1   **Special feature title**

2   Towards a mechanistic understanding of global change ecology

3

4   **Title**

5   Towards the general mechanistic prediction of community dynamics

6

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Abstract

1. "What controls the distribution and abundance of organisms"? This question, at the heart of the dynamics of ecological communities, would have been familiar to the earliest ecologists. Having lain effectively abandoned for many years, community dynamics today is a vibrant research topic of great conceptual interest with practical import for conservation, ecological management, ecosystem services and the responses of ecological communities to climate change.

2. We describe how modern coexistence theory can be applied to predict community dynamics through the use of demography. We explore the challenges that limit the deployment of this demographic framework, and the tools from phylogenetic and functional ecology that have been used to surmount them.

3. Finding existing tools not altogether sufficient, we propose the use of 'hard' functional traits and physiological tolerances of environmental conditions and low resource availability to extend the demographic framework so that the dynamics of a broader range of ecological communities can be accurately predicted.

4. We illustrate these new approaches with two case studies. Given the urgent need to accurately forecast the dynamics of ecological communities, we hope that many ecologists will adopt these tools.

Objective

The objective of this contribution is to outline the most promising techniques, as we see them, to predict community dynamics in the medium term. By community dynamics, we mean changes in species composition and relative abundance through time or over environmental gradients. By medium term, we mean 5-10 generations into the future, a timeframe that varies enormously among organisms. It represents an important frontier to advance, however, as it is the scale at which extrapolations from current community structure tend to break down, and yet, given anthropogenic effects on global climate and to environments around the globe, it is relevant to conservation, restoration and ecological management (Agrawal et al., 2007; Clark et al., 2001). Notably, ecologists already have predictive ability over such scales in a few circumstances. Following decades of research, we can make strong, empirically grounded predictions about the dynamics expected, for example, upon the abandonment of agricultural land (Horn, 1974; Norden et al., 2015). Even so, ecologists' ability to accurately predict community dynamics remain frustratingly limited. For example, we currently have little ability to predict changes in tree relative abundance over 200 years in tropical rain forests, or invertebrate species composition over five years in temperate vernal pools.

        Improving our predictive ability would be of great conceptual interest, yielding insight into long-standing questions in community ecology. For example, many ecological communities are puzzlingly rich in competing species despite a lack of obvious niche partitioning at the scale of individual patches, resulting in what Hutchinson (1961) famously described as a "paradox of the plankton". Conceptual gaps also remain in understanding how the strength and nature of interspecific interactions vary over space and time and thereby generate variation in community

63   structure (Agrawal et al., 2007; Chamberlain, Bronstein, & Rudgers, 2014; Hairston,

64   Smith, & Slobodkin, 1960). These classic problems deserve general answers.

65   We begin by outlining the most-promising current approach, based on the

66   estimation of demographic parameters relating to stabilising and equalising

67   coexistence mechanisms (Chesson, 2000b), which has scored notable successes

68   (Adler, Ellner, & Levine, 2010; Kraft, Godoy, & Levine, 2015; Levine & Hille Ris

69   Lambers, 2009). Essential to any accurate prediction is the identification and

70   minimization of uncertainties (Clark et al., 2001), so we next explore the challenges

71   that limit the current approach. We discuss the tools derived from phylogenetic and

72   functional ecology that have been used to surmount these challenges, and their

73   limitations. We conclude by presenting two ongoing investigations that employ

74   complementary techniques, 'hard' functional traits and physiological tolerances, to

75   further extend the demographic approach. We see them as offering the most

76   promise to generalise the demographic framework, thus facilitating accurate

77   predictions of community dynamics of a wide variety of ecosystems.

78

79   **Background**

80   25 years ago, Pianka (1992) declared that "Community ecology… remains a

81   primitive and embryonic science". He was correct in many ways. Ecologists have

82   debated the controls on population sizes and community structure since the dawn of

83   ecology as a science, and conceptual approaches to community dynamics had

84   proliferated (Fig. 1). Nevertheless, their application stalled because most of the

85   underlying theory, with the exception of limiting similarity (MacArthur & Levins, 1967)

86   was qualitative. The lack of mechanistic quantitative theory precluded accurate

87   predictions of community dynamics (Vellend, 2016).

88   Two publications re-founded community ecology on a more rigorous basis at

89   the turn of the millennium. The first, Hubbell's 'neutral' theory (2001), set forth a

90   model of community dynamics and biogeography of extreme parsimony. Though its

91   assumptions of species equivalence were derided as unrealistic (McGill, Maurer, &

92   Weiser, 2006), it was simultaneously lauded for its capacity to accurately describe

93   aspects of community structure, such as relative abundance distributions, with a

94   scant handful of parameters (Volkov et al., 2007). As deriving similar predictions for

95   species-rich communities from traditional niche-partitioning theory would require

96   unmanageably many parameters to be estimated (Chase & Leibold, 2003;

97   Silvertown, 2004), neutral theory led ecologists to radically reconsider their approach

98   to community dynamics. The previous year, Chesson (2000b) had synthesised niche

99   theory with an earlier formulation of neutral theory (Hubbell, 1997). He categorised

100   coexistence mechanisms as either equalising, which minimise average fitness

101   differences between species, or as stabilising, which intensify negative relationships

102   between population density and per-capita population growth rate. Chesson's

103   synthesis was highly influential because of its generality. For the first time, the

104   dynamics of any community could be investigated on the basis of the demography of

105   its component populations, so long as the growth rate of each population and the

106   intensities of interactions between them could be estimated.

