European Journal of Soil Biology 52 (2012) 78–83

Contents lists available at SciVerse ScienceDirect

European Journal of Soil Biology

journal homepage: http://www.elsevier.com/locate/ejsobi

Original article

Stable isotope evidence for marine-derived avian inputs of nitrogen into soil, vegetation, and earthworms on the isle of Rum, Scotland, UK

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A R T I C L E I N F O

Article history:
Received 20 March 2012
Received in revised form
25 June 2012
Accepted 16 July 2012
Available online 27 July 2012
Handling editor: Bryan Griffiths

Keywords:
Guano
Sea birds
Manx shearwater
Puffinus puffinus
Earthworm

A B S T R A C T

The largest breeding colony of Manx shearwaters (*Puffinus puffinus*) in the world is found on the Isle of Rum in the inner Hebrides of Scotland. We collected a feather, guano, soil, vegetation, and earthworms near shearwater burrows to determine whether inputs of nitrogen (N) from guano were incorporated into belowground foodwebs. For comparison, similar samples were collected from a nearby plot that was experimentally fertilised 40 years prior. The shearwater feather had the highest level of ^{15}N enrichment (+18‰), followed by guano (+12‰). Soil (+7.5‰) and vegetation (+5.7‰) collected at the burrow entrance were enriched with ^{15}N relative to those collected at 2 m or more away (+0.5 to +3.1‰ for soil, and −2.5 to −4.6‰ for vegetation). In contrast, soil inside the fertilised plot had δ^{15}N ≈ 0, but was enriched with ^{15}N away from the plot edge. Earthworms collected from shearwater greens had enriched ^{15}N signatures relative to earthworms from the fertilised plot (+3.8 and −0.9‰, respectively). Our data suggest that available N is tightly cycled in vegetation and soil for decades, and that shearwater derived N is substantially assimilated by earthworms. Therefore, because earthworms do not occur outside areas of shearwater influence, the birds should be viewed as ecosystem engineers of soil invertebrate foodwebs on Rum.

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1. Introduction

The Isle of Rum, in the Inner Hebrides of Scotland is home to the largest single breeding colony (61,000 pairs) of Manx shearwater (*Puffinus puffinus* [Brunnich, 1764]) in the world [1]. These obligately piscivorous birds nest in burrows constructed on the nutrient poor, rocky slopes of the highest peaks (~800 m elevation) on the island. Soils around the entrances to burrows are enriched by frequent inputs of guano as the birds embark upon and return from feeding forays, and consequently, these soils support relatively lush vegetation in areas termed shearwater greens which occur around burrow entrances and sometimes extend several metres down-slope (Fig. 1). There have been numerous demonstrations of nutrient inputs derived from birds having dramatic influence on plant community composition and growth, and these effects may even have influence upon aboveground food-webs [e.g., [2,3]], but the fate of these inputs relative to belowground pools has been less well documented. Interestingly, inputs of guano with nitrogen derived from marine sources have been shown to have stable isotope δ^{15}N signatures that are distinct from other terrestrial pools of N, and these distinct inputs have been widely used as ecological tracers [4]. Stable isotopes of multiple elements (C, N, H, O, S) have been used in numerous demonstrations of bird dietary and trophic ecology, to reveal migration patterns, and increasingly isotopes are being used to trace avian sources of N into terrestrial and aquatic foodwebs [5–9].

Stable isotopes of carbon (^{13}C) and nitrogen (^{15}N) have been used successfully to document foodweb interactions belowground and in particular to elucidate the feeding ecology of earthworms in several ecosystems [e.g., [10–14]], but very few studies have yet examined the transfer of N from avian sources to macroinvertebrate consumer guilds in the detrital foodwebs of soil. In a study of arthropods inhabiting blue penguin burrows, Hawke and Clark [7] used stable isotopes to demonstrate that different invertebrate taxa collected within penguin burrows used different sources of C (either soil C or guano C), suggesting that these invertebrates partitioned the available avian derived resources in this community.

Burrowing sea birds (wedge-tailed shearwaters, *Puffinus pacificus*) are considered to be crucial in soil-formation processes on some islands [15], and the closely related Manx shearwaters are known to engage in similar behaviours as they excavate and clean their burrows prior to nesting. This type of physical modification of habitat has been termed ecosystem engineering [16], but the term is used in particular to identify species “that directly or indirectly

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1164-5563/$ – see front matter Published by Elsevier Masson SAS.
http://dx.doi.org/10.1016/j.ejsobi.2012.07.004

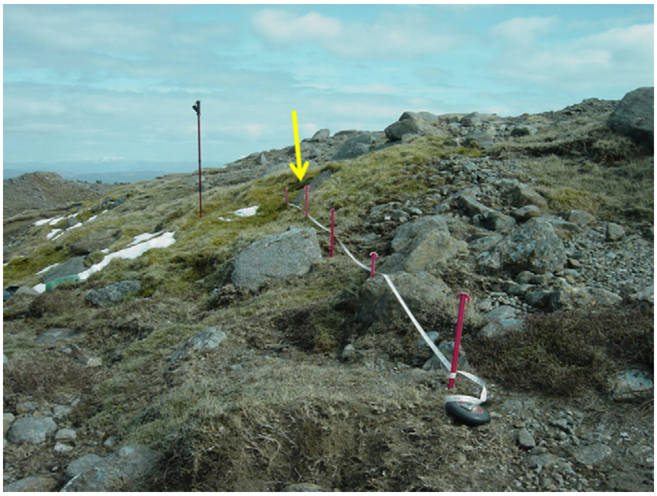

Fig. 1. Example of a shearwater "green". Note the contrast between vegetation near the burrow entrance (indicated by arrow) and that in the foreground. The stakes indicate 1 m intervals along the sampling transect away from the burrow entrance.

