1   **The Nature of *Espeletia* Species**

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16   *Abstract.*— Species are often regarded as basic units of study in biology, following the

17   presumption that they are real and discrete natural entities. But several biologists wonder if

18   species are arbitrary divisions that do not correspond to discrete natural groups of

19   organisms. Two issues must be addressed to solve this controversy, but few studies seem to

20   do so. The first is whether organisms form sympatric and synchronic groups that are

21   distinct in terms of phenotypes and genome-wide allele frequencies, often called "good

22   species." Alternatives to "good species" include "cryptic species," syngameons and, more

23   generally, cases in which phenotypes and genome-wide allele frequencies reflect

24   contrasting evolutionary histories. The second issue is the degree to which species taxa

25   (i.e., taxonomic classification at the species level) reflect natural groups of organisms or

26   constitute arbitrary divisions of biological diversity. Here, we empirically addressed both

27   issues by studying plants of the Andean genus *Espeletia* (Asteraceae). We collected a

28   geographically dense sample of 538 specimens from the paramo de Sumapaz, in the

29   Cordillera Oriental of Colombia. Additionally, we examined 165 herbarium specimens

30   previously collected by other researchers in this region, or from taxa known to occur there.

31   We tested for the existence of phenotypic groups using normal mixture models and data on

32   13 quantitative characters. Among 307 specimens with all 13 measurements, we found six

33   distinct phenotypic groups in sympatry. We also tested for the existence of groups defined

34   by genome-wide allele frequencies, using ancestry models and data on 2,098 single

35   nucleotide polymorphisms. Among 77 specimens with complete genomic data, we found

36   three groups in sympatry, with high levels of admixture. Concordance between groups

37   defined by phenotype and genome-wide allele frequencies was low, suggesting that

38   phenotypes and genome-wide allele frequencies reflect contrasting evolutionary histories.

39 Moreover, the high levels of admixture suggest that *Espeletia* plants form a syngameon in

40 the paramo de Sumapaz. To determine the extent to which species taxa corresponded to

41 phenotypic and genomic groups, we used data on 12 phenotypic characters to assign 307

42 specimens to species taxa, according to descriptions of species taxa in the most recent

43 monograph of *Espeletia*. This sample included 27 specimens cited in the monograph.

44 Remarkably, only one out of 307 specimens in our sample fell inside any of the phenotypic

45 ranges reported in the monograph for the species taxa known to occur in the paramo de

46 Sumapaz. These results show that species taxa in *Espeletia* are delineations of largely

47 empty phenotypic space that miss biological diversity.

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49 *Keywords*.— ancestry models, normal mixture models, species limits, species reality,

50 species taxa, sympatry, syngameon.

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62   Species are often regarded as basic units of biological diversity in ecology,

63   evolution, biogeography and conservation biology (Richards 2010; Sigwart 2018),

64   following the presumption that they are real, discrete natural entities (Coyne and Orr 2004;

65   Barraclough and Humphreys 2015). But some biologists, most notoriously botanists, have

66   persistent doubts about the existence of species. They see species as arbitrary divisions of

67   biological diversity that do not necessarily correspond to discrete natural groups of

68   organisms (Levin 1979; Raven 1986; Bachmann 1998). Darwin appeared to have

69   developed a similar view (Mayr 1982; Stamos 2007; Richards 2010; Mallet 2013 but see

70   De Queiroz 2011; Wilkins 2018), seemingly revealed in the concluding chapter of On the

71   Origin of Species: ''…we shall have to treat species in the same manner as those naturalists

72   treat genera, who admit that genera are merely artificial combinations made for

73   convenience. This may not be a cheering prospect, but we shall at least be freed from the

74   vain search for the undiscovered and undiscoverable essence of the term species'' (Darwin

75   1859). Moreover, it has been argued that Darwin's view on the nature of species may have

76   been shaped by interactions with botanists (Mayr 1982), and that botanists could have been

77   overly impressed by a few examples of fuzzy species limits (e.g., oaks, hawthorns and

78   blackberries) and wrongly assumed these "botanical horror stories" to be representative of

79   plant species overall (Diamond 1992). Yet, skepticism about the nature of species is still

80   common among botanists (Barraclough and Humphreys 2015; Hipp et al. 2019) and other

81   biologists (e.g., Hey 2001), as this fundamental question about the structure of biodiversity,

82   with major basic and applied implications, remains unsatisfactorily addressed (Barraclough

83   2019).

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85   Attempts to empirically solve the controversy about the nature of species would

86   ideally address two related but separate issues. The first is whether coeval individual

87   organisms form sympatric, distinct groups in nature (Coyne and Orr 2004). Sympatry,

88   defined in terms of the normal cruising range of individual organisms (Mayr 1947; Mallet

89   et al. 2009), and synchrony are stressed in this context because they imply opportunity for

90   two or more groups to merge via hybridization and introgression (Coyne and Orr 2004).

91   Additionally, temporal and spatial co-occurrence implies opportunity for competitive

92   exclusion. Therefore, distinct groups of organisms are unlikely to coexist for long unless

93   ecological niche differences between them are enough to offset respective differences in

94   population growth rate (Chesson 2000; Adler et al. 2007). In short, when sympatric and

95   synchronous, discrete groups of organisms are unlikely to be genetically and

96   demographically exchangeable (sensu (Templeton 1989)). Thus, sympatric and

97   synchronous, discrete groups of organisms are widely accepted as relatively

98   uncontroversial evidence of distinct, real units in nature (Mayr 1992; Coyne and Orr 2004;

99   De Queiroz 2007; Mallet 2007, 2008).

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101   The second issue is the degree to which taxonomic classification at the species level

102   accurately reflects distinct groups of individual organisms or constitute arbitrary divisions

103   of biological diversity (Rieseberg et al. 2006). To address this second issue about the nature

104   of species, it is paramount to distinguish the idea of species taxa (i.e., taxonomic divisions

105   at the species level) from the notion of species as biological units in nature (Hey et al.

106   2003). Species taxa do exist in the trivial sense of being human-made divisions,

107   documented in taxonomic treatments. Yet, species may not occur in nature as discrete,

108   sympatric and synchronous groups of individual organisms (Levin 1979; Raven 1986;

109   Bachmann 1998; Barraclough 2019). Moreover, even if species do occur in nature as

110   discrete sympatric and synchronous groups of individual organisms, human-made

111   taxonomic classification at the species level may not reflect such groups. By example, the

112   terms "splitter" and "lumper" were already used in Darwin's time to (often pejoratively)

113   describe taxonomists, including botanists, who divided biological diversity too finely and

114   too broadly into species taxa, respectively (Endersby 2009).

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116   These two issues about the nature of species may be empirically addressed in the

117   context of multiple, potentially contrasting species definitions (*sensu* (De Queiroz 1999)).

