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The status of the invertebrate fauna on the South Atlantic island of St Helena: problems, analysis, and recommendations

Alan Gray[1] · Vicky Wilkins[2] · David Pryce[3] · Liza Fowler[4] · Roger S. Key[5] · Howard Mendel[6] · Michael Jervois[4] · Axel Hochkirch[7] · Rebecca Cairns-Wicks[8] · Amy-Jayne Dutton[4] · Lourens Malan[9]

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Abstract
We present an analysis of the invertebrates of St Helena using an invertebrate conservation evaluation framework, to review invertebrate data, highlight knowledge gaps and prioritise invertebrate conservation needs that perhaps could be applied to other regions of the world. St Helena's invertebrate fauna has 891 genera and 1133 species. The fauna has a high level of endemism with 450 species (equal to 96% of all native species) but the total species richness now comprises many introduced species (664) with 93 species in 24 orders that are entirely novel to St Helena. The elevation ranges of native species appear to be narrow, most being confined to higher elevations above 500 m. St Helena has had a large number of probable extinction events; 30 insects, and 19 molluscs, and the threat of further extinctions remains high. The cumulative invertebrate extinctions on St Helena exceed the global background extinction rate on an island barely covering 122 km^2. We present actions and timelines to focus invertebrate conservation on St Helena; taxonomy, ecology, long term monitoring and invasive species control are priority areas to reduce extinction risk.

Keywords Extinction · Island biodiversity · Species richness · Endemism · Red List

Introduction

Over 19,000 species of described invertebrates have been assessed for extinction risk under IUCN Red List criteria, less than 2% of described invertebrates. Many more species remain undiscovered and as a result, many species could become extinct before being described (González-Oreja 2008). It is puzzling therefore that less than 100 species of insects have

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✉ Alan Gray
alangray@ceh.ac.uk

Extended author information available on the last page of the article

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been officially reported extinct during the last 600 years (Dunn 2005). This is undoubtedly a significant underestimate (Dunn 2005; Dunn et al. 2009; Hochkirch 2016) and more effort is required to address this through exploration, taxonomy, and a continuing commitment to catalogue biodiversity (Mora et al. 2011) and assess threats. There are many barriers to the effective conservation of invertebrates including: high species richness; poor taxonomic and ecological knowledge; limited data on distributions; complex lifecycles; poor or limited availability of skills; and a lack of social and political appreciation which can make invertebrate conservation a lower priority (New 2012). Recently Cardoso et al. (2011) recognised seven impediments to effective invertebrate conservation. A key response is for invertebrate conservation to develop tools to overcome these impediments and to appraise invertebrate conservation needs and priorities using appropriate evaluation frameworks. An ideal framework would facilitate the collation of existing information, and highlight knowledge gaps to give stakeholders the ability to evaluate evidence-based needs and priorities. We suggest that the seven impediments to invertebrate conservation (Cardoso et al. 2011), are also the foundation of an evaluation framework.

Islands have long been known to be disproportionately important to global biodiversity because of high levels of endemism that include invertebrates. There are over 3000 endemic arthropod species known from the Canary Islands (Fernández-Palacios 2010) and over 5000 endemics in the Hawaiian archipelago of which the arthropod fauna displays 98% endemism (Nishida 2002). Island invertebrates are also at the forefront of the extinction crisis, invertebrate extinction rates are considered to be at least ten times higher on islands than continental rates (Collen et al. 2012). In many islands, Cardoso et al's (2011) impediments are often acute because communities tend to be economically poorer and lack the specialised skills for invertebrate conservation. Islands are less species-rich than continental areas, and are geographically smaller, which means that it is cost effective to produce field guides for islands to aid conservation. An excellent island example is St Helena in the South Atlantic Ocean which has a rich invertebrate fauna of global importance (Churchyard et al. 2016). St Helena has a high level of invertebrate endemism (> 90%), with over 460 endemic invertebrates currently known. Isolation has led to invertebrate radiations, including the largest radiation of Tineidae known in any island or group (Robinson 2009) with at least 29 endemic species of *Opogona* (Hieroxestinae) possessing characters unknown in other species belonging to this genus (Robinson 2009; Robinson and Tuck 1997). Despite their scientific and global importance, until very recently few conservation initiatives or research studies had been undertaken on St Helena's invertebrates.

Here, derived from Cardoso et al. (2011) impediments, we evaluate the status of St Helena's invertebrates using Invertebrate Conservation Evaluation (ICE) framework to highlight invertebrate knowledge gaps. We outline the ICE framework, assess invertebrate conservation, and suggest priorities for St Helena.

Materials and methods

The ICE framework builds on the seven impediments of Cardoso et al. (2011) (relationships to the impediments are shown in italics and parentheses below) to include conservation planning and action. St Helena's invertebrate conservation is in its early stages so we naturally focus on points 1 and 2 of the framework but where appropriate we also review progress on points 3, 4 and 5.

Invertebrate conservation evaluation framework

(1) Knowledge—Regional invertebrate data to facilitate conservation:

   (a) Describe all invertebrate species present in the region (*the Linnaean shortfall*);
   (b) Invertebrate distribution, abundance, and changes in space and time (*the Wallacean and Prestonian shortfalls*)
   (c) Invertebrate ecological requirements, and resilience to environmental change (*the Hutchinsonian shortfall*)
   (d) Extinction threats and the efficacy of conservation management (*the Hutchinsonian shortfall*)

(2) Priorities—Regional invertebrate conservation priorities:

   (a) Priority species (Red List status global/national, endemic and native species)
   (b) Priority areas (Key Biodiversity Areas (KBAs) and protected areas)

(3) Increased awareness within:

   (a) Public (*the public dilemma*)
   (b) Conservation and science (*the scientific dilemma*)
   (c) Policy and decision makers (*the political dilemma*)

(4) Resources to facilitate long-term invertebrate conservation:

   (a) Sustainable finance and partnerships to achieve regional goals (*all*)
   (b) Increase regional capacity to identify, monitor and conserve invertebrates and their associated habitats (*all*).

Actions and timelines

At the end of each section, we have highlighted any actions we think are necessary for sustainable conservation on St Helena. We have tried not to replicate those actions from the St Helena invertebrate conservation strategy (Cairns-Wicks et al. 2016), although, some crossover is inevitable. The invertebrate strategy runs until 2021 which is also the timeframe for the St Helena sustainable development plan (Saint Helena Government 2012) so the proposed timelines here are linked to these.

