Co-evolution within communities

Tikhonov (2016)- An understanding of bacterial communities is currently very limited despite their widespread abundance e.g. human gut microbiota. Community level interactions of bacteria have been observed in which whole communities can displace others, but we don’t know why. It can be argued that bacteria behave as community unit, not in isolation. Direct cooperation/altruism need not be observed for bacteria to behave as communities- it can also depend on how bacteria interact with their abiotic environment. The cohesion of coalescing communities is dependent on the environment and the way in which the bacteria shape their environment to form niches. **One hypothesis from this model is that more niche packed communities should be more resistant to invasion. Therefore, communities with a higher level of co-evolution would have higher levels of persistence than naïve communities that have not experienced these events.** This has broad implications for our understanding of how communities of bacteria interact and form- such as within biomethane, soil and intestinal communities.

Levin (1970)- Different species can coexist if they are limited by different factors which are independent and the overlap of their ecological niches is ‘sufficiently small’. MacArthur (1958)-in the case where all species are resource-limited-comes close to saying this when he says that the proper statement of the Volterra-Gause principle is that "species divide up the resources of a community in such a way that each species is limited by a different factor.”

Freilich et al., (2011)- The high level of competition observed between species with mutual-exclusive distribution patterns supports the role of competition in community assembly. Cooperative interactions are typically unidirectional with no obvious benefit to the giver. However, within their natural communities, bacteria typically form close cooperative loops resulting in indirect benefit to all species involved.

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.** Therefore, the role diversity plays ininvasion resistance/success is unclear- co-evolution and niche packing may provide a better answer- specific interactions in a community context. ‘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.’ This paper places emphasis on community ecology- it is not just the individual interactions that matter, but also community context. However, it places invasion resistance due to environmental adaptation- discounting how organisms within communities adapt to each other.

Sierocinski et al. (2017)- When mixing biomethane communities of bacteria, entire community take over was observed. The most productive community dominated over the less productive one. Communities in which the members have become more adapted to their niches (Niche-packing hypothesis) are both more productive and more resistant to invasion. However, an alternative explanation is that the whole community is more productive because its members are better at exploiting resources than members of other communities. **The results of this study support the niche-packing hypothesis** as community coalescence was not related to methane production in a monotonic fashion- plus the second and third most productive communities were vastly underrepresented in final mixtures. Community diversity positively correlated with methane production, supporting greater niche packing.

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.

Gilpin (1993)- Competition occurs between communities of species when geographical barriers are removed. This often results in one community dominating against the other, with communities acting as ‘coordinated armies’. There is a level of cohesiveness between community members which allows them to act as a unit when in competition. Extrapolating the results of our study to other community systems.

Vermeij (1991)- Communities of organisms are coming into competition in the present day through anthropological interference (e.g. the building of the canal into the red sea). This is analogous to what has occurred historically, as shown by the fossil record, where the movement of landmasses has caused large-scale ecological interactions. When barriers between communities are broken, invasion is often one-sided, with one community invading the other but not the opposite. For example, the trans-Suez interchange has resulted in invasion of species (molluscs, crabs, fishes) from the Red Sea to the Mediterranean, but not the opposite. The fossil record has demonstrated, during the Pleistocene, a southward movement of savannah-adapted mammals and montane plants in which 11% of North American mammal genera invaded South America and only 2% from South to North. Some exchanges, such as late Miocene and Piocene were symmetrical. Such asymmetrical invasions have been noted throughout the fossil record, between northern and southern hemispheres, east and west and between tropics and temperate environments. These interchanges coincide with mass extinctions in the areas invaded.

Vermeij (1994)- Co-evolution can occur between individual pairs or within communities (diffuse)- interacting participants can be competitors, mutualists, predator/prey ect.

Rillig et al. (2015)- Whole bacterial communities are regularly displaced by the movement of their environment e.g. falling leaves, wind, food consumption and excretion. When different bacterial communities collide, they can be said to **coalesce (community coalescence)**. Research to date has focussed on migrations of metacommunities ie parts of communities rather than whole community interactions. Whole communities are mixed through dislocation of their abiotic habitat, rather than small migratory phases, resulting in changes in spatial structuring of the habitat. An understanding of this area has implications for medicine, agriculture and industry.

