Diversity-invasability relationship

Levine & D’Antonio (1999)- Review of D-I relationship and it’s evidence (plus method critique/review)- primarily ecological perspectives. Elton (1958) and MacArthur (1955, 1972) pushed the d-I relationship, further linking this to community stability (with invasability being one metric of community stability). The d-I relationship is established by more diverse communities being expected to fill more niches (niche-packing) and contain species which are impactful for invasability/invasion resistance. However, species can also be invasion facilitators and increasing diversity of some systems can open new niches (micro-heterogeneity of rhizosphere)- offering up debate about whether diversity will always scale with invasability. Invasability is also the function of factors at least in part independent of diversity- disturbance, resource availability, physical stress, competitors, consumers ect. (see paper for refs). Alls models reviewed find that as diversity increases, invasability decreases. Invasion is a probabilistic process, of which diversity is expected to decrease such probability of successful invasion. Propagule pressure can increase invasion success above diversity metrics through numbers alone.

Kimmunen et al. (2016)- Difficult to define invaders in microbial communities- species may have interacted historically (and so prior ecology and evolution cannot be excluded) and dispersal highways exist. Definition- any species not present prior to introduction/invasion. This can be extended to include growth of dormant microbial species which exist in a low metabolic state (thus removing them ecologically from the community) until reactivation. Invaders do not need to negatively impact the community to be invasive- effects can vary between species. Invasion literature typically can be divided into invader-centric research (invasive traits) and resident community-centric (community invasability).

See paper for summary on community ecology and invasability (could be helpful for building review framework).

Introduction

**Support**

* Diversity invasability relationship is correlative- higher diversity communities are more likely to fill niches that invaders exploit and alter environmental variables (niche modification)
* However, mechanisms underlying this relationship can create mixed evidence for D-I and diversity can prove insignificant or redundant in contrast to other mechanisms

Elton (1958)- high species richness should reduce invasiveness of communities (This paper is very commonly referenced)

Roughgarden (1976)- Partitioning of resources could be considered to be due to co-evolutionary processes in which there is a selection pressure for character displacement to avoid competition between species. This reduces niche overlap between species. Niche overlap has been reported to decrease with increasing species diversity (Pianka, 1973, 1974).

Dillon et al., (2005)- Investigated the effects of diversity in gut microbiota of locusts on invasibility by pathogenic bacteria. They found that species rich communities were more resistant to invasions.

Ridaura et al. (2013)- Gut microbiota from lean mice (more diverse) outcompeted the microbiota from obese mice (less diverse).

Bonanomi et al., (2014)- Microbiota invasions can have major impacts on ecosystems in their appearance and functioning, as well as cause diseases. In general terms, the invasion of an environment by new species is influenced by three main factors: (i) the number of propagules entering the new environment (propagule pressure); (ii) the characteristics of the invasive species (invasiveness); and, (iii) the susceptibility of the environment to invasion by new species (invasibility) (Lonsdale, 1999). This study showed that: fungistasis (inhibition of fungal growth) was positively affected by increasing microbial diversity; Diversity reduced the invasiveness of *P.chlororaphis* strain M71 to colonize the soil.

France and Duffy (2006)- Investigated how tropic level diversity affected invasion from other species at other trophic levels. Specifically- how species richness and identity of native crustacean grazers affects invasion of other native grazers at lower trophic levels in eelgrass mesocosms. Species richness of resident grazers reduced invasion of other mobile grazers (emphipods, isopods, sea slugs). No singular species identity was found to reduce invasiveness of the community. Species richness resulted in greater food consumption and, when competitors were removed, invasion was more successful- thus indicating competition for habitats and resources as being important for invasion resistance. Residents had a competitive advantage to invaders.

Kneitel and Perrault (2007)- Disturbances are commonly associated in communities and can directly affect the invasiveness of communities by changing resource supply rates and abundances of native species. The increased invasiveness of communities, following disturbance, is hypothesised to be due to reduced competition by residents either by lowering resident density or by lowering species diversity. This study investigated these hypotheses using rotifer and protozoa communities. Disturbances were found to decrease species richness by 53% but this was not affected by invasive species. Invader species richness and abundance significantly increased with disturbance and the success of invasion was dependent on disturbance itself. This study could not determine whether niche availability or dominant species identity affected invasion success.

