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ORIGINAL PAPER

Increases in invertebrate abundance and shifts in assemblage composition following rodent eradication on Lord Howe Island

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Abstract Invasive rodents represent one of the most serious threats to island ecosystems, affecting a wide range of native plants, vertebrates and invertebrates. While nearly ubiquitous on human-modified islands, the last four decades have seen the advent of targeted rodent eradications, which have generally resulted in positive impacts for biodiversity. Invertebrates, which are crucial to the functioning of island ecosystems, are known to be negatively impacted by rodents, but their response to rodent removal is less well understood. The largest rodent eradication on an inhabited island was undertaken in 2019 on Australia's Lord Howe Island, which successfully extirpated black rats (*Rattus rattus*) and house mice (*Mus musculus*) more than a century after their introduction. To examine the impacts of rodents on invertebrates on Lord Howe Island, we collected arboreal and terrestrial species and identified them to order. Samples were taken from 20 sites across the island's two main soil types, collected in two annual cycles pre- and post-eradication, respectively. Total invertebrate abundance increased after the eradication of rodents, alongside substantial shifts in assemblage composition, however ordinal diversity slightly decreased, albeit with strong seasonal variation. Orders with large increases in abundance included Isopoda and Blattodea, while the abundance of Coleoptera and Polydesmida did not change. In addition, the abundance of large invertebrates, which are presumably subject to stronger rat predation, rose dramatically following rodent eradication. While we cannot exclude an effect of extraneous environmental changes, our results suggest an ecological rearrangement following the relaxation of predation pressure and augment documented evidence of improved biodiversity outcomes for forest tree species, seabirds and land birds.

Keywords Predator eradication · Invasive species · Invertebrates · Lord Howe island · Ecosystem recovery · Restoration ecology

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Terence O'Dwyer and Maxim W. D. Adams have contributed equally to this work.

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Introduction

Introduced species are one of the most significant drivers of biodiversity loss on islands (Fernández-Palacios et al. 2021; Towns et al. 2006). Rodents in particular readily establish on islands and can precipitate declines across a broad swathe of taxa (Angel et al. 2009; Banks and Hughes 2012; Shiels et al. 2014; Towns et al. 2006). Human-commensal rats (*Rattus* spp.) and mice (*Mus* spp.) prey on a wide range of species, including mammals, birds, reptiles, amphibians, invertebrates and plants, which often results in long-term degradation of ecosystem functions such as pollination, seed dispersal, nutrient cycling and trophic regulation (Angel et al. 2009; Atkinson 1985; Auld et al. 2010; Campbell and Atkinson 2002; Cuthbert and Hilton 2004; Pender et al. 2013; Shaw et al. 2005; Shiels and Drake 2011; Smith et al. 2002; Towns et al. 2006Wanless et al., 2007). It is estimated that over 90% of the world's islands now harbour introduced rodents, and that these species have often been present for decades (Towns et al. 2006).

In the last 40 years, improvements in biological control methods have made it feasible to completely extirpate invasive species from insular habitats. This has effected a new paradigm in island conservation, centred on invasive-predator eradication (Russell and Broome 2016). To date, 842 successful rodent eradications have been undertaken on islands, and the biodiversity benefits are typically substantial, though variable across taxa (DIISE 2019; Holmes et al. 2019; Segal et al. 2021). In addition, the introductions of rodents to islands often occurred soon after human arrival and prior to detailed biodiversity surveys, resulting in incomplete understanding of their adverse impacts (Drake and Hunt 2009; Towns et al. 2006). Contemporary eradications and associated monitoring programs therefore provide opportunities to systematically investigate ecological rebound or trophic cascades, and to discern the consequences of historical rodent incursion.

Lord Howe Island (LHI), a small (<15 km^2) volcanic relic *ca*. 600 km east of Australia, is a well-documented example of an island adversely affected by introduced rodents. House mice (*Mus musculus*) probably arrived on LHI in the late 1860s (Hill 1869), while black rats (*Rattus rattus*) arrived in 1918 following the grounding of the *SS Makambo* (Nicholls 1953). Both species became widespread across the island, inhabiting built and natural environments. In the century that followed, rats were responsible for the extinction of five endemic bird taxa (Hindwood 1938), the extirpations of multiple invertebrate species and populations, and the declines of many additional species (Lord Howe Island Board 2007); the impacts of mice upon the fauna are less understood. Rats are also likely to have increased the extinction risk for two endemic palm species through predation of fruits (Auld et al. 2010). However, as robust biodiversity surveys were undertaken many decades after the arrival of rodents on LHI, the true extent of biodiversity loss remains unknown.

In response to these impacts, a rodent eradication program (REP) was carried out on LHI in 2019 to simultaneously extirpate both black rats and house mice. This was the largest such program ever undertaken on an inhabited island, utilising a combination of aerial, hand-broadcast and bait-station dispersal of the rodenticide Brodifacoum (Harper et al. 2020). A comprehensive success check in 2023 found no evidence of mouse or rat presence on LHI, indicating that eradication was successful (Lord Howe Island Board 2023). In recognition of the opportunity to study ecosystem recovery, as well as to address public and scientific concerns about the cost effectiveness and merits of rodent eradication (see LHIB, 2007), the REP included a multi-faceted biodiversity monitoring program to assess outcomes for island flora and fauna. This included monitoring of invertebrate assemblages, with samples collected both before (2016–17) and after (2023–24) the 2019 eradication. The response of invertebrates is of great scientific interest, not only for their contributions to ecosystem processes such as nutrient cycling, pest control and pollination, but also because studies of post-rodent eradication recovery on islands have typically focused on birds, mammals or reptiles (St Clair et al. 2011; Segal et al. 2021).

Where conducted, previous invertebrate surveys following rodent eradication or exclusion have documented highly heterogeneous impacts, ranging between decreases to substantial increases in total abundance or the abundances of individual species (Brittenden 2024; Gerlach 2005; Green 2002; Norbury et al. 2013; Samaniego-Herrera et al. 2017; Sinclair et al. 2005; Towns, 2009; Van Aarde et al. 2004; Vergara et al. 2021). Post-eradication changes in diversity are similarly variable, and do not necessarily correlate with changes in abundance (Holthuijzen 2021; Sinclair et al. 2005; Watts et al., 2014, 2020). While the removal of exotic predators may be expected to benefit invertebrate communities, the interruption of top-down regulation of island biota can have indirect consequences due to mesopredator release, new competitive dynamics, or release of invasive prey species (Baker et al. 2020; Bird et al. 2024; Bode et al. 2015; Borrelle et al. 2018; Kurle et al. 2021). Sustained rodent presence may also lead to the complete extinction of prey species, limiting ecosystem recovery following eradication (Vergara et al. 2021). However, in several of these studies, the impacts of rodent eradication were somewhat obscured by limited sample sizes or temporal variability (Norbury et al. 2013; Samaniego-Herrera et al. 2017; Sinclair et al. 2005). In addition, a number of studies only examined one or few invertebrate species (Brittenden 2024; Gerlach 2005; Newman 1994; Norbury et al. 2013; Watts et al., 2020), emphasising the need for larger-scale surveys to understand ecosystem-level changes in abundance and diversity.

