Pedobiologia 58 (2015) 33–39

Contents lists available at ScienceDirect

Pedobiologia - Journal of Soil Ecology

journal homepage: www.elsevier.de/pedobi

Microbial carbon concentration in samples of seabird and non-seabird forest soil: Implications for leaf litter cycling

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ARTICLE INFO

Article history:
Received 8 August 2014
Received in revised form 14 January 2015
Accepted 14 January 2015

Keywords:
Below ground
Carbon cycling
Litter decomposition
Nutrient limitation
Procellariidae
Stable isotope

ABSTRACT

The paucity of leaf litter in seabird forest is usually explained by litter burial in burrows, but burial by itself fails to address the processes controlling decomposition. We measured soil microbial C in samples from a Westland petrel (*Procellaria westlandica*) colony both within and outside the breeding season, and compared the results with two non-seabird forests. From the few studies of seabird soil microbial C, we initially hypothesised a soil microbial C concentration sequence of occupied burrows > unoccupied burrows > adjacent forest floor > non-seabird forest. Instead, the highest values came from non-seabird forest, a pattern consistent with published meta-analyses on the effects of N addition. Within the colony, highest concentrations were in forest floor soil and there was no burrow occupation effect. However, seabird forest soil microbial C followed a strong inverse relationship with soil δ^{13}C ($r = -0.58$; $P < 0.001$) as well as the expected relationship with total soil C ($r = 0.75$); the relationship with soil δ^{13}C in non-seabird forest was not significant ($P = 0.29$). We propose that soil microbes in seabird forest repeatedly process a single pool of increasingly refractory terrestrial soil C, facilitated by seabird guano priming of organic matter mineralisation. In this context, the paucity of leaf litter in seabird forest can be seen as a consequence of microbial C limitation in a nutrient-saturated system, an explanation consistent with recent theory.

Introduction

Mineralisation of terrestrial detritus is primarily driven by soil microbes (Hobara et al. 2014). As well as controlling nutrient availability for plant uptake (Gessner et al. 2010; McGuire and Treseder 2010), soil microbes also drive C and N fluxes to the atmosphere and to waterways. Multiple meta-analyses based on hundreds of studies have shown that N addition usually decreases soil microbial C (Treseder 2008; Liu and Greaver 2010; Lu et al. 2011). Conversely, P addition can either increase (Liu et al. 2012) or decrease (Groffman and Fisk 2011) forest soil microbial C regardless of the nutrient status of plants growing at the site (Turner and Wright 2014).

Dense colonies of breeding seabirds function as ecosystem engineers on islands and other remote landscapes free of mammalian predators (Polis et al. 2004; Mulder et al. 2011; Smith et al. 2011). Guano makes up the majority of seabird detritus, and guano N and P are deposited across the colony at rates large even by the standards of intensive agriculture (Furness 1991). Guano stoichiometry is both species- and diet-dependent, but is considerably more P-rich than typical soil and soil microbes (Burger et al. 1978; Cleveland and Liptzin 2007; Turner and Wright 2014).

The few published studies available show that seabirds (regardless of whether they inhabit burrows or nest above ground) seem to increase both microbial biomass and microbial respiration, and enhance bacteria at the expense of fungi. At an island to island spatial scale involving mostly burrow-nesting seabirds, Fukami et al. (2006) found that removal of seabird inputs via rat predation was associated with decreased soil microbial respiration. In soils adjacent to surface nesting seabirds, Wright et al. (2010) found increased microbial biomass and an increased importance of bacteria relative to fungi, but no effect on litter decomposition rates. Along the same lines, Osono et al. (2006) found that excreta from surface-nesting cormorants inhibited certain classes of fungi but decreased needle litter decomposition rates.

