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Review

An Aegean View on Non-Adaptive Radiations

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Abstract: The diversification of lineages sometimes exhibits patterns that are often described as 'radiations', which can be seen at various time scales, but researchers most often focus on a fast divergence of parental forms within short time spans. Adaptive radiations are widely discussed and have served as important showcases of Darwinian evolutionary processes. Other types of radiation have been identified, too, and several classifications have been suggested. Among these, 'non-adaptive radiations' remain controversial till today. Despite concerns on the conceptual basis of such a process, more and more cases of radiation that are described as 'non-adaptive' are published, and the continuously accumulating genetic/genomic data for more and more taxa seem to reveal extensive lineage diversification that is often not attributable to any apparent selective force. Given that allopatric divergence due to stochastic processes is presumably the cause of non-adaptive radiations, insular systems provide a rich pool of case studies. Using examples of lineage divergence from various taxa living on the Aegean islands, I discuss the processes leading to non-adaptive radiations in view of the alternative classifications of radiation by other authors, and show that such patterns may also result from a mixture of adaptive and non-adaptive processes.

Keywords: adaptation; divergence; evolution; genetic drift; geographic variation; speciation

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1. Introduction

The history of life on Earth is a history of lineage diversification over time that has led to the vast diversity we see today at all levels of living beings' organization. The diversification process does not unfold uniformly in time or space, with some lineages exhibiting slow rates and/or a narrow range of divergence, and others with fast rates and/or producing a wide range of forms. Such cases of fast and/or wide divergence of lineages are often called 'radiations' and have played an important role in the development of evolutionary and ecological theory [1]. We can describe radiation at different time scales, depending on the focus of our questions. In one broad, but also trivial sense, all biological evolution is a long-lasting radiation from a single common ancestor. On another scale, the divergence of dinosaurs or of their subclade, the birds, can also be described as radiations at large time scales [2]. Most of the discussion on radiation, though, focuses on the fast divergence of forms from a single ancestor in shorter time spans, usually within a few million or even thousands of years. Thus, the time scale is an important aspect of radiation, with the process(es) that guide them being another. Probably influenced by Darwin's observations on the Galápagos Islands' tortoises and birds, the concept of adaptive radiation has dominated the relevant literature [3,4]. This well-known process refers to the divergence of forms due to the action of different ecological stresses on different parts of the parental species' populations, i.e., due to selection acting towards divergent directions, resulting in the occupation of different niches by descendant lineages. Selection

here refers to natural selection sensu stricto, i.e., not including sexual selection. The latter was considered more recently in the frames of a different classification of radiations, as we will see below.

In the past century, though, it has been well-established that, in addition to selection, evolutionary change may be caused by other processes, too, such as genetic drift and meiotic drive, that are of a stochastic nature [5]. Hence, it would be possible, at least in principle, that such stochastic processes can also trigger radiation under the appropriate conditions. Nevertheless, the concept of 'non-adaptive radiation' was not easily accepted by evolutionary biologists until recently, and some are still quite reluctant to accept it [6]. This is mostly due to the fact that it is hard to exclude ecological factors from the explanation of any real radiation example, given that there may always be some effects that we have missed or which we have not yet developed the means to check for. This (admittedly controversial from an epistemological perspective) objection notwithstanding, the idea of non-adaptive radiation gradually gained support as more and more cases of fast and wide lineage diversification have been documented for which ecological divergence could not be reasonably assumed [1]. Furthermore, the almost exponentially accumulating genetic and genomic data for a wide range of taxa have revealed even more extensive divergence of lineages than what the phenotypes alone could show [7]. A large part of this divergence does not seem to fit any apparent ecological differences in the respective organisms' environments. In order to accommodate the wealth of patterns and inferred processes that have been reported in the last two or three decades, some authors have suggested alternative classifications of radiations that go beyond the adaptive/non-adaptive dichotomy. Herein, we shall attempt to address the issue of non-adaptive radiations in light of such theoretical work focusing on the role of insular systems in promoting relevant patterns. We shall use illuminating examples from the Aegean archipelagos' biota that underline the importance of this region for improving our understanding of eco-evolutionary patterns and processes.

