Diversity-Invasability Relationship: An Eco-Evolutionary Perspective

May cut to just considering eco-evo perspectives (rather than have diversity as a running theme- can be interjected?). Maybe something to discuss with Angus.

Structuring should be resident-community centric, as the D-I relationship is. Invader effects, with respect to diversity, will become more apparent when discussing future perspectives- coalescence ect.

Review purpose:

* Summarise evidence for and against the D-I relationship and suggest why evidence is inconsistent
* Combine ecological and evolutionary theory to explain why some communities and more or less invasable- linking this back to whether these theories coincide with diversity e.g. adaptive radiation increases niche packing, resource use and reduces niche opportunity by increasing diversity
* Provide future perspectives on how changing environmental conditions may alter invasion across the globe

Introduction:

* Background to invasion- invasive species, species movement (range shifts), micro-macro scales, past and future perspectives.
* Changing environmental conditions and mass biodiversity losses in recent years and projected into the future

No review done on D-I relationship since 1999- continued biodiversity loss, increased threats of invasion. New evidence for invasion from evolutionary perspectives.

* What is the D-I relationship? General idea why invasability is expected to decrease with increasing diversity
* Mixed evidence
* Evolutionary perspectives only recently begun to be considered- eco-evo dynamics of invasability are strong influences
* Define what invasion means for the purpose of this review- can be novel species or growth of dormant species (particularly for microbes)- Kimmunen et al. 2016

P1- Resource/niche use:

* How invaders and residents use resources/niches can determine invasability
* More diverse communities more likely to contain species which use same niches as invader. Species diversify (evolve) to fill niches (adaptive radiation, character displacement)- evolution and ecology correlate (diversity as a product of evolution).

-> interlink with species dominance here (why D-I relationship not always found- surrounding diversity redundant e.g. WS).

* However- Monopolisation of said resources depends on resource availability and invader species growth rate/competitive ability (e.g. red lionfish). When one species is key to invasion resistance (shared niche), an invader’s success will depend on being able to sequester resources faster to outcompete the resident.

Residents usually have an advantage through numbers (priority effect/monopolisation) but this can change…

* Disturbance can open niches/increase resource availability, making communities more invasable.
  + Increasing resources can remove correlate of diversity and invasability
  + Resident and invader success will be determined by resistance (evolution) to disturbance (e.g. antibiotics/ antibiotic resistance)

Case example- Clostridium difficile infections are kept under check by gut microbiome (resident advantage) but antibiotics deplete the microbiome, increasing resource availability and favouring antibiotic resistant species. C. difficile is antibiotic resistant (spores) and so can invade. This can prevent microbiome recovery without faecal transplant (re-establish resident diversity/advantage).

* Residents locally adapted (evolution) to their environment are more likely to sequester resources faster than an invader; filling up niches before invaders can dominate
* Section conclusion: diversity expected to scale with invasability under stable, disturbance free communities. Adaptation strong determinant of invasion success under variable conditions

P2- Niche modification/Ecosystem engineering

* How residents not only change niche availability but also ecosystem conditions (biotic and abiotic factors) can determine invasion success
* This is independent of diversity as it is strongly dependent on constituent species-> interlink with species dominance here (why D-I relationship not always found- surrounding diversity redundant if one species is main modifier/engineer)
* Effects can go both ways- invasion facilitation or resistance
  + Abiotic conditions- toxin production, pH change, oxygen levels, river flow, soil modification (pH, nutrients, toxins, oxygen, water)
  + Biotic conditions- suppression of competitors, pathogen build-up, public-goods
* Invaders can also alter environmental conditions, to the detriment or success of residents
* Adaptation- generalist species favoured (consistent with theory and invasive species traits) over specialist invaders as specialists are less likely to be adapted to resident conditions.
  + Locally adapted residents more likely to resist invaders unless invaders change local conditions (favouring invaders). Under change, generalist residents more favoured
* Conclusion: Whilst more diverse communities are more likely to shape their ecosystem in more dramatic ways, as a result of combined efforts, the direction this has on invasability depends strongly on constituent species effects and invader identity (plus invader effects). Under changing conditions, generalist species favoured and local adaptation could hinder residents if invaders modify niches

P3- Phylogenetic structure

* This links to community resource use and dominant/species ID- phylogenetic distances within a community mean species are more likely to use differing resources/niches which provides community stability (stable abundance of below)
* Whereas phylogenetic overlap (see Pseudomonas paper) between resident and invaders means resident communities are more likely to exclude invaders
  + Diversity- another correlative metric- more diverse comms more likely to cover more niche space and hold species phylogenetically close to invaders
  + Evolution- Within-community evolution can increase phylogenetic distance (character displacement/ adaptive radiation). Extents of allopatry (migration/gene flow) and ecological timescales are likely to interact here.

P4- Networks (i) Ecology

*Resident community:*

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

*Co-invasion:*

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

P5- Networks (ii) Evolution

* Long-term coevolution is hypothesised to increase mutualistic networks in communities (+/+), potentially increasing invasability by decreasing stability under change (increasing co-dependence)
* Local adaptation with antagonists (e.g. parasites) can increase competitive ability of invaders/residents

P6- Future perspectives

* Research: towards community coalescence. The above arguments yet to be tested in coalescence. Scaling of single to multi-invasion studies of testing and re-testing the above relationships.

Niche-packing hypothesis- potential scale of diversity with community success but coupled with evolution i.e. local adaptation, adaptive radiation, character displacement

* Ecology: Global climate change increasing invasion incidents. Predictions for the favour of generalist species over specialist due to selection against local adaptation. Biodiversity losses expected to continue #bleak

P7- Conclusion