Host community assembly modifies the relationship between host and parasite richness

Running title: Host community assembly and parasite diversity

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1 **Abstract**

2 Host and parasite richness are generally positively correlated, but the stability of this

3 relationship during community assembly remains untested. The composition of host

4 communities can alter parasite transmission, and the relationship between host and parasite

5 richness is sensitive to parasite transmission. Thus, changes in composition during host

6 community assembly could strengthen or weaken the relationship between host and parasite

7 richness. Host community assembly, in turn, can be driven by many processes, including

8 resource enrichment. To test the hypothesis that host community assembly can alter the

9 relationship between host and parasite richness, we experimentally crossed host diversity and

10 resource supply to hosts, then allowed communities to assemble. As previously shown, initial

11 host diversity and resource supply determined the trajectory of host community assembly,

12 altering post-assembly host species richness, richness-independent host phylogenetic

13 diversity, and colonization by exotic host species. Throughout community assembly, host

14 richness predicted parasite richness. As predicted, this effect was moderated by exotic

15 abundance: communities dominated by exotic species exhibited a stronger positive

16 relationship between post-assembly host and parasite richness. Ultimately, these results

17 suggest that, by modulating parasite transmission, community assembly can modify the

18 relationship between host and parasite richness, providing a novel mechanism to explain

19 contingencies in this relationship.

20

21

Introduction

23   Parasites are a major contributor to global biodiversity, yet parasite diversity remains

24   relatively underexplored, a problem that has spurred recent research into the drivers of

25   parasite diversity within host communities (Dobson *et al.* 2008; Kamiya *et al.* 2014; Johnson

26   *et al.* 2016; McDevitt-Galles *et al.* 2018). Through this research within host communities, the

27   positive relationship between host and parasite species richness has become one of the most

28   consistently documented relationships in disease ecology (Hechinger & Lafferty 2005;

29   Lafferty 2012; Kamiya *et al.* 2014; Johnson *et al.* 2016; Liu *et al.* 2016). Yet, whether this

30   relationship is robust to changes in host community structure over time remains poorly

31   understood, because few studies have quantified the relationship as host communities

32   assemble. During community assembly, the structure of host communities shifts over time in

33   response to biotic factors, such as species interactions, and abiotic factors, such as resource

34   supply to hosts (HilleRisLambers *et al.* 2011; Harpole *et al.* 2016). These shifts in host

35   community structure can alter parasite transmission (Johnson *et al.* 2013; Halliday *et al.*

36   2019), which could, in turn, alter the strength or direction of the relationship between host

37   and parasite richness. Thus, the relationship between host and parasite species richness might

38   depend on the manner in which host communities assemble (Johnson *et al.* 2016) (Fig 1).

39   Within host communities, the "host-diversity-begets-parasite-diversity hypothesis"

40   suggests that, because many parasites are specialized to infect a small number of host species,

41   increases in host species diversity should increase parasite diversity (Hechinger & Lafferty

42   2005; Poulin 2014). Empirical support for this hypothesis is widespread. For example, a 2014

43   meta-analysis found a consistent positive relationship between host and parasite richness

44   across 21 published studies (Kamiya *et al.* 2014). However, two recent studies highlight the

45   possibility for important contingencies in the nature of this relationship. Wood et al (2018)

46   observed that human activity decoupled the positive relationship between host and parasite

47   richness among reef fishes, attributing the contingency in the relationship between host and

48   parasite richness to a loss of parasite species with complex life-cycles. In another study,

49   Johnson et al (2016) observed that within host communities, the positive relationship between

50   host and parasite richness depended on the spatial scale of observation, attributing this

51   contingency to colonization opportunities (e.g., the propagule-pressure hypothesis; Levine

52   2000), which weaken at larger spatial scales. Colonization opportunities are fundamental to

53   metacommunity theory, suggesting that this contingency may be further understood by

54   considering parasites in that theoretical framework.

55   Metacommunity theory predicts that, all else being equal, regional richness can be

56   strongly influenced by dispersal and establishment of species among patches (Leibold *et al.*

57   2004; Holyoak *et al.* 2005; Logue *et al.* 2011). For parasites, transmission is the combination

58   of dispersal and establishment, so multiple parasite species in a host population or

59   community function as a metacommunity connected via transmission among host individuals

60   (Kuris *et al.* 1980; Sousa 1994; Mihaljevic 2012; Borer *et al.* 2016; Mihaljevic *et al.* 2018).

61   As such, metacommunity theory can be used to generate predictions about the relationship

62   between host and parasite richness. When dispersal and establishment (i.e. parasite

63   transmission) among patches (i.e., host individuals) is most limited, an "extinction vortex"

64   can occur as rare species are lost from local patches faster than they can colonize new

65   patches, leading to the eventual loss of those species in the entire metacommunity (i.e., host

66   community) (Gilpin & Soule 1986). Greater extinction rates of parasites in host communities

67   with low transmission could weaken the positive relationship between host and parasite

68   richness. In a metacommunity context, reducing dispersal limitation by increasing habitat

69   connectivity can alleviate this effect (Logue *et al.* 2011; Cornell & Harrison 2013).

70   Similarly, when parasite metacommunities are transmission-limited, an increase in parasite

71   transmission should strengthen the positive relationship between host and parasite richness

72 (Poulin 2004). Thus, the magnitude of parasite transmission among hosts could explain

73 variation in the relationship between host and parasite richness during host community

74 assembly.

75   Host community assembly involves change over time in community characteristics

76 that can alter parasite transmission, including host species richness, exotic host abundance,

77 and host phylogenetic diversity (Box 1) (Halliday *et al.* 2019). These changes in host

78 community characteristics may, in turn, be driven by a variety of biotic and abiotic conditions

79 including initial host richness and resource supply to hosts (Fig. 1). Consequently, the

80 impacts of initial biotic and abiotic conditions on host richness, parasite richness, and their

81 interaction may shift as host communities assemble.

82   This study examined whether the relationship between host and parasite richness in a

83 North Carolina old-field shifted during experimental host community assembly. Specifically,

84 we constructed experimental, native plant communities at two initial host diversity levels and

85 two levels of soil fertility, then measured how changes in post-assembly host richness, exotic

86 host abundance, and host phylogenetic diversity (together describing host community

87 assembly) influenced changes in parasite richness over three years. In previous analyses

88 using a subset of our data, we found that initial host diversity and resource supply to hosts

89 strongly influenced host community assembly, with consequences for exotic invasions,

90 disease risk, and host community trait distributions (Heckman *et al.* 2017; Halliday *et al.*

91 2019; Wilfahrt *et al.* 2019). Here, we show that, despite strong shifts in the structure of host

92 communities, host diversity begets parasite diversity during community assembly.

