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Coloniality, biogeography, and pedagogy

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Coloniality, biogeography, and pedagogy

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DISSERTATION

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DISSERTATION ABSTRACT

Coloniality, in which organisms are composed of repeated discrete structural units that are physically connected to each other, is a major evolutionary innovation. Since the first colonial animals appeared during the Cambrian Period, coloniality has independently evolved in several animal lineages including cnidarians, hemichordates, chordates, bryozoans, entoprocts, and annelids. Despite the prevalence of this trait, the mechanisms underlying broadscale biogeographic trends in coloniality remain untested. In this dissertation, I examined two global-scale biogeographic patterns related to coloniality in ascidians, a diverse group of chordates. In addition to this work, I also examined colonial animals through the lens of pedagogy. In Chapter 1, I investigated mechanisms underlying the latitudinal gradient in colonial ascidian richness. Using publicly available species occurrence data and abundance data from two large experimental networks, I demonstrate that this gradient is robust and likely driven by ecological mechanisms. In Chapter 2, I explored the relationship between coloniality and Rapoport's rules, the correlation between latitude and species' latitudinal or bathymetric ranges. Using species occurrence data, I show that ascidians demonstrate Rapoport's bathymetric rule possibly due to biogeographic variation in coloniality. Together, these findings indicate the need for more rigorous testing of the mechanisms underlying broad biogeographic patterns. In Chapter 3, I examined taxonomic bias in the animal diversity present in introductory biology course materials. Vertebrates, especially mammals, were overrepresented in textbooks and lecture slides, relative to their actual diversity. In contrast, invertebrates, including many groups of colonial animals, were underrepresented to varying degrees.

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TABLE OF CONTENTS

CHAPTER 1

Investigating ecological mechanisms for the latitudinal coloniality diversity gradient in ascidians

ABSTRACT

While there are many descriptions of biogeographic patterns in species diversity, fewer studies address the processes producing these patterns. Although colonial ascidians show a higher relative richness at lower latitudes and solitary ascidians show a higher relative richness at high latitudes, hypotheses for the mechanisms underlying this biogeographic pattern remain untested. Using publicly available species occurrence data from OBIS and GBIF, we demonstrate that this latitudinal ascidian coloniality diversity gradient is robust and exists independently of any longitudinal patterns or latitudinal variation in sampling effort, coastline length, or sample occurrence depth. We show that the higher relative richness of colonial species at low latitudes is driven largely by increases in the number of colonial species at low latitudes, as solitary species richness does not change with latitude. Many of the proposed hypotheses for this pattern suggest that increased competition and predation in the tropics could favor colonial ascidians because of their superior ability to survive competition and predation. If such forces were acting in ecological time, we should expect to find: 1) a latitudinal gradient in the relative abundance of colonial versus solitary species, not just in the diversity of the two forms, and 2) a higher proportion of colonial species at shallower depths, where predation and competition are generally stronger for marine organisms. When we analyzed abundance data from two large experimental networks, we found that the relative abundance of colonial ascidians peaked in the tropics, consistent with the proposed ecological hypothesis. The second prediction of the ecological hypothesis, that the proportion of colonial species should decrease with depth, was supported by our analysis of the species occurrence data. Latitudinal variation in predation intensity may explain why the relative abundance and relative richness of colonial ascidians were highest at 20° from the equator, rather than at the equator. Possible

historical and evolutionary mechanisms for the latitudinal coloniality diversity gradient remain unaddressed. Our findings indicate the need for more rigorous testing of the mechanisms underlying broad biogeographic patterns.

INTRODUCTION

The advent of global biodiversity databases (e.g., OBIS, GBIF) have made it easier to document biogeographic patterns in species diversity, but the mechanisms driving these patterns often remain the subject of vigorous debate. For example, most eukaryotic clades, aside from a few notable exceptions (e.g., molluscs, ichneumonids), increase in species richness from the poles to the equator (Hillebrand 2004). Although this biogeographic pattern, known as the latitudinal diversity gradient, has been recognized for over 200 years, there is no broad consensus on the primary mechanism(s) underlying this pattern (Kinlock et al. 2018). The explanations that have been proposed for this gradient include ecological hypotheses that focus on mechanisms of species coexistence and maintenance of species diversity, evolutionary hypotheses that focus on the rate of diversification (e.g. tropics as cradle or museum [Jablonski et al. 2006]), and historical hypotheses that focus on the duration and extent of tropical environments in the history of the Earth (Mittelbach 2007). Identifying the primary mechanism(s) driving the latitudinal diversity gradient is difficult because these explanations are not mutually exclusive and often generate similar predictions (Willig et al. 2003).

More recently, it has been suggested that more powerful, mechanistic tests of these biodiversity theories could be accomplished by moving beyond species richness, and instead focusing on other measures of diversity, such as functional diversity (Lamanna et al. 2014). Similarly, a focus on how traits change with latitude can offer mechanistic insights into latitudinal gradients of species diversity. One trait that is potentially important for understanding these gradients in marine organisms is coloniality. The first colonial animals appeared during the late early or early middle Cambrian Period, approximately 510 to 526 million years ago (Landing et al. 2018). Since then coloniality has independently evolved in several animal lineages including cnidarians, hemichordates, chordates, bryozoans, entoprocts, and annelids (Beklemishev 1969, Ruppert et al. 2004). Some of these lineages are almost exclusively colonial (e.g., bryozoans), while in others coloniality is exceedingly rare (e.g., annelids).

Ascidians (the largest and most diverse class of Tunicata, a subphylum of Chordata), like many other taxa, exhibit a higher diversity in the tropics than at high latitudes (Hiebert et al. 2019). The ratio of colonial species to solitary species also increases from the poles to the tropics (Moreno et al. 2014, Hiebert et al. 2019). Roughly 60% of the ~3,000 species of ascidians are colonial (Shenkar & Swalla 2011), and there have been multiple independent transitions to coloniality from solitary ancestors within this group (Swalla et al. 2000). This latitudinal pattern in coloniality in ascidians has long been anecdotally described (e.g., Jackson 1977, Kott 1981, Shenkar & Swalla 2011, Moreno et al. 2014), but rigorously quantified on a global scale only recently (Hiebert et al. 2019). Despite multiple studies describing this latitudinal coloniality diversity gradient, the mechanisms that generated or maintain this biogeographic pattern have not been established yet. Identifying the primary mechanism(s) underlying the latitudinal coloniality diversity gradient in ascidians could provide key insights into the consequences of coloniality not only for ascidians, but also for other marine animals.

Most of the proposed hypotheses for why there are more colonial than solitary ascidian species in the tropics rely on ecological mechanisms (e.g., Jackson 1977, Kott 1981, Hiebert et al. 2019). Biotic interactions, such as competition and predation, are generally stronger in the tropics (Schemske et al. 2009, Freestone et al. 2011, Ashton et al. 2022). Colonial organisms are thought to be better space competitors and less susceptible to predation than solitary organisms (Jackson 1977, Jackson & Hughes 1985). Empirical evidence for this colonial advantage is mixed. For example, solitary ascidians were more susceptible to predation than colonial ascidians in

Florida (Mook 1983), New England (Osman & Whitlatch 2004), and Australia (Lavender et al. 2014), but not in Brazil (Hiebert et al. 2019). Colonial ascidians were less palatable to fish predators (Stoecker 1980b) and had fewer macroscopic epibionts (Stoecker 1980a) compared to solitary ascidians in Bermuda, but were more palatable to fish predators than solitary ascidians in Florida (Koplovitz & McClintock 2011). It is difficult to generalize based on these studies because they generally use only a few taxa and lack the phylogenetic corrections necessary to make these comparisons robust.

Increased biotic interactions may increase the number of niche dimensions along which species can differentiate (Mittelbach 2007). Therefore, increased competition and predation in the tropics can lead to an increase in the number of available niches. These niches may be occupied more frequently by colonial ascidians than solitary ascidians if colonial ascidians have a superior ability to survive competition and predation. Occupying more niches means greater opportunities for differentiation and speciation, which could lead to a greater ratio of colonial species than solitary species in the tropics. While there is theoretical support for this hypothesized ecological mechanism for the latitudinal coloniality diversity gradient in ascidians, many of its corollary predictions have not been empirically tested yet.

In this study, we examine whether the latitudinal coloniality diversity gradient in ascidians can be explained by the ecological hypothesis that increased competition and predation at lower latitudes favors colonial ascidians. If this hypothesis is correct, then we should expect to find: 1) a latitudinal gradient in the relative abundance of colonial versus solitary species, not just in the diversity of the two forms, and 2) a higher proportion of colonial species not just at low latitudes, but also at shallower depths, where predation and competition are generally stronger for marine organisms (Harper & Peck 2016, Ashford et al. 2018). In addition, we address whether the latitudinal coloniality diversity gradient in ascidians is robust, by examining whether this pattern is confounded by a longitudinal pattern or latitudinal variation in sampling effort, coastline length, or sample occurrence depth. To examine these questions, we used a combination of ascidian species occurrence data from publicly available global biodiversity databases and ascidian abundance data from settlement plates that were deployed in bays and marinas around the world.

METHODS

Our overall approach was to first verify the overall pattern of a higher relative richness of colonial species at lower latitudes. Then, we examined whether our data was consistent with an ecological explanation for that pattern by examining relationships between: 1) latitude and the relative abundance of colonial ascidians, and 2) depth and the relative richness of colonial species. Finally, we investigated if the overall pattern of a higher relative richness of colonial species at lower latitudes was robust by creating models of species richness and relative richness that combined multiple predictors (latitude, longitude, sampling effort, coastline length, sample occurrence depth). All analyses were performed using R Statistical Software (v4.2.2; R Core Team 2022).

Ascidian species occurrence data collection

We retrieved ascidian species occurrence data from the publicly available Ocean Biogeographic Information System (OBIS 2022) and the Global Biodiversity Information Facility (GBIF 2022) databases. We started by downloading all records for the class Ascidiacea from both databases, which consisted of 236,865 records from OBIS and 319,879 records from GBIF. Data filtering consisted of several steps. We excluded all records not identified to species, missing coordinates, or missing a sampling year. We also excluded records of zero abundance or absence records. Using the package *CoordinateCleaner* (v2.0.20, Zizka et al. 2019), we removed spurious records with 0,0 coordinates or identical latitude and longitude using the functions *cc_zero* and *cc_equ*, respectively. Using the same package, we removed duplicate records (defined as records with the same species, latitude, longitude, species, and year) using the function *cc_dupl*. We also excluded records that were flagged as "country coordinate mismatch" by GBIF and "on land" by OBIS. We then visually inspected the remaining records plotted on a global map and removed any records that were obviously on land. Finally, we removed any records with species names that did not match the valid species names present in the Catalogue of Life (COL) checklist (Bánki et al. 2022). After all of our data filtering, we had 246,998 records total (116,084 from OBIS and 130,914 from GBIF), which included records from 1,912 species (65% of the 2,964 ascidian species listed in COL). We then assigned each species in the database a lifestyle (solitary or colonial) based on their original taxonomic description.

Ascidian abundance data collection

To gather ascidian abundance data, we leveraged existing settlement plate data from previously published studies by two research groups, the Smithsonian Environmental Research Center (SERC) and the Global Approach by Modular Experiments (GAME) program. Both research groups have conducted standardized surveys of fouling communities by deploying settlement plates at locations around the world. At each location, settlement plates are hung from docks or other structures, allowing marine fouling species to settle and grow on the plates for a specific period of time, before the resulting plate community is quantified. Previous studies have shown that settlement plates provide a sensitive and standardized method for assessing the composition of the marine fouling community at a given location (Marraffini et al. 2017).

