1    **Evolutionary ecology of specialisation: insights from phylogenetic**

2    **analysis**

3    Jana C. Vamosi[1], W. Scott Armbruster[2,3,4], and Susanne S. Renner[5]

4    *[1]Department of Biological Sciences, University of Calgary, Calgary, AB T2L 0Z3,*

5    *Canada*

6    *[2]School of Biological Sciences, University of Portsmouth, Portsmouth PO1 2DY,*

7    *UK[3]Institute of Arctic Biology, University of Alaska Fairbanks, Alaska 99709, USA*

8    *[4]Department of Biology, NTNU, N-7491 Trondheim, Norway*

9    *[5]Systematic Botany and Mycology, Department of Biology, University of Munich (LMU),*

10   *Munich 80638, Germany*

11   **In this Special Feature, we assemble studies that illustrate phylogenetic approaches**
12   **to studying salient questions regarding the effect of specialization in lineage**
13   **diversification. The studies use an array of techniques within a wide-ranging**
14   **collection of biological systems (plants, butterflies, fish, and amphibians are all**
15   **represented). Their results reveal that macroevolutionary examination of**
16   **specialisation provides insight into the patterns of trade-offs in specialized systems;**
17   **in particular, the genetic mechanisms of trade-offs appear to extend to very**
18   **different aspects of life history in different groups. In turn, because a species may be**
19   **a specialist from one perspective and a generalist in others, these trade-offs**
20   **influence whether we perceive specialisation to have effects on the**
21   **evolutionary success of a lineage when we only examine specialisation along a single**
22   **axis. Finally, how geographical range influences speciation and extinction of**
23   **specialist lineages remains a question rife with potential for further insight.**
24
25   1.INTRODUCTION
26
27          Specialisation is a repeated pattern in living systems, suggesting that there are

28   general mechanisms underlying its evolution. Clearly, every species interacts with only a

29   small subset of all other species and in only a subset of habitats. Thus, some constraints

30   on associations have simple explanations: biogeography and range limits preclude pairs

31   of species, or a species and a particular suite of environmental variables, from being in

32    the same vicinity. We do not currently have precise information on the extent to which

33    range limits enforce the levels of specialisation that we see in nature [1, 2]. Despite this

34    large knowledge gap, we have clear instances where species have access to many

35    potential mutualists or habitats, yet have evolved adaptations that restrict their

36    proportional usage [3, 4]. The evolution of these adaptations may themselves directly

37    affect the speciation process [5] or simply be associated with macroevolutionary and

38    macroecological patterns (e.g., diversification through correlated characters or reduced

39    geographical extent [6]). This Special Feature serves to highlight our current knowledge

40    on how evolution has produced clades and communities notable in their variation in the

41    level of specialization, despite a paucity of well-characterized pathways that might

42    produce such variation [7]. We focus especially on studies that employ a

43    macroevolutionary perspective to investigate (1) the evolutionary success of specialists

44    and (2) how specialisation is shaped by variation along multiple morphological and

45    environmental axes.

46

47    *(a) The Evolution of Specialisation*

48         Is specialisation a dead-end? A once-held view was that the evolution of

49    specialisation was a one-way street, with transitions back to a broader niche breadth

50    being restricted [8]. Recently, however, a growing number of studies of specialisation

51    indicate that transitions from specialisation to generalisation are possible [9, 10].

52    However, examinations of transitions in a phylogenetic context sometimes provide

53    conflicting results. In birds, transitions in the level of specialisation are rare [11]. Yet in

54    plants, there are many examples of reversals in specialisation [12]; for example,

55    pollinator breadth exhibits little phylogenetic signal [13]. Phytophagous insects also

56    exhibit equivocal results with transitions occurring in either direction [14, 15]. Thus,

57    evidence is mounting that specialisation is not an absolute "dead-end", even though a

58    disproportionate number of transitions may be in the direction of generalist to specialist

59    in some systems. However, the conditions and processes that lead to biases in transition

60    rates in one direction or the other remain poorly understood.

61        The envisioned pathway that would produce biased transitions from generalisation

62    to specialisation involves the idea of trade-offs, which however have proved elusive to

63    demonstrate empirically. The trade-offs might operate at the physiological level through

64    antagonistic pleiotropy [16]. For instance, C4 plant photosynthetic pathways have greater

65    efficiency in hot, dry environments, but lower photosynthetic rates in shaded, moist

66    environments [17]. Ecology could enhance the evolution of specialisation through

67    producing further genetic trade-offs. If a certain environment were more common (e.g.,

68    dry environments in the above example), deleterious mutations that affect the

69    performance in other environments might accumulate [18]. If these changes represented

70    loss-of-function mutations, reversals towards a generalist state would be rare. Whether

71    physiological or genetic trade-offs occur in tandem or independently is not well

72    characterized, nor is there much compelling evidence of irreversibility [12].

