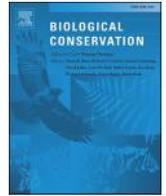


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Short communication



Co-benefits of soil carbon protection for invertebrate conservation

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ABSTRACT

The global decline in invertebrate diversity requires urgent conservation interventions. However, identifying priority conservation areas for invertebrates remains a significant challenge. We hypothesized that aligning the conservation of invertebrate biodiversity with climate change mitigation offers a solution. As both soil carbon storage and invertebrate biodiversity are positively influenced by plant diversity and productivity, a positive correlation can also be expected between SOC and invertebrate biodiversity. Drawing on >10,000 invertebrate observations organized into functional groups, and site-specific soil organic Carbon (SOC) measurements from Patagonia, the Peruvian Andes, and montane tropical rainforest, we examined the role of climate, soil, topographical position and land use for prediction of invertebrate biodiversity. We found that taxonomic and functional invertebrate diversity and abundance closely correlate with SOC stocks within ecosystems. Topographical position of sites, which was partly associated with SOC, was also important, whereas land use was of subordinate importance. We conclude that recent advances in predicting and mapping SOC can guide the identification of habitats within landscapes with high biodiversity and conservation value for invertebrates. Our findings stress the importance of linking global climate change mitigation initiatives that aim to preserve and restore SOC to efforts aimed at improving the conservation of invertebrates and the ecosystem services they provide, for the realization of mutual climate and biodiversity benefits.

Introduction

Major declines in invertebrate diversity and abundance have been observed in many regions leading to calls for more effective conservation (van Klink et al., 2020; Sánchez-Bayo and Wyckhuys, 2019; Seibold et al., 2019). Invertebrates (Fig. 1) are critically important ecosystem service providers (Dangles and Casas, 2019; Wong et al., 2019). Globally an estimated 80% of flowering plant species rely on invertebrates for pollination (Jordano et al., 2006), and between 235 and 577 billion US \$ in annual crop output is threatened by pollinator loss (Díaz et al., 2019) with major implications for food security and the other Sustainable

Development Goals (SDGs). Invertebrates are also important for pest control and for their role in the recycling of organic matter and soil formation (Gerrard et al., 1996). There are also disservices including herbivory of crops and disease transmission (Dunn, 2010). To support and sustain invertebrates requires the identification of high value areas for conservation. However, the characterisation of sites that are rich or poor in invertebrate species requires expertise and detailed study that is impractical over large regions.

In South America surrogate approaches (Beier and de Albuquerque, 2015) to assessing biodiversity such as coverage and inclusion of Holdridge Life Zones or flagship species (birds, mammals) have guided most

