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Chapter 3

Human-faunal interactions as drivers of phenotypic change in Southeast Asia

Samuel Ginot¹, Sirikorn Sripho², Thongchai Ngarmprasertwong³,
and Julien Claude^{1,3}

¹ Université de Montpellier, Institut des Sciences de l'Evolution de Montpellier (UMR5554), Montpellier, France

² Biology Program, Faculty of Science and Technology, Loei Rajabhat University, Loei, Thailand

³ Department of Biology, Faculty of Sciences, Chulalongkorn University, Bangkok, Thailand

Summary

Biodiversity is not just the number of species but one of its major aspects is the observable (or phenotypic) diversity of forms, present within and between species. This relates to biological evolution, natural selection, ecosystem functions and services, and conservation.

However important it may be, phenotypic diversity is still underlooked in conservation policies, or in models of biodiversity response to anthropogenic changes. Simply put, we still have no comprehensive idea of how phenotypic diversity interacts with human impacts. In the biodiversity hotspot of Southeast Asia, where drastic changes are ongoing, as in other tropical and economically growing areas, this gap is particularly visible and damageable. Indeed, booming cities and crops can be expected to cause major disruptions in diversity, both taxonomic (number of species) and phenotypic. The latter relates directly to the collapse of ecosystemic functions and services in anthropized areas, and should therefore be a priority at all levels: political, educational and scientific. On the other hand, it also relates to the rapid capacity of some organisms to adapt to human driven change, and these adaptations themselves can become a problem for the well-being of human societies, as well adapted organisms in that commensal context might generate new risks (e.g., pathogens) to human health and economy.

Here, we synthesize the standing knowledge of the influence of anthropogenic changes on phenotypic (morphological) diversity in vertebrates. With that in mind, we present a case study of five rodent species of different ecologies in Southeast Asia, with populations living in areas

more or less affected by anthropization. We show some examples in which the morphology of these animals is correlated with human land use. We also show that, within populations, species adapted to living with humans have less morphological diversity than other species, probably because they tend to disperse less.

These examples show that anthropo-ecosystems can modify the morphological traits and ecology of wildlife, and that middle or long-term monitoring of population traits is necessary to identify evolutionary responses to anthropic changes. The examples show that one can also take advantage of spatial heterogeneity in terms of environmental degradation to produce forecast models. We believe this should be generalized, as it is a great opportunity not only to solve fundamental questions related to evolution, but also to learn how the biosphere will change and adapt with the rapid environmental modifications of the Anthropocene. This is especially urgent in Southeast Asia due to its high biodiversity and fast anthropic changes.

Keywords: Agriculture, Morphology, Rodents, Urbanization

3.1 General context

Biodiversity is not limited to the number of species, but has many aspects, all of which are impacted and disrupted by human activities. An important but underestimated aspect is phenotypic diversity (sometimes known as disparity; Hunt and Rabosky, 2014, Villegger, 2008, Wills, 2001). The phenotype, in its broad definition, encompasses more or less conspicuous 'observable' aspects (characters or traits) of individuals: their morphology, behaviour, life history traits, performance traits, etc. (Violle et al., 2007, 2012; Villetiger et al., 2011). Phenotypic diversity should be of utmost interest to anyone keen on biology and conservation because it is linked with i) ecosystem functions and their services to humans (Jung et al., 2014; Norberg et al. 2001), ii) natural and artificial selection, which act directly on individual phenotypes, producing adaptation (Violle et al., 2007, 2012; Villetiger et al. 2011), and therefore iii) the resilience of populations facing changes, via adaptive or plastic responses (Hoffman and Sgro, 2011, Jung et al., 2014; Moran and Alexander, 2014). When phenotypic responses are insufficient, extinctions can happen, with the potential consequent collapse of ecosystems. Phenotype also has a great importance in terms of conservation simply by the aesthetic appeal of the diverse forms of living organisms to the public. Phenotypic diversity and how it will respond to environmental changes is therefore a key to our understanding of ecosystems evolution in the Anthropocene. Variation in phenotype is present at all scales from individuals to species, and should be included in any study aiming at understanding evolutionary responses (Jung et al., 2014; Moran et al., 2015). Although taxonomic diversity has proven useful in revealing the current

biodiversity crisis, it directly depends on the definition of the species concept, which is not the case for phenotypic diversity (Purvis and Hector, 2000). Some authors have suggested that specific diversity or biodiversity in general matters only because of its underlying phenotypic variation, which can relate to a function in the ecosystem (Loreau, 2000). It is past time we truly integrate the phenotype in global change biology. Finally the phenotype of organisms can also be used as an alarm when animal or plant populations are undergoing genetic or environmental stresses. In that case, normal development can be altered and new or extreme phenotypes can arise. Monitoring levels of phenotypic variability can reveal these stresses as some other morphological parameters such as fluctuating asymmetry level (Leung et al., 2001).