73        Notably, the difficulty of defining and detecting specialisation hampers our ability

74    to pinpoint its pathways and trade-offs. In the evolution of specialisation of plants on

75    pollinators, steep trade-offs (where adaptions improving the attraction or use of one

76    pollinator decrease the attraction or use of others) will generally favour specialisation

77    [19]. Studies on plant-pollinator specialisation in particular have provided many

78  examples showing how caution must be exercised in inferring fitness trade-offs from

79  morphological traits ("phenotypic specialisation", e.g., long corolla tubes [20]).

80  Classically, floral corolla tubes were one trait conceived as an appropriate indicator of

81  reduction in biotic partnerships (narrow corolla tubes suggesting efficient pollination by

82  hummingbirds and poor pollination by bees and vice versa for wide corolla tubes [21]).

83  Many cases of apparent specialisation on certain functional groups pollinators have been

84  observed to be, in fact, ecologically generalized (e.g. flowers with wide corollas are

85  visited by insect and birds [22-24]).

86       Characterization of trade-offs is further complicated because they can occur at

87  different scales and involve different aspects of a species' biology [25] (see *Axes of*

88  *Specialisation*).  This complexity has led to the somewhat perplexing view that trade-offs

89  are uncommon, at least in within-species comparisons [25]. Intriguingly, the elusive

90  nature of trade-offs spurred investigation of whether they were an essential condition - a

91  theoretical study by Muchhala and colleagues [26] demonstrated that the selective cost of

92  lost pollen alone is sufficient to drive specialisation even in the absence of trade-offs. To

93  date, there have been few phylogenetic comparisons, yet analyses of host-pathogen and

94  plant-pollinator associations suggest that the ability to incorporate a certain plant species

95  into diet breadth is correlated with phylogenetic distance [27-29]. This suggests that

96  specialisation on clades of hosts or mutualists is widespread and that the use of certain

97  hosts is indeed lost over evolutionary time-scales. Notably, this pattern is consistent with

98  trade-offs, but also consistent with ecological models of the loss of selection for

99  interacting with hosts or mutualists that are outside of a species' range.

100        From a macroecological perspective, there is one additional reason to expect the

101    appearance of dead-ends with transitions to the specialist state [6]. If specialists occupy a

102    narrow niche, they often also occupy smaller ranges [1], and endemics are more

103    susceptible to extinction [6, 30]. While some data suggest that the evolution of

104    specialisation is associated with evolutionary success in plants [31], habitat specialisation

105    is correlated with increased extinction risk in birds and bumble bees [32, 33]. If

106    specialists go extinct more frequently, most specialists will appear as young lineages on

107    phylogenetic trees [34] that have had less opportunity to transition to a generalist state

108    [10]. Species occupying a smaller range can also be less likely to speciate [35, 36]. Both

109    of these processes would produce a pattern whereby there are more extant generalist

110    lineages, each with the potential to transition to a more specialized state. Yet there are

111    examples that show empirical support for the opposite as well, with generalists exhibiting

112    higher extinction risk, at least in Odonata [37].

113        In this volume, we examine how "evolutionary success" in terms of speciation

114    and extinction rates varies with specialisation and document transitions between

115    specialisation and generalisation. Specialisation and generalisation in the diversification

116    of lepidopterans were examined for evidence of the musical chairs versus the oscillation

117    hypotheses [38]. Following a "musical chairs" model we might see that specialist clades

118    were more often transitioning between hosts, but remaining specialized, whereas in the

119    "oscillation" model we would predict that niche-breadth shifts (e.g. in phytophagy in

120    lepidopteran clades) from generalist to specialist would be more common. Rather than a

121    pattern of decreased diversification in specialist lepidopteran clades, Hardy and Otto find

122    more support for the Musical Chairs hypothesis [37]. In addition, they find a negative

123    relationship between host-plant breadth and diversification rates, with generalists

124    diversifying at lower rates because of their broad niches. This calls into question whether

125    specialisation can ever be considered a dead-end, at least in phytophagous insects. While

126    transitions to a more generalist state might be rare, host switching within specialist clades

127    is common and generates more species that are specialized, such that lowered

128    diversification rates will not be apparent. These patterns held despite the finding that

129    extinction rates were considerably lower in polyphagous lineages, suggesting that

130    specialists could potentially appear as evolutionary dead-ends due to declines in

131    persistence, but not due to trade-offs that prevent transitions back to a more generalized

132    state.

133          The Musical Chairs hypothesis may be clade-specific, as other patterns have been

134    seen in some plant-pollinator relationships. The shift from a specialized relationship (e.g.