107   Chesson's (2000b) synthesis, now referred to as "modern coexistence theory"

108   (Letten, Ke, & Fukami, 2017) is general, in the sense that it applies to all ecological

109   communities. Even so, its relatively abstract mathematical formulation limited its

110   application. Initial attempts to distinguish the relative strength of stabilising and

111   equalising mechanisms were based on the study of macroscopic patterns observed

112   in ecological communities. Niche-based and neutral models can generate very

113 similar relative abundance distributions, however, rendering such pattern-matching

114 exercises uninformative (Chave, Muller-Landau, & Levin, 2002; McGill, Maurer, &

115 Weiser, 2006). A new opportunity for predicting community dynamics was presented

116 when Adler et al. (2007) proposed a mechanistic operationalisation of Chesson's

117 synthesis.

118   To predict community dynamics from demography, first quantify the intrinsic

119 population growth rate of each target species, and the effects of those species'

120 abundances on the population growth rates of the other species of interest (Adler,

121 HilleRisLambers, & Levine, 2007). These are traditionally written as λ_i and α_{ij}, with i

122 and j representing distinct species. With estimates of population growth rates and

123 interaction coefficients in hand, build a demographic model including stabilisation

124 terms and fitness difference terms for each species (Adler, HilleRisLambers, &

125 Levine, 2007; Chesson, 2000b). Doing so is conceptually interesting, as it gives

126 insight into the mechanisms of coexistence operating in the community. The specific

127 form of the demographic model will depend on the life history of the organisms

128 examined and the nature of the interspecific interactions. Although originally

129 proposed to evaluate the importance of neutral- and niche-based coexistence

130 mechanisms, the Chesson-Adler demographic framework can be applied to predict

131 various aspects of community structure and dynamics. For example, Adler *et al*.

132 (2010) built a spatially explicit individual-based model to predict times to extinction

133 for each of their studied species, as well as a multi-species integral projection model

134 to predict the dynamics of population growth rates and asymptotic population sizes.

135

136 **Challenges to apply the demographic framework**

137   As Adler et al. (2007) note, the demographic framework "…require[s] considerable

138   data on species' performance and interactions across wide ranges of biotic and

139   abiotic variabilities, and also sophisticated quantitative techniques." In this section,

140   we elaborate on this comment, detailing the challenges that most strongly limit the

141   deployment of the demographic framework in the prediction of community dynamics.

142   First, and most simply, estimating population sizes of organisms that are shy,

143   nocturnal, fossorial, or otherwise difficult to detect is challenging. Moreover, the great

144   majority of species in any community are rare, complicating the estimation of their

145   population sizes (Rabinowitz, 1981).

146   Second, the life history of some organisms makes it difficult to estimate their

147   population growth rates and the sensitivity of their population growth rates to intra-

148   and interspecific density. Making observations over the complete lifespan of long-

149   lived individuals is often infeasible (Clark et al., 2010). In such cases, it can be

150   profitable to separately assess vital rates such as recruitment, individual growth,

151   survival and fecundity for each target species. Moreover, many species have

152   multiple pathways to fitness. For example, many species reproduce both clonally and

153   sexually, either sequentially, as in aphids (Aphidoidea, Hemiptera**)**, or

154   simultaneously, as in many plants. In the rare systems in which genets are easily

155   tracked, multiple fitness pathways cause little problem, but more often, only data on

156   ramets is easily available. Matrix population models are the traditional technique to

157   integrate vital rates over the lifecycle and estimate population growth rates (Caswell,

158   2001). They have been widely criticised recently, in favour of integral projection

159   models, which avoid the issue of into how many stages should the lifecycle be

160   divided (Ellner, Childs, & Rees, 2016). Long or complex life histories can be

161   accommodated through careful model construction, but only with detailed knowledge

162   of the target species.

163   Third, estimating interaction coefficients among co-occurring species can be

164   challenging. To quantify the density dependence of population growth rates

165   rigorously, it is important that the intensity of interactions among species be

166   integrated across life stages, as stabilising processes operating on one life stage can

167   be offset by destabilising effects at others (Adler, HilleRisLambers, & Levine, 2007).

168   For sessile organisms, especially plants, methods for estimating interaction

169   coefficients are well established. The degree to which number, size and distance to

170   neighbouring plants affect plant performance is the subject of a well-established

171   literature (Canham, LePage, & Coates, 2004). These methods have been further

172   refined through the inclusion of functional similarity and phylogenetic relatedness

173   among neighbours (Fortunel, Valencia, et al., 2016; Uriarte et al., 2010). With

174   extensive fieldwork, it is possible to estimate interaction coefficients observationally

175   (Clark et al., 2010; Purves et al., 2008). For mobile organisms, including most

176   animals, on the other hand, it can be challenging to model interactions between

177   individuals. Most mobile species face constraints in reproduction, however, which

178   can lead to breeding aggregations on localised limiting resources, such as flies

179   gathering on dung pats and explosively breeding frogs gathering in temporary pools.

