

Changes in non-marine mollusc populations in the Seychelles islands 1986-2012

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Abstract: Population changes in Seychelles terrestrial molluscs were investigated using monitoring data from 1986-2012 at 18 sites on the islands of Mahé, Praslin and Silhouette. Species with significant changes in populations could be categorised as fluctuating (populations increasing or decreasing at different times and in different localities), decreasing (significant declines in most occupied sites) or increasing (significant increases in most sites). Fluctuating species included the helicininid *Pleuropoma theobaldiana* and the streptaxids *Edentulina dussumieri*, *Seychellaxis souleyetianus* and *Stoerestele nevillei*. Two species were identified as increasing: *Subulina striatella* and *Leptichnoides verdcourtii*, both invasive species currently expanding their ranges. Five species are in decline in some sites but not others: *Augustula braueri*, *Imperturbatia constans*, *Silhouettia silhouettensis*, *Priodiscus serratus* and *Pachnouds ornatus*. 10 species are in decline: *Moominia willii*, *Edentulina moreleti*, *Glabrennea gardineri*, *G. silhouettensis*, *Nesokaliella minuta*, *Pachnods velutinus*, *P. kantilali*, *P. nigerxvelutinus*, *P. oxoniensis* and *Stylodonta unidentata*. Declines were attributed to habitat deterioration (*S. unidentata*), climate change (*M. willii*, *E. moreleti*, *G. silhouettensis*, *P. velutinus*, *P. nigerxvelutinus*, *P. oxoniensis*) or a combination of the two factors (*Augustula braueri*, *G. gardineri*, *N. minuta* and *P. kantilali*). Climate change takes the form of changes in rainfall patterns, most significantly a decrease in rainfall in the first quarter of the year. The reduction in rainfall is thought to cause increased mortality of juvenile snails, particularly for arboreal species. This results in the most rapid declines in the highest-altitude and most specialised species. Island snails may be particularly vulnerable to climate change impacts due to their poor dispersal ability and restricted ranges, especially when combined with habitat fragmentation and deterioration due to the spread of invasive plants. Further monitoring of invertebrate populations is needed to determine whether or not snails are particularly vulnerable and how widespread these impacts are.

Populations and ecosystems are thought to be changing in many parts of the world due to factors such as the spread of invasive species, exploitation and climate change. This is resulting in elevated extinction risk and ecosystem instability (Mace *et al.* 2005). Population declines are well established for some well studied vertebrate taxa but such data are scarce for most invertebrates. As a result assessments of threats of invertebrates are limited; 0.5% of terrestrial invertebrates have been assessed for the IUCN Red List (Gerlach *et al.* 2012). These assessments rely on the evidence of habitat degradation as an indication of population decline, sometime supported with range declines. There is a need for comprehensive assessments of the status of a wide range of invertebrate taxa to enable the true status of biodiversity to be determined. Whilst habitat and range changes may provide some indication of status changes population monitoring data are desirable to demonstrate real changes in population status. Such data are very rarely available for invertebrates, with most cases being butterfly populations (e.g. Van Sway *et al.* 2011); only 0.4% of Red Listed invertebrates have been listed

under population size criteria (according to Cardoso *et al.* 2012).

In the Seychelles islands Red List assessments have been undertaken for all non-marine plant and animal taxa (Gerlach 2012). Invertebrate assessments are based on habitat factors and changes in the frequency of collection over the past 150 years. Population monitoring data are not available for invertebrates, with the exception of molluscs. For snails and slugs quantitative population density data have been collected by the author since 1986 on several islands. Analysis of changes in density estimates over the past 36 years enables population changes to be evaluated, providing a more precise assessment of the conservation status of each species.

Methods

Mollusc populations were investigated in numerous sites across the majority of the islands of the Seychelles group between 1986 and 2012. Of these surveys 18 sites on the three largest of the granitic islands were surveyed on 2-10 occasions over these 36 years (Fig. 1). These sites support populations of all of the species recorded in the granitic islands.

Data collection

In each survey site data were collected at 10 randomly placed points. At each point the ground fauna was recorded by collecting a 1x1m square of leaf-litter. Each sample was sifted to remove large debris and record the larger snail species, and then snails extracting by Winkler extraction. The dried litter was finally searched by hand to remove any remaining snails and empty shells. The empty shells were not included in quantitative data but were used to supplement species lists. In addition each point was used as the centre of a 5x5m quadrat in which all trees over 2m height were identified to species and recorded. Each tree was visually inspected to a height of 3m above ground and all snails on the vegetation recorded. Each snail located in ground or vegetation quadrats was identified to species and assigned to categories of juveniles, subadult or adult. Individuals were assigned to the subadult category if they were approximately adult sized but lacked a lip at the mouth edge (usually associated with sexual maturity – pers. obs.). For species that do not normally develop a lip, the subadult category was not used and animals were considered adult if at least 75% of full adult size.

Four species were geographically highly restricted and focussed surveys were designed specifically for these. *Moominia willii*, *Edentulina moreleti* *Glabrennea silhouettensis* and *Dupontia levensonia* were only known from discrete habitat areas covering less than 0.5 hectares. In these areas the snails were either found in leaf litter (*G. silhouettensis*) and could be surveyed with the standard methods used for other species or were arboreal species restricted to the axils of the plants *Pandanus hornei* and *Dracaena reflexa*. In the identified ranges of the snails all accessible axils of these two plant species were examined for snails and the number of live snails recorded. In the case of *E. moreleti* snails were assigned to adult, subadult and juvenile categories, but only adults of the other species were located. Studies for these species dated from 1990-2010 for *G. silhouettensis* and 2000-2010 for the other species.

