Review Article　　*"Rodent Biodiversity Human Health and Pest Control in a Changing Environments"*

Rodent Biodiversity in Changing Environments

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ABSTRACT

Organisms adapt and evolve in response to environmental changes. Current changes in the environment occur at a rate and scale that are closer to those of mass extinction rather than of normal, background extinction. The response of species to global changes will depend on their ability to disperse and to acclimatize, as well as on their evolvability. The current view is that the high rate of current environmental changes impedes the evolutionary processes of adaptation to new conditions. Rodents, however, show a high potential to successfully adapt to changing environments over various time scales, including very rapid responses thanks to various characteristics of their life history, traits and plasticity. This paper briefly reviews the processes that allow rodents to respond to the challenges of changing environments, from the instantaneous plastic response to the paleontological perspective of long term evolution. Rodents indeed include very opportunistic and highly evolvable species, which may successfully overcome the ongoing changes, although some specialist species will inevitably be the victim of the adjustment of the communities to the human-driven modification of their environments.
Key words: rodents, community, changing environment, adaptation, evolution

INTRODUCTION

The biosphere faces ongoing global change by variations that are drastic both by their amplitude and rapidity. It raises scientific, societal and political concerns about the ability of the biosphere to respond to this complex cascade of processes, triggered by human activity, modifying landscapes and climate. Organisms, however, have faced changing environments throughout their evolutionary history. If sometimes catastrophic in the case of mass extinction, environmental changes are often a source of diversification and can thus benefit the building and maintenance of biodiversity. What determines the ability of a species, group of organisms, or even individuals, to successfully face a changing environment? The processes involved vary depending on the spatial and temporal scale of the changes. This paper provides a brief review of such processes, with a focus on rodents and the background question: how will the current rodent biodiversity face ongoing environmental changes?

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Rodents constitute a group of high interest in this context: they represent the most diverse order of mammals, with approximately 2000 species including nearly half of the mammalian species. The specific richness of this order results from a succession of radiations and shows the potential of adaptation and diversification in this group. In the context of human-driven environmental changes, rodents are notable for the number of species that have successfully adapted to anthropic habitats. For example, the house mouse (*Mus musculus*) and the black and water rats (*Rattus rattus* and *Rattus norvegicus*), have gained a world-wide distribution because of their association with humans. However, there are also species with a more restricted range, such as: the wood mouse *Apodemus sylvaticus* in Europe; the multimammate rats *Mastomys* in Africa; the bandicoot rats *Bandicota* in southeast Asia; and the rat *Niviventer* in China). Due to their successful acclimatization to being in the vicinity of humans and their efficient reproduction, many of these species are a pest for the human populations they influence, either due to deterioration of crops, spoiling of food stocks, or as vectors of various diseases. All these species pinpoint the high adaptive potential of some rodents and their ability to face changing environments even when triggered by human activity.

Rodent populations in changing environments: mechanisms of short-term response

   Adjustment to short-term fluctuation

   Rodents are usually small-bodied animals with a short life span. This is often associated with a relatively "fast" life history. These characteristics enable a rapid population response to short term variation, including seasonal fluctuations in, among others, temperature, humidity conditions and food availability (Vessey and Vessey, 2007).

   Response to this pace of variation mostly relies on behavioural adjustments. In temperate regions, the wood mouse *Apodemus sylvaticus* forages in the open landscape during summer time to exploit the crops, being then territorial, but retracts into forest during winter, sharing common shelters (Butet, 1994). Such short-term tracking of food availability by a change in the home range has been also observed in the African striped mouse *Rhabdomys pumilio* (Schradin and Pillay, 2006).

   These adjustments include a seasonal regulation of reproduction, with food availability and/or quality being one trigger for starting reproduction (Adler and Beatty, 1997; Leirs *et al*., 1994). Hence, behavioural plasticity in reproductive traits allows rodent species to adjust quickly to changing environments (Vessey and Vessey, 2007). In species displaying pluriannual dynamics, such as arvicoline rodents, seasonality of breeding has even been invoked as an important factor conditioning population explosions and subsequent crashes (Tkadlec and Zejda, 1998; Stenseth *et al*., 2003).

