**Eco-evolutionary perspectives on community coalescence**

Network interactions and evolution in coalescence:

* Competition and resource use- abiotic niches
* Trophic interactions- biotic niches
* Changing conditions (disturbance, ecosystem engineers)- how will communities respond and how does evolution shape this? Communities being destabilised by x, y, z will lose in coalescence.
* Manipulating evolution to understand how within-community dynamics influence between-community dynamics

May break this down to consider microbes then macro-organisms as a structure for evidence.

Coalescence introduction

* Coalescence occurs on all scales, expected to increase with global warming, medical and technological advances. Invasive species and disease spread (negatives); cure diseases, more efficient biotechology (positives)
* Conventional invasion research focussed on singular invaders and ability of communities to resist them. Increasing interest to community coalescence and co-invasion (which can be viewed as a type of coalescence in which coalescence is occurring between an in-situ community and exotic invaders)
* Specie exist in complex species networks- types and strengths of interactions matter for stability, stability matters for success in coalescence, evolution shapes species interactions within communities, therefore altering between-community interactions.

Include competition (resource use), trophic interactions, mutualisms (for this review- any case whether one species’ fitness is positively affected by presence of another). This has implications under disturbance from abiotic and biotic change

* Review purpose- Provide an overview of interlinking mechanisms of ecology and evolution to better predict coalescence outcomes (expand on initial proposals of Rillig et al. (2015) and Tikhonov (2016)), propose methods of testing these hypotheses and indicate what the results could mean for the future

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.

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).

**Observed coalescence + applications**

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.

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.

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.

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

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

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.

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

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.

**Evolutionary and community ecology**

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.

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.

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.

Evolution of networks: broad perspectives and implications

* Species form communities of complex species interactions
* Evolution shapes these interactions in their type and intensity
* Implications of networks on coalescence poorly considered

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

Competition: Evolution of niche packing and resource use

Cohesion and community success can hinge on principles from invasional biology that (Tikhonov, 2016):

* + Species which utilise differential resources should coexist (increasing cohesion)
  + Interaction outcomes between residents/invaders or, in coalescence, between species of differing communities are determined by which species can use resources faster to outcompete the other (assuming resources are finite- if resources are in surplus, species/communities can coexist)
  + Therefore-
    - Functional diversity- increased by adaptive radiation and character displacement. Not sufficient on its own however-
    - Local adaptation- adapted to specific resource type/niche (abiotic) and to the surrounding community to reduce competition (biotic). Specific species can hold central roles to community success by covering multiple niches (species dominance/top down selection)- being a superior competitor against a number of rival species could destabilise other community and ensure own-community success

**Coexistence, stability and cohesion**

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.”

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).

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

**Resource monopolisation**

Elton (1958)- high species richness should reduce invasiveness of communities

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.’

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.

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.

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?).

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.

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.

Luo et al. (2018)- Seasonality and nitrogen availability were the best indicators of invasive species abundance, not resident diversity or phylogenetic distances within the native community. In the region, nitrogen is the predominantly limiting factor for growth and thus its increases favour fast growing invasive over native species. Invasion success was also independent of other resources (light, water ect.) and propagule pressure. Had authors not controlled for the extrinsic factors, diversity would have scaled with invasability, suggesting the D-I relationship is based on correlative biotic and abiotic factors. Increasing resident biomass is a negative predictor of invasion success, suggesting priority effects/resource monopolisation/competition reduce invasions. The lack of relationship with phylogenetic diversity suggests that this was a poor measure of niche capture in the community, contrary to other studies.

Bennett et al. (2016)- Local species richness is determined by local (site specific) environmental factors i.e. heterogenous conditions can support more species due to fewer abiotic limitations. Consequently, such conditions can not only support more native species, but also more invasive species. Therefore, comparisons between sites, based on species richness and invasability, may result in positive relationships (Fridley et al. 2007). Species completeness includes the number of species excluded from a particular site- relative species richness. Species pool size reflects the potential pool size in a habitat (ignoring environmental conditions). Results support these predictions, using plant-based systems and seed establishments- sites with larger species pools offered greater biotic resistance and completeness was sometimes positively related to invasion. No overall universal relationship between invasion and diversity. Larger species pools were more likely to contain species conferring competitive resistance to invaders. Increased completeness coincided with increased establishment of growth, contrary to hypotheses that more complete communities should exert more resistance due to being more saturated and using more resources. It suggests communities remain unsaturated and completeness is representative of increased invasibility. Site productivity (shoot and litter biomass) were important determinants of resistance.

