Research overview

It is widely known that few species are common, while the majority of species are intermediately rare (Preston 1948). However, it is unclear why this pattern of commonness and rarity exists. There is a need to understand the mechanisms that predispose a species to be common or rare. The ultimate goal of my research is to gain a better understanding of the mechanisms that produce commonness and rarity in an ecological context. I will approach this question from three perspectives. First, I will explore the evolutionary basis of commonness and rarity by determining if commonness and rarity are phylogenetically heritable and if there are differences in the phylogenetic branch lengths among common and rare species. Second, I will identify if regional occupancy and abundance can be explained by life history traits. Third, I will determine if there are differences in regional spatial patterns of ecological and anthropogenically common and rare species that could distinguish between possible mechanisms of commonness and rarity.

Introduction

I will try to gain a better understanding of why species are common or rare through exploring whether persistance time, as estimated by phylogenetic branch length, is correlated with commonness and rarity. Research suggests that the extent of occupancy of a species geographic range is inheritable (Jablonski 1987, Hunt et al. 2005, Waldron 2007, but see Webb and Gaston 2003), and species with larger geographic ranges tend to have higher abundances (Brown 1984, Blackburn et al. 1997). However, geographic range size also fluctuates over time (Liow and Stenseth 2007, Gaston 2008), presenting an interesting conflict of information. If geographic range size (a proxy for abundance, and thus, commonness) is variable over time, then I would not expect range size to be inheritable. I am going to examine commonness and rarity more directly by asking if the occurrence (# occupied sites/ # of potentially occupied sites, both relative to and independent from range size) and average rank abundance (average species-richness corrected rank abundance) of species within a geographic range are more

similar among closely related species, and whether commonness (metrics mentioned above) is related to the branch lengths of the phylogeny.

Hypotheses

Based on previous results with the extent of occurrence, I would expect that more closely related species would have more similar occurrences and abundances. However, it is also possible that there could be no relationship between the relatedness of species and occurrence or abundance based on geographic range size fluctuating over time. Alternatively, if one species is widespread, can exploit many environments, and excludes closely related species, then I would expect that more closely related species would have less similar abundances and occupancies.

I will also test to see if phylogenetic branch lengths can predict commonness and rarity. Because the majority of species are intermediately rare, I would expect that there is no advantage to commonness or rarity, but rather that commonness is an alternate evolutionary strategy. If common and rare species do not have significantly different branch lengths, this would suggest that there is no advantage to commonness or rarity for persistence time of a species. In addition, commonness of a species could fluctuate throughout evolutionary time, which would also lead me to expect that there would be no difference in branch lengths between currently common or rare species. It is also possible that common species would have longer branch lengths. This could occur because common species are able to occupy more environments, and so are able to re-colonize more easily from local extinction events. Intermediately rare species could have longer branch lengths than common species if the smaller populations of rare species allows them to adapt more quickly to environmental change than common species. Commonness and rarity could also be part of the life cycle of a species. In this case, a species could start out rare, become common, and then decline into rarity before exinction. If branch lengths are intermediate for rare species and either short or long for common species, this would suggest that commonness is a more risky evolutionary strategy, resulting in either longer branch lengths (persistance time) or a rapid time to extinction (short branch length).

I predict that common and rare species will not have different branch lengths, because they are both equally successful strategies for continued persistence. A common species occurs under a wide

range of environmental conditions, but is less likely to be able to evolve quickly because of gene flow from other parts of the geographic range. However, it is likely to persist because it is already adapted for a wide variety of conditions. A rare species occurs under fewer environmental conditions, but is likely to be able to evolve more quickly, because of its smaller population size. Assuming that a rare species also possessed sufficient genetic diversity to allow it to evolve, a smaller population would allow evolution to proceed more swiftly across the entire population, allowing it to persist as well.

Methods

Data

To test my hypotheses, I will use data from the North American Breeding Bird Survey (BBS, Sauer et al. 2011), the Mammal Community Database (MCDB, Thibault et al. 2011.), and the North American Butterfly Association count data (NABA, North American Butterfly Association 2009). These datasets have a large geographic coverage, and phylogenetic trees are available for birds from the Bird Supertree Project (Davis, 2008), for mammals from the mammal supertree (Bininda-Emonds et al. 2007), and for butterflies from LepTree (LepTree Team 2012). For birds and mammals, published range maps are available from NatureServe (Ridgely et al. 2007 (birds), Patterson et al. 2007 (mammals)) and for butterflies, checklists of species are available from the Butterflies and Moths of North America (BAMONA, Opler et al. 2012).

