Priority effects- paper notes

Urban and Meester (2009)- Developed a model for two-species, three-patch evolving metacommunity with stochastic dispersal and mutation. Colonisation times manipulated with constant dispersal rates- how does early colonisation influence later competitive interactions? Model results- in the absence of evolution, first colonisers weakly dominate later colonisers due to neutral ecological drifts influencing first coloniser growth/extinction. In presence of evolution, the evolving species dominates non-evolving species. Therefore, localised evolution can increase priority effects.

Vanoverbeke et al. (2015)- Priority effects and evolution on community assembly- relative importance of ecology and evolution on community assembly- model. Community monopolisation effect- eco-evolutionary dynamic in which an early arriving community evolves to monopolise resources in a way which inhibits future colonisations. Time to locally adapt (and adaptively radiate) and dispersal times for future colonists can determine strength of priority effects. Simulation results- evolution interacts with ecology to determine community assembly. Support for early community monopolisation, even when 1-10 migrants move patches in each generation. Immigrant arrival success is determined by carrying capacity (spatial) of local community- if community is locally adapted, it is more likely to be at high densities and exclude immigrants. Gillespie (2004)- communities of Hawaiian island spiders originate from adaptive radiation of common ancestor and colonisation of pre-adapted species- interaction between evolution and species sorting (ecology) on community assembly. Anolis lizards- mostly adaptive radiation of ecomorphs. Birds- mostly species sorting.

Mihaljevic (2012)- Communities vary in complexity from simple competing guilds of species to complex trophic webs. Dispersal of species among localities (metacommunity) changes local community dynamics, leading to community structures that deviate from expected closed communities. In symbiont metacommunities, a host becomes a defined habitat from which species can disperse among communities. The how timing and dispersal structures a metacommunity depends on theoretical paradigms, environment heterogeneity and connectedness of host patches. Broad conceptual framework for the importance of evolutionary (LA) and community ecology on host-symbiont metacommunities.

Wittmann and Fukami (2017)- two species metacommunity model for species coexistence, engaging in local inhibitory priority effects. Mechanism- eco-evolutionary buffering- rapid evolution of traits determining species interactions. Inhibitory mechanism- production of toxins which are harmful to competitors but not conspecifics. Two genotypes of each species- one sensitive, the other resistant (at a cost). As a susceptible species becomes rarer, it becomes less beneficial to be resistant, so resistance is lost, allowing susceptible populations to recover. Therefore, under this scenario, species diversity and genetic variation is maintained via trade-offs even under PE.

Vass and Langenheder (2017)- PE review- includes stats and methods for testing and measuring PE

Gomez et al. (2016)- P. fluorescens local adaptation to the abiotic background (soil microcosm) affects the density of natural soil microcosm, whilst coevolving with phage.

Knope et al. (2012)- Diversity increases within communities by immigration (ecology) and diversification (evolution). This generates eco-evolutionary dynamics in which immigrants can pre-empt available niches, suppressing diversification- priority effects. This paper considers local adaptation, coevolution with phage and immigration history on Pseudomonas fluorescens diversity. Diversification was greater when genotypes were introduced before its competitor. Immigration did not influence focal genotype diversity when locally adapted in the absence of phage. When introduced first, focal genotypes dominate competitors in diversity and abundance , irrespective of evolution. The effect of evolution decreases over time, as focal species can pre-empt niches compared to their competitors. Previous evolution with phage prompted diversification- Possible mechanisms: Evolving with phage reduces resource competition, thus reducing selection for competitive ability; Genotypes previously evolved with phage diversified more quickly, increasing competition and more extensive diversification; Trade-offs between phage resistance and competitive ability, results in weak suppression of descendent mutants, allowing adaptive radiation.

Frossard et al. (2012)- Tenet in microbial and general ecology- structure determines function with respect to composition and diversity of biological communities, and the functions the communities drive. Support from direct community manipulations in which diversity is controlled. Indirect community manipulations, e.g. dilution series or fumigation, have yielded less support. Dilution/fumigation produce communities which are subsets of the original whereas assembled communities vary diversity and taxa composition. Third approach- analyse relationships between community structure and ecosystem function across spatial and/or temporal environmental change.