Main problems. Evolutionary biologists and ecologists alike have been aware of the importance of phenotypic diversity in the context of anthropization for decades, starting at least with Darwin's observation the appearance of melanic peppered moths in industrial areas (Majerus, 2008). Despite the ever increasing anthropic pressures, species' phenotypes remain understudied and under utilized in models (Hendry et al., 2008; Hoffman and Sgro, 2011; Moran and Alexander, 2014; Moran et al., 2015). This gap is especially wide for vertebrates and in tropical emergent and developing countries. The few examples to date in vertebrates are mostly found in occidental countries in long-urbanized contexts (BOX 1, Badyaev et al., 2008; Cox et al., 2020; Kern and Langerhans, 2018; Pergams and Lacy, 2007; Puckett et al., 2020; Snell-Rood and Wick, 2013; Tomassini et al., 2014; Yu et al., 2017). Other groups, notably plants and insects, have been more thoroughly studied, with several examples of positive responses of populations anthropized habitats, such as Darwin's melanic peppered moths (Francis and Chadwick, 2011). It is very damageable that not much is known for emergent countries such as those of Southeast Asia, especially considering that vertebrates are generally very vulnerable in their original habitats (habitat destruction, hunting, poaching), while at the same time being conspicuous members of the communities (Sodhi et al., 2004). On the economic side, it is also of prime importance to anticipate adaptative change as these changes might disrupt relationships in ecosystems, potentially generating new risks for humans. For instance: zoonotic risk, predation on human resources either directly from the top of the trophic chain for carnivores, or competition for resources produced by agrosystems with the adaptation of organisms to crops and food chain productions.

Solutions. To fill this gap in our knowledge, and to understand its implications for the conservation of species, two main types of studies can be put in place (Hendry et al., 2008). Allochronic studies, which follow and measure populations' responses and changes through time are very appealing and generally produce results of great quality. However, by nature, they require important efforts to obtain data and their duration (several years or decades) may not be affordable in the timeframe of anthropic changes and

BOX 1. Vertebrate phenotypic changes in anthropized environments (occidental countries).

In the British Red Squirrel, fragmentation of habitat led to isolation of populations. Cox et al. (2020) detected morpho-functional variation in the mandible of these isolated populations, with one of them particularly distinct from others. The diet of this particular population is notably supplemented with peanuts given by humans, which Cox et al. (2020) suggest could explain the change in mandible morphology and bite force.

In North Carolina streams, Kern and Langerhans (2018) found that two species of fishes had modified morphologies in urbanized vs. rural streams. Both species responded in opposite directions, but isolated populations (distinct streams) of each species showed parallel responses. Furthermore the changes were shown to be genetically determined, suggesting adaptation rather than plasticity as an explanation.

In Minnesota, Snell-Rood and Wick (2013) showed some tendency for urban populations of mammals to have greater cranial capacity than rural populations, although this was not true for all species they studied. They also showed that in some rural populations, cranial capacity tended to increase with time (since the 1940s), possibly due to increase anthropic effects in rural settings. These authors link this cranial change with cognition and behavioural plasticity, which may be selected for due to the novelty of anthropogenic environments.

Pipistrelle bats in Italy were shown to have increased in skull size after 1950 (Tomassini et al., 2013). This change was related to the concomitant increase of public lighting. Street lamps allowed the bats to catch larger preys by attracting moths and reducing their response to predators. This shift in food size may have driven the change in skull size.

Comparing museum collections and current populations of New York brown rats, Puckett et al. (2020) demonstrated directional selection pressures on craniofacial shape, over the last 120 years, possibly related with changes in available food.