93 Importantly however, the magnitude of the relationship between host and parasite richness

94 depends on characteristics of the host community that are linked to parasite transmission.

95

96 **Methods**

97   We performed this study in an old-field in Duke Forest Teaching and Research

98   Laboratory (Orange County, NC, USA), dominated by perennial, herbaceous plants. To test

99   whether initial host diversity and resource supply to hosts indirectly affect parasite richness

100   via changes in host community assembly, we experimentally manipulated native plant (i.e.,

101   host) richness with multiple community compositions at each level of richness, and soil

102   nutrient supply. This yielded a study that comprised 120 1m × 1m plots (5 replicate blocks ×

103   2 resource supply levels × 2 host richness levels × 6 native community compositions).

104   Because this study aimed to examine how plant and parasite community structure changes

105   over time, we did not weed plots to maintain richness (Fargione & Tilman 2005; Heckman *et*

106   *al.* 2017). Thus, the initial species richness treatments represent initial conditions and not the

107   richness of a plot after July 2012. The full details of the experimental treatments can be found

108   in Appendix A.

109   To establish initial host diversity, we assembled 12 planted communities at two

110   richness levels from a pool of six species: six monocultures and six five-species polycultures

111   where one species was excluded from each polyculture community. Plants were propagated

112   from seed at the University of North Carolina at Chapel Hill, then seedlings were

113   transplanted into the plots, spaced 10 cm apart.

114   We began resource supply treatments, hereafter referred to as the fertilization

115   treatment, in July 2012. Each plot was either fertilized with 10 g m^{-2} each of N, P, and K or

116   not fertilized. We applied slow-release forms of each nutrient each spring to alleviate nutrient

117   limitation within experimental communities during the growing season (Borer *et al.* 2014).

118   *Quantification of host community structure*

119   Each year, we visually quantified the percent cover of all plant species in each plot in

120   September using a modified Daubenmire method (Borer *et al.* 2014). We evaluated changes

121   in three components of host community structure to evaluate how experimental treatments

122   influenced host community assembly: post-assembly plant species richness, exotic plant

123   abundance, and the phylogenetic diversity of plant species. To quantify exotic plant

124   abundance, we classified species as exotic or native to eastern North America using the

125   USDA Plants Database (USDA & NRCS 2016), then assessed the relative abundance of

126   exotic species (hereafter, exotic abundance) as the ratio of the absolute exotic cover to the

127   total cover of all species within a plot. To quantify phylogenetic diversity, independent of

128   species richness, a phylogeny of all non-tree species was constructed using 'phyloGenerator'

129   (Pearse & Purvis 2013). Plant phylogenetic diversity was calculated using the ses.mpd

130   function in R package Picante (Kembel *et al.* 2010). This function uses a null-modeling

131   approach that measures the degree to which a plot is more or less phylogenetically diverse

132   than random, given the number of host species, weighted by their relative abundance.

133

134   *Quantification of parasite richness*

135   Following Lafferty and Kuris (2002), we define a parasite as any organism that

136   spends at least one life history stage living in or on a single host individual, causing a fitness

137   loss to the host. This definition includes all microbial parasites of plants and certain insect

138   parasites of plants, such as galling and leaf-mining insects, which spend a larval life history

139   stage parasitizing a single host leaf, but are transmitted by free-living adults that can seek out

140   host plants for their offspring (Halliday *et al.* 2017a, 2019).

141   Parasites were surveyed in each plot annually for three growing seasons in September,

142   which is the period of greatest parasite abundance in this system (Halliday *et al.* 2017b). In

143   2012, parasites were only surveyed on the six planted species (these species accounted for a

144   median of 78% of total vegetative cover per plot), and were measured by haphazardly

145   surveying five leaves on five individuals of each planted species in each plot.

146   In 2013, the composition of plots was characterized by a few common host species

147   and many rare host species (Heckman *et al.* 2017). Because common host species contribute

148   more to parasite abundance (Mordecai 2011; Heckman *et al.* 2016), parasites were measured

149   by haphazardly surveying one individual of each of the six most abundant non-planted

150   species across the experiment, as well as one individual of each of the six planted species that

151   were surveyed in 2012 (together, the surveyed species accounted for a median of 78% of total

152   vegetative cover per plot).

153   By 2014, the composition of host communities had shifted considerably from the

154   originally planted compositions (Heckman *et al.* 2017; Halliday *et al.* 2019; Wilfahrt *et al.*

155   2019). To estimate parasite richness in the assembled community, we maximized the number

156   of host species surveyed in a plot and across the experiment, by haphazardly surveying

157   parasites on five leaves on one individual of the most abundant host species, and then the

158   next most abundant species, iterating until the sampled species' summed cover accounted for

159   at least 80% of the plot's total plant cover. We surveyed one additional individual of all six

160   planted host species in each plot, regardless of cover. While this sampling method reduces

161   replication at the scale of host individuals within plots, it samples across leaf ages and

162   matches similar approaches for measuring community-wide responses at the plot scale (e.g.,

163   Pérez-Harguindeguy *et al.* 2013). Visual surveys were conducted following Halliday et al

164   (2017a, 2019). Briefly, parasites were categorized into morphospecies using morphological

165   and genetic characteristics (Table S1).

166   The number of host species, and thus individuals, surveyed varied among plots (min =

167   2, median = 5, mean = 7.9, max = 25 host individuals). We therefore performed "site-based"

168   rarefaction on the count of parasite morphospecies (Gotelli & Colwell 2001). In each plot, we

169   randomly sampled up to five host individuals, and counted the number of parasite

170   morphospecies in that subsample. We permuted this 999 times and took the average rarefied

171   parasite richness for each plot across those 999 permutations. Although insect and microbial

172   parasites may respond differently to host richness and fertilization (Halliday *et al.* 2017a), the

173   post-assembly data on insects were not sufficient to test for differences from microbes.

174   Therefore, rarefied parasite richness was calculated across all parasites, including insects and

175   microbes.

