

Patterns of hybridization and extinction in a tropical land snail

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Abstract

The extinction of a species of land snail from Seychelles, *Pachnodus velutinus*, is reported. This is the result of swamping by a hybrid taxon *P. niger* × *velutinus* following the movement of a hybrid zone. The hybrid zone movement and the extinction process were followed over the years 1986-1994.

Introduction

Numerous hybrid zones have been reported from a wide range of localities and taxa (Hewitt 1988). These may provide important insights into the processes that lead to full speciation from diverging sympatric genotypes or to convergence (introgression) following the breakdown of barriers between allopatric taxa.

Several patterns of fitness between hybrid and parental genotypes can be distinguished including equal fitness, one homozygote fitter than the others, heterozygote (hybrid) disadvantage, positive frequency dependence for homozygotes and hybrid advantage (Hewitt 1988). When one of the genotypes has an advantage over the others this tends to spread through the hybrid zone (Barton & Hewitt 1985). This is a feature of particular interest in understanding the potential instability of some zones and the speed of speciation or introgression. However, due to the rapid rates of gene flow that tend to occur in such situations there are relatively few reported examples of moving hybrid zones (Gill 1980; Hewitt 1988; Hillis & Simmons 1986; McDonnell, Gartside & Littlejohn 1978; Picozzi 1976; Yang & Sealander 1968). The study presented below describes one such case of a moving zone. This hybrid zone between two land snail species is unusual in that its composition was studied at regular intervals between its discovery in 1986 and the complete extinction of one of the parent taxa in 1994.

A hybrid zone occurs between species of the *Pachnodus* genus of land-snail (Mollusca; Gastropoda; Enidae) on the island of Mahé, Seychelles. These snails are largely arboreal (Gerlach 1991, 1994) and, unlike all other hybridizing snail species studied, have relatively high dispersal rates. Published studies of hybridization patterns in snails usually concern highly sedentary genera such as *Albinaria* (Shilthuisen 1995; Schilthuisen & Lombaerts 1995), *Cerion* (Gould & Woodruff 1986; Woodruff 1981) and *Partula* (Johnson, Clarke & Murray 1990; Johnson, Murray & Clarke 1993) where annual dispersal is in the region of only 3m (Murray & Clarke 1984). In contrast *Pachnodus* species may move some 220m annually (Gerlach 1994a). This relatively high dispersal rate raises the possibility

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of detectable dynamic movement of the hybrid zone as the small-scale environmental clines that restrict the *Albinaria*, *Cerion* and *Partula* hybrid zones can easily be crossed by *Pachnodus*.

The presence of a hybrid zone within the distribution of *Pachnodus* was first identified in 1986; since then it has been investigated on an annual basis. In 1994 it was discovered that one of the parent taxa had become extinct following a shift in the location of the hybrid zone. The pattern of movement of the zone observed between 1986 and 1994 is described below.

Identity of the hybrid taxon

The hybrid form *Pachnodus (Pachnodus) niger*×*velutinus* was described in 1994 (Gerlach 1994b) on the basis of shell and anatomical characters being intermediate between *P. niger* (Dufo, 1840) and *P. velutinus* (Pfeiffer, 1841). In this description the intermediate morphology was considered to be the result of hybridization between *P. niger* and *P. velutinus*, although evidence for the hybrid origin was not presented. The intermediate morphology could have arisen from hybridization, as suggested, or from incomplete separation of speciating taxa. The geographical distribution of characters allows these possibilities to be distinguished. Incomplete speciation would be expected to be characterised by clinal distributions of characters whereas hybridization could produce an apparently random distribution of intermediate characters. Mantle colouration does appear to follow a clinal pattern with pale forms being found in areas surrounding the range of the pale *P. vultinus*, however, there is no similar increase in the intensity of black pigment near the range of *P. niger*. Anatomical characters are constant and represent a combination of *P. niger* and *P. velutinus* states with no intergradation between them. The only variable character is the number of lateral radular teeth which cover the range of 188-192 as opposed to the constant 220 in *P. velutinus* and 181 in *P. niger* (Gerlach 1994b). The number of teeth does not fit any detectable pattern of geographical distribution with the full range being found in all populations. This lack of evidence of clinal patterns supports hybrid origin of the intermediate taxon.