Cerbrian et al. (2018)- Examined the relationship between resident species richness, in seaweed forests, and invasion by exotic algae species (*Lophocladia lallemandii*). A positive relationship was found between invasion success and resident species richness, consistent with theoretical hypotheses that the diversity-invasability relationship is not held at local scales. Native species are not necessarily the best exploiters of their own environment, nor are local environments entirely saturated- this means invaders can exploit unoccupied niches or better exploit residents’ niches. Increasing functional groups increase native algal abundance, facilitating Lophocladia invasion by providing multiple resources for colonisation.

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.

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

**Character displacement and adaptive radiation**

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).

Rainey & Travisano (1998)- P. fluorescens adaptive radiation into distinct morphotypes which monopolise resources differentially. Diversity maintained by negative frequency dependent selection.

Farrell (1998) hypothesized that specialisation on different angiosperm species led to the radiation of beetle species. The increase in herbivorous beetle genera correlates with the exponential increase of angiosperms beginning in the Cretaceous. Specialisation on angiosperms leads to rapid beetle speciation via coevolution. Evolutionary changes in plant host lead to incredible beetle radiations. It is important to note that this same pattern is observed in five different clades, indicating that the change in host type is driving this pattern.

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.

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

Ellis et al. (2015)- Character displacement in *Burkholderia cenocepacia* ecotypes within a biofilm system. Reduces competition to reach a stable equilibrium of coexistence.

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 (2000)- Pairs of stickleback species are found in several lakes. In each case one of the species is limnetic, foraging primarily on zooplankton in the water column, and the other is benthic, foraging on invertebrates in the sediments or clinging to vegetation. Solitary species are an intermediate form of the limnetic and benthic sticklebacks which feed on both zooplankton and invertebrates. The species pairs was the result of two colonisation events- the first causing intermediary forms, as observed in the solitary lake, and the second pushing the first species towards a more benthic lifestyle. The second species stayed more similar to its marine ancestor and adopted the limnetic lifestyle. Experiments were conducted with intermediary forms, showing that the addition of competitors caused character displacement and thus a reduction in completion (increase in growth rates). In particular, the addition of zooplanktivores favours benthic forms in the competing population. This was also shown to be frequency dependent with the addition of competitors (benthic or limnetics) causing reduced growth within the competitors and increased the growth rate of sympatric species. This demonstrates that character displacement is an adaptive change for escaping competition.

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.

Stuart et al. (2014)- Examined lizard populations of *Anolis carolinensis* for evidence of character displacement following invasion by *Anolis sagrei*. *A. sagrei* were introduced to three islands off the coast of Florida, which had resident populations of *A. carolinensis.* Perch height increased for *A. carolinensis* and this corresponded to larger toepads and more lamellae- allowing for better adhesion and grip. This morphological change occurred over 20 generations. Clear example of resource dependent character displacement. Alternative hypothesis were ruled out:

* Eggs were taken and reared in isolation of environment (garden experiment)- traits persisted showing a genetic linkage
* Migration of larger-toepad individuals (non-independent character divergence)- relatedness within islands was significantly greater than relatedness between islands which suggests limited gene flow
* Environmental differences- islands did not differ significantly in vegetated area, plant species richness, tree height ect. Which would have resorted in changes in mobility
* Ecological sorting- no differences between invaded populations. *A. sagrei* capable of invading every island

Grant and Grant (2006)- Character displacement was observed in Darwin’s finches (*G.fortis*) in 2004-2005 due to competition with *G.magnirostris*. During a period of drought, *G.magnirostris* specialised on *Tribulus* seeds which are not renewed during drought and can be consumed faster by *G.magnirostris* than *G.fortis*. This resulted in large-beaked *G.fortis* evolving smaller beaks to exploit mericaps, which larger beaked *G.fortis* and *G.magnirostris* cannot break into, thus giving them a selective advantage.

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.

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)

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.

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.

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

**Local adaptation and roles of specific species**

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

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

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.

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.

Gomez et al. (2016)- Preadaptation of P. fluorescens to soil microcosm before adding to soil community reduces soil community density

Trophic interactions

* How evolution with trophic levels affects community coalescence is determined by how trophic levels influence:
  + Functional diversity within a trophic level, and consequent resource use efficiency
  + Local adaptation towards hosts/parasites/predators- i.e. infectivity/ resistance towards sympatric versus allopatric populations.
    - And costs of coevolution i.e. competitive ability
  + Effects of trophic levels on overall community stability
* Understanding of trophic level interactions within communities is poor- consequently, a lot to be investigated on how trophic levels influence coalescence

Loeuille (2010)- May (1978) challenged Elton’s (1958) hypothesis that diversity promotes stability within communities. This paper models the effect of evolution on the diversity-stability relationship, finding that evolution decreases community stability at high levels of diversity, irrespective of interaction types or the costs of mutations. Trophic interactions are suggested to improve community stability, coinciding with other model findings’, but this effect decreases at high levels of diversity, thus preventing any stabilising effects. Similarly, mutualistic interactions are stabilising at low diversities but destabilising at high diversities. Thus, evolution stabilises dynamics within low-diversity communities for a variety of interaction dynamics, but this becomes destabilising at higher (more naturalistic) diversity levels.

