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ORIGINAL PAPER

Bellwether of the Canaries: anthropogenic effects on the land snail fauna of the Canary Islands

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Abstract Natural areas near human-modified landscapes experience factors that may affect local biodiversity at levels commensurate with natural environmental factors. The land snails of the Canary Islands provide excellent opportunities to evaluate the importance of anthropogenic agents in mediating the diversity and distribution of species. Land snails are particularly sensitive to disturbance and are an integral part of terrestrial ecosystems. This study analyzed the distributions and abundances of terrestrial macrosnail shell assemblages at 60 localities throughout the coastal scrub biome of the Canary Islands. This was accomplished using data on natural and anthropogenic variables to assess their relative importance in governing land snail diversity. A total of 34,801 dead shells represented a diverse malacofauna with highly localized endemism. Due to uncertain species identifications, samples from the 18 sites from the two easternmost islands are described, but excluded from statistical analyses. Regression tree analysis indicated that proximity to agricultural sites was the most important predictor of species diversity. Sites with no or very little agricultural area (≤ 0.167 km^2) within a 1 km radius had significantly higher richness and diversity. These results have implications for Canary Islands conservation. Protected areas that are patchworks of natural and agricultural landscapes are still subject to native biodiversity loss because of anthropogenic impacts even when the footprint of agriculture is small.

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Introduction

Anthropogenic landscape modification often has unintended ecological consequences on nearby species and communities (Fischer and Lindenmayer 2007). Crops, buildings, and infrastructure directly replace portions of natural systems. In addition, anthropogenic development can also obstruct species' movements across landscapes or contribute to environmental degradation through pollution or unnaturally high nutrient availability, which can produce haloes of radiating ecological impacts. Quantifying how anthropogenic activities impact the biodiversity of nearby landscapes is critical to successful conservation initiatives.

Historical records of biodiversity predating human modification tend to be rare and incomplete, limiting information on pre-disturbance baselines. When changes over time cannot be observed, some studies have successfully used changes over space instead, comparing community structure between disturbed areas and areas that are relatively pristine (McKinney 2008 and sources cited therein; McDonnell and Hahs 2008 and sources cited therein; Horsák et al. 2009, 2013; Lososová et al. 2011; Kolbe et al. 2016). Most of these studies sought to hold fixed the influence of natural factors by limiting the study area, for example, to a single city and its surroundings. Here, we constrain natural variability by focusing on a single biome found across a wide geographic range that is impacted by a variety of anthropogenic pressures. Conservation efforts often focus on areas that have not been developed and could be informed by studies focusing on human impacts that spread into natural areas. This could allow improved detection of situations in which a community may appear intact, but may actually be in a state of decline.

Here, we quantify the ecological impact of anthropogenic factors at a geographical scale directly applicable to conservation efforts. We focus our study on the semi-arid coastal scrub biome of the Canary Islands. We assess anthropogenic pressures on each site by quantifying nearby landscape modification. Native land snail diversity has been shown in other studies to be an early indicator of broader ecosystem disruption (McMillan et al. 2003; Čejka et al. 2008; Lososová et al. 2011; Yanes 2012a; Douglas et al. 2013). Because natural factors in the Canarian coastal scrub are fairly homogenous, biodiversity may be expected to be fairly constant unless affected by other factors. We hypothesize that proximity to human-modified landscapes has a negative effect on the diversity of native malacofauna of the Canarian coastal scrub.

Land snails are particularly advantageous for biodiversity assessments. After death, they often leave behind their shells, which can be plentiful and are easily collected. Land snail shell assemblages are a close match to the living assemblages from which they derive (Rundell and Cowie 2004; Pearce 2008; Thurman et al. 2008; Cernohorsky et al. 2010; Yanes 2012b; Albano 2014). These shell assemblages include many years to decades of accumulation. Such time-averaging reduces population fluctuations due to ephemeral variations in environmental factors (e.g., an unusually wet year). Instead, shell assemblages provide a rolling, long-term average composition of the living community, which is valuable for investigating long-term population trends and assessing community response to environmental change (Kidwell 2007; Pearce 2008; Albano 2014; Yanes 2012a). Unlike the multi-millennial ages of marine shell assemblages in many coastal settings (Kowalewski et al. 1998; Kidwell et al. 2005), Pearce (2008) found that land snail shells in a temperate forest had a half-life of 7.5–11.5 years and suggested this may be much longer in arid, carbonate-rich settings (like the Canarian coastal scrub). A variety of studies have taken advantage of these characteristics of land snail shell assemblages to study, e.g., urban–rural gradients (Horsák et al. 2009, 2013; Lososová et al. 2011), forest succession after logging (Douglas et al. 2013), anthropogenic impacts on live-dead fidelity (Yanes 2012a, b), national park management (Götmark et al. 2008; Bros et al. 2016), and heavy metal pollution (Regoli et al. 2006). Their use as sentinel species at a broad geographic scale, however, has not been tested.

Methods

Field methods

The coastal scrub biome's relatively consistent climate and vegetation throughout the seven Canary Islands allow the investigation of the biodiversity response in a single wide-ranging environment to a spectrum of anthropogenic impacts. For example, moisture availability is one of the most important natural factors controlling land snail distribution (Cook 2001), and the coastal scrub is relatively uniformly semi-arid. Average annual precipitation ranges from 150 to 400 mm among all sites, varying by about 100 mm among the sites on any given island. The coastal scrub also has fairly clear boundaries with adjoining biomes, abundant land snails with high preservation potential due to generally calcium-rich soils (Fernández Caldas et al. 1987), and is the only biome present on all seven islands. The coastal scrub also occurs near agriculture and urban development, as well as in relatively pristine areas.

To identify sampling sites, the European Environment Agency's (EEA) coordination of information on the environment (CORINE) land cover inventory (EEA 2013) was used. Human-modified areas were first broadly categorized as "agricultural" or "artificial" (the latter including urban, recreational, and industrial areas) following EEA (1995) nomenclature. Natural areas that the EEA identified as "sclerophyllous vegetation" within 5 km of the coast were considered coastal scrub. On each island, targeted areas included natural coastal scrub vegetation that was: (1) adjacent to or surrounded by agricultural and artificial landscapes; (2) in remote areas; or (3) somewhere in between. Within these areas, the presence of typical coastal scrub flora (e.g., *Euphorbia*, *Schizogyne*, *Launaea*, *Lycium* [Otto et al. 2006]), an elevation below 500 m a.s.l., and accessibility determined the placement of sites.