LHI is a suitable model system for further research of invertebrate responses to rodent eradication, as terrestrial invertebrates are exceptionally abundant and diverse, with > 1600 described species. Almost half are endemic to LHI (including the offshore islets), and the proportion of exotic species is relatively low (*ca.* 5%; Cassis et al. 2003). It is unknown how different components of the invertebrate fauna responded to rodents. In general, both *Rattus* and *Mus* species preferentially target larger invertebrates (length > *ca.* 10–13 mm; Angel et al. 2009; Towns et al. 1997; Watts et al. 2020), although their dietary preferences are strongly moderated by competition when they co-occur (Angel et al. 2009). The taxonomic compositions of invasive rodents' diets are also frequently dominated by Hemiptera, Araneae, Orthoptera, Coleoptera or Lepidoptera (reviewed by Shiels et al. 2014), yet the proportions of these and other orders in their diets vary greatly between islands (Harper & Bunbury 2015; St Clair, 2011) and have never been studied on LHI. Documented impacts of rodents on LHI are primarily at the species or population level, and mostly limited to macroinvertebrates. These include the losses of two endemic land snails (*Epiglypta howinsulae* and *Placostylus bivaricosus etheridgei*; Ponder 1997), 11 beetle species (C. Reid, unpub. data), the LHI population of the phasmid *Dryococelus australis* (now restricted to Ball's Pyramid; Priddel et al. 2003), and the near-extinction of the LHI population of the cockroach *Panesthia lata* (Adams et al. 2026; Carlile et al. 2018). In addition, the small islets surrounding LHI (which remained rodent-free) harbour comparatively high species diversity of spiders, ants and beetles, suggesting that these taxa may have experienced significant rodent predation on LHI (Cassis et al. 2003).

Here we present the results of comprehensive invertebrate sampling undertaken on LHI before and after the REP to examine whether: 1) invertebrate abundance and diversity increased following the REP, or whether recovery may have been moderated by other ecosystem processes; and 2) whether changes were ubiquitous across invertebrate orders and size classes, or whether certain groups responded more strongly to the REP.

Methods

Surveys

Invertebrate sampling was conducted at 20 sites across the lowlands on LHI (Fig. 1). To ensure balanced representation of both major soil types on the island, 10 sites were located on calcarenite bedrock and 10 were located on basalt bedrock (Fig. 1; Supplementary Table S1). These soil types correspond with a suite of potentially significant environmental variables: basaltic bedrock underlies the high-relief slopes of the island's northern and southern mountains, and sustains primarily closed forest; while calcarenite bedrock is found in LHI's central lowlands, produces comparatively nutrient-poor and alkaline soils, and sustains a mosaic of grasslands, shrublands and forests (Sheringham et al. 2016). Human settlement is also restricted to the calcarenite soils (LHIB, 2007). To allow for consistency in our sampling methods, all sites were located in closed forest, which is the dominant habitat on LHI (Sheringham et al. 2016). Each site spanned an area of *ca.* 100 m^2, and consisted of various tree, shrub and associated groundcover species (with ≥ 8 individual trees), and a substrate with varying amounts of leaf litter, soil