This study- determine links between bacterial community structure and microbial metabolic activities (enzyme activity) in soil and sediment.

Neither water availability nor direction of water exchange influenced enzyme activity. Temperature fluctuations over time accounted for a small amount of variation in metabolism. Dissolved organic carbon hypothesised to account for more diversity. Activities of carbon-, nitrogen- and phosphorus enzymes were unrelated to community structure (Structure was unrelated to function). This was likely due to the absence of clear spatial and temporal patterns in communities whereas enzyme activity all varied temporally.

Suggests community structure is determined by population growths/declines and random immigration- as such, leading to structures non-determinant of their background ecology.

Jones et al. (2017)- Propagule pressure- magnitude and pattern of arrival of invasive individuals. This can be independent of specific invasive traits. Communities and species are from water-filled beech tree holes- naturally coexisting. Communities constructed from three species combinations from 10 isolates- *Bacillus, Epilithonimonas, Flavobacterium, Pseudomonas* and *Staphylococcus*. Invaded by *P. putida*. Resident Pseudomonas had a significant effect on invasion success of P. putida, exemplifying community invasion resistance. Presence of other species non-significant. Earlier time of introduction- increased invasion success. Diversity had no effect on invasion success- primarily depended on species composition. Invasion success of P. putida against resident Pseudomonas further depended on propagule pressure in order to become established- as further highlighted by priority effects.

Pantel et al. (2015)- Presence of adapted Daphnia magna significantly influenced zooplankton community composition, leading to community that were more similar to one another than when with non-adapted D. magna. Effect of D. magna local adaptation varied among zooplankton taxa- some suppressed, some facilitated.

Louette & De Meester (2007)- Good refs for examples of PE in range of taxa. Introduced predators (midge larvae) into a Daphnia community to examine effect on strength of species sorting and PE. Priority effects of Daphnia species- first species becomes dominant. D. obtusa only dominant when first, S. vetulus third and no predation. Early resource monopolisation excludes superior competitor D. magna (D. obtusa extinct when second). Predation increased S. vetulus biomass by preferentially predating on Daphnia. Predation alters competitive interactions, thus affecting PE and community structure.

Rummens et al. (2018)- Bacterioplankton communities- whole-community priority of first pioneering community over another. First community not adapted to media, second community is- ensures priority effect is due to ordering and not adaptation. Variation in inoculation time lag (four treatments). Principal component analyses compare variation in community composition between treatments and inocula. Species sorting influenced. Euclidean distances compare effects of time lag to treatment in which communities are inoculated simultaneously. Increasing time lag- increasing resemblance of communities to the pioneer community. Three dominant OTUs in the pioneer community increased in relative abundance with increasing time lag. Dominant OTUs in the native community decreased with increasing time lag.

Tucker and Fukami (2014)- Environmental variability influences priority effects by changing species growth rates- if interaction is inhibitory, perturbations will slow growth of A species, allowing B species to grow. Reduced species growth- reduced priority effects. Species will vary in environmental sensitivity. Model community- nectar microbes- affect one another by competing for nectar resources (sugars, amino acids) and differentially influence nectar pH. Two yeast and two bacterial species.

Treatments- (i) simultaneous introduction of both yeast onto both bacteria, (ii) yeast first, 48hr, then bacteria, (iii) bacteria first, 48hr, then yeast.

Temp treatments- (i) constant 15C, (ii) spatial variability, 10C and 20C, (iii) temporal variability, 5- 25C daily, (iii) spatial and temporal variability.

Four metacommunity replicates- 4 x each treatment combo w/ temp

Results- strong priority effects- abundance strongly dependent on order and temperature. Constant temp, yeast first- yeast 1 only persisted. Temp variable- yeast 1 and bacteria 1 coexisted.

Bacteria first, constant temp- bacteria 1 only persisted. Temp variable- bacteria 1 and 2 coexisted.

Simultaneous introduction- yeast and bacteria 1 persisted, yeast and bacteria 2 went extinct. Persistence not influenced by temperature but abundance was.

Conclusion- environmental variation inhibits priority effects.

