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## **Why Do Some Lineages Radiate While Others Do Not? Perspectives for Future Research on Adaptive Radiations**

Rishi De-Kayne, Rowan Schley, Julia M.I. Barth, Luke Campillo, Catalina Chaparro-Pedraza, Jahnavi Joshi, Walter Salzburger, Bert Van Bocxlaer, Darko Cotoras, Carmelo Fruciano, et al.

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**1 Why do some lineages radiate while others do not? Perspectives for future research on adaptive  
2 radiations**

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4 Rishi De-Kayne (rishidek@gmail.com) <sup>\*,1</sup>, Rowan Schley (rowan.schley@gmail.com) <sup>2</sup>, Julia M.I. Barth  
5 (j.barth@unibas.ch) <sup>3</sup>, Luke C. Campillo (campillo@hawaii.edu) <sup>4</sup>, Catalina Chaparro-Pedraza  
6 (Catalina.Chaparro@eawag.ch) <sup>5</sup>, Jahnavi Joshi (jahnavi@csirccmb.org) <sup>6,7</sup>, Walter Salzburger  
7 (walter.salzburger@unibas.ch) <sup>3</sup>, Bert Van Bocxlaer (bert.van-bocxlaer@univ-lille.fr) <sup>8</sup>, Darko D. Cotoras  
8 (darkocotoras@gmail.com) <sup>9,10</sup>, Carmelo Fruciano (carmelo.fruciano@unict.it) <sup>11,12,13</sup>, Anthony J Geneva  
9 (anthony.geneva@rutgers.edu) <sup>14</sup>, Rosemary Gillespie (gillespie@berkeley.edu) <sup>15</sup>, Joseph Heras  
10 (joseph.heras@csusb.edu) <sup>16</sup>, Stephan Koblmüller (stephan.koblmuller@uni-graz.at) <sup>17</sup>, Blake Matthews  
11 (blake.matthews@eawag.ch) <sup>5</sup>, Renske E. Onstein (renske.onstein@idiv.de) <sup>18,19</sup>, Ole Seehausen  
12 (ole.seehausen@eawag.ch) <sup>5,20</sup>, Pooja Singh (pooja.singh@eawag.ch) <sup>5,20</sup>, Erik I. Svensson  
13 (erik.svensson@biol.lu.se) <sup>21</sup>, David Salazar-Valenzuela (davidsalazar@uti.edu.ec) <sup>22</sup>, Maarten P.M. Vanhove  
14 (maarten.vanhove@uhasselt.be) <sup>23</sup>, Guinevere O.U. Wogan (gwogan@okstate.edu) <sup>24</sup>, Ryo Yamaguchi  
15 (ryamaguchi@sci.hokudai.ac.jp) <sup>25,26</sup>, Anne D. Yoder (anne.yoder@duke.edu) <sup>27</sup>, and José Cerca  
16 (jose.cerca@gmail.com) <sup>28</sup>

17  
18 \* Corresponding author

- 19 1. Department of Ecology and Evolutionary Biology, University of California Santa Cruz, 95060, USA  
20 2. University of Exeter, Laver Building, North Park Road, Exeter, Devon, EX4 4QE, UK  
21 3. Zoological Institute, Department of Environmental Science, University of Basel, Vesalgasse 1, CH-4051  
22 Basel, Switzerland  
23 4. Department of Biology, University of Kentucky, Lexington, Kentucky, USA  
24 5. Department of Fish Ecology and Evolution, EAWAG, Swiss Federal Institute for Aquatic Science and  
25 Technology, CH-6047 Kastanienbaum, Switzerland  
26 6. CSIR-Centre for Cellular and Molecular Biology, Hyderabad, India.  
27 7. Academy of Scientific and Innovative Research (AcSIR), Ghaziabad, India  
28 8. CNRS, Univ. Lille, UMR 8198 - Evo-Eco-Paleo, F-59000 Lille, France

- 29 9. Department of Terrestrial Zoology, Senckenberg Research Institute and Natural History Museum,  
30 Senckenberganlage 25, 60325 Frankfurt am Main, Germany
- 31 10. Department of Entomology, California Academy of Sciences, 55 Music Concourse Dr., Golden Gate Park,  
32 San Francisco, CA 94118, USA
- 33 11. Institute for Marine Biological Resources and Biotechnology (IRBIM), National Research Council (CNR),  
34 Via S. Raineri, 86, 98122 Messina, Italy
- 35 12. National Biodiversity Future Center, Palermo, Italy
- 36 13. Department of Biological, Geological and Environmental Sciences, University of Catania, 95124 Catania,  
37 Italy
- 38 14. Department of Biology and Center for Computational and Integrative Biology, Rutgers University–Camden,  
39 NJ, USA
- 40 15. Department of Environmental Science, Policy and Management, University of California Berkeley, USA
- 41 16. Department of Biology, California State University, San Bernardino, 5500 University Parkway, San  
42 Bernardino, CA, 92407, USA
- 43 17. Institute of Biology, University of Graz, Universitätsplatz 2, 8010 Graz, Austria
- 44 18. Naturalis Biodiversity Center, Darwinweg 2, 2333CR Leiden, The Netherlands.
- 45 19. German Center for Integrative Biodiversity Research (iDiv) Halle -Jena-Leipzig, Puschstrasse 4, 04103  
46 Leipzig, Germany
- 47 20. Aquatic Ecology Division, Institute of Ecology and Evolution, University of Bern, Bern, Switzerland
- 48 21. Department of Biology, Lund University, SE-223 62 Lund, Sweden
- 49 22. Centro de Investigación de la Biodiversidad y Cambio Climático (BioCamb) e Ingeniería en Biodiversidad y  
50 Recursos Genéticos, Facultad de Ciencias de Medio Ambiente, Universidad Indoamérica, Machala y Sabanilla,  
51 Quito, Ecuador EC170103
- 52 23. Research Group Zoology: Biodiversity & Toxicology, Centre for Environmental Sciences, Hasselt  
53 University, Diepenbeek, Belgium
- 54 24. Department of Integrative Biology, Oklahoma State University, Stillwater Oklahoma, USA
- 55 25. Department of Advanced Transdisciplinary Science, Hokkaido University, Sapporo, Hokkaido, Japan
- 56 26. Department of Zoology & Biodiversity Research Centre, University of British Columbia, Vancouver, British  
57 Columbia, Canada, V6T 1Z4

58 27. Department of Biology, Duke University, Durham, North Carolina, USA

59 28. Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biosciences, University of Oslo,  
60 Oslo, Norway