180   Such aggregations offer opportunities to measure the strength of inter- and intra-

181   specific interactions, which may be negligibly weak at other stages of the lifecycle

182   (see *Sepsidae case study*, below).

183   Moreover, interaction coefficients need to be assessed across the natural

184   range of population density. A challenge in using observational data to do so is that

185   most species tend to be either common or rare throughout a study system

186 (Rabinowitz, 1981). Thus, regressions of observed population growth rates against

187 observed frequency often lack sufficient statistical power to yield satisfactory

188 estimates of interaction coefficients. An alternative is to generate experimental

189 communities at a range of densities, and to estimate interaction coefficients from

190 them (Levine, Adler, & Hille Ris Lambers, 2008; Levine & Hille Ris Lambers, 2009).

191 In species-rich communities, this approach can be simplified by modelling one target

192 species in competition with the aggregate community, essentially turning a many-

193 species community into a series of two-species systems, and repeating the process

194 for each species in the community (Adler, HilleRisLambers, & Levine, 2007; Kraft,

195 Godoy, & Levine, 2015). Data obtained from artificial communities can be used to

196 parameterise multi-species integral projection models that integrate over the

197 lifecycle, then estimate interaction coefficients and population growth rates for each

198 species (Adler, Ellner, & Levine, 2010).

199   Finally, incorporating environmental heterogeneity into the demographic

200 framework remains a challenging and open area of research (Agrawal et al., 2007;

201 Maron, Baer, & Angert, 2014). The degree to which population growth rates vary

202 along environmental gradients is little studied, and even less is known about

203 environmental effects on interaction coefficients. Should we expect uncorrelated

204 changes in community interaction coefficients along environment gradients, or can

205 we expect the rank order of interaction coefficients among pairs of species to remain

206 consistent? Although the degree of context dependence in interaction coefficients

207 has begun to be explored (Chamberlain, Bronstein, & Rudgers, 2014), general

208 answers to such questions remain unclear, and to our knowledge, no study has

209 investigated the environmental dependence of population growth rates and

210 interaction coefficients in species-rich communities (but see Griffiths, Warren, &

211   Childs, 2015). Fortunately, from the perspective of tractability, pairwise interaction

212   coefficients appear to be little affected by the presence of other species

213   (Chamberlain, Bronstein, & Rudgers, 2014). Acquiring data suitable for testing the

214   context dependence of interaction coefficients will require careful experimental

215   design (Levine et al., 2017; Maron, Baer, & Angert, 2014; see Two Ways Forward,

216   below)

217   Given this list of challenges, it is perhaps unsurprising that relatively few

218   investigators have employed the demographic framework to predict community

219   dynamics. Nor is it surprising that many researchers have turned to tools from

220   phylogenetic and functional ecology to overcome them.

221

222   **Addressing challenges through shared evolutionary history**

223   With access to phylogenetic data, it is possible to estimate the degree to which

224   shared evolutionary history structures ecological communities (Webb et al., 2002).

225   Access to these data has been facilitated by inexpensive sequencing and tree-

226   building (The Angiosperm Phylogeny Group, 2016; Webb, Ackerly, & Kembel, 2008).

227   Nevertheless, phylogenetic tools are not generally sufficient to generate clear

228   predictions of community dynamics (Gerhold et al., 2015). For example, mortality

229   rates of seedlings in a French Guianan rain forest increased with increased

230   phylogenetic relatedness of neighbours (Paine et al., 2012), even as the opposite

231   pattern was observed in a Panamanian forest (Lebrija-Trejos et al., 2014). More

232   importantly, phylogenetic information is generally the wrong tool to assess

233   interactions between species, as organisms can't detect each other's evolutionary

234   history. Rather, they detect only the present-day phenotype (Paine et al.,

235   2012). When ecologists observe phylogenetic community structure, they learn that

236   something is going on, but it is rarely clear what that thing is (Castillo, Verdú, &

237   Valiente-Banuet, 2010). Phylogenetic community structure is particularly difficult to

238   interpret without estimates of trait conservatism over the phylogeny. And if measures

239   of trait conservatism are available, then functional traits must also have been

240   measured. So why not use them directly? Thus, phylogenetic data is unlikely to

241   provide deep insight into community dynamics, unless interspecific interactions are

242   mediated by shared natural enemies. Since the natural enemies may have co-

243   evolved with the plants they consume, it is reasonable to think that they would, to

244   some degree, respond to shared evolutionary history (Paine et al., 2012).

245

246   **Addressing challenges through functional traits**

247   Functional traits, morphological or physiological attributes of organisms that affect

248   population growth rate through their relationships with vital rates (Violle et al., 2007),

249   hold great promise in the prediction of community dynamics (McGill et al., 2006).