The GAME data (described in detail in Canning-Clode & Wahl 2010) consisted of settlement plate data from 23 studies conducted at 16 sites in Europe, Asia, South America, and Oceania between 2003 to 2007. To standardize the sampling effort across sites, we only used the data from one study per site. At each site, six 15x15 cm polyvinylchloride (PVC) untreated control plates were submerged at 0.5 m depth for 5-8 months. The community composition on each plate was estimated by measuring the percent cover of all sessile species >1 mm in size, in steps of 5%. To facilitate the estimation of percent cover, a 15x15 cm plastic wire grid was laid over the settlement plates. A 1-cm wide margin at all sides of the panels was ignored to avoid edge effects. Total percent cover was allowed to exceed 100% when there were multiple layers of growth. We excluded any sites where there were no ascidians or “unknown” ascidians recorded, which resulted in 9 remaining sites (see Appendix, Figure 1.A1 for map of sites).

The SERC data (described in detail in Simkanin et al. 2016) consisted of settlement plate data from 363 sites around North America, Australia, and Hawaii collected between 2000 to 2017. We excluded sites where there were no ascidians recorded, which resulted in 270 remaining sites (see Appendix, Figure 1.A1 for map of sites) in 39 total bays. At the vast majority (93%) of sites, 5-6 14x14 cm PVC plates were deployed at each site, but the number ranged from 2-13 plates across all of the sites. Plates were deployed in late spring or early summer, during the usual peak of larval recruitment (colonization), and remained in the field for three months to allow sufficient community development. The community composition of each plate was estimated using a point count grid of 20 or 50 points per panel. The morphotaxa (e.g., ascidian, bryozoan, etc.) or bare space located under each point was recorded. For organisms directly attached to the panel, their structure (colonial or solitary) was also recorded.

Data Analysis

Latitudinal trends in the relative richness of colonial ascidian species

To examine how the proportion of colonial ascidian species varies with latitude and longitude, we sorted the species occurrence records into 10°x10° cells and calculated the proportion of ascidian species recorded in each cell that are colonial (Figure 1A). We excluded any 10°x10° cells with an insufficient sampling effort, defined here as fewer than 10 species recorded in that cell. To examine how the proportion of colonial ascidian species varies with latitude, we sorted the species occurrence records into 10° latitudinal bins and calculated the proportion of ascidian species recorded in each bin that are colonial (Figure 1B).

Latitudinal trends of solitary and colonial ascidian abundance

To examine how the relative abundance of colonial ascidians varies with latitude, we sorted the sites where settlement plate data was collected into 10° latitudinal bins. Given the paucity of sites in some of the latitudinal bins, we decided to collapse the bins by absolute latitude (e.g, so the sites 30-40°N and 30-40°S are in a single 30-40° bin). At each site, we calculated the proportion of panels with solitary ascidians and the proportion of panels with colonial ascidians, as measures of solitary ascidian abundance and colonial ascidian abundance, respectively. We chose to use the proportion of panels occupied by solitary or colonial ascidians, rather than the average percent cover of solitary or colonial ascidians, because with the small panels utilized in this data collection, the proportion of panels occupied is a better overall measure of a species' abundance at a given site than percent cover. For example, a species could be rare at a site but have a high percent cover on a single panel because it was able to colonize that particular panel first. We calculated the ratio of colonial to solitary proportions (by dividing the proportion of panels with colonial ascidians by the proportion of panels with solitary ascidians) to estimate the relative abundance of colonial ascidians at each site. Finally, we calculated the mean (± SE) proportion of panels with solitary ascidians, proportion of panels with colonial ascidians, and the ratio of colonial to solitary proportions in each 10° latitudinal bin.

Depth trends in solitary and colonial ascidian species richness

To examine how the proportion of colonial ascidian species varies with depth, we sorted the species occurrence records into depth bins. This required excluding any records that did not include a sampling depth, which resulted in 98,529 (40%) records retained. Because the number of records available declines exponentially with depth, we defined the depth bins logistically so there would be a more equal distribution of records per depth bin. So we defined the first depth bin from 0–2m (2^1 = 2m range), the second depth bin from 2–6m (2^2 = 4m range), the third depth bin from 6–14m (2^3 = 8m range), etc. There was a very small number of records (18 total; 0.02%)

with non-negative depths, so we chose to exclude them from this analysis. After sorting the species occurrence records into these depth bins, we calculated the number of solitary species, the colonial species , and the proportion of colonial species recorded in each bin.

Multivariable analysis of absolute and relative richness of colonial and solitary species

We built generalized linear models (GLMs) for two purposes. First, we wanted to examine whether the higher relative richness of colonial species at lower latitudes could be explained by some confounding factor. For example, if sampling depth was correlated with latitude, then the higher relative richness of colonial species at lower latitudes might actually be driven by depth instead of latitude. Second, we wanted to investigate how solitary and colonial ascidian species richness are related to various predictor variables. We did not take this approach with the abundance data because there were too few data points for this robust analysis.

We created separate models for our three response variables: 1) colonial ascidian species richness, 2) solitary ascidian species richness, and the 3) proportion of ascidian species that are colonial. We sorted the species occurrence records into 10°x10° cells and calculated the response variables listed above for each cell. Because depth was one of the predictors in our models, we excluded any records that did not include a sampling depth. We only included cells in our analyses with at least one record, which included 278 cells total (of the 648 10°x10° cells possible). Our models of colonial species richness and solitary species richness assumed a negative binomial error, as appropriate for overdispersed count data (Dunn & Smyth 2018). Our model of the colonial species proportion assumed a quasi-binomial error, which is used for overdispersed proportion data (Dunn & Smyth 2018).

All of the global models contained the following predictors (calculated for each 10°x10° cell): number of records, median record depth, latitude, longitude, and coastline length. We included the number of records as a predictor to account for differences in sampling effort across the cells. Coastline length was included as a predictor because it is an indicator of nearshore habitat availability. The number of records and median record depth for each 10°x10° cell were calculated directly from the species occurrence records. The latitude of each 10°x10° cell was calculated as the absolute distance the center of the cell is from the equator. Since the location of the prime meridian is arbitrary, we made longitude a categorical predictor in our models. The longitude categories were defined by 20° bins. The length of the coastline in each 10°x10° cell was derived from a global continents boundary shapefile, established by the Environmental Systems Research Institute (Esri). The shapefile provides a simplified boundary representation for all continents and larger islands. The world's continents were segmented into 10-degree cells utilizing the World Geodetic System (WGS) projection. Notably, the actual length of the coastline varies pending on tidal heights and other factors. This global global continent vector shapefile offers a simplified yet consistent and unbiased estimate of global coastline length. Number of records, median record depth, and coastline length were log-transformed to correct for non-linearity. Following these transformations, we standardized all continuous variables prior to analyses.

For each response variable, we initially built a global model with all of the predictors. We established there were no multicollinearity problems among our predictor variables by checking that the variance inflation factors (VIFs) were less than five. We also established there were no highly influential outliers (Cook’s distance >1) for any of our data points. We compared the performance of models with all possible combinations of predictor variables and assessed the performance of models, using either the small-sample size corrected Akaike information criterion (AICc) for the negative binomial models or the quasi-AIC (QAIC) the quasi-binomial models. We chose to report the top model. Model assumptions were verified by checking validation plots.

The *MASS* (v7.3.58.1, Venables & Ripley 2002) and *stats* packages (v4.2.2., R Core Team 2022) were used to fit the negative binomial and quasi-binomial models, respectively. Variance inflation factors (VIFs) were calculated using the *car* package (v3.1.1, Fox & Weisberg 2019). Model selection was performed using the *MuMIn* package (v1.47.1., Bartoń 2022).

RESULTS

Latitudinal trends in the relative richness of colonial ascidian species

The proportion of colonial species decreased towards the poles (Figure 1.1B), despite some variation among the 10°x10° cells within each 10° latitudinal bin (Figure 1.1A). The highest proportion of colonial species was 69% in the 10-20°S latitude bin, and the lowest proportion of colonial species was 29% in the 70-80°N latitude bin. Solitary species outnumbered colonial species (proportion <0.5) in all the 10° latitudinal bins north of 30°N and south of 50°S.

Latitudinal trends of solitary and colonial ascidian abundance

The abundance of solitary ascidians was highest at our sites furthest from the equator, with 72% of panels containing solitary ascidians on average at sites that were 60-70° from the equator (Figure 1.2A). The abundance of colonial ascidians was highest at our sites closest to the equator, with 64% of panels containing colonial ascidians on average at sites that were within 10° of the equator (Figure 1.2B). Generally, colonial ascidians were more abundant than solitary ascidians at sites closest to the equator, while solitary ascidians were more abundant than colonial ascidians at sites furthest from the equator (Figure 1.2C).

Depth trends in solitary and colonial ascidian species richness

The number of solitary species generally increased in the depth bins from 0-62m, reached a maximum of 232 species in the 62-126m depth bin, and then generally decreased with increasing depth (Figure 1.3A). The number of colonial species increased in the depth bins from 0-30m, reached a maximum of 484 species in the 14-30m depth bin, and then decreased with increasing depth (Figure 1.3B). In general, we found the proportion of colonial species decreased with depth (Figure 1.3C). At depths less than 126m colonial ascidians showed a higher species richness, while at depths greater than 126m solitary ascidians showed a greater species richness. The highest proportion of colonial species was 70% in the 6-14m depth bin, and the lowest proportion of colonial species was 12% in the 2046-4094m depth bin.

Multivariable analysis

In 10°x10° cells, the species richness of colonial ascidians and proportion of ascidian species that are colonial, both decreased with increasing latitude, even after accounting for effects of other potentially correlated variables. Both measures increased with the number of records per cell, decreased with the median depth of records in the cell, and varied significantly among some of the longitudinal bins (see Appendix, Table 1.A1, 1.A3). There was no relationship between colonial ascidian richness or proportion and coastline length.

After accounting for correlated variables, solitary ascidian species richness was uncorrelated with latitude, but increased with the number of records per cell, increased with the median depth of records in the cell, increased with coastline length in the cell, and varied significantly among some of the longitudinal bins (see Appendix, Table 1.A2).

DISCUSSION

Many studies have noted that there are more colonial ascidian species at low latitudes while solitary ascidian species are more numerous at high latitudes (Jackson 1977, Kott 1981, Shenkar & Swalla 2011, Moreno et al. 2014, Hiebert et al. 2019). However, previous studies have not explored whether this latitudinal coloniality diversity gradient could be explained by a longitudinal pattern (for example, driven primarily by high diversity in one region of the tropics) or latitudinal variation in some other confounding factor such as coastline length or sampling intensity. Using species occurrence data from two global biodiversity databases, OBIS and GBIF, we demonstrate that this latitudinal coloniality diversity gradient is robust. Our modeling results indicate the proportion of colonial species decreases with distance from the equator, even after accounting for longitudinal variation and latitudinal variation in sampling effort, coastline length, and sample occurrence depth. The higher relative richness of colonial species at low latitudes seems to be driven largely by increases in the number of colonial species at low latitudes. We found no relationship between latitude and solitary species richness.

The most commonly proposed explanation for the higher relative richness of colonial species at lower latitudes is the ecological hypothesis that increased competition and predation at lower latitudes favors colonial ascidians. Biotic interactions are generally more intense in the tropics (Schemske et al. 2009, Freestone et al. 2011, Ashton et al. 2022). Space is often the most important limiting resource in hard substratum environments with competition for space driving community assembly (Connell 1961, Dayton 1971, Paine 1974). Colonial organisms are thought to be superior space competitors in these environments because they can occupy additional space through somatic growth, while solitary organisms must rely on sexual recruitment (Jackson 1977). Colonial organisms are also hypothesized to be less susceptible to predation than solitary organisms because they can better survive and regrow following partial mortality (Winston 2010). Recently, Ashton et al. (2022) tested predator control of marine communities through standardized experiments across 115° latitude and found that the dominance of solitary ascidians was strongly reduced in the presence of predators, giving credence to the hypothesis that the dominance of colonial ascidians in the tropics is related to their increased resistance to predation.