Even if African lakes have played an important role in our understanding of radiation [8], insular systems seem to provide a far richer set of case studies. Islands offer more opportunities for faster divergence of populations in allopatry, both in cases where such divergence is driven by ecology and when it is driven by other factors. For non-adaptive radiations, in particular, insular systems of some form seem to be a prerequisite. Of course, from a biogeographical perspective, insular systems also include habitat islands, such as mountaintops and lakes, but most known cases of radiations still come from real, 'geographical' islands. Among these, isolated oceanic archipelagos provide a suitable template for adaptive radiations, since first-arriving taxa have a higher probability of finding opportunities for differentiation into empty available niches [9]. Given the generally longer existence of oceanic islands as islands compared to continental shelf ones, taxa on oceanic archipelagos often have ample time to diverge at species or higher levels. Continental shelf islands, on the other hand, might offer opportunities for non-adaptive divergence due to genetic drift or other processes. The generally lower isolation of these islands, coupled with their more recent formation as supersaturated fragments of the mainland, may inhibit adaptive divergence into empty niches. Such a process would be possible in such systems only in cases of extensive ecological variation among islands of the same archipelago. Furthermore, the shortage of available time since isolation should allow for lower-level divergence, such as found among populations of the same species or among species in superspecies complexes. This means that we would expect to see more extensive morphological divergence among distinct monophyletic taxa along oceanic islands, as in the case of Galápagos finches [10,11], whereas finer differentiation among populations of the same species (or superspecies in cases of increased evolutionary rates) along some ecological gradient or among different habitat types along continental shelf islands.

2. Approaches to Non-Adaptive Radiations

Rundell and Price [1] (p. 394) define non-adaptive radiation as 'lineage diversification with minimal ecological diversification, resulting in allopatric or parapatric taxa'. This definition connects observed distribution patterns (allopatry or parapatry) with the process that created them (minimal ecological diversification), leaving no space for other possible outcomes of this same process (e.g., sympatry). At the same time, the term 'minimal' seems vague, since it can accommodate a range of ecological diversification, from zero to a degree that can be subjectively considered as minimal. In contrast, the well-known process of adaptive radiation is usually framed in terms that are not restrictive regarding the distribution patterns. Hence, we can have species with a purely allopatric distribution, with parapatric, or even sympatric (e.g., some species of Galápagos finches, a classic example of adaptive radiation [10,11]). Therefore, it seems appropriate to define non-adaptive radiation in similar terms, focusing solely on the process and not on the pattern.

In the first explicit use of the term [12], non-adaptive radiation is defined more generally as 'evolutionary diversification from a single ancestor, not accompanied by relevant niche differentiation'. This definition is neutral in terms of resulting patterns, even though one may hold that it would be difficult to imagine the co-occurrence of ecologically similar sister-species. Indeed, most known cases that had been described as 'non-adaptive radiations' at that time referred to allopatrically distributed species [13–17]. Interestingly, Rundell and Price [1] did not consider the option of secondary dispersal that would lead to secondary sympatry of allopatrically speciated taxa. Such a case seems to have been exemplified in the study of annual killifishes [18]. Furthermore, one could make a more elaborate exploration of what is meant by 'allopatry', since sometimes the term is used in a sense that includes also 'micro-allopatry', whereas other times, it is not [19,20].

An important contribution to the discussion on possible mechanisms that lead to different kinds of radiations can be found in [21], where speciation is classified into two main categories, 'ecological' and 'mutation-order'. The latter type of speciation, based on the model of Mani and Clarke [22] for species divergence triggered by mutational order, which is distinct from genetic drift as it involves beneficial mutations, can be considered as a mechanism that leads to non-adaptive radiation. Even if this author considers ecological speciation to be far more common and better documented, 'mutation-order' speciation, together with genetic drift, could trigger divergence without niche separation. It is interesting to note that Schluter [21] includes speciation by sexual selection in the 'mutation-order' case when mate preferences or gamete recognition occur through fixation of different advantageous mutations in different populations. Cases of radiation due to divergence of sexual characters without ecological differentiation can be considered as examples of the 'non-adaptive' type, despite the strong effects of selection involved, as diverging taxa do not change their ecological niche. This perspective shares similarities with the generally neglected concept of 'reproductive drift' that had been suggested by Runemark [23,24] four decades ago, based on his observations of certain plants along the Aegean islands (Greece).

Remarkably, Simões et al. [25], in their review on radiations, do not even mention the non-adaptive type, but provide, instead, an alternative classification of radiations. These authors distinguish between adaptive and exaptive radiations on one hand, both of which would have been previously included under 'adaptive', and geographic and climatic radiations on the other. The latter, for many researchers, would have been identified as 'adaptive' in the sense that diversification is triggered by changes in climate, which can be considered as an ecological selective force. In addition, the authors also recognize 'disparification' and 'pseudoradiation' in cases where morphological divergence within a clade is increased without an increase in speciation rate. This latter view takes speciation rates as the defining factor of any radiation whatsoever. Of course, such an approach

leaves open the question of how to document actual change in speciation rates, especially in cases where it is impossible to have data on ancestral taxa of the focal lineage. This methodological issue notwithstanding, the only category that can be identified with non-adaptive radiation is what in [25] is called 'geographic' radiation.