In white-footed mouse from the New York area, Yu et al. (2017) described morphological differences between (sub-)urban and rural populations. Urban and suburban mice notably had shorter tooth rows than rural ones, a morphological characteristic related to the quality of the diet. The authors suggested that rural mice had lower quality diets, which required more chewing, leading to larger tooth rows.

In Arizona, two population of house finches were compared by Badyaev et al. (2008). One of the population was in its native desert habitat, and the other in an urban environment in Tucson. Both sites habitats were separated by 6-10km. The authors demonstrated that available seed hardness was causing divergent selection on the finches' beak morphology. This dietary adaptive change led to modifications of courtship songs between the populations, which in turn participated in the genetic isolation of populations, and maintaining of local adaptation.

Taken together, these studies show that vertebrates can and will adapt to anthropogenic changes, notably urbanization. However, it is still unclear how frequent these evolutionary trends are, and which factors allow them or impede them. Hendry et al. (2008) stated that '... Humans are an important agent driving phenotypic change in contemporary populations', but added that it remained uncertain whether these rapid phenotypic were explained by acceleration, i.e., populations in anthropized environments evolve faster, or by winnowing, i.e., populations that do not evolve fast enough disappear, leaving only fast-evolving ones. Acceleration and winnowing are not exclusive. It is interesting to note from these studies in vertebrates that diet-related changes are often reported, which suggests either a bias from researchers, or perhaps that diet is a large selective factor in anthropized habitats.

collapsing ecosystems, especially in fastly developing areas such as Southeast Asia. On the other hand, synchronic studies, comparing contemporaneous populations sharing recent ancestry can also bring understanding on their respective evolutions, without having to follow-up data collection over several years. Furthermore these studies can be completed by the use of museum collections and archeological samples to add a time dimension. Although more indirect than allochronic studies, synchronic studies can bring faster results. In the following section, we present results from one of such studies, showing evolutionary change in rodents living in contact with humans.

Several methods have been developed recently to measure and quantify phenotypic variation. Among these methods, ecologists have done much efforts to produce protocols to measure performance of organisms directly on the field. For instance transducers can now be used to monitor bite force (Aguirre et al. 2002), digital cameras and small experimental design can help to measure other trait performance such as running speed or other parameters (Tan et al., 2020). Other methods take advantage on computer development to measure some phenotypic attribute. For instance coloration patterns can be now analysed in very elaborated ways through computer vision (Lurig et al., 2021). Morphology is probably one of the easiest phenotypic traits to be monitored and large theoretical and mathematical progresses have been devoted to its study. It is at the core of morphometrics and one of its branches: geometric morphometrics. Geometric morphometrics allow the measure of size and shape variation and provide tools to relate morphological variation with ecological and genetic factors. The great advantage of these techniques for monitoring is that they can be quite cheap as just one camera and one computer are required to produce data and analyze it. Furthermore, most softwares devoted to morphometrics are free and available for instance in R (Claude, 2008).

3.2 A case study of morphological changes in Southeast Asian rodents

3.2.1 Introduction

In occidental countries, in which anthropic changes (notably urbanization) have become more mature, some studies show that species' phenotypes have been modified, sometimes to the point of genetic differentiation (BOX 1). Some of these changes appear to be adaptive, while other may be plastic. This study aims to start filling the gap for vertebrates in tropical hotspots, namely Southeast Asia, for which there is almost no study to date, and where strong anthropic changes are ongoing. This study brings preliminary comparative synchronic data for five species of rodents in various localities of continental Southeast Asia (Thailand, Lao PDR, Cambodia). It also aims at local scientists, with the hope that it can bring motivation to sample more thoroughly the region, bringing data that will inform policies in the region, but may also

be of interest globally especially in other economically growing tropical regions where large amounts of biodiversity are threatened. Although data brought in this study will be far from sufficient to built coherent conservation policies, we hope that decision makers may take the opportunity to support and sponsor their local scientific community to tackle this topic.