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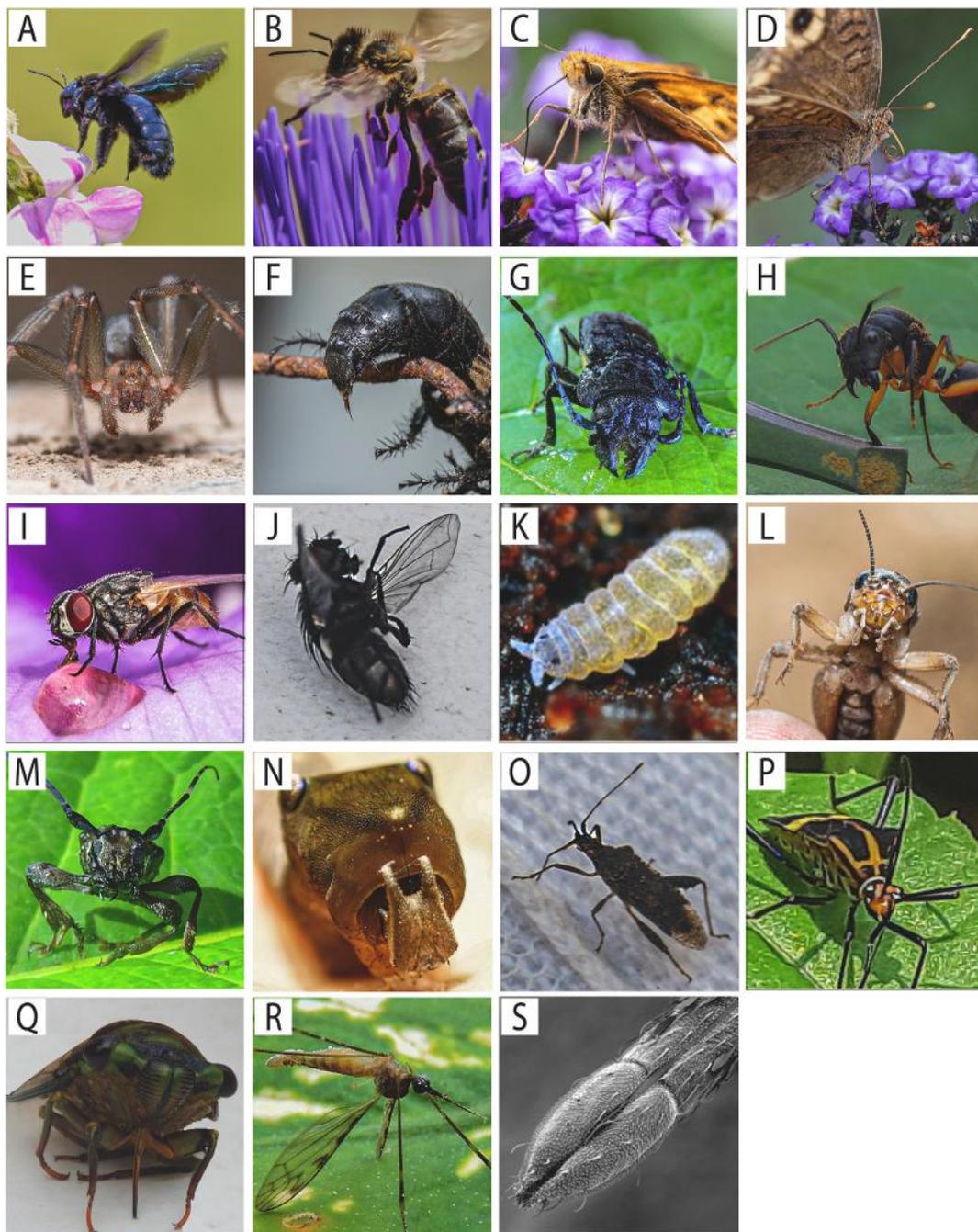


Fig. 1. Examples of invertebrates that generate ecosystem services (pollination, biological control and decomposition) and disservices (herbivory and disease transmission). Pollinators may possess bodies and legs covered with many hairs (A, B, C & D); and / or have hindmost legs in the form of a basket optimised for the transport of pollen (B). Examples of biological controllers (predators) are spiders (E); insects that possess needle like tail stings used to immobilize prey (F); and insects with mandibles in which the fore-section (incisor zone) is heavily serrated and optimised for handling prey (panels H and I). Decomposers, such as flies may possess sponge like proboscises that are optimised for the regurgitation of extra cellular enzymes and subsequent suction of food resources after said enzymes have had their effect (J, K, L). Collembolans (M) are another example, these small invertebrates are generally 1-3 mm in length and possess difficult to see internal mouthparts that consist of a series of plates optimised for grinding organic matter (photo credit: Philippe Garcelon). Examples of herbivores are insects with a highly developed molar zone on mandibles optimised for chewing plant material (N, O and P); and molluscs which possess tongues with numerous rows of small teeth, called radula, designed to shred foliage (Q). Insects with a hollow-needle-like feeding apparatus (U) can be either herbivores (R, S, T) or disease vectors (V and W). The scanning electron microscope image of the mosquito proboscis from: <https://emlab.uconn.edu/gallery/tip-of-mosquito-proboscis/#>.

conservation planning. It has often been assumed that protection of threatened vertebrates would also protect a broader range of biodiversity including invertebrates (Baldi et al., 2019; Dourojeanni, 2019). Yet, the efficacy of this surrogacy approach for conserving a wide range of biodiversity values remains unclear (Oberprieler et al., 2019; Schulze

et al., 2004). Further, to simplify coordination, it would be helpful if programs for biodiversity conservation could be linked to programs that address other Sustainable Development Goals, such as Goal 13, climate action (<https://sustainabledevelopment.un.org/?menu=1300>). Here we investigate how the protection of soil carbon stocks—widely

Table 1

Most parsimonious generalized least squares model of relative abundance of invertebrates, fit by Restricted Maximum Likelihood ($r^2 = 0.72$, $RSE = 0.044$; $df = 27/21$). LU = Land Use.

