Summary:

The primary aim of these notes is to summarize the grouping of coexistence mechanisms that we are hoping to apply during the workshop. These are largely based on the grouping from Palmer, 1994 (citation below), with some additional categories based on some more recent research. These are obviously not the only way to group coexistence mechanisms, but they seem to span a wide range of potential topics.

Note that I will use the terms "coexistence" and "persistence" interchangeably. "Persistence" here refers not to the consistent provisioning of particular ecosystem functions, but rather to the persistence of a particular arrangement of species (either in terms of fixed abundances, or at least bounded dynamics). These arrangements may not be "stable" in the strict sense (e.g. infinite persistence time, 100% probability of recovery from small perturbations), but rather refer to persistence over very long timespans.

Categories of coexistence mechanisms

Below, I briefly summarize the major categories of coexistence mechanisms that have been hypothesized in the existing literature. Rather than listing hundreds of "named hypotheses", I follow the methods of Palmer (1994), and list the general classes of mechanisms that are thought to be able to lead to competitive exclusion of all but one species. I have also expanded the Palmer framework somewhat to include some addition classes of mechanisms that were out of scope for the original review.

1. Proposed hierarchy from Palmer 1994

The following is a list of mechanisms posited by Palmer (1994) to be capable of violating Gause's competitive exclusion principle. Palmer suggests that any of these mechanisms can therefore lead to multi-species coexistence. Below each mechanism, I have included some basic information about how these mechanisms have been further sub-divided in the literature. Note that following Wright (2002), I have combined spatial and temporal heterogeneity into a single category.

Insufficient time for exclusion:

This category basically serves as a "null" for the remaining mechanisms, and is effectively defined as a case where the other mechanisms do not apply. Thus, it might be more appropriate to not list this as a "coexistence" mechanism, so much as a measure of the time that it takes for an unstable community to disassemble.

This hypothesis effectively encompasses any mechanism whereby transient dynamics lead to coexistence over observed temporal scales. Such transient coexistence are generally temporary, but can be long-lasting (e.g. the "gradual change hypothesis", or "alternate transient states") (Wilson 1990; Fukami & Nakajima 2011).

The primary insight behind this mechanism is that demographic stochasticity typically takes a very long time to drive species extinct, especially when initial population sizes are large (e.g.

centuries or millennia) (May 1973). This is also why Hubbell's neutral model can "appear" stable over small spatial and temporal scales (i.e. stochastic drift in population sizes only emerges over long time scales, while stability is typically measured as an instantaneous response) (Fig. 1) (Hubbell 2001).

Importantly, most mechanisms that have historically been placed in this category are actually a mixture of several mechanisms. For example, Hubbell's model retains an equilibrium number of species through a combination of *insufficient time* and *speciation*. Similarly, Connell's intermediate disturbance hypothesis (Connell 1978) can only explain long-term persistence of a community if rare species are disproportionately favored by disturbance (e.g. because of nonlinear growth responses, or unequal per-capita effects of the disturbance across species), which falls under the provenance of *negative density dependence* (Chesson & Huntly 1997; Fox 2013; Sheil & Burslem 2013).

Temporal and spatial heterogeneity:

Temporal and spatial heterogeneity are frequently invoked as potential drivers of coexistence. While these mechanisms have been rigorously studied in ecological theory, empirical studies are comparatively rare.

In general, theoretical models of spatial and temporal heterogeneity outline two broad types of mechanisms: *exogenous*, where a particular pattern in the environment such as a gradient in resource availability leads to heterogeneity, and *endogenous*, where species effects on their environment create heterogeneity in an otherwise homogeneous space or time series. This division is discussed at length in Amarasekare (2003). Models are also generally broken into *implicit* and *explicit* models, though this division is more common in spatial than in temporal systems.

For temporal heterogeneity, the most widely-used source is Chesson (1994). The model uses pairwise competition theory to show that coexistence via temporal heterogeneity requires one of two mechanisms: *relative nonlinearity* in species growth rates, or *temporal storage* caused by covariance between effects of competition and environment on species (note that while the proof appears to be for a multi-species system, the conditions that the proof meets are in fact based on the ability to invade when rare). Nevertheless, the model appears to be quite general, and may apply in diverse systems (though I have found no test of this assumption in the existing literature).

Importantly, Armstrong & McGehee (1980) demonstrate that temporal heterogeneity can arise endogenously in many systems. This can lead to potentially confusing results – e.g. a model with a single dynamic resource can sustain many species at equilibrium, e.g. due to relative nonlinearity in species growth responses to resource availability.