Van der Waaij et al., (1971)- CR drops immediately after mice were administered with antibiotics and recovery of CR results in profound changes to the intestinal flora. Which intestinal residents and the mechanisms of resistance are unknown.

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.

Amalfitano et al., (2015)- Our understanding of the invasibility of natural microbial communities in aquatic ecosystems is very limited by a lack of unifying theory and the complexity of these communities. Community compositions have been reported to change across both space and time, which may be the result of ecological niches changing in availability or the growth of rare versus dominant taxa. Diversity is expected to positively relate to invasion resistance on small spatial scales but be negative on broader scales. ‘Thus, we can assume that more stable (and ecologically complex, often but not always, more diverse) communities are also more efficient in the substrate utilization, and thus may leave less space for the establishment of non-native species.’ Environmental stressors which can influence invasiveness of communities: climate change (temp increase), pollution, resource fluctuations/availability and food web alterations. As temps increase, species (and presumably communities) are moving latitudes and in microbes, causing colonisations of warmer waters. The construction of artificial communities to test invasibility are invaluable (see paper for full detailing of experimental approaches).

Lozupone et al., (2012)- Disruptions of normal gut microbiota have been associated with conditions such as obesity, malnutrition, inflammatory bowel disease, neurological disorders and cancer. Diversity of human gut microbiota extends to over 1000 species of microbe. These communities are heavily affected by our diet, medicines and infection of neutral and pathogenic microbes. Diversity and stability of these communities also rapidly changes as we age, with greatest increases being observed in the first three years of age. This is the result of ecological succession in which initial colonisation is followed by consecutive compositional and functional changes to reach a relatively stable climax community. The sequences of succession in terms of community coalescence could have implications for later life health and disease. The gut microbiota generally exhibits resistance to invasion from other microbes, however there is some research with shows that it can be vulnerable to transplantation by invading communities. This effect was enhanced if resident communities were reduced with antibiotics.

Resilience to invasion is characterised by species richness- greater resource exploitation (fits into niche packing theory). Excessive nutrient consumption results in decreases in diversity as singular species grow to dominate microcosms, which is why obese individuals have lower diversity- this is coupled with reduced resilience to invasion. Resilience may also be affected by functional response diversity- the degree with which individual species in a community vary their ecosystem function as a function of their sensitivity to change. I.e. High FRD may allow niches to be quickly filled by other community members if one is compromised.

Phylogenetically related microbes have greater niche overlap and so experience greater levels of competition. Despite this, due to their shared environmental preferences, their abundances tend to be positively correlated.

Sources- C. difficile (opportunistic pathogen) expands into vacant niches after oral antibiotic administration. Coincides with increase in nutrient levels (niche vacancy). Most successful treatment is faecal transplants (reintroduction of diverse community) but some transplants are more effective than others. Unknown why microbiomes differ in stability- likely to be due to host-microbiome interactions as well as microbial interactions within the microbiome.

**Critique**

Shea and Chesson (2002)- Invasion occurs in two stages- transport of organisms to a new location and the establishment and increase of the new population. Whether a community provides niche opportunities (resource or enemy escape- see Brockhurst) is a strong determinant of invasion resistance of said community. Invasion success, when these resources are limited, is dependent on the invader being able to exploit those resources and have a higher capita growth, than the current resident. How hosts and residents respond differentially to environmental stressors is further a strong determinant in who will succeed in competition events. ‘The maturity concept might explain such community differences: communities that have had less time to assemble, and less time for their constituent species to adapt to the local conditions, are likely to have fewer species with broader niches. Their species might also have lower competitive abilities than those in communities that have had a longer time under their present environmental regime. These communities tend to be less invasion resistant. Maturity undoubtedly also affects invasion resistance through escape opportunities, but clear predictions in this area are not so apparent.’ **Studies which have suggested that diversity is a key mediator of invasion resistance can be contested in their validity as these communities often have high levels of exotic species which add to their diversity. In fact, some studies in agricultural systems have shown positive relationships between diversity and invasion success and this is hypothesised to be because increases in diversity can increase niche opportunities through interactions such as mutualisms.** ‘Invasion success depends not on filling a vacant niche but on being a better exploiter of resources or a better avoider of natural enemies than resident species.’