To evaluate the ecological hypothesis for the latitudinal coloniality diversity gradient we tested two corollary predictions and found support for both of them. The first prediction was that if there is a higher relative richness of colonial species at lower latitudes because increased competition and predation there favors colonial ascidians, then there should be a latitudinal gradient in the *relative abundance* of colonial versus solitary species, not just in the *species richness* of the two forms. Our analysis of ascidian abundance from settlement plates deployed worldwide showed the relative abundance of colonial ascidians generally decreases with distance from the equator. Unexpectedly, the relative abundance of colonial ascidians was highest not in the latitudinal bins closest to the equator (0-10°), but 20-30° from the equator. Our results (Figure 1.1) and Hiebert et al. (2019) have shown a similar depression in the ratio of colonial-to-solitary ascidian species richness around the equator, suggesting this departure represents some real phenomenon and that the two may be connected. Predation rates in other marine systems have been shown to peak at this same latitude and decline at the equator (Whalen et al. 2020), suggesting predation intensity as a potential mechanism driving the non-equatorial peak in coloniality.

The second prediction was that if lower latitudes have a higher relative richness of colonial species because increased competition and predation there favors colonial ascidians, then there should also be a higher relative richness of colonial species at shallower depths, where predation and competition are generally stronger for marine organisms (Harper & Peck 2016, Ashford et al. 2018). Our analysis of global ascidian species occurrence data showed that the proportion of colonial species generally decreased with depth. In contrast, a recent study quantifying ascidian communities in the Mediterranean Sea across depths ranging from 38-693m did not find a clear relationship between depth and the proportion of colonial ascidians (Arroyo et al. 2021). This suggests the large-scale biogeographic patterns described here might not be apparent at smaller, regional scales, especially those with limited depth ranges.

The higher relative richness of solitary species at higher latitudes and deeper depths has received less attention than the dominance of colonial species at lower latitudes and shallower depths, but there have been several hypotheses proposed to explain this phenomenon. First, much of the benthos in the Antarctic and deep sea is composed of soft sediment (Shenkar & Swalla 2011), and many ascidian species are unable to form attachments with this loose substrate (Millar 1971). Adaptations for living in this habitat, which include the development of filaments for anchoring to the sediment or morphological changes that allow an interstitial lifestyle, have evolved primarily in solitary lineages (Millar 1971). Second, soft sediment habitats are often subject to high sedimentation, which can inhibit ascidian filter-feeding and respiration (Torre et al. 2012, 2014). Solitary species possess an advantage over encrusting colonial species in these environments because they are often stalked and can use vertical growth to elevate their siphons above the substrate (Shenkar & Swalla 2011, Arroyo et al. 2021). Third, solitary ascidians generally have a higher potential for dispersal because they are usually broadcast spawners, while colonial species are typically brooders (Ayre et al. 1997). It has been suggested that this greater dispersal ability gives solitary ascidians an advantage over colonial ascidians in high latitude communities where anchor ice formation and ice scouring are frequent agents of disturbance (Shenkar & Swalla 2011).

While we demonstrated results that were consistent with the hypothesis that increased competition and predation at lower latitudes favors colonial ascidians, the higher relative richness of colonial species at lower latitudes could be due to some other unexplored mechanisms. Many processes, besides competition and predation, vary with latitude. For example, other biotic interactions such as mutualism, parasitism, and disease, are also generally more intense at low latitudes (Schemske et al. 2009). Although there is no evidence to suggest that these processes are important in shaping ascidian biodiversity patterns, we cannot rule out this possibility.

Furthermore, differences between colonial and solitary ascidian richness across latitude might be driven largely by historical or evolutionary processes rather than ecological processes. For example, colonial ascidians are more dispersal limited and show greater population differentiation (Ayre et al. 1997), which has been associated with greater diversification rates in other animals, such as beetles and spiders (Suárez et al. 2022) and New World birds (Harvey et al. 2017). Colonial ascidian lineages may simply have originated more frequently in the tropics, leading them to have a higher relative richness there. It was beyond the scope of this study to test evolutionary and historical hypotheses for the latitudinal coloniality diversity gradient. Ancestral state reconstruction has proven a useful method for understanding the evolution of coloniality in other animals, such as scleractinian corals (Barbeitos et al. 2010), hydrozoans (Cartwright & Nawrocki 2010), cnidarians (Kayal et al. 2018). Unfortunately, current phylogenies of Ascidiacea are insufficient for this approach because they are either: 1) constructed with a single or a couple markers (e.g., Stach & Turbeville 2002, Turon & López-Legentil 2004, Zeng et al. 2006, Tsagkogeorga et al. 2009, Pérez-Portela et al. 2009), leading to poorly resolved trees with low node supports and polytomies or 2) constructed with many markers but sparse sampling (e.g., Alié et al. 2018, Delsuc et al. 2018, Kocot et al. 2018), obscuring key transitions between solitary and colonial states.

There is evidence to suggest that other animals exhibit similar biogeographic patterns in coloniality as ascidians. For example, the few solitary bryozoan species that have been discovered have distributions largely restricted to deeper waters (Schwaha et al. 2019). Solitary scleractinian corals are generally absent from shallow tropical reefs but show wider geographic and bathymetric distributions than their colonial counterparts (Barbeitos et al. 2010). In corals, these biogeographic patterns have been attributed to the correlated evolution of symbiosis and coloniality in this group, which restrict most colonial species to the photic zone (Barbeitos et al. 2010). In contrast, hemichordates show opposite biogeographic patterns in coloniality to the taxa above. This group consists of solitary enteropneusts and colonial pterobranchs, with the distribution of most colonial pterobranchs, unlike solitary enteropneusts, largely restricted to deep sea and southern polar regions (Tassia et al. 2016). Uncovering geographic patterns in coloniality in these other groups and testing the mechanisms that drive these patterns could reveal key insights into the ecological and evolutionary consequences of coloniality in marine animals.

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FIGURES

Figure 1.1. Proportion of species that are colonial in 10°x10° cells (A) and 10° latitudinal bins (B). Only 10°x10° cells with at least 10 species recorded are shown. There is no bar for the 80° to 90°S latitudinal bin because there were no records available for that bin. The numbers inside the bars refer to the total number of species recorded in that latitudinal bin. The dashed line indicates equal proportions of solitary and colonial species.

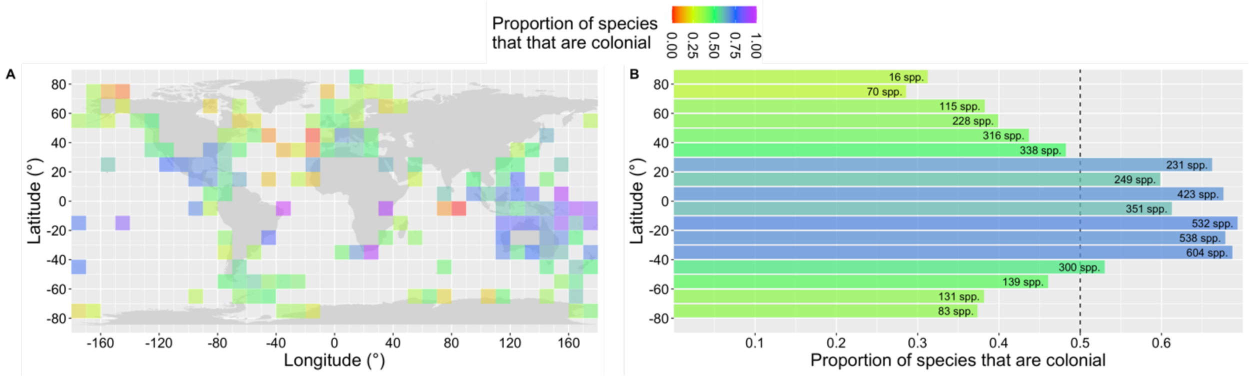


Figure 1.2. The mean (± SE) proportion of panels with solitary ascidians (A) and colonial ascidians (B), and the ratio of colonial to solitary proportions (C) in 10° absolute value latitudinal bins. The numbers inside the bars refer to the number of sites per latitudinal bin. The dashed line indicates equal proportions of panels with solitary ascidians and panels with colonial ascidians.

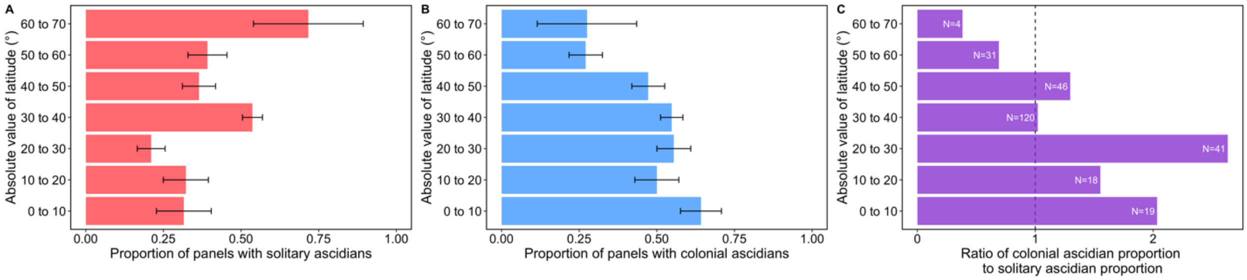
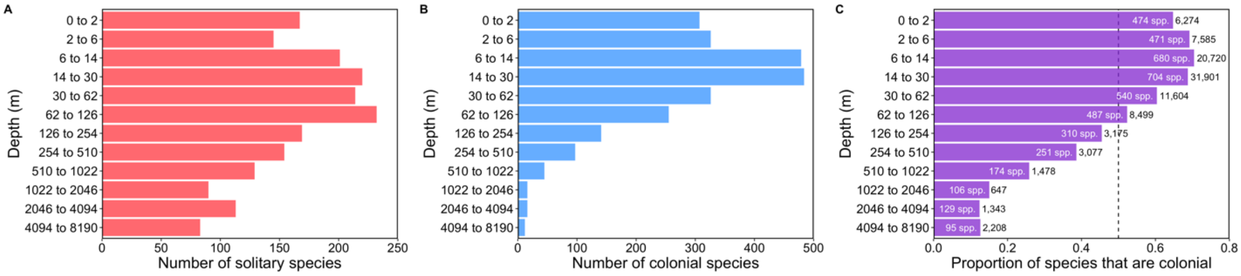


Figure 1.3. The number of solitary species (A), colonial species (B), and proportion of species that are colonial (C) by depth. Note, the depth bins are based on a log-scale. The numbers inside the bars refer to the total number of species recorded in that depth bin. The numbers outside the bars refer to the number of records from that depth bin. The dashed line indicates equal proportions of solitary and colonial species.



APPENDIX

Figure 1.A1. Sites where ascidian abundance data was collected, colored by dataset.

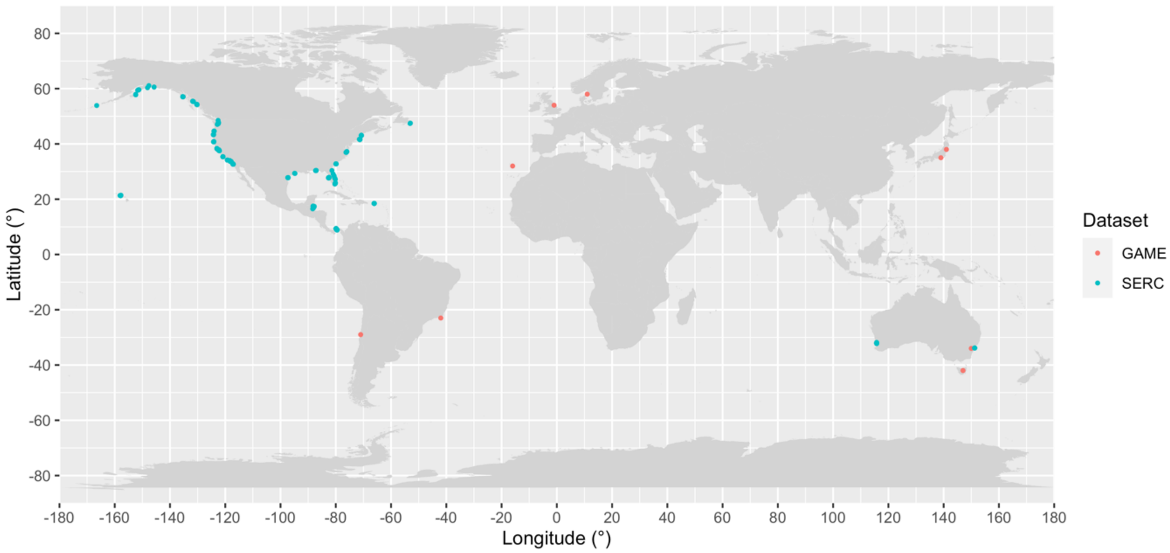


Table 1.A1. Model results from analysis evaluating potential predictors for colonial ascidian species richness. Results from the best model shown below. 'NA" indicates that the predictor was present in the global model, but not the best model. All continuous variables were standardized prior to the analysis. Significant predictors ($\alpha < 0.05$) shown in bold.