Southeast Asia is home to a very diverse murid rodent fauna, and likely constitutes the area of origin and diversification for many species (Marshall, 1977; Boonsong and McNeely, 1977; Pagès et al., 2010; Fabre et al., 2013). Rodents are of particular interest in the study of anthropogenic changes. They appear able to evolve and adapt quickly, notably with usage of human productions and waste. They can also colonize and live in human habitats, i.e., commensalism, or tolerate human presence and anthropization of habitats, i.e., synanthropy (Auffray et al., 1988; Brouat et al., 2007; Aplin et al., 2011; Thomson et al., 2014; Hulme-Beaman et al., 2016). In Southeast Asia most environments are anthropized (Sodhi et al., 2004), so most rodent populations can be considered as synanthropic to some extent (as defined in Hulme-Beaman et al., 2016), while some species may be occasionally or fully commensal. Studying phenotypic evolution in this context is of particular interest, since the use of niches made available by anthroposystems produces changes in feeding resources, predator presence, and social behaviours (BOX 1, Hulme-Beaman et al., 2016; Sanchez-Villagra et al., 2016). Here, our goal was to assess the potential anthropic drivers of morphological variation between and within populations of murid rodents in more or less anthropized localities. We compared various species, with different ecological characteristics, in their phenotypic responses.

3.2.2 Study sites and specimens

We studied five southeast asian murine rodents more or less closely associated to humans: *Rattus exulans*, a small commensal rat; *Rattus tanezumi*, a large, opportunistic rat which can thrive around and in urban areas ; *Mus caroli*, a small mouse found in association with flooded rice cultures; *Mus cookii*, a more mountaineous mouse, which is found in sloped agricultural areas; and *Maxomys surifer* a forest-dwelling rat which is less tolerant to human presence and influence on habitats (Morand et al., 2015). Table 1 shows a synthesis of the ecological characteristics of the five species studied here.

Specimens come from a total of 16 localities (Figure 1), from Thailand, Cambodia, Lao PDR, and Vietnam. All localities (spanning about 20km x 20km) are affected by some level of human-mediated changes, including the forested areas, which are secondary forests. Geographical data consisted of GPS coordinates of the capture points, obtained on the field. Around these coordinates, land cover data were obtained from the European Space Agency website (<https://www.esa-landcover-cci.org/>) to quantify the degree of anthropization (urbanization, agriculture) at the localities of capture. A buffer

of 20 km radius was taken on the 2012 global map with the R package raster (Hijmans et al., 2015) and rgdal (Bivand et al., 2015), and the landcover classification was simplified to 4 categories assigned respectively to water, crop, urban area, and forested area. Gross land cover characteristics are shown on Figure 1B.

For this study, we used in total 590 crania, and 593 mandibles of rodents, captured over several years of fieldwork across continental Southeast Asia in the framework of the CERoPath and biodivhealth SEA projects (www.ceropath.org) sampled from 2009 to 2016. We focused on the phenotypic variation of the skull (cranium and mandible) and quantified it using geometric morphometric approaches with homologous landmarks (Figure 2). Details of capture and specimen preparation can be found in Auffray et al. (2011) and Herbreteau et al. (2011). This morphological variation was then studied in terms of differences between species, populations and between individuals within populations (Figure 3-4). In that respect all configuration of landmarks were superimposed using Procrustes analysis and the ordination of specimen was described in the tangent shape space by the help of multivariate techniques (Principal component analysis, linear discriminant analysis). Full details about morphometric procedures can be found in Claude 2008 and 2013. All analysis were done in the R language and environment which is available as a free software under GNU General Public License (R Core Team, 2020). All specimens are kept in the osteological collections of the faculty of Veterinary Technology in Kasetsart University (Thailand), and of the Institut des Sciences de l'Evolution in the University of Montpellier (France).

Table 1. Synthetic table of the ecologies of the species studied here, based on conclusions from Morand et al. (2015). Synanthropy=capacity to live in human-influenced habitats. Commensalism=Using anthropic habitats as an ecological niche.

	Specialist/generalist*	Habitat	Synanthropy	Commensalism
<i>Ma. surifer</i>	Specialist	Forest	No	No
<i>M. cookii</i>	Intermediate	Agricultural fields (sloped)	Yes	No
<i>M. caroli</i>	Intermediate	Flooded agricultural fields	Yes	No
<i>R. tanezumi</i>	Generalist	Human settlements	Yes	Yes
<i>R. exulans</i>	Specialist	Human settlements	Yes	Yes

(*based on habitat specialization)