176

177   *Data analysis*

178   **Longitudinal model of parasite richness.** We first tested whether the relationship

179   between host and parasite richness would change over time as a function of initial host

180   diversity, fertilization, and their interaction by constructing a longitudinal linear mixed model

181   using the lme function in the nlme package (Pinheiro *et al.* 2016). In order to meet

182   assumptions of homoscedasticity, we added an identity variance structure (varIdent function)

183   by host diversity treatment (Zuur *et al.* 2009; Pinheiro *et al.* 2016). Each model included the

184   fertilization treatment, the initial host diversity treatment, post-assembly host species

185   richness, year of observation, and all interactions between these four variables as fixed

186   effects, plus block as a non-interacting fixed covariate. To account for temporal

187   autocorrelation, we included an AR 1 autocorrelation structure at the plot level in each model

188   (Zuur *et al.* 2009). We included planted composition as a random effect to ascribe differences

189   to initial host diversity only when differences in a response within a richness level (i.e.,

190   polycultures or monocultures) were smaller than differences between richness levels (Schmid

191   *et al.* 2002). This analysis tests the effect of the initial host diversity treatment after

192   accounting for variation in host composition. We used the pairs function in the lsmeans

193   package (Lenth 2016) to test whether treatment means were different in a given year, and

194   used the lstrends function to test whether the slope of the relationship between post-assembly

195   host and parasite richness differed among treatments and years. However, we caution the

196 comparison of treatment means among years, as sampling methodology for parasites varied

197 between years, as detailed above. In order to facilitate comparisons among responses and

198 clarify relationships among predictors, we reduced the model by removing non-significant

199 interactions (following Crawley 2007; Zuur *et al.* 2009).

200   **Structural equation model including community assembly.** The longitudinal

201 model of parasite richness tested whether the relationship between post-assembly host and

202 parasite richness changed over time as a function of experimental treatments. To explicitly

203 test the hypothesis that the relationship between post-assembly host and parasite richness is

204 altered by shifts in host community structure during community assembly, we performed

205 confirmatory path analysis using the lavaan package (Rosseel 2010). Specifically, we fit a

206 structural equation model (SEM) that included the treatment effects and their interaction on

207 three endogenous mediators (post-assembly host species richness, exotic host abundance, and

208 host phylogenetic diversity) measuring the outcome of community assembly (following

209 Halliday *et al.* 2019), as well as the effects of those three mediators on parasite richness (Box

210 Fig. 1). We tested the hypothesis that shifts in host community structure altered the

211 relationship between post-assembly host and parasite richness by fitting a second-stage

212 moderated mediation (Hayes 2015) including pairwise interactions between exotic host

213 abundance and post-assembly host richness (Box Fig 1 path m) and between host

214 phylogenetic diversity and post-assembly host richness (Box Fig 1 path n). The first half of

215 this model (Box Fig 1 paths a-i) uses the same data and is structurally identical to the paths

216 from the 2014 group in the multigroup model presented in Halliday et al (2019).

217   Experimental block was treated as a stratified independent grouping variable using the

218 lavaan.survey package (Oberski 2014). In order to meet assumptions of homoscedasticity and

219 multinormality, we logit transformed exotic abundance. All endogenous variables were mean

220 centered, following transformation, to improve interpretability and to eliminate non-essential

221   collinearity (Toothaker *et al.* 1991). In order to facilitate comparisons among responses and

222   clarify relationships among predictors, we reduced the model by removing non-significant

223   interactions (following Crawley 2007; Zuur *et al.* 2009), limiting model reduction to

224   exogenous (i.e., treatment) variables only.

225

226   **Results**

227   *Longitudinal model of parasite richness*

228   We first tested the hypothesis that the relationship between host and parasite richness

229   would change over time as a function of initial biotic and abiotic conditions by constructing a

230   longitudinal mixed model of parasite richness as a function of post-assembly host species

231   richness and its interaction with initial host diversity and fertilization. Consistent with our

232   hypothesis, there was a positive relationship between host and parasite richness, which

233   changed over time as a function of initial host diversity (Appendix B; Table S1). However,

234   fertilization did not affect the relationship between host and parasite richness over time

235   (Table S2), and so these interactions were removed from the model, yielding a reduced model

236   (Table S3).

237   In the reduced model, initial host diversity altered parasite richness, and this effect

238   varied over time (year p=0.001; initial host diversity × year p<0.0001; Table S3; Fig 2). In

239   2012, parasite richness was more than twice as high in polycultures as in monocultures

240   (p<0.001), providing strong evidence for the hypothesis that host diversity begets parasite

241   diversity, though that effect was reduced by 40% in experimentally fertilized communities

242   (fertilization × initial host diversity p=0.003). The positive effect of initial host diversity on

243   parasite richness weakened in 2013 (p=0.014), and by 2014, as the communities were further

244   colonized by non-planted host species, the positive effect from previous years became a

245   negative effect, though only in fertilized communities: parasite richness was 17% lower in

246   fertilized polycultures than in fertilized monocultures.

247   In the reduced model, the positive relationship between host and parasite richness

248   depended on initial host diversity (initial host diversity × post-assembly host richness

249   p=0.04), and this effect of initial host diversity changed over time (initial host diversity ×

250   post-assembly host richness × year p=0.01; Fig 3; Fig S1; Table S3). In 2012, there was a

251   significantly positive relationship between post-assembly host and parasite richness in

252   polycultures (p=0.03). This effect became non-significant as host communities assembled

253   over time (p_{2013}=0.42; p_{2014}=0.37). In contrast, there was no significant positive relationship

254   between post-assembly host and parasite richness in monocultures in 2012 or 2013

255   (p_{2012}=0.20; p_{2013}=0.87). However, the relationship strengthened over time, such that by

256   2014, there was a significant positive relationship between post-assembly host and parasite

257   richness in monocultures (p=0.004). This change over time in the relationship between post-

258   assembly host and parasite richness as a function of initial host diversity suggests that initial

259   host diversity altered the trajectory of host community assembly over time, thereby altering

260   the relationship between post-assembly host and parasite richness. The nature of this altered

261   trajectory is explored in the structural equation model.

262

263   **Structural equation model including community assembly**

264   The longitudinal mixed model of parasite richness indicated that the relationship

265   between post-assembly host richness and parasite richness changed over time as a function of

266   initial host diversity. That change may have been driven by shifts in host community

267   structure (i.e. community assembly). We therefore next tested the hypothesis that initial host

268   diversity and fertilization indirectly influenced post-assembly parasite richness via their

269   impacts on post-assembly host richness, exotic abundance, phylogenetic diversity, and their

270 interactions, using a structural equation model (Box 1). The data were well fit by this model

271 (Robust χ^2 p=0.288, RMSEA p=0.618, SRMR=0.075), though initial host diversity and

272 fertilization did not interactively influence any of the response variables (p>0.05; Table S4).