   Adjustment to instantaneous conditions may also occur in response to predation, as shown in bank voles suppressing breeding when exposed to cues of predator presence in their environment (Ylönen and Ronkainen, 1994).

   These cases exemplify the potential for an adjustment of life-history traits and behaviour allowing rodents to face changing environments. Yet, seasonality and predation are somehow for rodents a predictable component, since they have been exposed to these factors throughout their evolutionary history. The mechanisms of response to unpredictable changes may be different and their ability to adjust to new environments not as efficient.

   Acclimatization to new environments

   Murine rodents include Old World mice and rats. Their diversity is maximal in the tropical areas of Africa and especially Asia (Misonne, 1969). This pattern exemplifies their preference

for warm environments in contrast to arvicoline rodents. Yet the house mouse managed a successful adaptation in developing permanent feral populations on at least eight sub-Antarctic Islands (Berry *et al.*, 1978). Experiments on artificial selection for cold tolerance confirmed that adaptation to such conditions close to their physiological limits might achieve measurable results in about 10 generations, with heavier and fatter mice and more concentrated milk (Barnett and Dickson, 1989).

Arid environments are equally demanding in terms of metabolic requirements, and water-availability can vary dramatically within the distribution area of a species. This can lead to adaptive differences in the energetic strategy, as exemplified by house mice on Porto Santo Island (Mathias *et al.*, 2004). In order to understand the process underlying the adjustment to changes in the desiccating potential of the environment, a common desert rodent *Dipodomys* was cross-bred under either desiccating or water-abundant conditions (Tracy and Walsberg, 2001). The experience showed that developmental plasticity and acclimatization completely accounted for the existing intraspecific variability in desiccation resistance.

Such processes of phenotypic plasticity can operate quickly and therefore attenuate the action of an apparently drastic natural selection and contribute to the success of rodents in changing environments.

Stress and its estimation in wild populations

Despite this potential for acclimatization, some environmental conditions are less favourable than others to rodents, despite the fact that they may manage to survive. Partly because of societal anxiety and political concern, human-driven changes are often interpreted as potentially detrimental to wild species. Is this really the case? The problem is then to identify which conditions are really harmful.

Unfavourable conditions are often detected by an examination of life history traits, e.g. home range, size of the offspring and survival. Comparing such traits, one environment can appear to be less adequate for a rodent species than another, e.g. sand dunes compared with woodlands for the wood mouse *Apodemus sylvaticus* (Attuquayefio *et al.*, 1986).

Such an approach, however, does not reveal whether any adjustment to the environment concerned was efficient or not. Phenotypic traits can then be relevant indicators of poor living conditions. Developmental errors are likely to occur in stressful conditions, being either of genetic or environmental origin and a quantification of the level of perturbation would provide a measure of stress. Both sides of a symmetrically bilateral organism are supposed to be coded by the same genotype. Accordingly, a standard phenotype should express the perfect symmetry. Unless they are genetically determined, e.g. internal organs, any difference arising between the right and left sides of these organisms might be interpreted as a developmental perturbation inappropriately corrected. This kind of asymmetry, the so-called fluctuating asymmetry (FA), thus indicates a developmental instability (DI). Though the underlying mechanisms have been poorly identified, studies using FA have developed considerably over the past two decades.

Practically, appraising FA on a single metric trait consists of estimating the variance of the left-minus-right distribution in a population. Considering rodents, skull and teeth traits are often used to evaluate DI. While several methods exist to compile a global index of FA for several metric or meristic characters, the advent of geometric morphometrics allows an appraisal of the global asymmetry in a complex structure such as the skull or mandible (Auffray *et al.*, 1996; 1999a; Klingenberg *et al.*, 1998).

Several examples of developmental instability in natural populations of rodents due to

environmental changes are found in the literature. Using a synthetic index of FA, the populations of voles (*Apodemus sylvaticus*) have been shown to present higher levels of FA when they were closely located to Chernobyl (Ukraine). Obviously, in this case, radiation subsequent to the reactor accident at the nuclear power plant was supposed to have had a direct effect on the development of the animals (Oletsky *et al*., 2004). Populations of bank voles (*Clethrionomys glareolus*) presented higher levels of FA in a disturbed environment (extensive agriculture) when compared to traditional agricultural fields in northern France (Marchand *et al*., 2003). In that case, the fragmentation of habitat may have had several indirect consequences on rodent populations by restraining available resources, reducing the effective population size and favouring inbreeding. In Portugal, Mediterranean mice (*Mus spretus*) exhibited a higher level of FA in a polluted area (heavy metal soils around copper mines) than in control locations (Nunes *et al*., 2001). Rats and mice, as laboratory animals, were often used for testing potential environmental stressors in controlled conditions (for a review, see Hoffman and Parsons, 1991).