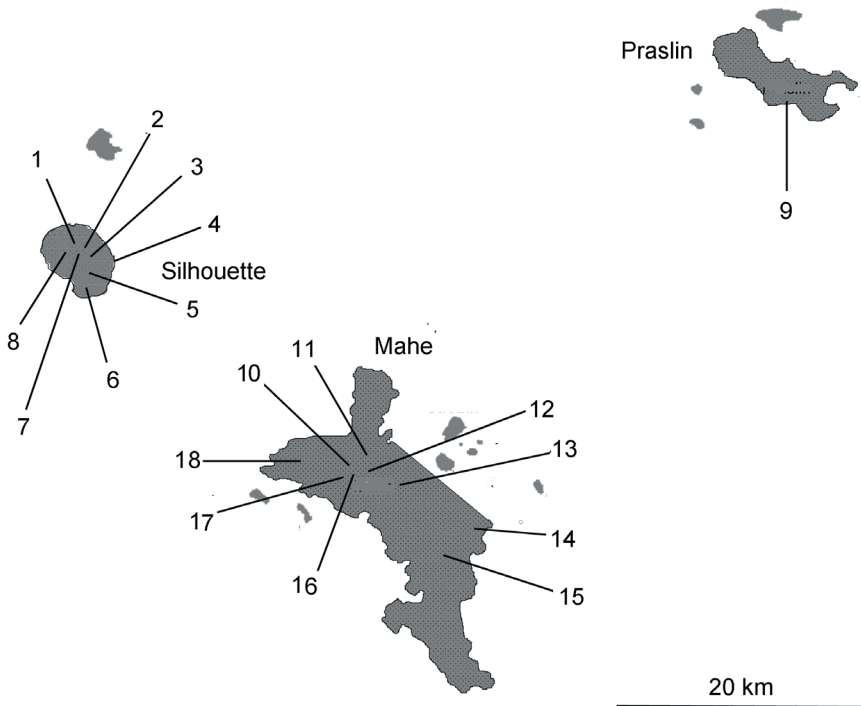
Most surveys were undertaken during the dry season, between June and

August. Some surveys were carried out in November-January and in March. Previous studies have shown that the survey techniques used here are not significantly affected by seasonal variation with no seasonal fluctuations in abundance of adult snails (Gerlach 1995), although reproduction of some species may be affected by climatic factors.

Environmental change

Habitat change was recorded in the same surveys. Plants were counted and identified in each quadrat; in 5x5m quadrats all trees over 2m tall were recorded, in 1m quadrats all plant individuals were counted. Impacts of invasive trees on forest conditions was investigated by recording light intensity levels at the base of 10 trees of each of the 5 most abundant invasive and native tree species in three sites on Silhouette: La Passe, Jardin Marron and Mon Plaisir. Light levels were recorded with a digital light meter (recorded as lux values). All light data were recorded within 10 minutes,

Fig. 1. Map of survey localities. 1 – Anse Mondon valley; 2 – Mon Plaisir; 3 – Jardin Marron; 4 – La Passe; 5 – Gratte Fesse; 6 – south peak; 7 – Pisonia forest; 8 – Mont Dauban; 9 – Praslin National Park; 10 – Congo Rouge; 11 – Trois Freres; 12 – Mission; 13 – Copolia; 14 – Mont Sebert; 15 – La Reserve; 16 – Casse Dent; 17 – Morne Blanc; 18 – Mare aux Cochons



minimising ambient changes in light levels.

Climatic factors were not recorded in the field sites but rainfall and temperature patterns were used from Gerlach (2010) based on data from fixed points (Seychelles Meteorological Office data for Mahé and Praslin islands, Nature Protection Trust of Seychelles data for Silhouette island).

Analysis

An initial analysis of population changes was undertaken by grouping data into three time periods: 1986-1990, 1991-2000 and 2001-2012. Data for each site was treated separately and comparisons made between these time periods for each site using a t-test. For species identified as having significant population changes in these time periods population change was analysed by regression of population against date.

Habitat change was evaluated using t-tests of data from 1986-2000 and 2001-2012. For this analysis plant species were tested individually and a separate analysis was undertaken grouping species into introduced and native species. Climatic change analysis used anomalies from the long term averages to identify periods of unusual rainfall. Annual and monthly data were examined.

The effects of location and of plant species abundance on snail populations was evaluated using a multiple analysis of covariance (MANCOVA) of the abundance of each species of snail, plant species, the total abundance of native and alien plant species and quarterly rainfall averaged over the previous five years. An exploratory analysis found that only one plant species and only first quarter rainfall had a significant impact on any snail species. The analysis was repeated using the abundance of *Cinnamomum verum* and first quarter rainfall. For each snail species data were only included from sites where the species had been recorded, thus avoiding the confounding effects of different geographical distributions.

Results

Snail population changes

Significant changes in species abundance are summarised in Table 1-2 and Fig. 2-4. Four species showed significant population changes but varied in the direction of change and geographical patterns (*Pleuropoma theobaldiana*, *Edentulina dussumieri*, *Seychellaxi souleyetianus* and *Stereostele nevillei*). Two species increased in abundance (*Subulina striatella* and *Leptichnoides verdcourtii*). 16 species were identified as being in decline (Table 1). All of these are mainly high forest species and 9 species declined at all occupied sites (*Moominia willii*, *Edentulina moreleti*, *Glabrennea gardineri*, *Glabrennea silhouettensis*, *Nesokaliella minuta*, *Pachnodus kantilali*, *Pachnodus nigerxvelutinus*, *Pachnodus ornatus* and *Pachnodus velutinus*). In addition *Nesokaliella intermedia* declined in all sites, but was too scarce for significance testing.

