1 **Not all traits are functional: the Panglossian paradigm**

2 Roberto Salguero-Gómez[1,*] & Daniel C. Laughlin[2]

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4 [1] Department of Zoology, University of Oxford, 11a Mansfield Road, OX1 3SZ, Oxford, United

5 Kingdom. ORCID: 0000-0002-6085-4433.

6 [2] Department of Botany, University of Wyoming, 1000 E. University Avenue, Laramie, WY

7 82071, USA. ORCID: 0000-0002-9651-5732.

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9 * Corresponding author:

10   Salguero-Gómez, R. (rob.salguero@zoo.ox.ac.uk)

11   https://salgo.web.ox.ac.uk/about-salgo

12   @Rob_SalGo

13

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17 Word count: 1,587 (Excluding abstract, glossary, and references)

18 Figures: 0

19 Tables: 0

20 Text box: 0

21 Glossary box: 359 words

22 References: 33

23

24 **Abstract**

25 The popularity of trait-based approaches continues to rise despite challenges in identifying strong

26 links between traits and organism performance. Here, we summarise evidence demonstrating that

27 not all traits appear to be functional, and discuss how life history theory and demography can help

28 elucidate which, how, where, and when traits gain functionality.

29

30 **Glossary**

31 **Alternative design:** different configurations of multiple traits' values that result in comparable

32 fitness outcomes.

33 **Functional trait:** morphological, physiological, phenological, or behavioural characteristics that

34 impact fitness indirectly via their effects on growth, survival, and reproduction [1].

35 **Fitness:** The number of surviving offspring produced by a parent. This measure of evolutionary

36 success is a function of two fitness components: the parent's ability for *survival* to a given point

37 where it can carry out *reproduction*.

38 **Fitness components**: Survival and reproduction.

39 **Life history trait**: a quantity that defines a key event along the life cycle of a species. Life history

40 traits emerge from trade-offs between vital rates. Examples include age at maturity, reproductive

41 window, post-reproductive life, mean life expectancy, clutch size, etc.

42 **Life history strategy**: combination of life history trait values that ultimately result in the way by

43 which the organism attempts to maximise its fitness in a given environment.

44 **Ontogeny**: The development of an organism, which is composed by different phases of

45 complexity. These phases typically range from the time of fertilisation until adulthood.

46   **Phenotype**: The set of observable traits of an organism resulting from the interactions of its
47   genotype with the environment.

48   **Selection gradient**: The slope relating how an organism's relative fitness –or its fitness
49   components– may change in response to a change in the value of one of its traits.

50   **Sensitivity**: A measure of how an emergent property of a system is affected by a small change in
51   one or more of its underlying components. In population models, a standard way to apply
52   sensitivities is to quantify the effect of vital rates, or its underlying drivers, such as traits, on
53   population growth rate.

54   **Structured population model**: Mathematical summary of the ways in which survival and
55   reproduction change across a trait (or combination of traits) of individuals in a population to shape
56   the dynamics of the population. Examples include life tables, matrix population models, and
57   integral projection models.

58   **Vital rate**: A demographic process that shapes the dynamics of a population, which ultimately is
59   a function of individuals' traits. In a simple size-based life cycle, these are typically survival,
60   growth, and (sexual) reproduction. However, other vital rates can also be considered depending on
61   the complexity of the life cycle of interest, such as clonal reproduction, shrinkage, fission/fusion,
62   migration, dispersal, and seed bank persistence.

63

64

Main body

66 Trait-based approaches provide a framework that transcends taxonomic and ecosystem boundaries

67 to evaluate how organismal attributes shape ecological processes [1]. However, the use of

68 **functional traits** in ecological and evolutionary research is not free of challenges. A key limitation

69 in trait-based approaches is their assumption that traits link an organism's **phenotype** to its **fitness**

70 [2]. A *trait* becomes *functional* when it allows researchers to link a measurable feature of an

71 organism (e.g., body size, specific leaf area) to processes that shape the performance of the system

72 [1]. Explicit in this definition is the need for functional traits to be good predictors of **vital rates**

73 and **fitness components**. Yet, this expectation is at odds with some empirical evidence [3].