Greischar & Koskella (2007)- Meta-analysis and review of parasite local adaptation. Consistent with view that parasites are ahead in coevolutionary cycles, 18 studies found evidence of parasite local adaptation and only 6 showed maladaptation. However, geographic distances varied alongside between-population comparisons, having implications for the validity of these studies. Very difficult to generalise host-pathogen coevolution across systems. High levels of migration, expected to homogenise populations whereas low-intermediate levels can facilitate local adaptation by increasing genomic variation on which selection can act. Results- highly migratory parasites more likely to be locally adapted. Generation time- low effect on local adaptation as parasites are ahead in cycle and track host genotypes regardless.

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.

Caronni et al. (2015)- Presence of a herbivore may increase invasibility by depleting native producers and freeing resources (this is assuming that the herbivore cannot eat the invader- at which point, local adaptation is important). Experimentally manipulated degradation by mimicking fish grazing in seagrass beds to test effect of trophic levels on invasion by invasive alga. Destruction of seagrass only increased invasion when areas were excluded from herbivores, showing that herbivory is not exclusive to natives- they can slow spread of invaders as well.

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.

Friman & Buckling (2013)- host/parasite/predator coevolution changes in community context in which all three are present. Coevolution influenced by community networks/trophic interactions

Friman & Buckling (2014)- Presence of phage and protists is hypothesised to increase evolution of bacterial virulence e.g. by selecting for public-goods production. Evidence remains ambiguous. Conflicting evidence also suggests that, for example, phage decrease bacteria virulence by slowing growth. Results- protists decreased virulence of P. aeruginosa due to pleiotropy in growth rate. Phage dampened this effect by reducing bacterial population sizes, thus limiting protist population size and consequential selection on bacteria. Phage alone did not directly influence bacterial virulence

Buckling et al. (2006)- Resistance to phage has growth costs in P. fluorescens via nutrient uptake pathways (surface modification).

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.

Mutualisms

* Can be important for resistance of invading species and communities
* But finicky- loss of one species leaves the other vulnerable e.g. loss of gut microbiome mutualists leaves human host susceptible to infection of C. difficle. Reintroduction of complex community only viable treatment as that contains (most) network interactions intact

King et al. (2016)- Examined evolutionary responses of resident microbe (Enterococcus faecalis) in the host (C. elegans) against the pathogen, S. aureus. Interactions between commensal and parasitic bacterium selected for defensive traits in the commensal bacterium, irrespective of host mortality- increased host survivorship was a by-product. E. faecalis also maintained mildly pathogenic effects against the host, demonstrating that it’s fitness effects are context dependent and of net benefit during a parasitic infection. Mechanistically, E. faecalis rapidly evolved increased activity of the superoxide production pathway

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

Murall et al. (2017)- Tilman (1999) used Elton’s (1958) hypothesis of invasion resistance to generate models of the D-I relationship regarding increased diversity leading to increased resource/niche use, thus conferring invasion resistance. However, weak interactions within resident communities are arguably greater stabilisers of communities, rather than diversity (McCann, 2011). Thus, invaders with high growth rates, and low mortality, are likely to be unaffected by diversity. Mutualistic networks between the host immune system and resident microbiota species can prevent invasion- e.g. S. epidermidis interacts with host keratinocytes to inhibit pathogenic S. aureus by triggering production of antimicrobial peptides by KCs; S. epidermidis also produces phenol-soluble modulins to improve AMP efficiency and signal to KCs to improve their cellular repair during infection (Grice and Segre, 2011).

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.

Disturbance

* Abiotic environment is changing due to extrinsic factors
* Species evolve under abiotic environment- in constant environments, local adaptation likely. Disturbance environment, species adapt to regimes.
  + Communities locally adapted to specific conditions less likely to be successful- this effect is exemplified under trophic cascades (i.e. x depends on y, x falls, y falls. So coalescence brought by disturbance into new environment- past evolution matters.
* How evolution could influence community success under environmental change:
  + Disturbance can increase niche space/resource availability so community most niche-packed (link back to first section) will monopolise resources faster
  + Evolution increases mutualistic networks so under changing conditions this will likely cause community destabilisation.