61

62

### 63 **Abstract**

64 Understanding the processes that drive phenotypic diversification and underpin speciation is key to  
65 elucidating how biodiversity has evolved. Although these processes have been studied across a wide  
66 array of clades, adaptive radiations, which are systems with multiple closely related species and broad  
67 phenotypic diversity, have been particularly fruitful for teasing apart the factors that drive and  
68 constrain diversification. As such, adaptive radiations have become popular candidate study systems  
69 for determining the extent to which ecological features, including aspects of organisms and the  
70 environment, and inter- and intraspecific interactions, led to evolutionary diversification. Despite  
71 substantial past empirical and theoretical work, understanding mechanistically how adaptive  
72 radiations evolve remains a major challenge. Here, we highlight a number of understudied  
73 components of the environment and of lineages themselves, which may help further our  
74 understanding of speciation and adaptive radiation. We also outline some substantial remaining  
75 challenges to achieving a detailed understanding of adaptation, speciation, and the role of ecology in  
76 these processes. These major challenges include identifying factors that have a causative impact in  
77 promoting or constraining adaptive radiations, gaining a more holistic understanding of features of  
78 organisms and their environment that interact resulting in adaptation and speciation, and  
79 understanding whether the role of these organismal and environmental features varies throughout the  
80 radiation process. We conclude by providing perspectives on how future investigations into the  
81 adaptive radiation process can overcome these challenges, allowing us to glean mechanistic insights  
82 into adaptation and speciation.

83

84 *In adaptive radiation and in every part of the whole, wonderful history of life, all the modes and all*  
85 *the factors of evolution are inextricably interwoven. The total process cannot be made simple, but it*  
86 *can be analyzed in part. It is not understood in all its appalling intricacy, but some understanding is*  
87 *in our grasp, and we may trust our own powers to obtain more. – G.G. Simpson, 1953*

88

## 89 **Background**

90 Understanding the origin and persistence of phenotypic, ecological, and species diversity, and how  
91 this diversity changes through time, is a fundamental aim of evolutionary biology. To achieve this,  
92 researchers have undertaken both theoretical and empirical investigations in a variety of biological  
93 systems. Study systems with high phenotype and species diversity, including adaptive radiations  
94 (ARs), constitute particularly promising and popular focal study systems. ARs are groups of related  
95 species characterised by common ancestry, and correlated ecological and phenotypic variation that  
96 facilitates the exploitation of ecological variation (trait utility; Schluter 2000). Species within an AR  
97 originate via a series of, often rapid, speciation events that occur concurrently with the colonisation of  
98 various ecologically differentiated niches (Schluter 2000). Due to the explicit connections between  
99 phenotypic differentiation and the evolution of reproductive isolation in the AR process, ARs often  
100 provide unique opportunities to study the links between ecological variation and adaptation along  
101 multiple axes of variation, speciation, and the ways in which species-rich communities persist through  
102 time (Schluter 1996; Givnish and Sytsma 2000; Wellborn and Langerhans 2015; Stroud and Losos  
103 2016). As a result, many ARs have become model systems for those wishing to disentangle the  
104 complex mechanisms underpinning phenotypic diversification, speciation, and species coexistence,  
105 with the aim of extending insights from these systems to better understand speciation as a whole  
106 (Martin and Richards 2019; Gillespie et al. 2020). To determine how evolution proceeds, many  
107 studies have aimed to pinpoint specific ecological factors that have either driven or constrained  
108 evolution and speciation within a given lineage (Grant 2017). Highlighting these features of  
109 organisms and their environment that drive or constrain evolution will help us understand the past  
110 evolution of clades, determine why some lineages radiate while others do not, and will also hint at the

111 predictability of evolution. Gaining a more mechanistic understanding of how and why some lineages  
112 undergo dramatic diversification and adaptation, and how adaptation and reproductive isolation are  
113 linked, will also provide insights into the future evolutionary trajectories of lineages, including, but  
114 not limited to, the response of lineages to climate and ecosystem change.

115

116 Researchers aiming to investigate factors that may drive AR often measure specific key aspects of the  
117 ecology across a clade, such as organism physiology, the environment, or interactions between  
118 organisms and their environment, and correlate these with the extent of species diversification within  
119 the clade. Significant positive associations between an axis of variation and diversification are then  
120 deemed representative of possible drivers of speciation and AR, and, likewise, significant negative  
121 associations are deemed representative of constraining factors (as in Wagner et al. 2012). ARs with  
122 independent instances of repeated diversification are particularly useful systems for undertaking such  
123 studies since they provide some degree of evolutionary replication and, depending on the types of  
124 ecosystems they span, can even act as natural experiments where biotic and abiotic conditions and  
125 traits vary between independent radiations (Salzburger et al. 2014). Studies that have linked specific  
126 organismal and environmental features with species diversity, have highlighted a number of potential  
127 drivers of AR, including genetic admixture and introgression between diverse lineages (Meier et al.  
128 2017; De-Kayne et al. 2022), sexual selection (Wagner et al. 2012), gene duplication (Brawand et al.  
129 2014), standing genetic variation (Choi et al. 2021), specific *de novo* mutations (Cerca et al. 2023), as  
130 well as broad-scale environmental biotic and abiotic features including energy (solar radiation or  
131 primary productivity), ecological opportunity (Wagner et al. 2012), and interactions between these  
132 and other environmental factors (Meier et al. 2019). However, despite these findings, and decades of  
133 research, robustly describing the role of these specific phenotypic features, the environment, and  
134 interactions between organisms and the environment, in the adaptation and speciation process during  
135 AR remains a challenge.

136

137 ***Outstanding challenges***

138 Correlating specific organismal traits, and biotic and abiotic factors of the environment with rates of  
139 diversification, or the establishment of reproductive isolation, is often insufficient to comprehensively  
140 identify the factors associated with diversification or to determine the mechanistic role of associated  
141 factors in the adaptation and speciation process. Studies that investigate only a small number of traits  
142 and environmental characteristics often oversimplify the many different interconnected axes of  
143 ecological variation that are important for species evolution and persistence and the processes that are  
144 involved in the evolution of new species. For example, without a comprehensive understanding of  
145 organismal and environmental variation it is difficult to distinguish whether factors associated with  
146 diversification contribute towards, or are essential for, lineage diversification, whether they play a key  
147 role but act in concert with other key factors, or whether they are simply indirectly associated with  
148 other causative factors that drive AR. Aiming to separate causal factors from factors which are  
149 spuriously correlated with diversification should be a major priority for future research on speciation  
150 biology. Making this goal of understanding the role of specific factors in AR even more challenging is  
151 the fact that many aspects of organisms and the environment are ecologically and evolutionarily  
152 intertwined. These links include different traits that co-vary within an organism, and environmental  
153 variables that are correlated with one another. Additionally, organismal traits vary in their degree of  
154 environmental-dependent expression and their expected responses to different selective agents (Felmy  
155 et al. 2022). To better understand the AR process we must therefore investigate organisms and their  
156 environment less simplistically and aim to demonstrate causality in the links between trait variation  
157 and fitness. This will involve moving away from selecting and measuring only a handful of individual  
158 organism and environmental features, and instead trying to tease apart the ecological interactions that  
159 facilitate the evolution of diverse ARs, especially by considering understudied and complex aspects of  
160 organismal and environmental variation. It will also be important to better understand which aspects  
161 of organisms and their environment are linked to avoid the pitfalls that these associations pose for  
162 correlative studies of diversification. We must also try to include assessments of the multitude of key  
163 ecological interactions and feedbacks present which undoubtedly moderate adaptation and, in the case  
164 of ARs, may eventually drive or facilitate speciation.