273 Therefore, we removed these interactions, yielding a reduced model (Fig 4, Table S5).

274   To model host community assembly, the structural equation model included

275 structurally identical paths, and the same data as the 2014 group from the model presented in

276 Halliday et al (2019). As shown in that model and in other results from this study system,

277 initial biotic and abiotic conditions determined the trajectory of host community assembly,

278 with host communities becoming increasingly divergent over time depending on initial biotic

279 and abiotic conditions (Heckman *et al.* 2017; Halliday *et al.* 2019; Wilfahrt *et al.* 2019).

280 Specifically, increasing initial host diversity increased post-assembly host richness, reduced

281 exotic host abundance, and increased richness-independent phylogenetic diversity of host

282 species. Fertilization reduced post-assembly host richness and increased exotic host

283 abundance, but had no significant effect on phylogenetic diversity of host species (Halliday *et*

284 *al.* 2019). Having re-analyzed this previously published first stage of the structural equation

285 model to quantify the effects of experimental treatments on host community assembly, we

286 then evaluated a novel second stage of the model (Box 1 Fig. 1) to test the hypothesis that

287 shifts in host community structure drive and moderate the effect of post-assembly host

288 richness on parasite richness.

289   As predicted, post-assembly host richness increased parasite richness (p=0.001),

290 supporting the hypothesis that host diversity begets parasite diversity (Fig 4). This effect was

291 moderated by shifting exotic abundance during community assembly: communities that

292 became heavily dominated by exotic species also exhibited the strongest positive relationship

293 between post-assembly host and parasite richness (p<0.0001; Fig 5; Fig S2), even though

294 exotic abundance did not directly influence parasite richness (p = 0.16). Parasite richness was

295   also lower in communities that became more phylogenetically overdispersed (p=0.026),

296   consistent with previous observations that more phylogenetically overdispersed communities

297   may exhibit lower parasite transmission. However, phylogenetic diversity did not alter the

298   relationship between post-assembly host and parasite richness (p=0.40). Together these

299   results indicate that, while the relationship between host and parasite richness is consistent,

300   the magnitude of this relationship depends on community assembly. Consequently, these

301   results support the hypothesis that host diversity begets parasite diversity, but reveal

302   important contingencies in how this relationship manifests over time.

303

304   **Discussion**

305   In this study, the relationship between host and parasite richness changed over time as

306   the host community assembled. Specifically, higher planted host diversity led to an initial

307   increase in parasite richness that weakened as the host community assembled, and the

308   ultimate relationship between post-assembly host and parasite richness was contingent on

309   how host community structure changed during community assembly. This represents, to our

310   knowledge, the first experimental evidence that the relationship between host and parasite

311   richness can change over time in response to shifting host community structure during host

312   community assembly. This result supports two recent studies that found that the relationship

313   between host and parasite richness was contingent on characteristics of host and parasite

314   communities (Johnson *et al.* 2016; Wood *et al.* 2018). Furthermore, host community

315   assembly is linked to parasite transmission (e.g., Joseph *et al.* 2013; Johnson *et al.* 2015;

316   Halliday *et al.* 2019), and our results suggest that contingencies in the relationship between

317   host and parasite richness during host community assembly can emerge as a consequence of

318   changing parasite transmission.

319   Our hypothesis that changes in parasite transmission during host community assembly

320   would modify the relationship between host and parasite richness was grounded in

321   metacommunity theory. According to metacommunity theory, the richness of species in a

322   metacommunity often depends on habitat heterogeneity, but this effect can be highly

323   sensitive to reduced dispersal and establishment among patches (Leibold *et al.* 2004). A host

324   community is a parasite metacommunity, with the richness of host species in the community

325   representing heterogeneity of parasite habitat (Johnson *et al.* 2016), and parasite transmission

326   representing dispersal and establishment of parasites among host individuals within that

327   metacommunity (Borer *et al.* 2016). Thus, parasite richness should increase with increasing

328   host richness, but this effect may be altered by parasite transmission. Parasite transmission, in

329   turn, can be altered by shifts in host community structure that take place during community

330   assembly (Johnson *et al.* 2013; Halliday *et al.* 2019). Exotic hosts contribute the most to

331   disease in this system (Halliday *et al.* 2019; Heckman *et al.* 2019), and consequently, the

332   abundance of exotic hosts modified the relationship between host and parasite richness,

333   supporting our hypothesis.

334   The relationship between post-assembly host and parasite richness was contingent on

335   the final abundance of exotic host species that resulted from community assembly. Many of

336   the exotic hosts that dominate Southeastern US old fields were introduced by humans from

337   fertilized pastures (Fridley 2008), benefit from experimental fertilization (Heckman *et al.*

338   2016, 2017), and are sensitive to initial host diversity. Previous analyses indicate that exotic

339   hosts also contributed most to parasite abundance in communities that they dominated,

340   suggesting that exotic host species may contribute disproportionately to parasite transmission

341   (Halliday *et al.* 2019). Consequently, we suggest that increasing exotic abundance may have

342   strengthened the relationship between host and parasite richness by alleviating dispersal

343   limitation of parasites in communities dominated by exotic species. This hypothesis, that

344   exotic host species contribute disproportionately to parasite transmission, relies on the

345   assumption that native and exotic hosts can share at least some of the same parasite species.

346   Nearly half (6/13) of the parasites infecting exotic host species were also observed infecting

347   native host species, providing some support for this assumption (Table S1).

348   The effect of exotic abundance on the relationship between host and parasite richness

349   is consistent with predictions grounded in metacommunity theory (Leibold *et al.* 2004;

350   Holyoak *et al.* 2005), but could this pattern be driven by the design of this study? In this

351   system, high exotic abundance typically results from increasing abundance of a few dominant

352   species (Heckman *et al.* 2017), suggesting strong competitive asymmetry. Consequently,

353   these dominant species are capable of reducing the abundance and richness of other species

354   (MacDougall *et al.* 2009), which, in addition to increasing parasite transmission, could

355   interfere with how parasite richness was estimated. If this were occurring here, we would

356   have under-sampled parasite diversity in heavily invaded host communities. But we found no

357   difference between the percent of host species surveyed in communities that were minimally

358   invaded (at least one standard deviation below mean exotic abundance; mean ± SD: 77 ±

359   10%) and communities that were heavily invaded (at least one standard deviation above mean

360   exotic abundance; mean ± SD: 83 ± 11%). This indicates that under-sampling of parasite

361   diversity in heavily invaded host communities was unlikely to contribute to our observed

362   results. In other systems, though, high exotic abundance can arise from increasing the

363   abundance of many sub-dominant species. These exotic species typically coexist with native

364   species by occupying distinct niches (MacDougall *et al.* 2009), which should have less

365   negative effects on the abundance and richness of other species. This may lead to increased

366   diversity in invaded host communities (Fridley *et al.* 2007), which could reduce parasite

367   transmission. Future studies could resolve these potential issues by experimentally

368   manipulating exotic abundance (or other drivers of parasite transmission) and host richness

369   simultaneously (Young *et al.* 2017). Nevertheless, these results highlight the value of our

370   dynamic community assembly approach for generating new hypotheses that could be tested

371   through direct manipulations of static host communities.

