the  
332 scenario envisaged by Power (1992) and the meta-analysis of Burkepille and Hay (2006) by  
333 which the extent of bottom-up control tend to overcome top-down forces in benthic high-  
334 productivity systems, and *vice-versa* in low-productivity systems. Moreover, in the shallow  
335 coastal systems, the propagation of both forces across multiple trophic levels tends to be  
336 prevented by compensatory effects driven by primary consumers. In more detail, the feeding  
337 pressure of suspension-feeders (Methratta, 2004), deposit feeders (Cheverie et al., 2014;  
338 Hamilton et al., 2006) and grazers (Gagnon et al., 2016), coupled with the intra-guild  
339 competition, can counteract and prevent the occurrence of trophic cascades, leading overall  
340 to community stabilization. A different scenario has been recorded in the pelagic Antarctic  
341 system, where the massive presence of penguins and petrels exerts a so strong predatory  
342 pressure on fish and zooplankton, to depress their abundance and hence resulting in a high  
343 ungrazed phytoplankton abundance and hence leading to a “wasp-waist” food web structure  
344 (Ainley et al., 2015).

345 Another issue that deserves to be mentioned is the effect of fish predators in lagoons and  
346 fish ponds, which historically posed a threat to fishing and angling activities. The case of  
347 cormorant (*Phalacrocorax* spp.) is maybe the most notorious: since the European Birds  
348 Directive was enacted in 1979, cormorant numbers increased alarmingly in many European

349 countries. The role of cormorants as active fish predators with very high food intake  
350 (Ridgway, 2010), together with the raised abundances, led to an increase of concerns about  
351 the potential conflicts with human fishing activities (Hobson, 2009; Leopold et al., 1998;  
352 Steffens, 2011; Vetemaa et al., 2010) and, consequently, to implementation of management  
353 programs of cormorant population. Nevertheless, other recent studies agree that this is an  
354 overblown issue as direct competition between cormorants and humans resources is limited  
355 by processes of niche and size segregation of exploited fish stock (Doucette et al., 2011;  
356 Troynikov et al., 2013; Žydelis and Kontautas, 2008). Only Klimaszyk and Rzymiski (2016)  
357 addressed the problem with a more holistic approach, highlighting that the environmental  
358 effects of great cormorants on aquatic systems are more complex than usually thought,  
359 because of the combined effects of chemical loading, microbial pollution and pathogen  
360 dispersion, alongside predatory pressure.

361 Lastly, there is strong evidence that swans exert a very high grazing pressure on vegetal  
362 biomass regulating the macrophyte community structure and triggering indirect effects on  
363 the whole ecosystems where they forage (Dos Santos et al., 2012; Hori et al., 2006). For  
364 this reason, they are considered as habitat modifiers and therefore the subject will be  
365 addressed in the next paragraph.

366

#### 367 **2.4.2 Non-trophic linkage (ecosystem engineers)**

368 Likewise terrestrial birds, also seabirds and waterbirds act as ecosystem engineers in  
369 coastal systems, as they can change the environment via mechanical processes, with  
370 potential direct or indirect consequences to other organisms (Green and Elmberg, 2013;  
371 Sekercioglu, 2006). Two are the main engineering processes acknowledged for seabirds  
372 and waterbirds respectively, but we will deal only with latter, as the former, namely the

373 burrow-nesting activity of colonial seabirds, influences the terrestrial coastal environment  
374 and therefore is out of the scope of the present review.

375 Differently, crucial engineering actions and processes are supported by waterbirds and  
376 shorebirds in wetlands. Possibly, the most abundant and significant avian ecosystem  
377 engineers in wetlands worldwide are the mute-swan *Cygnus olor* and the greater flamingo  
378 *Phoenicopterus roseus* with two major effects on submerged macrophytes and sediment  
379 properties. If the grazing activity by swans is conducted through destructive foraging  
380 methods that directly affect submerged macrophyte beds, the mechanical disturbance  
381 during bottom-feeding activities of flamingoes indirectly affects macrophytes (Gayet et al.,  
382 2012; Tatu et al., 2007). Alongside the obvious deleterious effects on aquatic vegetation,  
383 large waterbirds also limit the expansion of opportunistic macroalgae, finally resulting in a  
384 reduction of the negative effects of eutrophication in lagoons (Gayet et al., 2012). Moreover,  
385 while feeding at the bottom, flamingoes trample and uproot seagrass beds causing major  
386 bioturbation effects: sediment reworking and resuspension, nutrient mobilization to the water  
387 column and consequent increase of turbidity (Green and Elmberg, 2013; Rodríguez-Pérez  
388 and Green, 2006). In contrast with the foregoing example, higher turbidity can trigger a state  
389 shift to a turbid phytoplankton-dominated trophic state, which may further limit macrophyte  
390 growth (Rodríguez-Pérez and Green, 2006). At the same time, the higher spatial  
391 heterogeneity caused by sediment bioturbation may promote species diversity of benthic  
392 fauna (Widdicombe et al., 2000). Another engineering process indirectly driven by  
393 shorebirds in mudflats is the increase of sediment stability due to cascading effects driven  
394 by the predation of shorebirds on amphipods, which prey on benthic diatoms that secrete  
395 cohesion-inducing carbohydrates (Daborn et al., 1993; Hamilton et al., 2006).