165

166 Approaches that correlate organismal and environmental traits with speciation rate or the  
167 establishment of reproductive isolation also fail to account for both stochastic and non-linear  
168 relationships between differentiation and organismal or environmental features. To address this, it will  
169 be critical to identify when during the AR process factors associated with diversification play a  
170 mechanistic role, and if their contribution to diversification is consistent through time. Resolving the  
171 temporal importance of these factors will be important for determining how ARs proceed.  
172 Investigations that only associate contemporary trait variation and contemporary metrics of  
173 diversification may be particularly vulnerable to finding both false positive and false negative  
174 associations between specific factors and speciation. This challenge is particularly well-represented  
175 by the difficulty of determining whether ecological differentiation precedes or follows the  
176 establishment of reproductive isolation. Despite many narratives and proposed examples of ecological  
177 speciation, where ecological differentiation seems to precede speciation, the opposite, i.e., where  
178 ecological differentiation is thought to have developed after reproductive isolation and speciation is  
179 not uncommon. For instance, in Darwin's finches, character displacement and ecological  
180 differentiation occurred only after a degree of reproductive isolation had already accumulated (Lack  
181 1983). Additionally, an increasing number of examples of strongly reproductively isolated species  
182 groups that show only weak ecological niche differentiation have been noted, suggesting that  
183 speciation and ecological divergence are sometimes decoupled processes (McPeck and Gavrilets  
184 2006; Rundell and Price 2009; Svensson 2012, 2018; Cotoras et al. 2018; Czekanski-Moir and  
185 Rundell 2019). These challenges linked to our fundamental understanding of whether ecological  
186 differentiation promotes, constrains, or is neutral with respect to diversification are also shared with  
187 linking almost any intrinsic or extrinsic factor with speciation, and must be addressed to establish a  
188 deeper understanding of adaptive radiations and the speciation process more broadly.

189

190 Here, we highlight a number of complex aspects of ecology, including variation in organismal traits  
191 and environmental characteristics, which may play a role in the adaptive radiation process, and as

192 such, warrant more detailed future investigations. Despite being challenging to investigate, a better  
193 understanding of these complex components of ecology may help address the key outstanding  
194 questions relating to how adaptive radiations proceed that are posed in Box 1. We conclude by  
195 providing perspectives on how future investigations into adaptive radiations can address the  
196 challenges outlined above, with the aim of revealing how radiations evolve through time and the  
197 features of organisms and their environment that are important throughout the AR process.

198

199 **Box 1 – Key questions for investigating adaptive radiations.**

200 The environment:

- 201 • Do specific key abiotic or biotic factors drive or constrain AR?
- 202 • Is the presence or absence of these factors important or is the breadth or variation in the factor  
203 important?
- 204 • Does the multidimensional niche occupied by a lineage, rather than specific abiotic or biotic  
205 environmental conditions, impact the propensity for a lineage to radiate?
- 206 • Does the capacity for the abiotic and biotic environment to be modified by organisms in a  
207 lineage impact the propensity for the lineage to radiate?
- 208 • Does variation in abiotic or biotic conditions through time play a role in driving or  
209 constraining AR?
- 210 • Is ecological niche stability necessary for AR?

211

212 The organism:

- 213 • Do specific organismal features drive or constrain adaptive radiation?
- 214 • Is the presence and absence of specific key innovations important in facilitating AR or is it  
215 the breadth and variability of traits?
- 216 • Does variation in reproductive strategies across a lineage affect the likelihood adaptive  
217 radiation will occur?
- 218 • Does developmental variation play a role in AR?

219

220 **The Environment**

221 *The niche and ecological speciation*

222 The fundamental ecological niche describes the set of conditions in which a species can persist and is  
223 a central concept in ecology. Species within ARs are typically described as being adapted to different  
224 niches and, as such, understanding niche differentiation is key to understanding species diversification  
225 and species persistence during ARs. As an AR unfolds, there is an increase in overall occupied niche  
226 space by the radiating clade, either resulting from the broadening of the niche of an ancestral lineage  
227 followed by niche partitioning, or the budding off and subsequent colonisation of novel niche space  
228 by daughter species. Ecological speciation, the divergence of populations resulting from divergent  
229 selection along ecological axes, has been demonstrated to underpin diversification in many ARs  
230 (Schluter 2000; Nosil 2012; Matsubayashi and Yamaguchi 2022). As a result, understanding links  
231 between niche differentiation and AR is critical to determining the mechanistic role of ecological  
232 diversification in the adaptive radiation process. The emergence of intrinsic barriers to gene flow as a  
233 result of niche differentiation is largely thought to require differentiation across multiple ecological  
234 axes, rather than just one. This has been demonstrated in plants, such as in teosinte where species are  
235 differentiated across both temperature and soil chemistry (Aguirre-Liguori et al. 2019) and in animals,  
236 including Alpine whitefish which are differentiated across both water depth and diet (Doenz et al.  
237 2018). Sequential diversification across multiple different axes of differentiation including habitat,  
238 feeding morphology, and patterning, has also been proposed as the foundation for particularly  
239 dramatic levels of diversification in some ARs of cichlid fishes (Kocher 2004). Theory also suggests  
240 that intrinsic barriers to gene flow may evolve more easily when divergence occurs across multiple  
241 axes of variation (Chevin et al. 2014). As a result, accurately delineating the components that make up  
242 the multidimensional ecological niche occupied by different species within the radiation and  
243 determining how differentiation across each of these axes evolved will be critical to understanding the  
244 AR process (also see chapter by Germain et al., this volume).