118   In particular, species could be real units in terms of different properties acquired during

119   lineage divergence, including ability to interbreed, ecological divergence and reciprocal

120   monophyly among others. Despite the variety of possible species definitions, there has been

121   enduring interest in the reality of species in terms of two criteria: phenotypic and genome-

122   wide distinctiveness (Fig. 1, (Dobzhansky 1951; Grant 1957; Mayr 1963; Ehrlich and

123   Raven 1969; Levin 1979; Gould 2002; Coyne and Orr 2004; Rieseberg et al. 2006; Mallet

124   2013; Barraclough 2019)). Particular interest in these two species criteria seems to derive,

125   at least in part, from the influential view of species as well-integrated phenotypic and

126   genomic units, adapted to their physical and biotic environment (Dobzhansky 1951; Mayr

127   1963, see pages 518−540 in Gould 2002). According to this view, in sympatry and

128   synchrony most species are phenotypically distinct lineages, characterized by distinct allele

129   frequencies throughout the genome. This idea, according to which species can be

130   characterized as concordant phenotypic and genomic groups, corresponds to the

131   conventional species model (Barraclough 2019). Species that fit this model are sometimes

132   referred to as "good" species (Fig. 1a, (Templeton 1989; Allmon 2016)).

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134   There are several alternatives to the conventional species model. Species may show

135   very little if any phenotypic distinctiveness but differ in allele frequencies across many loci

136   (Fig. 1b). These species are known as "sibling"(Mayr 1963) or "cryptic" species (Bickford

137   et al. 2007; Fišer et al. 2018; Struck et al. 2018). Perhaps more controversial is the idea of

138   species characterized by phenotypic distinctiveness in the absence of differences in allele

139   frequencies across most loci (Fig. 1c), because it departs from the notion of species as well-

140   integrated units (Wu 2001). Syngameons are examples of this latter kind of species, where

141   phenotypic distinctiveness may be due to few loci, preserved despite interbreeding (Lotsy

142   1931; Grant 1971; Rieseberg and Burke 2001; Wu 2001) and the basis of meaningful

143   ecological and evolutionary units (Van Valen 1976; Templeton 1989). Finally, some

144   species may be characterized by discordant and non-nested sets of distinct phenotypes and

145   genome-wide allele frequencies (Fig. 1d). In this latter case, as well as in cryptic species

146   and syngameons, phenotypes and genome-wide allele frequencies might reflect contrasting

147   evolutionary histories incorporated into a single lineage (Arnold 2015; Barraclough 2019).

148

149   While the degree of concordance between distinctiveness in phenotype and genome-

150   wide allele frequencies (Fig. 1) have played a central role in debates about the nature of

151   species, there seem to be few formal tests of whether coeval individual organisms form

152   sympatric, distinct groups in nature according to these two criteria (Coyne and Orr 2004;

153   Barraclough and Humphreys 2015; Barraclough 2019), and whether such groups (if any)

154   correspond to species level taxonomic divisions (but see Rieseberg et al. 2006). Species

155   delimitation studies would seem particularly well-poised to directly address these two

156   aspects of the controversy about the nature of species. Several of these studies provide

157   powerful insights by focusing on inference of genomic groups among individuals thought

158   to represent different species taxa. Yet, because they are often not designed to measure

159   phenotypes nor formally infer phenotypic groups, such studies do not test alternative

160   species models in terms of concordance between distinctiveness in phenotype and genome-

161   wide allele frequencies (Fig. 1). Particularly illustrative in this context are cases in which

162   species are thought to be "cryptic" (Fig. 1b) because distinct genomic groups are found

163   within species taxa. Given this kind of evidence, the claim that species are "cryptic"

164   assumes concordance between species taxa (i.e., species level taxonomic divisions) and

165   phenotypic groups. But such concordance is often poor (Rieseberg et al. 2006) and should

166   ideally be tested as part of empirical studies on the nature of species (Fig. 2). In fact,

167   morphological studies of presumed "cryptic" species often find that such species are

168   actually phenotypically distinct (Allmon 2016; Korshunova et al. 2019).

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170   The paucity of empirical studies directly addressing the nature of species in terms of

171   concordance between distinctiveness in phenotype and genome-wide allele frequencies

172   may also partly reflect the recency of methods to formally infer the number of distinct

173   phenotypic groups in a sample of individuals. This inference should ideally be *de novo*

174   (Barraclough 2019), as opposed to validation of previously proposed species hypothesis.

175   Yet, commonly used approaches to the analysis of phenotypic data for species delimitation,

176   such as discriminant function analysis (McLachlan 2004), are designed to test for

177   differences between previously defined groups but not to infer the existence of such groups

178   (Cadena et al. 2018). Another common approach to the analysis of phenotypic data relies

179   on hierarchical clustering algorithms, even though phenotypic variation at and below the

180   species level is unlikely to be hierarchical. Thus, these algorithms force data into

181   hierarchical groups irrespective of whether such groups exist in nature(Crisp and Weston

182   1993; Queiroz and Good 1997). This problem is avoided by studies using ordination

183   methods, but then inference of groups is often based on unwarranted reduction of

184   dimensionality and subjective visual inspection of bivariate plots (Cadena et al. 2018). It is

185   only with the relatively recent availability of tools to fit normal mixture models

186   (e.g.,(Scrucca et al. 2016)) that these issues can be avoided (Ezard et al. 2010; Cadena et al.

187   2018). By contrast, *de novo* inference of genomic groups was widely adopted nearly two

188   decades ago, soon after the development of ancestry models (Pritchard et al. 2000). These

189   ancestry models, and subsequent refinements in their application (e.g.,(Verity and Nichols

190   2016, Lawson et al. 2018)), hold great potential for tests of species models defined in terms

191   of concordance between phenotypic and genomic groups (Fig. 1). Yet, for that potential to

192   be realized, approaches to *de novo* inference of phenotypic groups need to be widely

193   adopted too.

194

195   Yet another reason for the scarcity of studies leveraging modern data and methods

196   to directly address questions about the nature of species among synchronous and sympatric

197   organisms may relate to the current emphasis in systematic biology on studies designed to

198   sample the whole geographic distribution of a given monophyletic group. Due to virtually

199   inexorable logistical limitations, such emphasis results in species delimitation studies that

200   rely on geographically extensive and sparse sampling of organisms, as opposed to more

201   thorough samples of the organism co-occurring within localities or regions. The relative

202   merits of these two approaches to sampling, in terms of insights into species delimitation,

203   was a central issue for salient botanists of the XIX century that closely interacted with

204   Darwin, including Asa Gray and Joseph Dalton Hooker (Stevens 1997). In practice the

205   issue seems to have been resolved siding with Hooker, who emphasized geographically

206   extensive samples of closely related groups of organisms rather than intensive regional

207   samples. Thus, the sampling strategy of modern botanical collectors may be characterized

208   as "never the same species twice" (ter Steege et al. 2011), in reference to their (intended)

209   behavior in a single collecting locality. Currently, this approach to sampling is widely

210   practiced among non-botanists too, and results in a characteristic pattern in the locality data

211   derived from natural history collections: well-separated collection localities and few

212   specimens per locality (Sheth et al. 2012). No doubt, geographically extensive samples

213   have contributed dramatically to our understanding of species limits. Nevertheless,

214   geographically sparse sampling is insufficient to test species models, as defined in terms of

215   phenotypic and genomic groups (Fig. 1), with the relatively uncontroversial evidence

216   provided by studies of synchronic and sympatric organisms.

