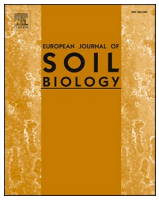
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Original article



The hidden shift: The role of exotic plantations in modulating soil arthropod communities in an arid island

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ABSTRACT

Reforestation with exotic species has often been used in arid and semiarid areas to restore degraded ecosystems. However, the effects of these plantations on soil biodiversity are still under debate. In the present study, we aimed to evaluate the long-term impacts (>60 years) of exotic plantations with *Acacia cyclops* and *Pinus halepensis* on soil biodiversity in an insular arid ecosystem of high ecological value. To do so, we study soil quality and soil arthropod communities in patches of vegetation under uniform edaphoclimatic conditions. Soil quality assessment was carried out by developing an ad-hoc Soil Quality Index (SQI) across seven sites, including two plantations (*Pinus* or *Acacia*), two degraded areas with a low cover of native species, and three sites with a high cover of native species. Whole organism community DNA (wocDNA) metabarcoding and barcoding were used to analyse key soil arthropod groups (Coleoptera, Acari and Collembola) recognized as habitat quality and biodiversity indicators. Our findings show that exotic plantations improved soil quality compared to degraded sites, with a considerable increase in the organic carbon pool, macronutrients and microbiological activity (SQI = 0.53 ± 0.12 *vs.* 0.29 ± 0.06). This improvement did not reach the values recorded in soils with a high cover of preserved native flora (SQI = 0.65 ± 0.12), with some exceptions. Richness of mesofauna and Coleoptera was lower in degraded areas (4.4 ± 1.6 and 0.4 ± 0.7, respectively) followed by exotic plantations (9.5 ± 2.6 and 1.2 ± 0.9) and permanent native vegetation (14.1 ± 5.5 and 2.2 ± 1.8). Soil quality significantly explained up to 52 % and 17 % of the variance in the richness of mesofauna and Coleoptera, respectively. While exotic plantations appear to prevent further land degradation in terms of soil quality, multivariate analysis shows that the structure of soil arthropod communities, particularly in *Pinus* plantations and to a lesser extent in *Acacia* plantations, differs significantly from that of soils in ecosystems with remnant native flora. These results highlight the need for a careful balance between biodiversity conservation and soil health management, especially in areas susceptible to desertification.

1. Introduction

Anthropogenic land cover alterations and land use intensification are the main drivers of ecological change and biodiversity decline in terrestrial ecosystems in the 21st century [1,2]. This transformation is largely influenced by the destruction of primary native forest habitats and their replacement by crops and exotic tree plantations [1,3]. Since 1990, the world has lost four million hectares of primary native forests while intensively managed plantations of exotic trees for productive purposes have grown by 2 % per year [2,4]. The use of exotic species for reforestation, rather than restoring native forests, has been a common approach to mitigate soil erosion and improve degraded and fragmented ecosystems worldwide [5,6]. Selected by their rapid growth, arboreal species from the genera *Acacia*, *Eucalyptus*, and *Pinus* have been widely planted around the globe to reforest habitats [7,8]. However, several studies warn that these plantations may host lower biodiversity levels

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compared to native ecosystems [1,5,7,9,10]. Despite the well-documented consequences of plantations with non-native vegetation on composition, structure and plant cover, and the recognized links between above- and belowground biological communities [11], our understanding of the impact of exotic plantations on soil properties and biodiversity is still limited [7]. This raises numerous questions regarding the effects of exotic plant species on soil fauna [2,12].

Soil invertebrates are a key component of terrestrial ecosystems. Their activities have significant impacts on soil properties and ecosystem processes and functions, including the maintenance of nutrient cycling, water storage and primary productivity [7,13,14]. These organisms directly or indirectly contribute to the decomposition of litter, the maintenance of soil structure and even directly influence on plant communities by selectively feeding on roots, leaves or seeds [15]. Given the sensitivity of soil invertebrates to environmental changes, macro- and mesofauna are often used as bioindicators of soil quality and to monitor ecosystem responses to management practices, underscoring their importance in conservation planning [16–19]. Understanding the influence of using exotic plant species in reforestation efforts can be especially important for soil arthropods due to the limited mobility and reduced distribution of many species [20,21], suggesting high vulnerability to habitat changes involving modifications in soil properties (e.g., soil temperature, water content, bulk density, organic matter and pH) or plant communities (e.g., species diversity and coverage) [7,8,22,23]. Yet, it is still unclear how different vegetation types induce changes in the soil environment and how these shifts, in turn, affect soil arthropod communities [12].

Previous studies have provided conflicting conclusions regarding the effects of exotic plants on the abundance, diversity, and composition of soil invertebrates. Plantations of exotic species are generally considered to negatively affect invertebrate communities compared to native ones [12,23–25], although some studies have found similar or even higher invertebrate diversity in plantations of non-native species [1,26,27], especially on degraded lands [8]. These discrepancies suggest that changes in macro- and mesofauna could be associated with the identity and composition of native soil fauna communities, the type of non-native plants involved in each case and/or the soil conservation status [2,7,15]. More evidence is therefore needed to draw consistent conclusions on the different responses to plantation type [12,15,28]; if responses depend on the local context, it is important that restoration programs include an adequate evaluation of the evolution of soil fauna communities in terms of diversity and community composition. Additionally, another important aspect to consider is that most research has concentrated on epigeal arthropods and temperate regions, while the effects on endogean arthropods within arid ecosystems have been generally overlooked [1,7,16,29,30].

In isolated regions such as the Canary Islands the impacts of non-native species can be particularly severe [31,32]. Even with their limited area and insular condition, the Canary archipelago hosts a high diversity of plant and animal communities, with a remarkable proportion of endemisms [33,34]. However, exotic plants have been frequently used to revegetate degraded arid and semi-arid habitats within the Canaries. Specifically, two species have been prominent in these revegetation efforts: *Acacia cyclops* A. Cunn. ex Don, an invasive coastal shrub [35,36], and *Pinus halepensis* Mill., a versatile conifer adept at colonizing degraded landscapes [37]. The consequences of introducing these species on insular ecosystems, particularly their effects on soil properties and soil biodiversity, are yet to be thoroughly investigated.

To address this knowledge gap, our study investigates the effects on soil properties and soil arthropods of a 60-years old reforestation with *A. cyclops* and *P. halepensis* within the arid environment of Lanzarote Island. We conduct comparative analyses among soils under degraded vegetation, soils with preserved native vegetation, and soils in revegetated (exotic-plantations) areas, across approximately 25 ha characterized by similar soil-climatic conditions (see Study area section). We measured soil quality by implementing the Soil Quality Index (SQI) [38,39] and studied (i) soil mesofauna communities of Acari and Collembola, recognized as soil bioindicators and analyzed together due to their shared ecological roles in soil processes [40–42], using whole organism community DNA (wocDNA) metabarcoding, and (ii) macrofauna communities of Coleoptera using barcoding, as this group serves as a reliable bioindicator and a predictor of broader community characteristics [43–46]. These molecular tools have been widely validated as both reliable and efficient for arthropod fauna characterization and for the detection of ecological trends [5,21,47–49]. Building on prior research into the effects of *Pinus* and *Acacia* monospecific plantations on soil properties (e.g., [2,12,50,51]), we hypothesize that these exotic plantations will decrease soil quality, potentially leading to diminished soil arthropod diversity and altered community composition. The two central questions guiding our inquiry are: *i)* Do *A. cyclops* and *P. halepensis* plantations lead to a decline in soil arthropod diversity, considering both species richness and community composition compared to soils under preserved native vegetation? and *ii)* How does the soil arthropod community vary across different soil quality conditions? This study aims to provide critical insights into the ecological consequences of reforestation with non-native species in fragile island ecosystems.

2. Material and methods

2.1. Study area

The study took place in Lanzarote, a volcanic island within the Canary Islands (Spain), located in the Atlantic Ocean between 29°14′41″ N and 28°50′28″ N latitude, and 13°28′06″ W and 13°47′46″ W longitude, roughly 130 km from the northwest African coast (Fig. 1). Lanzarote has an extreme aridity, and historically, intensive grazing and agricultural practices have played a significant role in accelerating soil erosion [52]. Only a fraction of the original vegetation and native flora persist, with the landscape now characterized by sporadic grasses and scattered drought-resistant shrubs, highlighting the severe ecological impact of past activities [52,53]. The study was conducted on a plateau perched atop a cliff approximately 580 m above sea level, spanning an area of about 25 ha, within the Altos de Famara landscape, a part of the Archipelago Chinijo Natural Park. Located along the northern coast of Lanzarote, this area falls under a designated protection scheme, underscoring its ecological significance and conservation priority (Fig. 1). Annually, this region receives an average of 225 mm of rainfall, primarily from October to March. The annual mean temperature is approximately 17.2 °C, with the coldest months averaging around 13.9 °C and the warmest months around 20.6 °C [54]. Intense solar radiation and moderate wind speed (~4.5 m s^{-1}) contribute to a reference evapotranspiration (ETo) of approximately 1400 mm per year [54; own data]. The dominant soils, Aridisols (particularly Paleargids and Calciargids; [55]), are highly erosion-prone due to their considerable clay levels, low organic matter content, and poor aggregate stability. This makeup restricts water infiltration, often creating numerous streams and gullies in unvegetated, sloped areas, known as badlands. The vegetation in the area forms a mosaic, ranging from patches of bare soil to regions that have preserved native vegetation, including areas reforested with pine and acacia trees.