Resource use

* Independent of diversity, the way in which the resident community and invader utilises niches can be a stronger determinant of invasability
* Resources can refer to nutrients, space ect.
* Priority effects are a general example of this as resident species/community monopolise resources, reducing invasion success
* Disturbances (e.g. antibiotics) can free up niches/resources, facilitating invasion

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

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.

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.

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

Eisenhauer et al., (2013)- Used *P.fluorescens* to investigate the role of niche dimensionality (resource richness) on community invasibility by *P.putida*. Invasion success was found to be determined by the presence of certain competitor genotypes which exploit the same resources as the invader in low niche dimensionality. Whereas, at high niche dimensionality, biodiversity was key to community invasibility- but only where there were few niches present. Invasion success relied heavily on the resource use of the resident and invader species in at high niche dimensionality. In contrast, at low niche dimensionality, invasion success relies on the presence of certain species and their use of resources.

Dukes, (2001)- How resistant a community is to invasion is hypothesised to be due to species diversity and the composition of particular species. More diverse communities are hypothesised to be more resistant to invasion because they reduce the available resources, thus reducing the niche breadth for invaders. This study investigated the effect of diversity on invasion success in grassland microcosms. It was found that functional diversity reduced community invasibility from *Centaura* by reducing resource availability but invisibility was not determined by species richness (with functional diversity held constant). However, species diversity did determine the lasting impact of invaders, finding that species from less diverse communities greater growth suppression from invaders when compared to species from more diverse communities.

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.

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.

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.

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).

**Niche modification**

* In addition to monopolising resources, earlier colonising species can modify niches in ways which facilitate or inhibit invasion
* Abiotic conditions- toxin production, pH change, oxygen levels
* Biotic conditions- suppression of competitors, pathogen build-up, public-goods

O’Loughlin & Green (2017)- Secondary invasions are synonymous to secondary infections, in which invasion or presence of a primary species facilitates invasion for the second. Successful invasion is dependent on resource availability, disturbance (type and frequency) and species composition- these can interact with disturbance affecting resource availability, resource availability affecting species composition and species composition driving disturbance. Primary invasions can alter these processes, facilitating secondary invasions. Includes examples of primary species invasion, habitat modification and secondary invasion

Simberloff & Von Holle (1999)- Analysed the frequencies of ‘invasional meltdowns’- the positive interactions among non-native species, also classifying other positive and negative interactions. +/- interactions were most common (156/254) with +/+ (10) almost as common as -/- (12) interactions. Specialist plant-pollinator interactions which are highly coevolved would likely be dependent upon co-invasion for mutual success in a new habitat e.g. fig plant could not reproduce until fig wasps were introduced as well. Dispersive mutualists such as exotic pigs in Hawaii, contribute to the spread of exotic plants- the pigs are also dependent on the introduction of protein-rich European earthworms, to reach large sizes. Environmental modification is also key for co-invasion- Asian water buffalo was introduced to eastern Australia and devastated native plant communities, compacted soil and altered hydrology of forests, causing high tree mortlity. This facilitated invasion of the central American shrub. Plants can further alter soil chemistry to facilitate invasion of other non-native species.

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.

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*.

Sources- humans produce non-digestable oligosaccharides which can only be digested with beneficial microbial flora (Bifidobacterium), suggesting hosts can modify niches within the gut to culture specific species and exclude pathogens. Links to species dominance (below)

**Species dominance**

* This strongly links to resource use and niche modification- specific species in communities (sometimes dominant) can contribute disproportionately to invasion resistance by monopolising more resources (generalists e.g. weeds), filling the same niche as the invader (species ID effects), niche modification
* More diverse communities are more likely to contain these species, but in their absence, absolute diversity can become insignificant
* Outside of resource use, invasion resistance and invasability can relate to the production and detoxification of resident/invader toxins/metabolites. This is more often related to species-specific rather than diversity based interactions (although more diverse communities are more likely to contain these species by probabilities)

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.

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.