74   Recently, the argument has been made that all traits are functional. Sobral [4] argues that,

75 because all traits did, do, or will at some point directly or indirectly affect fitness, the usage of

76 *functional* before *trait* is unnecessary. Here, using life history theory and demographic approaches,

77 we point out limitations in current trait-based approaches that have resulted in debates and

78 assumptions regarding trait functionality. Our goal is to remind researchers of a wealth of classical

79 literature from decades ago that rigorously evaluated adaptive value of organismal features, and to

80 help set the agenda for trait-based research towards more rigorous practices that will ultimately

81 improve the discipline's predictive ability to tackle the Holy Grail of Ecology: to predict complex

82 patterns from relatively easily measured traits [5].

83

Considerations on trait functionality: life history and demographic perspectives

85 Decades of ecological research have been devoted to the search for the Holy Grail of ecology [5].

86 At one level, this means establishing connections between traits and vital rates. The evidence thus

87 far is a mixed bag of successes [6] and failures [3]. However, the perception by some researchers

4

88 that traits are poor predictors of vital rates has left the discipline lukewarm regarding the promise

89 of these approaches [7]. This same sentiment has also percolated into ecosystem-level ecology,

90 where traits are used to predict properties such as carbon sequestration or nutrient cycling [8].

91 Contrary to the pessimism that emerges from some of those works, we argue that there is much to

92 be gained from classical life history theory and the substantial arsenal of demographic tools.

93 Below, we summarise how these two areas of knowledge can provide key insights in the discussion

94 of trait functionality.

95

96 **1. Trait functionality can be vital-rate specific**

97 Much research using trait-based approaches assumes the predictive ability of their traits on vital

98 rates [2], but it also assumes that a given trait predicts *all* vital rates of a system. Examining the

99 relationships between commonly used functional traits (seed mass, wood density, leaf lifespan,

100 specific leaf area [SLA], and leaf nitrogen concentration) and vital rate **sensitivities** for 222 plant

101 species worldwide, Adler et al. [9] showed that not all traits correlate with all vital rates. For

102 instance, seed mass positively correlates with the importance of survival on population growth

103 rate, but not with growth or reproduction, whereas SLA positively correlates with reproduction,

104 but none of the other vital rates.

105   The realisation that the functionality of a trait may be vital-rate specific begs ecologists to

106 clearly identify the demographic pathway(s) that most controls the system's performance. In this

107 regard, thinking of traits according to their role in resource acquisition *vs.* allocation [10] can help

108 link functionality to different demographic processes. For instance, root growth occurs in response

109 to a resource acquisition need, while flowering is the result of resource re-allocation from

110 maintenance. Life history theory can also offer important contributions to create *a priori*

111   expectations of trait vital-rate specific functionality, as it has already developed predictions based

112   on species' generation time, degree of woodiness, and habitat regarding the vital rate that

113   predominantly affects the mean fitness within the population [11]. Linking those vital rates to

114   specific traits that best predicts them holds the promise to drastically reduce the amount of data

115   collection and analytical work in trait-based approaches.

116

117   **2. Environment and ontogeny shape trait functionality**

118   Trait-based approaches have been applied to describe macroecological patterns of trait space.

119   Examples include leaf [12], wood [13], and root [14] trait spectra, as well as the spectrum of plant

120   and organ sizes [15]. While these large-scale analyses have provided key insights into trait

121   correlations, they have not examined the role of abiotic (e.g., drought) and biotic factors (e.g.,

122   competition) in shaping trait values. This is an important consideration when producing "big

123   pictures" of trait ordination, as trait data usually come from different locations with wildly different

124   a/biotic conditions, and where sampled individuals can range in **ontogeny**. As a result, these

125   approaches neglect key biological realities such as local adaptation or phenotypic plasticity.

126   Demographers have perfected the incorporation of environmental drivers in ecological

127   models while also explicitly mapping whole-species ontogeny. For instance, in the now widely

128   used **structured population models**, it is a standard practice to model vital rates as a function of

129   individual traits and the environment [16]. The simplicity of these demographic models, coupled

130   with their flexibility to accommodate a/biotic factors and individual traits –or even trait syndromes

131   [17]– means that researchers can simultaneously evaluate which traits are functional, for which

132   vital rates, in which ontogenetic state, and how these effects shape whole-population and

133   community dynamics [18, 19]. Importantly, by combining climatic projections, quantitative

134 genetics, and trait-vital rate relationships [20, 21], researchers can explicitly examine **selection**

135 **gradients** and predict how climate-driven trait shifts may shape upper-levels of biological

136 organisation. Moreover, by explicitly mapping individual ontogeny, researchers are able to track

137 how the functionality of different traits may change in regards to different vital rates with

138 individual age or size [6].