2.2. Soil sampling

According to Ref. [56], seven different sites were identified within the study area based on past soil management practices and current vegetation, as illustrated in Table 1. These sites include: *i)* soils from abandoned farmlands with highly eroded soil ('Badland'), *ii)* soils from abandoned farmlands suffering from sheet erosion ('Plain'), *iii)* lithic-mulch soils from abandoned farmlands recolonized by native plants ('Mulch'), *iv)* soils reforested with exotic species in the 1960s ('Pinus' and 'Acacia'), and *v)* natural, rich in native flora, grasslands and shrublands with remnant vegetation ('RemVeg') and herbivory

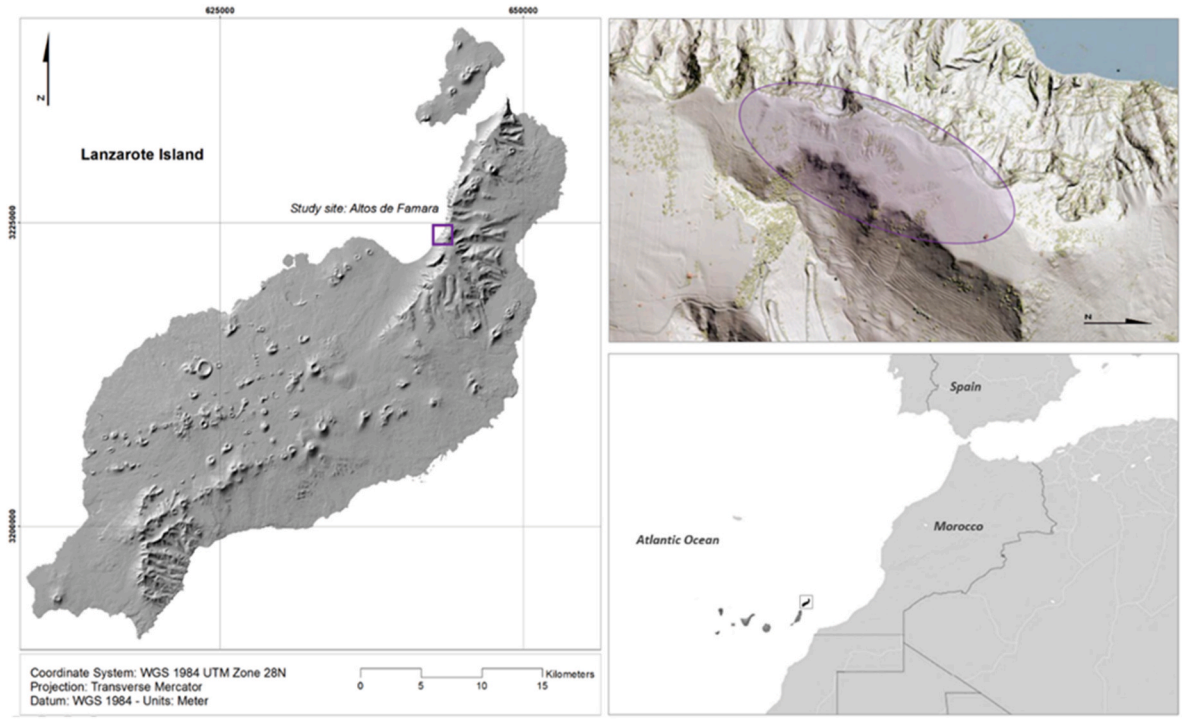


Fig. 1. Location of Altos de Famara in Lanzarote (Canary Islands, Spain).

exclusion ('HerbiExc' - inaccessible cliff). The complete plant inventories and key characteristics of these study sites are comprehensively detailed in Ref. [56]. Soil samples were collected in December 2020, following the first rainfall of the season to ensure comparable environmental conditions across sites. This timing allowed a meaningful comparison of soil arthropod communities across different soil conditions, as precipitation pulses are a major driver of biological activity in arid ecosystems [57]. For soil sampling, we partitioned each of the seven sites into seven 2.5 × 2.5 m experimental plots, except 'HerbiExc', which contained eight (total N = 50; see Table S1). Each experimental plot was segmented into four quadrants. From the topsoil (0–15 cm depth), we extracted soil near the center of each quadrant, merging these four subsamples into a composite sample weighing approximately 4 kg. These samples were homogenized and then split into three subsamples: one was air-dried for physical and chemical analyses, the second one was stored at 4 °C for biochemical analyses, and the third one was kept at room temperature for subsequent soil arthropod extraction. In addition, we used stainless-steel core samplers (100 cm^3–5 cm in diameter and 5 cm height) to extract an unaltered soil sample from the topsoil (5–10 cm depth) in each plot to determine bulk density.

2.3. Soil characterization and soil quality index development

Soil samples were sieved (<2 mm) before analysis. The different soil parameters were measured using the analytical techniques as follows: (a) physical parameters: bulk density (BD; ratio between soil mass dried at 105 °C for 24 h and total volume on soil cores), soil aggregate stability (AS; air-dried, sieved soil samples submerged in deionized water within bronze cylinders with a 200 μm mesh, and sinusoidally agitated for 3 min, based on [58], available water content (AW; calculated from the matric potential measured in Richard's chamber at −33 and −1500 kPa), soil texture (Txtr; Bouyoucos hydrometer method; then fine to coarse particles ratio); (b) chemical parameters: soil reaction and electrical conductivity (pH and EC; saturated paste extract), soil organic carbon (SOC; chromic acid wet oxidation method), soil labile organic carbon (SLOC; potassium permanganate oxidation), total nitrogen content (N; dry combustion using LECO CN828 equipment), available phosphorus (P; Olsen method); soluble cations (Ca^{2+}, Mg^{2+} and Na^{+}; from saturated paste extract by ion chromatography), sodium adsorption ratio (SAR; from soluble cations concentrations in the saturated paste extract), exchangeable sodium percentage (ESP_c; indirectly calculated from SAR values; [59]), assimilable potassium (K; 1N ammonium acetate extraction method at pH 8.2 followed by flame photometry analysis); and (c) biochemical parameters: microbial biomass carbon (MBC; chloroform fumigation-extraction method, [60]), soil basal respiration (BR; directly measurement of CO2 trapped in an alkali solution, [61]), β-glucosidase activity (bGlu; [62]); urease activity (Ure; [63]); and phosphomonoesterase activity (Phosp; [64]). All physical and chemical analysis were performed using standard methods [65].

The soil quality index (SQI) was developed to synthesize the information on the soil parameters studied following the methodology described by Refs. [38,39]. The process involved several steps starting with the detection of outliers (above or below three standard deviations around the median) and their replacement by regression imputation [66]. The soil properties were then transformed into unitless scores (S) ranging from 0 (lowest quality) to 1 (highest quality) to make them comparable, using transformation functions (Equations (1)–(3); [39]) according to their performance and based on previous literature (Table 2):

$$\textit{more is better} \rightarrow S_i = \left(1 + e^{-(b(x-a))}\right)^{-1} \quad (1)$$

$$\textit{less is better} \rightarrow S_i = \left(1 + e^{(b(x-a))}\right)^{-1} \quad (2)$$

$$\textit{optimum} \rightarrow S_i = 1 \bullet e^{\left(-\frac{(x-a)^2}{b}\right)} \quad (3)$$

where "S_i" is the soil property score, "x" is the parameter value, "a" is the soil property average, and "b" is $2\sigma^{-2}$ of the data.

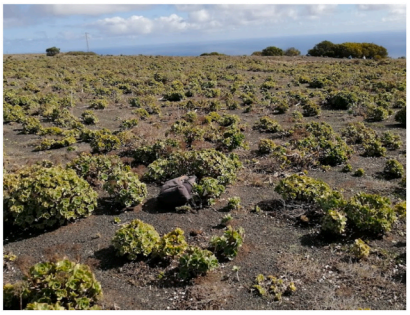
Even though the equations themselves use logistic and gaussian functions involving the mathematical constant *e* to handle variations and smooth excesses or deficiencies, these "more is better" and "less is better" approaches to transform soil quality parameters are valid as long

Table 1
Characterization of sampling sites within the study area.