Examples of non-adaptive or geographic radiation, with or without secondary sympatry, have become quite common in the literature and include a variety of taxa and geographic regions (for example, in addition to the above-mentioned cited work, see also [26–34]).

The case of Lake Malawi cichlid fishes [35] provides evidence for a mixture of adaptive and non-adaptive stages in radiations, and the authors suggest that non-adaptive divergence due to sexual selection should be common in later stages of radiations. Well-known cases where sexual selection plays an important role in radiation include Hawaiian *Drosophila* [36] and several birds [37–40]. Arnegard et al. [41], on the other hand, show that sexual selection may precede ecological divergence in an electric fish radiation.

Mendelson et al. [42] provide a general theoretical scheme and a classification of 'mutation-order' divergence due to sexual selection, suggesting that ecological divergence may also take place simultaneously, so that adaptive and non-adaptive radiations are not necessarily contrasting processes.

A few years earlier, Kamilari and Sfenthourakis [28] had presented evidence of a radiation that includes both adaptive and non-adaptive components in a species (complex?) of terrestrial isopod. The taxonomic issue notwithstanding, such a case raises some concerns about the traditional dichotomy in radiation's classification, since real organisms are continuously under the joint effects of selection pressures and genetic drift, especially when small insular populations are involved. The question then could be raised as to which process is the one that triggered speciation in the first place. Did reproductive isolation due to adaptive processes lead to the accumulation of other, non-adaptive features, or did genetic drift lead to divergence, whereas selection acted on already isolated populations? Or did the two processes act simultaneously, leading to the parallel divergence of different features? In the case of the terrestrial isopod in [28], presented in more detail below, several characters, both related and not related to mating, seem to have diversified stochastically, whereas one character not related to mating shows a latitudinal trend, presumably being under selective forces. The most plausible explanation involves genetic drift, given also that forms occupying the same latitude do show divergence in the other characters.

3. The Problem with Adaptation

Despite the rich literature on radiation and its characterization in terms of adaptation or the lack of it, notwithstanding, there are other issues with such a classification, too. The use of the term 'adaptation' and its connotations may be considered either tautological [43] or a 'just so story' (in the sense that led Gould and Lewontin [44] to their famous critique of the 'adaptationist program'). Even if the latter issue has led to a more careful and accurate documentation of 'adaptationist' explanations [45], the former still remains an important problem in defining and describing the products of natural selection. In a short version, this criticism is based on the fact that the description of natural selection as a process of adaptation to the environment leads to a vicious cycle of the form 'adaptation is the selection of the more adaptive variant'. Even if Olson and Arroyo-Santos [46] provide an interesting way out of the problem based on Bayesian logic, the heuristic value of treating vicious cycles as 'virtuous cycles' that promote understanding sounds more like a half-solution. On the other hand, the suggestion in [43] to completely abandon the term 'adaptation' and use, instead, a purely mechanistic, 'kinetics' description of the evolutionary process, offers a bold but straightforward solution. It is true that most evolutionary biologists were not

willing to take such a bold step, which explains why the use of 'adaptive' terminology has persisted without much change till today. Nevertheless, if we need to understand patterns and processes like radiation, we need to be careful with the use of concepts and terms. Some of the alternative classifications of the radiations discussed above may also be seen as a way out of the problem.

Another tentative solution could be the adoption of the terms 'adaptive' and 'non-adaptive' as a shorthand discrimination between a radiation process triggered by some apparent environmental factor(s) that select for different variants in different parts of the parental population and one that has resulted from genetic drift (or other stochastic processes) due to the isolation of parts of the parental population. Of course, in most cases, we can only attest the outcome of radiation, i.e., the species/variants that were produced after a certain amount of time, so we need some criterion to serve as evidence for the causal factor that initiated divergence. Calculated or reasonably presumed differences in the relative fitness of phenotypic characters that differentiate modern populations are the obvious choice. Even though we cannot unquestionably document the reality of such fitness differences, it is often useful to proceed with such a distinction in order to reach a deeper understanding of the processes that take place in nature. The examples from real cases given below may illuminate this view.

