This glossary (especially in the earlier part of the course) is a living document, and may be added to and/or ammended, so please take these definitions as a bit preliminary, and expect new terms to be added as we progress. Most definitions are from (Lomolino, 2016; Czekanski-Moir & Rundell, 2019). I'll likely start a separate glossary to talk about metrics of biodiversity (e.g., various species diversity indices and ways of comparing assemblages)

Adaptive radiation: (i) a pattern of species diversification in which a lineage of species occupies a diversity of ecological roles (Gillespie et al., 2001); and (ii) the evolution of ecological and phenotypic diversity within a rapidly multiplying lineage (Givnish, 1997; Schluter, 2000; Rundell & Price, 2009).

Beta diversity can be thought of as the difference between assemblages; in the context of patchy habitats it is sometimes formally defined as the ratio of gamma (regional, or landscape level) diversity to average alpha (local, or patch level) diversity. If a set, small number of species can occupy small habitat patches, increasing beta diversity among patches will necessarily increase gamma diversity.

Biogeography: the science that describes and develops causal explanations for all patterns in spatial variation of biological diversity. (Lomolino, 2016)

Coexistence: Siepielski and McPeek (Siepielski & McPeek, 2010) make the distinction between co-occurrence and coexistence of species, the latter of which implies some level of population stability among community members at the local scale that is stabilized by species traits and niches. This is in contrast to co-occurrence, where species' presence in a community is largely due to chance or larger-scale processes.

Community assembly: the construction and maintenance of local communities through sequential, repeated immigration of species from the regional species pool (Fukami, 2010, 2015). Vellend (Vellend, 2010, 2016) usefully suggests that species membership in assemblages at various scales is driven by the processes of speciation, selection, migration, and ecological drift.

Contingency: "...the effect of the order and timing of past events on community assembly." (Fukami, 2015). For our purposes, patterns are historically contingent if they require knowledge of previous events to understand. This is essentially the gedankenexperiment Stephen J Gould applies to the evolutionary history of major clades throughout the Phanerozoic, when he invoked the idea of "rewinding the tape of life." Historical contingency is consistent with **determinism**, whereby identical, niche-based interactions always have the same outcome. **Stochasticity** can also be involved, however, as in the "Lottery hypothesis" (Chesson & Warner, 1981; Pereira et al., 2015) in which arrival to a new habitat patch may be probabilistic, but the first species to colonize a habitat patch has deterministic impacts on subsequent community assembly patterns**;** see also: **priority effects**. Sterelny (Sterelny, 2016) has lots of thoughts on nuances of contingency, and other philosophers of science have weighed in fairly extensively.

Co-occurrence: refers to species that are found together by chance or because of larger-scale processes, like source–sink dynamics. **Neutral species** co-occur.

Dark diversity: the set of species that is absent from the local community, but could potentially colonize and establish in it (Pärtel et al., 2011; Lessard et al., 2012)

Deterministic process: For our purposes, when the same interaction results in the same outcome. In a probabilistic or **stochastic** process, the same interaction might result in different outcomes, perhaps falling along a probability distribution. In niche models of community assembly, for example, species traits are linked deterministically to presence in an assemblage. Ultimately, interactions that appear to have random outcomes may be deterministic in a complicated way we didn't (or can't) measure. Genetic determinism, for example, is often understood to mean you can perfectly predict a phenotype (and perhaps a person's success and place in society) from a genotype. You can easily reject strict genetic determinism without rejecting determinism in general, by allowing for the possibility of additional deterministic causes (e.g., gene-environment interactions) along a deterministic causal chain eventually leading to the phenotype. Many processes in ecology and evolution are best approximated by incorporating some degree of probability, which may be a result of our imperfect understanding of the system. For our purposes, though, we'll be most confident about calling a process "deterministic" if the causal pathway between our dependent and independent variables is relatively short and knowable. (see also discussion under **stochastic process**). We'll often say "random" or "stochastic" when we really mean "imperfectly predictable based on variables we did/can measure." **Priority effects** might be driven by deterministic species interactions (e.g., competition) that unfold following stochastic arrival order.