This study sampled 60 sites in the coastal scrub biome throughout the Canary Islands (Fig. 1). In general, more sites were sampled on larger islands, but at least six were sampled on each island. The methods prescribed by Cameron and Pokryszko (2005), and Coppolino (2010) were used to collect land snail specimens. Initial prospecting of sites ensured the presence of snails to maximize their abundance and richness. This practice is common for collecting macrosnails and helps to compensate for their patchy distributions and improves detection of rare species (Szybiak et al. 2009; Coppolino 2010; Bros et al. 2016). Field methods were designed to maximize efficient detection of macrosnails and did not include bulk sampling of soils, which has been suggested as the most effective method for detecting microsnails (snails with shells < 5 mm in their maximum dimension as adults) (Coppolino 2010). Furthermore, many microsnail species are burrowing, so their presence in mostly surficial samples may have more to do with soil processes than ecology.

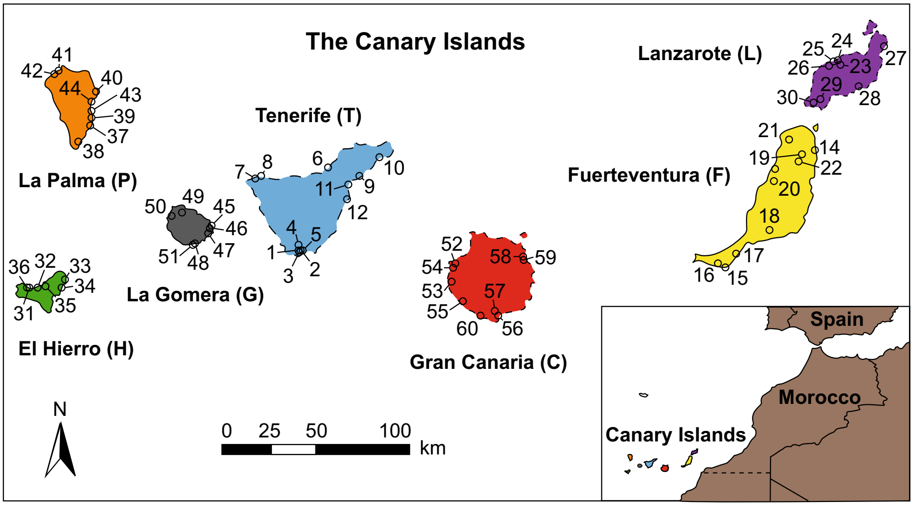

Fig. 1 Geographical location of the Canary archipelago and numbered collection sites. Island colors and abbreviations are used in some subsequent figures

Similarly, the fragility of microsnail and semislug shells probably leads to much lower persistence in the assemblage and, therefore, greater sampling bias against them (Cadée 1999; Ménez 2002; Pearce 2008). Therefore, microsnail and semislug specimens were excluded from quantitative analyses.

Workers marked out 30 by 30 m plots, then visually searched for and collected any dead snail shells for 1 h. Whenever found, living specimens were counted directly in the field, though diversity calculations only included data from the dead snail shells. Four workers collected specimens at each site in Tenerife, Fuerteventura, and Lanzarote; three workers in El Hierro; and two in La Palma, La Gomera, and Gran Canaria. The only exceptions were sites 23 and 24 in Lanzarote, and 45 in La Gomera, which had 3, 2, and 1 collector, respectively. Counts were rarefied to compensate for this discrepancy (see Statistical Methods).

Shells were commonly found on the soil surface, between or under rocks, or amongst plant litter. Only identifiable shells including the apex were counted. Species were identified by comparison with specimens from the mollusk collection in the Malacology Laboratory of the University of Cincinnati and the most recent literature (Ibáñez et al. 2006; Yanes et al. 2007, 2009, 2011a, b; Castro et al. 2012; Santana et al. 2013; Alonso and Ibáñez Alonso and Ibáñez 2015a, b, c), and with the assistance of local experts (see Acknowledgements).

Ten factors (natural and anthropogenic) were used to describe collection sites. These were selected from 40 environmental factors initially explored. When factors were strongly correlated—having an R^2 of 0.6 or greater—we selected the factor that was more general or more simply derived (see details in Appendix Table 3). The three independent anthropogenic factors included were: the total agricultural area within a 1 km radius of the site; the total artificial area (human-modified area other than agriculture) within a 1 km radius of the site; and the distance from the site to the nearest road of any kind. The six natural factors included were: the distance to the nearest stream; average minimum annual temperature; area of coastal scrub vegetation within a 1 km radius of the site; the dip of the site's slope; the northness of the slope's aspect (i.e., a slope facing due north = 1, due south = 0); and the eastness of the slope's aspect (i.e., a slope facing due east = 1, due west = 0). The tenth factor included was the patchiness of coastal scrub vegetation within a 1 km radius of the site, a factor influenced by both natural and anthropogenic forces. This final factor was measured as the total area of coastal scrub vegetation (km^2) within 1 km of the site, divided by total length of edges shared with other area types (km), and multiplied by π so a value of 1 indicated solid coastal scrub vegetation around the site, while, as area decreased and/or edge length increased, the value would approach 0. Topographical data were taken from the EEA Elevation map of Europe (EEA 2004). Climatic and population data were taken from the WorldClim global climate data set (Hijmans et al. 2005). All geographic analyses were performed using ArcGIS Desktop release 10.3 (ESRI 2014).

Statistical methods

Hill numbers (Hill 1973) were used to report diversity statistics. Following Chao et al. (2014), the three Hill numbers used are referred to as richness, Shannon diversity, and Simpson diversity, and are reported in units of species equivalents ("the effective number of equally common, equally distinct species" [Chao et al. 2014]). Most measures of diversity, including Hill numbers, are sensitive to sampling effort, and, as noted earlier, samples were collected with some variation in number of collectors (from 1 to 4). To mitigate this, samples were rarefied after Chao and Jost (2012). Rarefaction curves were created by finding a sample's expected richness at many subsample sizes. These demonstrated how richness increased with increased subsample size for each sample. Sample completenesses were reduced to that of the least complete sample (sample 33, having 73 individuals and an estimated completeness of 0.9867), such that each sample's rarefaction curve terminates at the same angle, allowing diversity measurements to be compared (Supplementary Material Table S1).