Parameter estimates variance structure (different standard deviations per stratum)	
Runoff * grassland	1
Runon * grassland	7.68
Runoff * forest	7.45
Runon * forest	6.27
Runoff * cropland-agroforestry	6.06
Runon * cropland-agroforestry	3.67

Model coefficients:				
	Coefficient	Standard error	t-value	P
Intercept	0.557	0.063	8.766	<0.001
Relative SOC	0.218	0.068	3.213	<0.005
LU-forest	-0.119	0.081	-1.471	0.16
LU-grassland	-0.310	0.058	-5.360	<0.001
Drainage-Runon	0.278	0.060	4.606	<0.001
Mean annual temperature	-0.081	0.027	-3.005	<0.01

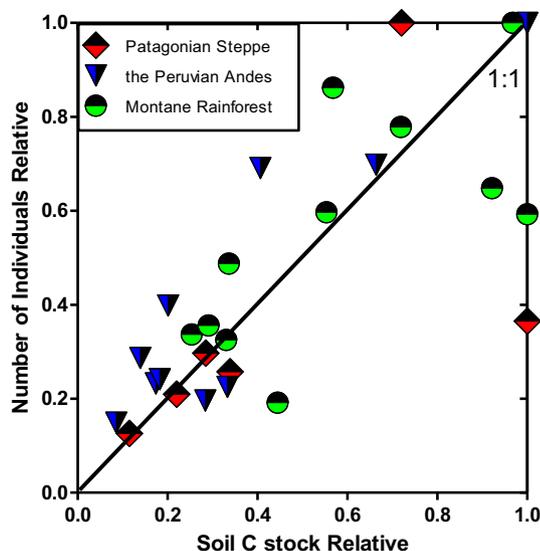


Fig. 2. The relationship between SOC and invertebrate abundance across sites in three regions. In total we sampled across 27 sites and captured and classified 10,083 individual invertebrates. Because sites were sampled across three very different biomes, we normalized both soil carbon stocks and invertebrate abundance to the maximum value of the respective variable recorded for each region. $y = 0.69x + 0.14$, $R^2 = 0.57$.

recognised as a key strategy for climate change mitigation (Rumpel et al., 2020)—could bolster the conservation of invertebrates and their associated ecosystem services.

While soil organic carbon (SOC) represents the largest terrestrial carbon (C) reservoir, holding three times the amount of C found in the atmosphere, this reservoir continues to suffer major losses due to human land use (Sanderman et al., 2017). The conservation of remaining SOC is a recognised global priority to avoid further exacerbation of the climate crisis (Bossio et al., 2020). Interestingly, conserving areas with highest SOC stocks might offer substantial opportunities to simultaneously protect threatened and other unique biodiversity (Kessler et al., 2012; Peri et al., 2019). Positive relationships between SOC and the richness of species, endemics and threatened taxa, have been found for plants, mammals, reptiles, amphibians and crustaceans (Sheil et al., 2016). Likewise variation in the abundance of invertebrates (i.e. nematodes, earthworms etc.) that are referred to as “soil taxa” have also been linked to SOC (Alegre Orihuela et al., 2019; Bardgett and van der Putten,

2014). However, for invertebrates that live on or above the soil surface and are not typically classified as “soil taxa” such a relationship had not been explored previously.

Aside from the increasing diversity of resources and niche opportunities for invertebrates in grazing and detrital food webs due to effects on plant diversity and productivity (Haddad et al., 2011) higher soil carbon may also provide a more stable resource base less affected by seasonal variations in climate. The greater stability of detrital compared to grazing food webs might favour the maintenance of invertebrate populations and diversity through time (Moore et al., 2004). The dominant functional groups of invertebrates at any given site are also expected to reflect the relative importance of the detrital vs the grazing food web.