Disparification: increase in the morphospace occupied by members of a clade through time (Ciampaglio, 2004; Ackerly, 2009); distinct from **diversification**, which we use here to mean an increase in the number of species in a clade through time. Nonadaptive radiations are expected to exhibit diversification with minimal disparification. **Diversification**: net increase in the number of species in a clade over time. Speciation minus extinction.

Ecological drift: random fluctuation in species abundances in an assemblage, analogous to genetic drift of allele frequency in a population (Vellend, 2010).

Ecological speciation: the generation of reproductive isolation between populations as a result of ecologically based divergent selection between environments, which can include both natural and sexual selection (Price, 2007; Nosil, 2012).

Fundamental versus **realized niche**: the total range of environmental conditions in which a species can survive (or functions and behaviors it can perform), versus those that it actually occupies (or performs). (Lomolino, 2016)

Fundamental versus **realized range**: the geographic distributions that a particular species may achieve based solely on its physiological and abiotic tolerances, versus the more-restricted distributions that result from barriers to dispersal and from ecological interactions among species. (Lomolino, 2016)

General dynamic model (GDM) **of oceanic island biogeography**: a conceptual and graphical model describing the sequential and highly regular changes in physiographic characteristics of islands which, in turn, affect the fundamen- tal process of biogeography (immigration, extinction and evolution) and, in turn, influence biological diversity during the geologic development an oceanic island from emergence to its geological maturation and ultimate submergence beneath the surface. (Lomolino, 2016)

Genetic drift: Changes in allele frequencies in a population through time (i.e., evolution) due to chance events of survival, reproduction, and inheritance

Geographic gradients: patterns of variation in characteristics such as those of species, communities, or environments along geographic clines including those of latitude, elevation, depth, isolation and area. (Lomolino, 2016)

Janzen–Connell–Thingstad dynamics: a family of negative density-dependent selection (NDDS) or negative frequency- dependent selection (NFDS) processes that are very similar, although Janzen–Connell is typically invoked by tropical forest biologists, whereas Thingstad's 'Kill-the-Winner' hypothesis is much more frequently cited in the marine phage literature [86,87].

Jordon's rule: [g]iven any species in any region, the nearest related species is not likely to be found in the same region nor in a remote region, but in a neighbouring district separated from the first by a barrier of some sort' (Anacker & Strauss, 2014) See also (Pigot & Etienne, 2015). This pattern is consistent with diversification arising from allopatric speciation. If there is substantial range overlap between two sister species, they then may have arisen by sympatric speciation.

Macroecology: study of the rules and mechanisms (processes) underpinning general patterns of ecology across scales (Brown, 1995; Shade et al., 2018)

Magic trait: a trait subject to divergent selection that also contributes to reproductive isolation. (Servedio et al., 2011; Nordén & Price, 2018)

Natural selection: differential survival and/or reproduction of classes of entities (alleles, genotypes, subsets of genotypes, populations, species) that differ in one or more characteristics.

Negative density-dependent selection (**NDDS**): sometimes referred to as ‘inverse’ density-dependent selection; selection that favors rare phenotypes. Although technically distinct, NFDS has similar effects on community-level dynamics, as frequency is often related to density. One way that NDDS and NFDS dynamics can arise is through species-specific pathogens, which will tend to lead to some variation of Janzen–Connell–Thingstad dynamics. Another possible way that NDDS or NFDS can occur is through sexual conflict (Svensson & Connallon, 2018; Kobayashi, 2019). Here we refer to population dynamics among (not within) species; that is, our discussion focuses on species richness rather than intraspecific genetic diversity.

Neutral species: species that are ecologically nearly identical to one another and that follow the neutral dynamics of a random walk in relative frequency as described by Hubbell (Hubbell, 2001); one of the four types of species in a community identified by (McPeek, 2017) based on their population dynamical properties.