In addition to sampling effort, differences in sampling quality among collectors was examined. To accomplish this, we compared the number of species each collector encountered at the 26 sites where all four were present. The median number of species encountered at a site was calculated and subtracted from the number of species each collector encountered. A Tukey's test (Tukey 1949) was performed on the resulting scores to detect whether any collectors encountered consistently more or fewer species. We were also concerned that diversity patterns across space may be influenced by geography (sites nearer each other might have similar diversities merely because of their proximity). Moran's I (Moran 1950) was calculated for diversity measures across all sites as well as for each island to test for spatial autocorrelation.

Rarefied richnesses at sites including introduced species were compared to those with only natives using Welch's *t* test (Welch 1947). This test was favored over the Student's t-test because of unequal sample sizes and variances. To detect signs of invasiveness (the negative impacts on native biodiversity due to introduced species), native diversity was compared between sites with and without introduced species.

Regression trees were used to evaluate the strength of the effects of natural and anthropogenic drivers on biodiversity (richness, Shannon diversity, and Simpson diversity). A regression tree is a machine learning technique that creates a hierarchical ranking of variables that best explain the distribution of a response variable. The algorithms use the predictor variables to recursively split the data into two groups until the total variance of the response variable is minimized. The variable that minimized the variance is considered to have the most explanatory power. The process is repeated on subgroups until further splits do not improve the model. To avoid overfitting, we used the one standard error rule (Breiman et al. 1984), which is a standard pruning procedure to remove splits that do not sufficiently improve the model. (Breiman et al. 1984; Lemon et al. 2003; Hothorn et al. 2015).

All statistical analyses were performed using RStudio vers. 0.98.1091 (RStudio Team 2015) and R vers. 3.2.4 (R Development Core Team 2016). Regression trees were produced using the party package (Hothorn et al. 2015). Rarefaction was performed with the iNEXT package (Hsieh et al. 2016).

Results

Land snail species composition and distribution

Sixty sites distributed among the seven Canary Islands yielded 34,801 land snail shell specimens. Sites varied in richness from 1 to 14 species and in abundance from 34 to 2,770 individuals.

Rarefaction of species richness (Fig. 2) illustrated the great range of richness and compositions encountered. For example, site 30 (Lanzarote) had a single species that was highly abundant, while site 6 (Tenerife) included fewer individuals than most sites, yet had 13 species and a rarefaction curve that does not approach anywhere near an asymptote (i.e., greater sampling effort would have probably yielded many more species). Rarefaction curves representing sites on the five westernmost islands were generally more similar, overlapping in Fig. 2, while Lanzarote and Fuerteventura had relatively depressed curves with low richness, despite large sample sizes. The number of species encountered on each island and their biogeographical characters are summarized in Table 1; threatened species are listed in Table 2; the Appendix includes detailed tables for each island (Appendix

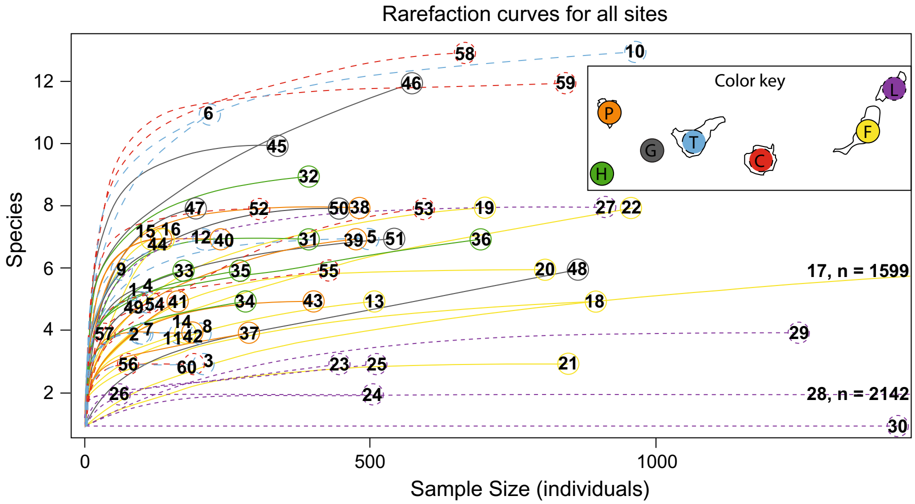

Fig. 2 Rarefaction curves for each site, color-coded by island. Inset map indicates color-coding; circled numbers indicate the sample site

Table 1 Summary of the number of large (> 5 mm maximum dimension) land snail species recovered from the coastal scrub biome on each island. The sums of values in each column are greater than the totals indicated because some species are found on multiple islands. Indigenous species are native but not endemic

Island	Species	Endemic species	Indigenous species	Introduced species
El Hierro	13	10	2	1
La Palma	10	7	2	1
La Gomera	22	17	4	1
Tenerife	20	15	4	1
Gran Canaria	22	18	2	2
Fuerteventura	13	10	2	1
Lanzarote	10	7	2	1
Total	84	72	8	4

Table 2 Endemic land snail species considered vulnerable (V), endangered (E), or critically endangered (CR) by the IUCN (2016) and encountered as shells in this study

Species and status	Island	Site(s)	Numbers of shells (by site)
Canariella bimbachensis V	El Hierro	31, 35, 36	85, 1, 171
Canariella fortunata V	Tenerife	6, 9, 10	58, 25, 98
Canariella hispidula V	Tenerife	11, 12	45, 34
Canariella huttereri E	El Hierro	33, 34	1, 76
Canarivitrina falcifera CR	La Gomera	47	1
Hemicycla eurythyra V	Tenerife	6	6
Hemicycla plicaria CR	Tenerife	11	15
Hemicycla pouchet V	Tenerife	10	109
Monilearia arguineguinensis CR	Gran Canaria	60	122
Monilearia granostriata CR	Fuerteventura	17	3
Napaeus isletae CE	Gran Canaria	58	21
Napaeus rupicola V	La Gomera	45, 49, 50	3, 2, 2
Obelus discogranulatus E	Fuerteventura	17	
Theba grasseti E	Gran Canaria	58, 59	37, 15
Theba impugnata V	Lanzarote	27	306
Xerotricha pavida E	La Palma	38, 40, 42	19, 18, 18

Table 4); and a spreadsheet compiling all sites and species is available as supplemental material.