250   Functional traits can be used to reduce the dimensionality inherent to species-rich

251   communities, as one can parameterise models on the basis of functional groups

252   rather than species (Laughlin, 2014). Alternatively, one can assess the degree to

253   which functional traits are associated with vital rates, then use integral projection

254   models to predict population growth rates (Adler et al., 2014). Their use by ecologists

255   has been facilitated by the standardisation of sampling techniques (Pérez-

256   Harguindeguy et al., 2013), and the development of global databases (Kattge et al.,

257   2011). Functional traits frequently vary within, as well as among, species,

258   contributing to variance in vital rates and thus population growth rates (Bolnick et al.,

259   2011). Albert et al. (2011) therefore suggest that intraspecific trait variation should

260   assessed and incorporated in regional- or local-scale studies of community

261   assembly.

262   Functional traits can be considered to lie along a continuum, from so-called

263   'soft' traits, which are easily measured but distal to vital rates and therefore to

264   population growth rates, to so-called 'hard' traits, which are more indicative of

265   physiology and therefore more directly associated with vital rates (Díaz et al., 2004;

266   Lavorel & Garnier, 2002; Weiher et al., 1999; Table 1). Soft traits indicate potential,

267   rather than realised vital rates, whereas 'hard' functional traits predict vital rates and

268   population growth rates more accurately, but are often are more time-consuming to

269   measure and require more-expensive equipment (Díaz et al., 2004; Pérez-

270   Harguindeguy et al., 2013). For example, leaf chlorophyll concentration is associated

271   with the potential growth rate of plants, given the ideal availabilities of light, water

272   and nutrients, and can be estimated in less than a second using the difference in

273   optical density at a pair of wavelengths (Coste et al., 2010). Photosynthetic rate, on

274   the other hand, indicates the effective net rate of photosynthate production, but takes

275   longer and requires a much more expensive infrared gas analyser (Table 1). So what

276   are the costs and benefits of 'soft' and 'hard' functional traits?

277   Like evolutionary relatedness, 'soft' functional traits are generally insufficient

278   to predict community dynamics. Vital rates are only moderately associated with 'soft'

279   functional traits (Paine et al., 2015; Wright et al., 2010). These weak relationships

280   occur, in part, because the trait-vital rate relationships are affected by environmental

281   conditions, which are rarely taken into account. For example, chlorophyll

282   concentration may misrepresent a plant's growth rate when its access to light or soil

283   resources varies. In such cases, photosynthetic rate would be a better indicator of

284   growth rate. Finally, and most damningly, the interpretation of functional traits is

285   complicated by inter-correlations among traits (Díaz et al., 2004, 2015), and their

286   potential for simultaneous associations with stabilising or equalising differences

287   between species (Kraft, Godoy, & Levine, 2015).

288

289   **Two ways forward**

290   *'Hard' functional traits*

291   We see the use of 'hard' functional traits and of physiological tolerances as

292   complementary methods to extend the demographic framework (Craine et al., 2012;

293   Violle et al., 2007). With hard traits, one can predict population growth rates and

294   interaction coefficients among species. They are a useful substitute in the many

295   cases when demographic data are not available or too costly to collect, and they can

296   be parameterised in models to predict community dynamics. The strength of this

297   approach is proportional to the strength of the relationship between the functional

298   trait(s) assessed and vital rates. Thus, we echo the advice of Díaz et al. (2004) for

299   investigators to use functional traits as mechanistically related as possible to vital

300   rates.

301   The use of hard functional traits come with two caveats. First, as they are

302   associated with actual, rather than potential vital rates, environmental conditions

303   influence their expression more than soft traits. To extend the previous example, the

304   soft functional trait of chlorophyll content is relatively independent of abiotic

305   conditions at the time of measurement, whereas photosynthetic rate is highly

306   context-dependent (Pérez-Harguindeguy et al., 2013). Thus, the signal that 'hard'

307   traits provide can be noisy, and can only be interpreted in the context of

308   environmental data. Thus, using them effectively requires not only their

309   quantification, but also determining the extent of their variation over relevant

310   environmental gradients. Moreover, as they are usually tissue specific, rather than

311   integrating over the entire organism, functional traits may trade off among the tissues

312   of an organism, obscuring their interpretation (Kraft, Godoy, & Levine, 2015).

313

314   *Physiological tolerances*

315   We further suggest the use of whole-organism physiological tolerances (also

316   referred to as physiological traits; Baltzer et al., 2008) to predict community

317   dynamics. A physiological tolerance is defined as the critical level of a particular

318   resource or environmental condition at which an organism can survive for an

319   extended period (Craine et al., 2012). In other words, it is the whole-organism

320   compensation point for that resource or condition. The relevant tolerances to assess

321   will vary depending on the organisms of interest and the environmental context. They

322   have been intensively investigated for certain taxonomic groups, such as lizards and

323   other ectothermic vertebrates (Buckley & Jetz, 2008; Kearney & Porter, 2009),

324   whereas as other taxa such as plants have received less attention (but see, for

325   example Koehler, Center, & Cavender-Bares, 2012).