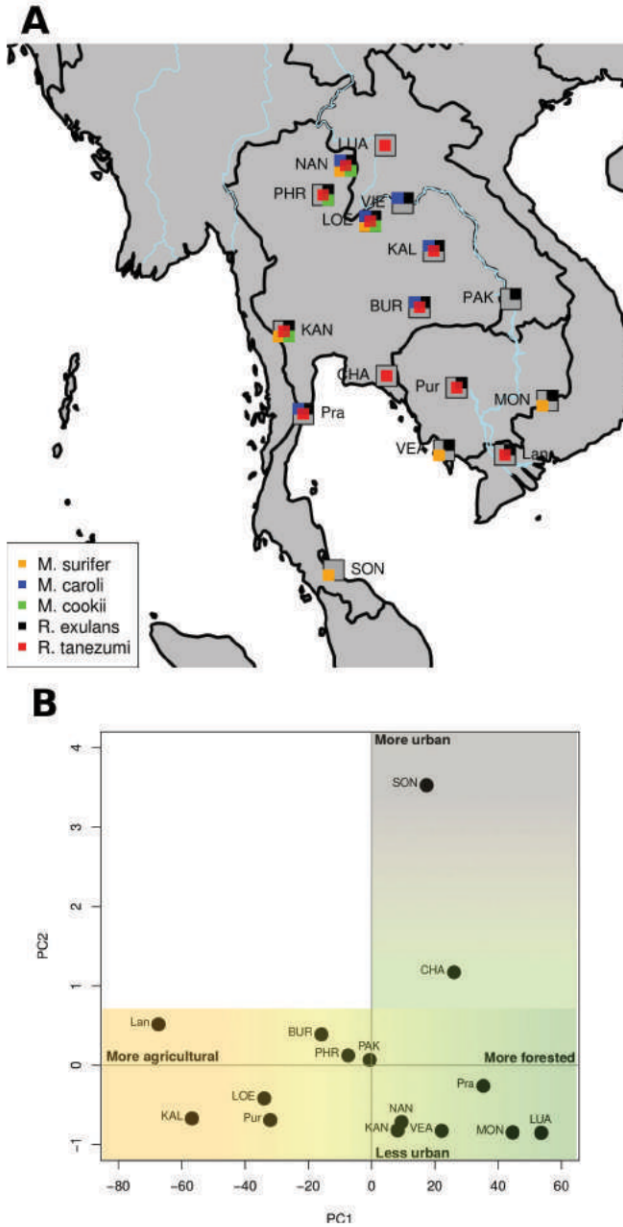


Figure 1. A) Map of continental South-east Asia, showing the localities sampled in this study, and the species caught in each. Abbreviations : CHA, Chantaburi (Thailand) ; KAL, Kalasin (Thailand) ; KAN, Kanchanaburi (Thailand) ; Lan, Cao Lanh (Vietnam) ; LOE, Loei (Thailand) ; LUA, Luang Prabang (Lao PDR) ; MON, Mondolkiri (Cambodia) ; NAN, Nan (Thailand) ; PAK, Pakse (Lao PDR) ; PHR, Phrae (Thailand) ; Pra, Prachuap (Thailand) ; Pur, Pursat (Cambodia) ; SON, Songklah (Thailand) ; VEA, Veal Renh (Cambodia) ; VIE, Vientiane (Lao PDR). B) PCA of localities based on land cover data.

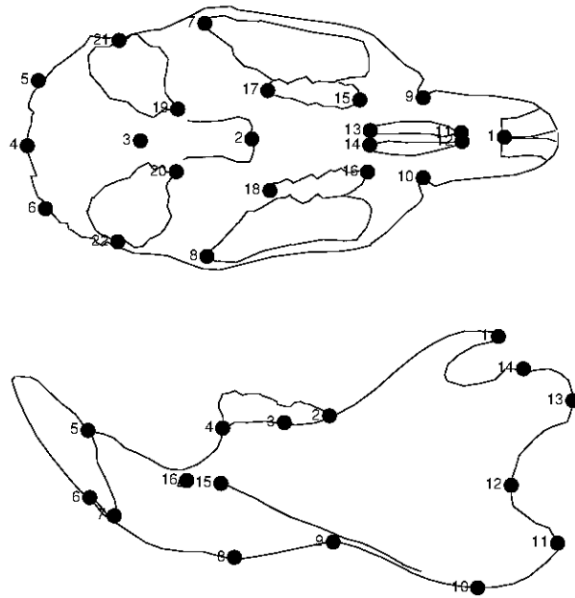


Figure 2. Outlines of the palatal view of the cranium, and lateral view of the mandible of *Rattus tanezumi*, displaying the landmarks used in this study.