245

246 In contrast, the expansion of the niche and ecological differentiation during AR may only occur after  
247 the establishment of reproductive isolation (Losos and Ricklefs 2009; Gillespie et al. 2020). A recent  
248 comparative study on sister species in vertebrates suggested that ecological speciation through niche  
249 divergence was much less common (<10% of trait sets) than non-ecological speciation where  
250 incipient species occupy similar niches (Anderson and Weir 2022), indicating that the importance and  
251 broader prevalence of ecological speciation in diversification may have been somewhat overstated  
252 (Rundell and Price 2009; Czekanski-Moir and Rundell 2019). Since empirical data has implicated  
253 such ‘isolation first’ diversification in ARs (Cotoras et al. 2018), more tests of this hypothesis across  
254 different ARs are needed. Identifying recent speciation events and assessing the degree of niche  
255 overlap between the resulting species might allow us to identify whether new species within ARs arise  
256 by occupying different niches, or whether this is achieved only after reproductive barriers have been  
257 established. Additionally, comparing closely related repeated cases of ecological divergence and  
258 measuring both niche occupancy of radiating lineages and levels of reproductive isolation may help  
259 disentangle the directionality, predictability, and mechanisms of divergence.

260

261 Despite the central role of niche theory in the AR literature, several challenges have prevented a more  
262 comprehensive integration of ecological niche theory with mechanistic evolutionary models of  
263 diversification. One challenge is that producing representative and comparative niche descriptions of  
264 organisms inhabiting complex environments is challenging, which may result in oversimplified  
265 characterizations of environmental variation, such as only characterising the trophic niche of species  
266 as either herbivorous or carnivorous, or the habitat use of fish as simply limnetic or benthic. Rather  
267 than capturing the multidimensionality of niches, such simplified descriptors often exclude other, key,  
268 aspects of ecology relevant to the persistence of species, including the range of abiotic and biotic  
269 conditions over which species can survive (Schluter 2000). Although more sophisticated ways of  
270 representing multidimensional niche space have been developed (e.g., the “*N*-dimensional  
271 hypervolume”; Blonder et al. 2018, which builds on foundational work by Hutchinson (1957)), the  
272 level of abstraction of these metrics, and the empirical data required to accurately implement these

273 methods, makes them impractical as well as difficult to interpret. As a result, an intermediate  
274 approach, where continuous ecological data is used to provide a more detailed and comprehensive  
275 overview of niche quantification rather than categorical descriptor, may be a solution. Intermediate  
276 approaches avoid the need for overly abstract metrics that aim to capture all variation (see chapter by  
277 Germain et al., this volume) but are still sensitive to the possibility that multiple interacting factors  
278 may be important for diversification. Without developing this kind of nuanced approach and aiming to  
279 understand niche variation more comprehensively, and how it might change over the course of an AR  
280 (Harmon et al. 2019), it will remain challenging to draw comparisons across systems and to highlight  
281 components of the niche critical to the AR process.

282

283 The frequent lack of knowledge on the temporal consistency of niche divergence (or lack thereof) also  
284 poses challenges for assessing its contribution to the divergence process. Although some aspects of  
285 the biotic and abiotic environment may remain relatively consistent through time, facilitating species  
286 divergence and persistence, other aspects of the environment vary. Such fluctuations likely result in  
287 dynamic selection pressures which vary over time. These potential changes pose a significant  
288 challenge for estimating links between niche variation in organisms estimated at a single  
289 contemporary time point, and metrics of diversification. For instance, the irregular cycles of  
290 disturbances in oceanic archipelagos can both create and remove niche space and ecological  
291 opportunity (Whittaker 1995; and even result in species extinction - discussed in more detail below)  
292 but these dramatic historical changes are not necessarily reflected by contemporary patterns of  
293 organismal and environmental characteristics. Furthermore, cases of putative multidimensional  
294 adaptation and ecological speciation are known to proceed in non-linear ways, with populations  
295 varying through time in their degree of adaptation to a given environment as well as the strength of  
296 reproductive isolation. For example, barriers to gene flow between species can become both stronger  
297 and weaker over time in response to a number of different factors including organismal and  
298 environmental changes. This has been demonstrated by extreme cases, where reverse speciation has  
299 occurred between previously ecologically differentiated and reproductively isolated species, which

300 may be caused by rapidly changing abiotic and biotic environmental conditions. For example,  
301 anthropogenically-induced eutrophication of lakes led to the breakdown of ecological niches and  
302 subsequently ecological distinctiveness and reproductive isolation between Alpine whitefish species,  
303 which were previously more genetically differentiated (Vonlanthen et al. 2012; Frei et al. 2022).  
304 Radiating species themselves likely have a feedback effect on ecosystems, and as such can also play a  
305 role in changing the ecological landscape (Matthews et al. 2016). Early in the radiation process  
306 species that evolve may modify existing features of the environment resulting in the alteration,  
307 creation, or even loss of niches, resulting in substantial effects on ecological differentiation and  
308 speciation. For example, the co-occurrence of green ecomorphs in *Tetragnatha* spiders has been  
309 suggested as a potential trigger of ecomorph diversification through competition (Cotoras et al. 2018).  
310 This temporal variation makes it particularly challenging to determine which features drive AR,  
311 particularly based on inference from the most common forms of data, that of single timepoints. Better  
312 utilising both ecological and evolutionary time-series data, including the ever-growing feasibility of  
313 sequencing historical specimens (as used in Frei et al. 2022), investigating the fossil or sediment  
314 record (for those species which readily fossilise or are preserved in sediment deposits; Ngoepe et al.  
315 2023), or undertaking chronosequence-based approaches that involve sampling across successional  
316 landscapes such as volcanic islands or areas of glacier retreat, will be key to disentangling the  
317 temporal components of niche differentiation during ARs. Data from multiple timepoints or  
318 timepoint-equivalents would allow us to investigate both contemporary patterns of niche  
319 differentiation and the historical trajectory of change.

320

### 321 ***Biotic interactions***

322 One of the most complex and challenging barriers to better understanding the ecology of organisms  
323 and links between ecology and adaptive radiation is the fact that individuals, populations, and species  
324 rarely persist in isolation. In addition to the interactions between organisms and their environment  
325 (discussed above), biotic interactions both within and between species are key features of ecosystems,  
326 impacting adaptation and speciation. However, the complexity and temporal variation in biotic

327 interactions poses a challenge to quantifying and fully integrating their role into our understanding of  
328 the AR process. Biotic interactions play a significant role in the evolution and maintenance of  
329 ecological communities, shaping the fitness, abundances, spatial ranges, and, ultimately, the  
330 evolutionary trajectories of species (Weber et al. 2017). Five main types of biotic interactions have  
331 been described - competition, predation, herbivory, parasitism, and mutualism (Krebs 1985). Each of  
332 these may constitute a cause and, or, consequence of phenotypic divergence and speciation, and  
333 different types of interaction may impact different stages of the AR process. Many biotic interactions  
334 have negative effects on organismal fitness. As a result, biotic interactions may impose or alter  
335 selection pressures and reduce the likelihood of diversification due to directional selection.  
336 Alternatively, biotic interactions can sometimes promote diversification by causing divergent natural  
337 selection (Nosil 2012).