Site		Description	Vegetation	Photography
Low native species cover	**Badland**	Highly eroded soils (less than 2 % plant cover) Avg. dist.[a] (m): 203.6 ± 121.5	Traces of *Launaea arborescens*, *Frankenia ericifolia*, *Helianthemum canariense*, *Sonchus pinnatifidus*, and *Aeonium lancerottense*	
	Plain	Soils affected by sheet erosion with an intermittent seasonal vegetation (6 % cover) Avg. dist. (m): 121.8 ± 75.7	Predominance of *Helianthemum canariense* and *Erodium* sp., with traces of *Scorpiurus sulcatus*, *Dipcadi serotinum*, *Emex spinosa*, and *Launaea arborescens* among others	
Exotic species	**Pinus**	Pinus halepensis plantations (60 years old, 95 % cover) Avg. dist. (m): 15.3 ± 7.4	Dominated by *P. halepensis* (82.9 % of cover), with presence of *Bupleurum handiense*, *Silene* sp., *Asparagus horridus*, *Helianthemum canariense*, *Asteriscus intermedius*, and others below 1 %	
	Acacia	Acacia cyclops plantations (60 years old, 90 % cover) Avg. dist. (m): 180.4 ± 145.6	Dominated by *Acacia cyclops* (91.4 % of cover), with presence of *Asteriscus intermedius*, *Ferula lancerotensis*, *Euphorbia regis-jubae*, *Sonchus pinnatifidus*, *Asparagus horridus*, and others below 1 %	

(*continued on next page*)

Table 1 (*continued*)

Site		Description	Vegetation	Photography
High native species cover	**Mulch**	Lithic-mulch soils from abandoned farmlands recolonized by native plants (50 years since abandonment, 55 % cover) Avg. dist. (m): 40.9 ± 19.9	Primarily covered by *Aeonium lancerottense*, accompanied by *Asteriscus intermedius*, *Sonchus pinnatifidus*, *Helianthemum canariense*, *Euphorbia regis-jubae*, and traces of other species	
	RemVeg	Multiespecific plant patches of native vegetation (90 % cover) Avg. dist. (m): 181.9 ± 125.8	*Lycium intricatum* dominates as a nurse species, unpalatable to herbivores, and is accompanied by *Sonchus pinnatifidus*, *Aeonium lancerottense*, *Asparagus horridus* and *Euphorbia regis-jubae* among others	
	HerbiExc	Soils situated on the cliff ledge, featuring rich native flora (around 26 species, 75 % cover) due to the exclusion of anthropic activities and herbivory Avg. dist. (m): 446.1 ± 266	Highest diversity. *Olea cerassiformis*, *Aeonium lancerottense*, and *Lavandula pinnata* are the most common, also *Euphorbia balsamifera*, *Convolvulus lopezsocasi*, and *Pistacia lentiscus*, among others	

[a] "Avg. dist." stands for "Average distance between plots within site" in meters.

as values remain within a normal range. For example, while higher MBC, BR, and enzymatic activities suggest better soil health, excessive levels due, for example, to the application of organic amendments rich in SLOC can result in less conservative cycling of organic matter. Hence, it should be recognized that optimal levels of these parameters may vary within the specific context of a study area, including its soil type, parameter ranges, and management practices.

Once the variables were transformed, highly correlated parameters were removed according to the predictive power score method (PPS; ppsr package in R) developed by Ref. [67]. This was done by discarding variables with PPS scores >0.5 from the SQI calculation. Variables not showing significant differences among sites based on a one-way ANOVA were also discarded. Finally, a principal component analysis (PCA; 'prcomp' function, based on a correlation matrix) was performed with the remaining variables to further select those to be finally represented in the SQI. PCs with eigenvalues approaching or exceeding 1, which also explained more than 5 % of the variance, were retained. Among the PCs retained for subsequent analysis, only variables with high factor loadings (i.e., absolute values within 10 % of the highest factor loading) were included in the SQI. When multiple variables were included within a single PC, we assessed redundancy by checking for multicollinearity among the variables using multivariate correlation (ppsr R package). When variables deemed redundant (correlation coefficients ≥0.8), we eliminated those with the lowest factor loadings from the SQI. Conversely, if factors exhibiting high loadings were uncorrelated, each was deemed essential and consequently retained in the SQI.

To finally build the SQI, the percentage of explained variation of each principal component provided the weight of the selected variables under a given component. To achieve a maximum SQI of 1, we divided the weight of each variable (defined as the percentage variance of the principal component) by the total weights of all variables incorporated into the SQI, thereby calculating the final weights. Every indicator was then multiplied by its corresponding weight to calculate the SQI according to Equation (4) [39], where PW is the PCA weighting factor and S is the indicator score.

$$SQI \quad \rightarrow \quad SQI = \sum_{i=1}^{n} PW \bullet S_i \tag{4}$$

This index was used to assess the potential influence of soil conditions on invertebrate communities, following the approach of [68]. The SQI calculation aimed to minimize redundancy among soil parameters while providing a comprehensive evaluation of habitat quality [39,69].

Table 2
Initial soil parameters included in the Soil Quality Index (SQI) developed ad-hoc for the study area.

Soil indicator	abbrv.	Reason for selection	Unit	Scoring curve
Bulk density	BD	Reflects soil compaction and porosity, influences the establishment of roots and biological communities	$g\ cm^{-3}$	less is better
Soil aggregate stability	AS	Measurement of soil structure, indicator of soil erodibility	%	more is better
Available water content	AW	Explains potential soil water availability and plant available water storage capacity	%	more is better
Soil texture (fine:coarse ratio)	Txtr	Related to soil physical fertility, water storage capacity in the soil and infiltration rate	–	optimum
Electrical conductivity	EC	Defines soil salinity, affecting plant growth	$dS\ m^{-1}$	less is better
pH	pH	Influences plant growth and metals availability. Affects the availability of macro and micro-nutrients	–	optimum
Soil organic carbon	SOC	Related to soil organic matter (SOM) levels and chemical fertility, improves aggregation and infiltration, increases water and nutrient availability. Constitutes resources for decomposers.	$g\ kg^{-1}$	more is better
Soil labile organic carbon	SLOC	SOC susceptible to short-term turnover	$mg\ kg^{-1}$	more is better
Nitrogen	N	Influences plant and microbial productivity, fundamental biomolecular structures contain it, vital nutrients to plant development	$g\ kg^{-1}$	more is better
Available phosphorus	P	Influences plant productivity, facilitates microbial breakdown of SOM, vital nutrients to plant development	$mg\ kg^{-1}$	more is better
Potassium	K	Enhances plant water regulation, vital nutrient to plant development	$mg\ kg^{-1}$	optimum
Exchangeable sodium percentage	ESP_c	Influence on the physical soil properties affecting aggregates stability and soil permeability to air and water	%	less is better
Microbial biomass carbon	MBC	Indicates bacteria and fungi communities' size	$mg\ kg^{-1}$	more is better
Basal respiration	BR	Indicates bacterial and fungal metabolic state	$mg\ C\text{-}CO_2\ kg^{-1}\ d^{-1}$	more is better
β-glucosidase activity	bGlu	Soil microbiological quality indicator, key in carbon mineralization	$nmol_{saligenin}\ g^{-1}\ h^{-1}$	more is better
Urease activity	Ure	Soil microbiological quality indicator, key in nitrogen mineralization	$nmol_{ammonia}\ g^{-1}\ h^{-1}$	more is better
Phosphomonoesterase activity	Phosp	Soil microbiological quality indicator, key in phosphorus mineralization	$nmol_{pnitrophenol}\ g^{-1}\ h^{-1}$	more is better

2.4. Soil arthropod extraction and DNA analysis

Soil arthropods were extracted from soil samples using a flotation–Berlese–flotation (FBF) protocol, following procedures described by Ref. [49] for wocDNA metabarcoding [70]. Each sample consisted of 2.5 kg of soil, which was first processed through flotation in water to separate the organic fraction. This fraction was then placed in a modified Berlese apparatus with a 1 cm metal mesh, over which a flexible and incomplete 1.5 mm mesh was placed to support the organic material, to capture specimens alive and preserve them in absolute ethanol. The extraction process was repeated every 72 h until complete dehydration, taking approximately three weeks. Specifically, for each sample, (i) macrofauna specimens from groups other than Coleoptera were discarded; (ii) all Coleoptera specimens including larvae were subjected to individual non-destructive DNA extractions by splitting specimens into parts or puncturing the body; and (iii) the remaining mesofauna (dominated by mites and springtails) was process for metabarcoding following procedures described in Refs. [20,21,49]. Prior to DNA extraction of each bulk sample of mesofauna, voucher specimens representing the main lineages of Acari and Collembola were selected and subjected to individual non-destructive DNA extractions. After that, samples of mesofauna were homogeneised with glass pestles and DNA extracted. All DNA extractions used a magnetic bead-based kit (Mag-Bind® Blood & Tissue DNA Kit, Omega Bio-tek) in a Kingfisher Flex robotic system (Thermo Scientific). To each DNA mesofauna extract we added 20 μl of the DNA extract obtained from vouchered Acari and Collembola retrieved from that sample.