4. The Aegean Perspective

The Aegean archipelago is an island-rich region, with more than 7000 islands and islets of various sizes and isolation levels [47], spread along a relatively narrow but clear ecological gradient, and with some variety in island ages. The vast majority of the islands are classified as continental (sensu [9]), but there are also continental fragments (Crete and surrounding islets, the Karpathos-Kasos group) and even a few oceanic ones (e.g., small islets around Thira) of recent age. The palaeogeography of the region is quite complex (Figure 1), with a history of repeated island separation and reunification into larger land masses or with nearby mainland (continental Greece to the west and Asia Minor to the east), especially during the Pleistocene glacial periods. Hence, the age of current continental shelf islands ranges from a few centuries to a few thousand years. On the other hand, the age of the islands that are considered as continental fragments (see above) can be traced back to the end of the Messinian Salinity Crisis [48], some 5 million years ago. Furthermore, the Aegean hosts a rich diversity of taxa, lying between two biodiversity-rich biogeographical regions, the southern Balkans and Asia Minor/Anatolia, with some influences from a third, namely northern Africa.

Consequently, the Aegean archipelago is expected to be a natural laboratory for testing many ecological and evolutionary patterns and processes, including radiations [49]. Indeed, as already discussed, some important examples of radiation come from this very region.

The plants of the *Nigella arvensis* alliance on the Aegean islands provide the most thoroughly studied case of non-adaptive radiation in this region [17,50–52]. The group of researchers working on this case has applied a combination of methodological approaches, convincingly showing that divergence among forms and species cannot be explained by selective processes, and has repeatedly attributed it to genetic drift.

Another case that has been studied in detail is the snail species in the genus *Mastus* [27]. This genus is distributed along several Mediterranean countries but has differentiated mainly in the Aegean (with 23 endemics out of 32 species in the genus overall), and more intensively on the island of Crete, where one can find 16 out of the 23 Aegean endemics. These snails exhibit limited variation in shell morphology but differ in other characters, such as the spermatophore shape, which do not show any geographically or ecologically consistent pattern. Furthermore, a molecular phylogeny recovered the monophyly of

the central-southern Aegean endemics, and cladochronology showed that divergence is old, having started sometime from 9 to 6 Ma. All these species share the same habitats and ecological features, and some can be found living close to one another in the same geographical locations. The authors examined this radiation from several perspectives, such as morphological, molecular, and ecological, and concluded that the only plausible scenario is radiation due to allopatric divergence of secondary sexual characters [27] (p. 1003).