Stoichiometric relationships drive the soil microbial processes that drive detritus mineralisation (Manzoni et al. 2008; Turner and Wright 2014). Departure within a system from an ideal stoichiometric relationship leads to disproportionate loss of the element present in excess (Rastetter et al. 2013), and (in principle) some degree of rate limitation. A recent formulation of the rate limitation aspect in the context of nitrogen saturation (Kopáček et al. 2013) emphasises the potential for microbial carbon limitation and increased bacteria: fungi ratios in soil systems where nutrient

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http://dx.doi.org/10.1016/j.pedobi.2015.01.002
0031-4056/

inputs have substantially disrupted long-standing stoichiometric relationships. In this context, the enhancement of bacteria in seabird soils (Wright et al. 2010) is most likely due to the low C:N ratio of seabird guano rather than the presence of labile, animal-derived C (Bastow 2012). Although interactions between C limitation and nutrient limitation are commonly observed (Kamble and Bååth 2014), the systems studied are often comparatively nutrient-poor.

Measurement of stable isotopic number ratios of C and N ($^{13}C/^{12}C$ and $^{15}N/^{14}N$, reported as $\delta^{13}C$ and $\delta^{15}N$) in various soil fractions complements traditional C:N stoichiometric approaches to organic matter cycling (Gleixner 2005; Craine et al. 2009; Prescott 2010). Patterns in the $\delta^{13}C$ of fresh plant litter, various fractions of soil organic matter and respired CO_2 serve to constrain models for organic matter transformations and turnover rates (Ehleringer et al. 2000). Notwithstanding a potential contribution from soil organic matter formed pre-1750 (the Suess Effect), the comparatively low $\delta^{13}C$ of CO_2 respired from soil explains the increased $\delta^{13}C$ of both older and deeper soil organic matter (Högberg et al. 2005). In contrast, foliar $\delta^{15}N$ typically indicates both soil and plant N status, with higher values reflecting a more open N cycle (Craine et al. 2009). Because the $\delta^{13}C$ and $\delta^{15}N$ of the marine environment is typically higher than on land, measurement of stable isotope ratios further facilitates studies of the soil ecology of seabird systems (Wainwright et al. 1998; Hawke 2004).

An immediately visible characteristic of forests supporting colonies of burrowing seabirds is the paucity of leaf litter (illustrations in Warham 1996 (Fig. 1.17, p52); Hawke 2004; Fukami et al. 2006), litter depth decreasing with increasing seabird burrow density (Towns et al. 2009). Explanations have typically focused on the seabirds themselves. Litter removal from the forest floor into burrows is widely reported (Warham 1996), and McKechnie (2006) measured litter incorporation at 33–96 g litter m^{-2} forest floor on seabird islands off southern New Zealand. However, this explanation is not particularly satisfying. Even if most leaf litter ends up in burrows, adult birds return any remaining detritus to the forest floor when they clean out their burrows at the start of each breeding season. Using incorporation into burrows as an explanation for the paucity of seabird forest litter is therefore contingent on rapid decomposition of the buried litter.

Burrow-nesting seabirds use their burrows to shelter both incubating adult birds and vulnerable nestlings, while adults walk the intervening ground to and from take-off trees and landing points. Consequently, a spatial structuring of soil microbial processes (Ettema and Wardle 2002) might be expected to parallel these different usages; burrows also support a specialist invertebrate fauna processing marine detritus (Hawke and Clark 2010; Hawke et al. 2013a). In this study, we initially hypothesised that soil microbial C concentration in a colony of burrowing seabirds would be higher in areas most affected by the birds (occupied burrows), and lower in unoccupied burrows and on the adjacent forest floor. We also hypothesised that microbial C would be higher in the seabird soil than in nearby forest with no seabird inputs and a low nutrient status. Our results did not support these hypotheses, so we used soil $\delta^{13}C$ and total soil C to explore potential C limitation based on the conceptual framework proposed by Kopáček et al. (2013) and the potential for guano-driven priming of soil organic matter mineralisation (Kuzyakov 2010).