Moominia willii and *Edentulina moreleti* were largely restricted to *Pandanus hornei* axils at Gratte Fesse on Silhouette, with single records from 300 m away at Mon Plaisir. The Gratte Fesse populations were first located in 2000 and declined to very low levels by 2010 (Fig. 4a-b). *Glabrennea gardineri* was recorded at low densities

Table 1. Significant changes in snail populations based on t-tests with 19 degrees of freedom

		1990 vs 2000		2000 vs 210	
		T	P	T	P
Natives	2. Mon Plaisir			2.399	<0.05
	3. Jardin Marron			2.112	<0.05
	7. Pisonia forest			-2.313	<0.05
	8. Mont Dauban			-2.521	<0.05
	9. Praslin NP			2.212	<0.05
	10. Congo Rouge	-2.332	<0.05		
	13. Copolia	-2.451	<0.05		
	14. Mont Sebert			-2.111	<0.05
	16. Casse Dent			2.167	<0.05
	17. Morne Blanc	-2.101	<0.05	-2.327	<0.05
Invasives	18. Mare aux Cochons			-2.270	<0.05
	6. south peak			3.899	<0.001
	18. Mare aux Cochons			-2.541	<0.05
<i>Pleuropoma theobaldiana</i>	7. Pisonia forest	2.329	<0.05	-2.099	<0.05
	9. Praslin NP			2.190	<0.05
	10. Congo Rouge	2.131	<0.05		
	13. Copolia	2.365	<0.05	-2.201	<0.05
	15. La Reserve	2.132	<0.05	-2.132	<0.05
	17. Morne Blanc	-2.165	<0.05	-2.221	<0.05
<i>Moominia willi</i>	5. Gratte Fesse			-2.912	<0.01
<i>Subulina striatella</i>	3. Jardin Marron			2.223	<0.05
	5. Gratte Fesse			2.101	<0.05
	6. South peak			2.117	<0.05
	9. Praslin NP			2.491	<0.05
	15. La Reserve			2.511	<0.05
	16. Casse Dent			2.521	<0.05
<i>Augustula braueri</i>	17. Morne Blanc	-2.112	<0.05		
<i>Edentulina dussumieiri</i>	7. Pisonia forest	2.132	<0.05	2.221	<0.05
	15. La Reserve	-2.145	<0.05		
	16. Casse Dent			-2.210	<0.05
<i>Edentulina moreleti</i>	5. Gratte Fesse			-2.998	<0.01
<i>Imperturbatia constans</i>	15. La Reserve	-2.431	<0.05		
<i>Glabrennea gardineri</i>	2. MonPlaisir	-2.232	<0.05		
	7. Pisonia forest	-2.322	<0.05		
	8. Mont Dauban			-2.311	<0.05
<i>Glabrennea silhouettensis</i>	8. Mont Dauban	-3.002	<0.01		
<i>Priodiscus serratus</i>	2. Mon Plaisir			-2.091	<0.05
<i>Seychellaxis souleyetianus</i>	10. Congo Rogue	2.333	<0.05		
	15. La Reserve	-2.495	<0.05		
<i>Silhouettia silhouettae</i>	7. Pisonia forest	-2.112	<0.05	-2.188	<0.05
<i>Stereostele nevilli</i>	2. MonPlaisir			-2.387	<0.05
	7. Pisonia forest	-2.501	<0.05		
	10. Congo Rouge	-2.451	<0.05		
	13. Copolia	-2.500	<0.05	-2.451	<0.05
<i>Nesokaliella minuta</i>	17. Morne Blanc	-2.887	<0.01		
<i>Pachnodus kantilali</i>	10. Congo Rouge	-2.903	<0.01		
	17. Morne Blanc	-2.869	<0.01	-2.331	<0.05
<i>Pachnodus niger x velutinus</i>	10. Congo Rouge	-2.198	<0.05		
	13. Copolia	-2.220	<0.05	-2.098	<0.05
	16. Casse Dent	-2.433	<0.05	-2.337	<0.05
	17. Morne Blanc	-2.865	<0.01	-2.438	<0.05
	18. Mare aux Cochons	-2.199	<0.05		
<i>Pachnouds ornatus</i>	15. La Reserve	-2.267	<0.05		
<i>Pachnodus velutinus</i>	10. Congo Rouge	-2.355	<0.01		
<i>Stylodonta unidentata</i>	3. Jardin Marron			2.122	<0.05
	7. Pisonia forest	-2.410	<0.05	-2.191	<0.05

Table 1. (continued)

		1990 vs 2000		2000 vs 210	
		T	P	T	P
<i>Stylodonta unidentata</i>	10. Congo Rogue	-2.322	<0.05		
	14. Mont Sebert	-2.210	<0.05		
	15. La Reserve	-2.102	<0.05		
	17. Morne Blanc	-2.112	<0.05		
	18. Mare aux Cochons	-2.433	<0.05		
<i>Leptichnodies verdcourtii</i>	16. Casse Dent	2.322	<0.05	3.155	<0.01

Table 2. MANCOVA of snail species abundance and environmental variables

Species	Variable	Df	SS	MS	F	P
<i>Moominia willii</i>	Cinnamomum	9	71.39	7.93	0.63	NS
	Q1 rain	1	207.86	207.86	16.51	<0.001
	Error	29	365.11	12.59		
	Total	39	644.36			
<i>Augustula braueri</i>	Cinnamomum	9	1608.03	178.67	2.23	<0.05
	Q1 rain	2	642.56	321.28	4.01	<0.05
	Error	78	6290.70	80.12		
	Total	89	8541.29			
<i>Edentulina moreleti</i>	Cinnamomum	9	159.21	27.69	2.15	NS
	Q1 rain	1	233.77	233.77	18.15	<0.001
	Error	29	244.72	12.88		
	Total	39	637.70			
<i>Glabrennea gardineri</i>	Cinnamomum	9	1820.61	202.29	2.62	<0.05
	Q1 rain	2	659.38	329.69	4.27	<0.05
	Error	87	6717.27	77.21		
	Total	89	9197.26			
<i>Glabrennea silhouettensis</i>	Cinnamomum	9	285.75	31.75	2.25	NS
	Q1 rain	2	325.38	162.69	11.53	<0.001
	Error	18	253.98	14.11		
	Total	29	865.11			
<i>Priodiscus serratus</i>	Cinnamomum	9	937.63	104.18	1.55	NS
	Q1 rain	2	642.52	321.26	4.78	<0.05
	Error	78	5242.38	67.21		
	Total	89	6822.53			
<i>Nesokaliella minuta</i>	Cinnamomum	9	1292.58	143.62	2.55	<0.05
	Q1 rain	2	1003.62	501.81	8.91	<0.01
	Error	48	2703.36	56.32		
	Total	59	4999.56			
<i>Pachnodus kantilali</i>	Cinnamomum	9	153.27	17.03	2.69	<0.05
	Q1 rain	2	184.82	96.41	15.23	<0.001
	Error	48	303.84	6.33		
	Total	59	641.93			
<i>Pachnodus nigerxvelutinus</i>	Cinnamomum	9	1464.12	162.68	1.98	NS
	Q1 rain	2	802.18	401.09	4.88	<0.05
	Error	78	6410.82	82.19		
	Total	89	8677.12			
<i>Pachnodus oxoniensis</i>	Cinnamomum	9	1306.62	145.18	1.65	NS
	Q1 rain	2	1036.52	518.26	5.89	<0.01
	Error	78	6863.22	87.99		
	Total	89	9206.36			
<i>Pachnodus velutinus</i>	Cinnamomum	9	183.06	20.34	2.23	NS
	Q1 rain	1	127.77	127.77	14.01	<0.01
	Error	9	82.08	9.12		
	Total	19	392.91			
<i>Stylodonta unidentata</i>	Cinnamomum	9	2518.92	249.88	2.22	<0.05
	Q1 rain	2	731.14	365.57	3.23	NS
	Error	288	32417.28	112.56		
	Total	299	35667.34			