The community structure of samples from Fuerteventura and Lanzarote (the two easternmost islands) was markedly different from that of the samples from the rest of the Canary Islands. Samples from these two islands had significantly lower diversities and evennesses compared with all other islands, despite typically higher abundances (Figs. 2, 3, 4). This is due in part to the dominant genus at all sites on Fuerteventura and Lanzarote being *Theba*, which includes many cryptic species. This made accurate species identification, and therefore diversity measurement, difficult (Greve et al. 2012). For these

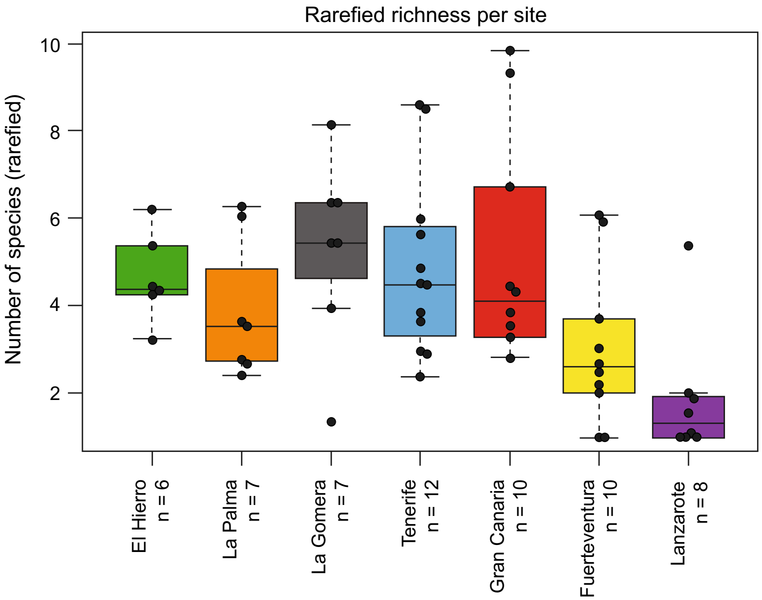

Fig. 3 Rarefied richness of land snails at each site from the coastal scrub biome across the Canary Islands, grouped by island. Sites are marked as black dots (horizontally offset for clarity in case of overlapping values); the upper and lower quartiles are the upper and lower sides of the boxes; medians are the lines within the boxes; and the whiskers terminate at the most distant point that is less than 1.5 × the interquartile range from the box

reasons, samples from these two islands are included in qualitative descriptions below, but were excluded from the quantitative analyses.

Eighty-four macro snail species from the coastal scrub biome, including 72 Canary Islands endemics, eight non-endemic natives, and four introduced species (Table 1) were recovered. Of these, subsequent analysis excluded six semislug species (terrestrial gastropods unable to retract fully into their shell) and five microsnail species. Specimens of *Ferussacia folliculus* were also excluded because, though they may reach 9 mm in length, all individuals encountered were smaller than 5 mm and were therefore subject to the same potential collection biases as microsnails. While not analyzed, abundances of recovered microsnails and semislugs are included in Appendix Table 4.

The great majority of macrosnail species encountered were highly endemic: 69 were single-island endemics and 27 of these were found at only one site and 23 at only two. Sixteen species listed as threatened by the IUCN (2016) were recovered (Table 2). These included *Monilearia arguineguinensis*, a critically endangered species that has sometimes been thought to be extinct (Fernández-Palacios and Whittaker 2008), but with shells making up ~ 60% of the site 60 sample. This further emphasizes the need for intensive and comprehensive land snail surveys in the Canaries, as the conservation statuses of most species are unknown or questionable.

Several species were found on multiple islands. *Theba geminata*, though almost certainly an endemic species complex (Greve et al. 2010, 2012), was encountered on three islands (Fuerteventura, Lanzarote, and Gran Canaria), with 12,364 shells (nearly as many as all other species combined) recovered from 20 sites. Where it occurred, *T. geminata* made up more than 50% of individuals in all but three sites. The Canary Island endemic

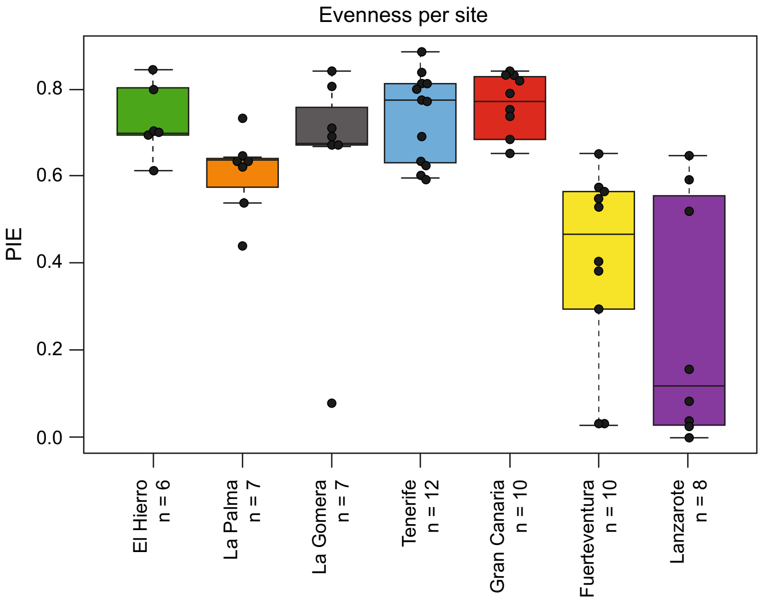

Fig. 4 Evenness, measured as PIE (the probability of interspecific encounter (Hurlbert 1971) of coastal scrub land snail communities across the Canary Islands, grouped by island. Sites are marked as black dots (horizontally offset for clarity in case of overlapping values); the upper and lower quartiles are the upper and lower sides of boxes; medians are the lines within boxes; and the whiskers terminate at the most distant point that is less than 1.5 × the interquartile range from the box

Monilearia persimilis was collected on Gran Canaria, La Palma, El Hierro, and Tenerife. Non-endemic native *Rumina decollata*—a well-known invasive species in North America (Cowie 2001a)—was encountered on all islands except Tenerife and La Palma. It typically made up ~ 10% of samples when present, but nearly 97% of the site 48 sample from La Gomera, with hundreds of individuals. The non-endemic native *Caracollina lenticula* was the only species found on all seven islands, occurring in all but eight samples.