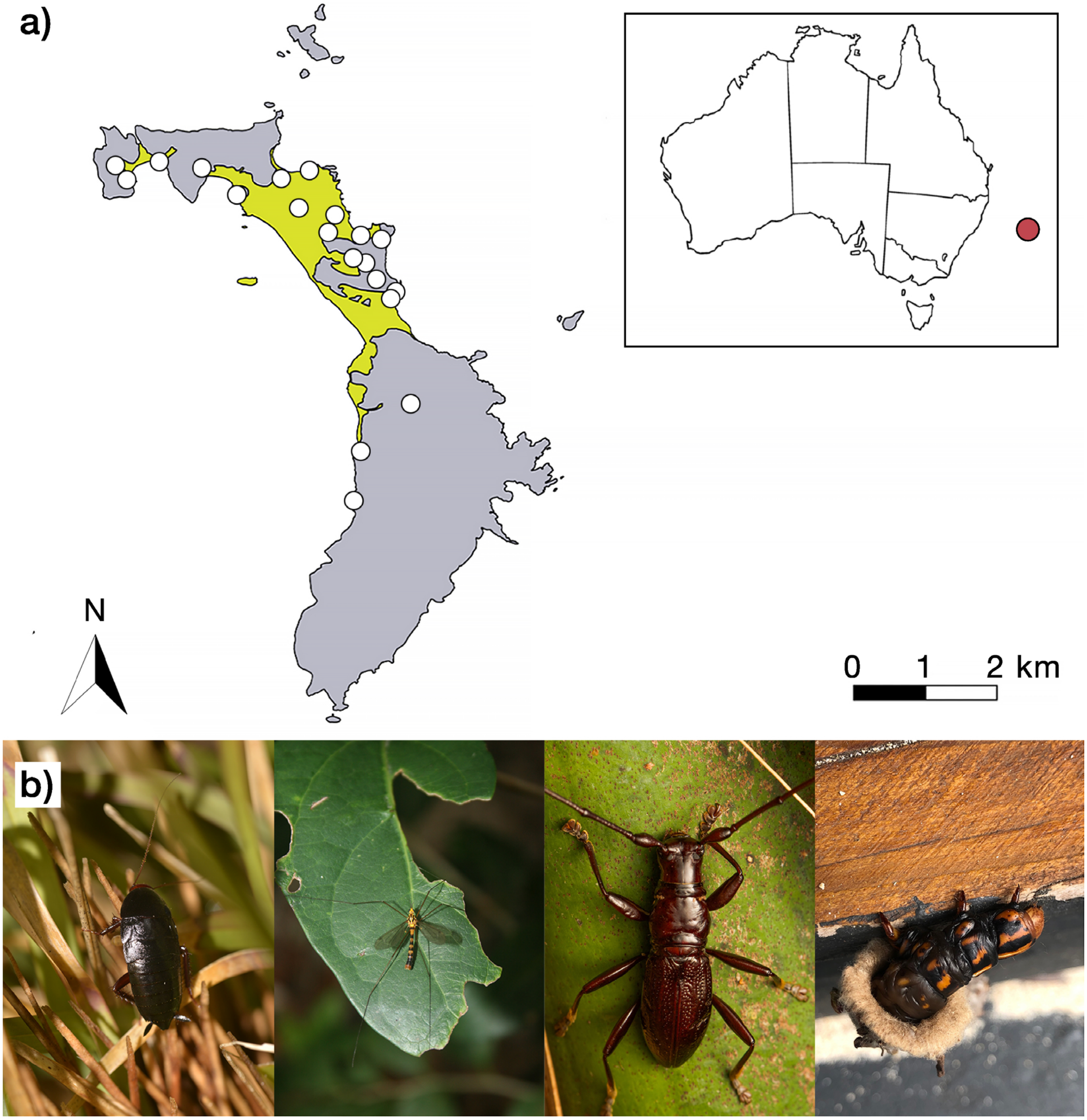

Fig. 1 **a** Locations of invertebrate survey sites on Lord Howe Island. Green shading: calcarenite bedrock, grey shading: basalt bedrock. Inset: location of Lord Howe Island relative to Australia. **b** Examples of Lord Howe Island invertebrates (from left to right): *Melanozosteria insularis*, *Nephrotoma lordhowensis*, *Xylotoles wollastoni*, *Metura falcata*. Photographs sourced from iNaturalist, from users *nicklambert*, *bush-tj*, *jamesbennettwild*, and *cherishnature13*, respectively

and bare rock. Surveys were conducted over two 12-month periods, one before (March 2016–February 2017) and one after (June 2023–May 2024) the eradication of rodents. In each period, we undertook collections every three months, directly following the end of each Austral season (i.e., in early March [representing the Summer collection], June [Autumn], September [Winter] and December [Spring]).

At each site, we collected both ground-dwelling and arboreal (specifically trunk-dwelling) invertebrates, using four separate survey methods. First, “tree wraps” were deployed on two adjacent trees with trunk diameter greater than 25 cm at breast height. Tree wraps were designed to mimic exfoliating bark, and consisted of a piece of corrugated cardboard (560 mm × 280 mm) with a piece of waxed cardboard stapled to the outside to increase the longevity of the wrap (modified from previous cardboard trap designs, e.g. Isaia et al. 2006; Tamaki and Halfhill, 1968). Both layers were wrapped around the trunk of each tree and held in place using an elastic strap. Two wraps were strapped to each tree on opposite sides of the trunk. Second, using the same two trees, we also deployed “tree blocks”, which mimic small hollows (modified from published “up traps”, e.g. Majer et al. 2001; Speight 2005). Each block consisted of a 150 mm wide × 200 mm long × 50 mm deep piece of pine wood with a 95 mm wide keyhole-shaped cavity recessed into the surface facing the tree, with a 25 mm wide opening facing towards the ground (Fig. 2). Four blocks were strapped to each tree. In two of these, the cavity was recessed to a depth of *ca.* 17 mm (permitting the entry of mice), and in two the cavity was *ca.* 9 mm deep (preventing access by mice). Tree wraps and blocks were deployed at heights of 1–1.5 m.

Third, a “roach hotel”, designed to mimic rotting vegetation and used in previous Blattodea studies on LHI (Carlile et al. 2018), was placed directly onto the forest floor between each sampled tree and in direct contact with soil substrate. The roach hotel consisted of three layers of corrugated cardboard (560 mm × 280 mm) topped by a piece of waxed cardboard. The cardboard pieces were held together with strapping tape and dampened with fresh water immediately before deployment. Fourth, we collected four leaf litter samples from each site: one approximately 3 m to the northern side and one approximately 3 m to the southern side of either tree. Leaf litter samples were collected at the time of recovery of other sampling equipment. Our collection methods did not encompass all microhabitats, most conspicuously omitting aquatic, subterranean and canopy-dwelling species. However, the aim of the study was to investigate the responses of invertebrates that were potentially targets of rodent predation. Ecological observations of invasive rats and mice indicate that they primarily hunt on the ground or in the lower reaches of trees (Bray 1994; Cox 1997).

Tree wraps, tree blocks and cockroach hotels were deployed for three months before invertebrate collection. To harvest invertebrates from the tree wraps, a plastic skirt was attached around the tree to catch any dislodged animals. The cardboard wraps were then removed and any invertebrates residing between the cardboard and the trunk were collected either by hand, with forceps, or with the use of a manual invertebrate vacuum. In some cases, larger, fast-moving invertebrates were immobilised with Servisol® electronic freezer spray before capture. The order and size of any escaping invertebrates were also recorded. Blocks were removed individually, and any residing invertebrates were collected as above. The cockroach hotel was dismantled by sequentially removing individual cardboard layers and retrieving any invertebrates present. Individuals located at the interface between the hotel and the soil were also collected. Finally, leaf litter samples were collected by pressing a stainless-steel circular cutter (25 cm in diameter) to the ground to cut through leaf litter, and retrieving all contained vegetative material and invertebrates into 150 um plastic bags. All other invertebrates captured were immediately placed into Ziploc® bags and wrapped loosely to prevent damage. Bags were sealed and refrigerated prior to processing. After each seasonal round of sampling, the sites were reset as above using a new pair of trees at least 1 m from the previously surveyed trees, and which had not been previously used in any previous collection ($n = 160$ roach hotels in total; $n = 320$ tree wraps and 640 tree blocks in total, across 80 unique trees).

Sorting and identification

Samples were manually sorted and identified to order. To extract invertebrates from leaf litter, the litter was emptied into a Tullgren funnel and placed above a collection jar containing 75% ethanol, then kept under a heat lamp for 48h (a sufficient period to completely dry leaf litter). Body measurements were taken using digital callipers or a ruler placed below a petri dish (measured to the nearest millimetre from the anterior margin of the head to the posterior margin of the abdomen). After identification, all samples were preserved in 100% ethanol or frozen at − 20 °C. As a result of irregularities in collection, such as clumped

Fig. 2 Cardboard tree wrap and wooden tree block strapped to a tree to mimic exfoliating bark and a tree hollow, respectively. Inset: schematic representation of a tree block. Dark shaded region incised to a uniform depth of either 9 mm or 17 mm. When deployed, the incised surface was positioned facing inwards against the tree with the opening directed downwards

distributions or large numbers of escapees, the orders Collembola, Lepidoptera and Polyxenida, and the family Formicidae, were excluded from statistical analyses. In addition, due to ongoing systematic uncertainty (Van Dam et al. 2019) and the subtlety of morphological differences, mites were only identified to the superorder Acariformes.

Statistical analyses

Analyses were undertaken using *R* v.4.4.2 in RStudio v. 2024.12.0. All invertebrates collected in a season from a given site were pooled across sampling methods (tree wraps, tree blocks, cockroach hotels and leaf litter samples; each such pool is hereafter referred to as a distinct "collection"). We then examined changes in total invertebrate abundance and diversity across collections. Total abundance was quantified from all invertebrates in a collection, including those that could not be identified to order.