For metabarcoding, the 3′- 418 bp of the COI barcode region was amplified using primers Ill- B- F [71] and Fol-degen- R [72] with modified tails corresponding to the Illumina P5 and P7 sequencing adapters for subsequent library preparation, as described in Ref. [49]. For each sample, three independent PCRs were performed, the amplicons were pooled and cleaned using AMPure XP magnetic beads. A limited-cycle secondary PCR amplification was done to add dual-index barcodes and the Illumina sequencing adapters (Nextera XT Index Kit; Illumina). Metabarcoding libraries were then sequenced on an Illumina MiSeq sequencer (2 × 300 bp paired-end reads), dedicating approximately 0.5 % of a flow cell to each library, producing paired reads (R1 and R2) with a dual tag combination for each sample.

Raw reads were quality checked in Fastqc [73], primers were trimmed using fastx_trimmer (http://hannonlab.cshl.edu/fastx_toolkit/), and quality filtered in Trimmomatic [74] with TRAILING:20. Subsequently, we used the USEARCH pipeline [75]: reads were merged (option mergepairs –fastq_minovlen 50, –fastq_maxdiffs 15), quality-filtered (Maxee = 1), retaining amplicons of 416–420 bp (–sort-bylength), dereplicated (–fastx_uniques), and denoised (–unoise3, –minsize 2). The latter included a chimera filtering step. Denoised reads from all the libraries, representing putative haplotypes, were combined and dereplicated to obtain a collection of unique sequences for the complete data set [76]. The unique sequences were assigned a taxonomy with the lowest common ancestor (LCA) algorithm implemented in MEGAN version 5 [77] based on the result of a BLAST search against a reference library including the NCBI nt database [78], and sequences from our local reference database. The LCA algorithm was run using default parameters. This high-level taxonomic assignment allowed extracting reads corresponding to Acari and Collembola, while excluding other taxa present in the bulk samples. Sequences corresponding to these two groups were used as input for metaMATE [79]. Within metaMATE, we identified verified authentic ASVs using the same reference library as above, and we tested the performance of alternative filtering on total read abundance, abundance by library, abundance by clade, abundance by clade and library, as well as synergies between total and clade-based abundance filtering (Supplementary materials text S1). We selected the filtering strategy resulting in the highest number of

estimated authentic ASVs with estimated non-authentic AVS contributing less than 5 % to final dataset. The finally surviving unique sequences were used to generate a community table with read counts (haplotype abundance) by sample against the complete collection of reads (i.e. reads before the dereplicating and denoising steps) using Usearch (-search_exact option). We use R-packages vegan [80] and cluster [81], to generate a UPGMA tree using F84 corrected genetic distances to define groups based on their genetic similarity, using a 97 % similarity threshold as a proxy to species here named as OTUs (operational taxonomic units). This information was used to generate a presence/absence community table at the OTU level that was used to perform statistical analyses.

For vouchered specimens, we Sanger sequenced the complete barcode fragment after amplification with primers Fol-degen-F and Fol-degen-R [72] as in Ref. [49]. Raw sequences were edited in Geneious Prime [82] and were assigned a taxonomy based on the result of two BLAST searches. The first one was carried out against the NCBI nt database [78]. The second search was performed using the BOLD systems database, which was accessed on the 12th of June 2023. The output from these searches was initially used to classify and identify the sequences to the greatest possible taxonomic resolution. All the specimens previously identified with these genetics tools were revised by the entomologist of the team (HL) to confirm the results or to improve their taxonomic identity. Finally, we consulted the Canary Islands Biodiversity Database (BDBC) [83] to determine the origin (native, introduced, endemic, etc.) of the identified Coleoptera specimens.

2.5. Statistical analysis

Statistical methods were performed using R version 4.3.0 [84]. All analyses were conducted independently for Coleoptera and mesofauna datasets using presence/absence tables. We have tested for significant differences among the seven types of vegetation/soils as defined in Table 1 in both, soil properties as recovered by the SQI, and species richness, by one-way ANOVAs followed by the post-hoc Tukey HSD.

Species accumulation curves were also estimated using 'specpool' and 'specaccum' functions from R 'vegan' package (version 2.5–7; [85]), and the relationship between the SQI and species richness was examined through a linear regression analysis with the lm function from the stats package in R. To satisfy the assumptions with a linear regression model, the richness values of both Coleoptera and mesofauna species were transformed using the natural logarithm.

Total dissimilarity across the communities was estimated, and pairwise community matrices were generated using total β diversity (Sorensen index, βsor) and its additive turnover (Simpson index, βsim) and nestedness (βsne) components [86] using the betapart package (version 1.6, [87]). Permutational ANOVAs were conducted over the community dissimilarity matrices using 999 permutations and the site (as defined by Ref. [56], Table 1) as the grouping factor. Homogeneity of variances among groups was tested using betadisper (vegan package) followed by ANOVA, indicating no significant differences in dispersion. Pairwise PERMANOVA tests were performed using the RVAideMemoire package with p-values adjusted by the false discovery rate (FDR) method.

2.6. Other computational tools

The relationship between SQI and mesofauna community structure was examined using non-metric multidimensional scaling (NMDS) with a Canberra dissimilarity matrix, alongside environmental fitting analysis through the 'envfit' function, also from the vegan package. Graphical networks for mesofauna and Coleoptera taxa distribution were constructed using the igraph package in R (version 2.0.2; [88]). These visualizations represent presence associations between taxa across different soil conditions, with node sizes scaled according to taxa's occurrence frequencies. ChatGPT large language model was utilized to assist in managing R code for analyzing data and generating graphs.

3. Results

3.1. Soil quality

Among the 17 soil parameters evaluated (see Table 2), 10 were selected as the final indicators for this study. According to the PPS method, Phosp and SOC were excluded due to their high correlation with SLOC and N, respectively. The other variables showed significant differences between sites according to a one-way ANOVA and were selected for PCA. The PCA results, used to calculate the SQI, are presented in Table S2. Five principal components (PCs) were identified, explaining 75.1 % of the variability in soil attributes. Variables bGluc, P, Ure, pH, and BD were excluded because they did not exhibit high factor loadings in any of the five PCs. All other variables exhibited high factor loadings in at least one of the five components. None of the selected variables within each PC demonstrated a correlation coefficient $\geq$0.8. The remaining variables for the SQI calculation include biological activities (MBC and BR) and concentrations of N and SLOC in PC1, all with a weighted factor of 0.38. Additionally, EC in PC2, Txtr and ESP_c in PC3, AW in PC4, and AS with K in PC5 are included (Table S2).

Significant variability in soil quality was observed across the surveyed locations (Fig. 2). The 'Badland' site registered the lowest mean SQI (0.24 $\pm$ 0.01), indicating notably poorer soil quality compared to the other sites, which mainly related to very low SLOC. In contrast, the 'HerbiExc' site reached the highest average SQI (0.71 $\pm$ 0.09), reflective of substantially better soil quality based on its balanced soil texture, high levels of biological activities, and elevated N content. 'Plain', 'Pinus', 'Acacia', 'Mulch', and 'RemVeg' sites displayed intermediate SQI values, with 'Plain' demonstrating statistically distinct SQI values and 'Pinus' being lower, but comparable in soil quality, to 'Acacia'. 'Mulch' and 'RemVeg' were noted for their relatively elevated mean SQI non-different statistically to the highest. The whiskers of the boxplots illustrated the spread of SQI values within each site, which demostrated the internal variability at each location. The analysis confirmed statistically significant differences in soil quality among the sites under investigation (ANOVA, $F(6,43) = 61.19$, $p < 0.001$). Overall, the findings suggest that sites with abundant native vegetation exhibit superior SQI scores compared to areas with sparse native vegetation (0.65 $\pm$ 0.12 *vs.* 0.29 $\pm$ 0.06). In contrast, areas with exotic plantations occupy an intermediate position, displaying an average SQI of 0.53 $\pm$ 0.11, as illustrated in Fig. 2.