326   Physiological tolerances differ from functional traits in that they integrate the

327   response of the entire organism to their environment, rather than being specific to a

328   particular tissue (Craine et al., 2012). For example, one can measure drought

329   tolerance as the difference in times to death between field capacity and un-watered

330   conditions (Kursar et al., 2009), rather than as the tissue-level functional traits of leaf

331   area, leaf water potential or stem vulnerability to embolism (Pérez-Harguindeguy et

332   al., 2013). Physiological tolerances do not, however, indicate the organ-level

333   mechanism(s) by which low-resource conditions are tolerated. Therefore, it can be

334   useful to measure them in conjunction with functional traits to infer the mechanisms

335   underlying changes in vital rates and therefore population dynamics.

336   A great advantage of studying physiological tolerances is that they explicitly

337   link vital rates to environmental conditions, making it possible to predict how

338   community dynamics will vary over environmental gradients. The most-relevant

339   environmental gradients over which population growth rates and interaction

340   coefficients vary will generally also be those most relevant for the assessment of

341   physiological tolerances (Kearney & Porter, 2009). One can investigate physiological

342   tolerances to the low availability of resources such as light or nutrients, or to abiotic

343   conditions, such as cold temperatures, flooding duration, or fire intensity. The

344   interpretation of such tolerances differs, in that the former are reduced by

345   competitors, whereas the latter are independent of the presence of competitors.

346   Tolerance can be evaluated as a change in individual performance along a gradient

347   of resource availability, even as interaction coefficients can be inferred as the degree

348   to which an individual reduces the availability of a resource to other individuals.

349   Interaction coefficients measured through the assessment of physiological

350   tolerances thus are closely related to the "effect traits" of Lavorel & Garnier (2002).

351   One can simultaneously estimate physiological tolerances and assess how

352   interaction coefficients vary over environmental gradients by exposing individuals of

353   a focal species to a range of resource availabilities, while simultaneously varying the

354   density of the aggregate community around each focal individual and monitoring the

355   availability of the relevant resource. No such study has been performed, to the best

356   of our knowledge, as the logistical challenges involved in doing so would be

357   substantial. Note that tolerances of abiotic conditions, such as temperature, would be

358   less uninformative in this regard, as they are rarely affected by the presence of

359   competitors. Exceptions could include cases in which competitors limit the access of

360   organisms to refuges or microclimates, for example, safe shelters from elevated

361   temperatures. Physiological tolerances of low resource availability therefore

362   complement the use of multiple functional traits by linking performance of whole

363   organisms to population growth rates and interaction coefficients over environmental

364   gradients.

365   Physiological tolerances can be assessed observationally or in field-based

366   experiments, for example using common gardens or reciprocal transplantations

367   (Craine et al., 2012). Purely observational studies can be stymied by atypical climatic

368   conditions, however. For example, flood tolerance may be assessed by transplanting

369   tree seedlings into a floodplain, but floods vary in size and duration, potentially

370   clouding the relationship between vital rates and particular environmental conditions

371   (Fortunel, Paine, et al., 2016). Thus, physiological tolerances are more informatively

372   assessed in experimental settings such as laboratories, controlled environment

373   facilities, or glasshouses, depending on the target organisms. Regardless of the

374   setting, the conditions and resources evaluated must be relevant to field conditions,

375   ideally spanning the entire natural range. The assessment of physiological

376   tolerances is hampered by a lack of standard protocols, which has led to much

377   debate about measurement techniques (for shade tolerance, see Valladares &

378   Niinemets, 2008). Establishing a consensus around experimental protocols for

379   estimating physiological tolerances should be a top priority.

380   A final challenge for the use of both physiological tolerances and hard

381   functional traits is that their measurement is typically labour-intensive, limiting the

382   number of species that can be feasibly studied. This issue can be addressed in three

383   ways. First, the careful selection of study species can yield community-level insight.

384   In species-rich communities, it is advisable to study relatively common species, as

385   they represent the majority of the individuals present and are the species most likely

386   to interact. Interactions among rare species are by definition rare, outside of

387   specialised host-parasite or mutualistic relationships. It is also advisable to select

388   species with typical functional traits, as these are most representative of the

389   community as a whole. A second way to address this issue is to assess soft

390   functional traits together with hard traits or physiological tolerances. This requires

391   little additional effort and allows the relationships among traits, and between traits

392   and tolerances, to be assessed. Thereby, the enormous amount of soft trait data

393   already available can be leveraged to yield further insight into community dynamics

394   (Kattge et al., 2011). Third, the use of standard measurement protocols would

395   facilitate sharing data among studies (Craine et al., 2012). Additionally, depending

396   upon study design, certain species, for example invasive or endangered ones, may

397   need to be included. Regardless, logistical constraints will rarely permit all co-

398   occurring species to be investigated, imposing an inevitable loss of precision in

399   predictions of community dynamics.