We tested whether abundance varied based on pre- or post-eradication status, Austral season and/or soil type using a generalised linear mixed-effects model (GLMM) in the package *lme4* v.1.1.37 (Bates et al. 2015), with sampling site included as a repeated measure. To account for overdispersion, we fit the data to a negative binomial error distribution. The significance of all main effects and interactions was estimated using progressive single-term deletions and likelihood-ratio tests (LRTs) in *lme4*, however only significant interactions are reported.

Ordinal diversity was estimated using a Hill-numbers framework. Hill numbers represent a unified, parametric family of diversity indices that estimate the effective number of taxonomic units in an assemblage, each assigning different weights to common or rare taxa based on a single exponent q (Hill 1973; Chao et al. 2014a,b). Briefly, when $q = 0$, the Hill number (hereafter $q0$) is equivalent to richness; $q1$ is equivalent to the effective Shannon entropy (a diversity metric weighting taxa by their abundance, emphasising evenness); and $q2$ is equivalent to the effective Simpson diversity (a diversity metric strongly emphasising common taxa and de-emphasising rare taxa). Unidentified invertebrates were excluded from Hill-number calculations. We assessed whether each Hill number varied based on pre- or post-eradication status, Austral season and/or soil type using linear mixed-effects models (LMMs) in *lme4*, once again including sampling site as a repeated measure. Preliminary visualisations of residual distributions confirmed that data met assumptions of normality, and Levene's method was used to test for heteroscedasticity. Where significant heteroscedasticity was found, we used the *varIdent* function in *nlme* v.3.1.168 (Pinheiro et al. 2025) to allow for unequal variances across years. The significance of main effects and interactions was estimated by fitting analyses of variance (ANOVAs) with type-III sums of squares in *lmerTest* v.3.1.3 (Kuznetsova et al. 2017), following recommendations of the *nmle* package.

We applied several analyses to examine whether assemblage compositions shifted following the REP. First, we assessed whether the relative abundances of all the orders varied pre- versus post-eradication, as well as between seasons, using a two-way permutational multivariate analysis of variance (PERMANOVA) in *vegan* v.2.6.10 (Oksanen et al. 2013). Data were first checked for homogeneity of dispersion using a permutational multivariate analysis of dispersion (PERMDISP). We conducted post-hoc comparisons of diversity in corresponding seasons before and after rodent eradication using one-way PERMANOVAs with Bonferroni corrections. Second, the similarity of invertebrate assemblages from individual collections was visually summarised using non-metric multi-dimensional scaling (NMDS) in *vegan*. NMDS was chosen to account for the non-independence and non-linearity of the data (based on preliminary analyses).

Due to the lack of temporal replication of season in our pre- and post-eradication samples, we implemented two methods to test whether our results were confounded by factors other than the rodent eradication itself. First, we checked whether patterns of invertebrate abundance were influenced by climatic conditions by testing whether abundance varied based on rainfall and/or temperature in the preceding month using a general linear model in *lme4*. Climatic data were collated from the Bureau of Metrology database (Bureau of Meteorology 2023). Second, we tested whether there was a relationship between invertebrate size and response to the REP, as larger invertebrates are subject to potentially higher levels of rat predation (St Clair et al. 2011). Multiple size thresholds have been used to define "large" invertebrates in studies of rodent predation (Bremner et al. 1984; Chown and Smith 1993; Craddock 1997; Samaniego-Herrera et al. 2017; St Clair et al. 2011; Watts et al. 2020), but for robustness we used the median published value and classified invertebrates as large (body length > 13 mm); or small (body length ≤ 13 mm; following Watts et al. 2020). Abundance was modelled as a function of year and size using a negative binomial GLMM in *lme4*. We also examined whether ordinal diversity (Hill numbers $q0$–2) varied based on year and/or size using LMMs and ANOVAs as described previously. Sampling site and season were included as random effects in these analyses.

Finally, we examined changes in the eight orders with the highest total abundances across all years and seasons. Using complete abundance data (i.e. not filtered for body length), we used negative binomial GLMMs in *lme4* to test whether the abundance of each order varied pre- and post-eradication, and/or between seasons (with site as a repeated measure).

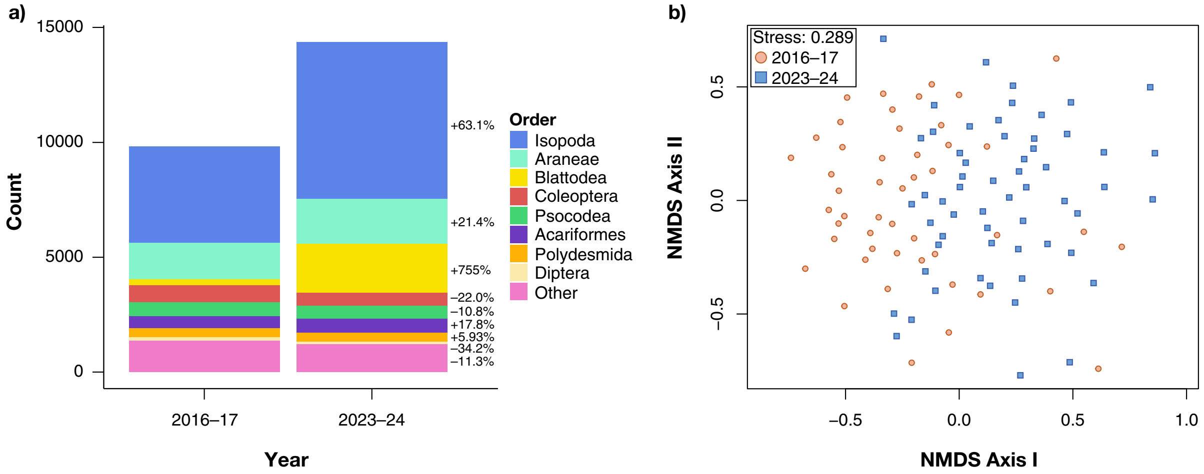

Fig. 3 **a** Proportions of invertebrate orders before and after rodent eradication. The eight most abundant orders are labelled. Percentage labels denote proportionate change in abundance between 2016–17 to 2023–24. **b** NMDS plot of invertebrate assemblages from all individual collections. Colours denote year of collection

Significance was tested using LRTs with progressive single-term deletions.

Results

Total abundance and ordinal diversity

We identified a total of 33 orders across all collections ($n = 25$ before eradication and $n = 28$ after eradication; 36 orders were present when including Collembola, Lepidoptera and Polyxenida; Supplementary Table S1). 24,209 invertebrates were collected in total, with 9,380 collected prior to eradication and 14,829 collected after eradication (Fig. 3a). Across all collections, the eight most abundant orders were (in descending order) Isopoda, Araneae, Blattodea, Coleoptera, Psocodea, the superorder Acariformes, Polydesmida and Diptera, which together comprised 89% of all captured invertebrates.