St Helena general description

Saint Helena, South Atlantic Ocean (15°58′S and 5°43′W), is a volcanic island around 12–14 million years old (Baker and Thorpe 2010) with an area of 121.7 km^2. It is a UK Overseas Territory (UKOT) and has a population of 4534 (St Helena Saint Helena Government 2016b). The nearest land is Ascension Island, 1,300 km north, with Africa lying 1,800 km east. The climate is subtropical warm and humid; temperature between 15 and 28 °C (Feistel et al. 2003; Taylor 2016) and annual rainfall ca. 500 mm at 435 m above sea level (masl). However, rainfall is orographic, and varies significantly with elevation and aspect over very short distances (Lambdon 2013). For example, the mean annual rainfall between 1977 and 1987 for Bottom Wood (435 masl) and Hutts Gate (630 masl) was 455 mm year^{-1} and 811 mm year^{-1} respectively (Mathieson 1990); the distance between these areas is approximately 3 km. The highest point is Diana's Peak on the Central Ridge at 820 masl. For invertebrates, the two main habitats are the arid zones, and the cloud forest and an agricultural area at mid elevation that is imperfectly known. The arid zones include the dry, rocky areas of the outer parts of the island, a desert caldera plain and the coastal fringe and cliffs. The cloud forest is the only remaining densely vegetated native habitat type and less than 40 ha remains, which is confined to high elevations above 650 m. However, only around 16 ha of this is considered to retain some original elements of the cloud forest and this is degrading. Less widespread are watery habitats which include permanent and ephemeral water bodies including freshwater and saline waters; pools, streams, springs, seepages, waterfalls and marshland (see also Lambdon 2013).

Review, surveying and invertebrate records compilation

All invertebrate records for St Helena with reliable location data were compiled from literature sources, surveys, reports and museum specimen data (BMNH and MRAC; see http://www.south-atlantic-research.org/ims-gis-data). In some cases, records could only be assigned an appropriate UTM grid reference locality associated with a place name (9% of the records). Species were classified as endemic (including sub-specific levels), introduced, native or unknown where the status could not be determined. Occurrence inside and outside each of the Key Biodiversity Areas (KBA) for St Helena (see Taylor 2016) was also noted.

Key biodiversity areas

Figure 1 shows a set of priority areas for biodiversity or Key Biodiversity Areas (KBA) recently identified for St Helena (Taylor 2016). We consider KBAs a very useful concept for invertebrates because very few statutory nature reserves are designated on the basis of threatened invertebrates. KBAs are selected using standardized, globally applicable, threshold-based criteria, driven by the distribution and population of species that require site-level conservation, and invertebrates are explicitly included (Eken et al. 2004; IUCN 2016). We used the full draft list of designated, proposed and potential KBAs, which included those highlighted in the St Helena invertebrate conservation strategy (Table 3) to encompass as large an area of potential invertebrate habitats as possible. We expect the KBA list to change over time as most invertebrates on St Helena have yet to be assessed using IUCN Red List criteria and including threatened Red List species is one criterion (Threatened Biodiversity Criterion A) for designation as a KBA (IUCN 2016).

Ecological data

Ecological research on St Helena is lacking, we therefore assume that the broader the elevation range an invertebrate species is generally found in, the greater the diversity of habitats or niches it is likely to be adapted to. Elevation range was estimated using the difference between maximum and minimum elevations where a species has been recorded. This is then defined as: Narrow (elevation range between 0 and 100 m), Narrow/Moderate

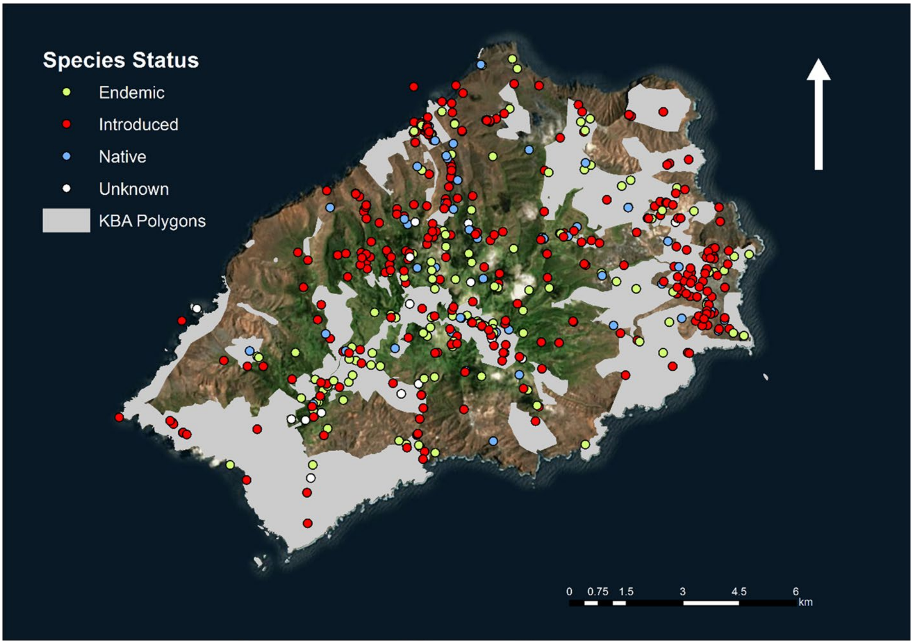

Fig. 1 The distribution and status of invertebrate records on St Helena, note that dots can overlap each other from the same locality and so may indicate multiple records for species of different statuses. Key Biodiversity Areas (KBAs) for St Helena are also shown see Taylor (2016)

(elevation range between 100 and 300 m), Moderate (elevation range between 300 and 600 m), and Wide (elevation range > 600 m). Habitat was determined using the broad classification in Lambdon (2013) and species' habitat associations were determined from the literature and collectors' notes where species were collected in one or a very few habitats or associated with particular species.

Extinction threat

We have included all species that have currently been assessed and pre-assessed under IUCN Red Listing criteria Version 3.1 and 2.1 (see IUCN 2001) and used expert opinion to assess the species where extinction is highly probable, e.g. species would be presumed extinct if no records exist since the 19th Century and/or when suitable habitat no longer exists.