135    pollination by few resin-collecting bees) to a generalized relationship (e.g. pollination by

136    many pollen-feeding insects) can be followed quickly by a reversal to a more specialized

137    relationship (e.g. pollination only by "buzz-pollinating" bees) [39]. This last example is

138    consistent with the oscillation hypothesis, which postulates that generalist lineages give

139    rise to specialist daughter species, but over time specialists can gradually add functions

140    and become more generalist. Similarly, in an analysis of pollinator breadth in

141    passionflowers, Abrahamczyk et al. [40] find that shifts are not disproportionately from

142    generalisation to specialisation. Instead, reliance on the sword-bill hummingbird

143    (*Ensifera ensifera*) appears to have evolved early on in a clade that then generated many

144    new species by allopatric isolation, some of which escaped from specialisation by

145    reducing their floral tubes, thereby being able to rely on a broader set of bird or bat

146    pollinators. In contrast to the idea that shifts in specialisation result in speciation

147    (pollinator shifts), Abrahamczyk et al. [40] find more evidence favouring biogeographical

148    shifts spurring the process of lineage splitting. In *Tritoniopsis revoluta* (Iridaceae)

149    Anderson et al. [41] report that pollinators vary geographically across the plant's range

150    and are closely associated with variation in floral traits, suggesting a strong role of

151    distribution and range in how biotic specialisation influences speciation (see *Range*

152    *extent, specialisation, and diversification).*

153        In summary, the studies in this Special Feature indicate that specialisation is not a

154    certain "dead-end" from an evolutionary perspective. First, transition from specialisation

155    to generalisation is possible and even prevalent in certain ecological contexts. Second,

156    specialisation in traits related to foraging or reproduction can be associated with

157    increased evolutionary success of some specialist clades, especially in specialist clades

158    that experience greater transition rates to different specialist states ("musical chairs"

159    pattern described above; Hardy and Otto [38]). Specialisation also need not by itself be

160    the driver of speciation. In the sword-bill-pollinated clade of passionflowers,

161    Abrahamczyk and colleagues find that specialized pollination is not the driver of

162    speciation but instead the precondition for successful species persistence in small

163    populations, which then adapt locally and evolve into separate species [40].

164        Hardy and Otto [38] raise the interesting point that the question of whether

165    specialisation influences speciation depends on how specialisation is defined: "One gray

166    area is how to define the relevant niche with respect to diversification, as generalists

167    along some axes (e.g., resource use) may be specialists along others (e.g., in host-

168    pathogen interactions). While theoretical models have shown that speciation is more

169    likely when phenotypes are multi-dimensional…this raises a challenge for empiricists

170    who must identify the phenotypic axes exhibiting the strongest diversifying selection in

171    order to detect relationships between niche breadth and speciation." Other authors in this

172    Special Feature also tackle the issue of multi-dimensional axes of specialisation.

173

174    *(b) The Axes of Specialisation*

175         Specialisation can be defined in a number of ways, and there are many ways to

176    expand the "Jack of all trades, master of none" paradigm. One way to define

177    specialisation is the breadth occupied by a species on niche axes. Most species probably

178    are a generalist on some axes and a specialist on others [16]. For example, some species

179    of *Dalechampia* (Euphorbiaceae) exhibit apparently compensatory

180    specialisation/generalisation on two pollination niches axes: specialisation on the

181    temporal axis (shorter duration of blooming season) is associated with generalisation in

182    the number of pollinator species used and vice versa [42]. A growing body of evidence

183    suggests that, while physiological trade-offs are uncommon, constraints may act to allow

184    for specialisation along alternate facets of a species' life history, e.g., where an advantage

185    with one biotic partner or in inhabiting one niche comes at the expense of dealing with

186    another [43-45]. Limits on floral specialisation may also accrue from conflicting selection

187    generated by herbivores or by abiotic factors. For example, specialisation on large bees

188    may select for large petals or bracts, but this may be countered by selection by herbivores

189    (that use the same cues to find host tissues) [46], selection for water conservation in xeric

190    environments [47, 48], or selection for rapid seed production in seasonal habitats [49-51].

191    Expanding the number of axes to include both biotic and abiotic specialisation can

192    also provide insight into the underlying forces that spur the evolution of specialisation.

193    For example, pollinators often select for larger corolla size, but such increases exert a

194    large cost in terms of water loss in dry environments [47, 48], as noted above. Without

195    information on the physical-environmental niche, it would be hard to ascertain why more

196    species do not display large flowers. Examining these trade-offs in a phylogenetic

197    framework can be a powerful approach to understanding the constraints on the evolution

198    of specialisation. Litsios et al. [52] provide evidence in this Special Feature of a negative

199    correlation between environmental tolerances (in temperature, salinity and pH) and host

200    specificities in clownfish and anemone mutualisms, which would likely confound

201    phylogenetic analyses of diversification along any single specialisation niche axis.