372   Increasing host phylogenetic diversity reduced parasite richness, consistent with

373   previous observations that more phylogenetically overdispersed communities may exhibit

374   lower parasite transmission (e.g., Parker *et al.* 2015; Halliday *et al.* 2019). These results are

375   in contrast to predictions grounded in the phylogenetic signal in parasites' host range (Box 1),

376   which suggest that, because more distantly related hosts are less likely to share pathogens

377   than closely related host species (Gilbert & Webb 2007), communities with higher

378   phylogenetic diversity may support more parasite species (e.g. via habitat heterogeneity;

379   Johnson *et al.* 2016). Experiments that explicitly cross host taxonomic and phylogenetic

380   diversity (e.g., Cadotte 2013) would help disentangle the conditions under which taxonomic

381   and phylogenetic diversity can have opposite, but non-interacting results.

382   Our hypothesis that increasing transmission during host community assembly would

383   alleviate dispersal limitation for parasites relies on the assumption that parasite communities

384   would be dispersal limited. This assumption appears to hold for some parasites of plants

385   (Mitchell *et al.* 2002; Laine 2005; Tack *et al.* 2014; Halliday *et al.* 2017a) and animals

386   (Sousa 1994; Esch *et al.* 2001; Byers *et al.* 2008; Mihaljevic *et al.* 2018). However, even in

387   systems where parasite dispersal does not appear to be particularly limiting (e.g., Richgels *et*

388   *al.* 2013; Dallas & Presley 2014; Ekholm *et al.* 2017), increasing transmission could still alter

389   the relationship between host and parasite richness. In a metacommunity, when species

390   richness is not dispersal-limited, mass effects (Logue *et al.* 2011; Cornell & Harrison 2013)

391   can reduce regional richness by overwhelming species sorting mechanisms that occur within

392   habitat patches. Similarly, when parasite distributions are not transmission-limited, an

393   increase in parasite transmission could weaken the relationship between host and parasite

394   richness (e.g., via mass effects), particularly if host generalists replace more specialized

395   parasites (Johnson *et al.* 2016). Thus, across a wide gradient in parasite transmission rate, we

396   hypothesize the effect of transmission rate on the relationship between host and parasite

397   richness to be nonlinear: a positive/strengthening effect at low transmission rate, and a

398   negative/weakening effect at high transmission rate.

399   While our results demonstrate that the relationship between host and parasite richness

400   can be moderated by shifting host community structure, they are nonetheless consistent with

401   the well-established "host-diversity-begets-parasite-diversity" hypothesis (Hechinger &

402   Lafferty 2005; Kamiya *et al.* 2014) . Consistent with previous experiments in other systems,

403   host richness most strongly predicted parasite richness immediately following establishment

404   of experimental host communities (Rottstock *et al.* 2014; Liu *et al.* 2016). This effect

405   weakened as non-planted hosts colonized experimental communities, but a significant

406   positive effect of post-assembly host and parasite richness remained even after two years of

407   community assembly. This latter result is consistent with the "host-diversity-begets-parasite-

408   diversity" hypothesis (Hechinger & Lafferty 2005), even after accounting for the moderating

409   effect of community assembly.

410   Together, these results demonstrate that the relationship between host and parasite

411   richness can be contingent on characteristics of host community structure that shift during

412   host community assembly. Thus by leveraging host community assembly, this study adds a

413   novel mechanism to a growing body of literature revealing key contingencies in this

414   relationship (Johnson *et al.* 2016; Wood *et al.* 2018). We suggest that contingencies in the

415   relationship between host and parasite richness may occur because characteristics of host and

416   parasite communities that shift during community assembly alter parasite transmission. More

417   specifically, parasite transmission may be altered simultaneously by multiple components of

418   host community structure that during community assembly shift in concert. For example,

419   experimental fertilization both increased colonization by exotic host species and decreased

420   host species richness (Heckman *et al.* 2017; Halliday *et al.* 2019). This covariance, in turn,

421   led to an indirect effect on the relationship between host and parasite richness: communities

422   that were more heavily invaded exhibited a stronger positive relationship between host and

423   parasite richness. Consequently, fertilization indirectly strengthened the relationship between

424   host and parasite richness. This study represents an important step forward by providing an

425   ecological mechanism to explain contingencies in one of the most consistently reported

426   patterns in disease ecology – the positive relationship between host and parasite diversity.

427

438

439   **References**

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630   **Figure legends**

631   **Fig. 1** Conceptual metamodel of community assembly altering the relationship between host

632   and parasite richness. During community assembly, biotic and abiotic drivers can determine

633   the trajectory of host community composition, which may, in turn, moderate the relationship

634   between host and parasite richness.

635

636   **Fig. 2** Longitudinal mixed model results showing the model-estimated effects of initial host

637   richness (monocultures orange; polycultures blue) and resource supply (unfertilized

638   communities on the left; fertilized communities on the right) on rarefied parasite richness

639   across three years. Large points represent the estimated treatment mean, error bars are 95%

640   confidence intervals, and small points show the raw data. The y-axis shows rarefied parasite

641   richness. Asterisks show significant effects ($p < 0.05$). Initial host richness increased parasite

642   richness but that effect weakened as host communities assembled, and ultimately reversed in

643   fertilized host communities.

644

645   **Fig. 3** Longitudinal mixed model results showing the model-estimated effect of post-

646   assembly host richness on rarefied parasite richness as a function of initial host diversity

647   (monocultures orange; polycultures blue) across three years. The y-axis shows the slope of

648   the relationship between post-assembly host richness and parasite richness. Points represent

649   the estimated effect of the experimental treatment on that slope (i.e., the interactive effect of

650   post-assembly host richness and initial host diversity on parasite richness). Error bars are

651   95% confidence intervals. The positive relationship between host and parasite richness that

652   was observed in polycultures in 2012 weakened over time, while the relationship between

653   host and parasite richness in monocultures strengthened over time, resulting in a positive

654   relationship in 2014.