Fig. 2. Changes in snail populations: alien and native species change in relation invasive plant abundance (proportion of trees identified as introduced). Bar charts: abundance of alien (blue) and native (red) snails, with standard errors of means. Map: levels of invasion coloured grey - suburban areas, green >60% invasives, blue 40-60%, yellow 25-40%, red <25%.

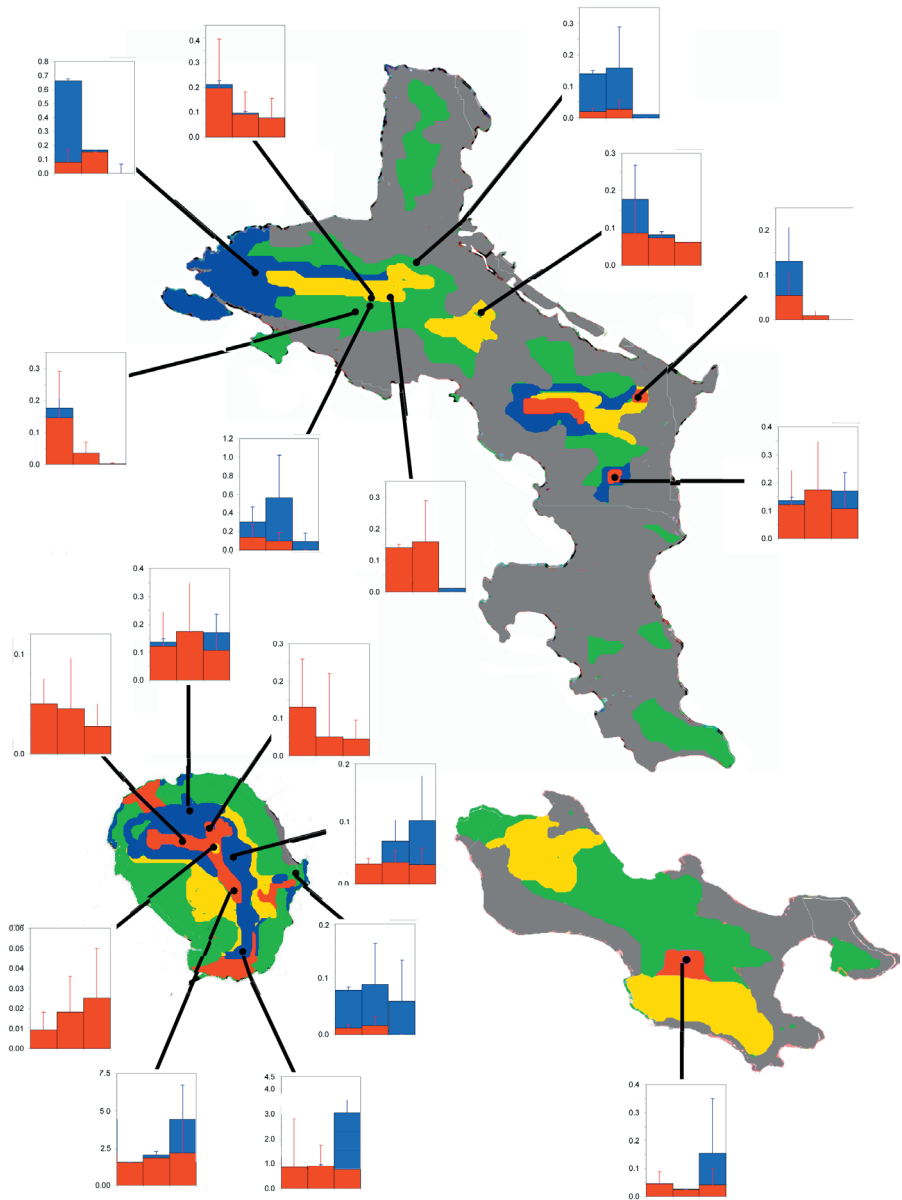
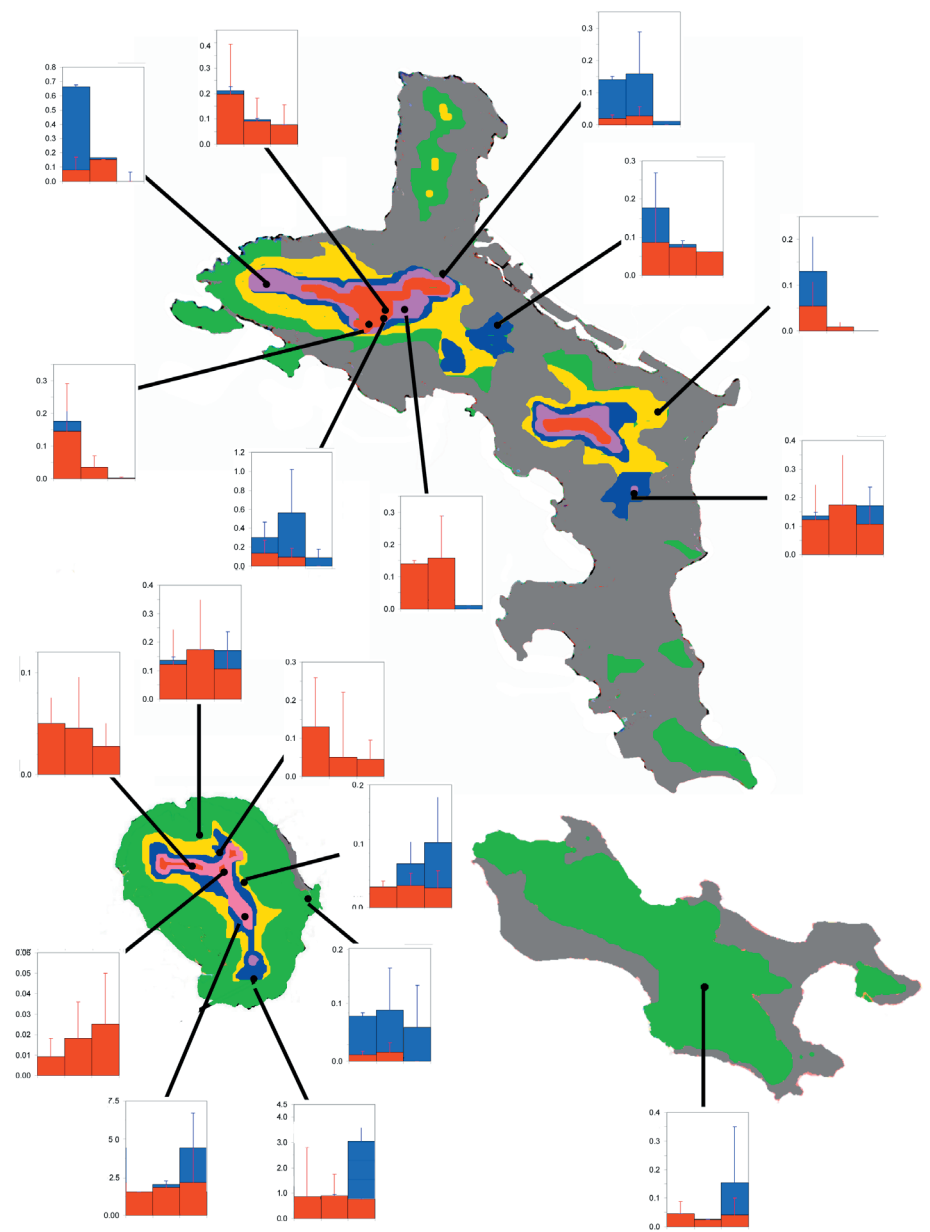