202    Further, if differential specialisation across resource axes is widespread, it may be a large

203    contributor to the local coexistence of specialist and generalist species [52], and provide

204    insight into the puzzling observation that specialists often do not outcompete generalists

205    [53].

206    Despite finding that multiple axes contribute to specialisation and interact to

207    influence its evolution [16], we have little information on whether abiotic or biotic factors

208    are more likely to drive specialisation, or whether dispersal and geographic range provide

209    environmental heterogeneity to spur initial transitions to specialisation. Muschick et al.

210    [54] examine these questions in this volume using the radiation of cichlids in Lake

211    Tanganyika, testing the idea that specialisation along multiple niche axes occurs

212    according to a common sequence of transitions. In these cichlids, subdivision of trophic

213    traits occurs in the early stages of adaptive radiation, while sexual communication traits

214    diversify late in the radiation. The phylogenetic analysis of Muschick and colleagues [54]

215    also finds limited support that specialisation along biotic niche axes (diet) precedes

216    specialisation along abiotic niche axes (macrohabitat).

217

218    *(c) Range Extent, Specialisation, and Diversification*

219         Environmental heterogeneity is a key factor both in the evolution of specialisation

220    and in the evolutionary success of the resulting lineage [7]. For example, if spatial

221    heterogeneity is such that the abundance of a commonly used host changes rapidly over

222    space (beta-diversity is high), this should accelerate the evolution of specialisation [41].

223    Much of the work in this area is done with herbivorous insects, with some studies

224    suggesting that generalisation is positively associated with large range size [55] and

225    others finding cases where a specialist can have a much larger range if its host species is

226    widespread [56]. Models of the evolution of specialisation that incorporate environmental

227    heterogeneity and associative mating indicate that these variables can result in a decrease

228    in gene flow between environments and contribute to speciation [7]. Anderson et al. [41]

229    examined pollinators in different parts of a plant species' range and found a close

230    association between floral traits and the traits of the pollinators in the region but did not

231    find strong evidence that these patterns greatly influenced gene flow and dispersal.

232    Presumably if selection pressures were consistent for generations, speciation could occur,

233    yet pollinators may be too variable between years [57]. Further work on the interplay

234    between dispersal, range, and beta-diversity would lend insight into how specialisation

235    evolves and persists as well as the propensity of these factors to lead to speciation.

236    Widely dispersing organisms are more likely to have opportunities to expand their

237    geographical range [58]. Species occupying large ranges should experience divergent

238    selection pressures upon their constituent populations; heterogeneity of selection

239    pressures may in turn provide selection towards generalisation across the entire species

240    (leading to its scoring as a generalist in a phylogenetic trait reconstruction that might use

241    just one accession to represent the species), but selection for different specialists at the

242    local population level. Bonetti and Wiens [59] find evidence in amphibians, however, that

243    the causal arrow could point in the opposite direction, with species with wide climatic

244    tolerances having the ability to persist in a greater number of locations than generalists.

245    Range size could then influence the heterogeneity in selection pressures from biotic

246    partnerships, allowing specialisation to evolve in other niche axes. Bonetti and Wiens

247    [59] find trait associations consistent with these expectations, with species having broad

248    tolerances for variation in temperature and precipitation rather than trade-offs in these

249    tolerances. For example, specialisation along the climatic niche can reduce range size and

250    set up conditions conducive to the evolution of specialisation along other niche

251    dimensions. Thus, we can observe associations in the levels of specialisation between

252    different axes of specialisation rather than trade-offs.

253

254    *(d) Conclusions and Future Directions*

255    Forister et al. [60] list a number of interesting unanswered questions in the

256    evolutionary ecology of specialisation. While they concentrated on plant-insect

257    associations, we attempt here to examine the process in a range of invertebrate and

258    vertebrate systems (butterflies, bees, hummingbirds, amphibians, fish lineages). The

259  problem of how to define specialisation remains. Generally, our view of trade-offs

260  appears to be widening, and this broadened perspective has the consequence of making

261  trade-offs more readily apparent. Whether or not trade-offs are observed depends on how

262  wide we cast the net; trade-offs do appear to be an important characteristic of

263  specialisation if we allow that they may operate between very disparate facets of a

264  species' life history (e.g., pollination and herbivory). Furthermore, the issue of dispersal

265  and range size presents further complicating factors, influencing the number and

266  combinations of conditions encountered (and therefore the trade-offs observed). Recent

267  studies indicate that the association between range size and niche breadth may vary in its

268  strength depending on niche position as well as the axes of the niche (dietary or habitat)

269  examined [61], suggesting that the complexity of these factors will provide an active area

270  of research for some time.