Total invertebrate abundance increased significantly after the rodent eradication ($\chi^2(1) = 14.962$, $p < 0.001$; Fig. 4a). Abundance also varied significantly between seasons, with lowest levels in Summer ($\chi^2(3) = 31.940$, $p < 0.001$; Fig. 4a). Across all seasons and years, abundance was significantly higher on calcarenite soil ($\chi^2(1) = 4.419$, $p = 0.036$).

There was a similar, significant interaction between the effects of year and season upon all three measures of ordinal diversity, whereby diversity strongly decreased in Autumn 2024 but remained constant or slightly decreased in other 2024 seasons (Hill number $q0$ [richness]: $F_{3,126} = 4.437$, $p = 0.005$; Hill number $q1$ [effective Shannon diversity]: $F_{3,126} = 5.063$, $p = 0.002$; Hill number $q2$ [effective Simpson diversity]: $F_{3,126} = 4.081$, $p = 0.008$; Fig. 4b–d). All three diversity metrics also varied with a significant interaction between season and soil type ($q0$, $F_{3,126} = 3.345$, $p = 0.020$; $q1$, $F_{3,126} = 3.222$, $p = 0.025$; $q3$, $F_{3,126} = 3.883$, $p = 0.011$). Total abundance and diversity are visualised per collection and soil type in the Supplementary Material (Supplementary Figure S1).

The relative abundances of all orders varied across collections with a significant interaction between year and season (PERMANOVA: $F_{3,152} = 2.356$, $p < 0.001$). Post-hoc analyses revealed significant differences between years in each of the four seasons (Supplementary Table S2). NMDS ordination tentatively supported this finding, with Axis I partially separating assemblages from 2016–17 and 2023–24 (albeit with very high stress, indicating that the plot only weakly fits the data; Fig. 3b). No groupings were apparent based on season or soil type.

There was no significant relationship between total invertebrate abundance and rainfall or temperature in the preceding month (rainfall: $t = -0.034$, $p = 0.975$; temperature: $t = -1.021$, $p = 0.365$),

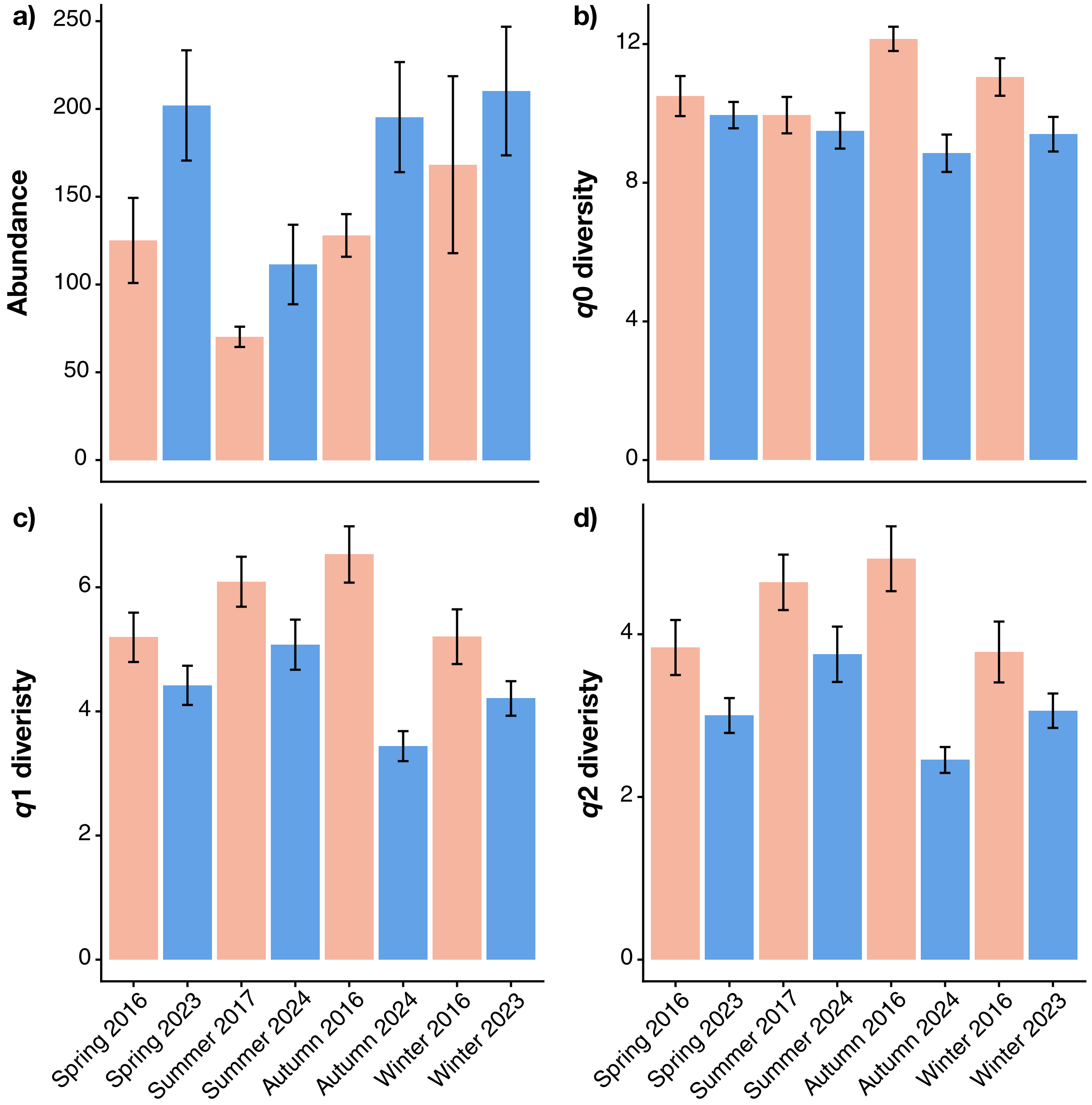

Fig. 4 Mean (±S.E.) abundance and ordinal diversity of invertebrates per site, stratified by season, before and after the eradication of rodents. **a** Total abundance. **b** Hill number *q*0 (ordinal richness). **c** Hill number *q*1 (effective Shannon diversity). **d** Hill number *q*2 (effective Simpson diversity)

nor any significant interaction between these factors ($t = 0.083$, $p = 0.938$), albeit based on a sample size of 8 points. Following filtering for large body size (body length > 13 mm), 15 orders remained in the data set ($n = 12$ in 2016–17, $n = 11$ in 2023–24; Supplementary Table S3). There was a significant interaction between year and size upon invertebrate abundance, with a steeper increase in the abundance of large invertebrates following the rodent eradication ($\chi^2(1) = 6.521$, $p = 0.011$; Fig. 5a). There were also significant interactions between year and size upon all diversity metrics, whereby the diversity of large invertebrates remained constant, while

