Northward range extension of an endemic soil decomposer with a distinct trophic position

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Ecological niche theory asserts that invading species become established only if introduced propagules survive stochastic mortality and can exploit resources unconsumed by resident species. Because their transportation is not controlled by plant health or biosecurity regulations, soil macrofauna decomposers, including earthworms are probably introduced frequently into non-native soils. Yet even with climatic change, exotic earthworm species from southern Europe have not been reported to become established in previously glaciated areas of northern Europe that already have trophically differentiated earthworm communities of ‘peregrine’ species. We discovered established populations of the earthworm Prosellodrilus amplisetosus (Lumbricidae), a member of a genus endemic to southern France, in six habitats of an urban farm in Dublin, Ireland, about 1000 km north of the genus’s endemic range. Not only was P. amplisetosus the dominant endogeic (geophagous) earthworm species in two habitats, it also occupied a significantly different trophic position from the resident species, as evinced by stable isotope ratio analysis. The suggested ability of this non-native species to feed on and assimilate isotopically more enriched soil carbon (C) and nitrogen fractions that are inaccessible to resident species portends potential implications of decomposer range expansions for soil functioning including C sequestration.

Keywords: decomposers; ecological niche; soil carbon; soil macrofauna; species introductions

1. INTRODUCTION

Scientists have long extolled the importance of beneficial soil macrofauna for soil ecosystem functioning. In particular, earthworms are a valued component of the soil fauna owing to their roles in decomposition, nutrient cycling and physical soil engineering [1]. However, in land areas not recolonized naturally by earthworms since the Late Quaternary glaciation, including some North American forests, recent invasions by non-native earthworms have had highly detrimental impacts on soils and ecosystems [2,3].

In northern Europe, including Great Britain and Ireland, earthworms recolonized glaciated areas during the Holocene, probably through a combination of natural and anthropogenic mechanisms such as farming and trade [3–5]. Almost all earthworm species found (outdoors) in northern Europe belong to the ‘peregrine’ group of about 33 holarctic Lumbricidae species that are now dispersed widely in temperate regions [6]. By contrast, records in northern Europe of any of the numerous endemic, non-peregrine species from southern Europe are sporadic, and full establishment has not been documented [3–5]. Notwithstanding the small total species pool, northern European earthworm communities are ecologically diverse, with coexisting species representing all three ecological groups, i.e. the endogeics (mineral-soil dwellers), epigeic (surface-litter dweller) and anecic (deep-burrowers) [4]. It is unlikely that major food resources (e.g. litter, dung, high-quality soil organic matter) are left unconsumed by these earthworm communities [7]. According to the ecological niche theory advocating stochastic competitive community assembly [8], it is therefore improbable that invading species can become established from introduced propagules. Even if new species were to become established in this situation, then they would be unlikely to have negative ecosystem effects as severe as those observed in earthworm-free, North American habitats [2,9], unless their resource use would differ markedly from that of resident species.

Here, we report the discovery in Ireland of established populations of the endemic southern European earthworm Prosellodrilus amplisetosus (Lumbricidae, Annelida). We also test the hypothesis that the trophic niches (defined as the use of soil carbon (C) and nitrogen (N) resources) of P. amplisetosus and of native earthworm species differ, by comparing natural C and N stable isotope compositions.

2. MATERIAL AND METHODS

(a) Earthworm survey

We conducted an earthworm survey on Airfield farm, Dundrum, Co. Dublin (53°17’ N; 6°14’ W, 75 m elevation), a 13.5 ha educational, urban, mixed farm. In March 2011, we surveyed 11 habitats distributed across the farm: reseeded pasture, reseeded pasture margin, old pasture, old pasture margin, meadow, deciduous wood, coniferous wood, compost heap, manure heap, formal garden and vegetable garden. The approximate habitat locations on the farm are illustrated in the electronic supplementary material, figure S1.

We excavated six soil blocks (25 x 25 x 25 cm) in each of the 11 habitats and extracted earthworms by hand-sorting. Then, we used 21 of a 0.2 per cent mustard oil (alyl isothiocyanate dispersed in iso-propanol) solution to expel deep-burrowing earthworms from each pit. In addition, we sampled a transect from the margin into the reseeded pasture at 0.5, 1.5, 2.5, 5.0 and 10.0 m. Earthworms were weighed alive, fixed in 4 per cent formalin and adults identified to species level using [4], and [5] in the case of P. amplisetosus.