	Estimate	**Std. error**	***z*-value**	***p*-value**
Intercept	**1.435**	**0.188**	**7.619**	**<0.001**
Log(records)	**1.323**	**0.056**	**23.534**	**<0.001**
Log(depth + 1)	**-0.423**	**0.064**	**-6.623**	**<0.001**
Log(coastline length + 1)	--	--	--	--
|Latitude|	**-0.316**	**0.058**	**-5.454**	**<0.001**
Longitude bin -160° to -140°	-0.434	0.315	-1.376	0.169
Longitude bin -140° to -120°	**-1.042**	**0.338**	**-3.080**	**0.002**
Longitude bin -120° to -100°	-0.394	0.350	-1.125	0.261
Longitude bin -100° to -80°	-0.513	0.271	-1.894	0.058
Longitude bin -80° to -60°	-0.432	0.242	-1.784	0.074
Longitude bin -60° to -40°	0.111	0.254	0.438	0.661
Longitude bin -40° to -20°	-0.140	0.287	-0.489	0.625
Longitude bin -20° to 0°	**-0.951**	**0.273**	**-3.483**	**<0.001**
Longitude bin 0° to 20°	-0.466	0.262	-1.781	0.075
Longitude bin 20° to 40°	-0.052	0.269	-0.195	0.846
Longitude bin 40° to 60°	**-0.796**	**0.317**	**-2.508**	**0.012**

Longitude bin 60° to 80°	**-0.828**	**0.413**	**-2.003**	**0.045**
Longitude bin 80° to 100°	-0.544	0.477	-1.141	0.254
Longitude bin 100° to 120°	0.458	0.285	1.606	0.108
Longitude bin 120° to 140°	0.471	0.259	1.820	0.069
Longitude bin 140° to 160°	0.446	0.246	1.813	0.070
Longitude bin 160° to 180°	0.340	0.249	1.368	0.171

Table 1.A2. Model results from analysis evaluating potential predictors for solitary ascidian species richness. Results from the best model shown below. Dashes indicate that the predictor was present in the global model, but not the best model. All continuous variables were standardized prior to the analysis. Significant predictors ($\alpha < 0.05$) shown in bold.

	Estimate	**Std. error**	***z*-value**	***p*-value**
Intercept	**1.869**	**0.128**	**14.641**	**<0.001**
Log(records)	**1.034**	**0.038**	**27.549**	**<0.001**
Log(depth + 1)	**0.218**	**0.043**	**5.125**	**<0.001**
Log(coastline length + 1)	**0.158**	**0.045**	**3.504**	**<0.001**
|Latitude|	--	--	--	--
Longitude bin -160° to -140°	-0.062	0.208	-0.300	0.764
Longitude bin -140° to -120°	-0.052	0.205	-0.252	0.801
Longitude bin -120° to -100°	-0.126	0.223	-0.565	0.572
Longitude bin -100° to -80°	-0.039	0.179	-0.220	0.826
Longitude bin -80° to -60°	-0.105	0.164	-0.640	0.522
Longitude bin -60° to -40°	-0.032	0.172	-0.184	0.854
Longitude bin -40° to -20°	-0.128	0.184	-0.694	0.487
Longitude bin -20° to 0°	-0.116	0.168	-0.686	0.493
Longitude bin 0° to 20°	**-0.496**	**0.174**	**-2.849**	**0.004**
Longitude bin 20° to 40°	**-0.497**	**0.197**	**-2.522**	**0.012**
Longitude bin 40° to 60°	-0.037	0.189	-0.193	0.847

Longitude bin 60° to 80°	0.212	0.214	0.989	0.323
Longitude bin 80° to 100°	-0.120	0.274	-0.439	0.660
Longitude bin 100° to 120°	0.281	0.201	1.399	0.162
Longitude bin 120° to 140°	0.236	0.179	1.318	0.188
Longitude bin 140° to 160°	**0.382**	**0.165**	**2.312**	**0.021**
Longitude bin 160° to 180°	0.114	0.172	0.664	0.507

Table 1.A3. Model results from analysis evaluating potential predictors for the proportion of ascidian species that are colonial. Results from the best model shown below. Dashes indicate that the predictor was present in the global model, but not the best model. All continuous variables were standardized prior to the analysis. Significant predictors ($\alpha < 0.05$) shown in bold.

	Estimate	**Std. error**	***t*-value**	***p*-value**
Intercept	**-0.422**	**0.200**	**-2.113**	**0.036**
Log(records)	**0.236**	**0.058**	**4.055**	**<0.001**
Log(depth + 1)	**-0.577**	**0.070**	**-8.297**	**<0.001**
Log(coastline length + 1)	--	--	--	--
|Latitude|	**-0.317**	**0.060**	**-5.252**	**<0.001**
Longitude bin -160° to -140°	-0.439	0.324	-1.353	0.177
Longitude bin -140° to -120°	**-1.256**	**0.322**	**-3.902**	**<0.001**
Longitude bin -120° to -100°	-0.389	0.354	-1.101	0.272
Longitude bin -100° to -80°	-0.281	0.267	-1.051	0.294
Longitude bin -80° to -60°	-0.393	0.238	-1.652	0.100
Longitude bin -60° to -40°	0.194	0.260	0.745	0.457
Longitude bin -40° to -20°	0.080	0.295	0.271	0.786
Longitude bin -20° to 0°	**-0.897**	**0.255**	**-3.518**	**0.001**
Longitude bin 0° to 20°	-0.340	0.257	-1.322	0.187
Longitude bin 20° to 40°	0.404	0.294	1.376	0.170

Longitude bin 40° to 60°	**-0.840**	**0.376**	**-2.232**	**0.026**
Longitude bin 60° to 80°	**-0.952**	**0.460**	**-2.071**	**0.039**
Longitude bin 80° to 100°	-0.527	0.640	-0.824	0.411
Longitude bin 100° to 120°	0.335	0.266	1.259	0.209
Longitude bin 120° to 140°	0.284	0.248	1.148	0.252
Longitude bin 140° to 160°	0.134	0.231	0.582	0.561
Longitude bin 160° to 180°	0.212	0.239	0.886	0.376

CHAPTER 2

Ascidians demonstrate Rapoport's bathymetric rule possibly due to biogeographic variation in coloniality

ABSTRACT

Rapoport's rules have been the focus of many studies and subject to much controversy over the last fifty years. Several authors have dismissed the generality of these rules, but these conclusions are tenuous given that most previous studies suffer from methodological constraints and lack null model comparisons. We investigated whether Rapoport's latitudinal and bathymetric rule apply to ascidians, a broadly distributed group of marine invertebrates, using a combination of empirical data and null models. In addition, we compared the ranges of colonial and solitary ascidians to assess whether the differing dispersal abilities of these species might contribute to the support of Rapoport's rules in this group. Our global analysis of the bathymetric distributions of 537 ascidian species demonstrated that the median bathymetric range increased with latitude for both the northern and southern hemispheres, which is consistent with Rapoport's bathymetric rule, although only the regression slope for the southern hemisphere was significantly greater than the slopes predicted by the null model simulations. Our global analysis of the latitudinal distributions of 803 ascidian species showed median latitudinal range decreased with latitude for both the northern and southern hemispheres, which is the opposite pattern predicted by Rapoport's latitudinal rule. However, the empirical regression slopes for both hemispheres were not significantly different from the slopes predicted by the null model simulations, indicating these patterns could be produced by chance and are not biologically meaningful. Our comparison of solitary and colonial ascidians demonstrated that solitary ascidians generally have larger latitudinal and bathymetric ranges. Given that the proportion of solitary ascidians increases with latitude, the greater ranges of

solitary ascidians may explain the correlation between latitude and bathymetric ranges in this group. Further studies are needed to establish the generality and resolve the mechanisms underlying Rapoport's bathymetric rules for marine organisms.

INTRODUCTION

Argentinian ecologist Eduardo H. Rapoport first noted that species at higher latitudes tend to have larger geographic ranges (Rapoport 1975/1982). Two decades later, the correlation between geographical ranges and latitude was coined Rapoport's rule by Stevens (1989). Stevens' explanation for this phenomenon, which is known as the climate variability or seasonal variability hypothesis, is that the greater seasonal variability at higher latitudes selects for species with greater climatic tolerances, which allows them to occupy larger geographical ranges. Using the same logic, Stevens later extended Rapoport's latitudinal rule to two other biogeographical gradients, elevation (Stevens 1992) and depth (Stevens 1996). Like species at higher latitudes, he reasoned species at higher elevations experience a greater range of climatic conditions, which should lead to broader tolerances and larger altitudinal ranges (Rapoport's altitudinal rule). Similarly, sea surface waters show greater seasonal variation in temperature at high latitudes. During the winter, shallow and deep waters are similarly cold at high latitudes. In contrast, at low latitudes, shallow waters remain warm and deep waters remain cool throughout the year. Consequently, marine species at higher latitudes should be expected to have broader depth ranges (Rapoport's bathymetric rule). Theoretically, Rapoport's phenomena could be detected along any biogeographically important gradient, such as gradients in soil moisture, salinity, or toxicity (Stevens 1996).

In the half century since Rapoport first made his observation about the relationship between latitude and range sizes, the generality of Rapoport's rules and the methods used to evaluate them have been questioned. While some subsequent studies have found support for

Rapoport's rules (e.g., Pagel et al. 1991, France 1992, Moreno et al. 2008, Fortes & Absalão 2004, 2010, Luo et al. 2011, Murphy et al. 2020), others have found no support (e.g, Rohde et al. 1993, Roy et al. 1994, Smith et al. 1994, Hughes et al. 1996, Anglielczyk et al. 2015, Macek et al. 2021), or even evidence for the opposite of Rapoport's rules (e.g., Hecnar 1999, Tomašových et al. 2015, Pie et al. 2021). Some studies have dismissed the universality of Rapoport's latitudinal rule and have suggested it is instead a local phenomenon restricted to high latitudes in the northern hemisphere (Rohde 1996, Gaston et al. 1998, Gaston & Chown 1999, Hernández et al. 2005). The totality of these studies has led some authors to conclude that support for the generality of Rapoport's rules is at best equivocal (Gaston et al. 1998, Hecnar 1999, Ruggiero & Werenkraut 2007), with some even downgrading their status as rules by instead labeling them instead as "Rapoport's effects" (Gaston et al. 1998).