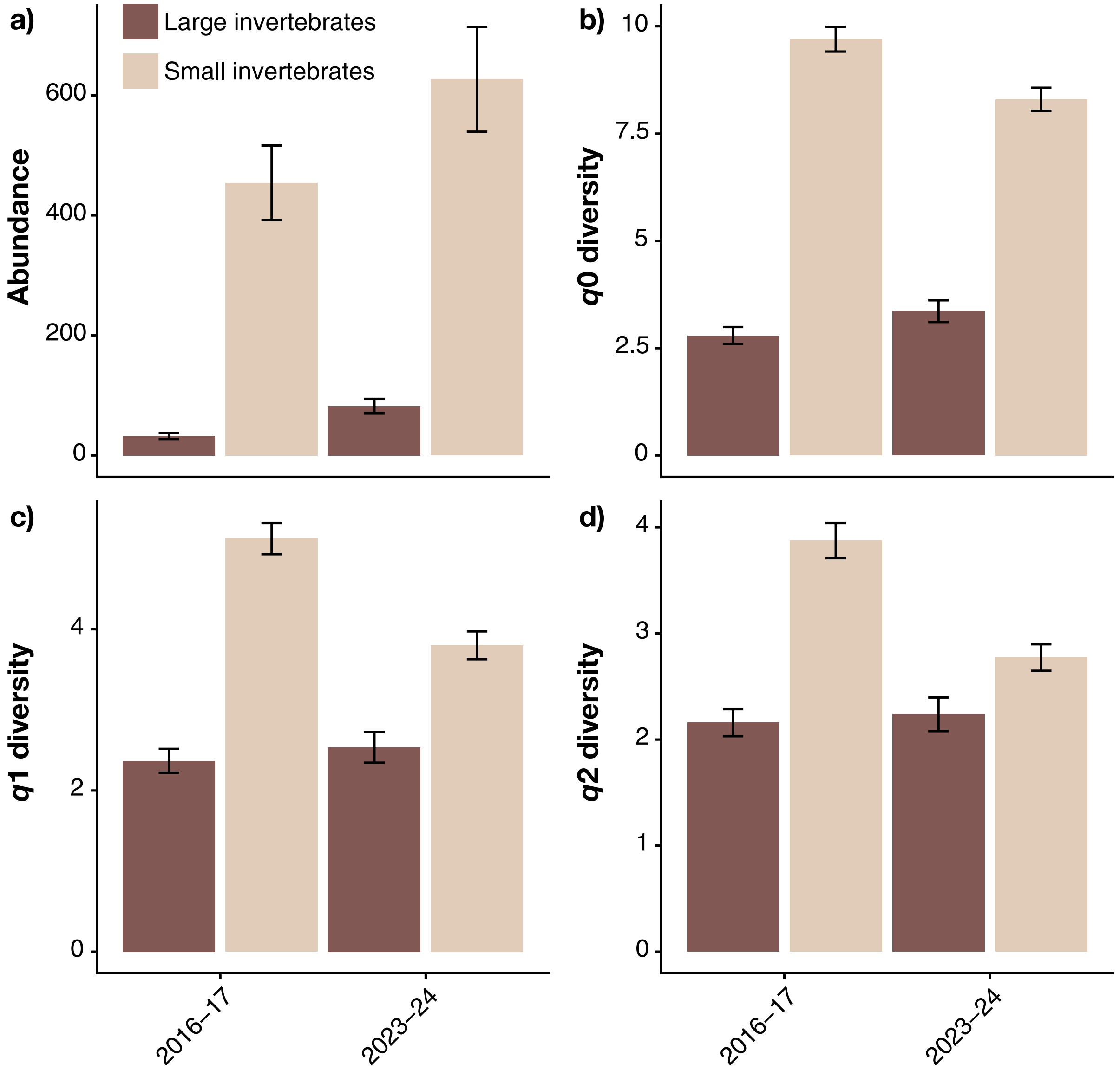

Fig. 5 Mean (±S.E.) abundance and ordinal diversity of invertebrates per site, before and after the rodent eradication, stratified by size. **a** Total abundance. **b** Hill number *q*0 (ordinal richness). **c** Hill number *q*1 (effective Shannon diversity). **d** Hill number *q*2 (effective Simpson diversity)

the diversity of small invertebrates decreased (Hill number *q*0 [richness]: $F_{1,126} = 5.684$, $p = 0.018$; Hill number *q*1 [effective Shannon diversity]: $F_{1,126} = 17.220$, $p < 0.001$; Hill number *q*2 [effective Simpson diversity]: $F_{1,126} = 17.850$, $p < 0.001$; Fig. 5b–d). Raw abundance and diversity data for each collection and size class are visualised in the Supplementary Material (Supplementary Figure S2).

Individual orders

There was a significant interact between year and season upon the abundance of Isopoda, whereby abundance increased substantially post-eradication in Spring, Summer and Autumn, but did not vary in Winter ($\chi^2(3) = 12.775$, $p = 0.005$; Fig. 6a). The abundance of Araneae also varied based on a significant interaction between year and season