For spatial heterogeneity, the most widely-cited source is likewise Chesson (2000). This paper decomposes drivers of spatial coexistence into three components: *relative nonlinearity* and *spatial storage* (which are directly comparable to their temporal analogs) and *covariance between growth rate and population density* (which has no temporal analog – though I must admit I'm not entirely sure why). Note, however, that this proof is also based on species abilities to invade when rare, and may therefore not apply in more diverse systems. Furthermore, Chesson uses a second-order Taylor series approximation of a spatially implicit model to derive this decomposition, which makes it unclear how general this method is (i.e. a second-order Taylor series expansion can only have three independent components).

Similar to the findings of Armstrong & McGehee, Bolker & Pacala (1999) used spatial moment models to demonstrate how endogenous heterogeneity can lead to coexistence. They break spatial coexistence into tradeoffs among three types of strategies: *competitive ability*, *dispersal ability*, and *exploitation ability* (i.e. rapid uptake of resources within a single site). Note that these are roughly comparable to Chesson's methods, and closely match Grime's strategy "triangle" (Grime 1974).

Multiple limiting resources:

There has been substantial theoretical and empirical work on resource limitation, primarily focusing on variants of Tilman's resource ratio theory (Tilman 1982; Miller *et al.* 2005). Though "classic" theoretical understanding suggests that n limiting resources can only support n coexisting species (Levin 1970), this rule has been shown to be easily violated given many different combinations of mechanisms (e.g. resources plus temporal or spatial heterogeneity) (Armstrong & McGehee 1980; Tilman 1982). Problematically, it can often be difficult to separate these mechanisms even in theoretical models (e.g. in systems with endogenous temporal heterogeneity). As such, most models of resource competition necessarily bleed into some of the other categories of mechanisms discussed here.

As far as I know, a major existing limitation to theoretical studies of resource competition is that there is no "standard" model for multiple resource limitation. For example, Tilman's resource ratio model has simple graphical solutions for systems with two limiting resources, but more complex analytical solutions are required for systems with three or more limiting resources.

In contrast, empirical studies relating to effects of multiple resources are relatively well-developed. These often show that adding excess quantities of limiting resources leads to species loss, and that adding multiple resources leads to the loss of additional species (Harpole & Tilman 2007; Harpole *et al.* 2016). Similarly, experimental addition of multiple resources often has interactive effects on community biomass (i.e. "non-additive" effects of resource addition) (Elser *et al.* 2007). Note, however, that these responses vary by system, and may be more prevalent in terrestrial than marine and aquatic ecosystems (Hillebrand *et al.* 2007).

Negative density dependence:

For our workshop, we are hoping to subsume this category into the other mechanisms, as many of the mechanism listed above lead to negative density dependence in one form or another. However, because it is listed in Palmer (1994), we also discuss it here.

This category refers broadly to any mechanisms that favor rare species over common species. It is therefore somewhat tautological, as it seems likely that negative density dependence is a necessary characteristic of a bounded population, which is a necessary characteristic of stable coexistence (Murdoch 1994).

Mechanisms categorized as *negative density dependence* in other reviews generally fall the "new" categories described in the next section – e.g. Janzen-Connell effects and plant soil feedbacks (Mills & Bever 1998; Wright 2002), which are arguably the result of *multi-species/multi-trophic* interactions. A potential reason for this is that, by his own admission, Palmer does not attempt to address multi-trophic interactions in his review.

I can think of two kinds of mechanisms that might be sufficiently distinct to warrant keeping this category. First, it can be a useful catch-all for mechanism that favor rare species, but for which the precise reason for this favoring is unknown (e.g. observation of depressed recruitment around conspecific adults) (Detto & Muller-Landau 2013). Second, some self-limiting mechanisms are arguably entirely endogenous. For example, in "cyclical succession", common species alter their environments in ways that favor rare competitors, leading stable cycles of coexistence (Wilson 1990). Again, however, if the precise mechanism behind these cycles is identified, then it could likely placed into a different category as well – e.g. manipulation of resource supply through niche construction (Kylafis & Loreau 2011).

Dispersal:

This category is primarily subsumed into the metacommunity framework that we will be discussing. Again, however, we include it here as one of the original mechanisms posited in Palmer (1994).

This category captures a wide variety of mechanisms, most of which rely on some sort of spatial heterogeneity (either in environmental conditions or in species compositions). As such, specific requirements for coexistence are probably similar to those that have been more rigorously developed for spatial heterogeneity.

In general, coexistence via dispersal can include four kinds of mechanisms (Leibold *et al.* 2004) (n.b. excluding *neutral* mechanisms, which I have sorted into other categories, and separately considering spatially implicit mechanisms). Note that metapopulation and metacommunity models can span the full range of these.

Fist, *mass-effect mechanisms* (e.g. global/local species pool models) assume that local community composition (or, more frequently, local community richness) is controlled primarily by a steady influx of immigrants from some outside pool. In general, these models assume that the local pool does not directly affect the global pool (MacArthur & Wilson 1967; Fukami & Nakajima 2011).