Materials and methods

Study sites

Three climatically-similar sites on the western coast of New Zealand's South Island (Fig. 1) were chosen. The seabird site south of Punakaiki (annual rainfall c. 2500 mm) hosts Westland petrels (*Procellaria westlandica*) and has been occupied by seabirds since at least the mid-1700s (Holdaway et al. 2007). The two non-seabird sites were near Saltwater and Okarito (rainfall c. 3100 mm), 175 km and 200 km to the south respectively. Saltwater Forest was selectively logged until 2002, whereas the Okarito site is comparatively undisturbed.

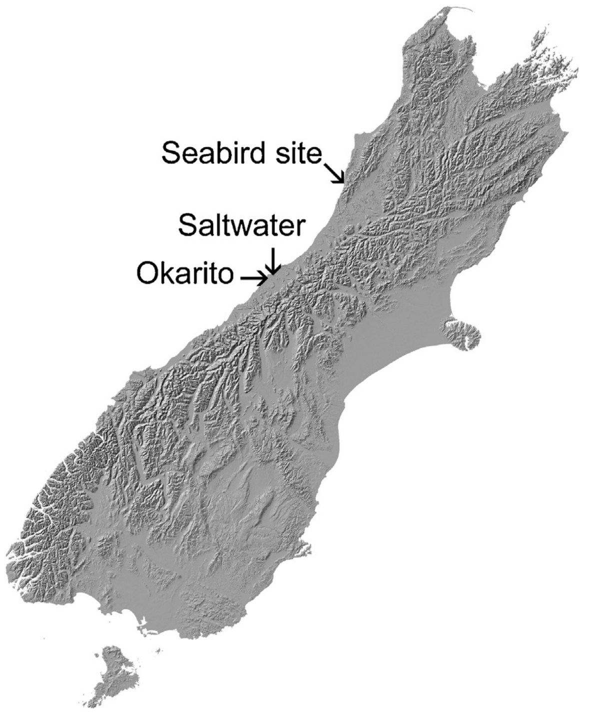

Fig. 1. Locations on the South Island (New Zealand) West Coast of the seabird forest site south of Punakaiki, and the two non-seabird sites at Saltwater and Okarito. Base digital elevation map courtesy of R. Holdaway.

The petrel sub-colony we sampled (colony 7 in Wood and Otley 2013; 42°08.8′S, 171°20.5′E) has a mean burrow density of 0.2 m^{-2} (Waugh et al. 2003) and occupies a steep, SSE-facing slope above Scotchmans Creek (Hawke 2004). The soil is a Dystrudept of silt loam texture developed on muddy sandstone parent material. Soil pH (H_2O) is 3.5–4.0. Soils at both Saltwater Forest and Okarito sites are developed on late Pleistocene glacial outwash. Our sampling at Saltwater Forest was on poorly drained terraces dissected with occasional small streams; soils are Alaquods and A horizon pH is 4.0 (Almond and Tonkin 1999). The topography we sampled at Okarito consists of low ridges and moderately steep-sided gullies on glacial moraines (Turnbull et al. 2003). Based on the detailed pedogenic investigations at Saltwater Forest (Almond and Tonkin 1999), soils at our Okarito site are probably Dystrochrepts with a pH of 3.5–4.0.

Seabird site vegetation is dominated by tree ferns (*Cyathea* spp.) and kamahi (*Weinmannia racemosa*), with scattered podocarps (especially matai *Prumnopitys taxifolia* and rimu *Dacrydium cupressinum*) and southern rata (*Metrosideros umbellata*) on the ridgeline. Vegetation at both non-seabird sites is podocarp-broadleaf forest dominated by rimu. The understorey at Saltwater Forest is more open, reflecting an ongoing recovery from logging. From nutrient limitation studies at the Franz Josef chronosequence (Richardson et al. 2004; Turner et al. 2012) 20 km south of Okarito as well as other New Zealand chronosequences (Parfitt et al. 2005; Coomes et al. 2013), both Saltwater and Okarito forests are likely to be P limited. The Franz Josef chronosequence is is developed on similar glacial outwash to both non-seabird sites. The soil age at our seabird site (c. 1000 years; Hawke 2004) and humid climate also suggest an underlying P limitation, but the modification of soil nutrient status