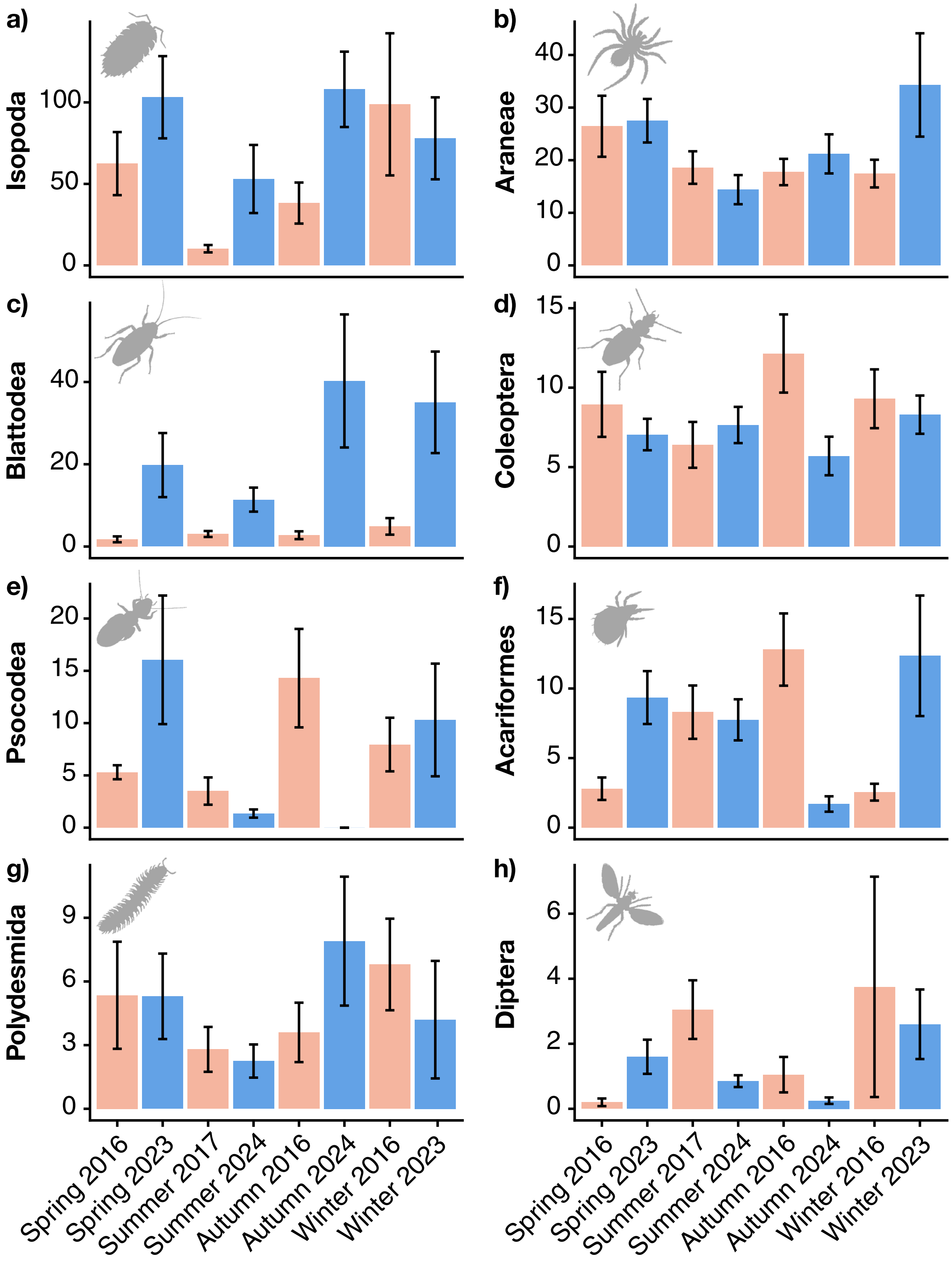

Fig. 6 Mean (±S.E.) abundance of individual orders per site, before and after the eradication of rodents. Inset graphics sourced from PhyloPic

($\chi^2(3) = 9.644$, $p = 0.022$; Fig. 6b), whereby abundance increased post-eradication in Winter only. The abundance of Blattodea increased significantly following the eradication ($\chi^2(1) = 75.365$, $p < 0.001$; Fig. 6c), as well as between seasons, with greatest abundance in Autumn and Winter ($\chi^2(3) = 9.956$, $p = 0.019$). There was no significant change in Coleoptera numbers before versus after the eradication ($\chi^2(1) = 3.336$, $p = 0.068$; Fig. 6d), nor between seasons ($\chi^2(3) = 1.859$, $p = 0.060$). There was a significant interaction between year and season upon the abundance of Psocodea ($\chi^2(3) = 84.301$, $p < 0.001$; Fig. 6e), with a sharp increase in Spring post-eradication but a decrease in Autumn. For Acariformes, abundance also varied based on a significant interaction between year and season ($\chi^2(3) = 59.180$, $p < 0.001$; Fig. 6f), whereby abundance rose steeply in Winter and Spring following the eradication, but decreased sharply in Autumn. The abundance of Polydesmida did not vary pre- versus post- eradication ($\chi^2(1) = 0.036$, $p = 0.850$; Fig. 6g) or between seasons ($\chi^2(3) = 4.007$, $p = 0.261$). Finally, we there was a significant interaction between year and season upon Diptera abundance ($\chi^2(3) = 21.120$, $p < 0.001$; Fig. 6h), for which abundance decreased in Summer and Winter following the eradication, while increasing somewhat in Spring.

Discussion

This study augments the few previous investigations of island invertebrate responses to rodent eradication (Green 2002; Samaniego-Herrera et al. 2017; Sinclair et al. 2005; Van Aarde et al. 2004). Overall, we observed an increase in total abundance and shifts in assemblage composition following the REP, consistent with expectations of release from rodent predation. We acknowledge that the lack of temporal replication before and after eradication introduces potential confounds on the results, and limits our ability to definitively link ecosystem shifts to rodent eradication alone. While our test for an effect of rainfall or temperature did not detect strong linear correlations with invertebrate abundance, the coarseness and small sample size of this approach precludes firm conclusions. It is also difficult to exclude the impacts of other environmental changes in the years between our samples, such as long-term climatic variations or the weed removals undertaken on southern LHI (albeit distant from our collection sites, and not targeting invertebrates). Nonetheless, by examining only the species that are more probable targets for rodent predation (body size > 13 mm), we found larger and more consistent increases in abundance following the eradication, and no declines in ordinal richness. Together, these results suggest that the broad increase in abundance was at least partially driven by the eradication of rodents, and that the rodent-suppressed component expanded especially substantially. That the abundance and diversity of insects were also strongly impacted by seasonal variation is consistent with some previous findings (Sinclair et al. 2005) and highlights the non-linearity of ecosystem recovery.

Due to the long history of rodent presence on LHI, it has remained an open question how different invertebrate groups were impacted by rodents. Our comparisons of dominant orders (representing *ca.* 90% of total abundance) revealed that Blattodea and Isopoda exhibited the largest and most uniform increases following the REP, while the abundance of Coleoptera and Polydesmida did not change, and the remaining orders responded primarily to season. We acknowledge that the exclusion of several orders from our analyses may have impacted these results. Following previous rodent exclosures or eradications, the orders with the most documented positive impacts are Coleoptera, Orthoptera and Mollusca (reviewed by St Clair, 2011). However, this result likely reflects taxonomic biases in the literature, as many previous surveys selectively focused on beetles or crickets, in particular larger-bodied species (e.g. Gerlach 2005; Rufaut and Gibbs 2003; Vergara et al. 2021; Watts et al. 2014; Watts et al. 2020). The few studies that examined whole-community responses to rodent eradication found more variable responses among Coleoptera (Bremner et al. 1984; Samaniego-Herrera et al. 2017; Sinclair et al. 2005). It is also noteworthy that many large-bodied Coleoptera and Mollusca species were extirpated by rodents on LHI prior to the REP (C. Reid, unpub. data; Ponder et al., 1997), raising the possibility that Blattodea and Isopoda compensatorily expanded solely in their absence. Only a handful of rodent-impact surveys have included cockroaches and isopods, with mixed responses (Craddock 1997; Sinclair et al. 2005; Towns 2009; Towns et al. 1997), although a recent investigation of invasive mouse diets suggested that they target detritivorous insects, including the orders Blattodea and Isopoda (Holthuijzen et al. 2023). It is not straightforward to generalise findings across disparate island systems with different invertebrate communities (Harper and Bunbury 2015; St Clair, 2011), however our findings suggest that these orders may be valuable indicator taxa for rodent predation.