Rillig et al. (2016)- Coalescent events in soil can happen because of intrinsic (natural ecological interactions) and extrinsic (external influences/disturbances) sources. Both of which can increase the heterogeneity of soils on spatial and/or temporal scales. Soils can differ greatly over small spatial areas in their physiochemical and community assemblage. Earthworms are key biological factors which mix microhabitats and expose soil microbes to the worm’s gut microbes. The disintegration of soil aggregates, pore spaces that provide microbial microhabitats, also coalescences communities as these aggregates can differ between being aerobic/anaerobic and have different physiochemical properties. Human-mediated or externally driven coalescence events occur by tillage flooding, litter-fall, outplanting, composting and the addition of manure. The effects of these events have been studied and understood but the community dynamics are understudied. Global warming further influences the frequency of these events, thus having greater implications to coalescence in soil systems. Interactions of microbial communities within soils has vast implications for plant-productivity, decomposition and nutrient cycling. The broader implications of coalescence involve changes in diversity and increased horizontal gene transfer which are related to topical issues of antibiotic resistance.

Rilig et al., (2016b)- Microbial communities are frequently mixed in microbiome engineering to increase the diversity of stock cultures. The outcomes of these interactions is hypothesised to change depending on whether whole communities (biotic and abiotic componenets) or extracts are used when mixing.

Kort et al., (2014)- Bacterial community coalescence occurs in kissing between human partners. The heterogeneity of the oral cavity is ideal for the proliferation of microbial diversity, supporting a wide range of species (an estimated 700 anaerobic species). Between couple tongue microbiota is much more similar than that of uncoupled individuals. Differences between couple and non-couple salivary microbiota were non-significant- saliva is a mix of bacteria from all areas of oral cavity and changes very quickly. The more frequently couples kissed, the more similar their salivary microbiota- no correlation with tongue microbiota. Findings suggest that the shared microbiota among partners is able to proliferate in the oral cavity, but the collective bacteria in the saliva are only transiently present and eventually washed out, while those on the tongue’s surface found a true niche, allowing long-term colonization.

Meadow et al., (2013)- Different teams of American Roller derby players have characteristic communities of skin microbes (on the upper arm- where contact occurs during the sport). After matches between teams, the overlap between communities increases ie. they become more similar after coalescence. This study didn’t consider long term changes- only that chimeric communities form immediately after matches and not how the communities change in the long term.

Bakken et al., (2011)- Treatment of *Clostridium difficile* infections (CDI) using antibiotics has resulted in disruptions of healthy bowel microbial communities, which would usually keep these infections from relapsing through the activation of antibiotic-resistant spores. Consequently, this creates more complications throughout the digestive tract. An alternative approach to treatment of CDI is to use Fecal Bacteriotherapy- the introduction of normal flora from donors to correct imbalances in gut microbiota created by its diseased state. FMT is the only therapy that restores the phylogenetic richness of the recipient's intestinal microbiota without prolonging the perturbation of the normal microbiotic composition.

Guo et al., (2012)- FT appears to be a safe and effective procedure. In most cases (83%) symptoms improved immediately after the first FT procedure, and some patients stayed diarrhoea free for several months or years. Although these results appear to be promising, the treatment effects of faecal transplantation cannot be determined definitively in the absence of a control group. Results from randomised controlled trials that compare faecal transplantation to oral vancomycin without or with a taper regimen will help to better define the role of faecal transplantation in the management of recurrent CDAD.

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.

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. Looked into resistance to isolate lines of pathogen (not communities) and further, which species of gut microbiota were important for resistance (results inconclusive)- didn’t look into whether individual species were important against community context.

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

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.

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.

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.

Hay et al., (2004)- Competitors as mutualists- Sponges typically form heterospecific communities of up to 12 individuals. Studies (Wulff, 1997) with particular species of these sponges have shown that heterospecific communities had greater growth rates and increased survivorship than when growing alone or with conspecifics. Each species has differing levels of susceptibility to predation, pathogens and physical disturbance- therefore, as a consortia, they may be able to resist environmental stressors.

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.

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).

Knowles et al (2013)- Coinfection of multiple parasitic species is highly documented in nature. These parasites can form infecting ecological communities which compete for host resources and interact with hosts through chemical/physical interfaces or through cellular interaction (immune system). Also come into contact with host microbiota. They studied within-host parasite communities in mice, demonstrating the interaction of co-infecting parasites (nematodes, *Eimeria/* protist). Treatment of nematodes resulted in 15-fold increases in *Eimeria* infection intensity- demonstrating that the parasites compete for resources. Communities were demonstrated to be highly stable in response to perturbations of nematode populations.

Brockhurst et al. (2007)- Increased diversity confers greater resistance to invasion (see paper for supporting reference).