338

339 Competition can be a powerful agent of character displacement and divergent natural selection, and  
340 has been described as underpinning some of the most iconic ARs, including Darwin's finches, where  
341 food competition and changes to song drove divergence in beak size and shape (Huber and Podos  
342 2006; Grant 2017). While this process may not directly establish barriers to gene flow between  
343 populations (and in many cases reproductive isolation may have already built up), competition can  
344 cause organisms to switch to new niches which might have indirect, but important, implications for  
345 ecological speciation (discussed above; Brown and Wilson 1956). However, despite being frequently  
346 invoked as a driving force for niche differentiation, few studies have demonstrated its existence and,  
347 more importantly, its intensity. While the existence of competition is typically demonstrated or  
348 inferred using various proxies such as measuring feeding traits, recording foraging place or time, gut  
349 content analysis, or field observations, an explicit characterization of its intensity is challenging and,  
350 as a result, rarely reported. Since a limitation on resource availability is often the selective force that  
351 drives niche differentiation, a better understanding of competition will be key for understanding the  
352 AR process.

353

354 Although comparatively less well studied, the roles of other biotic interactions including herbivory  
355 and parasitism in driving AR have also been investigated. The links between herbivory and  
356 diversification have mostly been studied from a macroevolutionary perspective (Wheat et al. 2007).  
357 For example, there has been substantial interest in whether diversification is associated with an  
358 expansion in novel chemical defences in different plant species, making them distasteful or toxic to  
359 some herbivores (e.g., in Burseraceae; Becerra et al. 2009), or whether declines in chemical defences  
360 have facilitated diversification (e.g., in *Asclepias*/milkweeds; Agrawal et al. 2009). Parasitism has also  
361 been noted in ARs (also see chapter by Vanhove et al., this volume), with some stickleback  
362 populations being less resistant to parasites than others, suggesting that selection against migrants and  
363 parasite-mediated post-mating isolation may drive divergence (El Nagar and MacColl 2016).  
364

365 Many biological interactions shape the selective pressures that diverging lineages are exposed to, and  
366 while many types of interactions might result in lower fitness, they may have varying impacts on AR.  
367 Although competition for resources may favour diversification, predation might have the opposite  
368 effect, hindering diversification (McGee et al. 2020; Chaparro-Pedraza et al. 2022). However,  
369 mutualism is also prevalent across ARs, and by their nature, interactions of this kind drive  
370 diversification by facilitating the occupation of new niche space and leading directly to reproductive  
371 isolation (e.g., reinforcement; Hopkins 2013). For instance, plant-pollinator mutualisms have been  
372 shown to play a key role in diversification in several plant clades. Orchids of the genus *Disa* are  
373 pollinated by nearly all major groups of pollinating insects, with evidence of repeated adaptation to  
374 similar pollinators (Johnson et al. 1998). Moreover, in the bee orchid (*Ophrys*) radiation, divergence  
375 in floral scent and flower morphology presumably to attract different bee species may underlie  
376 speciation through pollinator shifts (Baguette et al. 2020). As with many interactions, mutualistic  
377 interactions are not always static in their nature through time, and the breakdown of mutualistic  
378 interactions into parasitic interactions have also been indicated as fuelling AR (e.g., in the *Yucca*  
379 moths; Pellmyr and Leebens-Mack 2000). Determining whether the presence or absence of certain  
380 biotic interactions is a cause or consequence of AR is challenging, not least because the effect of these

381 interactions on diversification may not be consistent across taxonomic groups or through the radiation  
382 process. Radiations thought to be catalysed by competitive interactions, for example, may undergo an  
383 early burst of diversification, but this rate may decrease over time (Martin and Richards 2019). This  
384 change in the extent and strength of biotic interactions over time represents eco-evo feedbacks where  
385 the evolution of lineages occupying new niches has an impact on the selective pressures that other  
386 organisms experience (directly or indirectly).

387

388 In extreme cases, biotic interactions and abiotic environmental change may impact fitness or  
389 demography so severely that populations or species go extinct (Frei et al. 2022). The link between  
390 extinction and AR is likely situation-dependent, and the specific consequences of extinction may  
391 depend on the specific species or populations that go extinct and the rate and amount of extinction,  
392 i.e., local extinction or total species loss (Losos 2010). Extinction may have a range of effects,  
393 including the reduction or altering of the network of biotic interactions within an ecosystem. While  
394 extinction may lead to the vacancy of niches, translating into novel opportunities for surviving  
395 lineages, it may also lead to the collapse of niche space, for example through trophic cascades or  
396 indirect interactions. Although it has been suggested that high turn-over rates of species on islands are  
397 expected to promote AR (Gillespie et al. 2020), associating divergence with extinction is challenging  
398 because many lineages have gone extinct without tangible evidence. Whether it is possible to infer  
399 extinction rates from phylogenetic data alone is controversial and it remains a challenge to accurately  
400 determine the frequency of extinction (Stadler 2011). Understanding the link between speciation and  
401 extinction may be particularly important, and difficult, if species are often ‘ephemeral’, with  
402 speciation occurring readily but most species failing to persist through time (Rosenblum et al. 2012).  
403 This ultimately limits our understanding on whether extinction and the changes to biotic interactions  
404 that follow (as well as subsequent abiotic changes) have a net positive or negative effect on  
405 diversification, speciation, and specifically, AR.

406

407 **The organism**

408 *Life history*

409 The role of specific, key, organismal traits in underpinning AR has been the focus of the many  
410 investigations. This focus stems from the tight links between trait utility, where a given trait confers a  
411 fitness advantage in a given environment, and diversification across ARs. As a result, many have  
412 aimed to identify whether specific traits, or variance in traits, might make lineages more likely to  
413 undergo ecological diversification and/or facilitate the establishment and maintenance of reproductive  
414 isolation. Due to the tight link between adaptation and the establishment of reproductive isolation  
415 across ARs, traits that impact both the number and size of offspring, and how organisms interact with  
416 their environment may play important roles in driving AR. One such aspect of organismal trait  
417 diversity is variation in life history strategies, which relates to the consequences of reproductive  
418 strategies and their role in organismal diversification (Stearns 1992). These life history traits include  
419 age and size at maturity, the size and number of offspring, lifespan, and body size. Since these traits  
420 may directly contribute to the occupation of a given niche or vary because they are associated with  
421 traits under direct selection, life history variation across a given clade may play an important role in  
422 diversification and coexistence of radiating species during AR. Many ARs are associated with  
423 substantial interspecific differences in life history traits (Schluter 2000), although, as with much  
424 interspecific variation, determining whether this variation drove speciation or emerged following  
425 speciation is challenging. One of the most well-studied ARs that exhibit life history variation is the  
426 radiation of lungless salamanders of the family Plethodontidae (Weaver et al. 2020). While some  
427 species within the family exhibit little phenotypic variation and have been the subject of studies  
428 focussing on non-adaptive radiations (Kozak et al. 2006; Rundell and Price 2009; Czekanski-Moir  
429 and Rundell 2019), other members of this species-rich radiation (which includes around 500 species)  
430 exhibit complex life cycles and differ greatly in their ontogenetic development (with or without larval  
431 stages), body sizes, and their age at first reproduction (Bruce 1996; Mueller et al. 2004). Another  
432 example relates to the cichlid fishes in Lake Tanganyika, in which about 250 ecologically,  
433 morphologically, and behaviourally distinct species evolved from a common ancestor in ~10 MY