Fig. 3. Changes in snail populations: alien and native species change in relation to altitude (and climate change risk). Bar charts as Fig. 3. Map: grey – suburban; green <300m (low risk); yellow 300-400m, blue 400-500m; purple 500-550m; red >550m (high risk).



in the *Pisonia* forest and Mont Dauban in 1990 but not subsequently in either locality (Fig. 4c). *G. silhouettensis* was discovered in 1990 in a small area of Mont Dauban. It was recorded in the same locality in 1991 at lower densities, but has not been located since despite careful searching of the type locality and comparable areas in 2000, 2009 and 2010 (Fig. 4d). It is considered to be extinct. *Nesokaliella* showed rapid decline in *N. minuta* at Morne Blanc from 1988-1990; it was not recorded subsequently (Fig. 4e). In 2011 only one population was located (Praslin NP). These species were all significantly affected by rainfall but not invasive plants (Table 2).

The most significant declines were found in species of the genus *Pachnodus*. *Pachnodus* species at high altitude on Mahé declined rapidly from 1986-8 to 1991 for *P. velutinus* and *P. kantilali* (Fig. 4f & 4i). *P. nigerxvelutinus* also declined but at a slower rate (Fig. 4g). *Pachnodus* species at mid-high altitude on Mahé declined steadily from 1986, with decline most apparent from 1990. The lower altitude species on Mahé and on Praslin remained stable. On Silhouette rapid declines were recorded between 1990 and 2000 for high altitude *P. oxoniensis* (Fig. 4h) and *P. lionneti* in the *Pisonia* forest. The significantly declining species were all significantly affected by rainfall, and to a lesser extent invasive plants.

Stylodonta unidentata declined significantly in association with plant invasion, but not rainfall. These declines were only significant at Morne Blanc, Congo Rouge and Mare aux Cochons – Fig. 4j); non-significant declines were recorded at Mont Sebert and at La Reserve. One population increased in density; at Jardin Marron an increase was recorded following habitat restoration. These changes match habitat changes with notable declines in deteriorating sites, non-significant declines in stable sites and increases in the one restored site.