SOC is unevenly distributed across global ecosystems, with the highest concentrations being found at higher latitudes (Hengl et al., 2017), and hence does not covary with the latitudinal diversity gradient which, for most taxa, means an increase in species diversity from temperate to tropical latitudes (Mittelbach et al., 2007). There are however exceptions (Gaucherel et al., 2018) such as the tropical peat swamp forests (Posa et al., 2011). Nevertheless, the positive correlation between SOC and arthropod abundance and diversity is expected to predominantly manifest itself within ecosystems/landscapes, rather than across ecosystems. Here we test this possibility by compiling SOC stocks and invertebrate diversity within three south American ecosystems (the Patagonian steppe, the Peruvian Andes and the Peruvian montane rainforest) and assess the explanatory power of SOC as function of climate, soil, NDVI (a proxy of plant productivity), current land use, and the topographical position of the sampling site. Further, we investigate whether dominant the functional groups of invertebrates in the SOC – invertebrate gradient in each ecosystem can be related to the expected relative local importance of the detrital vs the grazing food webs.

Methods

We sampled invertebrates at 27 sites across three distinct ecosystems: 1) Cold arid steppe in southern Patagonia ($n = 6$ permanent plot sites within the PEBANPA network) (see Peri et al. (2019) for details); 2) Tundra like ecosystems in the Peruvian Andes ($n = 10$ sites, See Flores-Alvarez et al. (2018) and Vásquez et al. (2014) for details); 3) Montane tropical rainforest in the upper reaches of the Amazon catchment in Peru, known locally as the “ceja de la selva” or the “eyebrow of the forest” ($n = 11$ sites, see Ladd et al. (2018) for details). In all sites, soil carbon was assessed using soil pits dug to bedrock or 1 m depth and using the methods described by Vásquez et al. (2014). At each site we determined the dominant land use (grassland, forest or cropland-agroforestry) and classified drainage as either runoff or runon (for water) (Eldridge, 1996). Rainfall and temperature variables were obtained from the Worldclim dataset (Fick and Hijmans, 2017), potential evapotranspiration and aridity indices from the CGIAR-CSI GeoPortal, soil order from soilgrid250m (Hengl et al., 2017) and the mean, minimum, maximum and variance of normalized difference vegetation index (NDVI) was obtained from the European Space Agency (ESA) (<http://maps.elie.ucl.ac.be>, see their Land Surface Seasonality products).

Sampling took place in the Austral summer when invertebrate abundance was high (February 2016 in Patagonia, January 2016 in the Peruvian Andes, and December 2015 in Peru’s Montane Rainforest). At each of the 27 sites we deployed a single malaise trap and 4 replicates of the following trap types: bait (rotten meat), pitfall and pan (pollinator) traps for 48 h (see, https://www.youtube.com/watch?v=BYUs0wBh_zg). The pitfall and bait traps were fashioned from cylindrical 1 L plastic containers with a diameter of 10 cm and the pan traps from circular-yellow-disposable plates 20 cm in diameter. Diluted honey was added to the pan traps. All invertebrate samples were stored in alcohol for characterisation at the Universidad Científica del Sur in Lima, Peru, and classified into functional groups by the ecosystem services and