Analyses

Although ecologists typically think of rare species as those that are of low abundance or are habitat specific, taxonomic uniqueness or persistence of the species through time (ecological or evolutionary) have also been used as criteria (Gaston 1994). Drury (1974) and Rabinowitz (1981) used a three criteria classification system (range size, population size/local abundance, and habitat specificity/occurrence) to identify rare species. In the Drury-Rabinowitz framework, only one out of the three criteria must be "rare" for the species to be considered rare. I will compare a variety of measures of commonness to determine if the choice of metric impacts the results of the study. Differences among metrics of commonness and rarity, representing different axes of rarity, can help distinguish if there might

be differences in the mechanisms for commonness and rarity along different rarity axes. Commonness is most commonly thought of as a binary variable, where species are either classified as common or rare. While this will be one of my metrics, I would also like to treat commonness and rarity as a continuous variable. Commonness can be measured either based on the total number of individuals (abundance) or on the frequency at which a species occurs across the landscape (occupancy). I would like to compare species by relative commonness, which would be calculated by taking the average of the species richness corrected rank abundances throughout the geographic range of the species and then averaging that number with percent occupancy. I would also like to test the average species richness corrected rank abundance of a species with branch length as well as testing percent occupancy.

To obtain percent occupancies for a species, I will take the number of survey routes at which a species is recorded and divide that by the number of potential sites at which it could occur. This method will allow me to obtain an estimate of occupancy independent of the geographic range size or number of survey routes sampled. I will also calculate the percent occupancy relative to the area of occupancy of the species, which will be calculated by multiplying the percent occupancy by the area of the geographic range size. I will use an equal area projection for all range maps with a grain size of 1 km². The number of potential survey routes at which a species could occur will be determined by one of two methods. For birds and mammals, I will determine the potential number of survey routes by including all those sites which fall within the geographic range of that species using a geographic information system. For butterflies, I will use checklists to determine where the range limits fall, and include all the survey routes which fall within the geographic range. While checklists will be a coarser estimate of range size, I will only be comparing species within a taxon, so the data will be comparable.

I will perform a randomization test between phylogenetic branch lengths and occupancy (Waldron 2007) for the analyses for both questions. I will also use Pagel's λ (Pagel 1999) as implemented in the R package GEIGER (Harmon et al. 2007). While Waldron's (2007) method produced similar results to those obtained in the literature using Pagel's λ, he did not test his data using Pagel's λ. Waldron's (2007) phylogenetic randomization method is a randomization/resampling process which reshuffles the order of the dependent variable while keeping the independent variable static. Pagel's

lambda (Pagel 1999) is a maximum likelihood method. Using both methods, I will be able to determine if there is agreement between the methods.

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Introduction

Species that are common are more abundant and occur at many sites (Rabinowitz 1981). The majority of life history traits, at least for vertebrates, are factors that affect how many new individuals are produced (e.g., litter/clutch size, litters/clutches/year, age at first reproduction). I would expect that species with higher fecundity would be more abundant, therefore, I would expect that life history traits could be useful in predicting commonness of species. However, a problem with life-history traits is that there is a strong relationship between body size and life history traits (Roff 1992), and smaller species are more abundant than larger species. While body size clearly plays an important role in how abundant a species is, it is ultimately an unsatisfying answer. Charnov (1993) developed the idea of scale invariant numbers that encapsulate the rate of reproduction to arrive at an evolutionary explanation for observed allometric relationships. The idea of dimensionless numbers was further developed to identify the lifetime reproductive effort of a species (Charnov et al. 2007). While previous theory had suggested that the lifetime reproductive effort of a species would be different with different species and across different taxa, Charnov et al. (2007) observed that lifetime reproductive effort is the same across taxonomic groups.

As a continuum of species traits, r-K selection theory provides a convenient framework to think about species that are common and rare. Species that are more common might be expected to have traits that maximize reproduction. However, in the original sense of r-K selection, species would be expected to undergo both r- and K- selection at different times (MacArthur and Wilson 1967). This would suggest that traits that are the most beneficial in an r- selection scenario should be most common where species experience r-selection most of the time. Conversely, I would expect traits that are more beneficial in a K-selected scenario to predominate in a K- selection environment. This would suggest that there is not a single suite of traits that would predispose a species to commonness or rarity across all environments, but the suite of traits might change between ecoregions and over ecological and evolutionary time.