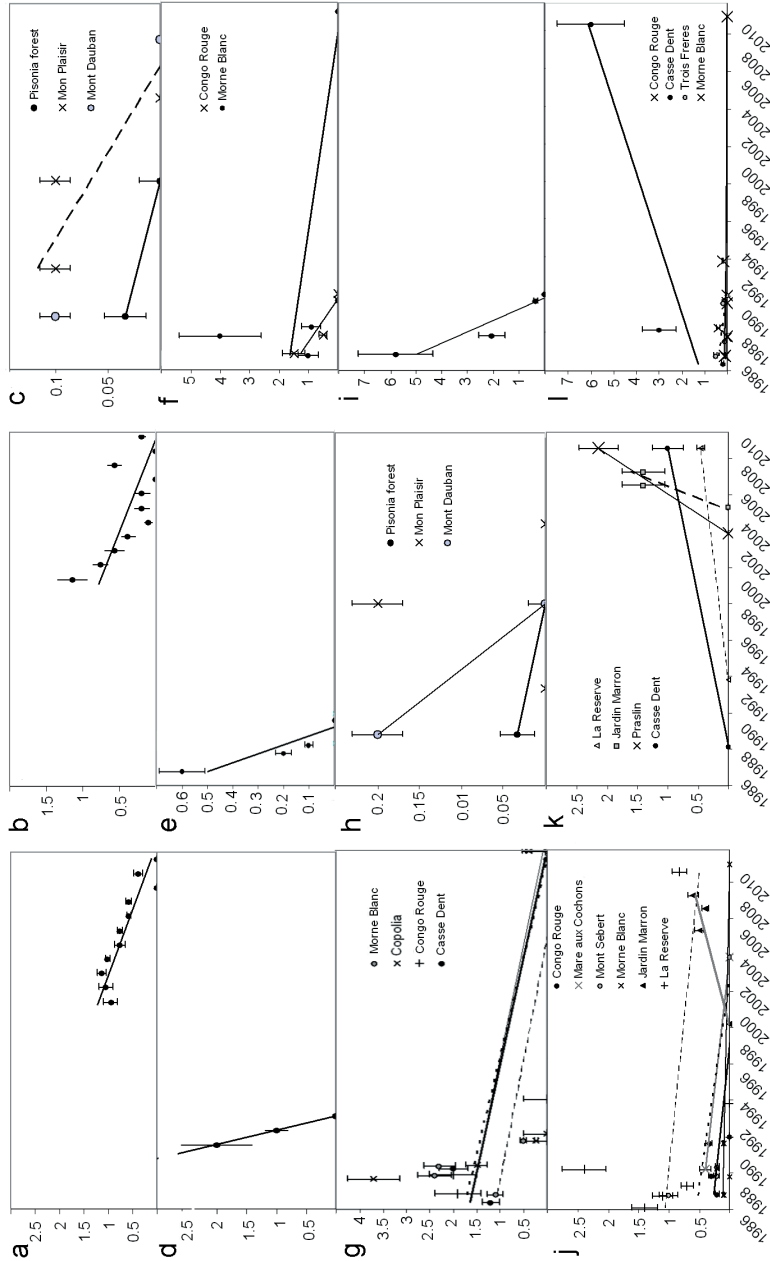
Increasing species (*Subulina striatella* and *Leptichonides verdcourti*) were not significantly affected by rainfall or plant species (Fig. 4k-l).

Habitat change

Significant changes in native and introduced plant densities are shown in Table 3. Tree density did not change at Trois Freres, Copolia, Praslin NP and the *Pisonia* forest, but a change in the balance between natives and invasives was apparent at Copolia where native seedlings decreased in abundance. Increases in invasion were apparent at Congo Rouge, Morne Blanc, La Reserve, Mon Plaisir and Mont Dauban. At Congo Rouge and Morne Blanc native seedling abundance also declined, and only invasive seedlings were recorded at Mont Dauban and Mon Plaisir. The only site with an increase in native trees and a decline in invasives was Jardin Marron, due to active management at this site from 2000-2010. At this site seedling abundance fluctuated significantly due weeding of invasives. Mon Plaisir showed increase in invasives but also an increase in natives due to regeneration of this site from a period of open habitat in 1990-2000. There is no general geographical pattern to habitat change, local factors (e.g. historical distribution of plantations) affecting forest dynamics.

Light level differences are shown in Fig. 5; relative light levels are calculated by dividing the recorded values by the average for that site.

Fig. 4. Changes in snail populations. a) *Moominia willii*; b) *Edentulina moreleti*; c) *Glabrennea gardineri*; d) *G. silhouettensis*; e) *Nesokaliella minuta*; f) *Pachnodus kantilali*; g) *P. nigerxvelutinus*; h) *P. oxoniensis*; i) *P. velutinus*; j) *Stylodonta unidentata*; k) *Subulina striatella*; l) *Leptichnoides verdcourtii*



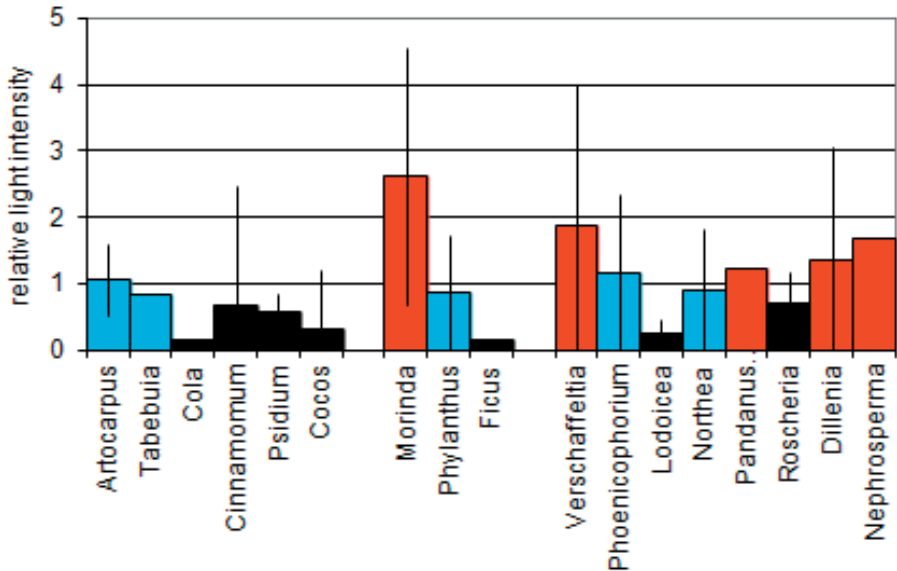
Climate change

No significant temperature changes were identified during the study period. Annual rainfall totals also did not change significantly but there was a notable change in rainfall seasonality, with a significant decline in rainfall in the first three months of the year (Fig. 6). The longest run of years with dryer than average first quarters was 2003-2011.

Table 3. Significant changes in native and invasive plant abundance between 1986-2012 and 1990-2012, T-test results with 19 degrees of freedom.