The **Neutral Theory of Molecular Evolution** asserts that most de novo mutations are either sufficiently deleterious in their effects on fitness that they have little chance of becoming fixed in the population, or are under such weak selection that they may become fixed as a result of genetic drift (Kimura, 1968, 1983; King & Jukes, 1969). Furthermore, the rate of substitution of neutral mutations between species is equal to the mutation rate. (definition from (Jensen et al., 2019); see also (Yoder et al., 2018)). See also (Ohta, 1973). But see (Kern & Hahn, 2018) for comments on the limitations of NTME.

Niche: the environmental conditions that allow a species to satisfy its minimum requirements so that the birth rate of a local population is equal to or greater than its death rate, along with the set of per capita effects of that species on these environmental conditions (Chase & Leibold, 2003; Fukami, 2015).

Niche conservatism: a pattern where closely related species are more ecologically similar to one another than would be expected based on their phylogenetic relationships. Niche conservatism is not expected in an adaptive radiation.

Nonadaptive radiation: lineage diversification with minimal ecological diversification, often (but not always) resulting in allopatric or parapatric taxa. ‘Minimal’ refers to slight differences among species that can accumulate in allopatry; for example, due to neutral evolution or slight differences in environments (Warren et al., 2014).

Nonecological speciation: the generation of reproductive isolation between populations that does not arise from divergent natural selection (Nosil, 2012). One potential mechanism by which nonecological speciation can occur involves the slow process of fixation of different and selectively favored mutations among allopatric populations.

Null hypothesis: from a pragmatic standpoint (i.e., for our purposes, for this course), a random relationship between the dependent and independent variables in which one is interested. Researchers in ecology often generate a distribution of species under the assumption that some process or causative agent is unimportant, but include some level of realism in processes that aren't ignored to generate the null. For example, Hubbell's Unified Neutral Theory of Biodiversity and Biogeography includes the processes of speciation, demographic stochasticity, and immigration, but does not include any information about trait-based differences among species. This model can be used to generate a null hypothesis against which to test the importance of niche-based community assembly or patterns of distribution. Models that have more realistic assumptions about the way speciation works have been put forward (Rosindell et al., 2010; Pigot & Etienne, 2015) that allow researchers to generate somewhat different null expectations against which to test the importance of niche-based processes on community assembly. Analogously, population geneticists interested in studying the strength of natural selection might generate a null hypothesis based on Hardy-Weinberg Equilibrium alone, or they might generate a null hypothesis of allele frequencies that incorporates genetic drift and mutation (and perhaps even gene flow) in a given effective population size. Some argue that the only way to advance our understanding of the world is by falsifying or failing to falsify null hypotheses.

Priority effects: a pattern whereby the outcome of competition for a resource is highly influenced by the (often stochastic) order of species arrival. For example, some types of wood-rot fungi will be able to exclude competitors only if they are established first (Fukami et al., 2010; Fukami, 2015). A related mathematical model of stochastic community assembly is the 'Lottery Hypothesis' (Chesson & Warner, 1981; Pereira et al., 2015).

Probability refuge: a metaphorical 'refuge' concept that Shorrocks and others (Shorrocks et al., 1979; Shorrocks, 1990; Sevenster & van Alphen, 1996; Ruokolainen & Hanski, 2016) invoke in the aggregation model to describe the niche space that opens for ecologically similar species when intraspecific competition is stronger than interspecific competition (e.g., due to aggregated egg laying and sibling competition in ephemeral patchy resources).

Sexual selection: selection on traits resulting from differential mating success, including access to different numbers of mates or to mates of differing quality (Price, 2007).

Sink species: species that are present only due to continual migration from other communities; one of the four types of species in a community identified by McPeek (McPeek, 2017) based on its population dynamical properties.

Source–sink dynamics: movement of individuals between high-quality (source) and lower-quality (sink) patches within a metacommunity, where populations in the sink are sustained only through migration.

Spatial scale: includes the concept of **grain**, the first level of spatial resolution possible with a given data set (sometimes called "resolution," e.g., (Lookingbill et al., 2011)), and **extent**, the total area of the study.

Spatial and temporal autocorrelation: the tendency for entities (e.g., environments, species, or biological communities) that are closer in space and time to be more similar than those that are further isolated or more disparate in time periods (Lomolino, 2016).