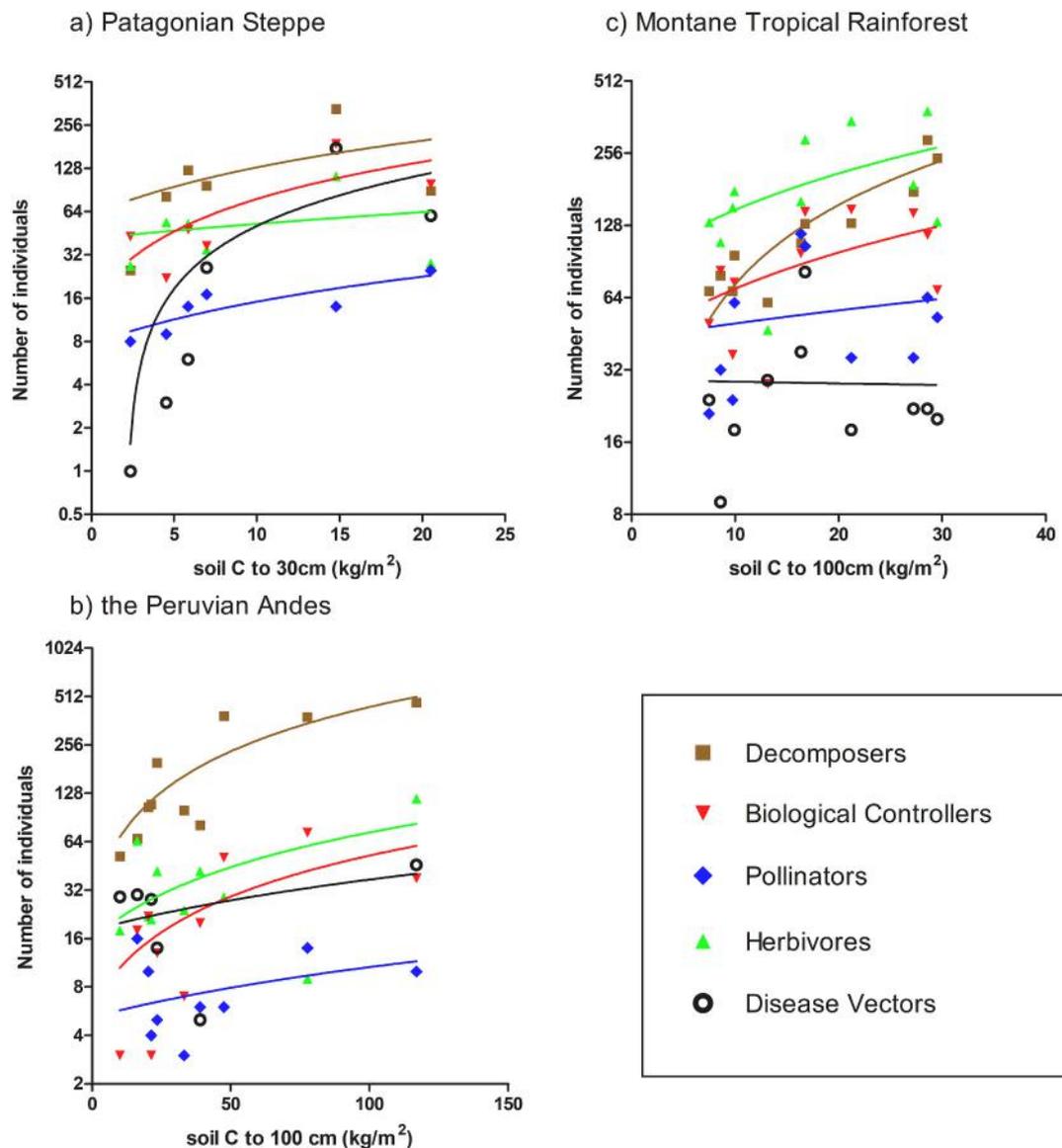


Fig. 3. The relationship between SOC stock and the absolute abundance of invertebrates classified according to the ecosystem service (decomposition [soil formation], pollination or biological control) or disservice (herbivory, disease transmission) that they provide. a) Patagonian Steppe: the r^2 values for simple linear regressions are as follows: 0.20, 0.05, 0.49, 0.71, 0.43, b) the Peruvian Andes \approx 4000 m.a.s.l, the r^2 values are as follows: 0.83, 0.34, 0.46, 0.12, 0.29, c) Montane Rainforest, the r^2 values are as follows: 0.83, 0.24, 0.30, 0.03, 0.00. For all three regions r^2 values correspond to values for decomposers, herbivores, biological controllers (predators), pollinators and disease vectors respectively. Across the three regions a total of 10,083 invertebrates were captured and then classified according to the ecosystem service or disservice.

disservices that they likely contribute (pollination, decomposition, pest control, herbivory, disease transmission).