3.2. Soil arthropod richness

The richness of Coleoptera species varied significantly across different sites, as evidenced by the ANOVA ($F = 7.466$, $p < 0.001$; see Fig. 3). Sites such as 'HerbiExc' and 'RemVeg' exhibited the highest species richness, with statistically significant distinctions from the 'Badland', 'Plain' and 'Pinus' sites. Areas with low native species cover hosted only two species ('Badland' and 'Plain', 0 and 2 species respectively), aligning with the Chao estimate and indicating a constrained diversity. Conversely, exotic areas contained nine species ('Pinus' and 'Acacia', 3 and 7 species, respectively), which is 69.8 % of the predicted Chao richness. Meanwhile, areas with high native species cover supported 26 species ('Mulch', 'Remveg' and 'HerbiExc', 5, 14 and 11 species, respectively), representing 74.1 % of their Chao richness, thereby demonstrating higher levels of diversity.

The mesofauna also exhibited notable differences in OTU richness across the study sites, as confirmed by the ANOVA ($F(6,43) = 14.63$, $p < 0.001$; shown in Fig. 3). 'RemVeg' emerged as the location with the highest mesofauna richness, closely followed by 'HerbiExc'. Upon examining mesofauna richness, it was observed that areas with low native vegetation cover were home to only 27 OTUs ('Badland' and 'Plain', 14 and 18 species respectively), regions with exotic vegetation supported 46 OTUs ('Pinus' and 'Acacia', 34 and 22 species, respectively), and areas characterized by high native vegetation cover boasted

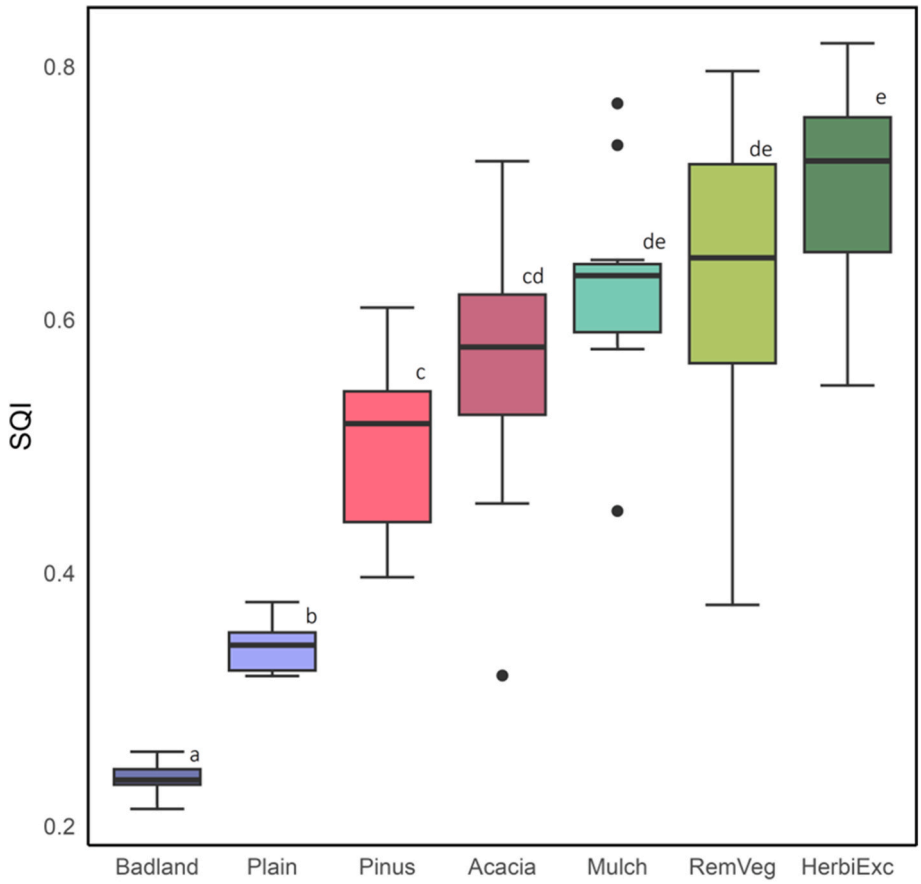


Fig. 2. Soil Quality Index (SQI) values from the seven study sites (n = 7–8). Boxes represent the middle 50 % of the data (interquartile range), with the line inside the box indicating the median; whiskers extend to show the range of the data excluding outliers, which are represented as isolated circles. Different letters above the boxes indicate significant differences among sites ($p < 0.05$) as estimated with one-way ANOVA followed by the post-hoc Tukey HSD.

a diverse array of 126 OTUs ('Mulch', 'Remveg' and 'HerbiExc', 30, 68 and 71 OTUs, respectively). These figures indicate detection rates in relation to the Chao estimates of 28.3 % for low native cover regions, 45.7 % for exotic vegetation cover areas, and 50.5 % for high native cover regions. The data denotes a moderate level of biodiversity under exotic vegetation but also suggests a possible underdetection of species across sites, which points to a need for more extensive surveying. For additional detail on the patterns of species/OTUs emergence and prevalence, refer to the species accumulation curves in Supplementary Figs. S1 and S2.

A positive relationship between the SQI and the logarithmic richness of Coleoptera and mesofauna species (linear regression) was found (Fig. 4). The analysis underscores a significant correlation, with the interquartile range (Q1 to Q3) of SQI associated with soils from exotic species plantations highlighted by a red band. For mesofauna, the strength of this relationship is particularly pronounced ($F = 49.95$, $p < 0.001$), explaining 52 % of the variation in logarithmic richness. In comparison, the Coleoptera data show a modest yet significant relationship ($F = 11.13$, $p < 0.01$), accounting for 17 % of the variability in richness. Additionally, the model indicates that for mesofauna, a one-unit increase in SQI predicts a 2.17 ± 0.31 change in richness, while for Coleoptera, the predicted change is 1.42 ± 0.43. These findings highlight the differential impact of soil quality on the richness of these two taxa.

3.3. Soil arthropod community structure

The network diagram in Fig. 5 offers a detailed view of the association patterns between beetle taxa and land use types. The diagram features a prominent green radial band, signifying soils with high native vegetation cover, which supports a rich array of beetle species. This biodiverse zone is distinguished by the presence of numerous endemic taxa, and notably, it is the habitat for four beetle species not yet formally described, suggestive of an important Linnaean shortfall on the knowledge of the soil fauna of the eastern Canary Islands. Conversely, the red band denotes soils covered with exotic vegetation, which sustains fewer than half the beetle taxa found in native conditions. The blue band, indicative of degraded soils with limited native vegetation, is sparsely populated, containing only two beetle taxa. Beta diversity metrics reveal a high species turnover rate (Similarity Index (SIM) of 0.94) within the beetle community, compared to a low nestedness component (SNE) of 0.03, which is particularly evident in exotic areas where only two out of nine taxa are unique to those conditions.

A small number of species are of uncertain origin, including members of the Elateridae, Curculionidae, and two Staphylinidae families. For a comprehensive listing of Coleoptera specimens including voucher numbers, locations, taxonomic identifications, Barcode of Life Data (BOLD) system matches, developmental stages, cluster IDs, and GenBank accession numbers, see Table S3 in the Supplementary Material. Additionally, the Supplementary Material includes a phylogenetic tree (Fig. S3) and a 'Photographic Appendix' of specimen images captured during the taxonomic identification phase.

With regard to mesofauna, β diversity showed a significant species turnover (SIM: 0.93) and a low level of nestedness (SNE: 0.03). Fig. 6 displays the non-metric multidimensional scaling (NMDS) analysis of its community compositions at the seven surveyed sites. Mesofauna communities in areas with low native species cover, specifically the 'Badland' and 'Plain' sites, exhibited distinct compositions, as shown by