3.2.3 Morphometric distinction between Muridae species

Based on our results, the five species studied here can be fairly well distinguished (Figure 4A) based on mandible shape (results for the cranium are similar). Some overlap is observed between the two species of mice, *Mus cookii* and *Mus caroli*. Overlap between the two rat species, *Rattus exulans* and *Rattus tanezumi* is also present, probably due to similarities in skull shape between small (i.e., juvenile) *R. tanezumi* and large *R. exulans*. However size can still allow to more accurately differentiate between those species. Finally, *Maxomys surifer* is clearly distinct from all other species, and mice are clearly different from rats. This shows first that morphometrics can be used as good taxonomic predictors as do genomic data. The advantage of morphometrics is that it does not requires to extract, purify and amplify DNA and that it does not requires important investments, as the price for good digital cameras has dropped in recent years.

3.2.4 Morphological variation within populations

Variation within localities was calculated, and bootstrapped. We found that populations of *R. tanezumi* and *R. exulans* had significantly less morphological variation than mice and *Ma. surifer* (Figure 3). The explanation for this result is probably a reduced tendency to dispersal in commensal populations, which is the case for *R. exulans* and to a lesser extent for *R. tanezumi*. This fits well with low genetic variation found within populations in African commensal rodents, compared with non-commensal sister species (Brouat et al., 2007).

3.2.5 Correlates between land cover and skull morphology

Non-neutral changes may also structure morphological differences between populations. These differences may be adaptive, although they may be plastic rather than due to heritable genetic variation. Shape and size examples illustrate this in the *R. tanezumi* specimens sampled here.

In *R. tanezumi*, we found that populations' average skull size was significantly ($p < 0.05$) positively related to the percentage of agricultural land cover around capture points (Figure 5). Larger size could be explained by higher-quality diet in anthropized localities, with more easily available resources in larger quantities and potentially higher caloric contents. Also related to diets, harder food items in anthropic environments may favor larger skulls that produce stronger bite forces. However, it is uncertain whether human-derived food resources are harder or softer than in the wild. Another explanation could be related to a rarefaction of natural predators of rats in these environments, although dogs and cats may replace them, relaxing selection of small and discrete individuals.

In any case, differences in mandible shape also appear in *R. tanezumi* (Figure 4B) between populations. Notably, two clusters appear to be separated in the discriminant analysis of localities (Figure 4B-C). The similarities between those clusters may relate to some geographical distinction (Figure 4C), with one cluster being found in Northern and Central Thailand, and the other in Southern Thailand, Cambodia, Vietnam, and more strangely in Northern Laos. The geographical pattern is therefore imperfect and may actually relate to other factors. From our data, there appears to be no relation between the clusters and the genetic differentiation between *R. tanezumi* and *Rattus* R3 that we have considered here as a conspecific (but see Pages et al., 2013). There is also no difference between the two clusters in the frequency of rats caught within or outside settlements, suggesting the difference does not come from a plastic effect related to life in settlements. Other ecological/ landscape or historical factors may be explaining those differences, such as the presence/absence of water bodies nearby, as one of the clusters is composed of mostly fluvial or coastal localities.

3.2.6 Discussion of case study results

Although our results are preliminary, they show the potential of this type of study, especially when carried over numerous localities with matching species in different contexts. Our results show that human influence can impact the phenotype of vertebrates in several ways.

First, anthropic changes and adaptation to anthropogenic habitats affect fluxes of individuals between localities. This has been known and demonstrated repeatedly with population genetics (e.g., Brouat et al., 2007), but here we show that this can also affect phenotypic variation. Phenotypic divergence (here morphological) can be at the basis of a reproductive isolation, and can in the