Quantifying priority effects- Pij = ln (D(i)ji / D(i)ij)

Pij as the log of the ratio between the abundance of strain i, time-averaged over days 4 through 10, when introduced after strain j, D(i)ji, and the abundance of strain i, also time-averaged over days 4 through 10, when it was introduced before j, D(i).

Zero- no priority effect; Positive- facultative priority effect; Negative- inhibitory priority effect.

Zee and Fukami (2018)- Effect of sympatric and allopatric evolution on PE. Sympatric evolution could weaken PE through character displacement or strengthen it due to similar competitive abilities between sympatric organisms. Study system- Pseudomonas fluorescens WS morphotypes. Calculated PE using Fukami (2014) equation. GLMM- effect of evolutionary history (sympatric/ allopatric), duration of evolution (1, 2, 7 weeks), observation timing (4-10 of community assembly) on difference in abundance of first and second species. Another GLMM- evolution history, evolution duration and phenotypic distance on strength and direction of PE.

T-tests- differences in species abundances of first and second species; strength of priority effects between sympatric and allopatric pairs.

Abundance through time- difference in abundance between first and second strain- metric of establishment success of second strain. High positive- first species dominant, lower/negative- better for second.

Short-term, but not long-term, sympatric evolution weakens PE. Short term- fast niche-partitioning. Long-term- increased competitive similarity among populations.

Peay et al. (2011)- More closely related species are more ecologically similar and so should compete more intensely- Darwin’s naturalisation hypothesis. Tested hypothesis in relation to PE in nectar yeast communities. Six species- total of 30 pairwise combinations. Day 0- first inoculation, Day 2- second inoculation- growth at 25C to day 5. Water treatment- negative control- species growth in absence of competition. 42 treatment combinations (21 two-species combinations x 2 introduction orders (including water treatment)) plus 10 negative water controls. Two way ANOVA- focal species abundance ~ order \* competitor identity. Bonferonni correction for multiple ANOVAs. Priority effects- invasion scores (see paper for equation). Negative growth for focal species upon introduction of a competitor. But negative effects absent when other species was introduced late. Order \* competitor identity interaction- significant for most but not all species interactions- some determined by competitor ID but not order (species effect). Growth inhibition greater for second species. Significant relationship between phylogenetic distance and invasion score. Some variation in PE by pairwise interactions explained by phylogenetic distance and ecological similarity among species. Closely related species- stronger priority effects.

Weslien et al. (2011)- Insects and fungi decay wood through successive stages. 15 year study. Hypothesised inhibitory priority effects for competition and facultative in niche modification. Hylurgops palliatus (bark beetle) facilitated colonisation of *Peltis grossa* (wood living beetle) whereas *Monochamus sutor* (wood-borer beetle) inhibited *P. grossa* colonisation. Abundance of *H. palliatus* was positively associated with *Fomitopsis pinicola* (wood decaying fungus) which is likely to explain the positive association between *F. pinicola* and *P. grossa*.

Flory & Bauer (2014)- Experimentally tested strength of indirect facilitation by invasive plants- *Microstegium vimineum* (stiltgrass) on *Alliaria petiolate* (garlic mustard). Also disturbed plots through raking. Number of Alliaria rosettes greater in control plots, however similar numbers in invasion treatment with heavy disturbance. Significant positive effect of Microstegium invasion on Alliaria plant biomass and silique production. Microstegium invasion significantly decreased biomass of native species- suggesting suppression of native plants facilitated Alliaria growth.

Huang et al. (2012)- Studied effect of generalist and specialist herbivory and strong/weak conspecific competition on native and invasive populations of Chinese tallow (*Triadica sebifera).* Herbivory significantly decreased both species biomass and stem height and this effect was greater for specialist than generalist herbivores in high, but not low, competition treatments. Invasive plants grew faster than natives and decreased native biomass. However, in the presence of herbivores, invasive plant growth decreased and tolerance towards herbivores was lower with increasing competition intensity.

Gioria et al. (2011)- Studied primary and secondary invasion of *Fallopia japonica* and *Gunnera tinctorial* (giant rhubarb)- both invasive species to Ireland- and invader effect on soil seed bank (richness, abundance and composition). *F. japonica* invasion decreased species richness and seed abundance greater than invasion of *G. tinctorial*. Couldn’t rule out extrinsic factors. Decline in diversity in *G. tinctorial* plots could have facilitated invasion of superiorly competitive *F. japonica*.