Locality	Tree changes				Seedlings			
	Natives		Invasives		Natives		Invasives	
	T	P	T	P	T	P	T	P
2. Mon Plaisir	2.111	<0.05	-3.001	<0.01	-2.879	<0.01	3.160	<0.01
3. Jardin Marron	2.978	<0.01	-3.121	<0.01			-2.395	<0.05
10. Congo Rogue			2.998	<0.01	-3.002	<0.01		
11. Trois Freres	-2.201	<0.05			2.132	<0.05		
12. Mission			2.405	<0.05			2.912	<0.01
13. Copolia			2.322	<0.05	-2.444	<0.05		
15. La Reserve	-2.199	<0.05	3.005	<0.01	2.501	<0.05	3.101	<0.01
17. Morne Blanc	-2.343	<0.05	3.100	<0.01			4.007	<0.001

Fig. 5. Relative light levels under different tree species, grouped as invasives (left 6), indigenous (centre 3) and endemic (right 8). Relative light levels coloured black <0.8, blue 0.8-1.2, red >1.2.



Discussion

The significant changes in snail populations could be divided into three categories: fluctuating species (with no clear pattern over the study period), increasing species and declining species. The most notable fluctuating species was *Pleuropoma theobaldiana*. This declined in one site from 1986-2012 (Morne Blanc) but has fluctuated, with periods of population increase and of decline, at five other sites (Copolia, Congo Rouge and La Reserve, *Pisonia* forest and Praslin NP). These sites cover a range of altitudes and are on different islands, with no identified common factors. The decline at Morne Blanc may be associated with the extreme habitat deterioration at this site, with populations at the other sites reflecting more normal unstable population dynamics in this species. In addition three of the carnivorous Streptaxidae show population increases in some sites and decreases in others and are also regarded as fluctuating. *Edentulina dussumieri* declined at La Reserve in the 1990s, and at Casse Dent in the 2000s, but increased in all periods in the *Pisonia* forest. *Seychellaxis souleyetianus* declined in the 1990s at La Reserve but increased in the same period at Congo Rouge. *Stereostele nevillei* declined at Congo Rouge and the *Pisonia* forest from 1990 but showed extreme fluctuations at Copolia. These are the three largest and most abundant streptaxids and population sizes probably reflect changes in the diverse prey species they consume.

Two species showed consistent population increases. *Subulina striatella* increased in the 2000s at six sites (Casse Dent, Gratte Fesse, Jardin Marron, Silhouette's south peak and in Praslin NP). *Leptichnoides verdcourtii* increased in all periods at Casse Dent, in addition this species was found commonly at La Reserve for the first time in 2011, although not in any quantified samples. Both species were introduced to the islands in the 20th century; *S. striatella* first recorded in 1962 and *L. verdcourtii* in 1986 (Gerlach 2006). These two species seem to be in a phase of active population expansion, with range expansion being apparent in *S. striatella* and *L. verdcoruti* increasing in abundance in higher-altitude sites where it was rare in the 1980s (Fig. 7).

Fig. 6. First quarter rainfall anomaly

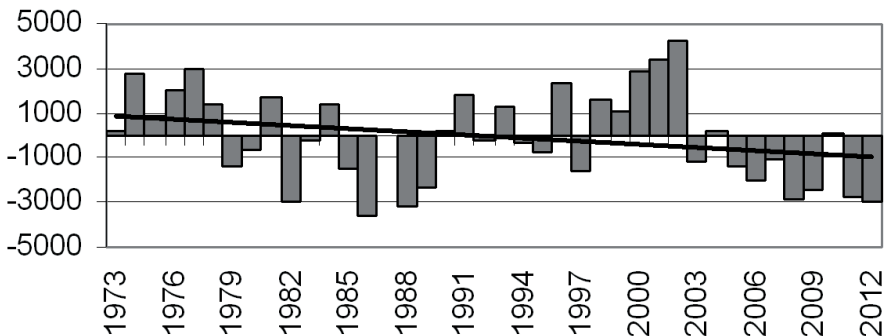
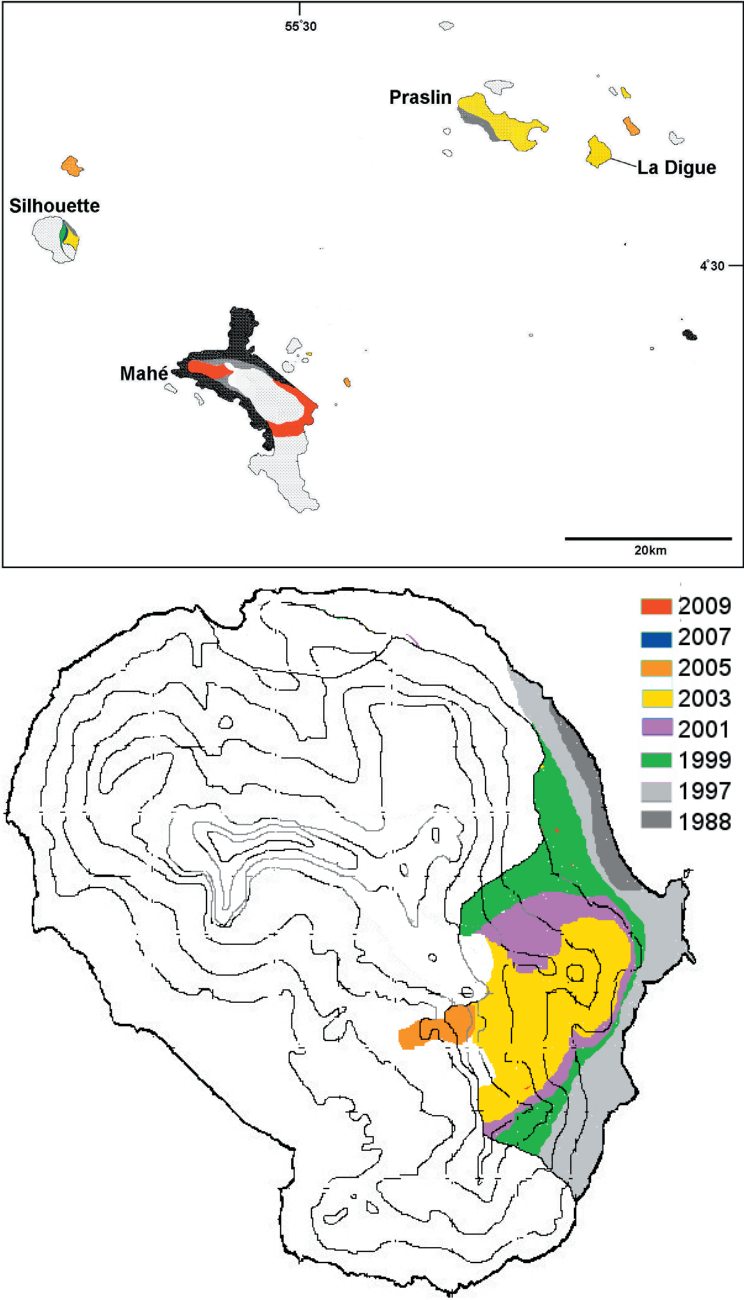