655

656   **Fig. 4** Structural equation model results for the final (reduced) model. Red lines are negative

657   effects (p < 0.05), blue lines are positive effects (p < 0.05), and dashed lines are non-

658   significant (p > 0.05). All coefficients are standardized. Correlations between errors are

659   denoted with double-headed arrows. Higher post-assembly host richness increased parasite

660   richness, and that effect was stronger in communities that, as a result of community

661   assembly, became more heavily dominated by exotic host species.

662

663   **Fig. 5** Effect of post-assembly host richness on parasite richness as a function of exotic host

664   abundance. Model estimated effects of standardized and centered exotic abundance on the

665   slope of the relationship between post-assembly host richness and parasite richness (i.e., the

666   interactive effect of post-assembly host richness and exotic host abundance on parasite

667   richness). The rug along the x-axis shows the distribution of the standardized and centered

668   empirical data. Communities that fall 0.5 or more standard deviations below the mean of

669   exotic host abundance show no relationship between host and parasite richness. Above that

670   level, the relationship between host and parasite richness becomes increasingly positive with

671   increasing exotic host abundance. Consequently, communities that became most dominated

672   by exotic species also exhibited the strongest positive relationship between host and parasite
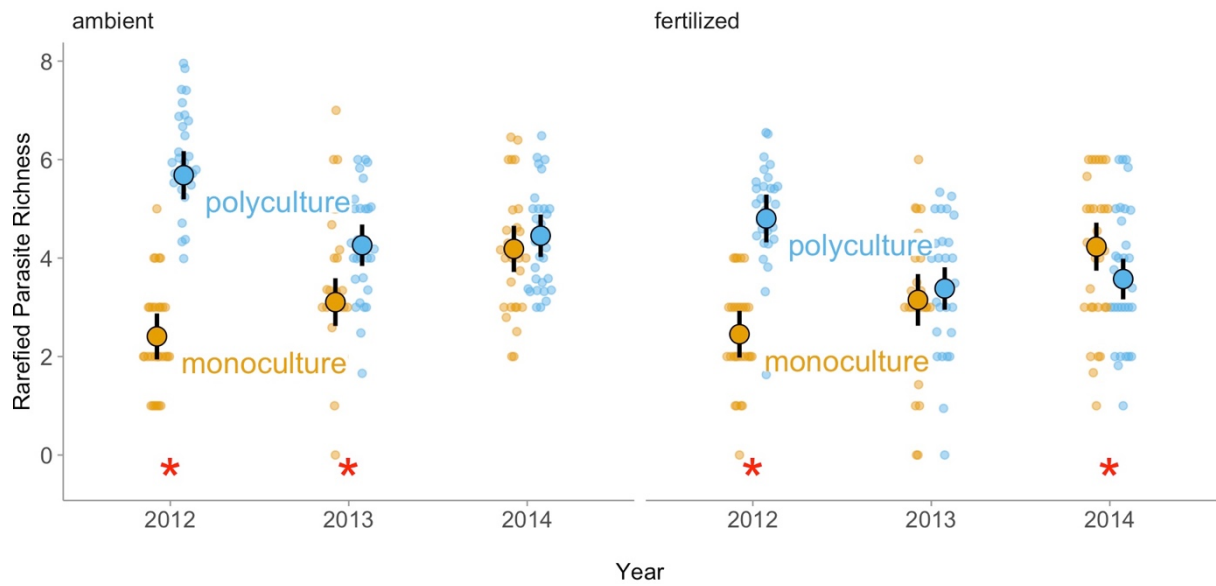
673   richness.

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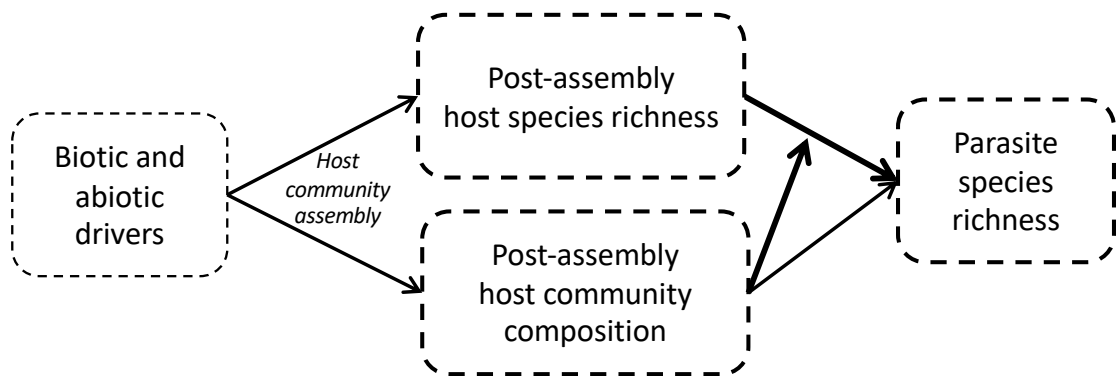
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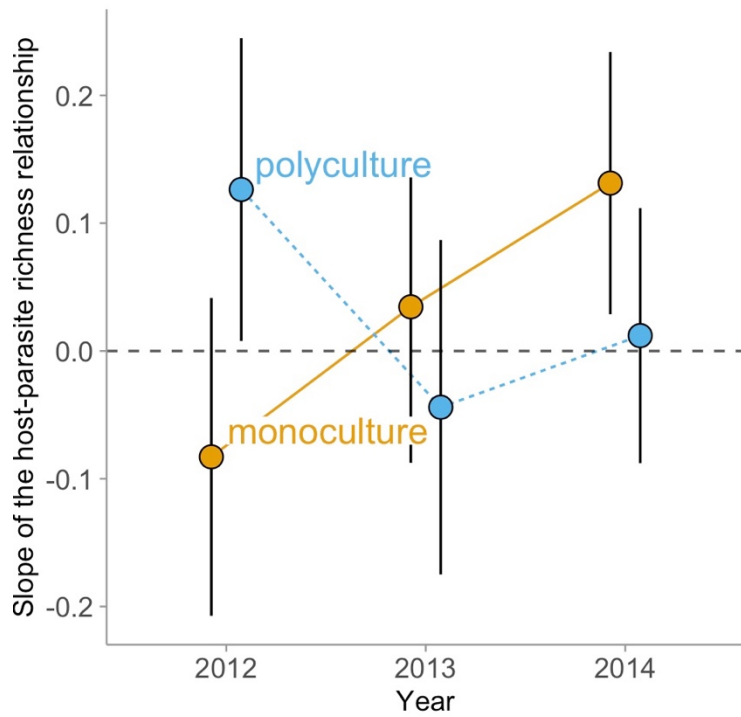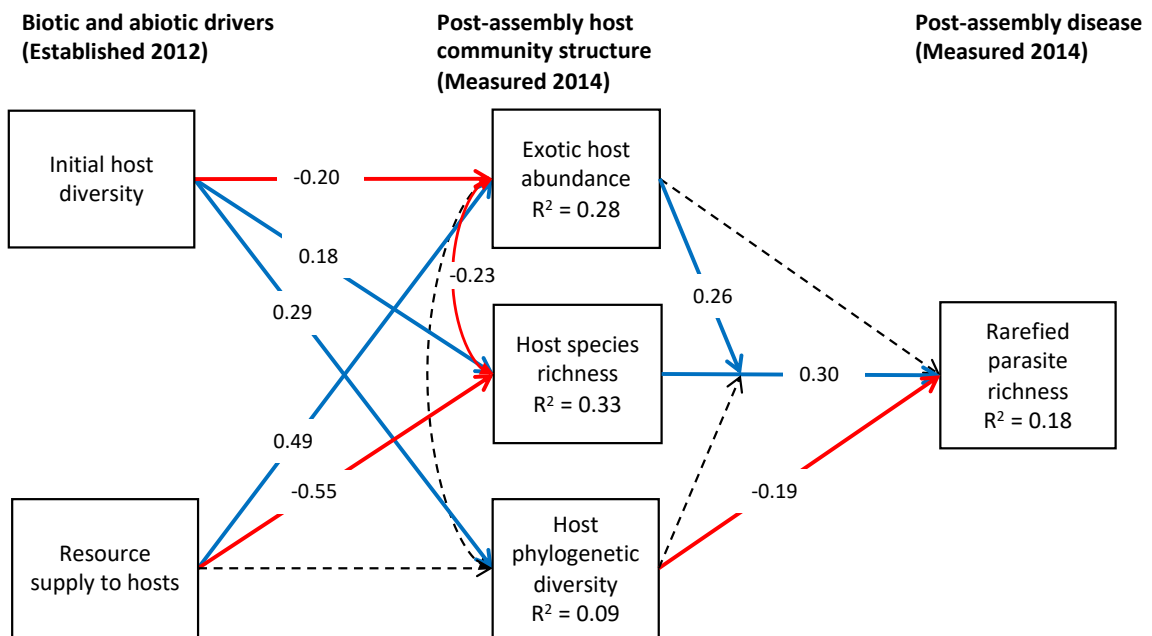**Fig. 1**