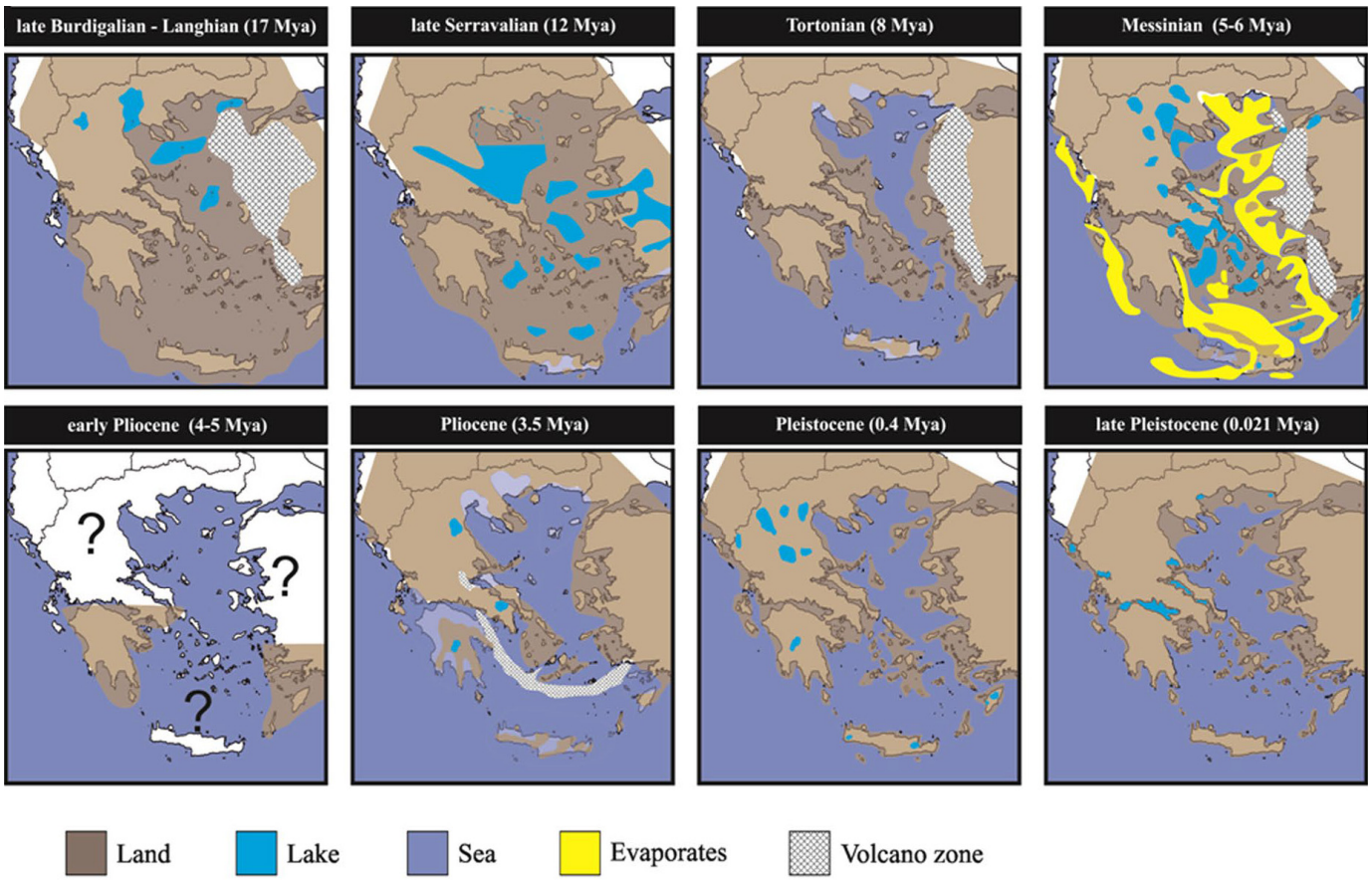


Figure 1. Palaeographical reconstruction of the Aegean region during selected periods from the Miocene to the present. Question marks mean no information for the respective regions. (From [49]).

The term 'non-adaptive radiation' was originally used by Gittenberger [12] in a discussion that used, as a prime example, the case of a snail genus that has been a puzzle for researchers for decades, namely *Albinaria*, which includes a large number of species distributed in eastern Mediterranean countries. Even though southern continental Greece (the Peloponnese) hosts a large variety of forms within a relatively restricted area, the genus is unexpectedly represented along the central Aegean islands with just a few species and forms. Nevertheless, the situation is quite different on the southern Aegean island of Crete, where one can find a huge variety of forms, classified into 31 distinct species [53]. These forms have been known to occupy very small areas, each sometimes very close to one another, without any meaningful geographical or ecological pattern. For example, the small (12 km^2) uninhabited and ecologically uniform islet of Dia, near the central-north coasts of Crete, hosts four distinct species, three of which form a monophyletic subclade within the genus that is endemic to the islet, and the other is an endemic of the Cretan archipelago [54]. At the same time, some 15 discrete and well-supported lineages (species?) have been revealed recently [55] by a genomic phylogeny on western Crete alone, some of which occur within very short distances. Among these, the species that were assumed to form two distinct monophyletic groups ('*A. candida*' and '*A. cretensis*' groups) show an almost star-like

radiation, while most 'species' are able to hybridize with one another. Delimitation of taxa cannot be made securely based on morphological characters, as these exhibit extensive variability even within species, not consistent with any apparent geographic or ecological pattern. It should be noted that most species of *Albinaria* live on limestone rocky outcrops that are scattered all around the Cretan landscape, while not all such habitats are occupied or densely inhabited. This suggests an abundance of 'empty niches' that can be attributed to relatively recent and extensive population fluctuations that are probably related to the climatic fluctuations during the repeated Pleistocene glacial-interglacial cycles, coupled with the restricted mobility of these small snails. In fact, very short dispersal distances in *A. coerulea* were estimated based on field experiments [56], and the authors suggested that such values can promote divergence of populations at a fine geographical scale, either by drift or by selection.

Terrestrial isopods are assumed to have a somewhat better dispersal ability than snails, as they are more active and mobile. Nevertheless, we can see a wide divergence of local populations among the Aegean islands in these animals, too. Despite the lack of a comparable taxonomic resolution of geographic variation among Aegean terrestrial isopods, available data on several taxa are strongly suggestive of radiation-type differentiation. The above-mentioned case of *Armadillo tuberculatus* [28,57] is probably the most evident among these, as each island and islet within the species' distribution range hosts a different morph. The range of differences may vary, but one can safely predict that, if the species is present on a not-yet-explored island, it will be represented there by a new variant. The morphological characters that have been found to vary (see Figure 2) include the ornamentation of the body (the size of 'tubercules'—short protuberances of the cuticle—in adults), coloration, the exact shape of pleotelson, and the shape of the first male pleopod-exopodite (a secondary sexual character in isopods). Furthermore, one population (on the island of Dia mentioned above) exhibits a character (a hollow triangle in the frontal line of the head) that deviates from the typical head structure found throughout the whole genus [57]. A preliminary genetic analysis of a few populations (unpublished data) has also shown extensive molecular divergence. Genomic analyses of many populations from all around the species' distribution range are underway. The aforementioned characters vary independently from one another, with many combinations occurring along the different islands.