Second, *structurally-specific mechanisms* (e.g. patch dynamic models) allow for coexistence because of a specific arrangement of sites or environmental features. For example, coexistence under such a mechanism might depend on the precise probability of dispersal among discrete habitat patches (Hanski 1994). These sorts of mechanisms have been rigorously studied in some experimental systems (e.g. Huffaker 1958), and are often applied for site-specific models, e.g. for conservation work (Hanski & Thomas 1994).

Third, *semi-structurally specific mechanisms* (e.g. species sorting) lead to coexistence along some sort of gradient (e.g. resources, environmental stress) (Tilman 2004; Muller-Landau 2010). Though the precise arrangement of sites does not influence outcomes following these mechanisms, the relative abundance of different types of sites or patches does.

Lastly, *structurally implicit mechanisms* depend merely on the existence of space, but do not require differences among patches. In general, coexistence depends on some sort of tradeoff among species abilities to disperse, and to compete and/or access resources locally (Tilman & Downing 1994; Bolker & Pacala 1999).

Lack of species interactions:

This category is more or less tautological. If species do not interact, then they do not influence one another and in theory should be able to coexist provided that each species is able to persist on its own. However, it is unclear how common this mechanism is in the real world, given that most aspects of ecological systems are influenced by one another, at least indirectly. We do not plan on considering this category much during the workshop.

2. Potential additions to Palmer 1994

Below are some potential other mechanism that are not listed in the Palmer (1994) review, but that have been highlighted as potentially important in subsequent work. In some cases, we hope to include these categories in our analyses in the workshop.

Speciation:

As demonstrated in Hubbell's neutral model, stable coexistence – in terms of the total number of species, though not the identity of those species – can be achieved if new speciation events are sufficiently frequent to offset extinction (Hubbell 2001). Similar mechanisms exist in extensions of MacArthur and Wilson's island biogeography model (Losos & Ricklefs 2009).

Multi-species interactions:

As discussed above in the ***Existing methods for detecting community stability*** section, a number of recent papers have suggested that the intrinsic role of complexity (both within and among trophic levels) have been under-appreciated in many frameworks of stable coexistence.

Within-trophic multi-species interactions appear to be particularly poorly understood, though they have long been known to influence dynamics in diverse communities (Lawlor 1979; Case & Bender 1981; Vandermeer 1991). In general, two types of within-trophic mechanisms seem to contribute to coexistence. First, *intransitive competition* (also sometimes called "circular networks") can lead to stable coexistence of diverse mixtures, even if subsets of species are not able to coexist (e.g. due to suppression of a potentially destabilizing competitor) (Connell 1978; Armstrong & McGehee 1980; Allesina & Levine 2011). These mechanisms are theoretically predictable from observations of pairwise interactions, though not necessarily using pairwise theory (e.g. the mutual invasibility criterion) (Levine *et al.* 2017). Second, *higher order interactions* describe mechanisms whereby the effects of two species on one another change depending on community composition (e.g. effect of A on B depends on presence C). By definition, this class of mechanisms cannot be detected based on pairwise interaction data. Consequently, it is unclear how common higher order interactions are (Levine *et al.* 2017), though recent theoretical work suggests that they could be highly influential in structuring diverse communities (Grilli *et al.* 2017).

Multi-trophic multi-species interactions include a broad array of well-studied mechanisms including Janzen-Connell effects (Janzen 1970), consumer-mediated plant-soil feedbacks (Mills & Bever 1998; Schnitzer *et al.* 2011), and apparent competition (Holt & Bonsall 2017). Note that these mechanisms have classically often been tested and attributed to negative density dependent processes. Importantly, however, many potential mechanisms contribute to negative density dependence, meaning that it alone is usually not sufficient to identify multi-trophic effects (Murdoch 1994; Wright 2002).

In addition to the well-studied mechanisms listed above, there are likely many more multi-trophic mechanisms that contribute to coexistence (e.g. Hillebrand *et al.* 2007; Lind *et al.* 2013; Filip *et al.* 2014; Plum *et al.* 2015). For example, grassland studies suggest that grazing by herbivores may be an especially important mechanisms that increases diversity by reducing light limitation (Borer *et al.* 2014). However, at least to my knowledge, as of yet there is no comprehensive review of multi-trophic coexistence mechanisms.

Large-scale/macro processes:

These include mechanisms that structure the diversity of ecoregions – e.g. issues of continental scale, historical biogeography, historical speciation rates, etc. (Rosenzweig 1995; Wiens & Donoghue 2004; Tilman 2011). Palmer specifically notes that he does not consider this class of mechanisms. Similarly, Ricklefs (2008) suggests that these may be the primary mechanisms responsible for structuring observed community composition, and that they have therefore been vastly under-appreciated in community ecology. That said, if we choose to follow the "local perspective" that I suggest below, then I think we may be able to safely disregard these larger-scale processes (e.g. by taking an external global community as "given", rather than trying to explain its composition).

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