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Fig. 2

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Fig. 3

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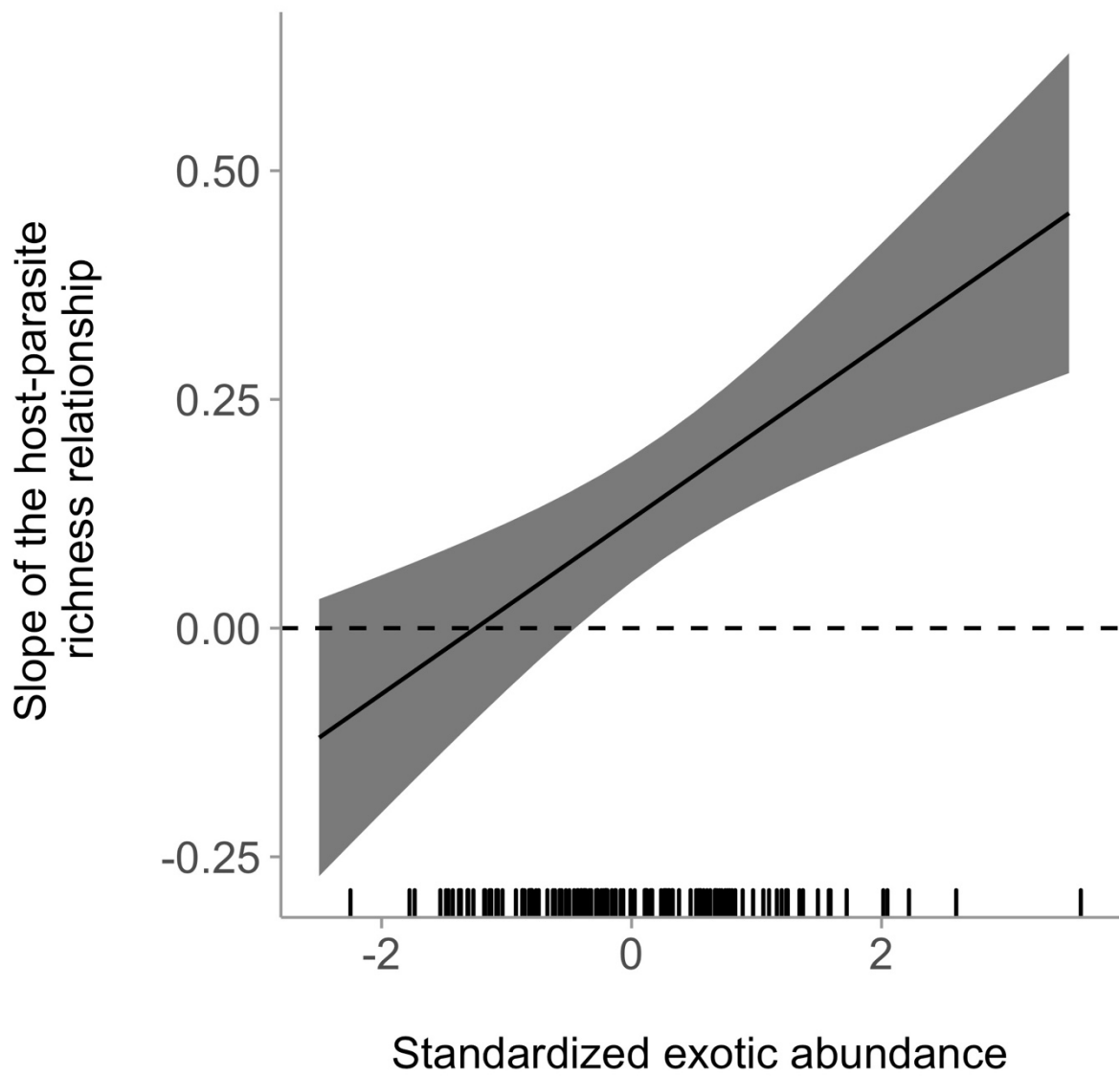684

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Fig. 4

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Fig. 5

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Box 1. Biotic and abiotic drivers of host community assembly can indirectly alter the host-parasite richness relationship.