Statistical analyses

As only a small number of species have been assessed under IUCN criteria, we used endemism to indicate species of conservation concern (Matenaar et al. 2015). Our statistical analyses relate to whether, KBA area, elevation and elevation variability (SD) relate to the species richness of endemic, native and introduced invertebrates. We know area affects species richness and so ask, do larger KBAs maintain more endemic invertebrates of conservation concern? Elevation and elevation variability are used to assess whether a diversity of ecological conditions is characteristic of species-rich KBAs e.g. the Central Peaks area may be more heterogeneous in conditions than the arid plains.

As with all species richness data, the number of species is strongly determined by the collecting or recorder effort in that area and our data do not have equitable collecting effort. The quality of our data however does not allow a direct measurement of recorder effort, (e.g. many historical records do not state the methods, the number of people or the time spent collecting) ruling out standard methods for correcting for recorder effort (e.g. Hassall and Thompson 2010; Hill 2012). We included the number of collecting visits per KBA as a proxy for recorder effort. We used Hierarchical Partitioning (HP) in preference to the other methods as HP has the ability to assess the independent contributions of relationships of each of the variables, even when the variables are strongly intercorrelated. The independent contributions of each of our explanatory variables were thus determined using HP, and the significance of each contribution was tested using bootstrapping (Chevan and Sutherland 1991; MacNally 1996, 2000; MacNally and Walsh 2004; Walsh and MacNally 2003). Data were analysed using R 3.3.1 (R Core Team 2016). Generalized linear models were used to examine the relationship between environmental variables and the abundance or occurrence of species. Models were fitted with Gaussian errors to total, endemic, native, introduced species richness (log transformed) and the environmental variables, collecting frequency in each KBA, KBA area (log transformed), mean elevation within each KBA and variability in elevation (SD).

Results and discussion

Describe all invertebrate species present in the region

10,509 invertebrate records were analysed, representing 57 Orders, 345 Families, 891 Genera and 1394 species. 167 species across many orders have uncertain taxonomic status. Their status as native, endemic also remains uncertain (Table 1). Of these, there are 35 species where endemism is suspected but further research is required to confirm that. The most taxonomically uncertain order is Hymenoptera (Parasitica, 58 species) followed by Diptera (20 species) and Araneae (13 species). Examples of uncertainty include the ant *Camponotus fabricator.* The type specimen was examined by Wetterer et al. (2007), it is anonymous, lacks locality data, cannot be attributed to a collector, and does not match its original description. Although only recorded on St Helena, it is also doubtful whether it can be regarded as endemic (see Wetterer et al. 2007). The eulophid wasp *Cirrospilus nireus* is similarly a doubtful species, as Francis Walker is well known for re-naming species that had previously been described.

Species new to science are still being discovered on St Helena (ca. 10 have been described in the last decade) because the level of sampling is still inadequate following the extensive Belgian expedition (Basilewsky et al. 1970–1977) and recent surveys. The St Helena mole spider (Lycosidae) is one example where scientific description is still lacking (Ashmole and Ashmole 2000). It is assumed endemic but the relationships with African Lycosidae are unclear and no systematic review exists. The St Helena Tineidae radiation has also been the focus of recent sampling but the evolutionary significance of this radiation has yet to be fully investigated.

Table 1 Numbers of St Helena invertebrate species in each order with uncertain taxonomy, 35 of these species are only known at the family level

Order	Endemic	Introduced	Native	Unknown	Total
Araneae	10			13	23
Coleoptera	7			3	10
Diptera	2	1		20	23
Entomobryomorpha				3	3
Haplotaxida				2	2
Hemiptera	6	4		6	16
Hymenoptera: Aculeata			1		1
Hymenoptera: Parasitica	2		1	58	61
Isopoda	1			1	2
Lepidoptera (Tineidae)	7			1	8
Poduromorpha				3	3
Pseudoscorpionida				1	1
Psocodea		1	1	3	5
Stylommatophora				2	2
Symphypleona				2	2
Tanaidacea			1		1
Thysanoptera				1	1
Tricladida				2	2
Zygentoma				1	1
Total	35	6	4	122	167

Where status is unknown information on whether the species could be considered as endemic, native or introduced was lacking

Actions and timelines

Taxonomic research on St Helena is currently a key knowledge gap and further collecting expeditions using a variety of methods are required for multiple taxa in all habitats. Targeted areas and species should be identified using the current distribution maps (see below). When funding for invertebrate projects is sought, taxonomic research, including molecular studies, should be fundamental components. Additional engagement with the invertebrate research community is also needed and a St Helena invertebrate research plan should be developed and implemented by 2021.

Invertebrate distribution, abundance, and changes in space and time

Over 1000 species have less than ten records and the distribution of records across St Helena indicates many areas where no records exist (Fig. 1). This may be partly due to data point aggregation but is also a consequence of under sampling. Within the current list of KBAs the following have over 100 records; Sandy Bay (118); Rupert's Hill (132); Stone Top Bay, George Island & Shore Island (190); Billberry Field Gut, Netley Gut, Bottom Woods & Deadwood (390); Prosperous (837) and The Peaks (2673). This suggests that at least 36 of the 43 KBAs require additional sampling effort. However, the vast majority of records are located outside the KBAs (5311) which may suggest further KBAs are necessary. In addition, the 'general countryside and urban areas' of St Helena have hardly been sampled for invertebrates. Casual observations indicate that at least some of the endemic species are present in abundance in these areas.

Population levels, and seasonal data are completely lacking for St Helena's invertebrates; it is therefore, currently impossible to assess population changes in space and/or time. A monitoring system is currently being developed in relation to restoration sites but it currently only covers the Peaks KBA and employs a limited range of sampling techniques. The Peaks are the most species-rich areas (Fig. 2), but they are also abundant in introduced species and both endemic and introduced species require study.

Action and timeline

It is clear from this evidence that distribution, spatial and temporal population studies are key knowledge gaps. This needs to be addressed to ensure that conservation actions are sustainable and to ensure invertebrate distribution. A clear key to this is the adoption of adaptive management techniques that incorporate distribution, and spatial and temporal population studies to underpin evidence based management actions. Management plans that are currently under preparation, need to adaptive, include research as a core component and should be in place by 2021 (see also Cairns-Wicks et al. 2016). It is essential that scientifically robust invertebrate monitoring protocols are established.