Brockhurst and Koskella (2013)- REVIEW- Co-evolution within communities is a currently expanding area of research- bacteria that have evolved to resist multiple phage (generalists) rather than singular phage (specialists) have greater fitness costs when grown in the absence of phage. Community co-evolution also has implications for how we understand how organisms adapt to novel biotic and abiotic environments.

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.

Crawley (1987)- “a community is invasible when an introduced species is able to increase

when rare.”

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.

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.

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)

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.

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.

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.

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).

Kolar and Lodge (2001)- Characteristics of invasive species- review.

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.

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

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.

Davis et al., (1998)- Dispersal and interactions between species of fruit fly can modify and disrupt links between temperature and species local presence or absence, and range- community context matters. Horizontal (competition) and vertical (enemy-victim) interactions will therefore distort predictions based on individual species acting in isolation, as has been the paradigm of past research. This is particular with relevance to global warming.

McGill et al., (2006)- Research has focussed on pairwise species interactions which gives a poor insight into how species function within community contexts. Functional traits of species, e.g. metabolic rate, seed size, body size, photosynthetic rate, vary more greatly between species than within. Community ecologists must address biotic interactions (e.g. competition) within community contexts, however to separate out individual interactions is difficult. In many communities, interactions are diffuse. Which functional traits are important in competition and determining a species’ fundamental niche will be mostly determined by traits relating to resource acquisition and competitive dominance ranking.

Johnson and Stinchcombe (2007)- Community ecology focuses on the abundance, distribution and diversity of species within communities, without considering evolutionary factors such as genetic variation and mechanisms of evolutionary change. Our understanding of community context with reference to evolution is poorly understood and has received little attention in research. Genetic variation itself has an influence on community patterns and the heritability of communities. These measures provide a basis for predicting how changes in one species (community variable) affect other aspects of that community. Studies have yet to investigate this. We need a better understanding of the intersection between evolutionary history and contemporary ecological forces, such as competition, predation, mutualism, disturbance and stochastic processes. If community context affects the expression of genetic variation or the strength of natural selection, microevolution within communities will vary in accordance to the factors governing said community. Some evidence is presented in communities, such as those of farming ants, cultivated and parasitic fungi, that interactions of multiple species leads to co-diversification. Evolutionary processes over short and long timescales can influence community dynamics and patterns. Likewise, ecological interactions among species within communities can influence micro- and macroevolutionary processes and patterns.

O’Brien et al., (2013)- Interacting selection pressures can have a major impact on the microevolutionary trajectories of bacterial populations. Therefore, the interactions of multiple species within communities is hypothesised to have a major role in the structuring of microbial communities.

Weber et al., (2017)- Species interactions can generate stabilising or directional selection pressures which can contribute to patterns of evolutionary stasis, divergence or convergent phenotype evolution. Decades of microevolutionary studies have compellingly shown that species interactions can directly impact factors such as genetic divergence, range/population size, hybridization, the evolution of reproductive isolation, and the persistence of young species.

Coexistence between species is dictated by the rate and amount of trait divergence that reduces competition. This can shape interspecific interactions in evolving metacommunities.

LaRue et al., (2016)- Newly introduced populations to habitats, in the attempt of restoring communities, will likely be under selection to undergo rapid evolutionary change. This may result in decreases in initial population size, growth rate and mean fitness; the continual persistence of restored populations will depend on the selection pressures and diversity within them. No studies have considered the effects of evolutionary change in restored populations on intraspecific and interspecific ecological dynamics. Evidence suggests that interacting species that do not share a recent coevolutionary history may impose strong selection pressures on one another (Fussman et al., 2007; Palkovacs et al. 2009; Crutsinger, 2016). Therefore, introducing different populations from different sources could generate evolutionary dynamics during the initial stages of community assembly and establishment.

Friman and Buckling (2013)- They investigated how selection imposed by a predator (protist) and a parasite (bacteriophage) affects the evolution of hosts defences and how this also affects pairwise coevolutionary dynamics. When coevolved with protist or phage in isolation, bacteria evolved specialised defence strategies, resulting in pair-wise co-evolutionary dynamics and an arms race of infectivity/predation and defence. However, when a protist was present, bacteria rapidly gained and lost phage resistance and the presence of a protist also decreased monotonic increases in resistance and infectivity, which indicates a breakdown in arms-race dynamics. The breakdown of arms-race dynamics, with bacteria gaining and losing phage resistance in 4 weeks, is indicative of a shift towards fluctuating-selection dynamics, however this could not be ambiguously identified. Protist populations decreased towards the end of the experiment and this was associated with increased phage infectivity.