Mutualisms mean invasion of species x is dependent on invasion of species y so if species x fitness is hampered by natives or non-optimal conditions, species y can’t invade. If either species is absent during coalescence, the other can’t invade.

* + However, if a community evolves under stress- less likely to form mutualistic networks (not favoured) and adaptations to multiple niches selected (generalist traits)- disturbance history shapes community evolution and stability under coalescence
* Species, and their communities, shape their environment (biotic disturbance). On the opposing side, invaders can shape ecosystems/communities e.g. soil legacies, toxin production, pathogen build up ect. This can push conditions in favour for whatever community is adapted to if not resilient to change.

**Evolution to ecosystems- local adaptation (section introduction)**

Macel et al. (2007)- Simultaneously tested soil versus climate local adaptation. Grass and legume chosen- legume has symbiotic nitrogen-fixing bacteria in rhizosphere. Grasses- negative feedback interactions with their rhizosphere community due to pathogen-build up (can negatively affect other grass species). Evidence of climate adaptation in soil species. Genomic differentiation and differential responses of legumes to soil and climate conditions but no clear pattern. Climate and soil interacted on measures of plant responses. No evidence of soil adaptation- could be due to design.

**Disturbance and community responses**

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.

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.

Koerner et al. (2015)- Fluctuating resource hypothesis- when resources exceed consumed by community, invasiveness increases. Longitudinal invasional study in context of climate change experiment- manipulating precipitation regimes to increase variability of rainfall and water availability. Plant based study. Controlled invader identity and propagule pressure. Larger pulses in rainfall did not increase invasion success by establishment or persistence-in years where significant, invasion was significantly lower. Thus, time between rainfall altered invasibility more than number of rainfall events. More diverse and dense native communities had higher invasibility- factors favouring higher diversity/density favour invasion or community alleviates stressful conditions (temperatures, moisture). Invasion success was greatest in years of highest resource availability- independent of variability.

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.

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.

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.

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.

**Ecosystem engineering**

Hufbauer et al. (2011)- Invader local adaptation can impact invasion success e.g. to a particular disturbance regime, stable environment (Lee and Gelembiuk, 2008). Human-altered habitats may pre-adapt species to specific conditions, allowing them to invade similar environments across space and time- termed Anthropogenically-induced adaptation to invade (AIAI). Humans homogenise habitats in agriculture, transportation systems, forestry and urbanisation, as examples. As environments become more homogenised, it will be an evolutionary advantage to be adapted to said environments for both local fitness and to invade other environments when dispersing- this will contribute to biotic homogenisation, in addition to active anthropomorphic abiotic homogenisation.

Lee and Gelembiuk (2008)- disturbance regimes may select for traits in species which promote invasability e.g. growth/reproductive rate, evolvability (mutation, recombination rates), phenotypic plasticity, generalist phenotypes

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. This is hypotheissed to be resulting from coevolution. Links to species dominance (below)

Vaginal microbes lower pH of environment which prevents bacterial and viral colonisation (Danielsson et al. 2011); and resident microbes (in a nematode model) produce bacteriotoxins which kill S. aureus (King et al. 2016).

Clause et al. (2016)- Evidence suggesting that worms alter soil properties and ingest non-native plant seeds which promote their germination over native plants- thus favouring co-invasion.

Altieri et al. (2010)- Native cordgrass and ribbed muscles cause a facilitation cascade which increases native biodiversity and invasion success of the Asian shore crab in New England, by ameliorating light intensity and wave stresses. Therefore, stress alleviation by foundation species generates conditions both favourable to diversity and invasion, thus creating a positive diversity and invasion relationship.

Bassar et al. (2010)- Species can alter ecosystem function. This can create ecological and evolutionary feedback loops which reciprocally influence one another. Presence of predators shapes how guppies evolve and consequently how they shape their environment. Predation selects for smaller guppy size and reduces overall guppy abundance and biomass. Life history traits shift towards earlier maturity and production of more offspring. These changed increase per-capita food availability.

Common garden experiment. Treatments- high and low predation. Measured guppy evolutionary responses to predation and their impact on ecosystem structure (algae, invertebrate, detrital standing stocks) and function (gross primary productivity, community respiration, leaf decomposition, nutrient flux). HP guppies- higher algae standing stocks, higher area-specific GPP, lower biomass-specific primary productivity, lower invertebrate standing stocks, lower leaf decomposition rates. HP guppies more food selective. More ammonia secretion at low densities.

