Priority effects – Notes

**Tucker and Fukami 2014**

**Variation in order of species arrival among sites drive local communities to divergent succestional trajectories – affects coexistence = priority effects**

1. Sutherland JP. 1974 Multiple stable points in natural communities. Am. Nat. 136, 859 – 873.

2. Sutherland JP. 1990 Perturbations, resistance, and alternative views of the existence of multiple stable points in nature. Am. Nat. 136, 270– 275. (doi:10. 1086/285097)

3. Drake JA. 1991 Community-assembly mechanics and the structure of an experimental species ensemble. Am. Nat. 137, 1– 26. (doi:10.1086/285143)

4. Chase JM. 2003 Community assembly: when should history matter? Oecologia 136, 489– 498. (doi:10.1007/s00442-003-1311-7)

5. Mergeay J, De Meester L, Eggermont H, Verschuren D. 2011 Priority effects and species sorting in a long paleoecological record of repeated community assembly through time. Ecology 92, 2267 – 2275. (doi:10.1890/10-1645.1)

6. Kennedy PG, Peay KG, Bruns TD. 2009 Root-tip competition among ectomycorrhizal fungi: are priority effects the rule or the exception. Ecology 90, 2098– 2107. (doi:10.1890/08-1291.1)

**Citation #4 – variable results of priority effects importance – but causes of variation – still much unknown**

**4, 7-9 – potential causes of variation**

7. Knowlton N. 2004 Multiple ‘stable’ states and the conservation of marine ecosystems. Progr. Oceanogr. 60, 387– 396. (doi:10.1016/j.pocean.2004.02.011)

8. Jiang L, Patel SN. 2008 Community assembly in the presence of disturbance: a microcosm experiment. Ecology 89, 1931 – 1940. (doi:10.1890/07-1263.1)

9. Fukami T, Dickie IA, Wilkie JP, Paulus BC, Park D, Roberts A, Buchanan PK, Allen RB. 2010 Assembly history dictates ecosystem functioning: evidence from wood decomposer communities. Ecol. Lett. 13, 675– 684. (doi:10.1111/j.1461-0248.2010.01465.x)

**Environmental variability affect priority effects through changes in species growth rates**

16. Loeuille N, Leibold MA. 2008 Evolution in metacommunities: on the relative importance of species sorting and monopolization in structuring communities. Am. Nat. 171, 788– 799. (doi:10. 1086/587745)

**High growth species = greater priority effecst – pre-empt resources and modify habitats to hinder or facilitate establishment of late arriving species**

17. deFreitas MJ, Frederickson AG. 1978 Inhibition as a factor in the maintenance of the diversity of microbial ecosystems. J. Gen. Microbiol. 106, 307 – 320. (doi:10.1099/00221287-106-2-307)

18. Tilman D. 1980 Resources: a graphical-mechanistic approach to competition and predation. Am. Nat. 116, 362 – 393. (doi:10.1086/283633)

19. Facelli J, Facelli E. 1993 Interactions after death: plant litter controls priority effects in a successional plant community. Oecologia 95, 277 – 282. (doi:10. 1007/BF00323500)

**Predictions are not necessarily straightforward, however, because whether priority effects are weakened or strengthened may depend on the relative nonlinear response of different species to environmental conditions. For example, imagine a situation where priority effects are weak in a constant environment, with one species (species A) always outcompeting another (species B) regardless of arrival order. If species B is less sensitive to environmental variability (e.g. because of a storage effect [20]), showing a lesser decline in growth rate than species A, the two species may become competitively similar in a variable environment, making the outcome of competition dependent on arrival order. Thus, priority effects would, in this case, be strengthened by environmental variability**

20. Chesson P. 2000 Mechanisms of maintenance of species diversity. Annu. Rev. Ecol. Syst. 31, 343 – 366. (doi:10.1146/annurev.ecolsys.31.1.343)

**Evidence indicates the presence of inhibitive priority effects among some of these nectar-inhabiting species [30]**

**It has also been suggested that microbial species affect one another via pre-emption of resources (amino acids and sugars) in nectar [30],**

30. Peay KG, Belisle M, Fukami T. 2012 Phylogenetic relatedness predicts priority effects in nectar yeast communities. Proc. R. Soc. B 279, 749 – 758. (doi:10.1098/rspb.2011.1230)

**This is a consumer–resource model that considers two competing species’ interactions as a result of the consumption of limiting resources**

* **Limiting resources a key point here**

**Taken together, our results suggest that temperature variability can promote the coexistence of nectar-inhabiting microbial species by counteracting priority effects in a metacommunity in which new flowers repeatedly emerge as local habitats for species colonization.**

**Peay, Belisle and Fukami 2012**

**late-arriving species experiencing strong negative effects from early-arriving species**

**priority effects stronger among more closely related species**

* Hypothesise that priority effects in floral visitation sequences may be stronger at intraspecific level than interspecific interactions

**In general, early arriving species experienced little negative effects from later arriving species, whereas late-arriving species attained final densities far below their monoculture growth potential**

**While both species did increase in abundance, it is possible that Mimulus nectar is not their primary habitat—S. bombicola, for example, was originally isolated from honey [43]. This type of habitat filtering has previously been shown to result in phylogenetic clustering of yeasts in nectar [44].**

-Important as blueberry and raspberry perhaps not primary resource of either species however both are highly generalist species

43. Rosa, C. A. & Lachance, M. A. 1998 The yeast genus Starmerella gen. nov. and Starmerella bombicola sp. nov., the teleomorph of Candida bombicola (Spencer, Gorin & Tullock) Meyer & Yarrow. Int. J. Syst. Bacteriol. 48, 1413 –1417. (doi:10.1099/00207713-48- 4-1413)