Species abundance distribution: depicts the number of individuals (N) of each species in a sample, and is often expressed as a relationship between the logarithm of N plotted against species rank (from the most to the least abundant species) (Shade et al., 2018).

Species–area relationship: relates the number of species (S) to the area of the plot (gray squares) in which species richness is sampled (A). In the nested SAR, larger areas should be therefore contiguous and should encompass all the smaller areas. However, empirical SARs are often constructed based on much smaller samples, which are assumed to be representative of the whole contiguous and mutually adjacent areas (Shade et al., 2018).

Species-level neutral model: all species are equivalent; they have the same chance of immigration, extinction and speciation (Rosindell et al., 2011).

Stochastic extinction: When population fluctuations (i.e., ecological drift) drive a species extinct. Analogous to allele fixation due to genetic drift. From (Roughgarden, 1975): "...even in a constant environment, the population size could fluctuate due to chance events in the reproductive success of the finite number of individuals in the population." See especially (Wright & Hubbell, 1983), and (Hubbell, 1979): "we may expect to observe substantial differentiation of the relative abundance of species in natural communities as a result of purely random-walk processes-a kind of "community drift" phenomenon."

Stochastic process (including extinction): a random, or probabilistic process, as opposed to a **deterministic** process, in which the same interaction will always produce the same outcome. See notes above about **contingency**. You can get pretty deep into the weeds pretty quickly if you start to really unpack the philosophy of this stuff... E.g., (Illari & Russo, 2014) (p82) write "... we should not confuse predictability with determinism. Second we should not confuse determinism with causality. Much work in the philosophy of causality has been devoted to spelling out and defending a *probabilistic* concept of causality. Besides the scholars mentioned above, Wesley Salmon also tried to provide a causal account of primarily physical phenomena that are not deterministic (Salmon, 1980b; Salmon, 1984). The distinction between determinism/indeterminism and predictability is also related to the next issue. Paul Humphreys (1990, sec17) distinguishes between 'theories of probabilistic causation' and 'probabilistic theories of causation.' In theories of probabilistic causation we aim to provide a conceptualization of causal relations that are inherently probabilistic, stochastic, chancy, or indeterministic. So we may well talk about ‘indeterministic causation.’ In probabilistic theories of causation we aim to provide a probabilistic characterization or modelling of causal relations that may or may not be probabilistic in themselves. In this second case we may either admit that there exist cases of deterministic causation and indeterministic causation, or we could hold that causation is all deterministic, but our modelling of causal relations is probabilistic because we don’t have complete knowledge or because of measurement error.” Elsewhere, (Jaynes, 2003) (p536) writes: “Indeed, there is no such thing as a “stochastic process” in the sense that the individual events have no specific causes. One who views human diseases or machine failures as “stochastic processes,” as described in some orthodox textbooks, would be led thereby to think that in gathering statistics about them he is measuring the one controlling factor - the physically real ‘propensity’ of a person to get a disease or a machine to fail - and that is the end of it.” Or, more succinctly, on page 26: “...no amount of analyzing coin tossing data by a stochastic model could have led us to the discovery of Newtonian mechanics, which alone determines those data.” For our purposes, there may be a genuine probabilistic relationship between, e.g., presence of an allele and expression of a trait, or the presence of a phenotype and a particular competitive outcome, but there was a genuine string of cause-and-effect relationships that deterministically leads to a particular outcome that’s grounded in a real, physical world. Or, there might not be... who knows. Stochastic processes, like circles and fractals, might not be precise realities, but they are sometimes useful approximations of the patterns we observe. In the case of patterns like demographic stochasticity and ecological drift, fluctuations in population abundance may be caused by deterministic processes that are too manifold to measure.

Tobler’s first law of geography (spatial autocorrelation): originally described by Tobler (1970: 236) in the observation that “Everything is related to everything else, but near things are more related than distant things.” In modern terms, this describes positive, spatial autocorrelation or the very general tendency for the environmental or biological characteristics of sites to decrease in similarity as distance between those sites increases. (Lomolino, 2016)

Walking-dead species: species that are slowly being driven extinct by the ecological conditions that they experience within the community; immigration will not rescue them; one of the four types of species in a community identified by McPeek (McPeek, 2017) based on its population dynamical properties.