One reason that previous studies have drawn such different conclusions, besides focusing on different regions and taxa, is the different methods they have employed to test the rules. A meta-analysis of several studies on Rapoport's latitudinal rule demonstrated that the method of analysis used to show latitudinal variation in range size is a strong moderator of the magnitude of Rapoport's pattern (Ruggiero & Werenkraut 2007). Two of the most commonly used methods of analysis, Stevens' (1989) method and Rohde et al.'s (1993) midpoint method, suffer from several statistical problems. Stevens' method involves dividing the study area into latitudinal bands and calculating the mean (or median or mode) latitudinal range for all species found within each band. This method has been criticized because: 1) the latitudinal bands are not independent because many species occur in more than one band (but see Fortes & Absalão 2004), 2) wide-ranging species occur in more than one band and therefore have more influence in the analysis, and 3) species richness generally decreases with latitude, so low-latitude species with wide ranges have a disproportionately large effect on the mean latitudinal range of higher latitude bands, which can lead to a spurious Rapoport effect (Rhode et al. 1993, Pintor et al. 2015). The midpoint method is similar to Stevens' method in that the study area is divided into latitudinal bands, but the average latitudinal range is only calculated for species whose latitudinal midpoints fall within each band. This method has been criticized because: 1) the exclusion of species that are present in an latitudinal band but whose midpoint doesn't fall within the band doesn't make ecological sense (they are subject to the same abiotic and biotic factors as species whose midpoint falls within the band), and 2) this method suffers from inherent geometric constraints (i.e., only small ranging species could have their midpoint at high latitudes) (Fortes & Absalão 2004), which could lead to a spurious inverse Rapoport effect. More recently, studies have addressed these statistical challenges by using randomization to compare results to appropriate null models (e.g., Lyons & Willig 1997, Arita et al. 2005, Ribas & Schoereder 2006, Moreno et al. 2008, Macek et al. 2021). Statistical approaches for evaluating Rapoport's rules that do not involve null models are not able to distinguish between stochastically and deterministically generated patterns (Ribas & Schoereder 2006). The lack of null models in most previous studies of Rapoport's rules calls into question the conclusions drawn about the generality of the rule by analyzing such studies.

Since Rapoport's rule was first conceptualized, other mechanisms have been proposed, besides the climate variability hypothesis, to explain this pattern. One hypothesis, known as the differential extinction hypothesis, suggests the correlation between geographical ranges and latitude may be present because species at high latitudes with narrow tolerances underwent differential extinction due to climate change and glaciation (Stevens 1996, Gaston et al. 1998). This hypothesis is less likely to apply to the southern hemisphere or marine environments, where the impact of earth's climatic variation is thought to be less important (Stevens 1996, Gaston et al. 1998). Another hypothesis, known as the competition hypothesis, suggests that the high species richness in the tropics results in higher competition, which may limit range sizes (Stevens 1996, Gaston et al. 1998). Other mechanisms, related to land area or biogeographical boundaries, have also been proposed (Gaston et al. 1998). As with several other macroecological patterns, no single mechanism may be adequate to explain all instances of Rapoport's rules (Gaston et al. 1998).

Ascidians, also known as sea squirts, are the largest and most diverse class of Tunicata (Shenkar & Swalla 2011). This paraphyletic group is composed of roughly 3,000 described species (Shenkar et al. 2019), which are exclusively marine but have radiated to occupy a diversity of habitats, ranging from shallow water to the deep sea (Holland 2016). Ascidians present an interesting opportunity to test the validity of Rapoport's rules because these patterns may be driven by a novel mechanism in this group. Coloniality has evolved multiple times within Ascidiacea (Swalla et al. 2000), and roughly 60% of all described ascidian species are colonial (Shenkar & Swalla 2011). Colonial species tend to be brooders with a shorter larval duration, while solitary species tend to be broadcast spawners with a longer larval duration (Tarjuelo & Turon 2004, Brown & Swalla 2012). Consequently, solitary species tend to have much greater dispersal abilities than colonial species (Ayre et al. 1997), which suggest they may also have larger geographic or bathymetric ranges. Solitary species are also more likely to inhabit deeper depths because they can survive better in soft sediment habitats, which are difficult to attach to and often have high sedimentation rates (Millar 1971, Shenkar & Swalla 2011, Arroyo et al. 2021). Given that the ratio of solitary-to-colonial species increases from the tropics to the poles (Hiebert et al. 2019), we might expect to find the geographic and bathymetric ranges of ascidians also increasing with latitude. In this study, we test the validity of Rapoport's latitudinal and bathymetric rules in ascidians using a combination of empirical data and null models. In addition, we test whether the latitudinal and bathymetric ranges of ascidians differ by lifestyle (colonial vs. solitary), which would lend support to the novel mechanisms for Rapport's rules proposed above.

METHODS

We gathered ascidian species occurrence data from the publicly available Ocean Biogeographic Information System (OBIS 2022) and the Global Biodiversity Information Facility (GBIF 2022) databases. We began by downloading all records for the class Ascidiacea from both databases, which included 237,156 records from OBIS and 319,371 records from GBIF.

Data filtering consisted of the following steps. First, we excluded all records that were not identified to species, missing coordinates, missing a sampling year, had negative (above sea level) depths, or were records of absence or zero abundance. Second, using the package *CoordinateCleaner* (v2.0.20, Zizka et al. 2019), we removed spurious records with 0,0 coordinates or identical latitude and longitude using the functions *cc_zero* and *cc_equ*, respectively. Using the same package, we removed duplicate records (defined as records with the same species, latitude, longitude, species, and year) using the fiction *cc_dupl*. Third, we removed records that were flagged as "country coordinate mismatch" by GBIF and "on land" by OBIS. Fourth, we plotted the remaining records on a global map and excluded any records that were obviously on land, based on a visual inspection. Finally, we removed records with species names that were not considered valid according to the Catalogue of Life (COL) checklist (Bánki et al. 2022). After these data filtering steps, we had 248,389 records total, which included records from 1,929 species (65% of the 2,964 ascidian species listed in COL). We then assigned each species in the database a lifestyle (solitary or colonial) on their original taxonomic description.

To exclude species that were insufficiently sampled to estimate their ranges, we only analyzed species with more than 10 records, which included 803 species with a total of 244,383 records. This is the dataset we used for all analyses focused on latitudinal ranges. For analyses of bathymetric ranges, we excluded records without a depth reported. This smaller dataset consisted of 98,973 records total, which included records from 1,574 species. Again, we excluded species with 10 or fewer records, which resulted in 537 species with a total of 95,464 records for the bathymetric analyses.

We determined species' latitudinal ranges as the one-dimensional distance between the minimum and maximum latitude recorded for that species in our dataset. Bathymetric ranges were defined as the one-dimensional distance between the minimum and maximum depth recorded for that species in our dataset. We tested for Rapoport's rule in the latitudinal and bathymetric distributions of ascidians using Stevens' method, which is considered less sensitive to geometric constraints and more intuitive for interpretation of range size patterns than the midpoint method (Macek et al. 2021). For our analysis of latitudinal ranges, we calculated the median latitudinal range of all the species present in each 5° degree latitudinal band and then performed a linear regression of median latitudinal range on latitude. For our analysis of bathymetric ranges, we calculated the median bathymetric range of all the species present in each 5° degree latitudinal band and then performed a linear regression of median bathymetric range on latitude. We chose to calculate the median rather than the mean because the median is less influenced by outliers, and species' latitudinal and bathymetric range size distributions are right-skewed within each latitudinal band, making the mean an inappropriate representation of central tendency (Roy et al. 1994, McCain & Knight 2013). Ideally we would control for phylogeny in our analysis, as some previous studies have done (e.g., Blackburn & Ruggiero 2001, Diniz-Filho & Tôrres 2002, Cruz et al. 2005), but unfortunately there is not yet a complete phylogeny available for ascidians.

To distinguish between stochastically and deterministically generated patterns, we compared our empirical patterns to those generated by simulated null models. Following Arita et al. (2005), we built null models by randomly moving species ranges along the latitudinal domain, without changing their size. Each species was randomly assigned a new position, with the constraint that their range cannot protrude beyond the "soft" boundaries of -78.5° to 81.2° (the maximum and minimum latitude recorded across all the species in our datasets). Following this randomization procedure, we calculated the median latitudinal or bathymetric range for all of the species present in each 5° degree latitudinal band and performed the same linear regression as with the empirical data. Thus, our null model varied the latitudinal position of ranges, while maintaining the same number of species and distribution of range sizes. We performed 10,000 simulations for both our latitudinal and bathymetric analyses to generate a frequency distribution of linear regression slopes. We compared empirical slopes to the distribution of null simulated slopes. We used the percentile of the null distribution that corresponded with the value of the empirical slope to calculate a p-value. For example, if the empirical slope occurred in the lower 2.5% or upper 2.5% of the simulated null distribution of slopes, then the empirical slope was significantly different than expected by chance alone (i.e., two-tailed test, $\alpha = 0.05$).

To compare the latitudinal and bathymetric ranges of ascidians by their lifestyle (solitary vs. colonial), we used Mann-Whitney U tests. We chose to use this non-parametric test, rather than a parametric t-test, because the ranges were not normally distributed. All analyses were performed using R Statistical Software (v4.2.2; R Core Team 2022).

RESULTS

Ascidian latitudinal ranges varied from 0.02° to 146.8°, with a median range of 31.4° (IQR = 14.5-50.2°; N = 803 species; Figure 2.1A). Ascidian bathymetric ranges varied from 0.1m to 6300.7m, with a median range of 169m (IQR = 51.6-754.1m; N = 537 species; Figure 2.1B).

Median latitudinal range decreased with latitude (Figure 2A) for both the northern ($\beta = -0.36$, $R^2 = 0.53$, $P < 0.001$) and southern hemispheres ($\beta = -0.28$, $R^2 = 0.87$, $P < 0.001$). However, the slope of these regressions did not differ significantly from the slopes predicted by the null model simulations (Figure 2.2C; $P = 0.12$ and $P = 0.64$ for the northern and southern hemispheres, respectfully).

Median bathymetric range increased with latitude (Figure 2.2B) for both the northern ($\beta = 7.96$, $R^2 = 0.79$, $P < 0.001$) and southern hemispheres ($\beta = 15.3$, $R^2 = 0.88$, $P < 0.001$). The empirical regression slope for the northern hemisphere was marginally significantly greater than the slopes predicted by the null model simulations (Figure 2.2D; $P = 0.09$). The empirical regression slope for the southern hemisphere was significantly greater than the slopes predicted by the null model simulations (Figure 2.2D; $P < 0.001$).

Overall, solitary ascidians had a significantly larger latitudinal range (Mann-Whitney U test; $P < 0.001$) and bathymetric range (Mann-Whitney U test; $P < 0.001$) than colonial ascidians (Figure 2.3). Colonial ascidians had a median latitudinal range of 26.2° (IQR = 11.5-43.6°, N = 481 species) and median bathymetric range of 66.0m (IQR = 33.0-208.5m, N = 277). Solitary ascidians had a median latitudinal range of 37.8° (IQR = 21.6-65.1°, N = 322) and median bathymetric range of 549m (IQR = 121.6-2051.0m, N = 260).

DISCUSSION

To our knowledge, our study is the first to apply Rapoport's rules in ascidians and the first to explore novel mechanisms for these patterns related to coloniality and dispersal. Our analysis, which included a comparison between empirical and null data, found support for Rapoport's bathymetric rule, but no support for Rapoport's latitudinal rule.

Other studies of marine organisms have failed to find support for Rapoport's latitudinal rule. For example, a study of eastern Pacific marine molluscs found that their latitudinal ranges were uncorrelated with latitude (Roy et al. 1994). Similarly, an analysis of marine teleosts from the Indo-Pacific and Atlantic oceans did not demonstrate Rapoport's latitudinal rule (Rohde et al. 1993). A study of western Pacific, eastern Pacific and western Atlantic marine bivalves found an inverse relationship between range size and latitude, which is the opposite of Rapoport's bathymetric rule (Tomašových et al. 2015).

There are several reasons why Rapoport's latitudinal rule may not apply to marine organisms. Stevens (1996) predicted that Rapoport's latitudinal rule is unlikely to be found in the marine environment because the distribution of marine organisms is three-dimensional, rather than two-dimensional. Tomašových et al. concluded that even though tropical species have narrower thermal ranges than high-latitude species, the nearly constant temperatures over wide areas of the tropics allow tropical species to achieve larger latitudinal ranges. In addition, the distribution of the water masses that are influenced by the global circulation of the marine currents could obscure the influence of latitude (Fortes & Absalão 2010). Furthermore, deep water varies little in temperature over the seasons or with latitude, so analyses of Rapoport's latitudinal rule that include both surface and deep water organisms are less likely to find a correlation between latitudinal range sizes and latitude (Stevens 1996). In contrast, freshwater organisms live in a relatively thin layer of water, and so they do generally exhibit Rapoport's latitudinal rule (Stevens 1989, France 1992, Rohde et al. 1993, Blanchet et al. 2013, Swaegers et al. 2014, but see Outomuro & Johansson 2019).