If FA may provide an interesting signal on the suitability of habitat, it may also fail to provide a reliable indication on the origin of disturbance. A study on mole rats (*Spalax ehrenbergi*) in Israel has considered several populations and numerous features related to these natural populations or their habitat: geographic and climatic variables, soil type, genetic features (karyotypes, heterozygosity, genetic diversity) and parasitic load. A general trend of increasing FA together with altitude and indurate soil was observed. However, the fact that environmental and genetic variables are highly covariant renders it difficult to disentangle the origins of developmental instability (Auffray *et al*., 1999b).

Mid-term response to changing environments: adaptation and adjustment of the communities
Building of gradients

Many of the previous cases have shown the potential for short-term acclimatization of rodents. This has allowed them to have a rapid response to changing environments; yet the amplitude of the response is limited by the potential of developmental plasticity and acclimatization. In the long run, natural selection should act to fix some traits involved in adaptation to the new conditions. Fine-tuning of adaptation is partly counteracted by gene-flow from surroundings environments (Lenormand, 2002). Despite this buffering effect, adaptation to local conditions can build if selection is strong enough. Such a clinal variation in metabolic characteristics is exemplified by cold adaptation in the house mouse *Mus musculus domesticus* (Lynch, 1992). Yet, at this scale, adaptation can concern phenotypic characteristics other than those varying with plasticity and acclimatization. Clinal environmental variations often include a series of physical factors that in turn cause variations in vegetation and hence, of the food available. This will select traits associated with nutrition, including skeletal and dental characters such as mandible and teeth. Phenotypic expression of patterns of clinal selection has thus been observed in various rodents (Fadda and Corti, 2001; Duarte *et al*., 2000). The establishment of such gradients can be quite rapid on an evolutionary time scale. An example of this is the latitudinal gradient in the mandible and molar shape observed through western Europe in the wood mouse *Apodemus sylvaticus,* built up since the end of the last glacial maximum, when the species migrated northward from refugia to re-colonize deglaciated areas (Renaud and Michaux, 2007).

Changing climate triggering diversification: vicariance and refugia

Species do not always have to adapt in order to respond to changing environment. The

simplest way to cope with environmental changes is often to track the same habitat by shifting their area of distribution. In this case, no special metabolic or phenotypic adaptation will occur, but one species can be split into several separate isolates that will diverge progressively in the prolonged absence of gene flow.

The glacial cycles that have characterized the Earth's history since the Pleistocene, caused many such fragmentations within species and may hence be viewed as a stimulating factor of diversification. Widespread glaciers durably hindered exchanges among wood mice populations from both sides of the Alps, leading to the significant differentiation of northwestern and Italo-balkanic clades within *Apodemus sylvaticus* (Michaux *et al.*, 2003). In the same way, the bank vole *Clethrionomys glareolus* (Deffontaine *et al.*, 2005; Kotlik *et al.*, 2006) or the east Mediterranean mouse *Mus macedonicus* (Orth *et al.*, 2002) repeatedly retracted into various refugia during glacial cycles, leading to the differentiation of geographic lineages.

Such processes are not exclusive to temperate regions. Sub-tropical environments were also affected by the glacial cycles, that were expressed there as alternatively arid and more humid phases. Hence, forest and open-field species were alternatively expanding and retracting. Such a process was likely the cause of a morphological differentiation in tooth morphology between central versus eastern Africa in the forest rusty-nosed rat *Oenomys hypoxanthus* (Renaud, 1999). Persistent biogeographic barriers can act over an even-longer time scale, causing differentiation of many species across these boundaries. This was the case with the Dahomey gap in Africa that separates west Africa from the central African forest block. This "gap" corresponds to a zone of lower rainfall between the Volta and the Niger rivers, the rivers themselves acting as a barrier to dispersion for small mammals. The disjunction of forest habitat caused by this gap has led to a

speciation in allopatry in several rodent species, e.g. *Oenomys* (Renaud, 1999), the African wood mouse, *Hylomyscus* (Nicolas *et al.*, 2006), and the multimammate rat *Mastomys* (Robbins and Van der Straeten, 1989). Environmental changes may alternatively strengthen or weaken such barriers, favouring speciation or contact between the populations.