217

218   In sum, despite noteworthy efforts (e.g., (Cavender-Bares and Pahlich 2009)), the

219   debate about the nature of species remains unsatisfactorily addressed by empirical studies,

220   due at least in part to the scarcity of germane analysis of phenotypic data and the emphasis

221   of species delimitation studies on geographically extensive rather than locally intensive

222   sampling of individual organisms. Here we contribute to the empirical resolution of the

223   debate by testing alternative species models (Fig. 1) and, also, by assessing the degree to

224   which taxonomic divisions at the species level (i.e., species taxa) accurately reflect the

225   phenotypic and genomic distributions of coeval, sympatric individual organisms (Fig. 2).

226   We aim to present a case study characterized by geographically dense sampling of

227   organisms, and the use of formal approaches to i) *de novo* inference of groups of organisms

228   in terms of phenotype and genome-wide allele frequencies, ii) measure the degree of

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229   concordance between distinctiveness in phenotype and genome-wide allele frequencies, and

230   iii) the concordance between species taxa and distinctiveness in phenotype and genome-

231   wide allele frequencies. We are unaware of empirical studies about the nature of species

232   that employ these approaches on a geographically dense sampling of individual organisms.

233   Yet, such studies are needed to empirically settle the debate about the nature of species.

234

235   We focused on *Espeletia*, a genus in the plant subtribe Espeletiinae (Asteraceae)

236   that is endemic to the northern Andes (Monasterio and Sarmiento 1991; Rauscher 2002;

237   Cuatrecasas 2013; Diazgranados and Barber 2017) and often dominant in high elevation

238   ecosystems known as "páramos" (Ramsay and Oxley 1997). This genus appears to have

239   undergone a very rapid radiation starting around 2.7 Ma (Madriñán et al. 2013; Pouchon et

240   al. 2018). *Espeletia* species are suspected to commonly produce inter-specific hybrids, even

241   between distantly related species (Pouchon et al. 2018), and, nevertheless, maintain

242   phenotypic and ecological integrity (Berry et al. 1988; Diazgranados 2012; Cuatrecasas

243   2013; Diazgranados and Barber 2017). In one of the (two) prefaces of the most recent

244   Espeletiinae monograph (Cuatrecasas 2013), Harold Robinson wrote: "The recent origin,

245   the high specialization and the complex structure of the often large plants, added to the few

246   barriers to hybridization in addition to geography, even at the intergeneric level, presented

247   many complications for the monographic study." Indeed, along with other plant genera

248   such as oaks (*Quercus*), hawthorns (*Crategus*) and blackberries (*Rubus*), *Espeletia* may be

249   a "botanical horror story" (Diamond 1992) from which we may learn much about the nature

250   of species.

251

252   **MATERIALS AND METHODS**

253

254   *Study Region and Taxa*

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256   We studied plants of the genus *Espeletia* occurring in the páramo de Sumapaz. This

257   páramo encompasses 1,780 km^2 in the Cordillera Oriental of the Colombian Andes, south

258   of Bogotá, and includes the high elevation areas of Parque Nacional Sumapaz. Annual

259   average temperature varies spatially between 2 and 10 °C and annual rainfall between 500

260   and 2000 mm. According to the most recent *Espeletia* monograph (Cuatrecasas 2013),

261   seven species taxa in the genus *Espeletia* occur in the páramo de Sumapaz: *Espeletia*

262   *argentea* Humb. & Bonpl.*, Espeletia cabrerensis* Cuatrec., *Espeletia grandiflora* H. & B.,

263   *Espeletia killipii* Cuatrec., *Espeletia miradorensis* (Cuatrec.) Cuatrec., *Espeletia*

264   *summapacis* Cuatrec. and *Espeletia tapirophila* Cuatrec. The monograph also explicitly

265   mentions the occurrence of infra-specific taxa in the páramo de Sumapaz for three of the

266   seven species taxa: *Espeletia argentea fma*. *phaneractis* (S.F.Blake) A.C.Sm., *E.*

267   *grandiflora spp. grandiflora var. attenuata* Cuatrec., *E. grandiflora spp. subnivalis*

268   Cuatrec. and *Espeletia killipii var. chiscana* Cuatrec.

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270   *Specimen Collection*

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272   To sample *Espeletia* species we defined the limit of the páramo de Sumapaz as the

273   3,000 m elevation isocline, based on the Aster digital elevation model with 30 m resolution

274   (https://asterweb.jpl.nasa.gov/gdem.asp). Thus defined, the páramo de Sumapaz was

275   divided into quadrants of 2 x 2 km. We sampled 34 of these quadrants by randomly

276   choosing two 30 × 30 m grid cells (of the Aster digital elevation model) in each band of

277   100 m elevation (Fig 3). We sampled a total of 219 grid cells of 30 × 30 m. In each grid cell

278   we collected at least one specimen of each seemingly different phenotype. Additionally, we

279   collected specimens opportunistically to further document the occurrence of different

280   phenotypes across the páramo de Sumapaz. In total we collected 538 specimens of

281   reproductive *Espeletia* plants, all deposited in triplicate at the herbarium of the Jardín

282   Botánico de Bogotá José Celestino Mutis (JBB).

283

284   *Phenotypic Distinctiveness*

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286   *Morphological characters.*— We measured thirteen morphological characters in

287   *Espeletia* specimens from the páramo de Sumapaz (Table 1). Except perimeter of the

288   synflorescence axis, all these characters were used by Cuatrecasas (2013) to delimit

289   *Espeletia* species taxa from the páramo de Sumapaz. We additionally included the

290   perimeter of the synflorescence axis because in the field this character seemed useful to

291   distinguish putative species. Whenever possible, we measured all thirteen characters in

292   each of the 538 specimens we collected. Additionally, we measured as many of the thirteen

293   characters as possible in each of 165 specimens from páramo de Sumapaz, or from taxa

294   known to occur there, that were collected by other researchers and deposited in the

295   Herbario Nacional Colombiano (COL), at the Instituto de Ciencias Naturales, Universidad

296   Nacional de Colombia. Out of these 165 specimens, 97 were explicitly mentioned in the

297   *Espeletia* monograph by Cuatrecasas (2013), including types for all but one (*Espeletia*

298   *argentea*) species taxa that, according to Cuatrecasas (2013), occur in the páramo de

299   Sumapaz.

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301   When possible, each one of the thirteen morphological characters was measured in

302   three separate structures per specimen (as mentioned before, specimens were collected in

303   triplicates), and analyses were based on average values per specimen to account for intra-

304   individual variation. The length of synflorescence axis was measured in the field to the

305   nearest centimeter. All other measurements were done in the herbarium after the specimens

306   were dried. To measure leaf blade length and width we photographed leaves on a standard

307   background including a millimeter ruler and then processed the respective images using

308   *Image J* (Schindelin et al. 2012). Capitulum diameter, length and width of the corolla of the

309   flowers of the disc, length of the corolla of the flowers of the ray, and length of the tubes of

310   the disc were measured to the nearest hundredth of a millimeter. All morphological data is

311   available as Supplementary Material in Appendix 1.