271      From a conservation perspective, specialists are some of our most charismatic

272  species, with the sword-billed hummingbird and the ca. 50 species of plants that

273  completely depend on it for pollination being a striking example. Thus, specialist species

274  often receive greater conservation attention than do generalists [62]. Although there is

275  evidence that specialists can exhibit superior competitive strategies in their element (for

276  foraging and/or reproductive assurance) [63], there is also evidence that their greater

277  reliance on a smaller subset of species puts them at greater risk of extinction [64].

278  Historically, a central question raised about specialisation was whether it commonly

279  represented a dead-end [65]. From a macroevolutionary perspective, specialist clades

280  may play a particularly important role in generating additional species at high rates due to

281  host switching (the Musical Chairs process; see [38]), and this process would tend to

282    make many specialists species appear "young" on phylogenies. With the current

283    conservation focus on the phylogenetic uniqueness of a given species [66], one

284    implication is that the "young" nature of many specialists may put them at lower

285    prioritization for conservation. Additionally, while there is little evidence to suggest that

286    specialisation is irreversible or associated with lower speciation rates, specialist clades

287    can experience higher extinction rates. Elevated speciation rates may buffer specialist

288    clades from being lost to extinction to a certain extent [67], but further research should

289    examine which specialist clades may be at the limits of the compensatory effects of

290    speciation and experiencing net declines in species richness.

291        Network studies are providing some valuable insight into how specialisation

292    varies among communities. However, while connectance (the number of links between

293    trophic levels compared to the maximum possible) is often equated with stability, loss of

294    specialists will appear as increased connectance in networks [68]. Additionally, gain of a

295    high proportion of weedy generalist species in numerous communities will result in

296    lowered beta-diversity and more homogeneous community composition over larger

297    spatial scales [69]. While these two outcomes would suggest that we lose biodiversity

298    despite increasing stability in networks, there are at least two reasons to suggest that

299    specialists may be as robust as generalists to environmental perturbations. First, specialist

300    species often rely on generalist partners (i.e., networks tend to be asymmetrical and

301    nested) [70, 71]. Second, as exemplified in clownfish in this Special Feature, generalist-

302    specialist trade-offs across multiple resource axes will act as a buffering force, such that

303    specialists in bipartite networks may be habitat generalists, thus providing a further

304    balancing mechanism that allows for coexistence of species [52]. Recent studies have

305 incorporated macroevolutionary and phylogenetic approaches into network studies to

306 reveal the influence of shared traits on forming network interactions [28, 64], and the new

307 metrics currently emerging [72] will likely further provide an important link between the

308 influences of evolutionary history, traits, and environmental heterogeneity.

309        In summary, specialists can experience greater evolutionary success compared to

310 their generalist counterparts, possibly due to the very trade-offs that often drive

311 specialisation. In cases where we observe specialisation along a number of different niche

312 axes, historical range size may provide insight into how suites of specialized traits arise in

313 lineages. Some of these insights would be impossible to gain without using a

314 macroevolutionary perspective, and the studies in this issue highlight how comparative

315 phylogenetic analysis sheds light on general principles underlying the evolution and

316 persistence of specialized interactions.

317

318 **REFERENCES**

319 1. Williams S.E., Williams Y.M., VanDerWal J., Isaac J.L., Shoo L.P., Johnson C.N.
320     2009 Ecological specialization and population size in a biodiversity hotspot:
321     how rare species avoid extinction. *Proc Natl Acad Sci USA* **17**, 19737-19741.
322 2. Devictor V., Clavel J., Julliard R., Lavergne S., Mouillot D., W. T., Venail P.,
323     Villeger S., Mouquet N. 2010 Defining and measuring ecological
324     specialization. *J Appl Ecol* **47**, 15–25.
325 3. Fenster C.B., Armbruster W.S., Dudash M.R. 2009 Specialization of flowers: is
326     floral orientation an overlooked first step? *New Phytologist* **183**(3), 502-506.
327 4. Buckley L.B., Davies T.J., Ackerly D.D., Kraft N.J.B., Harrison S.P., Anacker B.L.,
328     Cornell H.V., Damschen E.I., Grytnes J.-A., Hawkins B.A., et al. 2010 Phylogeny,
329     niche conservatism and the latitudinal diversity gradient in mammals.
330     *Proceedings of the Royal Society B: Biological Sciences.*
331     (doi:10.1098/rspb.2010.0179).
332 5. Kay K.M., Sargent R.D. 2009 The role of animal pollination in plant speciation:
333     integrating ecology, geography and genetics. *Annual Review of Ecology,*
334     *Evolution and Systematics* **40** 637-656.