400   The beginning of the physiological tolerance approach is illustrated by

401   Maynard et al. (2015), who correlated the distributions of three termite species with

402   climatic variables across the eastern United States. They demonstrated dramatic

403   interspecific variation in thermal tolerances, then mined the ecological literature to

404   determine the abiotic and biotic predictors of each species' distribution. Maynard et

405   al. (2015) identified the primary correlates of termite distribution and abundance,

406   illuminating the gaps in knowledge and setting the stage for experimental studies to

407   predict the dynamics of temperate termite communities. Engelbrecht and colleagues,

408   on the other hand, illustrate an end of the process, by predicting tropical forest

409   community composition on the basis of drought tolerance. As forests on the Isthmus

410   of Panama span a strong rainfall gradient, Engelbrecht et al. (2007) assessed the

411   drought sensitivity of tree seedlings in dry and irrigated plots in a common garden.

412   They coupled these observations with data on species distributions and soil moisture

413   availability. Drought sensitivity predicted species distributions at regional

414   (Engelbrecht et al., 2007) and local scales (Comita & Engelbrecht, 2009), owing to

415   interspecific variation in mortality rates during droughts (Kursar et al., 2009). Thus,

416   changes in soil moisture induced by global climate change are likely to alter tree

417   distributions and community dynamics.

418

419   **Case studies**

420   *Community dynamics on ephemeral patches: a case study of Sepsidae (dung flies)*

421   Although most recent empirical work on community dynamics has focused on plants,

422   there is considerable scope for extending the demographic framework to predict the

423   dynamics of animal communities. Among the most tractable of animal communities

424   are those comprised of short-lived species that complete their life cycles on discrete

425   ephemeral patches of organic matter (Horn & MacArthur, 1972). Ephemeral patch

426   communities encompass a high proportion of global biodiversity and include species

427   that rely on carrion, dung, deadwood, plant tissue, fungi, fruit, flowers, short-lived

428   water bodies, or host organisms to complete their development. Such communities

429   are often highly species-rich despite strong competition and a lack of obvious niche

430   partitioning within patches, making species coexistence especially intriguing (Finn,

431   2001). They are often highly amenable to experimentation, as the rapid turnover of

432   patch resources facilitates community manipulation, sampling, and replication, and

433   the patch environment itself can typically be controlled and measured during

434   observation. Obtaining population size estimates for ephemeral patch competitors in

435   the field, on the other hand, is often prohibitively difficult.

436   The coexistence of competitors in ephemeral patch communities is widely

437   assumed to be dominated by the stabilising mechanism of intraspecific versus

438   interspecific aggregation (Chesson, 2000a; Duthie, Abbott, & Nason, 2014, 2015). In

439   general, when conspecifics aggregate within or among patches, intraspecific

440   competition increases relative to interspecific competition, facilitating coexistence.

441   Mechanisms causing conspecific aggregation include the behaviour of females

442   ovipositing onto patches in clutches (Takahashi, 2007), and variation among species

443   in patch attractiveness or accessibility, which generate spatial and temporal

444   heterogeneity in species distributions (Chesson, 2000a; Duthie, Abbott, & Nason,

445   2014; Heard, 1998). The mechanisms modulating aggregation may be directly linked

446   to hard functional traits, such as individual longevity, wing loading, egg load and

447   larval feeding rate, enabling the prediction of community dynamics (e.g., Duthie,

448   Abbott, & Nason, 2015).

449   Black scavenger flies are a family of flies (Sepsidae, Diptera) especially

450   amenable to a trait-based approach to predict community dynamics. Sepsids occur

451   worldwide, and 10 species that occur in Scotland form the basis of this case study.

452   Flies are easily located and collected while mating on dung in the field and can be

453   maintained in large numbers under laboratory conditions. We measure traits

454   hypothesised to affect aggregation, and therefore competition, under controlled

455   conditions. The malleability of dung pats and short generation time of flies facilitate

456   the estimation of population growth rates and interaction coefficients through

457   pairwise invasion experiments across a density gradient of resident species (Fig. 2).

458   Unhatched eggs and larvae are collected from dung to measure the sensitivity of

459   each developmental stage to competition (Blanckenhorn et al., 2013). Moreover, we

460   measure dung mass before and after the invasion experiments to estimate

461   decomposition rates, thereby linking species composition and functional traits to a

462   key ecosystem function. Consequently, Sepsids are a promising model system to

463   address fundamental questions in community dynamics and ecosystem functioning.

464   We use Sepsidae to extend the demographic framework as well. Following

465   the approach of Kraft et al. (2015), the set of functional traits measured on each

466   species is conceptualised as points in multidimensional trait space. Then,

467   competition coefficients are correlated in multidimensional trait space with niche

468   differences and fitness differences between species pairs. This approach can identify

469   the functional traits that are most relevant to coexistence (Table 1), and provides a

470   whole-organism perspective that is critical to consider, because it cannot be

471   assumed that species are simply the sum of univariate traits (Kraft, Godoy, & Levine,

472   2015). Rather, combined effects of traits might be critical for predicting both niche

473   differences and fitness differences between species. By adopting this whole-

474   organism perspective, it should be possible to predict the recruitment of Sepsidae

475   species from field populations of ephemeral patch competitors.