Andersson et al. (2014)- Bacterial communities in rock pools- effect of contemporary and past environmental conditions on composition. Samples taken between 16 rockpools (spatial) and on two day intervals for 9 days (temporal). Bray-Curtis similarities between communities- indicated community changes between days 1 and 9. Environmental conditions (e.g. salinity) explained variation in community composition. Past environmental conditions were a greater determinant on community composition than contemporary. Possible hypotheses- consistent dry and warm weather prior to rainfall could have increased adaptation of bacterial community to stable conditions; time lag of compositional change in response to salinity; priority effects of resistant taxa or early immigrants expand into niche space when conditions change due to rapid adaptation.

Kennedy et al. (2009)- PE in mycorrhizal fungi root colonisation. Four species- pairwise colonisations/invasions. 6 two species combinations, reciprocals= 12 total combinations. Control- no spores added to rule out contamination. Early colonisation inhibited colonisation of second species for three of studied species.

Symons and Arnott (2013)- Fluctuating resource hypothesis- Priority effects, through niche pre-emption/community monopolisation, can interact with the effects of disturbance by altering resource availability. Disturbance has been shown to increase invasability in terrestrial systems, freshwater and marine systems. This study investigated invasability of communities following disturbance over time. Model- zooplankton communities, varying nutrients, salinity and dispersal time. Sampling before invaders, 2 days after addition of zooplankton community and every 9 days for 28 days from experiment start. Two way and three-way ANOVA. Permutation ANOVA- test for diversity invasability and resource invasability relationships; test FRH- whether invasability was related to the abundance of the resident community.

Invasability decreased as time between disturbance and dispersal increased- support for FRH). Demonstrative of priority effects of the resident community.

No relationship between diversity (Shannon-weaver indices and species richness) and invasability. Invasability increased with resource availability- so resource supply, independent of diversity, influence invasability.

Devevey et al. (2015)- Inhibitory priority effects in co-infecting Borrelia strains. Infection of first strain inhibited infection and transmission of second strain. Most likely due to resource exploitation. Three strains, four mice per treatment (9).

Mergeay et al. (2011)- Paleocological study on priority effects in Daphnia communities under repeated variations in natural lake-levels (8 fluctuations over 1800 years). Dormant eggs from at least 100 years. Fossil record for ~1800 years using sediment samples- genetic and morphological ID. 10 Daphnia species total, 6 frequently present. Priority effect strongest during highstands than lowstands- under lake swelling, resident community could expand into new environment and colonise it first, prioritising resources.

Grman and Suding (2010)- Plant communities can establish priority effects through direct competition and soil legacies. Soil legacies is the state of the soil after plants have been removed (e.g. seasonal die-off for annuals), this can be in nutrient levels, soil pathogens and mutualists and allochemicals which can influence colonisers of same or different species. Simultaneous colonisation- exotics outcompeted natives. 5 weeks after first coloniser, second coloniser (native or exotic) growth was inhibited. Exotic prior communities exhibited stronger priority effects via competition. Exotics also altered soil which reduced growth of native colonists. No effect of native legacies on colonisers.

Von Holle et al. (2003)- Plants can inhibit and facilitate succession and growth of other plant species. Allelopathy- inhibitory effect of one plant onto another through the production of chemicals, released into the soil (Rice, 1984)- may result in invasion resistance.

Mallon et al. (2015)- No general theory linking diversity-invasion relationships, more diverse communities generally resist invasion more than less diverse communities. Fluctuating resource hypothesis- resource pulses will decrease competition between residents and invaders. Created 10 communities of 30 species; 12 of 15; 24 of 5 and sterile soil control. E. coli invasion. Nutrient and resource use/niches quantified. Increased levels of species richness reduced niche availability for invaders, causing progressive elimination from communities. The effect linking diversity to invasion was removed using resource pulses, indicating that community niche pre-emption is the mechanism related to community invasion resistance.

Study did not look at specific species- species competitive interactions (see Jones, 2017- specific species/ niche competitors important. Diversity scales with invasion resistance by being more likely to contain these species (ecology) and limiting evolution by niche pre-emption)

Some studies find diversity-invasion relationship in absence of resource use. Other ecological (e.g. phage, protists) and evolution (LA) to consider.