335 6.     Colles A., Liow L.H., Prinzing A. 2009 Are specialists at risk under
336         environmental change? Neoecological, paleoecological and phylogenetic
337         approaches. *12*, 849–863.
338 7.     Whitlock M.C. 1996 The Red Queen beats the Jack-of-all-trades: the
339         limitations on the evolution of phenotypic plasticity and niche breadth.
340         *American Naturalist* **148**, S65-S77.
341 8.     Moran N.A. 1988 The evolution of host-plant alternation in Aphids: evidence
342         for specialization as a dead end. *Am Nat* **132**, 681-706.
343 9.     Armbruster W.S., Baldwin B.G. 1998 Switch from specialized to generalized
344         pollination. *Nature* **394**(6694), 621.
345 10.    Schluter D. 2000 *The ecology of adaptive radiation*. Oxford, Oxford University
346         Press.
347 11.    Brandle M., Prinzing A., Pfeifer R., Brandl R. 2002 Dietary niche breadth for
348         Central European birds: correlations with species-specific traits. *Evol Ecol*
349         *Res* **4**, 643–657.
350 12.    Barrett S.C.H. 2013 The evolution of plant reproductive systems: how often
351         are transitions irreversible? *Proc Roy Soc Lond B* **280**, 20130913.
352 13.    Sargent R.D., Vamosi J.C. 2008 The influence of canopy position, pollinator
353         syndrome, and region on evolutionary transitions in pollinator guild size. *Int*
354         *J Plant Sci* **169**, 39-47.
355 14.    Nosil P. 2002 Transition rates between specialization and generalization in
356         phytophagous insects. *Evolution* **56**, 1701-1706.
357 15.    Nosil P., Mooers A.O. 2005 Testing hypotheses about ecological specialization
358         using phylogenetic trees. *Evolution* **59**, 2256-2263.
359 16.    Poisot T., Bever J.D., Nemri A., Thrall P.H., Hochberg M.E. 2011 A conceptual
360         framework for the evolution of ecological specialisation. *Ecol Lett* **14**, 841–
361         851.
362 17.    Edwards E.J., Osborne C.P., Strömberg C.A.E., Smith S.A., Consortium C.G.
363         2010 The origins of C4 grasslands: integrating evolutionary and ecosystem
364         science. *Science* **328,**, 587–591.
365 18.    Jasmin J.-N., Kassen R. 2007 On the experimental evolution of specialization
366         and diversity in heterogeneous environments. . *Ecol Lett* **10**, 272-281.
367 19.    Castellanos M.C., Wilson P., Thomson J.D. 2003 Pollen transfer by
368         hummingbirds and bumblebees, and the divergence of pollination modes.
369         *Evolution* **57**, 2742-2752.
370 20.    Ollerton J., Killick A., Lamborn E., Watts S., Whiston M. 2007 Multiple
371         meanings and modes: on the many ways to be a generalist flower. *Taxon* **56**,
372         717–728.
373 21.    Faegri K., van der Pijl L. 1979 *The Principles of Pollination Ecology*. Oxford,
374         Pergamon Press.
375 22.    Aigner P.A. 2006 The evolution of specialized floral phenotypes in a fine-
376         grained pollination environment. In *Plant–pollinator interactions: from*
377         *specialization to generalization* (eds. Waser N., Ollerton J.), pp. 23–46.
378         Chicago, University of Chicago Press.
379 23.    Aigner P.A. 2004 Floral specialization without trade-offs: optimal corolla
380         flare in contrasting pollination environments. *Ecology* **85**, 2560–2569.