The origin of this taxon was further investigated by obtaining laboratory crosses between individuals of different populations. Pairs of the three taxa were maintained at 20°C and 90% humidity. In all cases wild-collected juvenile snails were used in the crosses to eliminate the possibility of sperm storage producing misleading results. All three taxa bred true. In the intermediate taxon the number of lateral radular teeth remained variable with no significant correlation between parental and offspring radular formulae. Offspring shell colour was indistinguishable from that of the darkest parent. Crosses between the taxa consistently produced the morphology of the intermediate taxon with the characteristic reproductive anatomical structures (Gerlach 1994b), the full range of radular formulae and the dominance of the darker colouration. All of these data

are congruent with a hybrid origin, supporting the classification of the intermediate taxon as the hybrid *Pachnodus niger* × *velutinus*.

Numbers of offspring produced by various crosses carried out in 1988 and 1989 are shown in Table 1. No significant differences in the mean numbers of eggs or the hatching rate were detected. From these crosses and from dissections of wild-collected snails (Gerlach 1994b) it was concluded that in 1987 the fully fertile hybrid *P. niger* × *velutinus* was present in an area surrounding *P. velutinus*. (Fig. 1)

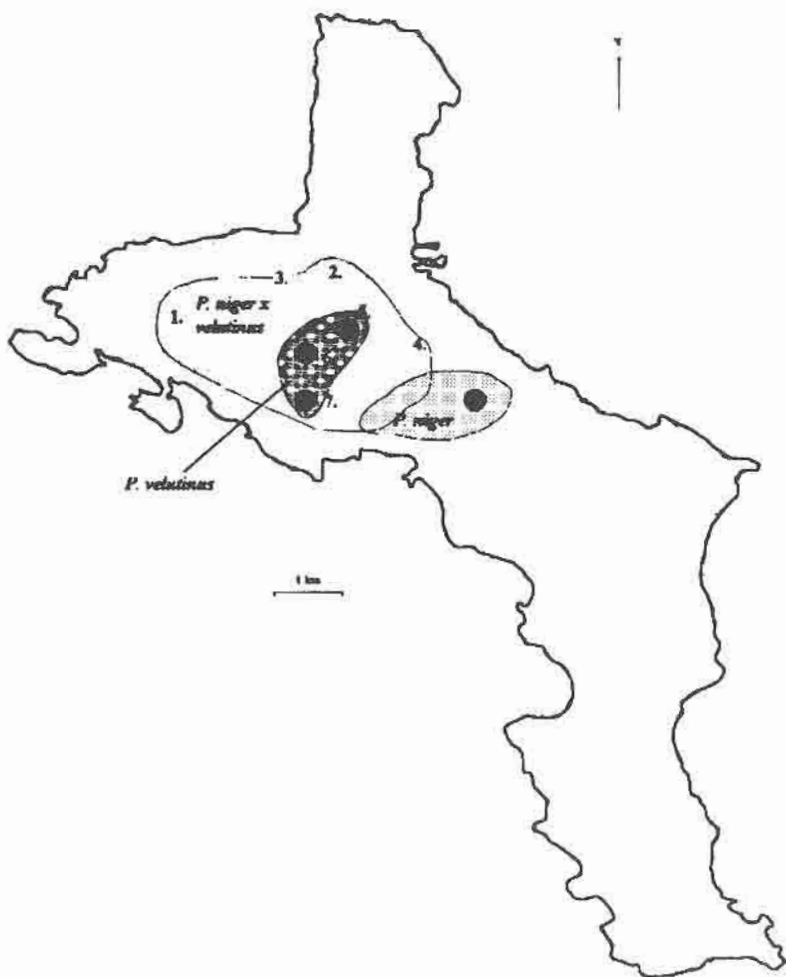


Fig. 1. Ranges of *P. velutinus*, *P. niger* and *P. niger* × *velutinus* in 1972. Scale bar = 1 km. Sites mentioned in the text are numbered.