139

140 **3. The functionality lies in trait syndromes, not single traits**

141 Organisms cannot easily be reduced to single dimensions. The phenotype is the combination of all

142 the key traits that, together, provide the necessary building blocks upon which natural selection

143 operates. Attempting to predict a single vital rate from a single trait does not allow researchers to

144 explore trait trade-offs. Moreover, life history theory has demonstrated that fitness can be

145 maximised in multiple, different ways through the combination of different traits [22].

146 Recent approaches inspired by **alternative design** theory [23] have shown that trait

147 syndromes predict vital rates better than single traits [24, 25]. The recognition that trade-offs shape

148 organismal performance has resulted in demographers turning to the quantification of **life history**

149 **traits**, as these explicitly take into account how vital rate trade-offs produce viable **life history**

150 **strategies** [22]. Two parallel efforts at mapping plant trait space using "functional" traits [15] and

151 life history traits [26], show a remarkable degree of similarity. Diaz et al.'s work [15] demonstrates

152 that two principal component axes explain ~75% of variation in six commonly used plant traits

153 (plant height, leaf area, seed size, wood density, LMA, and N content). These axes correspond to

154 a dominant spectrum of plant size, and another one reflecting the leaf economics spectrum.

155 Salguero-Gómez et al.'s work [26] similarly shows two dominant axes that explain ~70% in plant

156 life history traits (generation time, rate of actuarial senescence, age at maturity, shrinkage rate,

157 growth rate, reproductive rate, degree of parity, net reproductive output, and reproductive

158 window). In this case, the two axes correspond to the fast-slow continuum and an axis that explains

159 variation in reproductive strategies. The plant size spectrum is correlated with the fast-slow

160 continuum, and it may be that the leaf economic spectrum explains variation in reproductive

161 strategies [9]. Therefore, traits and trait syndromes can be mapped onto life history strategies [27,

162 28].

163

164 **Reinventing the wheel of the Panglossian paradigm**

165 Current debates on trait functionality evoke feelings of *deja vu*. Over 80 years ago, Large [29; p.

166 300] famously stated 'the just-so stories of adaptive trait evolution throughout the late nineteenth

167 and early twentieth century tempted biologists away from the straight and narrow path of Science

168 into the brothels and gin-palaces of unbridled hypothecation'. Similarly strong sentiments appear

169 throughout the life history literature [30]. Sobral [4] presents an eloquent view of why the adjective

170 "functional" should be dropped when using the noun "trait": if traits had, have, or will have

171 adaptive value, all traits are functional and the qualifier is redundant.

172   We suggest that qualifiers have an important role and that the utility of Violle's definition

173 is that the onus is on the researcher to determine whether the trait is functional or not [31]. What

174 good are traits whose effect on fitness is so indirect that it is difficult to establish, or whose effect

175 is long gone for current and future ecological performance? These debates remind us of old

176 discussions about the function of the human appendix, or the spandrels of San Marco. It appears

177 that the Panglossian paradigm has persisted [32].

178   We agree with Sobral [4] –and many others before [1, 2]– that the term "functional trait"

179 can be overused. "Trait" by itself can be perfectly acceptable. Here, we have presented three

180 considerations to advance more rigorous ways to test which, when, where, and how traits are

181 functional: (i) trait-vital rate specific effects, (ii) environmental and ontogenetic correlates, and

182 (iii) selection on syndromes rather than single traits. For each of these, we have shown how life

183 history theory and demography may provide useful quantitative frameworks. Metcalf and Pavard

184 [33] argued that all evolutionary biologists should be demographers due to the importance of

185 species' demography in evolutionary processes. Here, we extend such a suggestion to biologists

186 using trait-based approaches, since the demographic lens allows researchers to test for the

187 functionality -or lack thereof- in traits of interest.

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