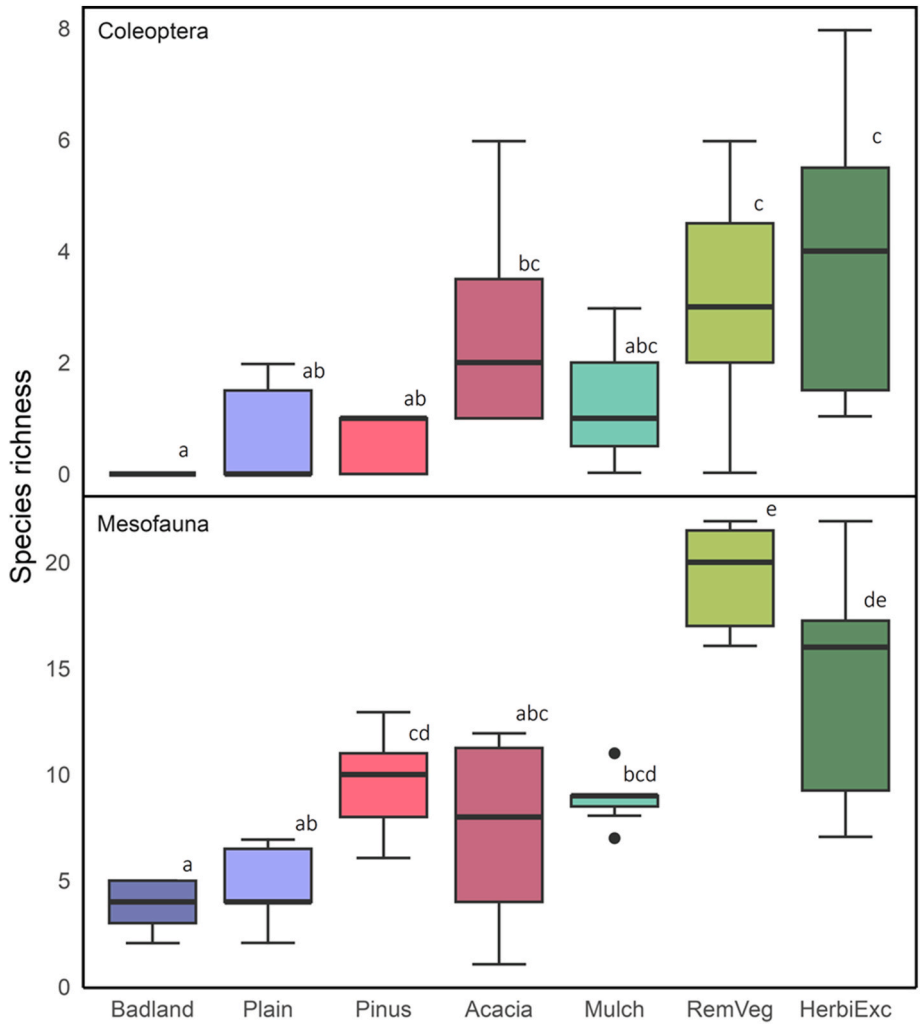


Fig. 3. Species richness for both Coleoptera (top; n = 7–8) and mesofauna (bottom; n = 3–8) communities from the seven study sites. Boxes represent the middle 50 % of the data (interquartile range), with the line inside the box representing the median; the whiskers show the range of the data excluding outliers represented as isolated circles; different letters indicate significant differences among study sites ($p < 0.05$) as estimated with one-way ANOVA followed by the post-hoc Tukey HSD.

their separation from other sites. This segregation underscores the unique mesofauna community structure associated with these land use types. While the centroids of 'HerbiExc', 'RemVeg', 'Pinus', 'Acacia', and 'Mulch' share a common space, 'RemVeg' is notably differentiated along the NMDS1 axis, suggesting a distinctive community composition. The close proximity and overlap of 'Pinus', 'Acacia', and 'Mulch' indicate similarities in their mesofauna communities. Additionally, environmental fitting analysis corroborates a significant correlation between SQI and mesofauna community structure ($p < 0.001$), with SQI explaining approximately 48.79 % of the observed variation. The orientation of the SQI vector within the NMDS space illustrates the gradient of soil quality, positioning the sites along this vector according to their increasing SQI values.

The clustering patterns identified through graphical analysis were statistically tested using pairwise PERMANOVA. The results indicate no significant differences in the mesofauna communities between 'Badland' *vs.* 'Plain' ($p = 0.074$), 'Acacia' *vs.* 'Pinus' ($p = 0.109$), and 'Acacia' *vs.* 'HerbiExc' ($p = 0.096$). The rest of the sites did show significant differences (Table S4).

Supplementary Fig. S4 offers critical insights into the presence of introduced species across soils with differentiated vegetation cover. The data show that soils subjected to degradation have the highest incidence of introduced species, at 11.11 %. This figure is modestly reduced in soils with exotic vegetation cover, where introduced species make up 8.70 %. In contrast, soils with robust native vegetation cover demonstrate the lowest incidence, at a mere 3.97 %. Full dataset detailing mesofauna lineages and their occurrence frequencies in relation to vegetation cover is thoroughly compiled in the Excel file within Table S5 of the supplementary materials. Raw data from metabarcoding libraries is available through dryad: DOI: 10.5061/dryad.n5tb2rc6p.

4. Discussion

The intricate dynamics between vegetation type and soil quality underscore the profound impact of plant species composition on soil ecosystems [89]. The variability in soil quality, as evidenced by various measures including the SQI, observed in areas with exotic species compared to native vegetation zones indicates that while exotic plantations can ameliorate some aspects of degraded soils, they do not replicate the soil quality levels associated with indigenous flora. This phenomenon is crucial for understanding how different revegetation strategies contribute to or detract from soil health in ecological restoration projects. Exotic plantations, often introduced to rehabilitate degraded lands, play a complex role in modifying soil characteristics [90]. These changes are not merely a reflection of the introduced species' ecological traits but also an interaction with the existing soil biota and physicochemical conditions [91]. Such insights are vital for managing soil resources in a way that promotes both biodiversity

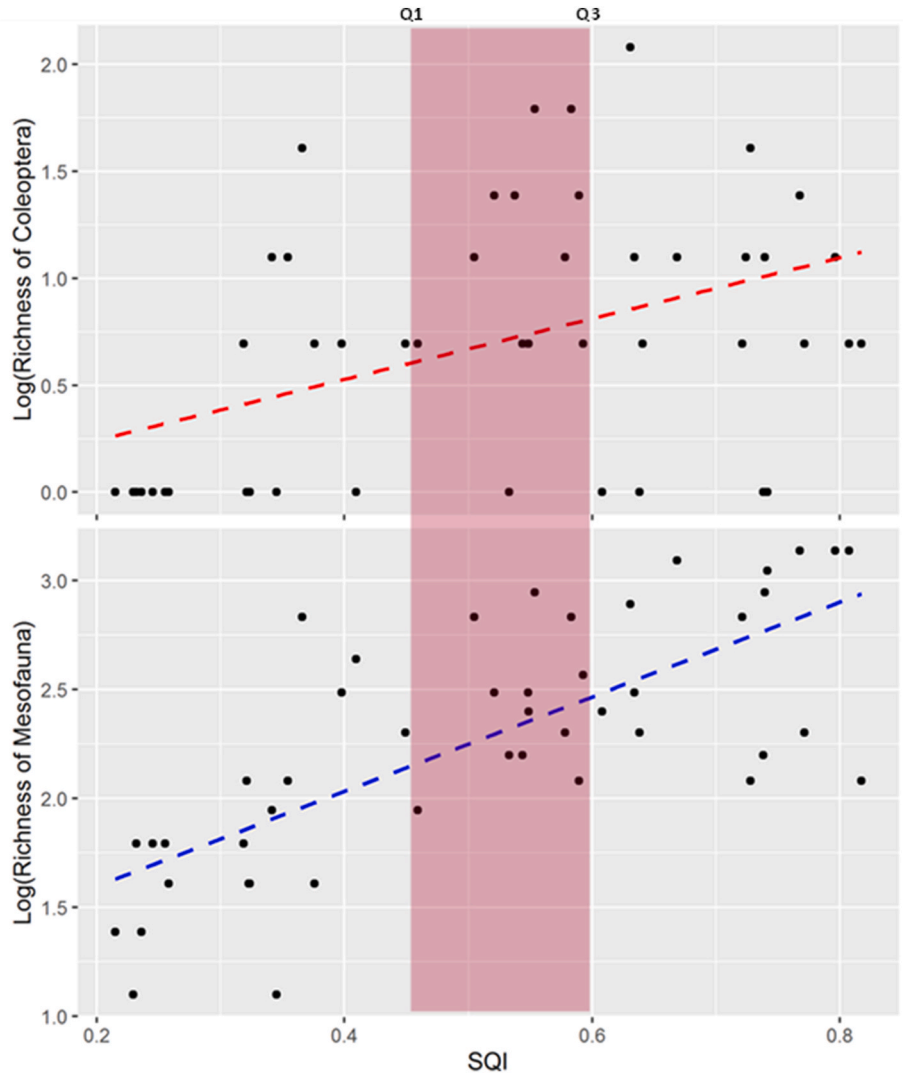


Fig. 4. Linear regression analysis illustrating the relationship between the Soil Quality Index (SQI) and species richness for Coleoptera (top) and mesofauna (bottom). Red band indicates the interquartile range (Q1 to Q3) of SQI corresponding to exotic species plantation. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

conservation and soil functionality, particularly in sensitive or degraded ecosystems. Given these variations in soil quality associated with vegetation cover types, it is reasonable to assume that they will impact the structure and diversity of soil arthropod communities [8].