Table 1. Results of crosses between the taxa (means and standard errors)

Cross	Origin	Number of clutches	Number of eggs	% successful hatchings
<i>P. niger</i>	wild	5	26.6±4.2	92.6±4.0
<i>P. velutinus</i>	wild	5	24.2±1.6	90.6±9.5
<i>P. niger</i> / <i>P. velutinus</i>	wild	6	25.0±3.6	91.3±9.7
<i>P. niger</i> × <i>velutinus</i>	wild	15	24.6±7.8	80.0±23.2
<i>P. niger</i> × <i>velutinus</i>	F ₁ captive	8	20.9±4.8	90.8±8.3

Table 2. Differences between the three taxa

	<i>P. velutinus</i>	<i>P. niger</i>	<i>P. niger</i> × <i>velutinus</i>
Shell thickness (mm)	<0.5	1.0-2.5	0.5-1.5
Rectum colour	banded	white	banded
Number of lateral radula teeth	220	181	188-192
Shell colour	beige	black	variable

History of the *Pachnodus* hybrid zone

The first definite specimens of the hybrid taxon *Pachnodus niger* × *velutinus* were collected on 15th July 1986 (Gerlach 1994b).

Three characters are of particular note in the hybrid form: typically the shell is strong, the rectum (visible through the shell) marked with black and white bands and the radula formula is highly variable. In *P. velutinus* the shell is very poorly calcified and in some specimens no significant inorganic layers underly the fragile periostracum whilst *P. niger* shells are always well calcified (Gerlach 1994b; Van Mol & Coppois 1980). The rectum is clearly banded in black and white in *P. velutinus*, but is white in *P. niger*. The radula formulae are different in *P. velutinus* and *P. niger* but do not exhibit any intraspecific variation. These characters are compared in Table 2. There are also significant differences in reproductive anatomy (Gerlach 1994b). These three characters allow preserved material to be identified and can also be applied to some historical descriptions.

The first record of a probable hybrid dates from 1880 (Möbius, Richters & Martens 1880). A dissection of a specimen of '*Bulimus velutinus*' gives the number of lateral teeth on the radula as 190 which would fit within the range for the hybrid, indicating the occurrence of hybridisation in the 1800s. The large collection of *Pachnodus* in the Musée Royale de l'Afrique Centrale, Tervuren, collected in 1972 (Van Mol & Coppois 1980) does not include any hybrids. This suggests that hybrids were uncommon or localised at that date, however no specimens were collected from the area between the main ranges of *P. niger* and *P. velutinus*. The 1972 ranges of the parent taxa are shown in Fig. 1.

Study methods

During 1987 field studies showed that the hybrid was distributed throughout all suitable areas of damp forest in the north of the island. *P. velutinus* could only be found at Congo Rouge whilst *P. niger* remained in the centre of the island without having suffered any apparent range contraction since 1972.

In order to study the process of range expansion of the hybrid a series of sites were visited during July & December/January of each year. These months are normally the driest and wettest months respectively, thus the data collected cover any seasonality that may be present in distribution patterns. A set route was walked at each site and the number of *Pachnodus* found was recorded. These were recorded as four distinct morphs:

- a. *P. velutinus* - light colour, thin shell, banded rectum
- b. *P. niger* × *velutinus* (light) - light colour, thick shell, banded rectum
- c. *P. niger* × *velutinus* (dark) - dark colour, thick shell, banded rectum
- d. *P. niger* - dark colour, thick shell, pale rectum

The number of visits to each site varied, most effort was concentrated on repeat surveys of Congo Rouge where *P. velutinus* persisted.

The sites examined are listed below and marked on Fig. 1.

1. Mare aux Cochons
2. Trois Frères
3. Le Niol
4. Copolia
5. Morne Seychellois (*P. velutinus* present in 1972)
6. Congo Rouge (*P. velutinus* present in 1972)
7. Morne Blanc (*P. velutinus* present in 1972)

Results

Only dark morphs of *P. niger* × *velutinus* (morph c.) were present at sites 1., 2. and 3. The changes in abundance of each form at the other four sites are recorded in Table 3.