All the invertebrates from all 27 sites were first classified to broad taxonomic groups using the system of Triplehorn et al. (2005). For the Hymenoptera (Fernández and Sharkey, 2006), Coleoptera (Bouchard et al., 2011) and Diptera (Craig, 2011) identification keys were more narrowly on these specific groups were used. When information on the feeding ecology of the above groups was described in the above keys, we used that information. In cases where knowledge of feeding ecology was unavailable the specimens were examined under a light microscope and then classified to ecosystem service category based on own observations of functional traits. In addition, we classified the 1859 invertebrates captured in Argentina to morphospecies.

We identified variables that significantly contributed to explaining relative invertebrate abundance using multivariate approaches. Collinear variables were removed based on stepwise calculations of variance inflation factors (VIF), retaining only variables with VIFs

smaller than <3 . Retained variables were land use (LU) and drainage class (drain), SOC, aggregated maximum NDVI (from hereon NDVI), soil water content, soil order, Mean Annual Temperature, and Mean Annual Precipitation. We normalized both SOC and invertebrate abundance by expressing measured values in relation to the maximum recorded values in each of the biomes. Thus, all values of normalized SOC and invertebrate abundance (from here on relative abundance and relative SOC) ranged between 0 and 1. All continuous explanatory variables were standardized by subtracting the mean value and dividing by twice the standard deviation.

We constructed a linear mixed effects (LME) model including sampling region as a random variable and compared this with a generalized least squares (GLS) model (fixed components containing all variables and up to second-order interaction terms) using the *nlme* package for R (Pinheiro et al., 2019). To resolve heterogeneity in the normalized residuals, we applied a fixed variance structure in the GLS for SOC and a corrective variance structure for the different levels of LU, drainage, and

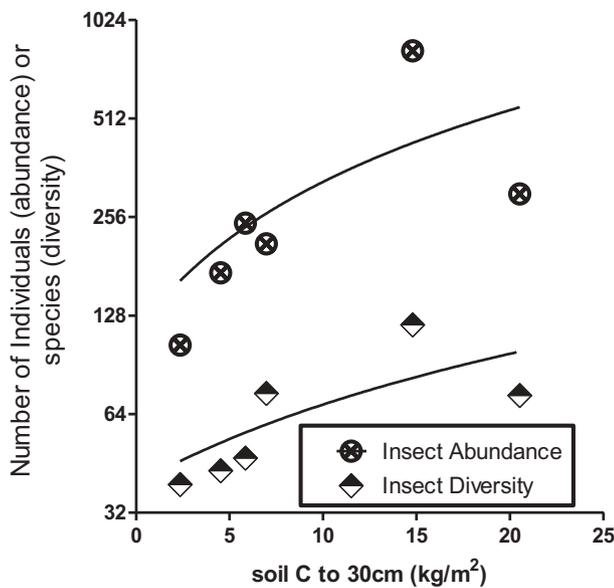


Fig. 4. The relationship between soil carbon stock and invertebrate diversity and abundance across 6 sites in the PEBANPA network of permanent plots in southern Patagonia. 1859 invertebrates classified across the 6 sites. Regression statistics: invertebrate abundance: $y = 215 * \ln(x) - 112.64$, $R^2 = 0.42$, diversity: $y = 29.07 * \ln(x) + 8.8$, $R^2 = 0.56$. Note the log2 scale on the y axis.

their interactions. The Akaike information criteria (AIC) and likelihood ratio tests indicated no significant random effect, and therefore, we rejected the LME model and retained the more parsimonious GLS model. Next, we optimized the fixed effect structure through an iterative use of F and likelihood ratio tests. The standardized residuals of the selected model were normally distributed and showed no patterns with either the fitted values or any explanatory variables.

Results

The 10,083 invertebrates —mostly insects, but also myriapods, molluscs and spiders—collected across the 27 sites revealed a clear relationship with site characteristics. The most parsimonious GLS model explained 72% of the variation in relative abundance of invertebrates

and included four explanatory variables: relative SOC, land use, drainage and mean annual temperature (Table 1). Relative SOC alone accounted for 57% of the variance in invertebrate abundance across the three sampled landscapes (Fig. 2). The most parsimonious GLS model with the same variance structure but without SOC explained 60% of the variance and retained only land use and drainage class. NDVI was not retained in any of the selected models and a GLS based on this variable alone explained 27% of variation.