Four introduced macrosnail species were collected. There is no published evidence that human-introduced snail species in the Canaries have become invasive, generally defined as causing environmental or economic harm or harm to human health. There was no evidence that sites with introduced species had significantly different diversity than sites with only native species (Welch's t-tests, $p > 0.05$). As this study is focused on the drivers of native species diversity, and because introduced species may have different distribution patterns than native species—e.g., being more likely than native species to be synanthropic and exhibiting higher diversity in anthropogenically influenced areas (McKinney 2008; Horsák et al. 2013)—they were removed from all subsequent analyses.

While collectors tended to collect similar numbers of species, one of the four collected significantly fewer than one other (Tukey's test, $p = 0.0046$, see supplementary material Fig. S1 for details), while the numbers collected by the other three did not differ from each other. This one collector also contributed the fewest samples. To reduce variation caused by differences in collection effort while retaining the greatest amount of data, the ten samples contributed by this collector were excluded from further analysis (though they are included in the raw dataset, available as supplementary material).

In total, 13,808 native macrosnails were collected from 42 sites on the five westernmost islands. After rarefaction, subsequent analyses were conducted on 1937 representative specimens from these sites.

Environmental factors controlling biodiversity

Tests for autocorrelation revealed none at either the archipelago or island scales. Sites nearer each other geographically did not appear to be any more similar than more distant sites. Thus, spatial autocorrelation should not interfere with detection of the influence of the various environmental factors. Further details, correlograms, and variograms illustrating these results are available in the supplementary material (Figs. S2–S7).

The regression tree of richness (Figs. 5, 6) indicates that total area of agriculture within 1 km of the site had the greatest explanatory power. The first split was between lower-diversity sites with greater than 0.167 km^2 of agriculture within a 1 km radius, and higher-diversity sites with less. This variable explained 25.0% of the variance in richness between the groups. The larger and relatively less diverse group could be further split by the eastness of the slope's aspect, with a score of 1 indicating a slope facing due east, -1 due west, and 0 due north or south. This split occurred at 0.411, meaning that eastward facing sites tended to have lower diversity, while slopes facing all other directions generally had higher diversity. The Shannon diversity and Simpson diversity regression trees were very similar to the richness tree and may be found in the supplementary material (Figs. S8–S11). Cross validation errors for all trees are also shown in the supplementary material (Figs. S12–S14).

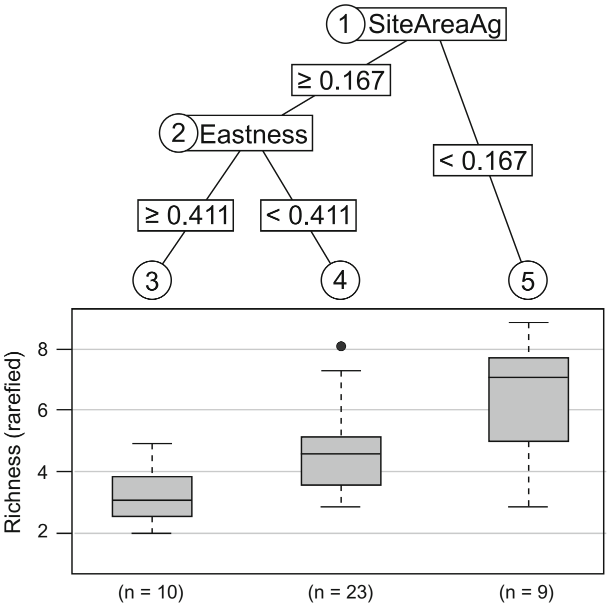

Fig. 5 Regression tree of land snail richness per site. Numbered circles represent nodes and the richness values of sites included in the terminal nodes (3–5) are illustrated as box plots. The primary split is at 0.167 km^2 of agricultural area within a 1 km radius of the site. The secondary split is at 0.411 eastness: those sites with higher values slope roughly to the east. The mean richness in species equivalents for each node is: Node 1, 4.6; Node 2, 4.1; Node 3, 3.2; Node 4, 4.5; Node 5, 6.3. Box plot midlines represent the median. Details of the splits are illustrated in Fig. 6

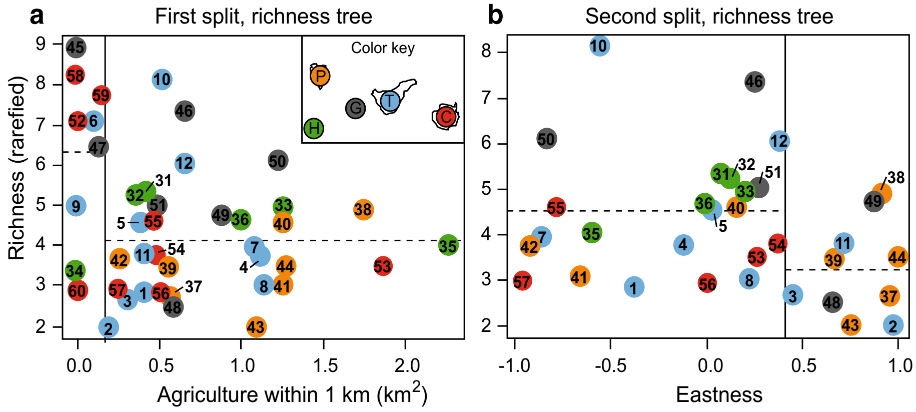

Fig. 6 **a** Details of the first split in the richness regression tree. The solid vertical line indicates where the algorithm split sites into distinct subgroups. The dashed horizontal lines indicate the mean richness for those subgroups, which are 6.3 and 4.1 species equivalents. **b** Details of the second split in the richness regression tree, which subdivides the subgroup of lower diversity (the right side of [a]). The mean richnesses for the subgroups are 3.2 and 4.5 species equivalents

Discussion

Qualitative observations

The land snail fauna of the Canarian coastal scrub includes a large majority of endemic species. Of 82 macrosnail species encountered, 72 were endemic to the Canaries and 69 were endemic to a single island. The coastal scrub of the five western Canary Islands supports 60 endemic snail species, nearly all of which are highly localized. These islands are rugged and the coastal scrub is divided by high and relatively wet ridges; barriers that may promote within-island allopatric speciation. Similar islands within an island patterns have been detected in Madeira (Cameron et al. 1996) and the Azores (Jordaens et al. 2009).