Invertebrate ecological requirements, resilience to environmental change

Knowledge of species' autecology is largely lacking on St Helena except for some well-known introduced invasive species studied elsewhere. Excepting taxonomic literature, endemic and native species knowledge is confined to several non-peer-reviewed publications that are largely faunisitic in nature (e.g. Ashmole and Ashmole 2000, 2004; Mendel et al. 2008). The one species with some detailed ecological information is the spiky yellow woodlouse *Pseudolaureola atlantica* where a species action plan now exists (Havery et al. 2016). Although Basilewsky et al. (1970–1977) includes useful general biological information, key knowledge gaps remain; life cycles, broader taxonomy, population genetics, habitat requirements etc., all remain largely unknown.

The majority of endemic and native species appear to be in either the Narrow or Narrow/moderate categories (Fig. 3) and are confined to higher elevations above 500 m where habitats are cooler and more humid. This could be an indication that these species have narrow ecological limits, and/or an indication of decreasing habitat, although, it may also be an artefact of under sampling. This distributional pattern is also repeated for the Narrow and Narrow/moderate introduced species (Fig. 3). This may suggest that some of these introduced species are still in the early stages of invasion or again it may be an artefact of under sampling. If most of the endemic species occupy a narrow niche, then populations are likely to be at extreme risk of extinction from environmental changes, particularly climate change and land use change, especially where populations are small. Much of the habitat at mid-elevations is deforeseted and degraded e.g. New Zealand flax *Phormium tenax*, which could also explain why many species are now artificially confined to the Peaks.

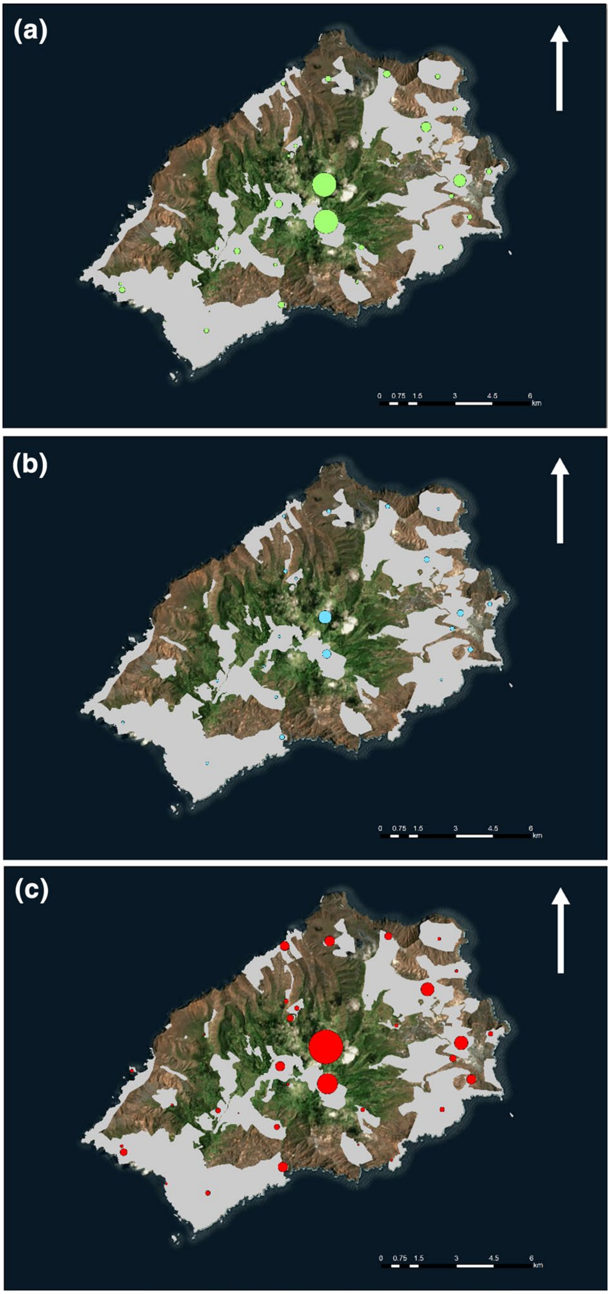

Fig. 2 Distribution of hotspots of species richness for **a** Endemic species, **b** Native species and **c** Introduced species. The central dot in each case represents the area outside the KBAs and the dot to the south represents the central Peaks area

Action and timeline

More research is clearly needed on species' ecology and habitat associations. Sustained inter-disciplinary research is needed to: assess the resilience of endemic species and