Explanations for these observations are as follows:

- Protists lowered bacterial populations, thus impacting phage densities. This reduced phage-bacterial interactions and therefore weakened the selection pressures for bacterial resistance. This also likely reduced genetic diversity of bacterial populations

- Defence against one enemy constrained defence against the other, generating a trade-off in defensive strategies and resulting in specialised rather than generalised defence. Resistance against both caused increased fitness costs than resistance against one alone. The exact extent of this trade-off is undetermined.

Gonzalez et al., (2012)- The use of next generation sequencing has allowed entire communities of microbes to be characterised, facilitating an abundance of research investigating microbial diversity. This has resulted in the production of a multitude of statistical models and tests which can determine how microbial communities vary across spatial and temporal scales.

Ashbolt (2015)- In the US alone, there are over 500 waterborne pathogens from viruses, bacteria, protozoa and fungi groups. The human norovirus can only bind and infect cells containing the histo-blood group antigen (HBGA) which is found on gut bacteria, thus facilitating infection. Infection with multiple pathogens- virus infection weakens gut microbiota- facilitates pathogenic microbe infection? Links to Brown paper- lysogenised bacteria can use phage to infect other bacterial colonies!

Spiers et al., (2002)- Investigates the genetics of WS morphotypes. Substantial phenotypic variation was found in growth rate and growth on LB v KB agar. WS defective morphs (SM) were competitively inferior to WS and could colonise the air-liquid interface. A wss operon, comprising of 10 genes, was identified as the area of the genome under selection for biofilm synthesis. Four of the genes were similar to genes found in other bacteria which are involved in cellulose biosynthesis. WS morphs appeared within 48 hours. Due to the heritable variation that exists between WS genotypes, it is likely that a variety of mutations can cause the WS mutants which are biochemically characterised by their overproduction of CLP (cellulose-like polymer). No genetic differences are highlighted between wss and wsp sequences, therefore the cause of the WS morphotype is likely due to mutations in regulatory cascades that link to the wsp operon and pass signals onto wss and wsp. This provides a complex link between genotype and phenotype for WS.

Rainey and Bailey (1996)-

McDonald et al., (2009)- WS genotypes are distinguished by LSWS- a single nonsynonymous nucleotide change in wspF which is a methyl esterase and negative regulator of the WspR dy-guanylate cyclase that is responsible for the biosynthesis of c-di-GMP (Malone et al. 2007), the allosteric activator of cellulose synthesis enzymes (Ross et al. 1987). This study found that mutations in the aws and the mws loci can generate the WS phenotype through the overproduction of c-di-GMP. Parallel evolution was found with mutations occurring repeatedly within the same loci e.g. 13/26 WS genotypes had mutations in wspF, 3 in wspE, 3 in awsX, 4 in mwsR, 2 in awsR and 1 in awsO. At least ~100 genes are associated with WS variation but it is not the number but the regulatory function of these genes which is important in the cascading role that they can have. The complexities of genetic architecture generate extensive genotypic and phenotypic variation. See paper for citations of parallel evolution

Bailey et al. (2015)- Parallel evolution of P. fluorescens in heterogenous environments.

Adams (2010)- Parallel evolution has occurred frequently in nature, with particular examples coming from vertebrates (sticklebacks, cichlids, lizards). This occurs due to similar abiotic and biotic selection pressures- the environment and the competition between species/morphotypes/individuals. Parallel evolution was found between two salamander species which exist in competition across a geographical gradient.

Tyerman et al., (2008)- Tested character displacement in E.coli populations grown in acetate and glucose broth. When grown in competition, divergence occurs. However, the degree of divergence was smaller in magnitude than in the convergent stage. This is hypothesised to be because (Schluter, 2000), the speed of divergence by character displacement is greatest when phenotypic distance is intermediate- therefore, after divergence occurs, further increments in divergent selection may not provide a competitive advantage, the same with regard to initial diversification.

Schluter and McPhail (1993)- Review- In northern hemisphere fish (sticklebacks), which have evolved in lakes, fish taxa have evolved variation in size and shape but partition lake resources in a very consistent way.

Rice et al., (2009)- Parallel character displacement found in spadefoot toads.

Pigeon et al., (1997)- Parallel character displacement- Lake whitefish

Taylor et al. (1996)- Genetic evidence for parallel life-history evolution and adaptive radiation in salmonids- selection against hybrids.