Zeta diversity measures the number of species shared by any number of assemblages or sites; an alternative to beta diversity that, rather than quantifying site-site distinctness, “provides an unbiased measure of multiple-assemblage similarity” Check out more here (Hui & McGeoch, 2014; Latombe et al., 2017)

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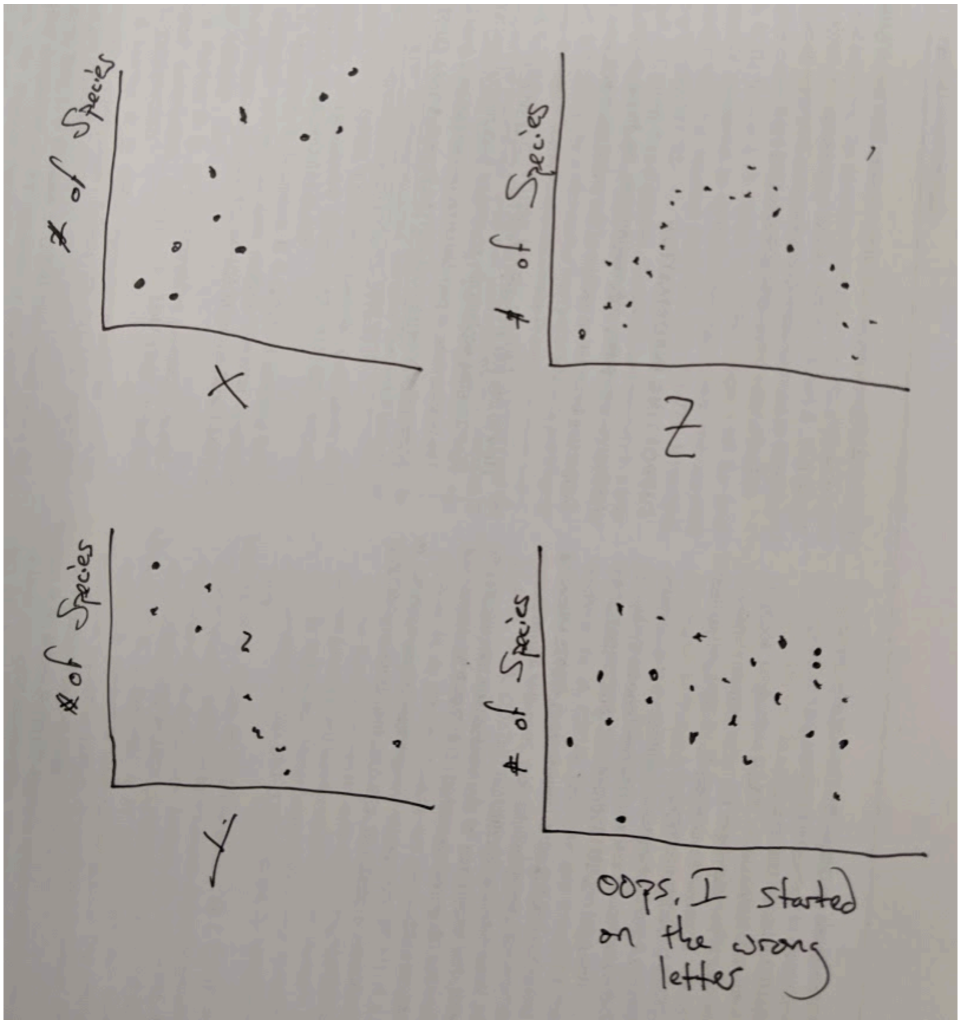
Statistical relationships:
In these graphs, we might consider X, Y, and Z to be **independent variables**, and the number of species in an assemblage to be the **dependent variable** of some type of experiment.
X is **positively correlated** with the number of species; Y is **negatively correlated**. Both X and Y are sometimes referred to as "monotonic" relationships, which means the sign of the relationship never changes (although the slope might: a relationship could be positive decelerating, for example, if it approaches an asymptote). Z has a **unimodal** relationship with the number of species. There are many unimodal relationships in ecology (and physiology, e.g., thermal performance curves for ectotherms; and economics, e.g., the Laffer curve).