Studies of Pacific Island systems have noted a marked homogenization of malacofauna with increasing anthropogenic impact (Cowie 2001b, c). This was not observed in the Canarian coastal scrub. Invasive species are the primary causes of homogenization, so their absence in the Canaries may explain this difference. Site 33, nearest to the airport on El Hierro, was the only site with a majority of non-native individuals. The abundances and proportions of native species, however, were not noticeably unusual relative to other sites on the island. Site 38, on the outskirts of the town of La Playa de Santiago on La Gomera, was also unusual in having a great abundance and near monoculture of the native species *Rumina decollata*. At the 14 other sites where it was present, it made up only ~ 7% of individuals on average.

The Canary Islands' native malacofauna has experienced no known historical extinctions. Yet their often small ranges, the ongoing development of the coastal scrub, and their sensitivity to even low levels of agricultural development suggest they are susceptible to human habitat modification.

Quantitative results

The results of this study indicate that the effects of anthropogenic factors on biodiversity in natural areas can be quantified when natural factors are sufficiently constrained. Regression tree analyses found that anthropogenic factors had greater power for explaining diversity than did natural factors. Although the environmental parameters explored in this study may not be the direct causes of diversity structuring, they are useful proxies for any ultimate causes. For example, our model recognizes agricultural impacts as the largest (negative) driver of native diversity: agriculture encompasses a wide range of human activities and impacts, including increases in the numbers of rats and other invasive species, and pesticide contamination. Many of these stressors may negatively impact snail species.

Values highlighted by nodes of the regression tree offer insight for conservation and landscape management, including indicating the impacts of agriculture on native snail diversity. Importantly, snail diversity is significantly impacted with remarkably little nearby agricultural development. The total area within a 1 km radius is 3.14 km^2, so an agricultural area of 0.167 km^2 is just 5% of the available space. Of the sites with less agriculture and overall higher diversity, three had no agriculture within 1 km, and the other six included agriculture only at the periphery of the 1 km radius (as opposed to a small area nearer the site). Götmark et al. (2008) similarly found land snails were highly sensitive to nearby agriculture. This result may provide a useful guideline for the establishment or expansion of protected areas for this unique biome.

All species richness and diversity regression trees had only one split beyond the primary one. It was within the greater agricultural area, lower-diversity subgroup and the dividing factor was eastness. Especially because our sites were not themselves directly modified by people (e.g., by leveling or excavating), the direction the slope of a site faces is an unequivocally natural factor. Orientation of a site probably affects temperature and moisture conditions, as well as vegetation composition and structure. The Canary Islands are subject to northeasterly trade winds that predominantly affect the islands' eastern sides. This alone may explain a systematic difference between east-facing sites and others. Alternatively, because these sites only include those with nearby agriculture, it may be an interplay between the two factors, e.g., eastern-facing slopes tend to host more impactful kinds of agriculture. As all three regression trees had very similar results, this pattern is robust even when more common species are weighted more heavily.

This study represents the first quantitative evaluation of the interplay of natural and anthropogenic factors on land snail diversity in the Canary archipelago. The statistical results, however, reflect total diversity rather than the member species that contribute to that diversity. Because each island has a somewhat different suite of members in its malacofauna, and there were relatively few sites per island, statistically meaningful evaluation of changes in community composition were not possible. Future studies in the region should incorporate additional sites and expand the number of plant biomes explored, and thereby permit further insight into the complex relationships exhibited by natural and anthropogenic factors in this eclectic island system.

Diversity of the native land snail fauna of the Canarian coastal scrub was negatively affected by close proximity to human-modified landscapes. This, coupled with the apparent lack of extinctions in the biota, suggests the geographic ranges of its constituent species are shifting. These species, many of which are known only from single valleys (IUCN 2016), are losing habitat to landscape modification, conversion, and development, as well as to the more subtle impacts that radiate far into natural areas from anthropogenic sources that were explored here. Few species have sufficient population data, but, of those that do, many are in decline and some are endangered (IUCN 2016). This study's results can inform efforts to keep this unique malacofauna intact. In particular, the seven Canarian Rural Parks and four UNESCO Biosphere Reserves are protected areas comprising a mosaic of natural and agricultural areas (Fernández-Palacios and Whittaker 2008). Unfortunately, our results suggest this interweaving of agriculture and natural habitats may not sufficiently protect some species with high sensitivities to agricultural factors.

The Canary Islands have been targeted for a variety of conservation efforts, especially after being designated part of the Mediterranean biodiversity hyper-hotspot (Myers et al. 2000). More broadly, land snails as a group have many vulnerable species worldwide, especially in island systems. Cowie et al. (2017) estimated that only 8.5–10% of molluscs had had their conservation statuses assessed by the IUCN, 34% of these being Data Deficient, though molluscs constitute 35% of known historical extinctions. Evaluating the health of land snail communities provides valuable information on an important group, can inform conservation efforts of vulnerable species, and may prove a logistically expeditious way of testing for and quantifying anthropogenic disturbance. This study adds to the growing consensus that assessments of land snail diversity are a useful and efficient way to measure biome disturbance. This includes the use of time-averaged assemblages, which provide valuable data on the enduring impacts of anthropogenic perturbations of local communities.

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Appendix

See Tables 3 and 4.

Table 3 Summary of measured environmental factors and the abbreviations used to encode them for analysis