Kamilari and Sfenthourakis [28] have found an ecological gradient in one of these characters (body ornamentation in adults), with northwestern populations exhibiting larger adult tubercules that tend to become smaller along a northwest to southeast gradient that could be related also to some ecological gradient, even though major climatic factors (such as precipitation and temperature) are not known to follow such a cline see [58,59]. All other characters vary in an apparently random pattern, not following any geographic or ecological (climatic or habitat) trend. It has to be noted that in most of the islands where this 'species' occurs, we can also find a closely related (congeneric) species that is distributed all around the Mediterranean countries, namely *A. officinalis*. Even though this taxon has been found to exhibit cryptic diversity on Cyprus [60], the populations from the Aegean belong to the same clade and show a low molecular diversity. The main difference between the two species can be found in their ecology, with the former being more stenoecious and the latter being a generalist that exploits almost all Mediterranean habitats. This difference is usually reflected in their population size, too, with the former being generally rarer and living in smaller populations, while the latter is abundant throughout its range. Some exceptions can be found in the southern parts of their distribution, where *A. tuberculatus* can be abundant too, especially at sites with extensive limestone. In fact, this species can be present in extremely dense populations on a few tiny limestone islets of the southeastern Aegean (personal observations). A minimum spanning tree analysis of male first pleopod shapes

based on a morphometric analysis failed to identify any relevance of the most probable shape transformation series with island distances or palaeogeographic connectance [28]. Hence, the most plausible scenario for the divergence of these forms is non-adaptive radiation, possibly coupled with adaptive change in ornamentation size. It is very hard to imagine any fitness advantage of one pleotelson or pleopod-exopodite shape versus another, given that many alternative forms exploit practically identical habitats and reach similar population sizes regardless of the differences in these characters. The only plausible scenario for their divergence is genetic drift due to the effective isolation of populations in different islands. Ongoing analyses will reveal the timing of diversification and hopefully find evidence of the possible effects of past population bottlenecks.



Figure 2. Some variants of the terrestrial isopod 'species' *Armadillo tuberculatus*. Top row: variation in coloration and body ornamentation. From left to right: morphs from the islands of Kea, Kythnos, and Crete. Lower rows: variation in the shape of the male pleopod-exopodite 1.

There are several other cases of wide divergence among geographically close and ecologically similar islands in terrestrial isopods, most of which have not been investigated yet. Nevertheless, the patterns observed are highly suggestive. These cases include, inter alia, the geographic variation in the pleotelson shape (ranging from narrow trapezoidal to truncated-triangular, Figure 3) in the 'species' *Armadillidium ameglioi*, distributed across several eastern Aegean islands and the neighboring mainland of western Turkey; the variation in the head, pleotelson, coloration, and granulation, in what has been called *Porcellio flavomarginatus* (Figure 4), most probably a species group that includes several distinct taxa along central and southern Aegean islands; and the variation and the differentiation of the genus *Ligidium* among the northern, central, and eastern Aegean islands [61,62]. A common theme behind all these cases is the narrow range of habitats occupied by each of these taxa. The first lives in dry sites with extensive limestone outcrops, the second can be found only in sparse locations rich in calcium content that are not necessarily dry, and the

third is restricted to a very narrow zone along streams and around springs, habitats that are very fragmented and subject to extreme seasonal fluctuations on Aegean islands.