312

313   *Estimating morphological groups.—* To estimate *de novo* the number phenotypic

314   groups among the measured *Espeletia* specimens, as well as the assignment of specimens to

315   such groups, we used the R package Mclust 5.0 (Scrucca et al. 2016) to fit normal mixture

316   models (NMMs, (McLachlan and Peel 2000)) to morphological data. The use of NMMs to

317   detect phenotypically distinct species assumes polygenic inheritance of phenotypic traits

318   and random mating; under these assumptions, gene frequencies would be close to Hardy-

319   Weinberg equilibrium, two or more loci would be near linkage equilibrium, and phenotypic

320   variation among individuals of a single species would tend to be normally distributed

321   (Templeton 2006). Thus, detection of two or more phenotypic normal distributions among

322   sympatric and synchronic organisms indicates the existence of two or more phenotypically

323   distinct species (Cadena et al. 2018), barring instances in which distinct normal

324   distributions reflect ontogenetic variation or phenotypic plasticity. The parameters of

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325   NMMs (e.g., means, variances and covariances) describe each phenotypic group as a

326   (possibly multivariate) normal distribution and can be estimated *de novo* from data on

327   phenotypic measurements (i.e., without *a priori* knowledge of species limits) using the

328   expectation-maximization algorithm (McLachlan and Krishnan 2008).

329

330   We used the Bayesian Information Criterion (BIC, (Schwartz 1978)) to measure

331   empirical support for different NMMs fitted to the morphological data (Fraley and Raftery

332   2002). We fitted NMMs that covered a wide range of the possible number of distinct

333   phenotypic groups, from a single group up to ten groups. This range amply bracketed the

334   number species taxa that, according to the most recent monograph of *Espeletia*

335   (Cuatrecasas 2013), occur in the páramo de Sumapaz: seven (see above section on *Study*

336   *Region and Taxa*). Before fitting MMNs, we rotated the phenotypic space using a principal

337   component analysis on the covariance matrix of the natural logarithm of the measurements

338   of thirteen morphological characters (Table 1). One of these characters, pairs of sterile

339   leaves per synflorescence, took on zero values, so we added one to this variable before the

340   logarithm transformation. We used R package Clustvarsel (Scrucca and Raftery 2018) to

341   reduce the dimensionality of the data by selecting the most useful set of principal

342   components for the discrimination of groups in NMMs, without *a priori* knowledge of the

343   groups (Raftery and Dean 2006; Maugis et al. 2009). We separately used algorithms

344   implemented in Clustvarsel that performed backward and forward selection of principal

345   components.

346

347   To avoid convergence of the expectation maximization algorithm on a local

348   maximum of the likelihood function, we ran five versions of the analyses based on NMMs,

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349   including reduction of dimensionality with package Clustvarsel, each using a different

350   approach for the initialization of the expectation maximization algorithm (Scrucca and

351   Raftery 2015). All five approaches to initialization are available in the package Mclust.

352   Each approach applies a different data standardization to obtain an initial partition of the

353   data via hierarchical agglomerative clustering (Scrucca and Raftery 2015), although the

354   reminder of the expectation maximization algorithm is run on the data on the initial scale

355   (i.e., the principal components of the covariance matrix of the natural logarithm of the

356   morphological measurements). Details of the analysis based on NMMs implemented in

357   package Mclust, including reduction of dimensionality using package Clustvarsel, are in the

358   R scripts available as Supplementary Material in Appendix 2.

359

360   *Distinctiveness in Genome-wide Allele Frequencies*

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362   *DNA extraction and genotyping-by-sequencing.*— Genomic DNA was extracted

363   using the QIAGEN DNeasy Plant Mini Kit (QIAGEN, Germany). DNA concentration was

364   quantified in R Qubit dsDNA HS Fluorometer (Life Technologies, Sweden). One 96-plex

365   genotyping-by-sequencing libraries were performed with MsII digestions (Elshire et al.

366   2011) and sequenced at LGC Genomics (Berlin, Germany). Readings were aligned based

367   on a previous study (Cortés et al. 2018) using a cluster of 283 *Espeletia* specimens, built

368   with 192 specimens from that study in addition to 96 specimens from this study. Filtering

369   of variants was done using a GBS-specific rule set with > 5 read count for a locus, > 5%

370   minimum allele frequency across all specimens, and ≥ 80% genotypes observed. This

371   filtering reduced the initial sample of 99 specimens to 77. The filtered dataset was

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372   inspected with TASSEL v. 3.0 (Glaubitz et al. 2014), resulting in a final set of 2,098 single

373   nucleotide polymorphisms (SNPs).

374

375   *Estimating groups according to genome-wide allele frequencies*.— To estimate *de*

376   *novo* the number of groups according to genome-wide allele frequencies among genotyped

377   *Espeletia* specimens, and assign specimens to such groups, we implemented ancestry

378   models in *R Maverick* package in R 3.3.1. (Verity and Nichols 2016). These models assume

379   that groups tend to be in the Hardy Weinberg equilibrium with their own set of allele

380   frequencies and that all loci are in linkage equilibrium (Pritchard et al. 2000). Yet, all

381   ancestry models we used allowed admixture. We evaluated ancestry models postulating a

382   wide range of number of groups among *Espeletia* specimens, from a single group up to ten.

383   Again, this range includes the number of species taxa that, according to the most recent

384   monograph of *Espeletia* (Cuatrecasas 2013), occur in the páramo de Sumapaz. R Maverick

385   assesses the number of groups using thermodynamic integration to obtain direct estimates

386   of the posterior probability of models, given the data and a prior distribution of model

387   parameters (Verity and Nichols 2016).

388

389   *Species Taxa*

390

391   To determine the extent to which species taxa corresponded to phenotypic groups

392   and groups based on genome-wide allele frequencies, we assigned specimens to species

393   taxa based on detailed descriptions in Cuatracasas (2013). In particular, for all species taxa

394   expected to occur in Sumapaz according to Cuatrecasas (2013), we obtained the maximum

395   and minimum values for twelve of the thirteen morphological characters in Table 1. We

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396   excluded from this analysis one of the measured characters, perimeter of the synflorescence

397   axis, because it was not considered by Cuatrecasas (2013), as already mentioned. Then, for

398   each specimen in our sample, we determined if the measured values for the twelve

399   characters fell within the ranges of each species taxa. We assigned a specimen to a species

400   taxon if the measurements for all twelve characters fell within the respective ranges

401   provided by Cuatracasas (2013).

402

403   *Concordance Between Groups Defined by Phenotype, Genome-wide Allele Frequencies*

404   *and Species Taxa*

405

406   To estimate the degree of concordance between the groups of specimens defined

407   according to phenotypes, genome-wide allele frequencies and species taxa we used

408   Goodman and Kruskal's tau statistic (τ, (Agresti 2002)) as implemented in R package

409   GoodmanKruskal version 0.0.2 (Pearson 2016). This statistic is based on measuring

410   variability as the probability that two items (specimens in our case) selected at random

411   belong to different groups. Thus, for an assignment of specimens to groups according to

412   phenotypes (P), variability equals the probability that two randomly drawn specimens

413   belong to different phenotypic groups, hereafter V(P). Likewise, for an assignment of

414   specimens to groups according to genome-wide allele frequencies (G), variability is the

415   probability that two randomly drawn specimens belong to different genomic groups,

416   hereafter V(G).

417

418   In contrast to other metrics of association between categorical variables (e.g., chi-

419   square, Cramer's V), τ is a potentially asymmetric measure of association (Agresti 2002).