Rapoport's bathymetric rule has generally received less attention compared to Rapoport's latitudinal rule. Nevertheless, an increase in bathymetric range size with increasing latitude (Rapoport's bathymetric rule) has also been found in Pacific Ocean fishes (Stevens 1996), Northeast Pacific fishes and northwest Atlantic gastropods (Smith & Gaines 2003), marine molluscs on the Pacific and Atlantic coasts of the Americas (Fortes & Absalão 2004), coastal cephalopod fauna in the western (but not eastern) margins of the Atlantic Ocean (Rosa et al. 2008), polychaetes along the Pacific coast of Chile (Moreno et al. 2008), marine bony fishes in 13 ocean regions around the globe with the exception of northern part of the Western Indian Ocean (Fortes & Absalão 2010), and South American Atlantic coast and adjacent Antarctic molluscs (Fortes & Absalão 2011). It is difficult to draw conclusions about the generality of Rapoport's bathymetric rule from these studies because only one of them (Moreno et al. 2008) employed a null model, which is necessary to distinguish between patterns driven by chance and those driven by biological or environmental processes (Ribas & Schoereder 2006).

While determining the exact mechanism(s) for Rapoport's bathymetric rule in ascidians is beyond the scope of this study, we did find evidence that was consistent with a novel mechanism related to coloniality and dispersal. Our analyses demonstrated that solitary ascidians generally have larger latitudinal and bathymetric ranges than colonial ascidians. The increase in the proportion of solitary ascidians increases with latitude (Hiebert et al. 2019) could therefore explain why ascidian bathymetric ranges also increase with latitude. This mechanism is unlikely to apply broadly to other marine invertebrates. Generally pelagic development and feeding larvae are rarer at higher latitudes (Thorson's rule; Thorson 1946, 1950, Marshall et al. 2012). Given that these traits are associated with greater dispersal abilities, most marine invertebrates should have greater dispersal abilities at low latitudes, which means that Rapoport's rule is predicted to not apply or be reversed for most marine invertebrates (Rhode 1999). More work is needed to resolve the exact mechanism(s) that produce Rapoport's bathymetric rule in ascidians, which may be difficult to establish, given how many biological and physical factors covary with latitude. Finally, establishing or rejecting the generality of Rapoport's rules in marine organisms will require many more studies that incorporate null models and mechanistic analyses.

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FIGURES

Figure 2.1. Latitudinal (A) and bathymetric (B) ranges of ascidian species (n = 803 and 537 species, respectively). Species are ordered in terms of their latitudinal range midpoint above and their depth range midpoint below.

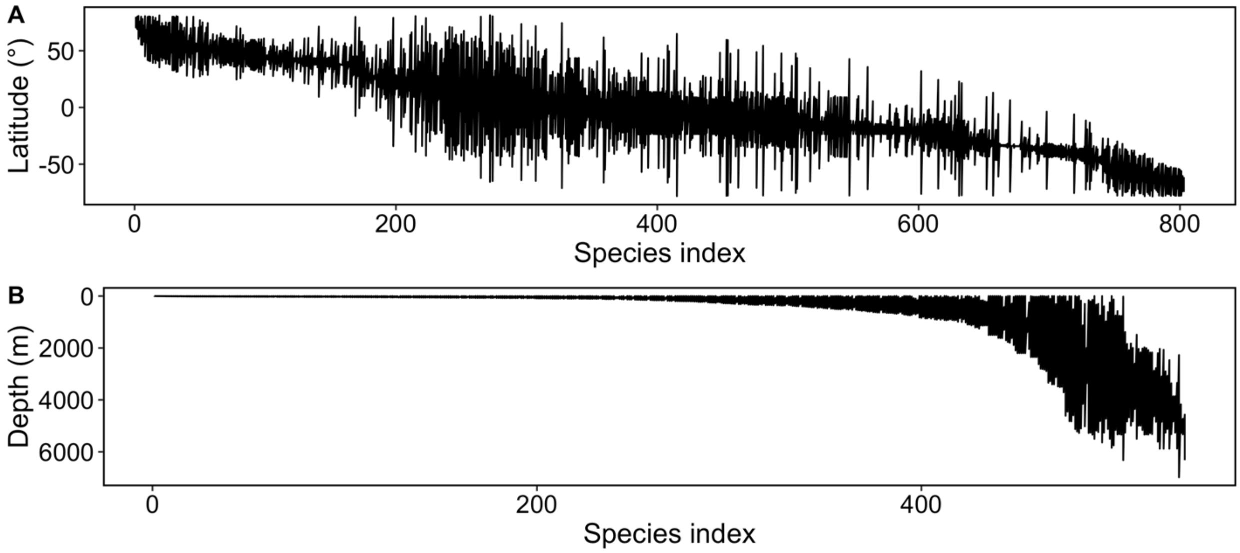


Figure 2.2. Latitudinal and bathymetric ranges of ascidians by latitude, based on empirical data and simulated null predictions. The top figures show the empirical median latitudinal range (A) and median bathymetric range (B) for all species present within each 5° latitudinal band. The bottom figures show histograms of the slopes of the regressions of median latitudinal range (C) and median bathymetric range (D) on latitude for the 10,000 null model simulations. The dotted lines represent the slopes for the empirical data. Regressions were conducted separately for the northern and southern hemispheres.

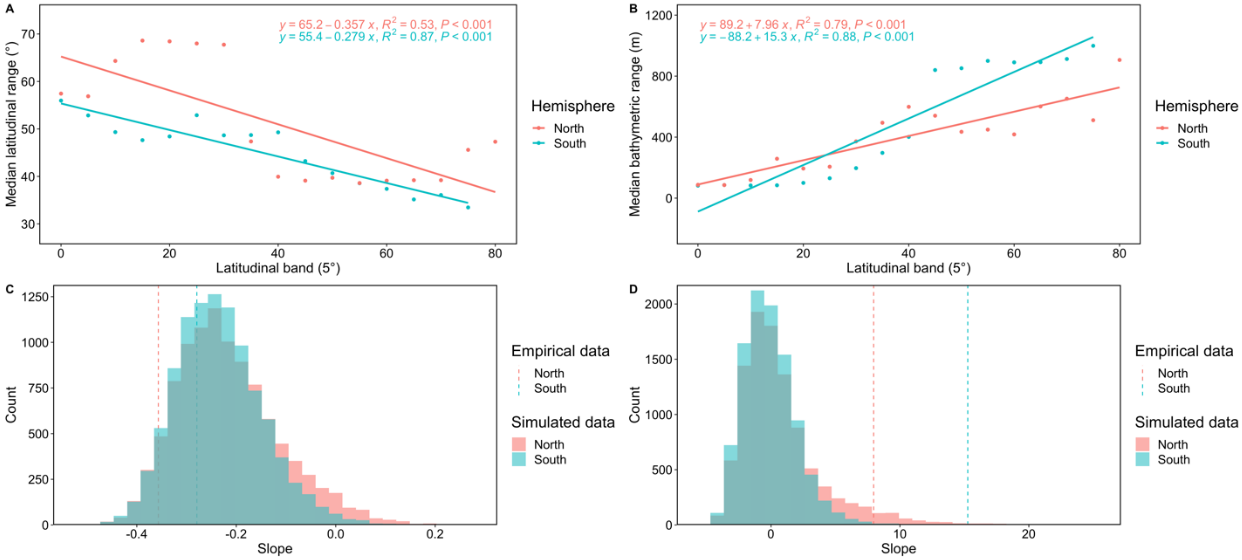
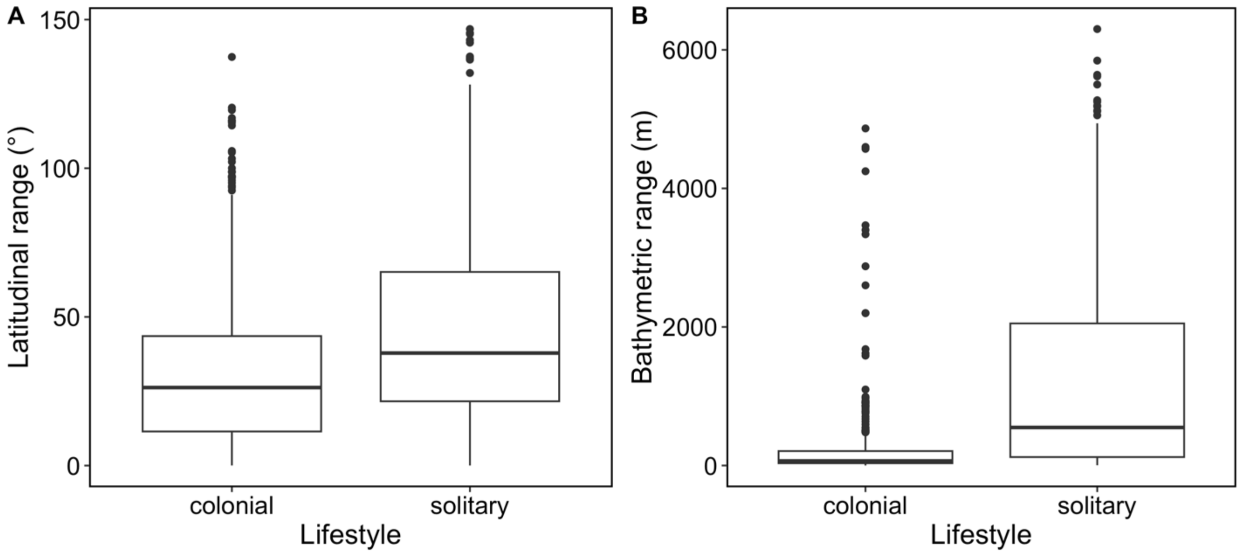


Figure 2.3. Latitudinal (A) and bathymetric (B) ranges of ascidians by their lifestyle (colonial, solitary). Samples sizes were 481 colonial species and 322 solitary species for the latitudinal range comparison, and 277 colonial species and 260 solitary species for the bathymetric range comparison.



CHAPTER 3

Taxonomic bias in representations of animal diversity in introductory ecology and evolution course materials

ABSTRACT

Though vertebrates make up only 5% of described animal species, they dominate our scientific research, informal environmental and naturalist educational tools, and popular media to a disproportionate extent. Despite the widespread documentation of vertebrate bias in these areas, the extent of vertebrate bias in biology educational materials is unknown. This study addresses the degree to which introductory ecology and evolution instructional materials disproportionately rely on examples from vertebrates and mammals. In particular, we address the following questions: 1) Which animal groups are over- or under-represented in introductory biology textbooks and lecture slides? 2) Are certain topics more or less taxonomically biased? 3) How do representations of animal diversity compare across textbooks and instructor teams? Ecology and evolution chapters from five major introductory biology textbooks and two sets of faculty lecture slide decks from a major public university were coded for animal imagery. Vertebrates were present in 47% of textbook figures with animals and 60% of lecture slides with animals, even though they account for only 5% of described animal species. Mammals, which represent only 0.4% of described animal species, were present in 47% of textbook figures with animals and 60% of lecture slides with animals. In contrast, many invertebrate phyla were underrepresented to varying degrees. Taxonomic bias may have negative consequences for student learning, even though mammal and vertebrate examples may be pedagogically advantageous at times.