Schluter et al. (2004)- Genetic and phenotypic parallel evolution in sticklebacks- number of bony lateral plates, body shape. Same QTL’s involves across populations.

Pfennig and Pfennig (2005)- Spadefoot toad species (*Spea multiplicata* and *Spea bombifrons*). *S. multiplicata* benefit by avoiding competition and mating interactions with *S. bom-bifrons* but at a cost in terms of offspring survival and reduced female fecundity. Trade-offs associated with ecological character displacement.

Ingley et al. (2016)- Trade-offs between speed and endurance in freshwater fish (*Brachyrhaphis*).

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Zhang et al (2009)- *Pseudomonas fluorescens* is a gamma proteobacteria which has three colonial morphs/phenotypes, each of which is adapted to exploit a particular niche- smooth morphs (SM) which occupy the liquid phase of the medium; wrinkly spreaders (WS) which produce and release polysaccharides in order to form a biofilm layer at the liquid/atmospheric barrier, thus allowing them to better metabolise oxygen; and fuzzy spreaders (FS) which occupy the bottom. The maintenance of cooperative behaviour in WS is supported by kin selected theory as individuals tend to form biofilms with daughter cells. SM have been reported to invade and exploit the cooperative behaviour of WS, without having to produce the costly polymers needed to form the biofilm. SM’s also impose costs to WS by weakening the structural integrity of the biofilm, making it more likely to collapse and release the WS into the anoxic environment. In this experiment, which involved exposing lines of SM and WS to contemporary, past and future lines, SM evolved to become better exploiters of WS and WS evolved to better resist SM. This work demonstrates a co-evolutionary cycle between co-operators and cheats.

Trade-off between biofilm production and cheat resistance in WS? - could have consequences for the maintenance of cooperation in WS.

How would evolution against other selection pressures e.g. interspecific competitors, affect WS/SM co-evolutionary dynamics? - In natural communities, selection pressures rarely occur in isolation

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.

This study focusses on species which have had no interactions before and so are adapting to entirely novel species- how would the introduction of migrants/other species, affect already co-evolved dynamics? E.g. Species which act as competitors for resources already exploited by pair-wise co-evolved species.

Impact on virulence? – multiple species infections increase virulence if co-evolved to sequester nutrients which are the waste products of other species. Would this be dependent on co-infection? See Alizon (2012)

**Effects of antagonistic coevolution- Phage causing population fluctuations in species X for which species Y is dependent- how would species Y respond? Would have important implications for understanding how phage therapy would impact already established bacterial communities such as within our intestines.**

Middleboe et al. (2003)- Marine bacterial lysates were used very efficiently by other bacteria thus influencing community compositions. This supports the ‘kill the winner’ hypothesis in which the most successful bacteria within a community is most affected by phage and so other bacteria benefit by reduced competition and acquisition to lysates. This helps to maintain diversity within bacterial communities.

Middleboe et al. (2001)- Interspecific competition for resources was the driving force of bacterial species diversity rather than viral lysis on specific viral strains. Phage-resistant

clones of bacterial host cells may constitute quantitatively important subpopulations of bacterial communities and (2) that the bacterial population dynamics and community composition are the result of a combination of viral lysis of specific bacterial populations and nonspecific flagellate grazing on the total bacterial assemblage.

Koskella et al (2011)- This study compared the relative fitness of populations of bacteria which had coevolved resistance to one (specialist) or multiple (generalist) phage types both with phage present and after phage was removed. There was no significant difference in fitness when coevolving with phage, which suggests that the costs of each type of resistance (e.g. broad antimicrobial peptides or CRISPR) have no overall difference in fitness cost; or that resistance to one phage facilitated resistance to other phage, potentially through the loss of particular receptors, thereby causing no further consequence to fitness. However, when grown in the absence of phage, generalist lines experienced significant fitness costs in comparison to specialist lines. This suggests that either- coevolution with multiple phage caused the build-up of multiple costly resistant genes or that decreased efficiency of selection resulted from drift and a lack of compensatory mutations. Therefore, this work would hint at fitness advantages of specialists over generalists in non-phage, competitive environments and demonstrates the context dependency of the fitness advantages of resistance.

What would the implications of co-evolution with multiple phages have with further required adaptation to abiotic components of the environment? This study used bacteria which were already adapted to their environment, but what would the need to evolve against multiple selection pressures have on overall fitness and speed of adaptation? E.g. trade-offs between adaptation to biotic and abiotic elements. This would model a circumstance of species migration to a novel environment with multiple selection pressures.