18

420   Thus, $\tau(P,G)$ measures the ability to predict genomic groups based on information about

421   phenotypic groups, while $\tau(G,P)$ measures the ability to predict phenotypic groups based on

422   information about genomic groups (Fig. 2):

423

424    $$\tau\,(P, G) = \frac{V(G)-E[V(G|P)]}{V(G)} \qquad \text{(equation 1)},$$

425

426

427    $$\tau\,(G, P) = \frac{V(P)-E[V(P|G)]}{V(P)} \qquad \text{(equation 2)},$$

428

429   where $V(G|P)$ is the probability that two specimens randomly drawn from a single

430   phenotypic group belong to two different genomic groups, and $V(P|G)$ is the probability

431   that two specimens randomly drawn from a single genomic group belong to two different

432   phenotypic groups. $E[V(G|P)]$ and $E[V(P|G)]$ are expected values of these quantities across

433   phenotypic and genomic groups, respectively. The values of $\tau(P,G)$ and $\tau(G,P)$ range

434   between zero and one. Values near one (zero) indicate high (low) predictive ability.

435

436   Asymmetry between $\tau(P,G)$ and $\tau(G,P)$ may arise because phenotypic groups may

437   predict genomic groups better than genomic groups may predict phenotypic groups, or vice

438   versa. Crucially, the different species models in Figure 1 imply particular asymmetries, or

439   absence of asymmetry between $\tau(P,G)$ and $\tau(G,P)$. "Good" species imply strong

440   concordance between phenotypic and genomic groups (Fig. 1a) and, therefore, little if any

441   asymmetry between $\tau(P,G)$ and $\tau(G,P)$. Both values should be high and statistically

442   significant. In other words, phenotypic groups should predict genomic groups well and vice

443   versa. In contrast, among "cryptic" species genomic groups should predict phenotypic

444   groups better than phenotypic groups can predict genomic groups, given that genomic

445   groups are nested within phenotypic groups (Fig. 1b). Thus, for "cryptic" species $\tau(P,G) <$

446    $\tau(G,P)$. The opposite is expected in syngameons because phenotypic groups are nested

447   within genomic groups (Fig. 1c) and, therefore, phenotypic groups should predict genomic

448   groups better than phenotypic groups can predict genomic groups. Finally, in the case of

449   discordant and non-nested sets of distinct phenotypes and genome-wide allele frequencies

450   (Fig. 1d), values of $\tau(P,G)$ and $\tau(G,P)$ would both be low and lack statistical significance.

451

452   Similar expectations can be described for concordance, as measured by τ, between

453   species taxa and phenotypic or genomic groups (Fig. 2). By example, when species taxa

454   correspond to phenotypic or genomic groups, τ values would be high, statistically

455   significant and symmetric. On the other hand, species taxa defined by "lumpers" would

456   each include several phenotypic or genomic groups. Given this nesting, the ability to

457   predict phenotypic or genomic groups based on species taxa would be low, even though the

458   ability to predict species taxa from information on phenotypic or genomic groups would be

459   high. The opposite would be expected for species taxa defined by "splitters." Finally, in the

460   case of non-nested discordance between species taxa and phenotypic or genomic groups, all

461   τ values would be low and lack statistical significance.

462

463   We evaluated the statistical significance of τ values using 1,000 iterations of a null

464   model that randomized the assignment of specimens to groups in one of the two categorical

465   variables being compared (phenotypic groups, genomic groups or species taxa, Fig. 2). We

466   calculated τ values for each iteration of the null model and thus constructed a null

467 distribution of 1,000 values. We estimated p-values for each test as the fraction of τ values

468 in the null distribution that were at least as extreme as the observed τ value.

469

470 *Sympatry*

471

472 To assess whether phenotypic and genomic groups were sympatric, we adopted an

473 operational definition of sympatry reflecting both potential for gene flow and geography

474 (Mallet et al. 2009). According to this definition, populations are sympatric when they have

475 geographic distributions within the normal cruising range of individuals of each other

476 (Mayr 1947), so that gametes of individuals are physically capable of encountering one

477 another with moderately high frequency (Futuyma and Mayer 1980). The normal cruising

478 range of individual organisms is determined by the distribution of distances between the

479 sites of birth and breeding (Mallet et al. 2009). Thus, both pollen and seed dispersal are

480 relevant to this operational definition of sympatry, although in *Espeletia* seed dispersal is

481 thought to be fairly limited (Berry and Calvo 1989; Diazgranados 2012; Gallego Maya and

482 Bonilla Gómez 2016). In sharp contrast, the pollen of *Espeletia* can travel considerable

483 distances via bumblebees (genus *Bombus*) and hummingbirds (Fagua and Gonzalez 2007);

484 except in some species that seem to be pollinated by wind (Berry and Calvo 1989).

485 Bumblebees home back to their nests from places 9.8 km away (Goulson and Stout 2001)

486 and regularly perform flights covering > 1 km (Greenleaf et al. 2007; Pope and Jha 2018).

487 Thus, we considered inter-group distances < 1 km as small enough for sympatry.

488 Accordingly, to estimate the degree of sympatry between a given pair of groups

489 (phenotypic or genomic), we measured the geographic distance between each specimen and

490   the nearest specimen that did not belong to the same group. We examined the resulting

491   distribution of inter-group distances to determine if groups were separated by < 1 km.

492

493   **RESULTS**

494

495   *Phenotypic Distinctiveness*

496

497   The morphological analysis included only 307 out of 703 specimens measured in

498   this study, because several specimens were missing values for at least one of the 13

499   characters studied (Table 1), most often flower traits. The procedure for dimensionality

500   reduction (Clustvarsel, see Methods) selected the first 12 principal components, out of a

501   total of 13, for discrimination of morphological groups in normal mixture models (NMMs).

502   This result was obtained regardless of whether the algorithm for reduction of

503   dimensionality employed a forward or backward search of principal components.

504

505   We found distinct phenotypic groups among the *Espeletia* specimens from páramo

506   de Sumapaz. In particular, the best NMM identified six morphological groups and had

507   substantially more empirical support than models assuming 1−5 and 7−10 groups (ΔBIC >

508   10, Fig. 4a). In this best model, the morphological groups appear to be fairly distinct,

509   because assignment of specimens to morphological groups entailed little uncertainty. In a

510   probability scale, assignment uncertainty exceeded 0.1 in only 3 out of 307 specimens.

511

512   In the best NMM model, three groups were relatively easily distinguished in the

513   morphological space defined by the first two principal components, mainly determined by

514   four characters: number of capitula per synflorescence, number of sterile leaves per

515   synflorescence, length of the cyma peduncle and sterile phyllary width (Fig. 5a). At one

516   extreme of this space, morphological group 1 was distinguished from the rest by having

517   few capitula per synflorescence and no sterile leaves along the synflorescence (extreme

518   right in Fig. 5c). At another extreme, morphological group 4 had the narrowest sterile

519   phyllaries, numerous capitula per synflorensese and the shortest cyma peduncles (upper

520   left in Fig. 5c). Finally, morphological group 6 can be distinguished from the rest by wide

521   sterile phyllaries, many capitula and several pairs of sterile leaves per synflorescence

522   (central lower part in Fig. 5c). The remaining morphological groups were better

523   distinguished in the morphological space defined by principal components 2 and 3, mainly

524   determined by leaf blade width, number of capitula per synflorescence, number of sterile

525   leaves per synflorescence, sterile phyllary width and length of the tubes of the flowers in

526   the disc (Fig. 5b). In this space, morphological groups 2, 3 and 5 were located along a

527   gradient of decreasing values for the number of sterile leaves per synflorescence (Fig. 5d).