Mächler & Altermatt (2012)- species traits & disturbance on invasion success. Traits usually associated with invasion success include size, trophic level or growth rate. Measured invasion success and community compositional changes of the resident community. Invading species- 8 protist, 1 rotifer- originated from natural ponds. All obligate or facultative bacterovores, some also feeding on smaller protists. Three autotrophs. Resident community- protists, rotifers, microbes from natural pond. Invading species identity significant for success, disturbance alone was not but there was a significant interaction between the two factors- meaning disturbance increased success for some species but decreased success for others. (+) correlation between growth rate and invasion success. Undisturbed communities had a higher microbial density and a tendency for higher diversity- not very strong effects and effect of diversity for invasability. Other traits non-significant. Suggested differential invasion success by species due to differing effects on niche/resource availability.

Yang et al. (2017)- Effect of community diversity (species richness) and composition (species identity effect) on pathogen invasion success on a resource availability gradient. Model- bacterial communities (5 closely related species to invader- 31 communities total), invading plant pathogen bacterium (*Ralstonia solanacearum*). Increasing resident community richness and resource availability had a negative impact on relative invader density. Increasing resources favoured fast-growing species over the invader. Increasing community richness increased likelihood that communities contained species competitive to the invader across a wide resource gradient- species identity effects independent of resource availability. Three species identified to be important for invasion resistance. Species with high catabolic similarity (niche competition), more efficient at controlling invader density at low resource availability- effect vanished at high resource availability. Fast growing species more important at high resource.

Rivett et al. (2016)- Strength of ecological interactions during succession. Predictions- strongest in earlier succession by competitive exclusion; phenotypic changes occur to reduce interaction, increase fitness; labile substrates used early in succession, recalcitrant substrates during later succession. By the third prediction, if important, diversity should only scale with productivity during later succession- effect removed if resources used flexibly by species. Model- water-filled beech hole bacterial communities. Species richness- 1, 2, 4, 8, 16. Consistent with predictions, strength of interspecific interactions decreased over time which coincided with a shift in resource usage over the experiment from labile polysaccharides (hemicellulose) to fibrous cellulose. This shift in resource use is likely due to metabolic plasticity or rapid species sorting.

Roger et al. (2016)- Theory predicts more diverse communities have greater productivity, however experimental evidence is mixed. Species richness is the common metric for diversity but abundance, functional and phylogenetic diversity also matters. Can manipulate bacterial diversity using dilution-to-extinction approach- loss of rare, retention of common species. This study related ecosystem functioning of bacterial communities across three dimensions of diversity- number and abundance of species, functional diversity and phylogenetic diversity in a dilution-to-extinction experiment. Model- lakes microbes. No evidence of positive effect of diversity on ecosystem functioning. Phylogenetic diversity and abundance important. Possible explanations- few species important for functioning, regardless of diversity; high levels of redundancy- most species equally efficient at using resources. High redundancy is supported by functional diversity measures. FD was a poor predictor of functioning and correlated weakly with diversity. Phylogenetic diversity may be a better predictor of functioning than species and functional diversity.

Vall-llosera et al. (2016)- Opportunity hypothesis- invader utilises resources not used by resident community. Invaders more likely to encounter these opportunities if it is an ecological generalist and/or having requirements lacking in resident species. Competition hypothesis- invaders displace natives from niches via exploitative or interference competition. Study system- Red-billed Leiothrix (*Leiothrix lutea*). Opportunity hypothesis supported- little resistance from native community. No decline of native species. Lack of phylogenetic clustering, suggesting species sorting not apparent. Leiothrix behaved as a generalist and opportunist.

**Community monopolisation-** early monopolisation of resources by early immigrants by local genetic adaptation

**Metacommunity-** multiple local communities of interacting species which are connected by at least one dispersing species

**Niche preemption-** early immigrants deplete/decrease certain resources

**Niche modification-** habitat modification e.g. toxic metabolite production (could also be beneficial metabolites)

**Priority effects-** the effect of colonisation order on community dynamics e.g. species abundance and community properties (invasion resistance ect.)