476   The manipulability of this system also offers a promising way forward to

477   predict community dynamics under changing environmental conditions using the

478   demographic framework, and for linking demography to functional traits. The short

479   generation time of Sepsids enables multiple invasion experiments to be performed

480   simultaneously under controlled environmental conditions (Fig. 2). Though time-

481   consuming, invasion experiments to estimate all intrinsic population growth rates and

482   interaction coefficients can tractably be replicated across an environmental gradient.

483   For example, temperature strongly affects the functional traits of Sepsids, including

484   body size and development time (Blanckenhorn et al., 2013), and could therefore

485   modulate their population growth rates and interaction coefficients. Measuring these

486   traits and parameters across a range of temperature permits us to estimate the

487   sensitivity of community dynamics to environmental change. Such knowledge would

488   be valuable for better understanding and predicting the resilience of communities to

489   environmental change.

490

491   *Controls on distribution: a case study of tropical trees*

492   In tropical forests, water and light are two of the most important resources

493   shaping the vital rates of individual trees, and thus their distributions along

494   environmental gradients and community dynamics (Baltzer et al., 2008; Engelbrecht

495   et al., 2007; Valladares & Niinemets, 2008; Wright et al., 2010). As habitat

496   fragmentation, drought frequency and intense rainfall are set to increase in tropical

497   regions, a mechanistic understanding of the degree to which water and light

498   availability interact to control community dynamics will be essential for forest

499   managers to mitigate potential biodiversity loss.

500   Seeking strong predictors of vital rates and species distributions, we focus on

501   whole-plant tolerances to low resource availability and extreme environmental

502   conditions (Craine et al., 2012). We aim to predict vital rates, and thus community

503   dynamics, in areas for which demographic data is unavailable. More specifically, the

504   aim of this case study is to assess the degree to which physiological tolerances

505   predict observed spatial patterns of vital rates and community compositional

506   turnover. We hypothesise that integrating physiological tolerances with

507   environmental data will explain variation in species distributions at the landscape

508   level, as well as predict changes in species distributions under different climate

509   scenarios.

510   The rain forests of the Paracou Research Station, French Guiana, provide an

511   ideal situation to assess the influences of light and water availability on the

512   community dynamics of tropical trees. Permanent plots have been established in

513   which all trees > 10 cm diameter at breast height have been censused every 1-2

514   years since 1984. Hydrology & light availability also have been characterised in

515   these plots (Wagner et al., 2012). The survival and growth of saplings of 25 common

516   tree species have been monitored since 1992 in subplots nested within the tree plots

517   (Fig. 3a, b). This abundance of data allows us to characterise resource availability,

518   species distributions, and the vital rates of individual trees across the landscape.

519   From observation alone, however, the relative importance of these factors in

520   determining the distribution and relative abundance of each species is not evident

521   (Fig. 3b). Stated more precisely, the observed turnover in species composition

522   between floodplain and plateau forests could occur because floodplain-associated

523   species cannot tolerate the intensity of seasonal drought on the plateaux, or plateau-

524   associated species may be intolerant of the flooding regime in the floodplain

525   (Fortunel, Paine, et al., 2016).

526   We established a shadehouse experiment to assess the physiological

527   tolerances of tree seedlings to drought, flooding and shading (Fig. 3c). We work on

528   seedlings because of their experimental tractability, and also because seedlings are

529   expected to be more sensitive to fluctuations in soil water availability than adult

530   trees. We use shade-cloth to vary light availability over the range found in the forests

531   and impose three levels of water availability: drought (no watering since the

532   commencement of the study), flooding (water maintained above the soil surface) and

533   watering to field capacity, in a factorial split-plot design. For each of 11 species,

534   growth and survival are monitored at least weekly. We generate indices of tolerance

535   to flooding, drought and shading based on the differential survival and growth of

536   individuals in the various experimental treatments (Engelbrecht et al., 2007; Kursar

537   et al., 2009). We also measure a set of functional traits associated with the tolerance

538   of drought, flooding and shade, to assess their associations with the relevant

539   physiological tolerances (Table 1). The location of each individual in the shade

540   houses is mapped, allowing us to assess the effects of neighbourhood composition

541   on individual performance. Even so, our estimates of interaction coefficients between

542   species are weak, because the study does not include variation in neighbourhood

543   density. Including systematic variation in neighbourhood composition and density in

544   the experimental design would be more logistically challenging but would provide

545   stronger estimates of interaction coefficients.

546   We will predict the vital rates of growth and survival observed in the field as a

547   function of topographic position and physiological tolerance indices. We expect

548   statistical interactions between topographic position and physiological tolerances.

549   For example, if drought is the primary mechanism generating species turnover, then

550   we would expect elevated mortality risk for drought-intolerant species, but only on

551   the plateaux, which are relatively dry (Fig 4d). Once such relationships are

552   characterised for flooding, shading and drought, we will build individual-based and

553   integral projection models to predict the dynamics of our focal species under

554   scenarios of changing precipitation (Adler, Ellner, & Levine, 2010).