528

529   *Distinctiveness in Genome-Wide Allele Frequencies*

530

531   We found support for the existence of more than one genomic group among the

532   *Espeletia* plants we sampled from the paramo de Sumapaz. In particular, an ancestry model

533   with three groups had the highest empirical support, with posterior probability of almost

534   one (Fig. 4b). In this best ancestry model, however, the genomic groups did not seem

535   particularly distinct. One of these groups had only six specimens, all with a relatively low

536   proportion of alleles from other groups (Fig. 6a). The other two groups were much larger

537   (32 and 39 specimens) and included specimens with fairly high proportions of mixed

23

538   ancestry. Indeed, in both these groups specimens with more than 10% admixture were

539   nearly half the group (19 and 21, respectively), and fairly high values of admixture (> 20%)

540   were not uncommon (Fig. 6a). Moreover, six specimens with admixture values near 50%

541   suggest F1 hybrids among the three groups are not uncommon.

542

543   *Species Taxa*

544

545   The procedure to assign specimens to species taxa described by Cuatrecasas (2013)

546   resulted in only one specimen being assigned to any species taxa, out of a total of 307

547   specimens with data for all 12 relevant morphological characters (i.e., all characters in

548   Table 1 except perimeter of the synflorescence axis). In particular, one specimen collected

549   during field work for this study was assigned to *Espeletia killipii* Cuatrec. All other

550   specimens fell outside the ranges specified by Cuatrecasas (2013) for the species expected

551   to occur in the páramo de Sumapaz, including 27 specimens explicitly mentioned by

552   Cuatrecasas (2013). Among them are specimens labeled (i.e., determined) as *E. argentea*,

553   *E. grandiflora*, *E. killipii* and *E. summapacis* and the type of *E. tapirophila*.

554

555   *Concordance Between Groups Defined by Phenotype, Genome-wide Allele Frequencies*

556   *and Species Taxa*

557

558   The remarkable result presented in the previous section, whereby all but one of the

559   307 *Espeletia* specimens in our sample could not be formally assigned to any species taxa,

560   meant that we could not use the Goodman and Kruskal's tau statistic (τ, see Methods) to

561   estimate the degree of concordance between species taxa and groups defined by phenotypic

24

562   distinctiveness or genome-wide allele frequencies. This statistic assumes that specimens are

563   actually assigned to groups, but the morphological space defining species taxa (according

564   to Cuatrecasas 2013) was nearly void of specimens. Nonetheless, it seems fair to state that

565   concordance between species taxa and groups defined by phenotypic distinctiveness or

566   genome-wide allele frequencies was null, because species taxa could not predict assignment

567   of specimens to either phenotypic distinctiveness or genome-wide allele frequencies, and

568   visce versa.

569

570   The analysis of concordance between the classifications based on phenotypic

571   distinctiveness and genome-wide allele frequencies included 46 specimens, because several

572   specimens in the genomic classification were not in anthesis and, therefore, could not be

573   included in the phenotypic classification based on all morphological traits (Table 1). The

574   association between these classifications was not very strong, although it was statistically

575   significant in one direction. In particular, knowledge of phenotypic groups conferred

576   statistically significant but poor ability to predict groups based on genome-wide allele

577   frequencies ($\tau = 0.36$, p-value < 0.001). This weak concordance (τ ranges from zero to one,

578   see Methods) seems mainly due to the complete inclusion of morphological groups 2, 5 and

579   6 into single genomic groups (Fig. 6). However, each of the three remaining morphological

580   groups straddled two genomic groups. The association between classifications was even

581   weaker and not statistically significant when measured in terms of the ability to predict

582   assignment of specimens to phenotypic groups based on knowledge about genomic groups

583   ($\tau = 0.177$, p-value > 0.001). This result reflects the inclusion of multiple phenotypic

584   groups in each of the two genomic groups with most specimens (Fig. 6). We note, however,

585   that the genomic group with the smallest number of specimens included only

586   morphological group 4 (Fig. 6).

587

588   *Sympatry*

589

590   All phenotypic and genomic groups were sympatric, given the assumption that

591   inter-group geographic distances ≤ 1 km allowed gamete exchange via pollen dispersal by

592   bumblebees. All geographic distances between pairs of morphological groups were ≤ 1 km,

593   and the same was true for groups defined by genome-wide allele frequencies (Fig. 7).

594

595   **DISCUSSION**

596

597   Species are often regarded as basic units of biodiversity, but few empirical studies

598   seem to directly address two key issues in a long-standing debate about the nature of

599   species (Coyne and Orr 2004; Barraclough and Humphreys 2015; Barraclough 2019). One

600   of these issues is whether organisms form sympatric groups, distinct in terms concordant

601   phenotypic properties and genome-wide allele frequencies (Fig. 1). The other issue is the

602   degree to which taxonomic classification at the species level (i.e., species taxa) accurately

603   reflects distinct groups of individual organisms or constitute arbitrary divisions of

604   biological diversity. Here we addressed both issues by studying plants of the Andean genus

605   *Espeletia* (Asteraceae), based on geographically dense sampling of organisms in the

606   páramo de Sumapaz, and the use of formal approaches to *de novo* inference of groups of

607   organisms in terms of phenotype and genome-wide allele frequencies, as well as to

26

608 measuring concordance between groups defined by phenotypes, genome-wide allele

609 frequencies and species taxa.

610

611   To our surprise, we found that species taxa delimited in the most recent monograph

612 of the group (Cuatrecasas 2013) were mostly empty in the sense that they contained only

613 one of the 307 *Espeletia* specimens from Sumapaz in our analyses. In other words, we did

614 not find the species taxa of Cuatrecasas (2013) in nature. However, analysis of data on 13

615 morphological characters did reveal fairly distinct, sympatric phenotypic groups among the

616 *Espeletia* from Sumapaz. On the other hand, analysis of genome-wide allele frequencies

617 indicated somewhat indistinct, sympatric groups with high levels of admixture among the

618 *Espeletia* from Sumapaz. These phenotypic and genomic groups were only weakly

619 concordant. Therefore, among the various hypotheses regarding the nature of species, our

620 results seem most consistent with that in Figure 1c and d. The *Espeletia* from Sumapaz

621 seem to form discordant sets of distinct phenotypes and less distinct groups of genome-

622 wide allele frequencies, suggesting that phenotypes and genome-wide allele frequencies

623 reflect contrasting evolutionary histories incorporated into a single species. Next, we

624 explore implications of these results and potential caveats in our analyses.