The differential impact of exotic versus native vegetation on soil arthropod richness, particularly for key groups such as Coleoptera, Acari, and Collembola, highlights the nuanced interactions within soil ecosystems under varying vegetative covers. Our findings suggest that while exotic plantations moderately increase the richness of soil arthropods compared to degraded soils, they do not achieve the biodiversity levels observed in soils under preserved native vegetation after six decades. This pattern is evident in the richness of those groups, where areas with native plants support a more diverse and robust community. The presence of native vegetation appears to foster a more favorable habitat for soil arthropods, possibly due to more complex soil structures, higher organic matter content, and a more stable microclimate, all of which are less effectively replicated in environments dominated by exotic species. Furthermore, the intermediate levels of biodiversity in exotic plantations may reflect a transitional ecological state where soil conditions and available habitats have not fully developed to support the higher biodiversity seen in undisturbed native ecosystems. This observation underscores the importance of considering native species in ecological restoration efforts for soil rehabilitation and biodiversity conservation. While exotic species can serve as a short-term solution to prevent further soil degradation, their long-term impacts on soil biodiversity may require careful management to prevent potential imbalances in soil ecological functions [92].

The observed differences in Coleoptera communities across the three vegetation conditions—preserved native vegetation, exotic plantations, and degraded bare soils— shed light on the ecological roles these beetles play in soil ecosystems. The network diagram of beetle taxa associations reveals that soils with native vegetation support a broad array of beetle species, including detritivores such as members of the Scarabaeidae family, which play critical roles in nutrient cycling and soil structure formation and are particularly adapted to decomposing dense leaf litter and wood found commonly in native forest settings [93]. Also predatory beetles from the Carabidae family, which help control pest populations, thus supporting the overall health of the forest ecosystem [94]. Such diversity in functional roles supports a complex food web and a stable soil ecosystem, underscoring the richness of Coleoptera in these settings. Data also highlights the presence of endemic beetle species, which thrive specifically under native plant conditions due to their specialized relationships with the local flora and microhabitat conditions. These beetles often serve crucial ecological functions such as pollination, seed

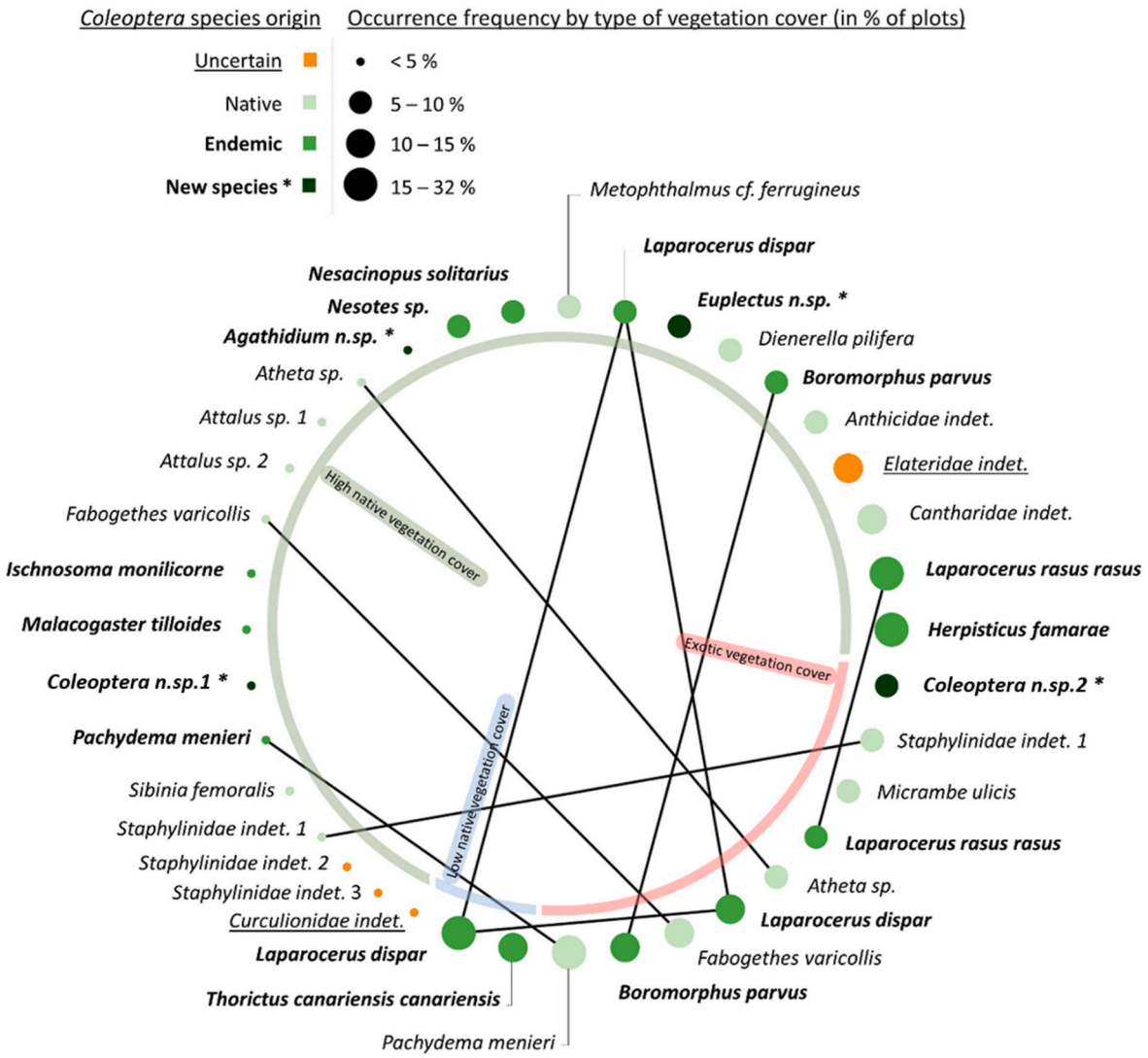


Fig. 5. Coleoptera taxa distribution network. Graphical representation of beetle taxa associations across varying soil conditions. The green radial band indicates high native vegetation cover soils ('HerbiExc', 'RemVeg', 'Mulch'), red for exotic vegetation cover areas ('Pinus', 'Acacia'), and blue for degraded soils with scant native vegetation ('Badland', 'Plain'). Interconnecting lines (edges) signify shared species across conditions. The node size is scaled to the taxa's occurrence frequency across vegetation types (expressed as a percentage of surveyed plots), while node color designates the species' origin (endemic, native, or uncertain, with asterisks (*) identifying species pending description). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

dispersal, and the breakdown of organic material, which are essential for maintaining the health and resilience of their native habitats [9,22,23,95].

In contrast, the Coleoptera communities in exotic plantations are less diverse and tend to be dominated by a narrower range of species, which might indicate a less complex trophic structure. Species from the Elateridae and Curculionidae families, known for their roles in decomposing plant material and influencing soil fertility, are common but yet the reduced diversity in these areas might indicate a less robust ecological network, impacting soil health and nutrient dynamics negatively. Curculionids, often known as weevils, are primarily herbivores, with many species having a significant impact on the plant materials they inhabit, both as larvae and adults. Their presence in exotic plantations is indicative of their adaptability to modified habitats where native competitors and predators may be less prevalent. These beetles might not adequately fulfil the ecological roles needed for a balanced soil ecosystem, potentially due to the homogeneity of the plant cover and the resultant lack of habitat diversity. In this regard, some studies have demonstrated that non-native plantations can have similar or even higher arthropod diversity than native species [12,22,27]. These observations could be attributed to factors such as plant species identity and diversity, soil quality [2,10,15], plantation age [8], and sampling methodologies employed.