Brockhurst et al. (2007)- Migration of pathogen-free (and naïve) bacteria to a population of bacteria and phage caused changes in the rate of coevolution and different rates of migration benefited either bacteria or phage. Low and high rates of migration accelerated phage evolution by increasing the proportion of the bacterial population which was susceptible to the phage without providing enough genetic variation in the low condition to provide benefit to the bacteria. This also caused the rate of coevolution to increase as phage are usually behind bacteria in the co-evolutionary arms race. Intermediate levels of migration benefited bacteria by increasing the amount of genetic variance for selection to act upon. This demonstrates that it is the lagging species (phage) which dictates the rate of coevolution and that gene flow has implications for co-evolutionary interactions, as predicted by the geographical mosaic theory.

Betts et al. (2016)- When bacteria are coevolved against 5 different types (diversity) of bacteriophage, rapid decreases and suppression of bacterial growth was observed. However, this resulted in increased inter-phage competition, resulting in decreases in phage populations and the evolution of broad phage resistance in bacterial lines, thus facilitating rapid recovery of bacterial populations. Therefore, phage diversity did not limit the evolution of bacterial resistance to phage.

Evolution of multiple phage against multiple hosts- niche specialisation to avoid competition or attempts at broad host infection?

Gorter et al (2015)- This study investigated whether parasite host range (number of genotypes phage can infect) and population diversity of phage affected the evolution of resistance in bacteria. Host range and diversity of phage populations did not affect the likelihood of resistance evolution, there was no correlation between parasite host range and breadth of resulting host resistance and hosts were more likely to be resistant to genetically similar parasites to those they had evolved resistance to than to genetically dissimilar ones. - The lack of correlation between host range and resistance probability is likely due to the limits in the evolution of molecular resistance mechanisms as singular mutations can impose resistance by changing the structure of receptors the phage has become specialised to

- The ability of hosts and parasites to be infected by and infect similar genotypes respectively indicates hosts and parasites are not specifically matched and are aspecific to some degree

- Bacteria are therefore able to evolve resistance to phages irrespective of their coevolved history which indicates why bacterial populations do not decline indefinitely from phage and can rapidly recover

Kassen et al (2000)- Diversity peaks at intermediate productivity

* Invasibility important to understand- conservation, health, agriculture, biotechnology
* A lot of research has been dedicated to understanding the characteristics of invasive species and the invasibility of communities but the only research to date which considers the how communities can invade other communities is theoretical and hasn’t been empirically studied.
* Niche-packing hypothesis- higher levels of within-community coevolution should have greater invasion resistance. Diversity and species identity have been suggested to be important. But diversity itself does not wholly determine how well resources are used in that environment- it also depends on coevolutionary interactions between species in that community.
* Communities of microbes are constantly coalescing
* Research has shown one community typically dominates another- mechanisms unknown (some also show chimeric communities)
* Most research has been dedicated to understanding within- but not between- community dynamics- is whole-community context important when understanding individual competitive roles?
* Pseudomonas fluorescens communities

If no sig-differences:

* Coevolution in this system acts to maintain variation (frequency dependent selection)- but does not act in a continuous fashion to further reduce niche overlap in a way which is unique to pairs of coevolved morphs. Coevolution is not unique but is consistent across coevolving communities/ parallel evolution.
* Coevolution/ character displacement is limited in the extent it can reduce niche overlap. Potential trade-offs with specialism v generalism. WS needs a degree of niche overlap with SM to acquire resources in the liquid media. Schluter 2000- weak selection for further diversification/niche separation.
* The variation itself in WS and SM morphotypes is not as a direct consequence from selection pressures from the specific SM morphotypes it is coevolving with. Genetic data to back up?
* Therefore, continuous coevolution does not implicate the efficiency with which communities use resources in its environment. Initial bouts of coevolution through character displacement would however be important in increases variation- niche packing hypothesis.
* Evolution and coevolution in this system is highly repeatable despite random mutation- same functional relationship- parallel evolution- niche separation consistent. Suggests that despite the complexity of between species interactions/ genetic architecture, so long as selection pressures from that species are consistent, the resulting coevolved characters will be too. Examples of parallel coevolved features.

Positive for conservation- suggests species from fragmented populations can be reintroduced providing abiotic and biotic conditions are similar.

* What is the difference between communities which on coalescence form chimeric communities v ones which outcompete one another? Mechanism still unknown.