Conservation biology has used species traits to predict which species have higher extinction risks. Geographic range size, endemicity, reproductive rate, and body size have been important indicators of extinction risk (Purvis et al. 2000, Cardillo et al. 2005), thus indicating that traits could be important in determining the commonness or rarity of species. However, the traits that predispose a species to be rare enough that it is of conservation concern may not be the same as for intermediate rarity. In addition, while these traits may be good predictors of extinction risk, several of these traits (body size, geographic range size, endemicity) are not satisfying explanations of rarity.

Both Charnov's lifetime reproductive effort and r-K selection theory suggest that there might not be a single suite of traits that predispose a species to commonness or rarity across all habitats. These theories indicate that the effects of differences in life traits may not produce a signature in commonness or rarity. Some success has been found in using species traits to predict extinction risk, but attempts to predict the commonness of species (primarily for invasion) have met with little generalizable success (Moles et al. 2008). I propose that commonness and rarity might be emergent properties that are not predictable through life-history traits.

Hypotheses

Invasive species tend to be common in their native ranges as well as the introduced range (Hierro et al. 2005). Recent work with invasive species suggests that while life history traits are useful in predicting invasibility, there is little generality among studies (Thompson and Davis 2011). If common

species and native species are comparable, as the work by Hierro et al. (2005) suggests, then I would not expect to observe a relationship between life-history traits and occurrence or abundance. However, recent work in community ecology indicates that plant functional traits are useful in predicting abundance at a local scale (Laliberte et al. 2012). If functional traits can be used to predict abundance of species at a local scale, perhaps life-history traits can be used to predict the abundance and occurrence of species at a regional or continental scale.

Methods

Data

To test my hypotheses, I will use data from the North American Breeding Bird Survey (BBS, Sauer et al. 2011), the Mammal Community Database (MCDB, Thibault et al. 2011), reptile community data gleaned from the literature (MiscAbundanceDB,Baldridge2012), and the life history trait database for birds, mammals, and reptiles (LHDB, Baldridge et al., in prep). These datasets have a large geographic coverage, and phylogenetic trees are available for birds from the Bird Supertree Project (Davis, 2008), for mammals from the mammal supertree (Bininda-Emonds et al. 2007). For reptiles, there is not an available supertree, so the taxonomy will be used as a substitute where a more detailed phylogeny is not available. While taxonomy is a less powerful indication of phylogenetic relationships, the addition of ectotherms to the analysis will provide a stronger test of the overall question, even though the specific test of the reptiles will be less strong than the birds and mammals. I will use the full set of life history traits available in the LHTDB for my analyses.

Analysis

I will determine percent occupancy as outlined in chapter 1. The abundance of a species will be counted as the average of all the ranks of a species at each local community, standardized for species richness as suggested by McGill (McGill 2011). I will test my hypothesis with a phylogenetic regression analysis, which will allow me to do variance partitioning among the life history traits, abundance, and phylogeny (Kemble et al. 2010).

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Introduction

One of the inherent problems of continental scale ecology is the difficulty of performing direct manipulations on the system. While intentionally manipulating the abundance and occurrence of species on a continental scale for an experiment would be highly unethical, humans have unintentionally manipulated the abundance and occurrence of species on a global scale. The unintentional anthropogenic manipulation of species by introducing species to new locations or by causing reductions in the total abundance or occurrence of species provides an opportunity to study patterns of commonness and rarity in a more experimental context.

Recent work in invasion ecology suggests that invasive species and native common species are successful for similar reasons (Thompson and Davis 2011) While this seems to be true at a local scale, it is unknown if spatial patterns of commonness and rarity are the same for ecologically common and rare species compared to anthropogenically common and rare species. If the spatial patterning is different between native and non-native common species, then differences in the spatial patterning of the distribution of abundance could indicate that different processes are operating to produce commonness in native and non-native species. If spatial patterns are the same between ecologically common and rare species and anthropogenically common and rare species, it is more likely that the same processes are operating for both groups. Because non-native species and species of conservation concern are common or rare through some human influence, the intensity of human disturbance provides a logical starting place to begin exploring potential differences between anthropogenically and ecologically common and rare species.