Table 3. Numbers of different morphs at the main field sites

Site	Morph	Year								
		1986	1987	1988	1989	1990	1991	1992	1993	1994
4.	b.	-	-	24	0	0	0	0	-	-
	c.	-	-	14	35	20	4	34	-	-
5.	b.	-	-	-	-	-	1	-	-	-
	c.	-	-	-	-	-	12	-	-	-
6.	a.	-	54	35	35	21	11	6	3	0
	b.	-	26	5	10	10	7	12	6	26
	c.	-	8	2	5	6	6	7	5	6
7.	b.	0	13	17	18	13	0	0	0	-
	c.	8	29	24	36	34	6	44	40	-

The presence of *P. velutinus* at Congo Rouge (Site 7) justifies more detailed consideration of this area. The site is shown in Fig. 2, using the habitat classifications of Gerlach (1993). This area can be divided into 5 sections (labelled on Fig. 2). The data for these 5 sections are given in Table 4.

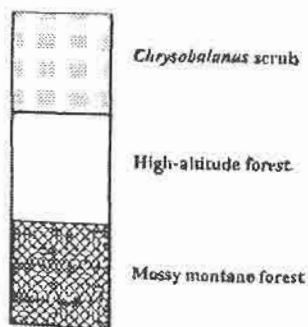
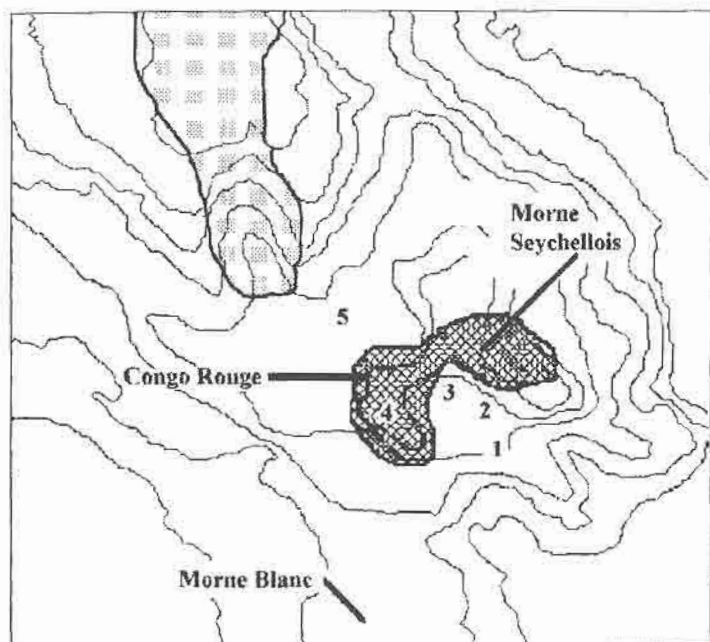


Fig. 2. Habitats and localities at Congo Rouge mentioned in the text.

Table 4. Numbers of different morphs at Congo Rouge

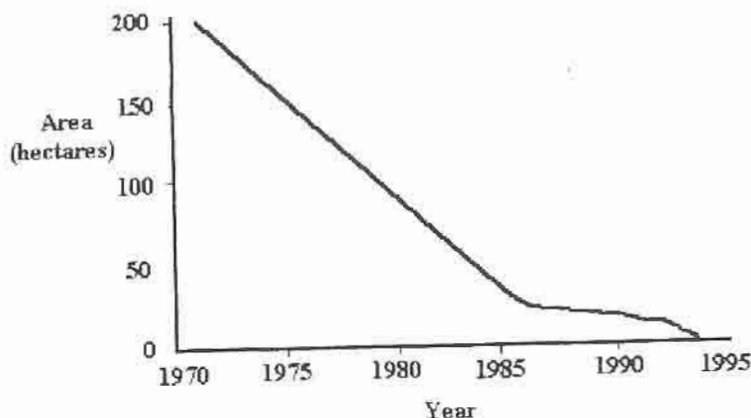
Area	Morph	Year							
		1987	1988	1989	1990	1991	1992	1993	1994
6.1.	a.	1	4	0	0	0	0	0	0
	b.	14	3	7	6	4	3	2	6
	c.	0	0	1	2	2	2	3	3
6.2.	a.	3	15	18	11	2	2	0	0
	b.	0	0	0	0	0	2	2	11
	c.	0	0	0	0	0	0	0	0
6.3.	a.	10	10	11	9	6	3	2	0
	b.	0	0	0	0	0	4	1	3
	c.	0	0	1	1	2	1	1	1
6.4.	a.	5	6	6	1	3	1	1	0
	b.	12	2	3	4	3	3	1	6
	c.	0	0	0	1	0	0	0	0
6.5.	a.	0	0	0	0	0	0	0	0
	b.	0	0	0	0	0	0	0	0
	c.	8	2	3	2	2	4	1	2