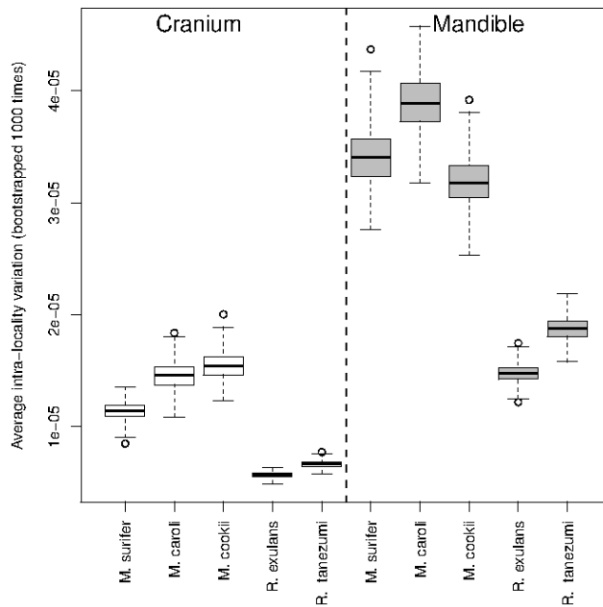


Figure 3. Boxplots of the average morphological variation within locality and within species, with error bars showing 95% intervals obtained by bootstrapping individuals 1000 times.

long term produce new species by allopatric speciation. However, limited phenotypic variation within populations can also reduce adaptive ability, which can cause extinction in case of abrupt changes.

Second, anthropized habitats can produce local adaptations, either by plastic or heritable changes. As synthesized in BOX 1, such adaptations have been demonstrated, and can be quite drastic in urbanized environments. Our case study shows that rural agricultural landscapes can also produce significant phenotypic changes in vertebrates, here in the skull of rodents, which may be adaptive. Therefore, scientists should not underestimate the selective pressures produced by agriculture on faunas. Such underestimation may come from a general feeling that cities are ‘more modified’ than agricultural areas from a subjective human point of view, but also from phenomena such as urban heat islands. The potentially strong selective pressures that may be found in agricultural landscapes can certainly affect phenotype rapidly, as illustrated by our results. This result is also coherent with the low taxonomic diversity sometimes observed there (while cities can paradoxically maintain larger numbers of species). These two observations combined should make scientists and decision makers more preoccupied with these agricultural environments, especially when they occupy most of the landscape as it is the case with intensive agriculture. In Southeast Asia, the rapid conversion of forests into various crops is an obvious direct threat on biodiversity as it destroys original habitat (Sodhi et al., 2004). We show here that it can also modify the biology of species.

In conclusion, our results, as well as those of others, suggest that much more attention should be paid to phenotypic evolution under anthropogenic