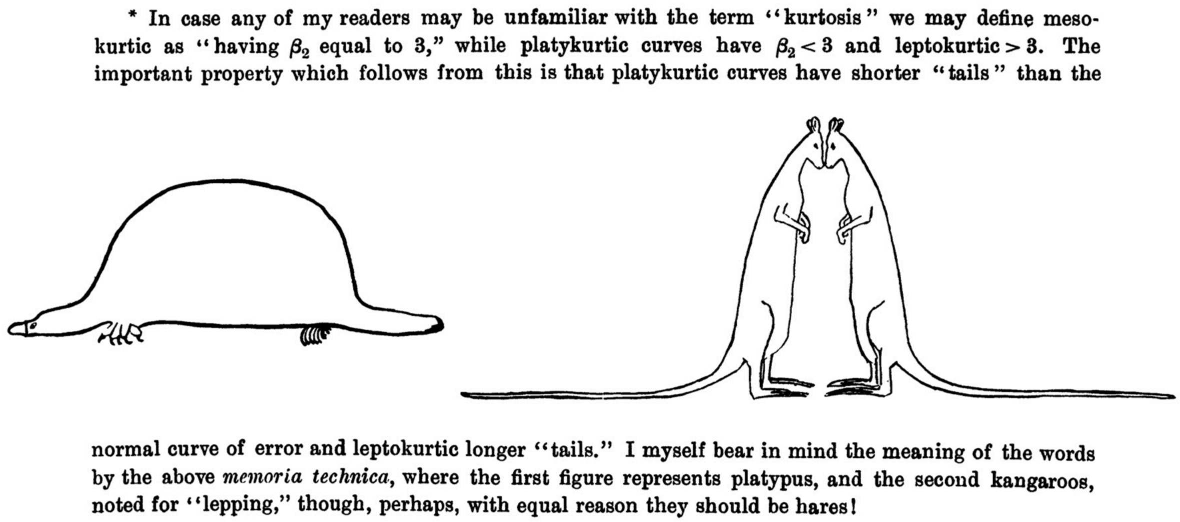
The "Oops I started on the wrong letter" variable has no statistically significant relationship with the number of species in a community.



Unimodal relationships make the scale of a study very important: if the study does not include the entire gradient found where life is, the unimodal nature of the relationship might not be apparent. For example, there is often a positive relationship between the mean annual temperature of a habitat and the species richness. However, if you also measure habitats that

stay above 45C all year, and include hotsprings and hydrothermal vents, you might see a decrease in the species-temperature relationship. Note that probability distributions can also be described as unimodal, bimodal, multimodal, etc. There are lots of names for probability distribution functions! Yay! https://en.wikipedia.org/wiki/List_of_probability_distributions
A popular family of PDFs in evolutionary biology is the Poisson distribution. Less popular, but very cool, is the Cauchy distribution. (cf. the Lévy distribution).

There are other ways of describing distributions, too. One way of talking about unimodal distributions is describing their kurtosis. A leptokurtic distribution is very tightly distributed about the mean, and so will look kind of pointy, whereas a platykurtic distribution has a broad distribution about the mean, and looks flatter. "Student" (William Sealy Gosset) has one of the most adorkable mnemonic devices for this ever:



*** In case any of my readers may be unfamiliar with the term "kurtosis" we may define mesokurtic as "having β_2 equal to 3," while platykurtic curves have $\beta_2 < 3$ and leptokurtic > 3. The important property which follows from this is that platykurtic curves have shorter "tails" than the normal curve of error and leptokurtic longer "tails." I myself bear in mind the meaning of the words by the above *memoria technica*, where the first figure represents platypus, and the second kangaroos, noted for "lepping," though, perhaps, with equal reason they should be hares!**

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