Hodgson et al., (2002)- Used *P.fluorescens* to investigate the role of diversity in invasion resistance of communities from invading genotypes. With increasing genotypic diversity, productivity increased and invasibility decreased. This was due to the increase in functional group diversity, which coincides with increased genotypic diversity. The dominance effect was the main mechanism driving relationships between diversity and both productivity and

invasibility. After controlling for the dominance effect (that a particular species contributes disproportionately to invasion resistance), there was no relationship between diversity and productivity, and only a weak relationship between diversity and invasibility. The dominance effect operated at the level of functional groups rather than genotypes: the presence or absence of WS genotypes was the best predictor of both productivity and invasibility. However, it has been strongly argued that the dominance effect is a statistical artefact of assembling random communities, and will have less impact on the productivity and invasibility of natural communities (Aarssen 1997; Huston 1997; Huston et al. 2000). We therefore determined the relative influence of other mechanisms in shaping the remaining weak relationship between productivity and invasibility.

Stecher et al., (2010)- Gut microbiota protect the body from infection of pathogenic bacteria by exhibiting colonisation resistance (CR). Less diverse gut communities in mice were more susceptible to colonisation from pathogenic bacteria (Salmonella, E.coli). However, the mechanisms behind CR are unknown- one hypothesis is that it is due to the interactions between the gut microbiota and the mucosal innate and adaptive immune system which keep the host in a competent defensive state. Alternatively, the gut microbiota directly suppresses pathogen growth by producing antimicrobial chemicals. Enterobacteriaceae were not found to mediate CR but indicated levels of CR. Conditions which renders gut microbiota less defensive include nutrient deficiencies, stress, illness and antibiotic treatment (history). This creates another level of risk for infections, which is particularly implicit for already high-risk groups such as the elderly, children, pregnant and immune suppressed.

Crawley et al., (1999)- In a 7 year longitudinal study, investigating the invasibility of grassland communities, they found no correlation between species richness and the number or biomass of invasive species. There were significantly more invasive species in the species rich plots, but the effects of species richness or functional types could not be distinguished. The main result of this study is that it is the identity of species which matters more than diversity itself within communities.

Emery and Gross (2006)- Investigated the effect of dominant species identity, abundance and the mechanisms utilised by dominant species on invasibility of field plant communities. *Andropogon* dominated plots were the least invasible whereas *Centaurea* and *Bromus* plots were most highly invaded. Whilst dominant species were identified in affecting invasion success, the mechanism could not be explicitly identified. Possible mechanisms: nitrogen removal from soils by C4 plants such as *Andropogon* as well as factors relating to light, soil nitrate and water availability. In this study, litter biomass, soil nitrogen and community species richness were the only significant predictors of invasion. Species richness was positively related to invasion by non-native species. This may be due to increases in micro-heterogeneity (see also paper regarding mutualisms). Relative abundance of dominants did not affect invasibility but does suggest that this relationship occurs after a 40% threshold.

Costello et al. (2014)- The ability of certain anaerobes to limit the invasion and growth of Clostridium perfringens in a diet-dependent manner is an example of competition for resources (Yurdusev et al. 1989). Bifidobacterium breve produces an exopolysaccharide (EPS) that protects it from the immune response; this allows it to compete for space and colonize the mouse gut at high loads in both the lumen and at the epithelial surface without inducing inflammation (Fanning et al. 2012). Even if invaders do gain a foothold, the indigenous microbiota can block lethality: in mice, some B. longum strains can protect against enterohemorrhagic E. coli-mediated death by inhibiting translocation of Shiga toxin from lumen to blood (Fukuda et al. 2011).

**Phylogenetic structure**

* This links to community resource use and dominant/species ID- phylogenetic distances within a community mean species are more likely to use differing resources/niches which provides community stability (stable abundance of below)
* Whereas phylogenetic overlap (see Pseudomonas paper) between resident and invaders means resident communities are more likely to exclude invaders

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

Jousset et al., (2011)- Investigated the role of genotypic dissimilarity and genotypic richness (genotype structure of communities) in invasibility of *P.fluorescens* of communities by *Serratia liquefasciens* MG1 which has similar niche coverage. Genetically dissimilarity increased invasion resistance of communities and were more productive which suggests that resources were used more efficiently in niche pre-emption. This contrasts to results suggesting that it is dominant genotypes which determine invasibility. Genotype richness also inhibited invasion through the production of toxins which peaked at intermediate genotype frequencies (relatedness)

Lessard et al., (2009)- The phylogenetic structure of ant communities was significantly different from random- individual taxa were more distantly related to each other. This suggests that competition shapes the structure of uninvaded communities by excluding taxa that are closely related (and so compete for a similar niche). Therefore, only distinct ant genera can coexist within communities. Invaded and intact communities did not vary in species richness but in community composition, resulting in different phylogenetic structure.