Discussion

As can be seen from these data the invasion of the area by *P. niger* × *velutinus* was relatively slow with considerable spatial and temporal overlap of this taxon and *P. velutinus*. The gradual decline of *P. velutinus* is concordant with the pattern that would be expected to result from genetic drift through non-assortative mating. The last individuals of *P. velutinus* were observed in the moist forest habitat of Site 6c. when they were coexisting with *P. niger* × *velutinus*.

The field data presented above demonstrate that since 1972 *P. niger* × *velutinus* has undergone a significant range expansion. By 1987 the hybrid was present in all low and mid-altitude forested areas in the north of the island. Invasion of the high forest appears to have been slower and in 1987 at least some of the hybrids occupying the high forest of Copolia, Morne Blanc, Trois Frères and Morne Seychellois retained the light colouration of the *P. velutinus* parent (morph b.). At this time this parent taxon was restricted to the mist forest area of Congo Rouge where it was present in some 23 hectares (the dampest and most climatically stable area of the island). By 1989 the pale colouration of *P. velutinus* had disappeared from the hybrid population which were now externally indistinguishable from *P. niger* (although they remained distinct in terms of their reproductive morphology). Over the years the range of *P. velutinus* has contracted (the change in the estimated area is shown in Fig. 3.) until by July 1994 no pure *P. velutinus* could be located.

Fig. 3. Range contraction of *P. velutinus* since 1972



This process of range contraction leading to extinction has a primary cause in the expansion of the hybrid. Possible explanations for this rapid extinction process lie in the nature of this particular hybridisation process and that of the hybrid zone. From the data in Table 2, it is clear that the hybrid taxon is fully fertile and suffers no hybrid disadvantage in terms of reproductive success. This would allow it to spread into the parent population in the absence of any selective disadvantage. For the zone to remain stable a degree of selection against the hybrid would be required. This can be calculated as

$$W^2 = (2.08L)^2 / S$$

where W = width, L = mean dispersal rate, S = selection against hybrids (Endler 1977). This assumes no assortative mating and equal selection against all hybrids. For *P. niger* × *velutinus* the stable hybrid zone must have been approximately 2 km wide. The mean dispersal rate is 0.22 ± 0.02 km per year (Gerlach unpublished data) giving $S = 0.05$. This low level of selection means that the stability of the zone could easily be disrupted by relatively minor changes in the level of selection caused by environmental fluctuations.

If the hybrid zone between *P. niger* and *P. velutinus* is assumed to have been stable prior to the anatomical studies reported above (including that of Mobius *et al.* 1880) then a process of slow genetic drift could be postulated as occurring over a narrow hybrid zone of approximately 2 km. The rapid range contraction since 1972 (on average some 9 hectares annually, with an initial peak of 18 hectares) requires that there be a significant element of hybrid advantage at