44. Herrera, C. M., Canto, A., Pozo, M. I. & Bazaga, P. 2009 Inhospitable sweetness: nectar filtering of pollinatorborne inocula leads to impoverished, phylogenetically clustered yeast communities. Proc. R. Soc. B 277, 747 –754. (doi:10.1098/rspb.2009.1485)

**The presence of amino acids in floral nectar and their role in pollinator visitation have been known for some time [48]. The differences between yeast species in amino acid consumption may thus have important consequences for plant pollinator visitation rates and determining the balance between mutualism and parasitism in the yeast-floral nectar symbiosis.**

48. Baker, H. G. & Baker, I. 1986 The occurrence and significance of amino-acids in floral nectar. Plant Syst. Evol. 151, 175 –186. (doi:10.1007/BF02430273)

**Toju, H Vannette, RL Gauthier, MPL et al. 2018**

**The order of species arrival during community assembly can promote or limit species coexistence (Palmgren 1926, Sutherland 1974, Drake 1991). These effects, termed priority effects, have been reported in a range of organisms, including plants (Grman and Suding 2010), animals (Alford and Wilbur 1985), fungi (Kennedy and Bruns 2005), protists (Louette and De Meester 2007) and bacteria (Devevey et al. 2015). These studies have shown that species that arrive early influence community development by competitively suppressing later colonizers or by modifying habitat conditions to some species’ favor and not others’ (Fukami 2015).**

**Nevertheless, our results are consistent with the hypothesis that priority effects, along with other factors influencing pollinator behavior and plant physiological status, structure nectar microbial communities within and across floral generations.**

**Regardless, persistent priority effects could in turn influence pollination and plant fitness, as we found previously that Neokomagataea (= Gluconobacter), but not Metschnikowia reukaufii, could negatively affect pollinator foraging and seed set (Vannette et al. 2013, Good et al. 2014).**

**Moreover, we used only one strain per species for the experimental inoculation, but strains can be phenotypically variable (Herrera 2014) and may therefore show different priority effects, which remains to be tested.**

* Phenotypic variation in floral visitation behaviour may be important

**Young et al. 2015**

**Such priority effects were the centerpiece of initial definitions of assembly theory, and are currently being explored as potential management techniques in ecological restoration, in particular to assist the establishment of less-competitive species in communities (Hobbs and Suding 2008; Porensky et al. 2012).**

**competitive suppression of native grass species by exotics**

**In particular, Vannette and Fukami (2014) they suggested that priority effects would be greater under higher resource availability (see also Kardol et al. 2013).**

**Vannette and Fukami 2014**

Niche components and priority effects A species’ niche can be viewed as consisting of three components, including niche overlap, impact niche and requirement niche (Fig. 1). Derived from Gause’s (1932) competitive exclusion principle and MacArthur & Levins’s (1967) limiting similarity concept, niche overlap refers to resource use similarity among co-occurring species, independent of their rate of resource consumption (Pianka 1973; Petraitis 1989). Based on Elton’s (1927) niche concept as a species’ role in the environment and Tilman’s (1982) theory of resource competition, the impact niche is defined as a species’ per capita influence on the environment through resource consumption and other modes of environmental modification (Leibold 1995; Chase & Leibold 2003). Finally, originating from Grinnell’s (1917) limiting factors and Hutchinson’s (1957) fundamental niche, the requirement niche describes the environmental conditions that affect a species’ survival, growth and reproduction (Leibold 1995; Chase & Leibold 2003). The contrast between the impact niche and the requirement niche is similar to that of ‘effects traits’ and ‘response traits’ (sensu Lavorel & Garnier 2002; Suding et al. 2008), where species with high impact and those with low requirement may be strong ‘effect competitors’ and ‘response competitors’, respectively (sensu Goldberg & Landa 1991). Recognising that these related, but distinct niche components may differentially determine how species interact, and assuming that interactions among species are generally weaker than interactions within species, one can propose the following hypotheses (Fig. 1): priority effects should be strong when (1) species display a high degree of similarity in resource use (high overlap), (2) early-arriving species strongly affect the environment (high impact) and (3) the growth rate of late-arriving species is highly dependent on the environment (high requirement). Emphasising multiple niche components, these hypotheses are firmly founded on classic niche-based theories of community assembly (Grinnell 1917; Elton 1927; Gause 1932; Hutchinson 1957; MacArthur & Levins 1967; Pianka 1973; Tilman 1982; Leibold 1995; Chase & Leibold 2003). Yet, to our knowledge, niche components have never been distinguished in empirical studies of priority effects.

The term priority effect is sometimes used to refer to cases where early-arriving species completely exclude late-arriving species. Here, because we are interested in quantitative predictions of the strength of the effects of species arrival order, we take a broader view and regard any significant effect of arrival order on the abundance, not just the presence or absence, of species as a priority effect.

By decomposing niche components, it was possible to predict nearly twice as much variation as explained by phylogenetic relatedness or overall ecological similarity (cf. Peay et al. 2012).

The potential scope of the niche-component hypotheses is broader than can be captured by the specific data from our experiment. For example, priority effects were mostly inhibitory in our experiment, but facilitative priority effects, where early-arriving species promote the growth of late colonisers, may also be common in natural communities (Callaway & Walker 1997; Bruno et al. 2003).

We suggest that both facilitative and inhibitory priority effects can be considered within the same niche-component framework.

We assumed in this study that intraspecific competition was generally stronger than interspecific competition, or that each species had a greater impact on the resources that were more limiting to themselves than to other species (Tilman 1982).