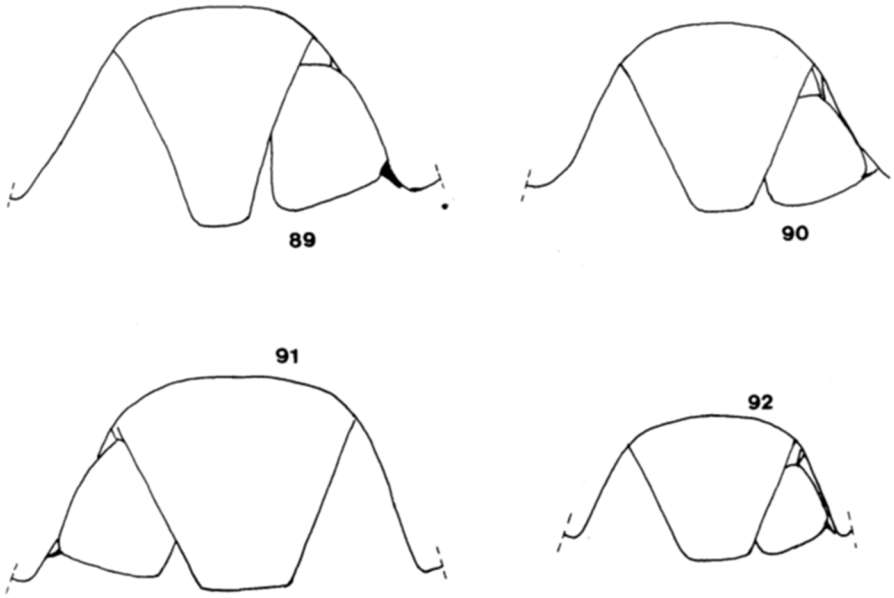


Figure 3. Some variants of the pleotelson in the terrestrial isopod 'species' *Armadillidium ameglioi*. Numbers correspond to islands of origin: 89 = Ikaria, 90 = Naxos, 91 = Amorgos, and 92 = Chalki. (From [61]).

There are several more cases of radiation-like divergence along the Aegean islands in Tenebrionidae beetles, such as in the genus *Dendarus* [63,64], in which monophyletic groups of Aegean species show a strongly suggestive concordance to the known palaeogeographic history of the area, the genera *Eutagenia* (the soil-living forms) and *Dailognatha*, and populations of the species *Zophosis punctata* [65]. The more taxa being studied across the Aegean islands, the more evidence of radiation-type divergence by geographic isolation (without any apparent role for ecological diversification), is revealed. Researchers working on the Aegean islands are well aware of this and most often seek explanations of such patterns in palaeogeography and not in ecology (see papers in [66]). Due to the repeated fragmentation and reconnection of the Aegean archipelago, coupled with extensive environmental changes during the Pleistocene, vertebrates have not generally followed similar patterns of divergence. Given their high mobility and generally longer generation times, any signal of divergence would have been lost by the secondary mixing of populations during the phases of land masses' reconnection, and the same is also true for flying insects. Nevertheless, some known cases involving mainly lizards seem to have retained signals of such geographical radiations, even though these are not very clear in terms of adaptive roles. The variation in scales in the gecko *Cyrtopodion kotschyi* [67] and the patterns of genetic variation in the *Podarcis erhardii* group [68], with many subspecies recognized according to morphology-based taxonomy, may belong to this case. Most studies on these taxa have focused on the identification of discrete lineages that have been based on molecular evidence or in the analysis of color polymorphisms related to behavioral features of the respective animals, while less attention has been paid to the seemingly non-functional variation in scales. The examples from invertebrates and plants, though, are more than enough to make a case for 'non-adaptive' radiations.