Natural factor	Code	Anthropogenic factor	Code
Island area, km[b]	IsArea[a]	Population density as of 2000, the most recent data available	HumPop
Island age, millions of years	IsAge[a]	Total length of roads within 1 km buffer, km	RoadDens
Number of biomes on island	IsHabDiv[a]	Distance to the nearest small road, km	Dist$_{\text{SmRd}}$
Island ruggedness, 3D/2D area ratio	IsRug[a]	Distance to the nearest highway, km	Dist$_{\text{MedRd}}$
Island's shortest distance to the African continent, km	AfricaDist[a]	Distance to the nearest freeway, km	Dist$_{\text{BigRd}}$
Annual precipitation mm, 50 year average	AnnualPrecip	**Distance to nearest road of any kind, km**	Dist$_{\text{AnyRd}}$
Maximum annual temperature °C, 50 year average	MaxAnnualT	Distance to the nearest agricultural area, km	Dist$_{\text{Ag}}$
Minimum annual temperature °C, 50 year average	MinAnnualT	Distance to nearest artificial surface, km	Dist$_{\text{Art}}$
Elevation in meters	Elevation	Distance to the nearest airport, km	Dist$_{\text{Air}}$
Dip of the sites's slope in degrees	Slope	Distance to the nearest urban area, km	Dist$_{\text{Urb}}$
Direction of slope exposition (N = 1, S = − 1)	Northness	Distance to the nearest dump or landfill, km	Dist$_{\text{Dump}}$
Direction of slope exposition (E = 1, W = − 1)	Eastness	Distance to the nearest recreational area, km	Dist$_{\text{Golf}}$
Coastal scrub area within 1 km of site, km^2	Area$_{\text{Scrub}}$[b]	Distance to the nearest industrial site, km	Dist$_{\text{Ind}}$
Edges of coastal scrub within 1 km buffer, km	Edge$_{\text{ScrubTot}}$[b]	Human-modified area of any kind within 1 km buffer, km^2	Area$_{\text{Mod}}$
Coastal scrub edge bordering natural features, km	Edge$_{\text{ScrubNat}}$[b]	Agricultural area within 1 km of the site, km^2	Area$_{\text{Ag}}$
Distance to the nearest stream, km	Dist$_{\text{Stream}}$	**Artificial area (not agriculture) within 1 km of the site, km^2**	Area$_{\text{Art}}$
A qualitative assignment of agricultural or urban influence	Impact[c]	Coastal scrub edge bordering agriculture, km	Edge$_{\text{ScrubAg}}$
Patchiness of coastal scrub area, area/edges, km^2/km	VegPatch	Edges shared between artificial and agricultural surfaces, km	Edge$_{\text{ArtAg}}$
		Coastal scrub edge bordering artificial surfaces, km	Edge$_{\text{ScrubArt}}$
		Edges shared between artificial and natural surfaces, km	Edge$_{\text{ArtNat}}$
		Coastal scrub edge bordering any human-modified surface, km	Edge$_{\text{ScrubMod}}$
		Whether site is part of a gov't designated natural area	Protected[3]

[a] Measurements of islands' parameters, not individual sites

[b] Measurements could result from natural or anthropogenic factors

[c] Categorical variables

Factors in bold are those used for statistical analyses. When groups of factors were correlated ($R^2 \geq 0.6$), the most general or simply derived factor was selected used. Sites in bold are therefore not correlated with each other ($R^2 < 0.6$)

Table 4 All species are endemic to the Canary Islands except [a]native but not endemic, and [b]introduced, [c]microsnails (species with maximum dimension < 5 mm as adults), [d]semislugs

Sites	13	14	15	16	17	18	19	20	21	22
Fuerteventura										
Canariella plutonia	–	–	3	2	–	–	2	3	–	173
Caracollina lenticula[a]	1	8	3	2	–	3	8	11	–	–
Ferussacia folliculus[b]	–	–	–	–	–	–	–	–	–	1
Granopupa granum[b,c]	–	–	–	–	–	–	–	–	–	3
Monilearia granostriata	–	–	–	–	3	–	–	–	–	–
Monilearia monilifera	115	1	2	2	4	6	345	309	5	4
Moniliaria multipunctata	8	–	–	2	–	1	–	–	–	–
Obelus discogranulatus	–	–	–	–	15	–	–	–	–	–
Obelus moderatus	–	–	–	122	–	–	–	–	–	–
Otala lactea[b]	–	–	1	–	–	–	1	–	–	1
Pomatias cf. *lanzarotensis*	–	–	6	2	1	–	2	–	–	4
Rumina decollata[a]	2	24	60	–	1	–	21	6	5	220
Theba geminata	563	201	77	60	1958	900	546	838	1222	1039
Theba cf. *clausoinflata*	–	–	–	–	–	221	–	–	–	–
Xerotricha lancerottensis	–	–	–	–	–	–	8	8	–	–

Site	53	54	55	56	57	58	59	60
Gran Canaria								
Caracollina lenticula[a]	1	28	59	10	7	6	18	46
Cernuella virgata[b]	–	–	–	–	–	2	64	–
Ferussacia folliculus[b]	–	–	–	–	–	1	–	–
Gibbulinella dealbata	–	–	–	–	–	18	–	–
Granopupa granum[b,c]	–	–	–	–	–	2	–	–
Hemicycla berkeleyii	–	–	–	40	13	–	–	–
Hemicycla ethelema	–	54	–	–	–	–	–	23
Hemicycla glasiana	–	–	–	–	–	–	91	–
Hemicycla guamartemes	–	–	260	–	–	–	–	–
Hemicycla psathyra	51	–	77	–	–	–	32	–
Insulivitrina nogalesi[d]	–	1	1	–	–	–	–	–
Monilearia arguinaguinensis	–	–	–	–	–	–	–	122
Monilearia caementitia	–	–	–	–	–	–	2	–
Monilearia persimilis	–	26	16	–	–	–	–	–
Monilearia phalerata	73	–	–	23	13	69	29	–
Napaeus interpunctatus	2	–	–	–	–	–	–	–
Napaeus isletae	–	–	–	–	–	21	–	–
Napaeus moquinianus	2	–	–	–	–	–	–	–
Napaeus sp.	–	–	–	–	1	–	–	–
Otala lactea[b]	2	–	–	–	–	16	15	–
Pomatias canariensis	–	–	–	–	–	183	58	–
Pomatias cf. *laevigatus*	–	6	13	–	–	–	–	–
Rumina decollata[a]	–	–	–	–	–	43	102	–
Theba geminata	461	–	–	–	–	95	403	–

Table 4 continued

Site	53	54	55	56	57	58	59	60
Theba grasseti	–	–	–	–	–	37	15	–
Xerotricha conspurcata[b]	–	–	–	–	–	–	12	–
Xerotricha cf. *orbignii*	3	–	–	–	–	173	–	–

Site	45	46	47	48	49	50	51
La Gomera							
Canariella discobolus	–	–	–	–	–	–	3
Canariella multigranosa	–	–	5	–	–	–	–
Canariella tenuicostulata	47	54	8	–	–	–	–
Canarivitrina falcifera[d]	–	–	1	–	–	–	–
Caracollina lenticula[a]	18	192	7	1	1	31	9
Gibbulinella cf. *macrogira*	2	1	–	–	–	–	–
Hemicycla fritschi	68	17	2	–	6	2	–
Hemicycla gomerensis	–	–	–	–	–	–	166
Hemicycla laurijona	–	–	–	–	–	–	284
Hemicycla paivanopsis	–	–	–	1	46	169	–
Hemicycla aff. *paivanopsis*	60	110	82	–	–	–	1
Hemicycla quadricincta	–	–	–	10	–	–	46
Napaeus bertheloti	8	1	–	–	–	–	–
Napaeus rupicola	3	–	–	–	2	2	–
Napaeus servus	–	–	–	–	–	22	–
Obelus mirandae	8	126	86	–	38	195	32
Otala lactea[b]	–	1	–	–	–	–	–
Pomatias cf. *laevigatus*	108	4	–	1	–	–	–
Pomatias cf. *lanzarotensis*	–	–	–	–	–	20	–
Retinella rochebruni	15	1	–	17	–	–	–
Rumina decollata[a]	–	3	3	833	–	–	–
Xerotricha adoptata	–	62	–	–	–	4	–