434 (Ronco et al. 2021), offspring numbers per clutch range between 5 and >10,000 (Konings 2015;  
435 Ronco et al. 2019) and egg sizes vary from ~1-8 mm (Kuwamura 1986; Konings 2015). While it has  
436 been shown that several trait-complexes such as body shape and mouth and jaw morphology show a  
437 strong phenotype-environment correlation in the Tanganyika cichlid radiation (Ronco et al. 2021), the  
438 causal links between the evolution of life history traits, ecology, and AR are unknown, despite an  
439 amazing variance in strategies.

440  
441 To better determine the role of life history variation in facilitating or constraining ARs, and to avoid  
442 the pitfall of mistakenly highlighting all variables that correlate in some way with life history  
443 variation, it will be important to investigate study systems that have varying degrees of diversity but  
444 with minimal trait variation outside of life history variation, ecological differentiation, and  
445 reproductive isolation. Future research should also identify whether a propensity to radiate is  
446 impacted by the variance in specific life history traits or in the presence or absence of specific key  
447 innovations. This could be achieved by assessing whether radiating lineages exhibit a wide range of  
448 age at maturity, body size at maturity, number and size of offspring, and by determining whether this  
449 variation is an emergent property and axis of early variation during AR. Ideally, replicated study  
450 systems of varying ages could also be used to determine whether life history variation is important  
451 throughout the AR process or whether it plays a more prominent role in facilitating divergence early,  
452 or late, in the AR process.

453

#### 454 *Eco-evo-devo*

455 The challenge of mechanistically understanding how ARs evolve is made even more complicated by  
456 the fact that variation within an organism's lifetime can also have considerable impacts on evolution.  
457 Although key traits are often measured on adult organisms, the multitude of phenotypic changes that  
458 occur throughout an organism's development represent important aspects of variation which can  
459 easily be overlooked. Capturing developmental variation may be critical for understanding both how  
460 speciation generally proceeds, and specifically how ARs evolve, because this variation can have

461 significant impacts on key lineage characteristics, including demographic rates, reproductive rates,  
462 and interactions with other organisms. For example, body size, which plays a substantial role in  
463 underpinning metabolic processes and ecological interactions (Woodward et al. 2005; Eklöf et al.  
464 2013), can increase four orders of magnitude throughout the lifetime of many fish species (Werner  
465 and Gilliam 1984), resulting in large, rapid, changes in the composition of populations and  
466 communities, and potentially contributing to the speciation process (Persson and de Roos 2013;  
467 Rudolf and Rasmussen 2013; Chaparro-Pedraza and de Roos 2020). Variation of this kind can, in  
468 turn, have substantial knock-on effects to population dynamics and biotic interactions. For example,  
469 an increase in the mortality rates of juveniles relative to adults could strengthen intraspecific  
470 competition, induce frequency-dependent selection, and potentially culminate in adaptive  
471 diversification (Chaparro-Pedraza 2022).

472

473 As a result, developmental variation has been studied across multiple ARs. This work has successfully  
474 highlighted a strong link between developmental variation, ecological opportunity, and ontogenetic  
475 shifts in habitats, diets, and resource requirements across ARs (Schluter 2000). Developmental  
476 changes occur across a variety of traits, meaning that over the course of their development and  
477 maturity individual organisms can vary widely in the ecological niches they occupy. For instance,  
478 predatory species that emerge from ARs and subsequently feed on other AR members have been  
479 described in various systems, including the African Lake cichlid radiations (Seehausen 2006), the  
480 Bahamas *Cyprinodon* pupfish radiations (Martin and Wainwright 2011), and the Lake Baikal  
481 amphipod radiation (Naumenko et al. 2017). Yet, because predators usually require an advantage in  
482 body size over their prey species (between 0.5 and 4 orders of magnitude; Heckmann et al. 2012), this  
483 ecological niche is typically only accessible for larger, older individuals.

484

485 In addition to modulating traits throughout an organism's lifetime, developmental variation can play a  
486 key role in differentiating species that result from AR and underpinning key innovations. A number of  
487 studies have investigated key morphological innovations that facilitate niche expansion during AR

488 (summarised in Miller et al. 2023). Developmental variation that impacts how organisms interact with  
489 their specialised niche has been demonstrated in Darwin's finches, where beak height, a key axis of  
490 ecological variation and a trait involved in the establishment of reproductive isolation via its impact  
491 on song (Huber and Podos 2006), is related to the expression of the *BMP4* gene during development  
492 (Abzhanov et al. 2004). Similarly, in the Hawaiian spiny-legs, individuals of the species *Tetragnatha*  
493 *polychromata* change their colour and subsequently their trophic niche during development (Brewer  
494 et al. 2015). It is therefore likely that different selective pressures affect these species throughout their  
495 lifetime. Trying to determine the role of ontogenetic trait and niche shifts in facilitating AR will  
496 involve characterising organismal traits across ontogenetic stages and constitutes a challenging, but  
497 essential, avenue of future research.

498

499 Despite the potential for ontogenetic niche shifts (heterochrony) to facilitate adaptive divergence, and  
500 play a role in the AR process, theoretical work has shown that developmental changes may, in fact,  
501 hinder the radiation process. For example, while piscivorous morphs attain the largest body size  
502 among the African Lake cichlid radiations (Seehausen 2006), and their distinct piscivore-specific  
503 morphologies have already developed at the larval stage, they do not realise these ecological niches  
504 until they are adults, with small-bodied juvenile cichlids of many different morphs still competing for  
505 similar resources (Singh et al. 2017). As a result, and despite the widespread nature of ontogenetic  
506 diet shifts in different animal lineages (Werner 1988), this increased competition at the larval stages  
507 can potentially hinder AR, even in the presence of extensive ecological opportunity (Ten Brink and  
508 Seehausen 2022).