In all three biomes the abundance of invertebrates belonging to the five ecosystem service categories increased with soil carbon stock (Fig. 3). Disease vectors in the montane rainforest zone were the only exception, with no detected correlation with SOC (Fig. 3C). The positive correlation between SOC stocks and the abundance of invertebrates was also found for species richness across the sample sites in Patagonia (Fig. 4). “Runon sites”, where water tends to accumulate, had average relative SOC and invertebrate abundance scores that were more than twice as high than the better drained runoff sites (Wilcoxon $W = 29$, $P < 0.01$ and $W = 20$, $P < 0.001$, respectively; Fig. 5). When clustering the data within these drainage classes, there was a clear trend towards higher median values of species richness in the order grassland ≤ forest ≤ cropland-agroforestry (all runoff) ≤ grassland ≤ forest ≤ cropland-agroforestry (at runon sites). At the runoff sites on cropland-agroforestry the relative abundances of invertebrates was even significantly higher than for grassland (post hoc Kruskal-Wallis test $P < 0.05$; Fig. 5b).

Discussion

Soil organic carbon proved to be an effective indicator of the diversity, abundance and ecosystem service provision by invertebrates. The mechanisms behind these relationships are unclear, but multiple factors appear likely. Soil organic carbon storage is positively associated with greater plant diversity and productivity (Chen et al., 2018, 2020; Keddy, 1994; Perner et al., 2005) which means more resources, and niches, also for invertebrates (Haddad et al., 2011). That land use had little detectable effect on SOC or invertebrates was surprising, as land use change from natural vegetation to cropland typically leads to SOC loss (Duarte-Guardia et al., 2020) and decline in invertebrates (Sánchez-Bayo and Wyckhuys, 2019). Probably the agroforestry and cropping systems we sampled were still too young to detect such trends. At the same time, we find more invertebrates at run-on sites, which are less likely to be water deficient than otherwise similar sites in the vicinity. Higher invertebrate abundance might be explained by the combination