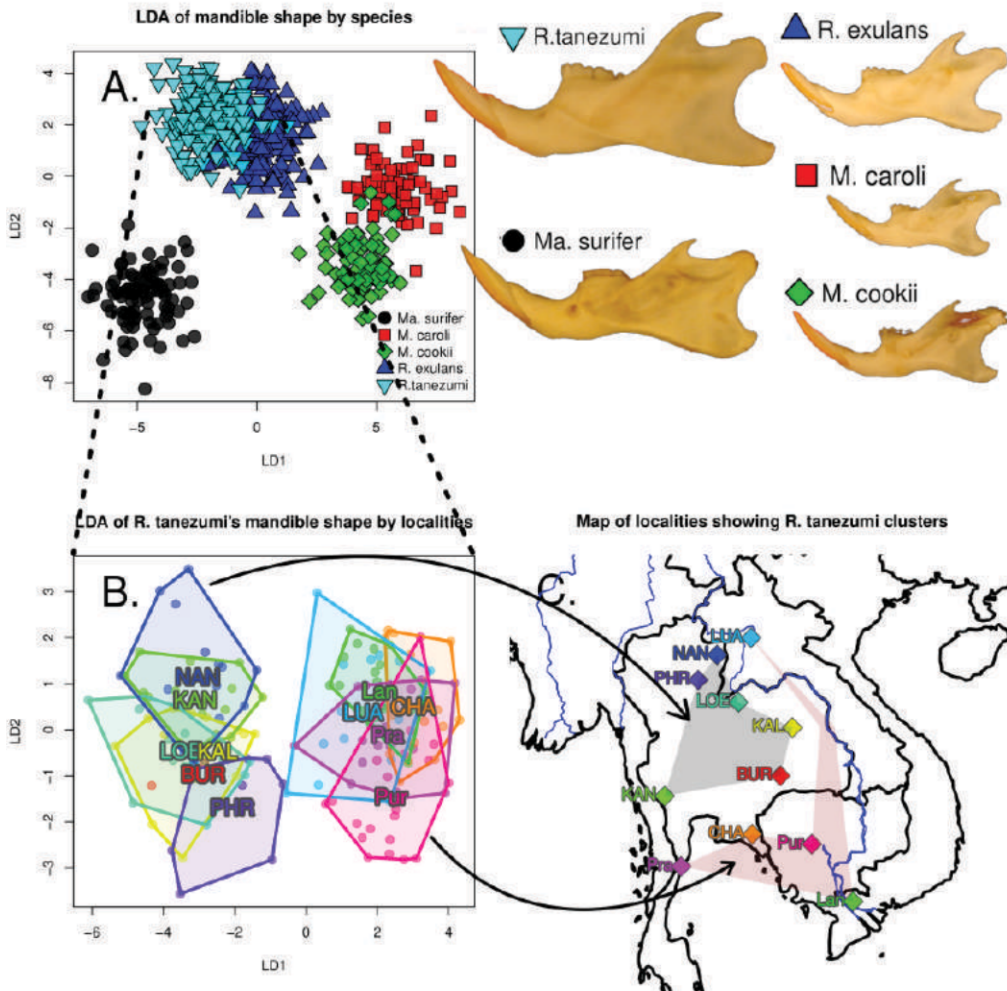


Figure 4. Morphological difference in the shape of the mandible of murid rodent species studied here. A) Linear discriminant analysis showing differences between the species, with photographic examples of mandibles included in the dataset. B) Linear discriminant analysis of mandible shape between populations of *R. tanezumi* at different localities. C) Map of continental Southeast Asia showing the localities corresponding to panel B), with the two clusters highlighted by grey polygons.

pressures, if we are willing to correctly model biodiversity's responses and take appropriate measures. Growing cities must obviously be a target (BOX 1), but our results show that rural areas where landscapes are becoming increasingly agricultural should also be monitored. Although long-term monitoring of populations may seem like the best way to go scientifically, the speed of anthropic changes may not allow them before ecosystems become unreversibly disrupted. Our example case study shows the value of comparative synchronic studies to assess the phenotypic evolution of populations. Historical data (museum collection, archeological samples) are a potentially good addition to these, as they will give a much needed time perspective. In Southeast Asia, local researchers and students could undertake such fieldwork, with support

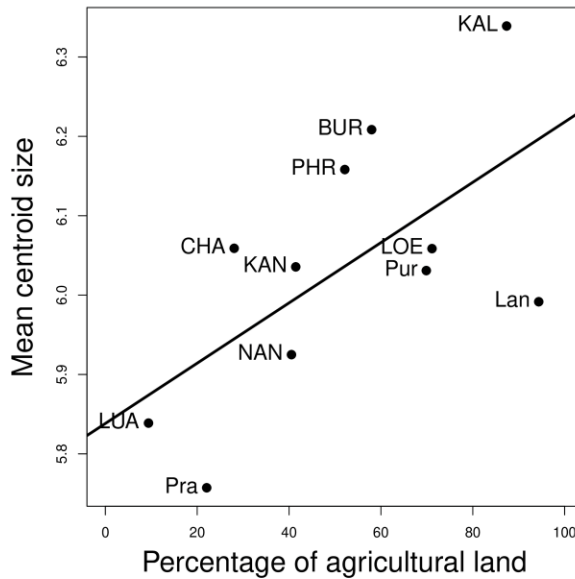


Figure 5. Correlation between the percentage of agricultural land around capture points and skull size for *Rattus tanezumi*.

from local authorities and help from inhabitants, notably farmers and hunters. Indeed, local researchers have easier access to localities nationwide, but also do not suffer from language and cultural barriers as foreign researchers do.

Perspectives. Understanding the part of phenotypic variation and adaptation in populations' and species' resilience to change can help produce better predictions on the near future of taxonomic and phenotypic diversity, but also on functional aspects of ecosystems (McMahon et al., 2011; Moran et al., 2015). Identifying in which conditions and how species and populations faced with anthropic changes can survive, can help build policies to maintain local indigenous species by mitigating both extinction (Wilcove et al., 2013) and homogenization (such as that produced by urbanization; McKinney, 2007). These aspects can be particularly beneficial for Southeast Asia, where changes are dramatic and rapid, and where biodiversity is large and has important ecological and socio-economical functions.

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