381  24.    Aigner P.A. 2001 Optimality modeling and fitness trade-offs: when should
382         plants become pollinator specialists? *Oikos* **95**, 177–184.
383  25.    Armbruster W.S. 2014 Floral specialization and angiosperm diversity:
384         phenotypic divergence, fitness trade-offs and realized pollination accuracy.
385         *Annals of Botany* **6**, plu003.
386  26.    Muchhala N., Brown Z., Armbruster W.S., Potts M.D. 2010 Competition drives
387         specialization in pollination systems through costs to male fitness. *Am Nat*
388         **176**, 732-743.
389  27.    Gilbert G.S., Webb C.O. 2007 Phylogenetic signal in plant pathogen-host
390         range. *Proc Nat Acad Sci USA* **104**, 4979-4983.
391  28.    Vamosi J.C., Moray C.M., Garcha N.K., Chamberlain S.A., Mooers A.Ø. 2014
392         Pollinators visit related plant species across 29 plant–pollinator networks.
393         *Ecology and Evolution* **4**(12), 2303-2315. (doi:10.1002/ece3.1051).
394  29.    Weiblen G.D., Webb C.O., Novotny V., Basset Y., Miller. S.E. 2006 Phylogenetic
395         dispersion of host use in a tropical insect herbivore community. *Ecology* **87**,
396         S62–S75.
397  30.    McKinney M. 1997 Extinction vulnerability and selectivity: combining
398         ecological and paleontological views. *Annu Rev Ecol Syst* **28**, 495–516.
399  31.    Crepet W.L., Niklas K.J. 2009 Darwin's second "abominable mystery": why are
400         there so many angiosperm species? *Am J Bot* **96**, 366-381.
401  32.    Julliard R., Jiguet F., Couvet D. 2003 Common birds facing global changes:
402         what makes a species at risk? *Glob Chang Biol* **20**, 148–154.
403  33.    Williams P. 2005 Does specialization explain rarity among British
404         bumblebees? A response to Goulson et al. *Biol Conserv* **122**, 33-43.
405  34.    Futuyma D.J., Moreno G. 1988 The evolution of ecological specialization. *Annu*
406         *Rev Ecol Syst* **19**, 207–233.
407  35.    Vamosi S.M., Vamosi J.C. 2012 Causes and consequences of range size
408         variation: the influence of traits, speciation, and extinction. . *Frontiers of*
409         *Biogeography* **4**(4).
410  36.    Owens I.P.F., Bennett P.M., Harvey P.H. 1999 Species richness among birds:
411         body size, life history, sexual selection or ecology? *Proc Roy Soc Lond B* **266**,
412         933-939.
413  37.    Suhonen J., Korkeamaki E., Salmela J., Kuitunen M. 2014 Risk of local
414         extinction of Odonata freshwater habitat generalists and specialists.
415         *Conservation Biology* **28**, 783–789.
416  38.    Hardy N., Otto S.P. this issue Specialization and generalization in the
417         diversification of phytophagous insects: tests of the musical chairs and
418         oscillation hypotheses. *Proc Roy Soc Lond B*.
419  39.    Armbruster W.S., Lee J., Edwards M.E., Baldwin B.G. 2013 Floral
420         paedomorphy leads to secondary specialization in pollination of Madagascar
421         *Dalechampia* (Euphorbiaceae). *Evolution* **67**(4), 1196-1203.
422         (doi:10.1111/evo.12002).
423  40.    Abrahamczyk S., Souto-Vilarós D., Jorgensen P.M., Renner S.S. this issue
424         Escape from extreme specialization:Passionflowers, bats, and the Sword-
425         billed hummingbird. *Proc Roy Soc Lond B*.

41. Anderson B., Ros P., Wiese T., Ellis A. this issue Intraspecific divergence and convergence of floral tube length in specialized pollination interactions. *Proc Roy Soc Lond B*.

42. Armbruster W.S., Herzig A.L., Clausen T.P. 1992 Pollination of two sympatric species of *Dalechampia* (Euphorbiaceae) in Suriname by male euglossine bees. *Amer J Bot* **79**, 1374-1381.

43. Gould F. 1979 Rapid host range evolution in a population of the phytophagous mite *Tetranychus urticae* Koch. . *Evolution* **33**, 791– 802.

44. Rasmann S., Agrawal A.A. 2011 Evolution of specialization: a phylgenetic study of host range in the red milkweed beetle (*Tetraopes tetraphthalmus*). *Am Nat* **177**, 728–737.

45. Kassen R. 2002 The experimental evolution of specialists, generalists, and the maintenance of diversity. *J Evol Biol* **15**, 173-190.

46. Pérez-Barrales R., Bolstad G.H., Pélabon C., Hansen T.F., Armbruster W.S. 2013 Pollinators and seed predators generate conflicting selection on *Dalechampia* blossoms. *Oikos* **122**, 1411-1428.

47. Galen C. 2000 High and dry: drought stress, sex-allocation trade-offs, and selection on flower size in the alpine wildflower *Polemonium viscosum* (Polemoniaceae). *American Naturalist* **156**(1), 72-83.

48. Lambrecht S.C., Dawson T.E. 2007 Correlated variation of floral and leaf traits along a moisture availability gradient. *Oecologia* **151**, 574-583.

49. Runions C.J., Geber M.A. 2000 Evolution of the self-pollinating flower in *Clarkia xantiana* (Onagraceae). I. Size and development of floral organs. *American Journal of Botany* **87**(10), 1439-1451.

50. Lambrecht S.C. 2013 Floral water costs and size variation in the highly selfing *Leptosiphon biolor* (Polemoniaceae). *International Journal of Plant Sciences* **174**, 74–84.

51. Mazer S.J., Paz H., Bell M.D. 2004 Life history, floral development and mating system in *Clarkia xantiana* (Onagraceae): Do floral and whole-plant rates of development evolve independently. *American Journal of Botany* **91**(12), 2041-2050.