396

### 397 **3. Resident vs migrant seabirds**

398 Seabirds display a vast array of migratory patterns, as well as sedentary behaviour. Their  
399 movement types cover from a daily short distance from nesting/roosting sites to feeding  
400 sites, up to seasonal inter-continental migrations for breeding, which involves substantial  
401 land- or ocean-crossings (Newton, 2007). If most seabirds disperse by flying, penguins and  
402 other pelagic seabirds migrate by swimming. In both cases, along these long journeys, the  
403 stop-over number, timing and duration greatly vary according to the species and the route  
404 involved, and therefore, the potential influence on the ecological processes of coastal areas  
405 may also vary significantly. The most relevant difference between migrant and resident birds  
406 is the pulsed or continuative nature of the habitat use. The migrant inputs represent  
407 “resource pulses”, i.e. brief events during which the ecosystems dramatically experience  
408 higher resource deposition, followed by long “interpulse” intervals during which the effects  
409 of the pulses can persist longer than the extinction of the pulses themselves (Yang et al.,  
410 2008). Similarly, also the predatory pressure exerted by top-predator seabirds represents a  
411 “pulsed event” of resource harvesting, linked to their presence. This alternation may  
412 primarily lead to changes in the community structure via extinction, invasion, or switch  
413 between alternative stable states (Bauer and Hoyer, 2014). Of course, there are some  
414 exceptions to the rule, such as tropical areas where wintering and summering breeding  
415 species alternate over the seasons, and hence the allochthonous input is not seasonally  
416 restricted (Lorrain et al., 2017). In contrast, alternative stable states have been observed in  
417 small coastal ponds under a resident gull colony, as an effect of the strong seasonal  
418 variability influencing productivity patterns (Vizzini et al., 2016).

419 Another aspect of the different timing of habitat use by resident and migrant seabirds is  
420 linked to their role as a contaminant and genetic linkage. If resident birds mirror and  
421 contribute to site-specific contamination, migrants accumulate and disperse contaminants  
422 from and to a wide range of geographical areas. Similarly, resident species and short-

423 distance migrants do not contribute much to the diffusion of pathogens and parasites, in  
424 contrast to migrants which facilitate long-distance dispersal events, according to their moult  
425 timing. The pronounced heterogeneity of the moulting patterns, namely moulting event i)  
426 prior the onset of migrations, ii) after the arrival at the breeding site, or iii) both prior and  
427 after, influences the probability of successful dispersal events, with higher probability in the  
428 second case (Coughlan et al., 2017).

429

#### 430 **4. Conclusions**

431 This review collected and summarized the existing literature about the role of seabirds within  
432 the ecological dynamics of coastal areas, demonstrating their great but overlooked role in  
433 driving a vast array of ecological processes, finally influencing the ecosystem functions and  
434 services (Table 1; Fig. 2). While cultural services provided by birds are historically  
435 recognized (Green and Elmberg, 2013), the seabird role in influencing directly or indirectly  
436 supporting and regulating services has been dramatically neglected so far. Here, we  
437 highlighted that, similarly to terrestrial systems (Polis et al., 1997; Sanchez-Pinero and Polis,  
438 2000), the dynamics of seabird-subsidized coastal systems is greatly donor controlled,  
439 highly depending on the amount of allochthonous input, although other biotic and abiotic  
440 factors play key roles in shaping the ecosystem response. In more detail, the interspecific  
441 competition between primary producers due to differing nutrient limitation (Powell et al.,  
442 1991; Wootton, 1991), the interaction with top-down forces (Bosman et al., 1986; Gagnon  
443 et al., 2016; Methratta, 2004), and, last, but not least, the intrinsic properties of the recipient  
444 systems, namely physico-chemical, geomorphological and hydrological drivers (Bauer and  
445 Hoye, 2014; Signa et al., 2012) shape the ecosystem response. Accordingly, interface  
446 systems, such as estuaries, lagoons and coastal ponds, that are preferential stop-over and  
447 breeding site for numerous birds, are also the most sensitive to the seabird/waterbird impact.

448 The environmental relevance of seabirds at a global scale, here outlined, highlights the need  
449 to explicitly consider seabirds in the coastal management plans and the development of  
450 conservation measures, as previously suggested by other authors (Bauer and Hoyer, 2014;  
451 Otero et al., 2018). Moreover, seabirds are highly sensitive to environmental drivers, such  
452 as habitat loss, coastal development and pollution, and global climate change, and are also  
453 highly threatened nowadays, according to the IUCN Red List ([www.iucnredlist.org](http://www.iucnredlist.org)). All these  
454 stressors can dramatically influence their abundance and distribution patterns modifying  
455 their functions within coastal systems and affect social benefits such as cultural, recreation  
456 and aesthetic value of coastal areas.

457 This scenario reveals an urgent need to further increase the current knowledge about the  
458 relationship between ecological functions of seabirds and coastal ecosystem functioning  
459 and services, with an interdisciplinary approach that integrates ornithology and ecology  
460 expertise. We strongly emphasize the need to improve the knowledge about seabirds  
461 functions, by ranking seabirds in functional guilds, that is a mandatory preliminary step to  
462 link the seabird functional traits with the service provided (Zoeller et al., 2020) and hence,  
463 the ecosystem effect traits. This approach could lay the foundations for future research in  
464 coastal areas worldwide, allowing to assess how future changes in seabird/waterbird  
465 abundance will influence the coastal functioning and the ecosystem services and goods that  
466 are vital for the human well-being in a global climate change context.

467

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471

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