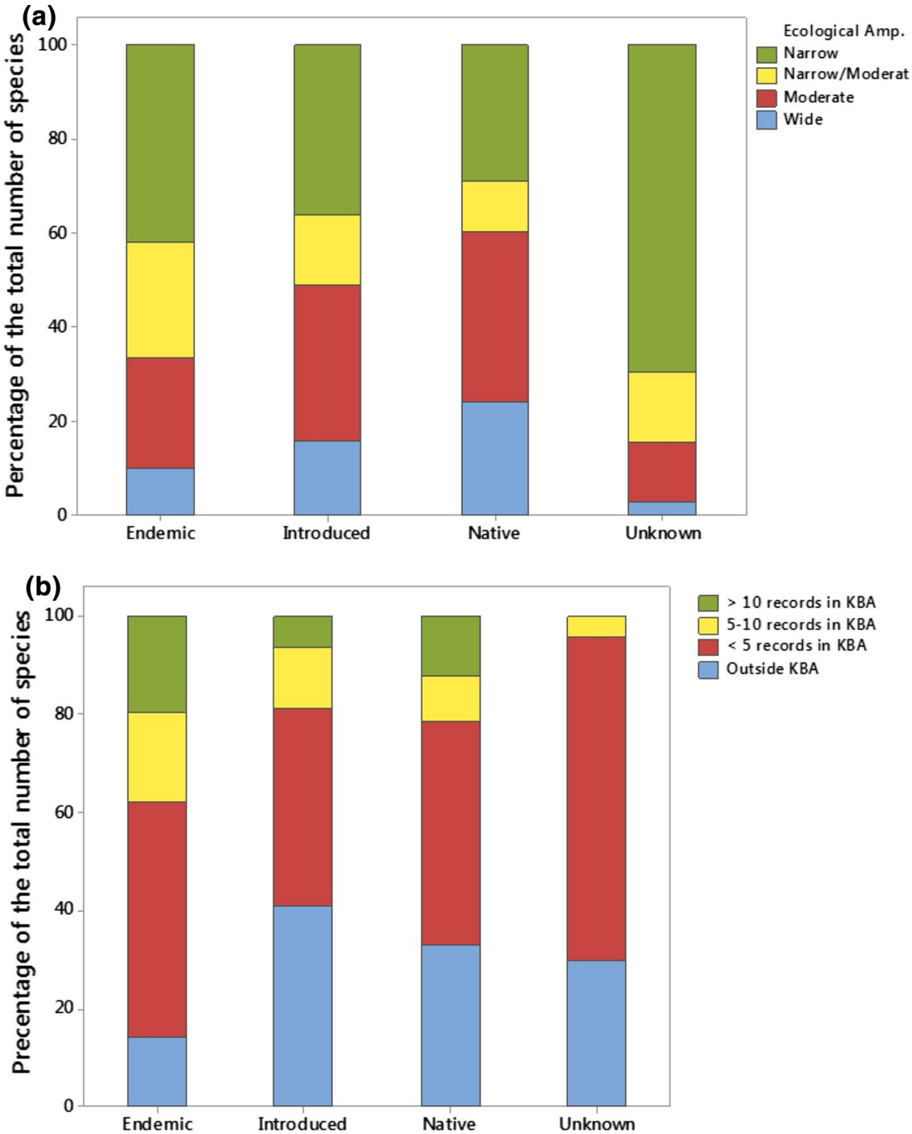

Fig. 3 **a** Percentage of species in three classes of elevation range defined by the altitudinal range of species records: Narrow (0–100 m), Narrow/Moderate (100–300 m) Moderate (300–600 m) Wide (> 600 m). **b** Percentage of St Helena endemic, native, introduced species and those of an unknown status found in KBAs by the number of records inside or outside of KBAs

habitats to environmental change; investigate population genetics and morphology to assess levels of adaptation within St Helena invertebrate populations; and climatic assessments and modelling, to predict resilience to climate change. These are undoubtedly long-term activities but research needs to be initiated by at least 2021 if extinction is to be addressed.

Extinction, threats and the efficacy of conservation management

There is a high level of probable extinction in the St Helena invertebrate fauna (Table S2: 28 insects and 19 molluscs). If this were reliable, then the number of insect extinctions from St Helena would increase the known global insect extinctions by more than 25%. The cumulative invertebrate extinctions on St Helena exceed the global background extinction rate, on an island barely covering 122 km^2 (Fig. 4). Extinct species declared on the Red List include the iconic Giant earwig, *Labidura herculeana*, the St Helena darter dragonfly, *Sympetrum dilatatum* and the giant ground beetle *Aplothorax burchelli*. It is also likely that the level of extinction on St Helena is an underestimate. There are no records from before the first wave of habitat destruction in the 17–18th Centuries which resulted in the degraded area known as the Crown Wastes (see Ashmole and Ashmole 2000) and the complete loss of mid-elevation ebony forest (*Trochetiopsis* spp.).

The distribution of extinct species appears quite widespread suggesting an island-wide effect (Fig. 4). Native habitats are now less than 1% of the original cover, and some phytophagus invertebrate species must have been confined to specific tree species and/or their associated faunas. Several of these tree species are extinct or wild populations have been reduced to a few trees e.g. *Lachanodes arborea*. Invertebrates have been introduced to control some of the plant extinction threats. For example, in the 1990s *Commidendrum robustum* was severely threatened by the introduced scale *Orthezia insignis,* the coccinellid predator *Hyperaspis pantherina*, was released on St. Helena in 1993 and increased numbers coincided with a 30% decrease in scale numbers (Fowler 2004). This appears to be have been successful; however, there has been little follow up since 1995, *C. robustum* is still threatened with extinction and in combination with other invasive species *O. insignis* may still be contribute to the lack of regeneration in core *C. robustum* sites.

Many of the invertebrate orders affected by extinction now have a high percentage of invasive species; for example, introduced Coleoptera and Araneae represent 40% and 57% respectively of the total species (Tables 2, 3). In other orders where extinction is not yet known, introduced species can dominate e.g., more than 80% of the Diptera are introduced (Tables 2 and 3). Many orders (24 of 52) are completely novel to St Helena solely represented by introduced species (Table 2). These data suggest an increase in competition, predation, and mutualism, are likely to interact with habitat loss to increase the probability of further extinctions. The extinction risk remains high (see Table 3); but in contrast to native species the ecology of some introduced species is known. An assessment of the non-native invertebrates on the island, was recently conducted (Key 2014) highlighting opportunities to control the invasion process. These include predator species such as springbok mantis, *Miomantis caffra* (Saussure, 1871) and European common wasp *Vespula vulgaris*. Introduced vertebrates have also been a problem historically e.g., goats *Capra aegagrus hircus* and pigs *Sus scrofa domesticus* and are likely to have impacted invertebrate communities through habitat destruction. Current problem species also include the guppy, possibly *Poecilia reticulate*, mynah birds *Acridotheres tristis*, rats *Rattus rattus* and *R. norvegicus*, mice *Mus musculus*, gecko *Hemidactylus frenatus*, and frogs *Strongylopus grayii*, all of which have altered predator–prey relations. Herbivores such as rabbit *Oryctolagus cuniculus* (Linnaeus, 1758) are also continuing to alter habitat structure and thereby impact invertebrates. Control of some of these species has been demonstrated in other islands (e.g. Daly 2009; Howald et al.