52. Litsios G., Kostikova A., Salamin N. this issue Host specialist clownfish are environmental niche generalist. *Proc Roy Soc Lond B* **this issue**.

53. Remold S. 2012 Understanding specialism when the jack of all trades can be the master of all. *Proc Roy Soc Lond B* **279** 4861-4869.

54. Muschick M., Nosil P., Harmon L.J., Salzburger W. this issue Ecological niche dimensionality and the stages of adaptive radiation of cichlids within Lake Tanganyika *Proc Roy Soc Lond B* **this issue**.

55. Dapporto L., Dennis R.L.H. 2012 The generalist-specialist continuum: Testing predictions for distribution and trends in British butterflies. *Biol Cons* **157**, 229-236.

56. Bridle J.R., Buckley J., Bodsorth E.J., Thomas C.D. 2013 Evolution on the move: specialization on widespread resources associated with rapid range expansion in response to climate change. *Proc Roy Soc Lond B* **281**, 20131800.

471 57. Lázaro A., Nielsen A., Totland Ø. 2010 Factors related to the inter-annual
472 variation in plants' pollination generalization levels within a community.
473 *Oikos* **119**(5), 825-834.
474 58. Davies T.J., Pedersen A.B. 2008 Phylogeny and geography predict pathogen
475 community similarity in wild primates and humans. *Proc Roy Soc Lond B* **275**,
476 1695–1701.
477 59. Bonetti M., Wiens J. this issue Evolution of climatic niche specialization: a
478 phylogenetic analysis in amphibians. *Proc Roy Soc Lond B*.
479 60. Forister M.L., Dyer L.A., Singer M.S., Stireman J.O., Till J.T. 2012 Revisiting the
480 evolution of ecological specialization, with emphasis on insect–plant
481 interactions. *Ecology* **93**, 981-991.
482 61. Slatyer R.A., Hirst M., Sexton J.P. 2013 Niche breadth predicts geographical
483 range size: a general ecological pattern. *Ecol Lett* **16**, 1104-1114.
484 62. Filippi-Codaccionia O., Devictorb V., Basa Y., Julliarda R. 2010 Toward more
485 concern for specialisation and less for species diversity in conserving
486 farmland biodiversity. *Biological Conservation* **143**, 1493–1500.
487 63. Ehinger M., Mohr T.J., Starcevich J.B., Sachs J.L., S. P.S., Simms E.L. 2014
488 Specialization-generalization trade-off in a Bradyrhizobium symbiosis with
489 wild legume hosts. *BMC Ecology ,* **14**, 8.
490 64. Rezende E.L., Lavabre J.E., Guimaraes P.R., Jordano P., Bascompte J. 2007
491 Non-random coextinctions in phylogenetically structured mutualistic
492 networks. *Nature* **448**, 925-928.
493 65. Kelley S.T., Farrell B.D. 1998 Is specialization a dead end? The phylogeny of
494 host use in dendroctonus bark beetles (Scolytidae). *Evolution* **52**, 1731-1743.
495 66. Jetz W., Thomas G.H., Joy J.B., Redding D.W., Harmann K., Mooers A.O. 2014
496 Global distribution and conservation of evolutionary distinctness in birds.
497 *Curr Biol* **24**, 919–930.
498 67. Heard S.B., Mooers A.O. 2000 Phylogenetically patterned speciation rates and
499 extinction rates change the loss of evolutionary history during extinctions.
500 *Proc Roy Soc Lond B* **267**, 613-620.
501 68. Poisot T., Gravel D. 2014 When is an ecological network complex?
502 Connectance drives degree distribution and emerging network properties.
503 *PeerJ* **24688835**.
504 69. Cadotte M.W., Borer E., Seabloom E., Cavender-Bares J., Harpole S., Cleland E.,
505 Davies K. 2010 Phylogenetic patterns differ for native and exotic plant
506 communities across a richness gradient in Northern California. *Diversity and*
507 *Distributions* **16**, 892-901.
508 70. Vazquez D.P., Melian C.J., Williams N.M., Bluthgen N., Krasnov B.R., Poulin R.
509 2007 Species abundance and asymmetric interaction strength in ecological
510 networks. *Oikos* **116**, 1120-1127.
511 71. Ashworth L., Aguilar R., Galetto L., Aizen M.A. 2004 Why do pollination
512 generalist and specialist plant species show similar reproductive
513 susceptibility to habitat fragmentation? *Journal of Ecology* **92**, 717-719.
514 72. Poisot T., Canard E., Mouquet N., Hochberg M.E. 2012 A comparative study of
515 ecological specialization estimators. *Methods in Ecology and Evolution* **3**, 537-
516 544.

517
518