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Impacts of protected colonial birds on soil microbial communities: When protection leads to degradation

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ABSTRACT

Colonial nesting and roosting birds can degrade their habitat by soil salinization, eutrophication, and acidification associated with excessive deposition of avian excreta. We studied the impact of a protected wading bird colony on soil microbial communities from cork oak woodlands in Doñana National Park (SW Spain). Over one year we analyzed soil properties (pH, salinity, soluble N and P forms, extractable organic carbon - EOC -), microbial activity (basal respiration, community-level physiological profile, extracellular enzyme activities) and community structure (fungal, bacterial and archaeal terminal restriction fragments -TRFs-) along a gradient of bird nesting intensity. Bird nesting largely impacted soil chemical environment, with increases from 25 to 500 μS cm^{-1} in soil salinity, from 6 to 725 mg kg^{-1} in soil P, from 5 to 22 mg kg^{-1} in $N\text{-}NH_4$, and from 5.4 to 245 mg kg^{-1} in $N\text{-}NO_3$ between the extremes of the nesting intensity gradient in the wet season. Most of these chemical changes were enhanced in the dry season. We observed positive linear or log-linear relationships between the bird nesting footprint on soils (indicated by an integrated soil chemistry index) and microbial biomass, basal respiration and most of the studied enzyme activities. This was likely due to the concurrent increases in EOC along the avian intensity gradient, which counteracted the negative impacts of salinity. Soil P and EOC were the main drivers for fungal, bacterial and archaeal TRFs diversity. Bacterial TRFs richness and diversity index decreased along the avian intensity gradient in the dry season, while archaeal TRFs diversity increased in those soils highly salinized by excess of avian excreta deposition. Our study clearly shows that this oversized bird colony has profound effects on soil chemistry and biological activity, and highlights the need for a re-evaluation of management strategies in this protected area, towards a greater consideration of soil processes in conservation priorities.

1. Introduction

Oversized animal populations may have profound effects on soil biogeochemical cycles in terrestrial ecosystems, for instance by reducing C inputs belowground due to overgrazing (Raiesi and Asadi, 2006; Mchunu and Chaplot, 2012), and by providing nutrient inputs through faecal deposition. This is the case of those systems used by birds for nesting or roosting, where soil acidification, eutrophication and salinization might occur due to the deposition of large amounts of guano, which is highly enriched in N and P salts (García et al., 2002a,b; Ligeza and Smal, 2003; Zwolicki et al., 2013). The increase in waterbird protection initiatives and the drastic expansion of seagulls during the last two decades have resulted in a growing number of areas affected by ornithogenic soil degradation, which has been reported in Mediterranean and Atlantic islands (García et al., 2002b; Baumberger et al., 2012; Otero et al., 2015), forest and wetland ecosystems in Europe (Kutorga et al., 2013), the Great Lakes in North America (Hebert et al., 2005) or lakeside forests and islands in Australia (Baxter and Fairweather, 1994; Bancroft et al., 2005) and Japan (Hobara et al., 2005; Katsumata et al., 2015).

Piscivorous birds transport N and P from their wide feeding areas into their nesting and roosting habitats, which might release plant and soil microbial nutrient deficiencies in environments with

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nutrient-poor soils (Speir and Ross, 1984; Wait et al., 2005; Tscherko et al., 2003; Sigurdsson and Magnusson, 2010; Korsten et al., 2013; Adame et al., 2015; Irick et al., 2015). However, in those systems where the size of the bird colony is too large, detrimental effects on plant or soil microbial communities may occur due to the excess of nutrients and salts in soils (García et al., 2002a; Ellis, 2005; Ellis et al., 2006; Wait et al., 2005). Excess of guano deposition can lead to N saturation in soils, resulting in C limitations for soil microbes that enhance organic matter decomposition (Hawke and Vallance, 2015), or in decreased rates of litter decomposition by fungi due to the formation of acid-insoluble lignin-like substances in plant biomass to immobilized excreta-derived N (Osono et al., 2006a).

Some studies have shown that excessive avian excreta inputs can alter the structure of soil fungal and bacterial communities, with decreases in fungal growth (Osono et al., 2002, 2006b), mycorrhizal and myxomycetous richness (Adamonytė et al., 2013; Kutorga et al., 2013), and the fungi:bacteria PLFA ratio (Wright et al., 2010) in those soils highly fertilized by birds, in comparison to nearby control sites. Most of these studies, however, have focused mainly on a single microbial group, and information about the relative impact of guano deposition on the diversity of different microbial groups is still lacking. While bacteria might be more affected than fungi by changes in soil pH (Lauber et al., 2008; Rousk et al., 2010), fungi appear to be more affected by increased salinity and nutrient inputs than bacteria, as suggested by several studies reporting decreases in fungal dominance in response to salinization (reviewed in Rath and Rousk, 2015) and long-term N or P fertilization (Bradley et al., 2006; Wallenstein et al., 2006; Demoling et al., 2008; Rousk et al., 2011a). The impact of fertilization by birds on archaeal community remains to be studied. Recent works have reported a greater sensitivity of archaeal than bacterial and fungal communities to disturbances in soils with a long history of N-fertilization (Pereira e Silva et al., 2012), so it is likely that the archaeal community is highly responsive to fertilization of the soils from these bird habitats.

