Co-selection paper notes

Species can interact to increase functionality or growth of another. In ecological selective processes e.g. invasion, this can result in co-selection. Possible ecological and evolutionary mechanisms (note: some interact and overlap):

* Co-evolution (niche-partitioning; see other notes)
* Cross-feeding
* Local adaptation
* Priority effects (see other notes)- inhibitive or facultative
* Ecosystem engineering
* Trophic complexity- parasites, predators

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).

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.

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.

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.

Ames et al. (1991)- Study on effectiveness of rhizobia on cowpea growth in presence of vescular-arbuscular mycorrhizal (VAM) fungi in sterilised and non-sterilised soil. Cowpea growth was inhibited in sterilised soils, irrespective of rhizobia and VAM pairing. In non-sterilised soils, two rhizobia sp. significantly improved cowpea growth, especially when paired with VAM, *Glomus pallidum*.

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.

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

Faust & Raes (2012)- Microorganisms exist in complex communities of positive, negative or neutral interactions. Mutualism- both species benefit. Commensalism- one species benefits without helping or harming the other species. Cross-feeding aka syntrophy. Amensalism- one species harms another without direct benefit to self-e.g. metabolic by-products, pH, toxins. Interpretation of the ecological relevance of these relationships is far from easy. For instance, a positive relationship can be due to cross-feeding, co-aggregation in biofilms, co-colonization, niche overlap or other reasons, whereas a negative relationship may result from amensalism, a prey–predator relationship, competition, and so on. In addition, relationships can be time-lagged (for example, if one species increases its abundance at a certain moment, another species might only disappear at a later time). Multiple regression techniques can illuminate complex network relationships outside of pairwise combinations by tracking species abundances with change of other species’.

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?).

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.

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.

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

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

Barthell et al. (2001)- Studied role of invasive honeybees in establishment of invasive yellow star-thistle (*Cebtaurea solstitialis*). Honeybees were dominant visitors, in contrast to other pollinators. Seed set numbers increased in treatments which facilitated largest honeybee visitation rates, whilst exclusion of honeybees decreased seed set rates.

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.

Groscholz (2005)- Introduced crab species preferentially predates on native clams and facilitates the historic (50 yr) population expansion of an invasive clam species.

Ren et al. (2013)- This study investigated synergy of *Pseudomonas lutea, Ochrobactrum rhizosphaerae, Arthrobacter nitroguajacolicus, S. rhizophilia, Xanthomonas retroflexus, Microbacterium oxydans* and *Paenibacillus amylolyticus.*

*S. rhizophila, X. retroflexus, M. oxydans* and *P. amylolyticu* showed high biofilm synergy, increasing biofilm biomass by 300% when growth together versus in isolation.

Uses qPCR as a method of quantifying bacterial growth and interactions.

Ren et al. (2015)- Follow up study showed that the four species community biofilms were dominated by X. retroflexus but the abundance of said species, and other species in the community, is dependent on the presence of others- weak growth in monoculture or lower diversities. Therefore, high synergy is achieved in these biofilms via cooperative mechanisms. This is suggested to be in accordance with the ‘Black Queen’ hypothesis in which bacteria increase co-dependency due to loss of trait functions- in this case, bacteria may form multispecies biofilms to ‘group together’ to cooperate or biofilm formation could be lost in some species. “The key to whether bacterial species compete or cooperate may lie in their potential for long-term coadaptation and degree of niche overlap.” Potential evolution between bacteria hypothesised.

Rigg et al. (2016)- Symbiotic and pathogen microbes are essential for plant communities and individual success. ‘Manipulation of microbial communities has been used in a wide variety of restoration and rehabilitation projects to promote success (Jasper 2007; Eviner and Hawkes 2008; Zoë et al. 2009). For example, inoculation of a critically endangered orchid with a mycorrhizal fungus prior to translocation improved success (Zoë et al. 2009).’ This generates coalescence events between translocated and native microbial communities.

Growth and condition of the Wollemi pine was independent of resident microbiota during translocation. Resident microbiomes were structured by soil properties, vegetation composition and light gradients. Wollemi pine altered bacterial communities over time in soil and roots and maintained a distinct fungi community within its soil and roots from the surrounding environment.

Rúa et al. (2016)- Conifers and mycorrhizal fungi are hypothesised to have co-diversified 200 million years ago and now form obligate mutualisms. Plants exchange carbon for nitrogen, phosphorus and micronutrients from the fungi. Needles of conifers are heavily colonised by needle bacterial endophytes (microorganisms living within plants). Results suggest relationships between specific ectomycorrhizal fungi and bacterial endophyte communities- fungi Cortinarius I was significant in structuring the endophyte community, along with fungi Sarcosphaera whose importance had a negative correlation with Cortinarius (one important and the other not depending on environmental conditions). The evolutionary implications of these ecological interactions would be an interesting avenue of future research.