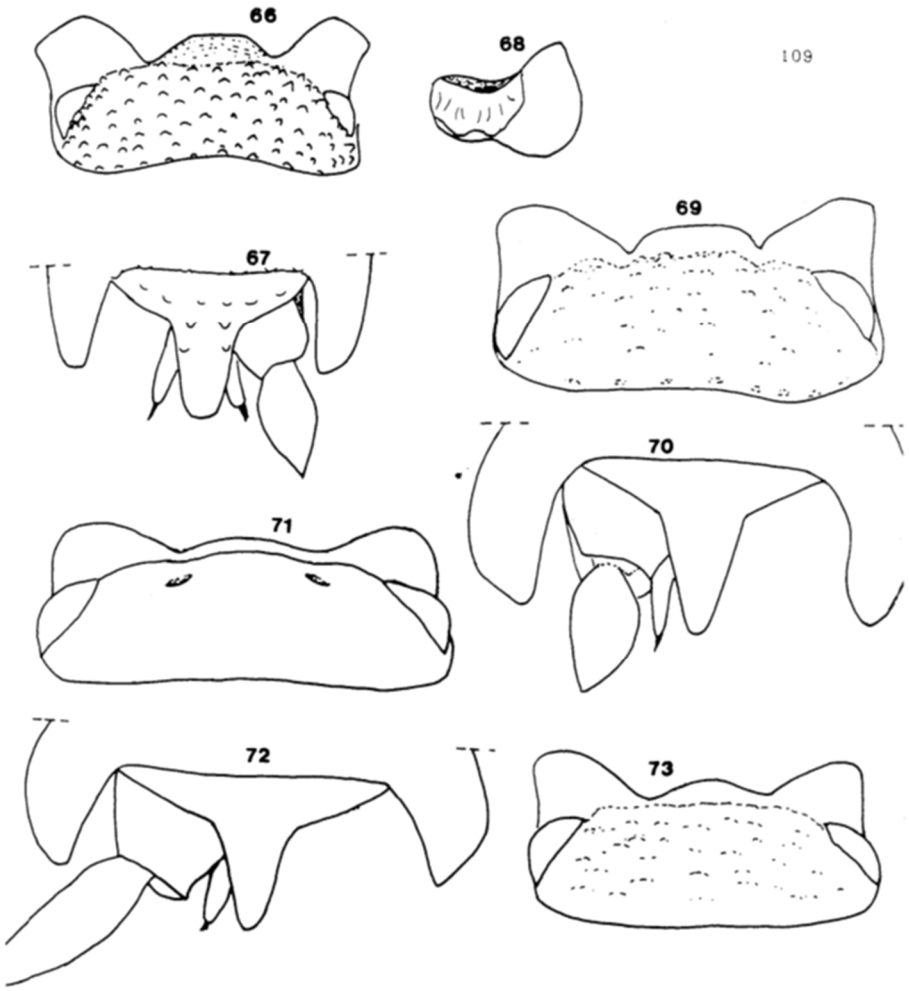


Figure 4. Part of the variation found in the head and pleotelson (both in dorsal view) of the terrestrial isopod 'species' *Porcellio flavomarginatus* across the Aegean islands. Numbers indicate islands of origin: 66–68 = Serifos (68 shows the first male pleopod-exopodite that also exhibits variation, not depicted herein), 69–70 = Mykonos, 71–72 = Kos, and 73 = Syros. (From [61]).

5. Do We Still Need Adaptive/Non-Adaptive Interpretations of Radiation?

It has become clear that radiations involve several processes that cannot be easily classified in a binary manner, either in terms of adaptation or other. Hence, is the whole discussion on adaptive versus non-adaptive radiations irrelevant? As we have shown above, there are several classifications that take completely different approaches and use different terminology altogether. Even though these views are important for our better understanding of these patterns, I will attempt to support that the classical dichotomy is still relevant.

At first, it is important to distinguish between the processes taking place during radiation from the factors that have triggered them. Population divergence during radiation may include both selective responses to environmental variability and stochastic phenomena such as genetic drift. At the same time, we should note that not all of the species that occur in the same environmental setting radiate. It is well known that species vary in evolutionary potential so that evolution may take place at different rates among taxa, mainly due to (subtle or more extensive) differences in their niche, particularly regarding their position in the specialist-generalist spectrum. Other factors are also involved, like the structure and mechanics of their genome, demographic parameters, as well as variations in

environmental/geographical conditions at critical times in the respective lineage history (e.g., the particular period when they first arrived at an archipelago). Hence, one way to classify radiations is the identification of the conditions that sparked the process of fast and wide divergence of the original population. The cases of sister (or at least very similar) species occupying the same region for a similar time period are valuable for such studies: If one such species has not radiated while the other has given rise to a multitude of forms, then we can narrow down the range of possible factors affecting the radiation. Such sympatry may be due to niche differences, to character displacement, or even to mutualistic interactions (see also [69]), with each of these cases demanding different explanations of uneven divergence patterns. The pair of *Armadillo* spp. on the Aegean islands described above is a promising case study for such an approach, with niche differences being the most probable factor of uneven divergence.

Sometimes, we can find enlightening clues in the pattern we observe today. For example, the case of African lake cichlids strongly suggests the initiation of divergence as a response to empty ecological niches. On the other hand, the cases of *Albinaria* spp. on Crete, *Mastus* spp., and *Armadillo tuberculatus* along the Aegean islands cannot be attributed to such ecological divergence, so a more thorough exploration is needed to identify the triggering factors. In fact, as explained above, the most plausible explanation for all these cases is genetic drift acting on small, isolated populations that are produced by mainland fragmentation into the islands.

Therefore, regardless of the processes that took place while the original populations had started to diverge, the trigger of radiation in the cichlid case is adaptation to new niches, while in the others, it is 'non-adaptive', stochastic effects. Natural selection has surely played a role in the subsequent divergence of these lineages, as all populations should have to deal with many environmental challenges at their home range in the passage of time, especially if the ecological conditions varied from place to place. It is also plausible to assume that selection would have increased diversity by pushing different populations/species in different directions, either in a concise pattern (e.g., in cases of ecological gradients) or more haphazardly. Still, this does not change the fact that the radiation had been initiated for different reasons in each case. The distinction between adaptive from non-adaptive radiations, then, can provide an informative description of triggers. Of course, other classifications can also showcase various other aspects of the process; hence, they should not be viewed as contradictory or mutually exclusive.

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