555

556 **Conclusions**

557 Our motivation is to enhance the generality and tractability of predicting community

558 dynamics, especially for species-rich communities, on the basis of the Chesson-

559 Adler demographic framework. Although powerful, this framework is difficult to

560 operationalise in its raw form, and has thus primarily been applied to low-diversity

561 annual plant communities (but see Adler, Ellner, & Levine, 2010). Phylogenetic data

562 and soft functional traits have been useful for the analysis of community structure but

563 are less informative for the prediction of community dynamics. Instead, we advocate

564 the use of hard functional traits and physiological tolerances, as they provide

565 opportunities to predict community dynamics without a complete reliance on

566 demographic data. Moreover, they provide a mechanistic way to incorporate the

567 variation imparted to ecological communities by environmental gradients, over which

568 population growth rates and interaction coefficients vary. Incorporating

569 environmental variation is essential for making predictions in the face of

570 anthropogenic effects, especially over large spatial or temporal scales. Given the

571 urgent need for ecological forecasting (Clark et al., 2001), we hope that ecologists

572 will adopt these approaches, extending the range of ecosystems for which accurate

573 predictions of community dynamics are possible.

574

575 **Author contributions**

576 CETP conceived the ideas for this review and lead the writing of the manuscript. AD

577 and ABD contributed the case studies. All authors contributed critically to the drafts

578 and gave final approval for publication.

579

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584

Data Accessibility

586 This paper does not include any data

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827   **Table**

828   **Table 1. Hard versus soft traits.** Examples of 'hard' and 'soft' functional traits

829   associated with key vital rates for the animals and plants used in the case studies. In

830   general, it is easier to measure hard functional traits and vital rates on animals than

831   on plants. For example, fecundity estimates are relatively easy to measure for many

832   insects (as egg load), but obtaining the equivalent data for long-lived trees may

833   require decades of field observations of seed production and complicated modelling

834   (Clark et al., 2010; Purves et al., 2008).

	Dung flies		Tropical rain forest trees	
Vital Rate	**Hard trait**	**Soft trait**	**Hard trait**	**Soft trait**
Survival	Life span	Ovigeny index	Life span	Wood density
Growth	Ingestion rate	Body size	Photosynthetic rate	Foliar chlorophyll concentration Wood density Maximal stature
Fecundity	Egg load	Abdominal mass	Seed production	Above-ground biomass

835

836   **Figures**

837   **Figure 1. Milestones in the prediction of community dynamics.** Each milestone

838   is indicated by a key reference in the development of that concept or technique,

839   rather than its first mention in the literature. See also Figure 3.6 in Vellend (2016).

840

841

842

843   **Figure 2. Overview of the dung fly case study.** We study 10 species of Sepsidae

844   co-occurring in Scotland to link species functional traits to biodiversity and the

845   ecosystem function of decomposition. Key functional traits are measured for A) fly

846   eggs, B) larvae and C) adults. D) We perform invasion experiments in which a mated

847   female of species *i* (black) oviposits on dung patches that vary in the density of

848   ovipositing females of species *j* (red). We repeat this experiment for all combinations

849   of species *i* and *j* (including *i* = *j*) over a temperature gradient. Intrinsic growth rates

850   (λ_i) can be calculated from the number of offspring that eclose from empty patches,

851   and competition coefficients can be calculated by estimating how the eclosion rate is

852   reduced by increasing conspecific (α_{ii}) or heterospecific (α_{ij}) density. Values of λ_i, α_{ii},

853   and α_{ij} can then be used to calculate niche differences and fitness differences. Dung

854   decomposition can be estimated from the difference in dung mass from oviposition to

855   eclosion. Differences in trait values between all pairwise combinations of species *i*

856   and *j* will be calculated. Univariate correlations between each of these trait value

857   differences and stabilising niche and average fitness differences can be estimated,

858   and model selection can be used to identify combinations of traits that best describe

859   niche and fitness differences (Kraft *et al*. 2015). Similarly, trait values and differences

860   can be associated with decomposition rates. Artwork by A. C. Duthie.

861

862   **Figure 3. Overview of the tropical trees case study.** A) The abundance of

863   saplings of 25 common canopy trees has been monitored eight times since 1992 in

864   960 permanent plots at Paracou Research Station, French Guiana. The sapling plots

865   are distributed in an 8x8 grid in each of 12 6.25 ha permanent tree plots, in which

866   light availability, soil moisture and flooding frequency have also been assessed.

867   Point types and colours indicate the topographic position of each plot. B) The

868   abundance of one species (*Virola michelii*, Myristicaceae), is proportional to the size

869   of the black circles. C) Methods for physiological tolerance testing, in which 11 target

870   species (indicated by varying point types) are factorially exposed to varying water

871   and light availabilities. D) Prediction of field mortality risk from estimated species

872   physiological tolerances. The hypothetical result shown in panel D would indicate

873   that interspecific variation in drought tolerance contributes far more to spatial

874   variation in species composition than does variation in the tolerance of flooding or

875   shading, as drought intolerant species suffer elevated mortality rates, but only on the

876   relatively dry plateaux.