INTRODUCTION

Only 5% of described animal species are vertebrates (Bánki et al. 2022), which are characterized by the presence of a backbone or spine. Although invertebrates (animals that lack a backbone or spine) make up the vast majority of animal species and dominate the planet in terms of their sheer numbers, biomass, and ecological impact (Wilson 1987, Black et al. 2001), they are almost universally underrepresented in our society (Table 3.1). This taxonomic bias towards vertebrates has been documented in everything from scientific research efforts (Clark & May 2002, Pyšek et al. 2008, Rosenthal et al. 2017, Titley et al. 2017) and databases (Troudet et al. 2017, Vickers et al. 2021), to reintroduction projects (Seddon et al. 2005), endangered species lists (Black et al. 2001), zoo collections (Brereton & Brereton 2020), children's media (Sousa et al. 2017, Vrla et al. 2020, Hooykaas et al. 2022), and social media posts (Heathcote 2021). Even within vertebrates there is often a strong taxonomic bias, with mammals receiving the lion's share of representation (e.g., Christoffel & Lepczyk 2012), despite accounting for less than 9% of vertebrate species (Bánki et al. 2022).

Recently, efforts to characterize representations of animal diversity have expanded to college biology textbooks. Stahl et al. (2020) surveyed contemporary conservation biology textbooks and found they were significantly biased in their taxonomic coverage of Earth's biodiversity relative to its actual biodiversity. For example, mammals accounted for 31% of all examples referring to a specific species or group, despite comprising less than 1% of all described animal species (Bánki et al. 2022). Similarly, the most species rich class of animals on the planet is insects, which make up about 65% of all described animal species (Bánki et al. 2022); however, when Gangwani & Landin (2018) examined insect representation in introductory biology textbooks from the last century, they found that content dedicated to insects decreased by more than 75% in recent textbooks (published since 2000) compared to books published before 1960. These studies suggest that not only do taxonomic biases exist in college textbooks, they may even be becoming more extreme.

Textbooks play a central role in shaping undergraduate biology courses. Because many instructors adopt a required textbook for their courses (French et al. 2015) and rely on materials in the instructor edition (e.g., downloadable figures, test banks, and PowerPoint slides) to develop their courses, textbooks often strongly influence what and how instructors teach. Students depend on textbooks as one of their primary means of learning the course material (French et al. 2015). Thus textbooks, while conveying foundational concepts, also have the potential to directly or indirectly impact students' understanding (or misconceptions) of animal diversity. To our knowledge, there have been no studies yet that have quantified the representation across all animal groups in introductory biology textbooks or lecture materials.

Here, we address this gap in the literature by examining representations of animal diversity in introductory biology (ecology and evolution) course materials at a large public university in California. We investigate the following questions: 1) Which animal groups are over- or under-represented in introductory biology textbooks and lecture slides? 2) Are certain topics more or less taxonomically biased? 3) How do representations of animal diversity compare across textbooks and instructor teams? Our inquiry was focused on depictions of animals in course materials, rather than text, because figures have been shown to facilitate engagement, arouse interest, and often significantly improve learning (Levie & Lentz 1982, Mayer 1989, Carney & Levin 2002, Wiley et al. 2017). We share the results of our analysis and provide guidance on selecting animal examples for course materials.

METHODS

Our overall approach to document the animal imagery in introductory biology course materials (textbooks and lecture slides) and compare those representations to actual animal diversity. Below, we explain how we selected what course materials to analyze, provide the details of our image coding methodology and analysis, and describe our statistical analyses.

Content Selection

We chose five textbooks to analyze, representing the most commonly adopted textbooks for introductory biology courses in the United States from each of the major publishers (Table 3.2). Within each textbook, we selected chapters related to content from ecology and evolution. Since each textbook arranges this content in slightly different ways, the number of chapters analyzed differs between textbooks. We included in the analysis all chapters in each textbook's ecology unit and evolution unit with two exceptions: first, the Cengage textbook contains within its evolution unit a chapter on primate evolution which had no corollary in the other textbooks and so was excluded; second, the OpenStax text does not arrange its chapters into units, so chapters were identified which covered the relevant content. Lastly, chapters relating to inheritance were also included (though these were located in the genetics unit of the textbooks) as the course under study also includes inheritance. The topics covered by these selected chapters include populations, communities, ecosystems, the biosphere, inheritance, evolutionary processes, speciation, conservation, behavior, and the history of life.

In addition to textbook chapters, we also analyzed faculty lecture slides covering ecology and evolution content. One course in the introductory biology series, Biosciences 2B: Introduction to Biology, Evolution and Ecology, was chosen for analysis in this study. Biosciences 2B is the first course in the introductory biology series and is required for all 11 majors in the College of Biological Sciences as well as 23 of the 29 majors in the College of Agriculture and Environmental Sciences as well as some majors in other colleges (e.g., Psychology). Other courses in the introductory series either have no taxonomic focus or are required for a much smaller cohort of majors on campus. Consequently, this course reaches a large number of students (~1400 per quarter) and serves as the primary mode of exposure to taxonomic diversity for a large number of majors. This course is taught by a rotation of several faculty teams. Lecture slide decks were gathered from the Fall Quarter 2022 two instructional teams (A and B). All slides used for instruction of lecture content were included in the analysis

(Table 3.2). These teams were used for this analysis as Team A has taught the course the longest (since its inception in 2008) and includes the course faculty lead, while Team B teaches the course the most frequently (2-4 sections per academic year). Consequently, these teams have the largest impact on the structure and operation of the course, as well as on student experience in the course. Sharing of instructional materials across all teams is high and all instructional teams share the same course learning goals; consequently, variation in lecture content is relatively low. One of the instructional teams is an author on this paper; however, instructional materials were developed for this course prior to the conception of the study and were not altered during the development or implementation of the project. Additionally, this author did not code their own course materials. Since this study is focused on instructional materials, it is not considered human subjects research, and is exempt from IRB review.

Image Coding Methodology

We coded all the numbered figures within the selected chapters of with each textbook. The use of only numbered figures provides a clear standard for inclusion of content, excludes solely decorative graphics that are not referenced by the text, and has been applied by other textbook analyses (e.g., Wiley et al. 2017). Some textbooks included an opening image in each chapter that was not numbered, which were also included in the analysis. Tables, boxes, and any other unnumbered images were not included in the coding analysis. Each numbered figure was treated as a single coding unit, even if there were lettered subparts to the figure. Within each lecture slide deck, we coded all individual slides. Each individual slide was treated the same as a numbered figure in the textbook chapters.

We coded all animal imagery to the phylum of the animal depicted, or (for Phylum Chordata) to subgroups within the phylum. We also recorded figures that contained no animal imagery and figures that contained animals that could not be identified to phylum level (e.g., ‘zooplankton’ or extinct species that cannot be assigned to modern phyla). Current phylum designations were taken from the Catalogue of Life (Bánki et al. 2022). Consequently, the coding scheme included 38 possible codes: one code for ‘no animal depicted’, one code for ‘non-specific phylum depicted’, one code each for the 32 non-Chordate animal phyla, and four Chordate codes (Human, Non-Human Mammal, Non-Mammal Vertebrate, Non-Vertebrate Chordate). Each code was used to record presence/absence of that phylum or group, meaning that multiple images of, or an image of multiple individuals of, the same phylum or group was not counted more than once. A single image can contain multiple phyla or Chordate groups. To be coded as present, an animal of that phylum must be visible in the image, not simply named in the figure or caption. Deceased or fossilized animals were considered depictions of animals. A portion or subpart of an animal (e.g., a single limb or organ) were not considered depictions of animals. Only animal imagery was coded; images containing other organisms (plants, animals, fungi, etc.) were coded as “no animal depicted.” Examples of coding for textbook figures and lecture slides is illustrated in Table 3.3.

Statistical analyses

All authors coded lecture slides and textbook figures. Training on coding began with an introduction to each of the 33 animal phyla as well as the groupings within Chordata (specifically mammals, vertebrates, and non-vertebrate chordates). As a group, we discussed a ‘training’ set of textbook images taken from chapters not included in the analyses. Once we were all comfortable with the training figure set, each of us separately coded a practice chapter (Chapter 1 of *Life: the Science of Biology* by Hillis et al. 2020). To determine the reliability of the image coding, we performed an interrater reliability on the practice chapter coding. Interrater reliability was measured with Cohen's Kappa for all codes that were assigned in the practice chapter across all pairwise coder comparisons (Appendix, Table 3.A1). Cohen’s Kappa values reflect the degree to which different coders apply the same code to the same variable (in this case a textbook figure or lecture slide) and are more reliable than other correlation metrics, such as percent agreement, which do not account for chance agreement between coders (McHugh 2012). Only coders with average Cohen’s Kappa values greater than 0.8 were used in subsequent analyses. Each textbook chapter and lecture slide deck were assigned to at least two different coders. If more than one coder met the 0.8 threshold, then the coder with the highest Cohen's Kappa value was used in subsequent analyses. The coders used in analyses exhibited an average Cohen's Kappa of 0.89, which reflects "strong" agreement between the coders (McHugh 2012).

We used Fisher's exact tests of independence ($\alpha = 0.05$) to test whether the proportion that each phylum was represented in the course materials (textbook figures or lecture slides) was significantly different from the proportion of described animal species belonging to that phylum. To conduct these tests, we constructed two-way contingency tables, where the first row contained the total number of animal species (1) belonging and (2) not belonging to the phylum of interest, and the second row contained the number of textbook figures or lectures slides (1) belonging and (2) not belonging to the phylum of interest. The proportion of described species within each phylum was gathered from the Catalogue of Life (Bánki et al. 2022). All analyses were performed using R Statistical Software (v4.2.2; R Core Team 2022).

RESULTS

Across the five textbooks, we analyzed 1199 figures, 658 (55%) of which included a depiction of an animal. A total of 2,039 lecture slides were analyzed from the two instructor teams, 1,017 (50%) of which included a depiction of an animal. Most of the textbook figures (85%) and lecture slides (85%) with an animal depicted included only one phylum.

Overall representation of vertebrates, mammals, and invertebrates

Overall, 80% of textbook figures and 83% of lecture slides with animals contained vertebrates (including mammals). Mammals (including humans) were present in 47% of textbook figures with animals and 60% of lecture slides with animals. Invertebrates were present in 33% of textbook figures with animals and 31% of lecture slides with animals.

Overall representation of groups within chordates

Of the textbook figures with chordates, 58% included non-mammal vertebrates, 45% included non-human mammals, 18% included humans, and 0.8% included non-vertebrate chordates. Of the lecture slides with chordates, 44% included non-mammal vertebrates, 32% included non-human mammals, 51% included humans, and 0.1% included non-vertebrate chordates.

Number of animal phyla in ecology and evolution course materials

We recorded 9 (27%) of the 33 total animal phyla in the textbook figures and 15 (45%) in the lecture slides. In both cases, about one-third of the phyla present were significantly overrepresented and one-third of phyla were significantly underrepresented relative to their described number of species (Figure 3.1A and 3.1B, Fisher's exact test: $p < 0.05$; Appendix, Table 3.A2). In total, eighteen (55%) phyla, representing 0.5% of all described animal species, were not represented in either the textbook figures or lecture slides (Figure 3.1C).

Comparing representations of animal diversity by topic

Among the ecology and evolution textbook topics analyzed, we found the greatest animal diversity in communities, with an average of 5.2 phyla represented per textbook (Figure 3.2). Among lecture slide decks, evolutionary processes had the greatest diversity of phyla, with an average of 9 phyla represented per instructor team. Inheritance had the lowest animal diversity in both the textbook figures and lecture slides with an average of 2 phyla represented in both sources, chordates (i.e., humans and other mammals) and arthropods (i.e., fruit flies).

Comparing representations of animal diversity by source

The proportions of animal phyla represented were similar across the textbooks and lectures slides of each instructor team (Figure 3.3) suggesting that the larger number of phyla in lecture sides results from rare inclusions of certain phyla (Figure 3.1B). The most commonly depicted phylum across both the textbook figures and lectures slides was Chordata (present in 81% and 83% of the figures/slides with animal depictions, respectively). The second most commonly depicted phylum across both the textbook figures and lecture slides was Arthropoda (present in 25% and 22% of the figures/slides with animal depictions, respectively).