Rodents within community: ecological processes, phenotypic expression?

Previous sections provided a brief review of the possible responses of a single species to environmental changes. Yet, any species is part of a small-mammal community that will influence its habits and ability to cope with changes. The coexistence of several rodent species within a community relies on resource partitioning. This is achieved by exploiting various microhabitats within a mosaic landscape (Price, 1978; Decher and Bahian, 1999) and by the differential exploitation of the resources, for example larger rodents consuming larger seeds (Brown and Lieberman, 1973). Further aspects of habitat use can contribute to segregation among species, such as vertical segregation (Sekijima and Soné, 1994) or temporal heterogeneity (Ben-Natan *et al.*, 2004).

Hence, behavioural aspects strongly contribute to this fine-scale resource partitioning. Yet, exploitation of food of a different size or composition can be related to characteristics of the feeding apparatus. Accordingly, rodent species within communities are structured according to the size or shape of teeth (Millien-Parra and Loreau, 2000; Dayan and Simberloff, 1994), showing that resource partitioning has a phenotypic expression.

Changing environments affect the distribution of microhabitats and hence, the composition of the rodent community. The effect of changing productivity is obvious - less productive habitats cannot support as many species as richer ones (Brown and Lieberman, 1973). Yet,

changing environments may also act on rodent communities by modifying the structure of landscapes. The equilibrium model of island biogeography (MacArthur and Wilson, 1963) predicted a relationship between the number of species and the area of an island. Progressive impoverishment would not be random but would result in assemblages of fewer species as a subset of the species present in richer communities, according to their efficiency in sharing resources. The island theory can be applied to many continental contexts, habitat fragmentation leading to "island-like" patches of a given habitat. Indeed, the composition in desert rodent assemblages has shown the predicted nested pattern in species composition (Patterson and Brown, 1991).

A well-known case of such "island-like" structure combined with an impact of climate change is displayed by the rodent community of the Great Basin of western North-America, where island-like mountain ranges are surrounded by "seas" of desert shrublands. These habitat islands are the remnants of a former contiguous network of mountain habitats fragmented by Holocene climate warming. This resulted in a progressive impoverishment of the fauna in the relict patches (Brown, 1971).

Long-term evolution in changing environments

Competition among species, resource partitioning and adjustment to the local environment occur in a reduced time and space scale. In contrast, radiation and evolutionary trends document long-term outputs. Can similar processes be identified at different time scales as determinants of biodiversity in rodents?

Within rodents, the subfamily Murinae exemplifies one episode of diversification originating 12-14 Myrs ago and leading today to approximately 120 genera and 550 species in Europe, southeast Asia, Australia and Africa (Wilson and Reader, 2005). This radiation includes diversification according to numerous aspects of

the ecology, including diet (in most cases omnivorous but also herbivorous, insectivorous, worm eaters and seedeaters) and life habits (cursorial, arboreal, burrowing, amphibious, richochetal). This diversity in diet and life habits has a phenotypic expression in the diversity of the mandible shape, with convergent shape for omnivorous versus herbivorous rodents (Michaux *et al.*, 2007). Confronting molecular and morphological evolutionary rates provides further evidence that within omnivorous generalist rodents, differences in mandible shape accumulated slowly and progressively with time. In contrast, the occurrence of an ecological specialization triggered an acceleration of morphological evolution and a departure from a phenotypic drift pattern (Renaud and Michaux, 2007). Hence, both phylogenetic history and ecological strategy appear crucial in determining the patterns of diversification.