We identified, allowed to evacuate their guts, weighed, freeze-dried and powdered. Five individuals of each species were used except Aporrectodea longa for which only two specimens were available. Adults were used except for Lumbricus spp. (all juveniles) and Aporrectodea caliginosa (four juveniles, one adult). Worm tissues were analysed using an Elemental Analyser—Isotope Ratio Mass Spectrometer (Europa Scientific Mass Spectrometer, 20–20) at Iso-Analytical Ltd. (UK), and results are expressed in delta per mil (%o) notation. Analytical precision (s.d., n = 5) for powdered bovine liver reference material (δ13C = −21.60‰, δ15N = 7.65‰)


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3. RESULTS

We recorded high earthworm abundances (115–635 individuals m\(^{-2}\)) and species richness (4–12 species per 25 cm sample) from a transect in the reseeded pasture. MANOVA revealed significant differences among the six cosampled species in \(^{13}\)C and \(^{15}\)N (Wilk’s \(F_{10,36}=17.9, \ p<0.001\)). The C and N isotope biplot (figure 2a) showed that \(P. \text{amplisetosus}\) had a distinct trophic position compared with all other soil-feeding species and, when tested separately, was significantly more isotopically enriched than the nearest (and morphologically most similar) endogeic species, \(Aporrectodea \text{rosea}\) (Wilk’s \(F_{2,7}=7.6, \ p<0.05\)). Litter-feeding \(Lumbricus\) spp., also showed an expected trophic difference (less enriched in \(^{13}\)C and \(^{15}\)N; figure 2a).

The distinct isotopic composition of \(P. \text{amplisetosus}\) among endogeics (figure 2a) was not simply an effect of body size (figure 2b), because juvenile \(A. \text{caliginosa}\) were smaller than \(P. \text{amplisetosus}\) but isotopically less enriched (by 0.71‰ and 2.29‰ in \(^{13}\)C and \(^{15}\)N). The C : N ratio of \(P. \text{amplisetosus}\) was higher than that of the other endogeic species analysed (figure 2b), but neither body mass nor C : N ratio was a significant covariate in MANCOVA (\(p>0.10\)).

4. DISCUSSION

All lumbricid species recorded in Great Britain and Ireland, including the few recent additions, are peregrine species or belong to peregrine genera [4,11]. By contrast, the genus \(Proscolaelodes\), comprising about 25 species, has a small, endemic range in the Aquitaine region of southwestern France, with a few species occurring in northern Spain, Sardinia and northern Africa [5,12]. The established \(P. \text{amplisetosus}\) populations in Dublin represent a northward range extension for the genus of about 1000 km. A previous record of a single adult \(P. \text{amplisetosus}\) from a farm in County Louth, Ireland [13], together with sporadic records from single, agricultural locations in Galicia, Spain [14] and Burgundy, France [15], could suggest that this species’ geographical range is expanding.

The extent and speed of northward range extensions, as well as the agents and climate factors, are well-documented for economically important taxa such as invasive terrestrial arthropods [16] and plant pests [17]. Soil decomposer species, by contrast, are not considered pests or a biosecurity risk, yet they are

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**Table 1.** Number of earthworm species, mean total abundance and biomass (all earthworms, adults and juveniles) in each habitat (\(n=6\), s.d. in parentheses).