Fig. 7. Range expansion in *Subulina striatella*. Top – distribution in the granitic islands; bottom – distribution on Silhouette island. The species also colonised Denis and D’Arros by 2003



Of the 10 species that declined, the species that declined across their ranges are all high altitude species (*Moominia willii*, *Edentulina moreleti*, *Glabrennea gardineri*, *G. silhouettensis*, *Nesokaliella minuta*, *Pachnods velutinus*, *P. kantilali*, *P. oxoniensis*), species which declined in only some sites are more varied in their altitude adaptations, and declines were recorded in their highest altitude sites. The genus *Nesokaliella* covers a range of altitudes, with rapid declines in the high altitude *N. minuta* which was restricted to deteriorating habitat, and in *N. intermedia* on Silhouette which declined in all areas, irrespective of habitat quality. A third species, *N. subturritula*, is the most widespread species of the genus and occurs at lower altitudes than the others, declines were not recorded in this species.

Declines in the populations of Seychelles snails can be attributed to two main causes: habitat deterioration and climate change. Habitat deterioration includes changes in forest characteristics, as indicated by the data showing increasing depth of shade cast by the main invasive species (such as *Cinnamomum verum*). This would change the conditions in the leaf litter, affecting litter-dwelling snails and, more obviously, would affect the epiphyte flora and the associated arboreal organisms. Habitat appears to be the primary factor affecting *Stylodonta unidentata* and is a contributory factor for *Augustula braueri* (but only locally), *Glabrennea gardineri*, *Nesokaliella minuta* and *Pachnodus kantilali*. Climate is a significant factor affecting the high-altitude specialist species (*Moominia willii*, Streptaxidae and *Pachnodus* species). *Nesokaliella* may be affected by a combination of both factors, the most significant declines being found in *N. minuta* which occurs at high altitude in the most seriously deteriorating sites on Mahé island. The fact that *N. intermedia* has declined even in areas with improving habitat suggests that climate is a significant factor. It is probable that recorded declines in *Pachnodus* species are due to a combination of both factors. Climate has a major impact on Seychelles snail populations through rainfall patterns affecting recruitment; hatchlings of *Pachnodus* species require high levels of humidity (>90% at all times – pers. obs.). If low humidity occurs adults of most species (except the extinct *P. velutinus* – Gerlach 1996) enter aestivation and can tolerate hours, or days of relatively dry conditions. Lowland species can survive several weeks in this state. Hatchlings and small juveniles however are unable to do this and die within hours of humidity dropping below 90%. This means that prolonged dry periods will result in high levels of juvenile mortality, affecting population structure. Non-arboreal species would be better able to withstand dry conditions, the deeper layers of litter retaining moisture for longer, thus fewer terrestrial species show population declines. Those that are in decline are the most high-altitude specialist species (e.g. *Glabrennea* spp.). Mid- to low-altitude species are adapted to variable climates with periods of low humidity. They are thus more tolerant of the dry conditions that are associated with the decline of the high altitude species.

Until recently the forest ecosystems of the Seychelles islands were relatively intact and documented extinctions were attributed to direct hunting (birds, crocodiles and tortoises: Stoddart 1984) or to early lowland forest clearance (the snails *Pachnodus ladiguensis* and *P. curiosus*: Gerlach 2006). The synergistic interaction of accelerating alien plant invasion (Kueffer *et al.* 2004; 2010) and climate change are now causing significant declines in high-forest species. Climate change is expected to combine

with habitat loss and fragmentation to increase species loss (Schindler 2001; Opdam & Wascher 2004; Brook *et al.* 2008). Climate change risk is greatest for isolated or fragmented populations that are unable to move in response to changing climates (Brook *et al.* 2008). The forest habitats of the Seychelles habitats are not highly fragmented but the high-altitude habitats are isolated and small in area, in addition snails have low mobility and so may be at particular risk. Whether or not Seychelles snail populations have experienced similar declines in the past as a result of natural climatic fluctuations is not known. There is no palaeoecological record comparable to that used to demonstrate prehistoric droughts in Mauritius (Van der Plas *et al.*, 2012). Even if prolonged dry conditions do occur as part of natural processes present day populations may be particular prone to extinction risk due to the impacts of habitat degradation caused by invasive species and population fragmentation resulting from both habitat change and development.

Invasion may also be increasing due to the effects of climate change (Van der Wal *et al.*, 2008; Mantyaka-pringle *et al.* 2012), although this has not been investigated in Seychelles. With a largely stable equatorial climate and only a recent human history (human settlement dating from 1772) the Seychelles islands are unlikely to be unusually vulnerable to these factors. Accordingly, it is to be expected that synergistic impacts of habitat deterioration and climate change will be occurring throughout the world. Further monitoring of invertebrate populations is needed to evaluate how significant these are elsewhere. Monitoring of snail populations is recommended due to their slow movement, easy detection and comparatively easy identification.

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