modulate the availability of resources to other species, by causing physical state changes in biotic or abiotic materials." [16]. Shearwater greens (burrowing and nesting areas) are recognized among Scottish Natural Heritage land managers as a distinct habitat type, and cover approximately 30 ha in aggregate on Rum [17]. Additionally, previous sampling of earthworms on Rum revealed that greens surrounding the entrances to shearwater burrows were among the only locations where earthworms could reliably be collected at high elevations [18]. Manx shearwaters are therefore appropriately viewed as ecosystem engineers (*sensu* Jones et al. [16]), as they actively construct and maintain habitats that would otherwise not be available to earthworms.

Objectives for this study were to characterize natural abundance $\delta^{15}N$ signatures of soils, vegetation, and soil invertebrates in the vicinity of active Manx shearwater burrows, and to compare isotopic signatures of shearwater green samples with similar material from artificially fertilised plots at high elevation.

2. Materials and methods

2.1. Site description

The Isle of Rum is a 10,650 ha reserve owned and managed by Scottish Natural Heritage. The site has a maritime climate with cool summers and warm winters, and 3000 + mm of rainfall annually at higher elevations. Sampling for this study was conducted on the upper slopes of Hallival Peak (>500 m elevation) in the south-eastern quadrant of the island. Soils on the ultrabasic upper slopes are deep brown earths which have weathered in place, and which have very low native fertility [19].

2.2. Field methods

Sampling was accomplished on two separate sampling trips (28–30 July 2007 and 13–15 April 2008). Although these two sampling trips were separated by 3 months relative to the season of the year, shearwaters on Rum actively nest, breed, and rear chicks from approximately the third week in March until the second week of October, and shearwater droppings can be found around burrow entrances continuously from spring until autumn [17]. Sampling involved collection of a Manx shearwater feather, shearwater guano, soil, vegetation, and earthworms from two different sites on the upper slopes of Hallival peak on Rum. Specifically, samples were taken from shearwater-impacted soils, and from an experimental plot (10 × 10 m) where fertiliser (NPK) was applied at 650 m elevation in 1965, 1967, and 1968 (Details for the historical treatment of this plot are given by Ferreira and Wormell [20]). We selected representative Manx Shearwater burrows from the north flank of Hallival peak, just below the summit (the same aspect as the fertiliser plot). For all sites, soil sampling involved using a hand-trowel to take a roughly cylindrical sample approximately 5 cm in diameter to a depth of 10 cm (or rarely to the depth where solid rock was encountered). Vegetation sampling at all sites consisted of clipping a 10 × 10 cm plot of all vegetation immediately adjacent to the site where soil was sampled. Of necessity, this involved the collection of multiple species of plants at each site. Although we did not attempt to identify or quantify particular species within our samples, previous research in these systems has documented that shearwater greens share attributes of the *Festuca/Agrostis* grasslands found at lower elevations on the island, with the exception that shearwater greens typically have a greater component of mosses and a smaller component of herbs than the lower elevation grasslands [17]. The turf of shearwater greens was composed mainly of *Festuca vivipara*, *F. rubra*, *Agrostis tenuis*, and *A. stolonifera* [17], whereas vegetation in areas on the margins of the shearwater greens was more characteristic of highland heath and contained patchy cover of *Calluna vulgaris*, *Molinia* spp., and *Vaccinium* spp (K.R. Butt, personal observations). Vegetation on the fertiliser plot was similar to that found on shearwater greens, and was dominated by mosses and grasses, principally *F. vivipara*, *Rhytidiadelphus squarrosus*, and *Hypnum cupressiforme* [21].

Soils and vegetation were sampled at 1-m intervals along transects spanning from a burrow entrance into soil that was not impacted by guano inputs. Five burrow transects on two separate greens were sampled across the hill slope. Each green surrounded multiple burrow entrances, and for statistical purposes, the burrow is the experimental unit. Burrows were intentionally selected on the criterion that a 4-m transect would extend (approximately by 2 m) past the visible influence of shearwater activity on vegetation (Fig. 1). For three transects, sampling was extended such that soils and vegetation were also collected at 6 and 8 m distances. Earthworms were collected by turning over stones in the vicinity of the burrow transect on and around the green. Mustard extractions [22] were attempted, but found to be ineffective for earthworm collection in this situation. Efforts at earthworm collection were unsuccessful in soils that were more than 1.5 m from the burrow entrance (i.e., in soils not directly on the green).

Similar sampling was conducted in three transects crossing the edge of the historic fertiliser plot. In this case, sampling transects were centered on the edge of the plot with soil and vegetation samples collected at the plot edge in addition to 2.5 and 5 m inside and out of the plot. Earthworms were collected by turning stones and peeling back small amounts of turf around large stones along the sampling transects. Efforts to collect earthworms away from the fertiliser plot using recognised techniques were unsuccessful. All earthworms collected from both shearwater greens and from the fertiliser plot were immediately placed in 70% ethanol until they could be analysed for stable isotope content.

2.3. Laboratory analysis

Soils and vegetation samples were initially air-dried (~18 °C) before being sealed in plastic bags and transported for stable isotope analysis. Prior to analysis, soil and vegetation samples were oven-dried (45 °C), and then ground to a fine powder in a Spex 3000 mixer/mill. Stable isotope and total N analysis were conducted on a Finnegan Delta-C continuous flow isotope ratio mass