this time. There are three main morphological differences between the hybrids and *P. velutinus* from which to account for such an advantage: reproductive tract anatomy, radula variability and increased shell thickness. Given that there is no obvious reproductive advantage in the hybrid form (Table 2.) the first character is of uncertain value. The radula would have a selective value were it not for the variability in the hybrid form; variation would allow the taxon as a whole to exploit minor differences in food resources but this would be more likely to lead to specialisation into a number of radula morphs than to continuous variation. This leaves the shell which has two obvious functions. Firstly it acts as a protection device; given that *P. velutinus* survived in considerable numbers between 1836-1972 (Dufo 1840; Van Mol & Coppois 1980) the thin shell cannot have been a major disadvantage. The second function would be to reduce water loss by sealing off the upper body surface. This may provide the key to the problem. When humidity levels drop below 70% most *Pachnodus* species enter aestivation (pers. obs.). This is not achieved by the formation of a complete epiphragm but rather by the secretion of a partial seal around the edge of the aperture and the substrate. The substrate must be a reasonably flat surface and accordingly in seasonally dry areas characteristic double hemispheres (formed by the two sides of the divided sole of the *Pachnodus* foot) of thick dry mucus can be found on the fronds of the birds nest fern *Asplenium nidus* L.. This aestivation behaviour was observed in captivity in adults of all taxa, except *P. velutinus*. In *P. velutinus* survival required a humidity constantly in excess of 80%, below this they rapidly desiccated and died.

Considerable changes have occurred in the forests of Mahé. Although forest cover is largely complete at present, this is almost entirely secondary. Within the historic range of *P. velutinus* extensive areas were cleared for tea and timber plantations in the 1960s (Piggott 1968; Sauer 1967). This change in forest distribution and structure would be expected to have had some effect on the local climate of the surrounding forest. It may be that the probable decrease in humidity of the partially cleared mid-altitude forest may have resulted in *P. niger* × *velutinus* having a selective advantage over the thin shelled, desiccation prone *P. velutinus*. With such an advantage the spread of *P. niger* × *velutinus* into the low and mid-altitude range of *P. velutinus* would be expected. In the higher areas where the humidity rarely falls below 95% the selective advantage would be absent but the large source population of *P. niger* × *velutinus* surrounding the *P. velutinus* remnant would lead to genetic swamping through random mating patterns. The reduced rate of range contraction in 1987-93 corresponds to this switch from hybrid advantage to genetic swamping.

The above hypothetical process of selective advantage and random drift would lead to the observed pattern of apparently rapid invasion of low to mid-altitudes and a slowing of the rate of invasion as shown in Fig 3. The hybrid form would have no advantage over the *P. niger* parent which was the original source of

the low desiccation tolerance and thus the hybrid zone would remain stable at its southern edge.

This event is one of the few cases where an extinction process has been followed to its conclusion. It is also one of the few observed cases where the process, hybridisation, has been largely natural although habitat disturbance may have speeded up the event. There have been no previously reported cases of hybrid advantage resulting in the total extinction of one parent species. Reports of moving zones refer either to hybrid disadvantage as in birds (Moore & Buchanan 1985; Yang & Selander 1968) and frogs (McDonnell *et al.* 1978) or to hybridization occurring in connection with other, more important, demographic influences such as major habitat change or competition (Gill 1980; Moore & Koenig 1986; Picozzi 1976; Short 1969). The hybrid zone reported above demonstrates that hybrid superiority is possible and can lead to extinction of at least one of the parental taxa. Furthermore a zone developing as a result of secondary contact may remain stable indefinitely but can be disrupted by environmental changes; once instability develops, the process of expansion of the zone and extinction of parental taxa may be extremely rapid.

Three explanations have been proposed to account for the persistence of hybrid zones following secondary contact. These are the ephemeral zone hypothesis, the dynamic equilibrium model and the geographically bounded hybrid superiority model. The first of these leads either to speciation (if the parental taxa are sufficiently divergent to result in hybrid unfitness) or to fusion (where the hybrid acts as a bridge for introgressive hybridization). The second results in stability despite selection against the hybrids; under this model a broad contact zone develops. In the hybrid superiority model the hybrid has an advantage in a restricted area which leads to a stable, narrow zone. Of these three the last has been favoured as a general explanation as it is the only model to account for the persistence of narrow, stable zones (Heaney & Timm 1985; Moore 1977). The data presented in this study suggest that a narrow hybrid zone formed as a result of the geographically bounded hybrid superiority model can shift into the ephemeral zone form following environmental change. This means that no single explanation need apply to a hybrid zone throughout its history. Changes in the environment can disrupt the underlying processes such that stable zones may become zones of speciation or of introgression.

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