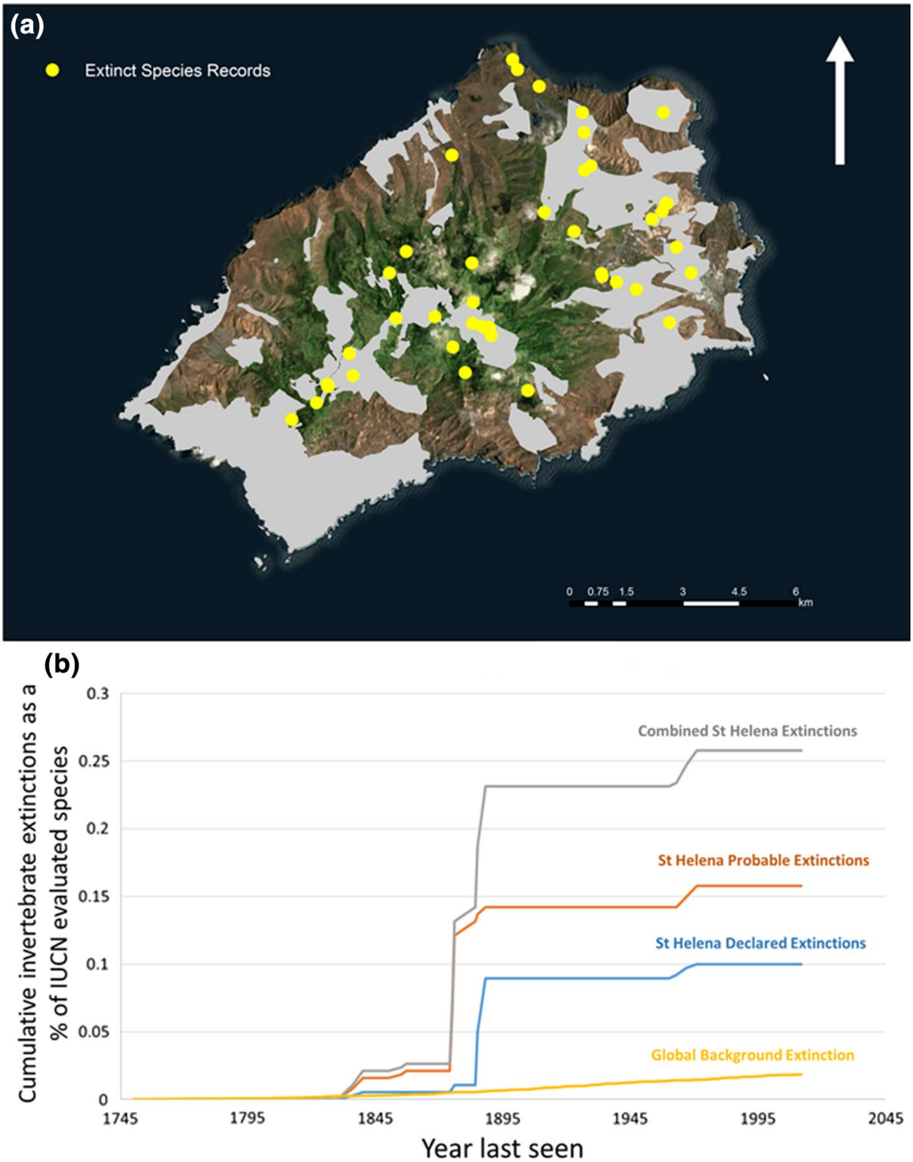

Fig. 4 **a** Distribution and number of records for probable extinct invertebrate species on St Helena. **b** Comparison of global extinction rate (Pimm et al. 2014) and the cumulative number of invertebrate extinctions on St Helena from 1750 until the present

2010; Nogales et al. 2004) and Cousine in the Seychelles offers a model example of where island restoration can be completed (Samways et al. 2010a, b). Invasive species control has yet to be attempted on a wide scale on St Helena but we suggest that rats, mice, rabbit, frogs, guppies, European wasp and mantis should be the initial focus for any large scale control programme.

Table 2 Status and number of species in each of the orders in the St Helena invertebrate fauna

Order	Endemic genera	Endemic species	Native	Introduced	Percentage of introduced taxa
Amphipoda		1		1	50
Araneae	15	42		55	57
Archaeopulmonata				1	100
Blattodea				10	100
Coleoptera	134	166	1	113	40
Dermaptera		1		3	75
Diplura				4	100
Diptera	1	18	3	93	82
Embioptera				1	100
Entomobryomorpha				9	100
Geophilomorpha		1		2	67
Haplotaxida				21	100
Hemiptera	32	43	1	78	64
Hoplonemertea				1	100
Hygrophila				1	100
Hymenoptera: Aculeata		6		23	79
Hymenoptera: Parasitica	5	11		37	77
Hymenoptera: Symphyta				1	100
Isopoda		8		14	64
Julida				6	100
Lepidoptera	5	59	3	46	43
Lithobiomorpha		1		3	75
Macrostomida		1			0
Mantodea				1	100
Neuroptera		2		3	60
Odonata		1	1		0
Oribatida		28		20	42
Orthoptera	4	5	2	3	30
Parasitiformes		5	1	12	67
Podocopida		2			0
Poduromorpha				6	100
Polydesmida				3	100
Polyxenida				3	100
Polyzoniida				1	100
Prostigmata		9		10	53
Pseudoscorpionida	4	5		3	38
Psocodea: Anoplura				2	100
Psocodea: Phthiraptera			7	4	36
Psocodea: Psocoptera		7		13	65
Pulmonata				3	100
Sarcoptiformes				6	100
Scolopendromorpha		1		2	67
Scorpiones				1	100
Scutigeromorpha				1	100

Table 2 (continued)

Order	Endemic genera	Endemic species	Native	Introduced	Percentage of introduced taxa
Siphonaptera				6	100
Spirostreptida				1	100
Strongylida				1	100
Stylommatophora	20	23		18	44
Symphyla				3	100
Thysanoptera		1		10	91
Tricladida	1	2		1	33
Zygentoma		1		4	80

The proportion of introduced to native species calculated on the assumption that species with low level of taxonomic confidence are what we currently assume them to be

The spread of novel habitats has changed the vegetation dynamics and altered the distribution of indigenous vegetation (Table S1 and see Lambdon 2013) and altered ecological conditions. As many native and endemic species appear to have narrow to moderate elevation ranges this may suggest greater habitat specificity and less adaptation to novel habitats. However, some species may be able to adapt, *Pseudolaureola atlantica* has been found on non-native plants, particularly *Solanum mauritianum* in quite high densities and a number of endemic saproxylic beetles are found in decaying wood of *Erythrina caffra* and *Ulex europaeus*. *Opogona* spp. have also been collected from lichens growing on introduced trees in novel habitats. This suggests that more evidence is needed on the interactions between native and introduced species.

In 2012 construction of the new airport at the eastern edge of an endemic invertebrate-rich site, Prosperous Bay Plain, resulted in the loss of habitat for some threatened species (see supplementary material) further population declines are also likely. The airport opened in October 2017 with the explicit aim of attracting up to 30,000 tourists a year, there is currently no monitoring programme to identify what impact this will have on invertebrates.