Here, we analyzed soil microbial activity and diversity along a gradient of bird nesting in a large colony of wading birds established in a cork oak woodland at the Doñana National Park (SW Spain). This park is one of the most important bird reserves in Europe, where a large colony of wading birds established on the cork oaks and other tree species located in the ecotone between the woodland and the marshland in the 1947–1948 (Bernis and Valverde, 1954). Since then, the increase in the size of the bird colony has resulted in some detrimental effects on the trees. In a previous study we showed that the observed cork oak decay in this woodland was explained by the effects of nesting birds on soils (mainly soil salinization and fertilization, García et al., 2011). After 46 years of bird protection, the risk of death for centenarian and planted cork oaks in the area occupied by the bird colony was over twofold higher than for trees outside the nesting area (Fedriani et al., 2016).

We explored the ornithogenic impact on soil microbial communities during two contrasting seasons, through the analysis of their activity (basal respiration, mineralization of low molecular-weight C compounds and enzyme activities), and diversity (fingerprint profiling of fungi, bacteria and archaea) along a gradient of bird nesting intensity. We expected that in these naturally acidic and N- and P-poor soils, where microbial biomass and litter decomposition are strongly limited by a low P availability (Aponte et al., 2010, 2012), moderate inputs of guano would increase N and P availability, resulting in increased microbial biomass, basal respiration and extracellular enzyme activities. Under high nesting intensity conditions, however, we expected that the excess of salts and nutrients would negatively impact these variables. Thus, our first hypothesis is that the positive relationships between bird input intensity and microbial activity variables are not linear, but peak at intermediate levels of bird input intensity. Likewise, we expected a higher richness of Terminal Restriction Fragments (TRFs) at intermediate nesting intensities, but a decrease in richness at high bird nesting intensities due to the strong selective pressure imposed by soil acidification, hypersalinization and hyperfertilization. We expected that the changes would be particularly marked for the fungal community, in agreement with the reported decreases in fungal dominance in soils in response to fertilization and salinization (Wallenstein et al., 2006; De Vries et al., 2006; Rath and Rousk, 2015). Thus, our second hypothesis is that the decline in TRF diversity under high nesting intensity conditions is stronger for fungi than for bacteria or archaea.

2. Material and methods

2.1. Study site

Doñana National Park is located in SW Spain, and comprises about 30,000 ha of clayey marshlands and about 25,000 ha of dunes, sparse forests and shrublands on sandy soils (Montes et al., 1998). This National Park is one of the main wintering areas for birds in Europe (Rendón et al., 2008), as well as one of the most important areas for waterbird nesting in Western Europe (Ramo et al., 2013). The park is protected since 1969 and was declared as Biosphere Reserve in 1981 and as World Heritage Site in 1994. Climate is Mediterranean with an average annual rainfall of 550 mm and an average temperature of 16–17 °C.

Cork oaks in the area grow on acidic, nutrient-poor sandy soils, and are formed by a few thousand scattered centenarian trees (savannah-like woodland). Our study was conducted in the ecotone between the woodland and the marshland, which is locally known as “La Vera de Doñana”, where a colony of wading birds established in 1947–1948. The colony, ranging from 150 to 13,000 pairs of birds depending on the marsh flood level (Ramo et al., 2013), is composed by seven species: white stork (*Ciconia ciconia*), spoonbill (*Platalea leucorodia*), grey heron (*Ardea cinerea*), little egret (*Egretta garzetta*), cattle egret (*Bubulcus ibis*), squacco heron (*Ardeola ralloides*) and black-crowned night-heron (*Nycticorax nycticorax*). Birds intensively use cork oak trees as nesting sites, which often results in physical damage to the trees as well as in increases in soil salinity due to guano deposition (García et al., 2011).

2.2. Sampling design

Soil sampling was conducted in autumn 2012 and repeated at end of summer 2013, outside the nesting season (February to July). During the autumn (wet season), the influence of the bird colony on soil processes was expected to be lower, due to the leaching of guano during rainy events. Maximum accumulation of guano was expected to occur by the end of summer, just after the end of the nesting season and coinciding with the period of lowest rainfall.

The study was conducted across three levels of bird nesting intensity (low, medium, high), established based on the records of tree occupation by birds during the 1998–2012 period. Trees in the high nesting intensity (HNI) category had been used by birds during at least the last 13–15 years, with a number of nests per tree per year ranging between 12 and 75; trees under medium nesting intensity (MNI) had been occupied for 7–12 years, with an average annual occupation per tree ranging from 6 to 26 nests; trees in the low nesting intensity category (LNI) had had none to less than 2 nests per tree annually, been occupied by birds for a maximum of 4 years between 1998 and 2012.