625

626   Normal mixture models (NMMs) revealed distinct, sympatric morphological

627 groups, which suggests the existence of six, non-cryptic *Espeletia* species in Sumapaz, thus

628 ruling out scenarios depicted in Figure 1a and e. This conclusion is based on the

629 assumptions needed to apply NMMs to species delimitation based on phenotypic characters

630 (Cadena et al. 2018), including polygenic inheritance. We are not aware of studies of the

631 genetic architecture of morphological characters in *Espeletia*. However, studies of

27

632   quantitative trait loci (QTL) in confamilial species suggests that morphological characters

633   (including some in Table 1) are determined by QTL of small effects (relative to the

634   variance of inter-specific backcross populations, Lexer et al. 2005), as expected for

635   polygenic inheritance. Two additional assumptions implicit in the application of NMMs to

636   our context are that morphological groups do not reflect ontogenetic variation or

637   phenotypic plasticity (Cadena et al. 2018). Given that all specimens included in the analysis

638   were adult reproductive plants, we expect only negligible ontogenetic effects. Also,

639   morphological groups seemed to share environments, at least broadly defined, as suggested

640   by extensive sympatry (Fig. 6). In sum, the assumptions required by the application of

641   NMMs seem to be reasonable for our study system.

642

643   We found evidence of three sympatric groups of *Espeletia* specimens from

644   Sumapaz, characterized by different allelic frequencies across the genome. This finding is

645   based on ancestry models that assume Hardy-Weinberg equilibrium and linkage

646   equilibrium within groups (Pritchard et al. 2000). These models are often taken as a useful

647   but rough approximation to reality, and it may be unwise to place much emphasis on any

648   single value for the number of genomic groups (in our case 3). It may be more useful to

649   consider the entire distribution of posterior probabilities for the number of genomic groups

650   (Verity and Nichols 2016). Nonetheless, in our case the posterior distribution for the

651   number of groups takes a value close to one for 3 groups and close to zero for all other

652   values (Fig. 4b). Thus, it seems reasonable to conclude that there is strong support for *the*

653   existence of three genomic groups. However, in contrast to the morphological groups, these

654   genomic groups seemed indistinct and characterized by high levels of admixture (Fig. 6a).

28

655   In fact, admixture values near 50% for several specimens in our sample suggest that F1

656   hybrids among the three genomic groups may be common.

657

658   The weak concordance between phenotypic and genomic groups suggests that the

659   nature of *Espeletia* species in Sumapaz resembles that depicted in Figure 1d. However, the

660   genomic groups are poorly differentiated (Fig. 6a). Therefore, the nature of *Espeletia*

661   species in Sumapaz may be more similar to the hypothesis depicted in Figure 1c, a

662   syngameon. In both cases (Fig. 1 c and d) phenotypic and genomic distinctiveness reflect

663   contrasting evolutionary histories (Doyle 1997; Maddison 1997; Szllosi et al. 2015). This

664   lack of agreement may be due to the fact that a general scan of the allele frequencies across

665   the genome may not represent small and atypical parts of the genome that determine

666   phenotypic distinction. For instance, in a syngameon frequent hybridization and

667   introgression may homogenize large sections of the genome of different species that,

668   nonetheless, remain phenotypically distinct due to selection on relatively few loci, as seems

669   to be the case in some oaks (Van Valen 1976; Templeton 1989, Hipp et al. 2019). This idea

670   is consistent with high admixture levels in our sample of *Espeletia* from Sumapaz,

671   suggesting that F1 hybrids among genomic groups are common (Fig. 6a), and with previous

672   studies of *Espeletia* that inferred hybridization between distantly related taxa (Pouchon et

673   al. 2018), measured high crossability between species taxa (Berry et al. 1988) and observed

674   putative hybrids between several pairs of species taxa (Cuatrecasas 2013; Diazgranados and

675   Barber 2017).

676

677   We did not find the species taxa described in the most recent monograph of

678   *Espeletia* (Cuatrecasas 2013) for the páramo de Sumapaz. This result suggests that species

29

679   taxa are not even arbitrary divisions of biological diversity, as proposed by botanists (Levin

680   1979; Raven 1986; Bachmann 1998) and suggested by Darwin (1859). Far more

681   disconcerting, species taxa in *Espeletia* appear to largely miss biological diversity,

682   delineating mostly empty phenotypic space. We wonder if this result is unique to our study

683   taxa and region. We note, however, that formal, specimen-based exploration of descriptions

684   of species taxa in multidimensional phenotypic space is rarely carried out. This is no small

685   matter, given that species are considered basic units of biodiversity in ecology, evolution,

686   biogeography and conservation biology (Coyne and Orr 2004; Richards 2010; Barraclough

687   and Humphreys 2015; Sigwart 2018). In this study we provided an example of how such

688   exploration may be accomplished. In any case, our findings regarding species taxa strongly

689   suggest the need to revise species limits in *Espeletia*, in addition to the taxonomic changes

690   above the species level suggested by Pouchon et al. (2018).

691

692   **ACKNOWLEDGMENTS**

693

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919   **FIGURES LEGENDS**

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921   **Figure 1.** The nature of species in terms of phenotypic and genomic distinction. **a)** "Good"

922   species are well-integrated units characterized by concordant phenotypic groups (colored

923   points) and genomic groups (delimited by dashed lines). **b)** "Cryptic" species are

924   phenotypically indistinct but differ in allele frequencies across many loci. **c)** Syngameons

925   are characterized by distinct phenotypic groups in the absence of differences in allele

926   frequencies across many or most loci. **d)** Distinct, discordant and non-nested phenotypic

927   and genomic groups. In **b-d** phenotypes and genome-wide allele frequencies reflect

928   contrasting evolutionary histories.

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930   **Figure 2.** Illustrative example of degree of concordance between phenotypic groups,

931   genomic groups and species taxa. Black dots represent a sample of sympatric and

932   synchronic individuals, and rectangles represent groupings of this sample individuals

933   according to different criteria. The top and middle rows of dots show phenotypic and

934   genomic groups estimated *de novo*, respectively. The differences between phenotypic and

935   genomic groups illustrates an instance of "cryptic" species (Fig. 1b). The lower row of dots

936   illustrates an instance of species taxa defined by a "lumper." The arrows on the left

937   represent a single test of concordance between phenotypic and genomic groups. This test

938   involves two values of the Goodman and Kruskal's τ statistic, as illustrated by the two

939   arrows on the left. In particular, $\tau(P,G)$ measures the ability to predict genomic groups

940   based on information about phenotypic groups, while $\tau(G,P)$ measures the ability to predict

941   phenotypic groups based on information about genomic groups (see equations 1 and 2). The

942   double headed arrows on the right represent two tests of concordance, one between species

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943   taxa and phenotypic groups, and the other between species taxa and genomic groups. For

944   simplicity, only one arrow is shown for each of these latter tests, even though each entails

945   two values of the Goodman and Kruskal's τ statistic.

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947   **Figure 3.** Topographic map of the study region, delimited by the contour of 3,000 m of

948   altitude, according to the digital Aster elevation model

949   (https://asterweb.jpl.nasa.gov/gdem.asp). The study region was divided into quadrants of 2

950   × 2 km (gray grid). We sampled 34 of these quadrats (black squares). In particular, in each

951   of these 34 quadrants we sampled two 30 × 30 m cells in each band of 100 m altitude,

952   chosen randomly based on the Aster digital elevation. For example, the 2 × 2 km quadrant

953   shown to the left of the figure has five elevation bands (as indicated by the color scale).