Action and timeline

Invertebrate extinction risk remains high on St Helena but an invertebrate conservation strategy (Lukenbach et al. 2016) was recently developed. The strategy highlights the high-level threats and issues that invertebrates face (e.g. see Table S1): introduced species, climate change, and a lack of resources as drivers of extinction. Nevertheless, there is a complete lack of long-term monitoring coupled with a need for increased resources and scientific research. Put simply, continuity is one of the biggest problems St Helena faces, long-term monitoring and funding are needed to assess the success of conservation management and the impact of construction projects on ecological communities. Funding should be targeted towards a monitoring programme for endemic species particularly those that have very restricted distributions (i.e. those with a restricted elevation range). This programme could involve a fixed set of conservation sites using standardised collection protocols (e.g. time sampling using beating, sweeping, pitfalls, cold searching etc.). In addition, funding is also needed to carry out targeted survey work to determine the status of species that are considered probably extinct e.g. those endemic species that have not

Table 3 St Helena invertebrate species currently assessed as threatened or near-threatened under IUCN Red Listing criteria version 3.1

Family	Species	IUCN status	Likely cause
Anthribidae	*Homoeodera compositarum*	NT	Decline in habitat quality; increased predatory invasive species
	Homoeodera edithia	CR	Decline in habitat quality; loss of endemic host plants; increased predatory invasive species
	Homoeodera elateroides	CR	Decline in habitat quality; increased predatory invasive species
	Homoeodera major	CR	Decline in habitat quality; increased predatory invasive species
	Homoeodera scolytoides	CR	Airport construction. Decline in habitat quality; increased predatory invasive species
Charopidae	*Helenoconcha relicta*	CR	Decline in habitat quality
Crambidae	*Helenoscoparia nigritalis*	NT	Increased predatory invasive species
Drosophilidae	*Scaptomyza horaeoptera*	VU	Decline in habitat quality; increased predatory invasive species
Salticidae	*Paraheliophanus jeanae*	VU	Increased predatory invasive species
	Paraheliophanus napoleon	CR	Decline in habitat quality; increased predatory invasive species
	Paraheliophanus sanctaehelenae	VU	Decline in habitat quality; increased predatory invasive species
	Paraheliophanus subinstructus	VU	Decline in habitat quality; increased predatory invasive species
Scarabaeidae	*Mellissius adumbratus*	EN	Airport construction. Decline in habitat quality
Scheloribatidae	*Scheloribates evanescens*	EN	Decline in habitat quality; increased predatory invasive species

CR critically endangered, *EN* endangered, *VU* vulnerable, *NT* near threatened been recorded since Basilewsky et al. (1970–1977). Further survey work is also required to determine the suitability of the current set KBA's to determine if these need to be expanded (see also below).

Priority species (Red List status global/national, endemic and native species)

Currently 16 invertebrate species (from 94 to be completed) have been assessed as threatened or near threatened using the IUCN Red List categories and criteria (Table S2). However, 94 species only constitute 19% of the endemic fauna. An expanded priority list of key endemic species, good quality habitat, and key restoration sites would be a more effective way for invertebrate conservation than just using the current Red List. Ideally, these species and sites would be good indicators of population dynamics and habitat quality, and be responsive to environmental change. As the mole spider has not yet been described, a Red List assessment cannot be completed but it would undoubtedly be critically endangered.

Action and timeline

This is the practical approach was suggested in the conservation strategy (Cairns-Wicks et al. 2016) but a full priority list should be completed by 2019. Recently, the IUCN SSC Mid Atlantic Island Invertebrates Specialist Group was established as the Red List authority for the Mid-Atlantic islands including St Helena; this key achievement should ensure the success of the Red Listing process on St Helena. The taxonomy of the mole spider needs to be progressed urgently.

Priority areas (KBAs and protected areas)

400 of the 466 (86%) endemic species and 65 of 97 (67%) native non-endemic species are found in KBAs, providing high complementarity of species of conservation concern. 72% of species with unknown status and 59% of introduced species are also found inside KBAs. The hierarchical partitioning analyses indicated that area of KBA and number of collecting visits are significant parameters in the models (Table 4); none of the other variables were significant. Number of visits is consistently the most important variable and is indicative of under sampling, which needs addressing. Area is also an important variable indicating that the size of conservation areas may be important (cf. MacArthur and Wilson 1967). The high elevation KBAs appear to form a core set of invertebrate conservation sites but additional sampling may reveal other important sites. St Helena currently has 23 National Conservation Areas, three are National Parks, six are Nature Reserves, five are Important Wirebird Areas and nine are Historic Conservation Areas. Whilst the National Park, Nature Reserves and the Important Wirebird Areas are the primary focus of conservation efforts, they do not fully address the conservation of invertebrates (see Taylor 2016).

Action and timeline

KBAs are a more flexible approach to identify new invertebrate sites than declaring further statutory protected sites. KBAs can be more rapidly periodically reviewed and redefined than statutory designation allows in response to new data. In the longer term, KBAs may then be designated statutory sites. A review of current compliment of KBAs should be

Table 4 Hierarchical Partitioning of the relationships between environmental variables and species richness

<table>
<tr><th rowspan="3">Dependent variable</th><th colspan="6">Fraction of regression relationship attributable to independent variables (%) according to Hierarchical Partitioning</th></tr>
<tr><th colspan="3">Including area outside KBAs</th><th colspan="3">Only KBAs</th></tr>
<tr><th>Number of collecting visits</th><th>KBA Area</th><th>R^2 value for GLM regression (%)</th><th>Number of collecting visits</th><th>KBA Area</th><th>R^2 value for GLM regression (%)</th></tr>
<tr><td>Total spp. richness</td><td>69.9</td><td>28.7</td><td>75.6</td><td>81.9</td><td>27.3</td><td>68.4</td></tr>
<tr><td>Endemic spp. richness</td><td>62.1</td><td>38.4</td><td>61.6</td><td>70.5</td><td>39.3</td><td>53.5</td></tr>
<tr><td>Native spp. richness</td><td>60.0</td><td>25.7</td><td>62.3</td><td>67.6</td><td>19.8</td><td>51.2</td></tr>
<tr><td>Introduced spp. richness</td><td>70.0</td><td>25.1</td><td>73.9</td><td>82.8</td><td>22.8</td><td>65.9</td></tr>
</table>

The overall R^2 is derived from a Generalized Linear Model (GLM) using all the variables measured. The explained variation is partitioned into the individual contributions of each of the nine variables by Hierarchical Partitioning (HP) (each contribution is a percentage of the overall R^2). Non-significant contributions are omitted and all relationships were positive

KBA key biodiversity areas

completed by 2021 and this should be done in conjunction with Red Listing priority species as occurrence of Red list species is a requirement of KBA designation (IUCN 2016).