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.

**Networks**

*Resident community:*

* Network interactions (positive and negative) can increase or decrease community stability, against invasion, depending on their strength and direction
* Models predict that positive interactions (+/+) can destabilise communities by creating positive feedbacks (risk of co-extinction or overdominance) whereas negative interactions (+/-) create negative feedbacks- restabilising a community.
* E.g. Antagonists (parasites, predators) can provide stability by reducing interaction intensities. Also, see local adaptation

*Co-invasion:*

* Equally, invading species can interact to increase co-invasion success (either simultaneously or sequentially) by altering environmental conditions, suppressing competitive species (see niche modification)
* Invader-invader interactions allow species to circumnavigate diversity effects by suppressing key resident species and opening niches
* More diverse communities will contain more network interactions, but the direction and strength of these interactions can increase or decrease stability among resident species and co-invaders. Therefore, diversity is a poor proxy in this regard for predicting community invasability.

Coyte et al. (2015)- Microbiome stability research- models based on individual and two-species models. Microbiomes are more diverse with multiple species interactions. Competitive interactions are found within microbial communities but it is also assumed that metabolic cross-feeding occurs in microbiomes to facilitate its function. Interactions include cooperation (+/+), competition (-/-), exploitation (+/-), commensalism (+/0) and amensalism (-/0) in microbial networks. Model- pure cooperation, mined-interaction and competitive networks- increased diversity destabilises the community. Increasing proportion of cooperative networks- decreases likelihood of stability. Cooperation causes a destabilising effect by creating species-species interactions and positive feedbacks. Therefore, one species decreasing in abundance with decrease others. Host trade-off- microbiome stability and metabolic efficiency versus ecological stability.

Ecological competition improves stability, however high species numbers are destabilising. Although increasing species numbers is a destabilising process, competition creates negative feedback loops which have a stabilising effect. Similar effects are observed with exploitative species, including phage.

Host mechanisms of stability: Spatial structuring which inhibits microbial interactions; nutrient provision e.g. epithelia frucose release, thus providing alternate carbon sources to cross-feeding

Wei et al. (2015)- The structure of microbial communities can produce strong predictions of function and stability of eco-systems e.g. nestedness and connectedness. Study system- soil-borne bacterial pathogen, *Ralstonia solanacearum*, which causes bacterial wilt in 200 different plant species. This bacterium has to invade resident communities and reach a threshold density before becoming virulent. This study focused on bacterial competition networks as mechanisms linking composition, invasion success and disease spread in tomato plants. Model bacterial communities- five phylogenetically related (non-virulent) *Ralstonia* spp. species from rhizospheres. Resource competition patterns of pathogen and resident species on 48 labile carbon sources typical of rhizosphere (network properties characterised). 31 different communities- all possible combinations of five species with varying richness and composition. High connectedness- all species can use resources similarly, reducing niche opportunity e.g. generalist networks. Nestedness- trophic interactions between generalist and specialist species. In resource competition, nestedness can have a destabilising effect due to competition between specialist (few resource links) and generalist (many resource links) species. Therefore, high nestedness- less stable, lower invasion resistance.

Results- Increased diversity reduced invasion success however, networks are a better predictor of invasion resistance than diversity. Stabilising configurations (low nestedness, high connectance) with clear niche overlap with pathogen reduce invasion success, resulting in lowest levels of wilt disease. Niche overlap was less important than nestedness and connectivity which suggests intra-community competition dynamics are as important as resource monopolisation. Diversity was also linked to invasion resistance outside of resource use, suggesting additional mechanisms for invasion resistance e.g. colonisation ability of rhizosphere and roots, environmental alteration (toxin production?).