The temporal dynamics of such a diversification can be observed in fossil lineages. The interpretation of morphological changes in terms of phylogeny and ecology is then crucial, since only morphological remains can be found in paleontological deposits, and especially the small but resistant teeth in the case of the rodents. Molar teeth are known as good phylogenetic markers (Misonne, 1969), but their shape is also related to diet in modern rodents, allowing inference of the ecology of past taxa based on their fossil remains (Renaud *et al.*, 2005).

A survey of Mio-Pleistocene murine rodents in southwestern Europe pointed out first, the importance of changing environment in opening new niches and allowing diversification. During this period, a trend of decreasing temperature led to the opening of an initially-forested landscape. Starting from a generalist ancestor associated with forest habits, the increase of grassland allowed evolution towards grass-eating exhibited by *Stephanomys*, a rodent with a particular dental morphology interpreted as an

adaptation to herbivory (Renaud *et al*., 2005). In the same deposits, however, the lineage leading to the modern wood mouse *Apodemus* displays a rather stable dental morphology, suggesting few ecological changes throughout the 10 Myr record. The discrepancies in the evolutionary trends as a result of the same environmental change suggest that one rodent colonized grass fields which represented new habitats related to global cooling, while the other tracked its original habitat that remained present as forest patches in a mosaic landscape.

In this case, changing environment is a key factor in triggering evolution, but the response of the rodents is still conditioned by the ecological strategy adopted. This latter aspect was likely related to interspecific interactions. In fossil deposit, segregation in size and/or shape of the tooth morphology between the different species (Renaud, 1999) provides evidence of resource partitioning similar to what has been observed in modern communities (Dayan and Simberloff, 1994; Ledevin, 2007).

Rodents and the ongoing human-driven changes

Previous examples show evidence of a high adaptive potential in some rodents to face changing and new environments. The two lineages of fossil rodents, however, exemplify that the ecological strategy may condition the long-term success: while the generalist wood mouse is still flourishing today, the specialist *Stephanomys* was not able to cope with the highly variable Pleistocene climate and became extinct around 1.8 Myrs ago (Renaud *et al*., 2005). In a similar way, opportunist species like the house mouse and rats are evidently successful in disturbed or anthropic habitats, but other species might be less successful in coping with the range of perturbation occurring due to human activity.

Endemic rodents on islands illustrate such a negative impact of human activity and related changes on wild fauna (Amori and Clout, 2003). Many of these endemic rodents disappeared during archeological or modern times on islands. Among others *Microtus* (*Thyrrenicola) henseli* and *Rhagomys orthodon* on Sardinia and Corsica became extinct during Roman times, presumably due to the progressive introduction of alien species that started at the beginning of the Neolithic period (Vigne, 1992). *Malpaisomys* and *Canariomys* became extinct on the Canary Islands, probably due to several factors: alien predator species like dogs; competition with the introduced house mouse, *Mus musculus;* and possibly introduced parasites or diseases (Michaux *et al*., 1996). It is noteworthy, that one of the few endemic rodents to have successfully faced human arrival with its cortege of changes is the Cyprus mouse, *Mus cypriacus* (Cucchi *et al*., 2006). Phenotypically close to continental mice, it likely displays similar adaptability and proved competitively superior in its local environment on Cyprus to the invading house mouse.

One might argue that insular rodents evolved into a context characterized by a release in interspecific competition and predation, making them especially sensitive to the arrival of human-related fauna. Changes in the landscape due to agricultural practices are nevertheless recognised as having strongly affected rodent communities, directly changing the available resources, fragmenting the suitable habitat, or affecting the distribution of the predators (e.g. Delattre *et al*., 1999; Hansson, 1999). Traditional agricultural practices may contribute to a high local diversity by maintaining a variety of resources (Decher and Bahian, 1999), whereas more intensive human impact may favour invasive species. Investigation of a rodent community close to the city of Boulder, Colorado found that suburban landscapes had a negative effect on the abundance of native rodents, whereas the house mouse was not affected (Bock *et al*., 2002)

Predicting the evolutionary output of the

ongoing global change on rodent communities would require too much complex modelling coupled to detailed field observations. Some conclusions emerge, however: rodents are probably on the whole highly adaptable and prone to adjust rapidly to new environments. For sure, some species will successfully cope with human-driven changes as they have up until now. This process, however, may select for some opportunistic species showing adequate life-history traits to the detriment of more specialist species.

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