509

510 Evo-devo studies have already provided evidence of developmental variation underpinning important  
511 aspects of variation across ARs, but the degree to which analogous developmental changes may play a  
512 key role in facilitating AR in different taxa is unclear. Instances of re-use and re-wiring of  
513 developmental networks and developmental variation being associated with evolutionary innovation  
514 appear to be especially widespread across ARs (e.g., the evolution of morphological novelty via the

515 re-wiring of ancestral gene-regulatory networks in cichlid radiations; Mehta et al. 2021; Singh et al.  
516 2021). One classic example of evolutionary innovation being associated with developmental variation  
517 is the functionally decoupled oral and pharyngeal jaws of cichlid fishes (Liem 1973). Recent work  
518 shows that varying levels of modularity between the two jaws in younger versus older cichlid  
519 radiations may play a role in their propensity to diversify (Conith and Albertson 2021). Evolutionary  
520 developmental mechanisms have also given rise to key innovations and AR in plants (Fernández-  
521 Mazuecos and Glover 2017), including the evolution of flowers, which enabled radiation through  
522 plant-pollinator interactions (Grimaldi 1999). Early-diverging lineages of the angiosperm radiation  
523 exhibited lower floral development specialisation and were species-poor, in contrast to the species-  
524 rich groups with highly specialised flowers such as orchids (Melzer and Theißen 2016).

525 Developmental changes in the floral tube and stigma have contributed to the AR of *Petunia* in South  
526 America, giving rise to 20 species in <3 MY (Reck-Kortmann et al. 2014). Ecological speciation in  
527 *Petunia* spp. has been linked to molecular changes in the R2R3-MYB family of transcriptional  
528 regulators that modulate plant floral development (Yuan et al. 2013). In the iconic AR of Hawaiian  
529 silverswords, it has been found that diverse species of trees, shrubs, mats, and vines have evolved  
530 from ancestral tarweed with major shifts in body plans as a result of regulatory changes in  
531 developmental pathways in <6 MY (Purugganan and Robichaux 2005).

532

533 Future research focusing on identifying differences in development between radiating species will be  
534 important to understand how eco-evo-devo contributes to speciation and AR, as links between evo-  
535 devo variation and a mechanistic understanding of speciation and AR remain tenuous and largely  
536 species-specific. For example, frameworks such as West-Eberhard's flexible-stem hypothesis (2003),  
537 which suggests that ancestral developmental plasticity sets the stage for AR, have aimed to  
538 mechanistically link developmental variation and AR. However, evidence supporting this hypothesis  
539 is scarce, as founder populations of most ARs no longer exist and have usually not left a substantial  
540 fossil record from which developmental variation can be studied. This has made it particularly  
541 challenging to identify causative aspects of developmental variation that may be critical for lineages

542 to radiate. Future studies investigating the link between developmental variation and adaptive  
543 radiation should also investigate the role of developmental plasticity, which has been thought of as an  
544 important precursor to the emergence of evolutionary innovations, a feature of ARs (West-Eberhard  
545 1989; Moczek et al. 2011). The presence of developmental plasticity in a lineage may have a strong  
546 influence on the propensity for a lineage to radiate since it may act as an avenue for species to  
547 colonise previously unoccupied niches (Hunter 1998), provided that these changes become heritable  
548 (genetic assimilation).

549

### 550 **Next steps – perspectives for future adaptive radiation research**

551 In our pursuit of better understanding how ARs evolve and the role of different aspects of organisms  
552 and their environments in driving or constraining AR two broad barriers remain: 1) overcoming the  
553 limitations of studying the diversification process with data from only one, or a limited number of,  
554 timepoints; and 2) separating mechanistic links between, often simplified, ecological factors and  
555 diversification from indirect, sporadic, or spurious, associations. These challenges are not unique to  
556 understanding AR, and a better understanding of both will also help disentangle the speciation process  
557 more broadly. Additionally, there are a number of complex aspects of ecology (some of which are  
558 outlined above) which, despite exhibiting substantial variation across ARs, have yet to be fully  
559 integrated into our understanding of how and why some lineages diverge while others do not, and as  
560 such are ripe for future investigations into ARs.

561

### 562 ***Assessing variation through time***

563 To better understand the mechanistic role of organismal or environmental factors in AR, and  
564 speciation more broadly, future studies should focus on trying to address questions in Box 1 while  
565 accounting, where possible, for the possibility that the factors that drive diversification act at specific  
566 timepoints in the AR process. This will involve expanding on correlative investigations based on data  
567 from a single timepoint and into time-series based investigations that involve the collection of data  
568 spanning organismal traits, environmental characteristics, links between organisms and their

569 environment as well as the establishment of phenotypic and genomic differentiation through time. For  
570 example, measuring trait values within and between sister taxa at multiple timepoints will help  
571 determine whether changes in reproductive isolation or genetic divergence are positively correlated  
572 with trait change across time. While such approaches may not be possible in many old radiations,  
573 where contemporary dynamics in traits and reproductive isolation may be heavily influenced by short-  
574 term environmental stochasticity, producing and analysing time-series data across systems where  
575 evolutionary replicates are known to be of different ages may be particularly valuable. This approach  
576 will help characterise the trajectory of phenotypic diversification and will reveal whether species are  
577 becoming more or less differentiated over time. Future studies may consider measuring changes in  
578 phenotypic differentiation between timepoints i.e.,  $\Delta P_{ST}$  and changes in gene flow or reproductive  
579 isolation between timepoints i.e.,  $\Delta RI$ . These studies would help determine whether the role of  
580 different lineage and environmental characteristics in driving diversification is consistent across  
581 timepoints, indicating a constant key role of a given organismal or environmental characteristic, or  
582 whether variation in these associations through time reflects a scenario in which different factors play  
583 key roles at different parts of the radiation process. Future theoretical work should also aim to  
584 complement empirical investigations by explicitly including variable organismal traits, environmental  
585 conditions, and interactions to determine the ranges of conditions over which we might expect to see  
586 ARs persisting through time, resulting in more realistic and testable neutral expectations. This  
587 combination of theoretical and empirical studies would also help identify the role of chance and  
588 historical contingency, or a mixture of predictability and chance, in the evolution of ARs (see chapter  
589 by Roesti et al., this volume).