Rivett et al. (2018)- Multi-species bacterial invasions into communities. Model- invaders and communities from water-filled tree holes. Increasing invader diversity (co-invasion) increased invasion success. Invasion success was also highest at earliest colonisation time (co-inoculation with community) and had higher short-term effects on community composition. Consistent with role of priority effects on invasion success. Positive pairwise invader interactions decreased with later invasion into resident communities.

Lu et al. (2018)- Facilitative interactions between invading species can result in an ‘invasional meltdown’, in which their negative effects on the resident community are amplified- increasing invasability of present and future invasions. Ecological co-selection phenomenon is demonstrated in coalescence studies (e.g. Pawel’s). Depending on the type and direction of such interactions, this can result in ‘top-down’ cohesiveness, in which the fitness of subordinate species in dependent on dominant; or ‘bottom-up’ cohesiveness in which subordinate members amplify the fitness of dominant species. 8 natural microbiomes from soil and plant sources. Outcomes of coalescence can be quantified using Bray-Curtis similarities to invaded vs coalesced communities (before/after) and Jaccard indices. 56 community coalescence, 56 dominant pairwise. Weak dominance effect found- coalescence outcomes not determined by dom-dom competition. Invasion success of dominants increased in presence of rarer species (bottom-up selection).

Livingston et al., (2013)- In oceanic microbial communities, coexistence is the predominant outcome for coalescence events with no general increase in extinction events. Many evolutionary processes have been highlighted as being responsible for these patterns including character displacement, co-evolution, phylogenetics, species range evolution, trade-off surfaces or post-contact ecological community assembly involving rapid reassembly through species interactions and environmental heterogeneity. However, some models suggest that communities can displace or dominate others (e.g. the dominance of Northern mammal fauna in place of the Southern). The mixing of two non-random communities results in asymmetry in community assemblage whereas the mixing of two random communities results in equal numbers from both. Non-random communities are hypothesised have greater local stability but is highly sensitive to community composition as only 29% resulted in asymmetry (Gilpin, 1994).

In this study, they investigated the effects of trophic structure on community coalescence in aquatic microbes. Treatments- mixing competitive (C) and/or trophic (T) communities with each other. Asymmetrical outcomes for community coalescence were found. Previous research indicates that asymmetry at the community and guild level is influences by assembly history. CC mixes only resulted in significant asymmetry and these had more guilds and more species per guild- the competitive interactions results in extinctions, which is in line with Gilpin’s predictions.

Lawrence et al (2012)- This study examined interspecies coevolution on used and unused beech tea. This was investigated by measuring growth rates of species A-D on used and unused beech tea- e.g. if growth rates decreased on used tea, then species were using the same resource whereas if growth rates increased then species had evolved to use the waste products of the other species within the community. Coevolution within these artificial communities caused increased cooperation between pairwise species/ reduced negative interactions. Species B and C adapted to their biotic environment by evolving to exploit the waste products of other species whereas species A evolved to exploit a different carbon source in the abiotic environment, thus escaping competition with the other species. This resulted in species A-C becoming less adapted to their abiotic environment as they had become more dependent on the biotic conditions created by the other species. Contrastingly, species D became more adapted to the abiotic environment by exploiting other macromolecules. The strength of this study is that it demonstrates co-evolutionary interactions between more complex communities of bacteria and how interspecies interactions can cause evolution and diversification of species into new biotic and abiotic niches.

He et al., (2014)- It has been suggested that community structure is important in colonisation resistance, but due to the complexity of communities, this has not been empirically proven. This study identified three key bacterial species, within mice oral cavities, as being part of a colonisation resistance pathway. These species were- *S. saprophyticus* (the ‘Sensor’), *S. infantis* (the ‘Mediator’) and *S. sanguinis* (the ‘Killer’). *S. saprophyticus* could produce diffusible signals to *S.infantis* which stops suppressing *S. sanguinis*’s ability to produce H₂O₂ which then inhibits invading E.coli.

Eiler et al. (2012)- Bacterioplankton communities (freshwater)- co-occurrence patterns among bacterial groups and correlations to environmental properties on a temporal scale. Most DNA reads associated with phylum Actinobacteria (38%), also Verrucomicrobia, Proteobacteria and Bacteroidetes- depending on season. Networks over time enabled detection of time-lagged interdependencies and succession patterns. This revealed co-occurrence patterns between community members (tribes- phylogenetic cladistics) and environmental variables. Analyses suggest closely related phylogenetic groups have high functional redundancy and/or similar ecological roles in the environment. Network interactions were suggestive of conducive (facultative) and inhibitory mechanisms- for example, two groups were positively associated with phosphorus but negatively associated with respective abundance, suggesting they compete for resources. Different groups also showed high numbers of associations, suggestive of interdependencies.