Increased awareness

There has been extensive work to raise public awareness of invertebrates on St Helena. Over the last five years there have been 170 education events with 2995 opportunities for children to learn in the three primary schools and one secondary school and through the Forest Schools programme (Table S3). This includes the development of loan boxes of bug exploring equipment together with a wide range of educational materials. Thirty-nine teachers have been trained on invertebrate education and they continue to integrate invertebrates into lessons and wider school activities. There have also been wide reaching media articles and most residents have been exposed to invertebrate media and events in some way. An invertebrate reference collection in the Museum of St Helena (ca. 2500 specimens representing and 420 species) and a St. Helena invertebrate field guide are also being developed to increase engagement, understanding and improve local skills.

The introduction of the new Environmental Protection Ordinance (EPO) in 2016 (Saint Helena Government 2016a), is a recent example of increased awareness of policy makers. The EPO gives endemic invertebrates protection under the law for the first time ever. These types of policy are particularly important given the projected increased tourist activity on the island. However, policy needs to be flexible and adapt to the needs of the island invertebrates and periodic reviews are essential. One of the key threats to invertebrates is invasive species hence biosecurity is another key area and the Government biosecurity team now have responsibility for both port and airport. This team is tasked with managing impacts, monitoring, collecting baseline data, and mitigating damage. Recent public alerts have included the European paper wasp *Polistes dominula* and the harlequin ladybird *Harmonia axyridis* which now seem to be establishing. The sustainability of this approach depends on long-term funding and developments in tourism are likely to have profound effects on biosecurity. All the monitoring and baseline data collection are currently undertaken by projects funded through external resources (see Table S4); this is unlikely to be sustainable. In addition, St Helena has a high turnover of trained staff and periodic access to training is likely to be necessary. Ideally, core funding would alleviate this risk but this is unlikely to occur in the current economic climate, other options are therefore required, green tax or citizen science may be productive areas.

Action and timeline

The continual advancement of the public engagement strategy within the confines of the existing invertebrate strategy needs periodic review. In addition, a strategy for scientific research on St Helena that gives guidance to scientists on delivering measurable impact whilst researching on St Helena would be invaluable. The current public engagement strategy should be reviewed, a scientific engagement strategy completed and the EPO policy mechanism reviewed by 2021. In addition, the issue of funding for core training and monitoring activities needs to be reviewed and the option of a green tax and the potential for or citizen science explored by 2020.

Sustainable finance and partnerships to achieve regional goals

A big challenge to sustainability is long-term funding. St Helena Government funding is dependent on foreign aid so susceptible to changing politics overseas. The St Helena National Trust is dependent on grants and philanthropic donations, but aims to move towards self-sustainability through business and scientific services. The move towards economic independence will be a challenging one but given St Helena's globally important biodiversity a balance needs to be struck between making use of, but protecting, natural resources including invertebrates. Whether nature-based tourism can play a part of sustainable funding in the future remains to be seen as a local mechanism to raise taxes from tourism does not currently exist.

Action and timeline

Consideration needs to be given to sustainable funding for conservation and research on St Helena and the potential for income from tourism. This was not addressed in the current sustainable development plan (Saint Helena Government 2012) but a new plan will be prepared for the period from 2021, we strongly suggest that these areas need addressing in the new plan.

Increase regional capacity to identify, monitor and conserve invertebrates and their associated habitats

St Helena is one island in the South Atlantic and other islands face similar problems although at different scales. Regional initiatives to bring together invertebrate scientists, conservationists and policy makers through institutions such as SAERI and groups like the

IUCN SSC Mid Atlantic Island Invertebrate Specialist Group increase regional capacity. However, the permanency of these institutions cannot be guaranteed so the continuation of invertebrate initiatives at regional levels through policy would allow some level of communication to be maintained.

Conclusions

The key findings for our study of St Helena's invertebrates suggest there are significant opportunities for research, on taxonomy, ecology and population biology to address spatial and temporal aspects and to address resilience to environmental change. The current level of extinction on St Helena has reached major proportions. Conservation action is needed to monitor and survey of priority endemic species with restricted distributions, and key sites that have been under sampled. Further, additional Red List assessments, an expansion of the KBA network and large-scale control of invasive species also need to be addressed. Focusing on the management of invasive species as the most significant threat in the KBAs is likely to provide long-term protection and reduced extinction threat. A clear success in recent times has been the level of public engagement and continuation of these approaches is a key area. A further challenge is sustaining adequate funding but there are key commitments from both governmental and non-governmental organisations for the conservation of invertebrates but more needs to be done. Given its status as a UK Overseas Territory, the UK Government must make UKOT invertebrate conservation a higher priority and provide adequate support to prevent further loss of globally important species (*c.f.* Churchyard et al. 2016).

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Affiliations

Alan Gray[1] · Vicky Wilkins[2] · David Pryce[3] · Liza Fowler[4] · Roger S. Key[5] · Howard Mendel[6] · Michael Jervois[4] · Axel Hochkirch[7] · Rebecca Cairns-Wicks[8] · Amy-Jayne Dutton[4] · Lourens Malan[9]

[1] NERC Centre for Ecology and Hydrology, Bush Estate, Penicuik, Midlothian EH26 0QB, UK

[2] Mid Atlantic Island Invertebrate Specialist Group, c/o IUCN, The David Attenborough Building, Pembroke Street, Cambridge CB2 3QZ, UK

[3] Pink Grove, Levelwood STHL IZZ, St Helena Island

[4] St Helena National Trust, Broadway House, Jamestown STHL 1ZZ, St Helena Island

[5] The Old Black Bull, Carthorpe, Bedale, North Yorkshire DL8 2LD, UK

[6] Natural History Museum, Cromwell Road, London SW7 5BD, UK

[7] Department of Biogeography, Trier University, 54286 Trier, Germany

[8] Mount Pleasant House, Sandy Bay STHL IZZ, St Helena Island

[9] Environmental Management Division, St Helena Government, Jamestown STHL IZZ, St Helena Island