954   Therefore, we sampled 10 cells of 30 × 30 m, two in each elevation band of 100 m, as

955   indicated by the black squares within the 2 × 2 km quadrant.

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957   **Figure 4**. Empirical support for **a)** normal mixture models assuming different number of

958   morphological groups and **b)** ancestry models assuming different number of groups defined

959   by genome-wide allele frequencies among *Espeletia* from páramo de Sumapaz. The normal

960   mixture model with highest empirical support has 6 morphological groups while the best

961   ancestry model distinguishes 3 genomic groups.

962

963   **Figure 5.** Six phenotypic groups detected by normal mixture models among *Espeletia*

964   specimens from paramo de Sumapaz, as seen in the morphological space dtermined by the

965   first 3 principal components. A subset of 6 characters largely determined these 3 principal

966   components (**a**, **b**), where phenotypic groups can be distinguished (**c**, **d**). Arrows in **a** and **b**

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967   display the contribution of characters to principal components (loadings), and circles show

968   the expected length of arrows if all characters contributed equally. Arrows exceeding this

969   expectation contribute most significantly and are labeled. In **c** and **d**, ellipses show regions

970   within 1 standard deviation of the multivariate mean of each phenotypic group, and

971   symbols represent specimens according to morphological groups (M1 to M6).

972

973   **Figure 6.** Three genomic groups detected by ancestry models among *Espeletia* specimens

974   from paramo de Sumapaz and concordance with phenotypic groups detected by normal

975   mixture models (Fig. 5). **a)** assignment of specimens to genomic groups. Each specimen is

976   represented by a stacked bar showing admixture proportions in color. Labels at the top

977   indicate specimen assignment to genomic groups (G1 to G3). **b)** Assignment of specimens

978   to morphological groups (vertical axis, symbols as in Fig. 5). Some specimens in the

979   gnomic groups could not be classified into phenotypic groups because they were missing

980   morphological characters. There was low concordance between genomic and

981   morphological groups, as seen in low values of the Goodman and Kruskal tau statistic (τ).

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983   **Figure 7.** All pairs of **a)** phenotypic and **b)** genomic groups were sympatric, < 1 km apart.

984   Contiguous areas above 3,000 m of elevation (gray, black contour) constitute the paramo de

985   Sumapaz, separated from the paramo de Chingaza in the northeast. Specimen collection

986   localities are shown as symbols according to phenotypic and genomic groups, as in Figures

987   5 and 6, respectively.

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991   **Table 1.** Thirteen morphological characters measured in *Espeletia* specimens from the
992   páramo de Sumapaz to test for the existence of phenotypic groups.

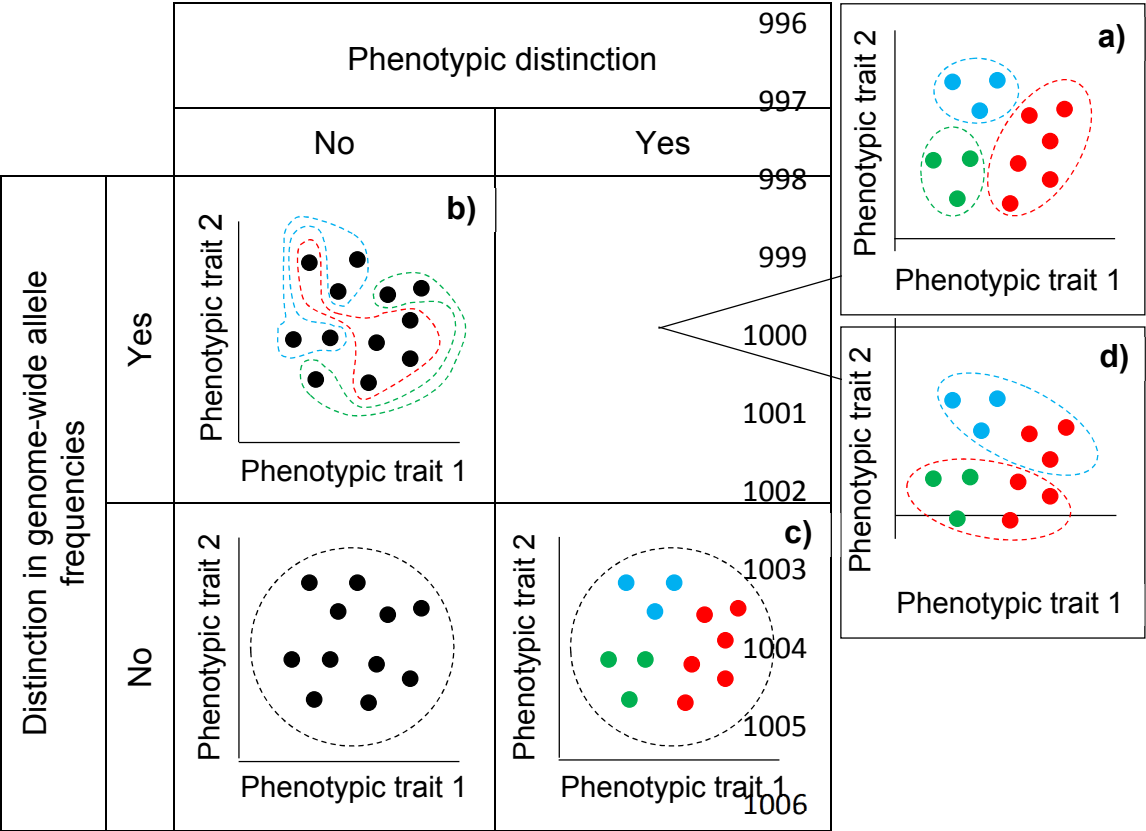| Character number and name	Character description
1) Leaf blade length	Distance from the apex to the base of the leaf blade (excluding the leaf sheath).
2) Leaf blade width	Width of the leaf blade at the widest part.
3) Number of capitula per synflorescence	Count of the number of capitula in a single synflorescence.
4) Capitulum diameter	Diameter of the capitulum, omitting the ligules of the flowers of the radius.
5) Number of pairs of sterile leaves per synflorescence	Count of the pairs of leaves in the infertile (or vegetative) part of the synflorescence axis.
6) Length of the synflorescence axis	Distance from the base of the central capitulum in the terminal cyme to the base of the synflorescense axis.
7) Synflorescence axis perimeter	Perimeter around the synflorescence axis at 10 cm from the base (avoiding areas near sterile leaves).
8) Terminal cyme peduncle length	Length of the peduncle of the central capitulum in the terminal cyme.
9) Sterile phyllary length	Distance from the apex to the base of the sterile phyllary subtending capitula.
10) Sterile phyllary width	Width of the sterile phyllary subtending capitula, at the widest part.
11) Length of the corolla of the flowers in the disc	Distance from the distal tip of a corolla lobe to the base of the tube of the flowers in the disc.
12) Length of the corolla of the flowers in the ray	Distance from the distal tip of the ligule to the base of the tube of the flowers in the ray.
13) Length of the tubes of the flowers in the disc	Distance from the base of the tube to the widening of the corolla of the flowers in the disc.

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1011 Figure 1

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Figure 2

Longitude (degrees)

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Figure 3

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Figure 4

Figure 5

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Figure 6

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Figure 7