Despite the increases in abundance and shifts in assemblage structure, we found neutral to negative changes in ordinal diversity, irrespective of the metric used. It appears that reciprocal increases and decreases across orders resulted in similar or lower levels of richness and evenness between years. As with abundance, the positive diversity impacts of the eradiation were concentrated in larger invertebrates, which only comprised a minority of the data set. While our coarse taxonomic resolution precludes comment on changes at the species level, even more granular studies of invertebrate communities have not consistently found increases in diversity following rodent eradications, suggesting that the present results may not be an artefact of taxonomic resolution (e.g. Green 2002; Samaniego-Herrera et al. 2017; Sinclair et al. 2005; Van Aarde et al. 2004; but see Palmer and Pons 1996). Small or non-existent increases in prey diversity are not unusual following invasive predator removal on islands, as population growth may be suppressed by interspecific interactions, resource limitation or rebounds of native predators (Baker et al. 2020; Bird et al. 2024; Borrelle et al. 2018; Kurle et al. 2008; Towns et al. 1997). The abundance of native predators appears to have risen following rodent eradication on LHI, based on surveys of insectivorous birds (O'Dwyer et al. 2023). Our opportunistic captures of geckos also revealed a two-fold increase in their abundance (unpub. data), though this result should be interpreted with caution until confirmed by formal surveys. Likewise, the expansion of larger invertebrates may have increased competition and predation pressure upon smaller taxa, potentially explaining the decreases in the latter's diversity—evenness in particular—on LHI.

This study offers a broad view of invertebrate recovery. The overall pattern points towards a turnover in invertebrate assemblage compositions, as has been observed following rodent eradications on Kapiti Island (Sinclair et al. 2005), Mexican tropical islands (Samaniego-Herrera et al. 2017) and Macquarie Island (M. Houghton, pers. comm.). The long-term ecological consequences of such shifts are difficult to predict. While ecological niches and functional groups were not recorded, orders with large increases consist primarily of detritivores and decomposers, which may have downstream implications for nutrient cycling. Monitoring isotope and nutrient ratios in soil and/or invertebrates has proven effective is in tracking the restoration of island ecosystem processes following rodent eradication (Jones 2010; Nigro et al. 2017). However, this would require monitoring on a decadal scale, as shifts in decomposition and nutrient cycling require 5–10 years to produce noticeable improvements in soil isotope composition (Jones 2010). Ideally, any such program would also be combined with further monitoring of invertebrate assemblages. More robust temporal replication is vital to affirm the conclusions outlined here, as seasonal variation was of comparable magnitude to the signal of the REP, and it may be many years before the ecosystem reaches a stable equilibrium (Courchamp et al. 2003; Jones 2010; Kuile et al. 2021).

While our results suggest positive impacts for LHI's invertebrates, predator eradications often do not restore ecosystems to their pre-disturbance trajectories (e.g., Bode et al. 2015). Ecological dynamics may have been permanently altered not only by rodents, but also by concomitant environmental changes or incursions of other invasive species, neither of which were considered in our analyses. It is plausible that invasive invertebrates are among those experiencing significant increases following the REP, as on nearby Blackburn Island (*ca.* 750 m from LHI), habitat restoration has inadvertently allowed for the establishment of non-native isopods (M.W.D. Adams, pers. obs.). There is growing recognition that eradications of invasive species should also consider non-target exotic species, especially those previously subject to competition or predation (Ballari et al. 2016). A planned genetic study using the samples collected here will provide additional detail on the invertebrate diversity now present on LHI. Key questions to be addressed by this work include the impact of the REP upon different feeding guilds, native versus non-native invertebrates and fine-scale taxonomic diversity. Comparisons of species in different trap types will also illuminate any changes in habitat use, an understudied ecological impact of rodents (Brittenden 2024) that is overlooked by surveys focusing purely on abundance.

Our invertebrate sampling was a single component of a broader biodiversity monitoring program. It was previously found that the rodent eradication had a major positive impact on the breeding success of black-winged petrels (*Pterodroma nigripennis*; O'Dwyer et al. 2023). The removal of rodents also appears to have benefitted a range of land birds, including Lord Howe woodhens which have increased more than seven-fold since the REP (O'Dwyer et al. 2024). This species primarily consumes soil dwelling invertebrates (Miller and Mullette 1985) and their rapid increase following the eradication may have been facilitated by the increase in large invertebrates. Conversely, the rapid increase in woodhen abundance might be limiting the growth of some invertebrate populations, and it would be valuable to monitor the top-down effects of woodhen predation upon long-term invertebrate recovery. The contrast between the heterogeneous shifts in invertebrate assemblages and the more straightforward increases in bird abundance is notable but not unprecedented (reviewed by St Clair, 2011; Watari et al. 2011). Birds were historically top predators on LHI and their recovery is presumably less impacted by mesopredator release. It is nonetheless promising that changes are already evident across trophic levels, as the benefits of rodent eradication can require up to decades to manifest, especially for indirectly impacted taxa (Bird et al. 2024; Jones 2010; Philippe-Lesaffre et al., 2023; Towns 2009). Further planned components of the biodiversity benefits program include an assessment of little shearwater (*Puffinus assimilis*) breeding success and a focused study of the impacts on geckos, which will provide valuable insights as LHI continues to recover.

Invertebrates are often omitted from environmental monitoring programs, including on islands (reviewed by Samaniego-Herrera et al. 2017; Ward and Larivière 2004). Many groups are poorly described or taxonomically unstable; and even modest collection efforts can yield large sample sizes that require significant effort to process. There is also a lack of standardised collection protocols and balanced sampling regimes (reviewed by Brown and Matthews 2016; Neville and Yen 2007; Webb et al. 2022). Despite these challenges, we demonstrate that a relatively simple sampling design, with coarse taxonomic resolution, can illuminate ecosystem dynamics following rodent eradication. This highlights the benefits of the REP as both a conservation and biodiversity management measure, as well as an experiment to examine the consequences of rodent invasion.

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Declarations

Conflict of interest The authors declare no conflicts of interest.

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