Degraded soils with minimal vegetation cover host impoverished Coleoptera communities, often lacking the diversity and biomass of more vegetated soils, and primarily support generalist species that survive under harsh conditions. The presence of only two beetle taxa in these areas underscores the significant impact of vegetation cover in supporting functional biodiversity within the soil ecosystem. This stark contrast in beetle diversity and community structure across different vegetation conditions highlights the substantial influence of vegetation cover and management on soil biodiversity and the corresponding ecological processes. Specific beetle species identified in degraded soils, such as *Laparocerus dispar* (primarily a detritivore) and *Thorictus canariensis canariensis* (part of the saproxylic beetle group) are adapted to challenging conditions characterized by reduced organic matter and structural complexity. The presence of these beetle species in degraded soils can be seen as an indicator of the beginning stages of ecological succession, where even minimal organic inputs are crucial for initiating recovery processes. This highlights the importance of these beetles not

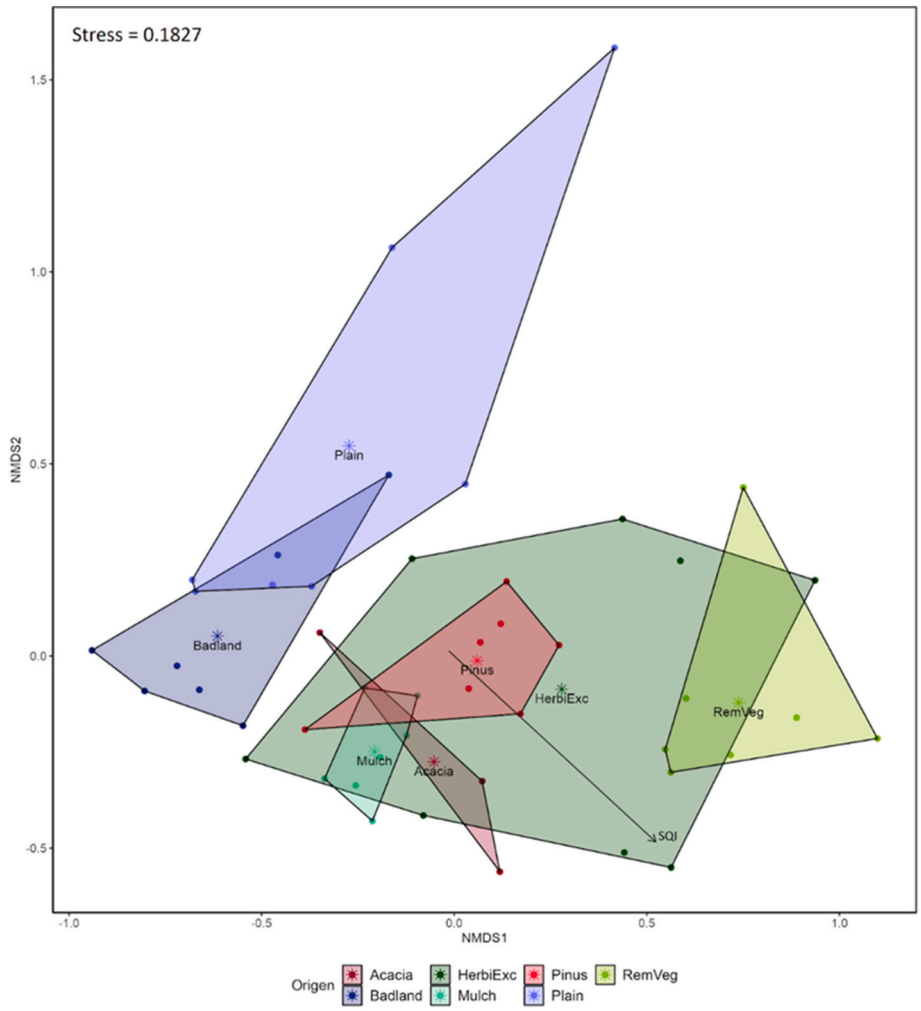


Fig. 6. Non-metric multidimensional scaling (NMDS) representation of mesofauna communities at the seven study sites (n = 3–8); site centroids are marked with asterisks in matching colors. The direction of the SQI vector in the NMDS space delineates the gradient of soil quality. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

only in terms of biodiversity but also for their ecological functions which support soil recovery and sustainability.

With regards to mesofauna, the pronounced correlation between mesofauna richness and the SQI observed in this study outstrips the correlation seen in coleopteran communities. This highlights the sensitivity of mesofauna to changes in soil quality, suggesting that these organisms could serve as more accurate bioindicators of soil health improvements or degradations. Unlike coleoptera, which are influenced by a broader range of environmental factors beyond soil quality, mesofauna such as acari and collembola seem to respond more directly to the conditions quantified by the SQI, such as organic matter content, nutrient availability, and microbial activity [16,19].

This significant relationship emphasizes the integral role that mesofauna plays in maintaining soil structure and fertility, primarily through their contributions to the decomposition process and nutrient cycling. The disparity in sensitivity to soil quality between mesofauna and coleoptera might also be attributed to the different ecological niches and life history traits of these groups, with mesofauna often being more intimately connected with the soil microenvironment [14].

In exotic plantations, while there is an improvement in mesofauna richness compared to degraded soils, the community structure does not reach the complexity or diversity seen in native vegetation areas. This divergence highlights that while exotic plantations may improve certain physical soil properties, they do not fully mimic the ecological roles of native species, which support in our study system richer and more diverse mesofauna communities, as seen in other studies [40]. This finding suggests that the introduction of exotic species may disrupt existing soil arthropod communities, potentially altering ecosystem processes such as nutrient cycling and soil structure maintenance. For example, some pine plantations, which produce more recalcitrant litter, seem to host a lower diversity and abundance of soil arthropods [12]. The authors argue that this result might be associated with the accumulation of litter rich in inhibitory compounds, which could negatively impact decomposition activity reducing soil arthropod diversity. However, they point out that certain groups of organisms (e.g, springtails), can proliferate under these conditions, possibly due to the presence of fungi capable of degrading lignin in resistant litter [12,96]. The increased presence of introduced species in exotic plantations, as observed in our study, reinforces the importance of preserving strong native vegetation to mitigate the effects of invasive species and ensure the stability of ecosystems.

Furthermore, the significant impoverishment of mesofauna in degraded and bare soils underscores the critical role of vegetation cover in maintaining soil biodiversity. These environments, characterized by low SQI values, demonstrate how severely reduced ecological processes can hamper the recovery of functional soil ecosystems. The minimal presence of mesofauna in these areas points to a disrupted ecosystem where essential ecological processes are severely hampered, emphasizing the need for soil and vegetation restoration efforts that prioritize ecological function alongside biodiversity conservation [97]. The data

also emphasize the importance of considering the ecological roles of different mesofauna species when assessing the impact of vegetation changes on soil health. For instance, the presence or absence of acari and collembola as key species can greatly influence the rate of soil recovery and the sustainability of ecosystem processes.

Previous research within the same study area by Ref. [56] evaluated the effects of plantations on microbial communities, including bacteria and fungi. Building on this foundation, the present study complements these findings by incorporating higher trophic levels, thereby providing a more comprehensive understanding of the ecological dynamics and ecosystem services that underpin the sustainability of natural systems [98]. It is also important to highlight that most of the literature predominantly relies on traditional sampling techniques, such as pitfall traps [1,22,95], while only a few studies have employed more advanced methods like metabarcoding [5]. By addressing these gaps, this study provides valuable insights into the ecological consequences of using exotic species in reforestation efforts, particularly in arid insular ecosystems. These findings enhance our understanding of soil-vegetation-fauna interactions and support decision-making in land management and restoration planning, promoting approaches that improve both soil health and biodiversity conservation.

5. Conclusions

This study elucidates the integral role of the Soil Quality Index (SQI) as a robust tool for assessing soil condition, specifically within ecosystems subjected to varying vegetation covers. Notably, the SQI strongly correlated with the richness of soil arthropod communities (i.e., Coleoptera; Acari and Collembola), affirming the effectiveness of those groups as bioindicators of soil health. These findings underscore the significant ecological shifts induced by exotic plantations compared to native vegetation. Exotic plantations, predominantly composed of *Acacia cyclops* and *Pinus halepensis*, have been shown to enhance soil quality in comparison to degraded landscapes. However, they do not achieve the soil complexity and community richness observed in areas with native flora. This divergence highlights the critical ecological value of native vegetation in supporting more complex soil communities and maintaining higher richness within the studied groups, which can contribute to ecosystem stability.

The implications of these findings are profound for restoration ecology. The transition towards native flora in restoration practices is not merely a preference but a necessity for the re-establishment of complex soil arthropod communities essential for ecosystem stability and resilience. Careful consideration must be given to the selection of plant species in restoration projects, ensuring a meticulous selection process to generate multispecies communities that facilitate restoration and ensure the recovery and health of soil ecosystems. This study not only adds to the growing body of evidence supporting the superior ecological benefits of native vegetation but also provides actionable insights for land management and restoration practices. By fostering a deeper understanding of soil health dynamics and community interactions under different vegetative covers, we can better strategize restoration efforts that are ecologically sound and sustainable, ensuring the preservation of biodiversity and the resilience of ecosystems in face of environmental changes.

CRediT authorship contribution statement

Adolfo Perdomo-González: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Investigation, Formal analysis, Data curation. **Raquel Pérez-Reverón:** Writing – review & editing, Writing – original draft, Visualization, Validation, Investigation, Data curation. **Marta Goberna:** Writing – review & editing, Visualization, Validation, Supervision, Resources, Investigation. **Heriberto López:** Writing – review & editing, Validation, Data curation. **Paula Arribas:** Writing – review & editing, Validation, Methodology, Investigation. **J. Alfredo Reyes-Betancort:** Writing – review & editing, Validation, Investigation. **Carmelo Andújar:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Methodology, Investigation, Formal analysis, Data curation. **Francisco J. Díaz-Peña:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ejsobi.2025.103724.

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