Site	31	32	33	34	35	36
El Hierro						
Canariella bimbachensis	85	–	–	–	1	171
Canariella huttereri	–	–	1	76	–	–
Caracollina lenticula[a]	245	117	–	–	154	369
Hemicycla maugeana	–	86	25	101	57	82
Insulivitrina canariensis[d]	4	7	–	1	4	–
Monilearia persimilis	34	44	27	–	33	50
Napaeus gruereanus	–	3	–	–	–	–
Napaeus subsimplex	10	46	–	–	–	1
Obelus cf. *mirandae*	–	–	–	6	–	–
Otala lactea[b]	–	–	99	–	–	–
Pomatias cf. *canariensis*	5	83	–	–	–	–
Retinella hierroensis	–	–	18	98	–	–
Rumina decollata[a]	–	–	2	–	–	–

Table 4 continued

Site	31	32	33	34	35	36
Vitrea contracta[a,c]	–	5	–	–	–	1
Xerotricha orbignii	9	1	–	–	23	18

Site	23	24	25	26	27	28	29	30	23	24	25	26
Lanzarote												
Canariella plutonia	–	–	–	–	90	–	–	–	–	–	–	–
Caracollina lenticula[a]	1	5	15	–	110	–	5	–	1	5	15	–
Ferussacia folliculus[b]	–	–	–	–	6	–	–	–	–	–	–	–
Hemicycla sarcostoma	–	–	–	–	3	–	–	–	–	–	–	–
Monilearia monilifera	25	–	–	–	597	–	3	–	25	–	–	–
Otala lactea[b]	–	–	1	–	39	–	–	–	–	–	1	–
Pomatias lanzarotensis	–	–	–	–	19	–	–	–	–	–	–	–
Rumina decollata[a]	–	–	–	12	–	–	8	–	–	–	–	12
Theba geminata	585	712	699	50	–	2261	1554	1810	585	712	699	50
Theba cf. *geminata*	–	–	–	–	–	509	–	–	–	–	–	–
Theba impugnata	–	–	–	–	306	–	–	–	–	–	–	–

Site	37	38	39	40	41	42	43	44
La Palma								
Canarivitrina taburientensis[d]	1	–	2	–	–	–	–	–
Caracollina lenticula[a]	103	136	202	58	90	24	78	66
Cecilioides acicula[b,c]	–	–	–	–	–	–	–	1
Cornu aspersum[b]	–	12	2	10	–	–	8	–
Ferussacia folliculus[b]	–	15	1	–	–	–	5	–
Gibbulinella dewinteri	11	4	10	–	5	–	–	8
Hemicycla fuenterroquensis	–	4	–	–	1	7	–	–
Insulivitrina solemi[d]	–	–	–	5	–	–	–	5
Monilearia persimilis	172	277	243	121	65	139	307	50
Napaeus encastus	–	–	–	20	–	–	–	–
Napeus subgracilior	–	14	14	–	–	–	–	2
Retinella lenis	–	–	–	5	–	–	2	–
Vitrea contracta[a,c]	–	–	–	–	1	–	–	1
Xerotricha pavida	–	19	–	18	–	18	–	–
Canarivitrina taburientensis[d]	1	–	2	–	–	–	–	–

Site	1	2	3	4	5	6	7	8	9	10	11	12
Tenerife												
Canariella fortunata	–	–	–	–	–	58	–	–	25	98	–	–
Canariella hispidula	–	–	–	–	–	–	–	–	–	–	45	34
Caracollina lenticula[a]	3	60	184	63	292	98	53	78	70	208	147	78
Ferussacia attenuata[c]	–	–	1	–	–	–	–	–	–	–	–	–
Ferussacia folliculus[b]	–	–	–	–	–	–	–	–	–	4	–	–
Gibbulinella dewinteri	–	–	–	–	–	10	–	–	–	6	–	–
Granopupa granum[b,c]	13	8	1	5	9	–	–	–	–	–	–	–

Table 4 continued

Site	1	2	3	4	5	6	7	8	9	10	11	12
Hemicycla bethencourtiana	–	–	–	–	14	–	–	–	–	–	–	77
Hemicycla bidentalis	–	–	–	–	–	5	–	–	–	93	–	–
Hemicycla consobrina	6	4	8	26	66	–	–	–	–	–	–	–
Hemicycla eurythyra	–	–	–	–	–	6	–	–	–	–	–	–
Hemicycla plicaria	–	–	–	–	–	–	–	–	–	–	15	–
Hemicycla pouchet	–	–	–	–	–	–	–	–	–	109	–	–
Hemicycla sp.	–	–	–	–	–	–	–	–	2	–	–	–
Insulivitrina lamarkii[d]	–	–	–	–	–	1	–	–	–	–	–	–
Monilearia persimilis	–	–	–	–	–	21	25	116	3	–	–	–
Monilearia phalerata	80	90	58	28	246	–	28	85	1	449	–	8
Monilearia aff. *woodwardia*	–	–	–	–	–	–	–	–	–	5	–	–
Napaeus baeticatus	–	–	–	–	–	11	–	–	–	32	–	–
Napaeus variatus	–	–	–	–	1	59	–	–	3	–	–	7
Otala lactea[b]	–	–	–	–	–	–	–	–	1	68	–	–
Pomatias laevigatus	–	–	–	–	17	3	–	–	–	129	–	15
Pupoides coenopictus[a,c]	–	–	–	–	–	–	–	–	–	–	–	–
Vitrea contracta[a,c]	–	–	–	–	–	3	–	–	–	1	–	–
Xerotricha conspurcata[b]	–	–	–	–	–	1	–	–	–	–	–	–
Xerotricha orbignii	–	–	–	8	23	1	27	1	–	7	48	1

Based on information from Ibáñez et al. (2006), Yanes et al. (2007, 2009, 2011a, b), Núñez and Núñez (2010), Castro et al. (2012), Santana et al. (2013), and Alonso and Ibáñez (2015a, b, c)

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