^ results additionally reflected in succession of the infant gut microbiome with co-occurrences of taxonomic groups (Koenig et al. 2010)

Johnson et al. (2008)- Interactions between invasive rusty crayfish, Chinese mystery snails and native snail populations. Rusty crayfish decreased populations of two snail species by >90%- predation effects. Chinese mystery snails compete with native snails, decreasing their abundance. Rusty crayfish and Chinese mystery snails had a combined negative effect on snail populations, greater than their individual effects. Predatory effects, however, lessened competitive interactions, reducing their direct effect.

Buric et al. (2009)- Two co-occuring invasive crayfish species- Orconectes limosus, Dikerogammarus villosus. D. villosus predates on juvenile O. limosus (3rd-5th developmental stages). O. limosus could only predate on D. villosus when itself was at the 5th development stage- relative size made it a poorer predator.

Preston et al. (2012)- American bullfrogs co-occur with non-native fish (i.e. sunfish, bass, mosquitofish). Studied combined effect on amphibian taxa at the aquatic larvae stage. Predictions- mosquitofish predators would decrease amphibians and zooplankton; bullfrog larvae would decrease native grazers (anuran larvae, snails). Mosquitofish reduced treefrog survival from 74% to 7%, newt survival from 97% to 6% and no effect on toad survival. Toads developed more rapidly with MF. Bullfrogs decreased toad biomass. No MS- bullfrog interaction. Zooplankton became undetectable with MS.

Green et al. (2011)- Invader-invader mutualism between yellow crazy ant (*Anoplolepis gracilipes*) and honeydew-secreting scale insects (*Tachardinia aurantiaca*) facilitates secondary invasion of giant African land snail by killing red land crabs- predators of GALS. Study examined between- population expansion/invasion on Christmas island. Tethered GALS to measure mortality rates. Propagule pressure was an important determinant of GALS invasion success. GALS had a greater survival in YCA supercolonies and persisted 115 times longer than in their absence, due to predation from RLCs. Invader-invader mutualism of YCA and HSI increase propagule pressure of GALS, increasing invasion success.

Evolutionary mechanisms

**Local adaptation**

* Evolutionary mechanisms of community stability and invasion resistance- can increase diversity but this is secondary to the invasion mechanisms listed above
* Locally adapted species are more likely to occupy distinct niches (adaptive radiation, character displacement) and be adapted to using local resources
* LA of resource use allows residents to monopolise resources faster than invaders (PE) and restrict diversification (AR) of invaders to use resources- species sorting and evolutionary restriction of invaders
* Additionally, across trophic levels, local species will have co-evolved with local parasites and predators, to which invaders will likely be more vulnerable

Brown et al., (2006)- Microbes are capable of killing competitors through the release of toxins/bacteriocins (allelopathy). Microbes that carry phage can also use phage in a similar way as they use toxins. This study focussed on E.coli and associated phage which can be horizontally transmitted by lysis or vertically transmitted in a dormant state (lysogenized bacteria). Vertical transmission, whilst rare, gives the host protection from lysis. Whilst hosts face direct costs of replication of the virus and increased risk of lysis, they can be indirectly beneficial by killing competitors. This advantage is most beneficial when the resistant hosts are rare as phage can then quickly spread through the competitors. In thus study, when susceptibles were common, competition was initially neutral, followed by rapid phage growth then competitive neutrality and phage decline. The decline coincides with the lysogenisation of the susceptible bacteria. Therefore, the advantages of spite versus the use of phage are dependent on the relative frequencies of the competitors. Invader offence will utilise phage more as invasion occurs more as minorities whereas defence will utilise spite where frequencies of residents are higher.

Gomez et al. (2016)- preadaptation to soil microcosm of Pseudomonas fluorescens had stronger decreases in soil microbiome diversity. Resource monopolisation by local adaptation.

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.

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.

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.

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.