Hypotheses

If non-native species and native species have equal access, ability, and time to colonize the same sites, and perform equally well, I would expect that abundances and percent occupancy throughout the geographic range will be comparable, following the type of peak-tail distribution described by Brown (1984). The peak-tail distribution describes a peak of abundance within the geographic range, with abundances tapering off toward the edges of the range (Brown, 1984, McGill, in prep.). The peak-tail

distribution was originally called the abundant-center hypothesis (Brown, 1984), but while empirical evidence did not support the idea that the peak always fell within the center of the range, it did suggest that there is typically only one to a few main peaks of abundance within the geographic range (Sagarin and Gaines, 2002, McGill, in prep.)   Another possibility, given the same conditions described previously, is that abundances and percent occupancy throughout the geographic range will be comparable, but the non-native species will have many peaks of abundance throughout the geographic range, resulting in a very heterogeneous spatial structure that does not follow the typical peak-tail distribution observed in native species. If non-native species tend to be more dominant at sites than native species, I would expect that non-native common species will have higher abundances at a site. However, non-native species may not have had equal access or time to colonize an area, therefor I would expect that non-native species would have lower percent occupancy than native common species. If non-native species are more dominant than native species, but have had less access to sites or time to colonize sites, I would expect that the spatial structure of the geographic range would not follow a peak-tail distribution, but would instead be very heterogeneous. However, it is possible that non-native species could both be more dominant and follow a peak-tail distribution, if non-native species and native species have had equal access, and time to colonize sites.

While some of these predictions are based on the assumptions that non-native species and native species have equal access, ability, and time to colonize the same sites, I expect that there are differences between native and non-native species in the ability to access sites, resulting in the non-native species having a more heterogeneous spatial distribution due to the increased likelihood of non-native species to be introduced to disturbed areas. Because I expect that human disturbance will be an important factor in determining the spatial distribution of native and non-native species, I will explicitly test the effects of human disturbance on native and non-native species. I predict that non-native species will have distributions that are positively correlated with human disturbance, while native common species will have distributions that are negatively correlated or have no relationship to human disturbance.

I predict that anthropogenically rare species will have lower abundances overall and lower percent occupancy than ecologically rare species, while still maintaining a peak-tail distribution.

Anthropogenically rare species are rare due to some human influence, whether it be from overexploitation, habitat loss, disease, etc. Thus, I predict that anthropogenically rare species will have distributions that are negatively correlated with human disturbance, while ecologically rare species will have distributions that are negatively correlated or have no relationship to human disturbance.

Methods

Data

To test my hypotheses, I will use data from the North American Breeding Bird Survey (BBS, Sauer et al. 2011) and the Forest Inventory Analysis (FIA, Woudenberg et al. 2010). Identities of invasive species are well documented in each of these groups, and the sampling effort is geographically widespread. For non-native species, I will also compile a list of times since introduction. The life history trait database (LHDB, Baldridge et al., in prep.) will be used to estimate generations times for the birds, and additional data will be compiled to estimate generation times for the trees. With generation time and time since introduction, I will then estimate generations since introduction. After dividing species into common and rare species, I will determine if a species is ecologically or anthropogenically rare by consulting the IUCN Red List (IUCN 2012) and local or regional threatened and endangered species listings. If the species is not on either the IUCN Red List or state or federally listed, it will then be considered to be ecologically rare. If a species is on the IUCN Red List or state or federally listed, but has been listed due to characteristics of that species (i.e, endemic to a small geographic area) rather than an anthropogenic cause (overexploitation, habitat destruction, etc), then it will be considered an ecologically rare species.

To test the influence of human disturbance on anthropogenically and ecologically common and rare species, I will use the Human Footprint map layer at a grain size of 1 km² (HF, Last of the Wild, 2005). The Human Footprint environmental layer is derived by calculating a human influence score and then normalizing the data by biome for a final value from 0 for minimal impact to 100 for maximum impact. The human influence score takes into account eight variables, including human population

density/sq. km, distance to railroads, distance to major roads, distance to navigable rivers, distance to coastlines, the level of nighttime lights, whether an area is urban or rural, and land cover type.

Analysis

I will perform an initial graphical exploration of the data in R. After initial exploration of the spatial structure of the data, it will then be possible to determine the most appropriate methods for a formal statistical analysis, following the guidelines presented by McGill (2011). The initial exploration of the data will be done with a first order spatial interpolation technique, while the human disturbance analysis will be carried out with a second order spatial analysis technique, such as a spatial regression technique (McGill 2011). Generations since introduction will be included as an additional explanatory variable in the analyses for native and non-native species. The final statistical analyses will be carried out either with one or several of the various R spatial statistics packages.

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