590

### 591 ***Separating correlation from causation***

592 Studying repeated diversification amongst closely related species may be one of the few ways to  
593 avoid the pitfalls of trying to compare the causes and outcomes of speciation across taxonomic clades.  
594 Experimental approaches where abiotic or biotic factors are modified are also excellent ways to  
595 understand their impact in speciation (Rice and Hostert 1993), niche occupation, and coexistence

596 (Pringle et al. 2019). For instance, raising different populations of *Drosophila melanogaster* on  
597 similar or different food mediums allows a quantification of the degree of reproductive isolation  
598 between pairs of populations (Rice and Hostert 1993). In their review of lab experiments aimed at  
599 understanding speciation, Rice and Hostert (1993) concluded that reproductive isolation evolved more  
600 readily when populations evolved in different environments, compared to when populations had  
601 evolved in similar environments (although a subsequent meta-analysis of research published since has  
602 failed to find any empirical support for this claim; B.J. Jarret et al. unpubl.). Findings from  
603 experimental evolution approaches can help address key questions, including identifying the role of  
604 ecological differentiation in speciation (discussed in more detail above; MacLean 2005; Stelkens and  
605 Bendixsen 2022), and can subsequently be used to guide investigations in natural systems such as  
606 ARs. Furthermore, ARs with independent instances of repeated diversification are particularly useful  
607 systems for undertaking such studies since they provide some degree of evolutionary replication and,  
608 depending on the types of ecosystems they span, can even act as natural experiments where biotic and  
609 abiotic conditions and traits vary between independent radiations (Gillespie 2004; Mahler et al. 2013;  
610 Cerca et al. 2023).

611  
612 ***Are islands the answer?***

613 Undoubtedly, some natural systems lend themselves to addressing outstanding questions in ARs more  
614 than others, particularly with regard to overcoming the challenges outlined above. ARs that are  
615 relatively simple, or even manipulatable, where it is possible to understand organismal and  
616 environmental variation and metrics of diversification without resorting to oversimplifying  
617 ecosystems are particularly valuable. While many ARs do not fulfil these criteria, with some  
618 particularly complex and speciose systems being almost antithetical to a desired simplified system,  
619 island radiations represent compelling study systems to address some of the most pressing questions  
620 posed in Box 1 while overcoming the challenges outlined above. Island radiations that include islands  
621 of different ages may help us establish the trajectory of change in phenotype and reproductive  
622 isolation and instances where similar variation has evolved independently across islands may help us

623 better understand causative factors that drive or constrain differentiation (also see chapter by Illera et  
624 al., this volume). Semi-isolated island ecosystems including volcanic oceanic islands, mountain tops,  
625 and expansive lake systems are known to harbour a substantial number of the world's ARs, and as a  
626 result have already formed the basis of a significant amount of research into ARs (Losos and Ricklefs  
627 2009; Gillespie et al. 2020; Schenk 2021; Cerca et al. 2023; Miles et al. 2023). Additionally, since  
628 islands have historically been the focus of substantial ecological investigations, we often have a  
629 particularly detailed understanding of their biodiversity, climatic variation, and even the mechanisms  
630 that led to their formation (MacArthur and Wilson 1967; Simberloff and Wilson 1969; Whittaker et  
631 al. 2008; Valente et al. 2020). This glut of information for many island systems lends itself for teasing  
632 apart the topics outlined above, and opens the door for more detailed investigations with the power to  
633 look across spatial and temporal scales. Perhaps unsurprisingly, given the number of empirical  
634 examples of island ARs, theoretical work has confirmed the suitability of island archipelagos for AR  
635 (Kagawa and Seehausen 2020), as a result of the metapopulation dynamics that can play out across  
636 discrete areas of suitable habitat.

637

638 Islands also have a number of unique features which may have promoted ARs, including an  
639 abundance of fluctuating geographic barriers which may have provided important opportunities for  
640 populations to establish in allopatry, prior to (or in the absence of) ecological differentiation, allowing  
641 the subsequent accumulation of differences through genetic drift and founder effects. These dynamics  
642 have been well-documented in highly diverse plant radiations on Andean 'sky-islands', in which  
643 glaciation led to 'flickering connectivity' between diverging populations on mountaintops (Nevado et  
644 al. 2018; Flantua et al. 2019). Additionally, instances of secondary contact between isolated  
645 populations may also lead to character displacement through directional selection (Lack 1983). This  
646 scenario has been proposed for explaining diversification across the *Tetragnatha* spiny-leg radiation,  
647 where multiple species that represent green morphs are thought to have emerged and subsequently  
648 segregated from one another geographically. Eventually, when multiple green morphs come into  
649 secondary contact in the presence of open niches, competition is thought to lead to directional

650 selection and the evolution of novel ecomorphs (Cotoras et al. 2018). Similarly, the rearrangement of  
651 dispersal barriers and the establishment of hybrid variants upon secondary contact has also been  
652 suggested as a way of generating diversity via strictly neutral processes (Sefc et al. 2017). Repeated  
653 cycles of disturbance on islands, such as volcanic eruptions, may also drive diversification through the  
654 creation and modification of environments, providing the opportunity for geographic isolation  
655 (Carson et al. 1990; Vandergast et al. 2004) and ecological variation (e.g., silverswords adapted to  
656 different lava substrates; Robichaux et al. 1990).

657

658 Finally, other features of islands, such as the degree of unbalanced taxonomic variation on oceanic  
659 islands or the total absence of specific taxa (e.g., non-flying mammals), may facilitate rapid  
660 diversification. The absence of specific clades may offer lineages the opportunity to occupy new  
661 niches, leading to extreme phenotypic and ecological variation. For instance, the plant family  
662 Asteraceae comprises mostly herbs and shrubs, but across different archipelagos tree-like forms have  
663 evolved repeatedly (Cerca et al. 2022). This in turn may provide opportunities for taxa able to  
664 colonise and establish to occupy niches that were not available across their original ranges, facilitating  
665 extreme phenotypic and ecological variation.

666

667 Islands may therefore form valuable study systems for advancing our understanding of speciation and  
668 the evolution of ARs by allowing us to identify the role of complex aspects of ecology in driving  
669 diversification, in turn overcoming some of the most difficult challenges facing the field. Systems  
670 with independent radiations with varying degrees of diversity, which have evolved on neighbouring  
671 islands (including oceanic islands or lakes) with varying ages and ecology may be particularly fruitful  
672 for future research into ARs. Future research should also continue to take advantage of valuable  
673 island-like lake systems which preserve evidence of historical diversity in the form of remains and  
674 fossils stored in sediment deposits, as these remains provide unique opportunities for disentangling  
675 how ARs evolve (as in Muschick et al. 2018 and Ngoepe et al. 2023).

676

677 **Concluding remarks**

678 ARs provide the opportunity to glean a mechanistic understanding of adaptation and speciation and  
679 the aspects of ecology, including various organismal and environmental traits, which underpin these  
680 processes. While it is currently unclear which factors drive or facilitate AR across taxa, future studies  
681 that aim to address this knowledge gap should purposefully focus on identifying causative factors and  
682 determining the role of different factors at various stages of the AR process. Future research should  
683 not shy away from complex aspects of ecology (outlined above) and should aim to avoid overly  
684 simplistic descriptions of key organismal and environmental features. These detailed future  
685 investigations will help advance our understanding of the remarkable phenotypic and species diversity  
686 we observe across ARs, the predictability of this diversification, and how applicable these processes  
687 are for the speciation process more broadly.

688

689

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