Host community assembly involves change over time in community characteristics in response to a variety of biotic and abiotic conditions. Here, we consider three characteristics of host communities that change over time during community assembly and can alter parasite transmission: host species richness, exotic host abundance, and host phylogenetic diversity. We consider these changes in host community structure in response to two potential drivers: initial host diversity and resource supply to hosts.

Increased resource supply often reduces host species richness by decreasing the number of limiting resources that species compete for (Box Fig. 1, path h; Harpole *et al.* 2016), increases the abundance of exotic species by favoring species adapted to resource-rich environments (Box Fig. 1, path g; Huenneke *et al.* 1990; Heckman *et al.* 2017), and reduces phylogenetic diversity by favoring clades with specific resource uptake and allocation strategies (Box Fig. 1, path i; Mayfield & Levine 2010). Furthermore, communities that assemble from higher initial diversity may experience a legacy effect, with these host communities maintaining higher richness during community assembly (Box Fig. 1, path b; Mouquet *et al.* 2003), being more likely to resist invasion by exotic species at small and intermediate spatial scales (Box Fig. 1, path a; Levine & D'Antonio 1999; Fargione & Tilman 2005), and promoting colonization by species from different clades with low niche overlap, resulting in increased phylogenetic overdispersion (Box Fig. 1, path c; Mayfield & Levine 2010; Pavoine & Bonsall 2011). By altering parasite transmission, these concurrent shifts in host community structure might alter the relationship between host and parasite richness as host communities assemble.

Shifts in exotic host abundance during community assembly might alter the relationship between host and parasite richness. Parasite richness often increases with host

718   richness, because higher host richness represents a more diverse pool of resources for

719   parasites (Box Fig. 1, path k; Kamiya *et al.* 2014). However, exotic species often initially

720   escape the parasites that infected them in their native range (Mitchell & Power 2003;

721   Mitchell *et al.* 2010; Heger & Jeschke 2014), potentially leading to lower parasite richness

722   (Box Fig. 1, path j) and weakening the relationship between host and parasite richness (Box

723   Fig. 1, path m) by reducing transmission in exotic-dominated communities. Alternatively,

724   introduced hosts can also acquire infections from closely related native hosts (Parker *et al.*

725   2015) or via repeated introductions over time (Mitchell *et al.* 2010; Stricker *et al.* 2016).

726   Successful exotic species are often more competent hosts for the parasites that can infect

727   them (Han *et al.* 2015; Young *et al.* 2017), which could increase parasite transmission in

728   exotic-dominated communities (e.g., Halliday *et al.* 2019). Thus shifts in exotic host

729   abundance could strengthen or weaken the relationship between host and parasite richness,

730   depending on characteristics of the host and parasite communities (Box Fig 1, path m).

731   Shifts in host phylogenetic diversity during community assembly might alter the

732   relationship between host and parasite richness. More distantly related hosts are less likely to

733   share pathogens (Gilbert & Webb 2007). Consequently, communities with higher host

734   phylogenetic diversity, independent of species richness, may support more parasite species

735   (Box Fig. 1, path l), potentially strengthening the relationship between host and parasite

736   richness in phylogenetically overdispersed host communities (Box Fig. 1, path n). However,

737   as host phylogenetic overdispersion increases, parasite transmission is expected to decline via

738   a phylogenetic dilution effect (Parker *et al.* 2015; Liu *et al.* 2016; Halliday *et al.* 2019),

739   which could reduce parasite species richness and weaken the relationship between host and

740   parasite richness in phylogenetically overdispersed host communities (Box Fig. 1, paths n, l).

741   Thus, drivers of community assembly that favor higher phylogenetic overdispersion could

742 either increase or reduce parasite richness, while simultaneously strengthening or weakening

743 the relationship between host and parasite richness.

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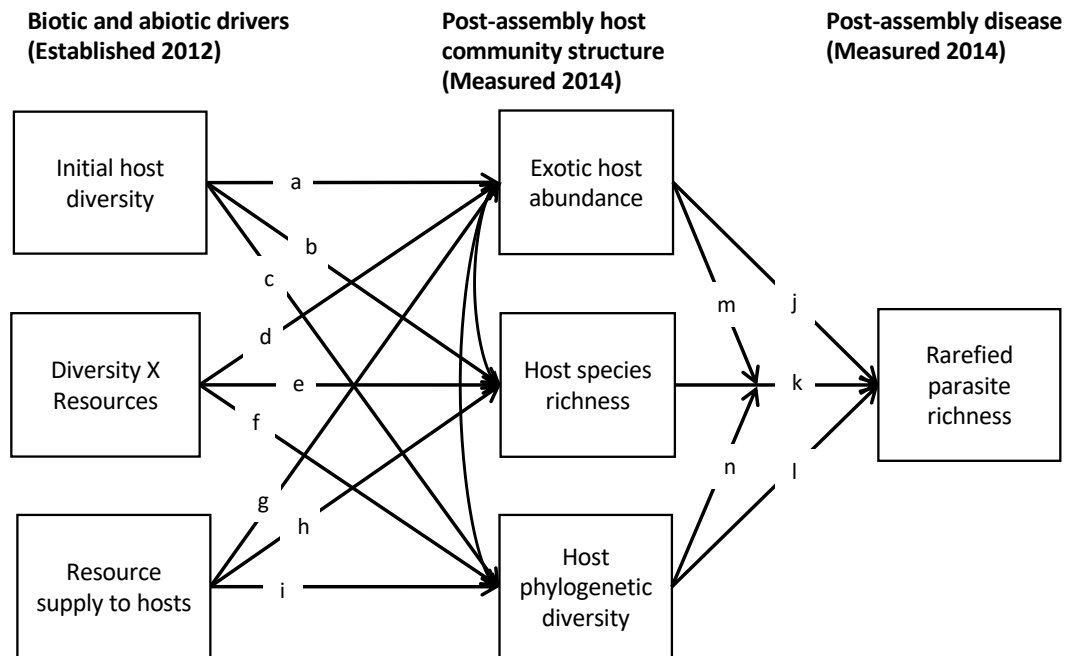
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747 **Box 1 Fig 1.** Measurement model representing the hypothesized effects of initial host

748 diversity and resource supply on parasite richness, mediated by post-assembly host

749 community structure. Paths are labeled a-n for reference in the text. Paths a - i represent the

750 effects of experimental treatments on community assembly (the model's first stage). Paths j -

751 n (the model's second stage) test the hypothesis that shifts in host community structure

752 altered the relationship between post-assembly host and parasite richness. Specifically, paths

753 j - l represent direct effects of the final plant community in 2014 on parasite richness. Paths m

754 - n represent the moderating effect of shifting community structure on the relationship

755 between host and parasite richness.

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