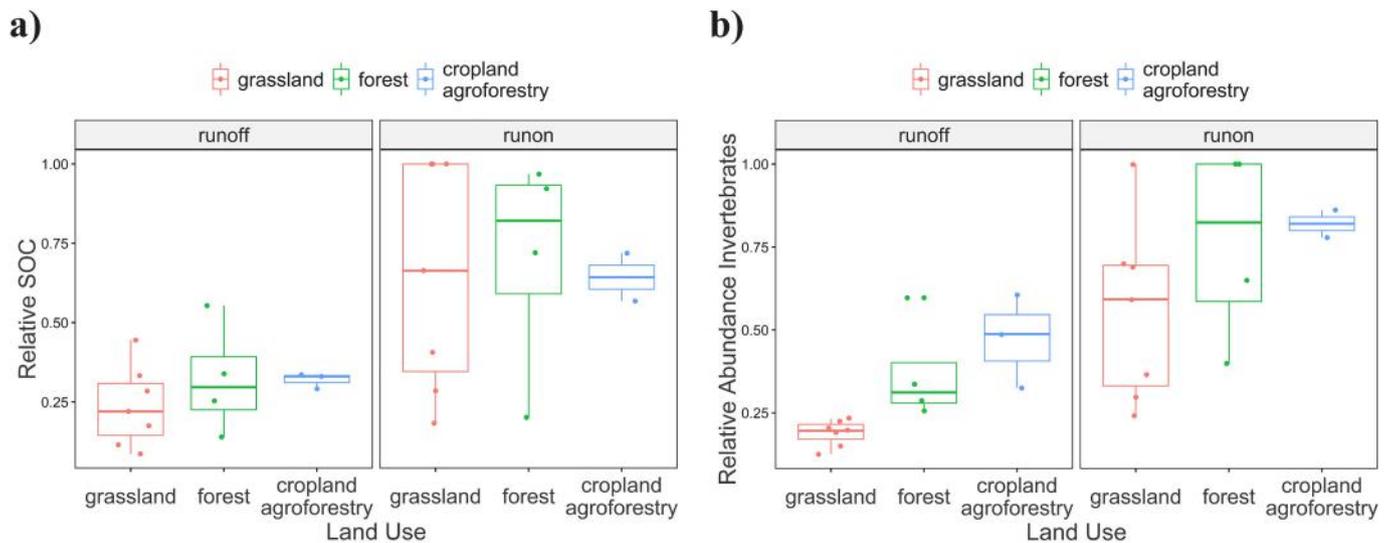


Fig. 5. Comparisons of relative SOC (a) and abundance of invertebrates (b) sampled at 27 sample sites spread across cold arid steppe in southern Patagonia ($n = 6$); tundra like ecosystems in the Peruvian Andes ($n = 10$) and Peruvian montane tropical rainforest ($n = 11$), according to drainage class and current land use at sampling sites. Runon sites are those located at lower end of a slope where water accumulated, whereas runoff sites are those located higher up the slope.

of higher availability of food resources due to higher plant productivity and more favourable habitat conditions related to lower drought stress and possibly lower temperature extremes. Nonetheless, questions remain as to how generalizable the SOC-invertebrate correlation might be across global ecosystems. Possibly in ecosystems where high SOC is linked to adverse environmental conditions such as extreme inundation or low temperatures (e.g. permafrost) the correlation between SOC and biodiversity may begin to fray? Additional measurement in a wider diversity of ecosystems are needed to clarify these possibilities.

The dominant invertebrate functional groups varied among regions in accordance to our expectations. Biomes with pronounced seasonality (Patagonia and the high Andes) were dominated by decomposers. In these seasonal climates, dead biomass accumulates from deciduous and annual vegetation due to dry seasons and annual temperature cycles increasing the importance of the detrital trophic pathway. In contrast, in the evergreen montane tropical rainforest zone, where a significant percentage of the ecosystem carbon stock is in the form plant foliage, herbivores dominated over decomposers. The positive correlation between SOC and the abundance of disease vectors in the seasonal biomes likely reflects productivity, making these habitats more attractive to warm-blooded animals (Sheil et al., 2016). The value of these SOC rich wet microhabitats as relatively stable refugia when other environments are subjected to episodic droughts and heat events, may also be influential. In non-seasonal biomes such as the montane tropical rainforest zone, the higher and more widely distributed availability of food resources and the reduced need for shelter for warm-blooded animals may lead to their occurrence being independent of SOC. The ubiquitous presence of phytotelmata in the montane rainforest zone may also spatially expand the possibilities for breeding of disease vectors such as mosquitoes. Detailed studies using isotopic approaches to map the predominant trophic pathways in these landscapes could help to confirm or refute these hypotheses (Schneider et al., 2004).

Our findings add to others highlighting a positive relationship between SOC and biodiversity values at a range of scales (Sheil et al., 2016). SOC is a useful surrogate, or indicator variable, for many other site properties. High SOC levels result from a favourable combination of factors including climate, topography, soil parent material, management, etc. (Duarte-Guardia et al., 2019, 2020; Peri et al., 2019). Despite these complexities our ability to predict and map soil organic carbon has advanced impressively (Hengl et al., 2017; Manning et al., 2015). We propose that the strong correlation between SOC and other important conservation values can guide conservation priority setting and related mapping initiatives. Important especially for continents like South America where the required experts with “boots on the ground” are scarce or absent (Wilson, 2017).

Our finding that invertebrate abundance and diversity both increase with increasing SOC stocks suggests that climate change mitigation initiatives that aim to preserve and restore soil C, such as the 4p1000 initiative (Chabbi et al., 2017; Rumpel et al., 2020) or RECSOIL (FAO, 2020), the FAO's vision for re-carbonization of global soils, may also have relevance for biodiversity conservation. Many other important ecosystem services like water storage capacity, soil heath and plant productivity are closely linked to both SOC and biodiversity (Keesstra et al., 2016). The alignment of strategies to mitigate climate change and conserve biodiversity thus represents a major win-win opportunity in our efforts to achieve the SDGs.

CRediT authorship contribution statement

BL conceived the study. AR-F, AV-A. and AL-T classified the invertebrates. PLP and WA contributed soil C data. BL, ET, WA, NB, DS, TT and IS-D. drafted the manuscript. All authors provided input.

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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