Evolution and ecology occur on similar timescales to impact ecosystem functioning.

Newbold et al. (2015)- The worst affected areas of human land use had a reduced species richness of 76.5%, abundance by 39.5% and rarefaction-based richness by 40.3%. (see above study for further stats). McGill (2015)- Article of Newbold paper- Over the past 500 years, human land use has caused species richness to decline within small plots of land by 8.1% when averaged across the globe, alongside a 10.7% decline in individual organisms. Greatest negative impacts came from the introduction of cropland and pasture. Biodiversity is further estimated to be reduced by 3.4% in the next 100 years. Potential publication bias as positive effects are less likely to be published, although not expected to impede the results greatly. Also potential bias as land which was previously forest or grassland was not distinguished. Regardless, below study is best empirical database on the effects of land use on biodiversity.

Future perspectives

**Global warming**

Dossena et al. (2012)- Increasing temperatures can fasten the emergence of aquatic invertebrates and increase total flux of organisms from aquatic to terrestrial environments. Temperature can therefore affect benthic community size and structure which is driven by the effects of temperature on metabolism and species interactions. This study suggests that the rising temperatures of global warming can alter the structure and functioning of aquatic ecosystems. Increasing temperatures affected size structure of benthic communities but did not affect diversity or evenness. Higher trophic levels were met with decreasing biomass as a consequence of the link between trophic level and body mass, and metabolic rate and temperature. Therefore, as temperatures rise so do metabolic rates which can only be supported if resources increase- consequently larger organisms decrease due to resource limitation. This has consequences for predator-prey interactions.

Friberg et al. (2009)- Temperature was found to affect both macroinvertebrate community structure and diversity. Taxa richness was constant across temperature gradient with declines in evenness and species overlap with increasing temperatures. However, this may be partially due to the fact that Iceland is relatively young. Filter feeder numbers increased with temperature which corresponded with increases in *Simulium vittatum*. Scrapers were the dominant feeding group but were not affected by temperature. Leaf decomposition was correlated with temperature which reflects higher microbial activity. Nutrient loading was suggested to increase with temperature which would make freshwater ecosystems more susceptible to eutrophication.

O’Gorman et al. (2012)- The effects on global warming are difficult to predict because it operates on large spatiotemporal scales and interactions with multiple anthropogenic stressors. Short term effects include acclimation of physiological or behavioural traits whereas long term effects include changes in body size distributions, local extinctions and invasions as well as eventual evolutionary adaptation. Icelandic streams are ideal study sites for studying the effects of global warming whilst controlling for environmental and geographical gradients- ‘natural global warming experiment’. Body size of organisms are expected to change, via adaptation or range shifts, as organisms tend to be larger in colder climates (Jame’s rule). Warming could also shift community compositions to favouring smaller species, giving them a competitive advantage. Species living at their thermal limits are likely to be driven extinct at rising temperatures whereas species which are more eurythermal could expand range. These changes are likely to have cascading effects through ecosystems.

Metabolic rate increases exponentially with temperature, so when combined with reduced body sizes (which have greater mass specific metabolic rates), energy demand of communities are set to increase. Starvation risk increases as ingestion efficiencies and energetic efficiencies decrease. Increased metabolic rates are likely to impact energy transfer throughout food webs. Faster decomposition could release stored organic carbon which could influence nutrient cycling and fluxes, as well as carbon emissions if it is released as a greenhouse gas.

They observed changes in biomass of some key species, indicating changes in trophic biomass pyramids. Rising temperatures reduced the similarity of macroinvertebrate and meiofaunal assemblages. It additionally simplified food web structure with reduced trophic transfer efficiency. All ecosystem process rates increased asymmetrically.

Support for Jame’s rule was limited with macroinvertebrate showing some deceases in body size with temperature but most showed no change.

Diet breadth of trout increase with temperature and body size. This led to an increase in similarity of diet with prey availability in warmer streams. As larger trout should be faster and more adept at spotting prey, activity and encounter rates are set to increase with temperature. Heightened metabolic rates may force trout to undertake a generalist lifestyle which may contribute to the reduced diversity and simplicity of food webs with temperature.

Warmer food webs were less complex with fewer species and feeding links and a lower linkage density and connectance.

Biofilm respiration rates increased with temperature regardless of whether they were from cold or warm streams. Temperature dependence for respiration rate was found to be consistent among biofilm assemblages from different streams. Biofilms consist of autotropic organisms such as green algae, cyanobacteria and diatoms, as well as heterotrophs such as ciliates and meiofauna.