<table>
<thead>
<tr>
<th>habitat</th>
<th>no. of species</th>
<th>individuals (m(^{-2}))</th>
<th>biomass (g m(^{-2}))</th>
</tr>
</thead>
<tbody>
<tr>
<td>reseeded pasture</td>
<td>12</td>
<td>635 (226)</td>
<td>195 (89)</td>
</tr>
<tr>
<td>reseeded pasture margin</td>
<td>10</td>
<td>555 (244)</td>
<td>140 (50)</td>
</tr>
<tr>
<td>old pasture</td>
<td>10</td>
<td>544 (105)</td>
<td>185 (61)</td>
</tr>
<tr>
<td>old pasture margin</td>
<td>7</td>
<td>184 (95)</td>
<td>91 (60)</td>
</tr>
<tr>
<td>meadow</td>
<td>9</td>
<td>504 (442)</td>
<td>107 (109)</td>
</tr>
<tr>
<td>deciduous wood</td>
<td>9</td>
<td>306 (136)</td>
<td>156 (102)</td>
</tr>
<tr>
<td>coniferous wood</td>
<td>4</td>
<td>115 (175)</td>
<td>72 (53)</td>
</tr>
<tr>
<td>compost heap</td>
<td>12</td>
<td>371 (514)</td>
<td>90 (125)</td>
</tr>
<tr>
<td>manure heap</td>
<td>6</td>
<td>138 (136)</td>
<td>38 (40)</td>
</tr>
<tr>
<td>formal garden</td>
<td>5</td>
<td>309 (84)</td>
<td>42 (20)</td>
</tr>
<tr>
<td>vegetable garden</td>
<td>9</td>
<td>171 (215)</td>
<td>36 (41)</td>
</tr>
</tbody>
</table>

was 0.02‰ and 0.06‰ for C and N. We used MANOVA to compare isotopic compositions (\(\delta^{13}\)C and \(\delta^{15}\)N) of species, and MANCOVA of endogeic species data with individual worm biomass and C : N ratios as covariates (Minstaa v. 16) to rule out that the latter two factors caused artefactually distinct isotopic values [10].

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**Figure 1.** (a) Mean abundance (adults m\(^{-2}\), \(n=6\)) of the four endogeic earthworm species (\(A. \text{caliginosa}, Allobophora chlorotica, A. \text{rosea} \) and \(P. \text{amplisetosus}\)) in 11 habitats. See table 1 for total abundances. (b) Number (adults) of \(P. \text{amplisetosus}\) and all other earthworm species (per 25 \(\times\) 25 \(\times\) 25 cm sample) from a transect in the reseeded pasture.
likely to be transported frequently. The European earthworm distribution has not been mapped formally [11,12], and hence range shifts or expansions have not been documented systematically.

The high earthworm abundances and species richness observed at Airfield are comparable to those in similar habitats across Ireland [18]. The six habitats in which *P. amplisetosus* was recorded had between five and 12 native earthworm species, including three endogeic species (*Al. chlorotica*, *Ap. caliginosa* and *A. rosea*) that are among the most widespread and successful of all peregrine lumbricid species [5]. Stable isotope data suggest strongly that *P. amplisetosus* is the most extreme soil-feeder of all endogeic, geophagous species. Its isotopic elevation was not related to body size or biochemical composition; in fact the higher C : N ratio of *P. amplisetosus* tissues implied a higher lipid content and thus a more negative δ13C value [10], and smaller body size in endogeic species was associated with lower δ15N values in a previous study [10]. A possible mechanistic explanation for this distinct trophic position among endogeics is that *P. amplisetosus* assimilates C and N from other soil organic matter fractions. Perhaps it consumes soil organo-mineral particles containing soil organic matter fractions that are more microbially processed and hence more 13C and 15N enriched [19] than those consumed by resident endogeic species. A depth effect is unlikely in a reseeded (ploughed) pasture soil.

While the suggested exploitation of unused soil C and N resources by *P. amplisetosus* concurs with niche theory and explains this species’ invasion success, it also has potential implications for soil functioning [9]. If soil decomposer taxa such as *Prosellodrilus* expand their ranges, facilitated by climatic change, they might access and mobilize soil organic C pools that are unavailable to resident species. Southern species could also stay active longer under drier conditions. This novel feeding activity could potentially counteract the beneficial effects of resident species [1] on C and N dynamics, soil C sequestration and also soil physical properties.

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![Figure 2](http://rsbl.royalsocietypublishing.org/)

Figure 2. (a) Carbon (C) and nitrogen (N) stable isotope composition of five co-occurring earthworm species and juvenile *Lumbricus* spp. (means ± s.d., n = 5 except *Ap. longa* n = 2). (b) Mean biomasses and mean C : N ratios of the four endogeic species (mean ± s.d., n = 5 except *Ap. caliginosa* n = 4 juveniles, n = 1 adult).


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