DISCUSSION

We found that textbook figures and lecture slides disproportionately used examples of vertebrates and mammals compared to their representation in terms of described animal species diversity. Overall, 80% of textbook figures and 83% of lecture slides with animals contained vertebrates (including mammals), even though vertebrates account for only 5% of all described animal species (Bánki et al. 2022). These results demonstrate that vertebrates were present in textbook figures and lecture slides 16 to 17 times more than expected given the proportion of described animal species that are vertebrates. Mammals (including humans) were present in 47% of textbook figures with animals and 60% of lecture slides with animals, despite representing only 0.4% of all described animal species (Bánki et al. 2022). These results indicate that mammals were present in textbook figures and lecture slides 64 times and 86 times more than expected, respectively.

In contrast, many invertebrate phyla were underrepresented to varying degrees in the course materials. Arthropods and molluscs were significantly underrepresented (relative to their actual species richness) in both the textbook figures and lecture slides (Figure 3.1), while chordates, cnidarians, and echinoderms were significantly overrepresented in both the textbook figures and lecture slides (Figure 3.1). Over half of the described animal phyla don’t appear at all in the textbook figures and lecture slides that we analyzed. Overall, invertebrates represent 95% of all described animal species (Bánki et al. 2022) but were present in only 33% of textbook figures with animals and 31% of lecture slides with animals.

It is important to note that while this study focuses on representation of diversity of animal groups, the same questions could be asked for representations of other taxonomic groups. In particular, bias towards animal representation over other groups of living organisms such as plants (Schussler et al. 2010, Brownlee et al. 2021) and fungi (Madrazo and Hounshell 1979) has been documented in K-12 and college educational materials. In addition, there may be other axes of diversity besides species diversity that are important to instructors, such as body plan diversity or other trait diversity. To assess whether the bias we describe here can or should be corrected, it is necessary to understand both the reasons underlying the disproportionate use of the vertebrates and the consequences of this bias for student learning goals.

Causes and Consequences of Taxonomic Bias in Instructional Materials

The degree of vertebrate bias varied minimally across the five textbooks analyzed in this study (Figure 3.3), in part due to a high degree of similarity in figures relating to 'classic' examples. For example, all behavior textbook chapters included in this analysis contained a figure of the male three-spined stickleback (*Gasterosteus aculeatus*) fixed-action pattern studies (Tinbergen 1952). Conversely, the degree of vertebrate bias varied markedly across topics (Figure 3.2). Within the textbooks the most diverse content related to community ecology, which might be expected since explicitly focusing on multiple trophic levels and species interactions lends itself more easily to including a variety of types of animals. Inheritance content represented the fewest phyla (Figure 3.2), which also might be expected since inheritance chapters tend to focus heavily on humans and other mammals, Mendel's pea plant experiments, and *Drosophila* research.

Lecture slide decks included many more phyla than textbook figures across all topics except inheritance (Figure 3.2), though the proportion of vertebrate representation was similar between lecture and textbook content (Figure 3.3) indicating that the representation of these additional phyla in lecture materials was rare. The instructors represented in this analysis primarily study plants and marine invertebrates, so the disproportionate vertebrate representation is not due to their research focus and may be less extreme than other introductory biology courses. Some topics within the introductory biology course analyzed here, such as functional diversity, lend themselves to including more phyla, as an explicit goal of these lectures was to expose students to the breadth of functional variation and explore tradeoffs in resource acquisition, stress tolerance, predator defense, etc.

Taxonomic bias has been documented in a wide variety of applications, including children's media, environmental education, and scientific research (Table 3.1). Consequently, the vertebrate and mammal bias documented in this study may be borne out of a general cultural bias towards these groups as well as limitations in scientific research on other taxonomic groups around which course content can be structured. It is difficult to tease apart where this bias originates given that it is so ubiquitous. While it is beyond the scope of individual instructors or scientists to address these biases, if exposure to organismal diversity is an important course goal, instructors can choose examples that better represent the full diversity of animal phyla.

However, it is not the goal of every biology course to teach students about biological diversity. Many biology degrees include separate requirements for coursework that explicitly covers the diversity of life meaning that explicit incorporation of taxonomic diversity as an objective of an ecology and evolution course may not be necessary. The course analyzed in this study is a prerequisite for such an organismal-diversity focused course, which reduces the importance of educating students on animal diversity explicitly in the course assessed here. Instead, ecology and evolution courses may wish to (and indeed frequently do) focus on functional group diversity, and processes that shape biodiversity such as niche partitioning and speciation.

Even so, instructors and textbook authors/publishers should consider what aspects of ecology and evolution students lose when the diversity of animals in examples is limited. In other words, how does a vertebrate (and mammal) focus in instructional content overemphasize traits and strategies of these groups and/or fail to represent the full diversity of traits and strategies such that general understanding of ecology and evolution are impaired? For example, discussions of K and r selection in life histories commonly depict mice and other rodents as r-selected; however, all mammals are to some degree K-selected when compared to invertebrates such as insects and bivalves. Consequently, a mammal bias fails to illustrate the full continuum of life history traits seen in animals. Similarly, a vertebrate (and mammal) focus would fail to illustrate the unique adaptations of sessile organisms such as corals and sponges for accomplishing tasks that students may think require movement, such as obtaining food and finding mates. On a more fundamental level, a vertebrate (and mammal) bias may negatively impact students' understanding of foundational concepts. For example, studies have suggested that ignoring the ubiquity of streamlined and miniaturized invertebrates can lead students to misconceptions that evolution is progressive and favors complexity (Czekanski-Moir & Rundell 2020).

When Is Taxonomic Bias Appropriate or Useful in Instruction?

We are not arguing that animal representation in textbooks and lecture materials should perfectly reflect described species diversity. In some instances, active bias in favor of vertebrates and mammals might be pedagogically advantageous. First, a bias towards human examples might be advantageous in some content. Incorporating personal genotyping data into genetics content can improve students' perceptions, attitudes, and knowledge of genetics (Burghardt et al. 2021) and can also be used to address misconceptions relating to supposed genetic differences between human populations (Donovan 2016). One of the instructional teams analyzed in this study takes this approach by using their own family's 23andMe results to illustrate multi-generational inheritance patterns, and highlighting human population genetics research that refutes the idea of biological races (e.g., Jorde & Wooding 2004).

Second, a bias towards representation of mammals and vertebrates may be pedagogically useful when covering content that is especially difficult or foreign to students.

Introductory biology textbooks have a higher frequency of vocabulary that is new and unknown to students than many other fields (Thonney 2016). Coupling unfamiliar content and terminology with unfamiliar organisms may inhibit students' understanding of the underlying ecological or evolutionary principles and require more instructional time. For example, both instructional teams analyzed in this study use the Labrador retriever coat color example to illustrate epistasis (Templeton et al. 1977). This concept and term is new to most students in the course and so teaching the concept around an animal that students know well may be easier for students to grasp than an example using an animal that is more foreign to students.

For these, and possibly other, reasons, the goal of animal representation in instructional materials should not be to match described species diversity, but instead to make conscious, pedagogically-sound decisions on how to represent animal diversity in course content to best support students' learning of course content and counter student biases in understanding. As outlined above, in some cases, inclusion of animals that are very foreign to students could inhibit learning and using humans and common pet species will make concepts seem more relevant. However, in other cases, broad representation of the impressive variety of animal forms and functions is critically necessary for students to develop an adequate understanding of the diversity of life. Furthermore, increasing the diversity of examples could be a powerful tool for attracting students to the study of ecology and evolution. In particular, faculty should move beyond repeating the examples illustrated in textbooks associated with their courses and intentionally incorporate more diverse examples. Indeed, in its initial *Vision & Change: A Call to Action* report in 2010, the American Association for the Advancement of Science (AAAS) warned faculty to "look beyond existing textbooks for course resources since strict adherence to texts can impede reform" (p9, AAAS 2011). Towards this end, we provide options for invertebrate examples in common evolution and ecology course content (Table 3.4) and list online repositories for case studies and lesson plans (Table 3.5) which faculty can incorporate into their own courses and to which faculty can submit their own content.

CONCLUSION

This study documents disproportionate representation of a single animal phylum (Chordata) in ecology and evolution instructional materials, including faculty lecture slides from a large R1 institution and textbook imagery from the most adopted textbook of five major academic publishers. This taxonomic bias may be born out of wider cultural biases towards vertebrates, which has been documented in research, conservation, environmental education, and popular media and poses pedagogical concerns by 1) failing to fully represent the diversity of animal species and their traits and strategies, and 2) reinforcing students' misconceptions about animal diversity and vertebrate abundance. While focusing on familiar organisms may serve important pedagogical roles in some cases, textbook authors/publishers and introductory biology instructors should critically review the representation of animal diversity in their content to ensure that students are exposed to invertebrate species and their unique traits, life histories, and ecological roles.

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FIGURES & TABLES

Figure 3.1. Representation of different animal phyla in (A) textbook figures and (B) lectures slides relative to the number described species. The proportion of figures/slides from each phylum is plotted against the actual proportion of described animal species in that phylum. Values were log transformed for clarity. The 1:1 line is shown (dotted); phyla that appear above the line in blue are significantly (*p*<0.05) overrepresented in course materials and phyla that appear below the line in pink are significantly underrepresented in course materials. For the phyla that appear in black in (A) and (B), there was no significant difference between the proportion of described species in those phyla and the proportion of figures/slides containing those phyla. 18 phyla were not present in either textbook or lecture imagery: Acanthocephala, Chaetognatha, Dicyemida, Gastrotricha, Gnathostomulida, Hemichordata, Kamptozoa, Kinorhyncha, Loricifera, Micrognathozoa, Nematomorpha, Nemertea, Onychophora, Orthonectida, Placozoa, Sipuncula, Tardigrada, and Xenacoelomorpha.

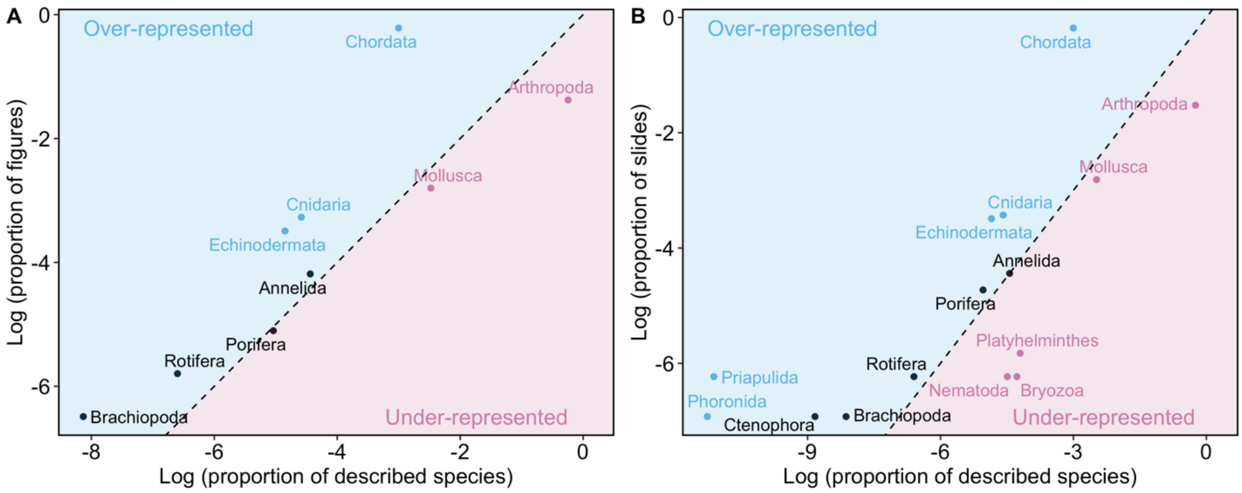


Figure 3.2. Average (± SE) number of phyla present per topic. Red bars show data for the lecture slides (n = 2 instructor teams). Blue bars show data for the textbook figures (n = 5 textbooks). The single bars for “Behavior” and “Other” reflect that there were no lectures on behavior and no “other” category for the textbook data.

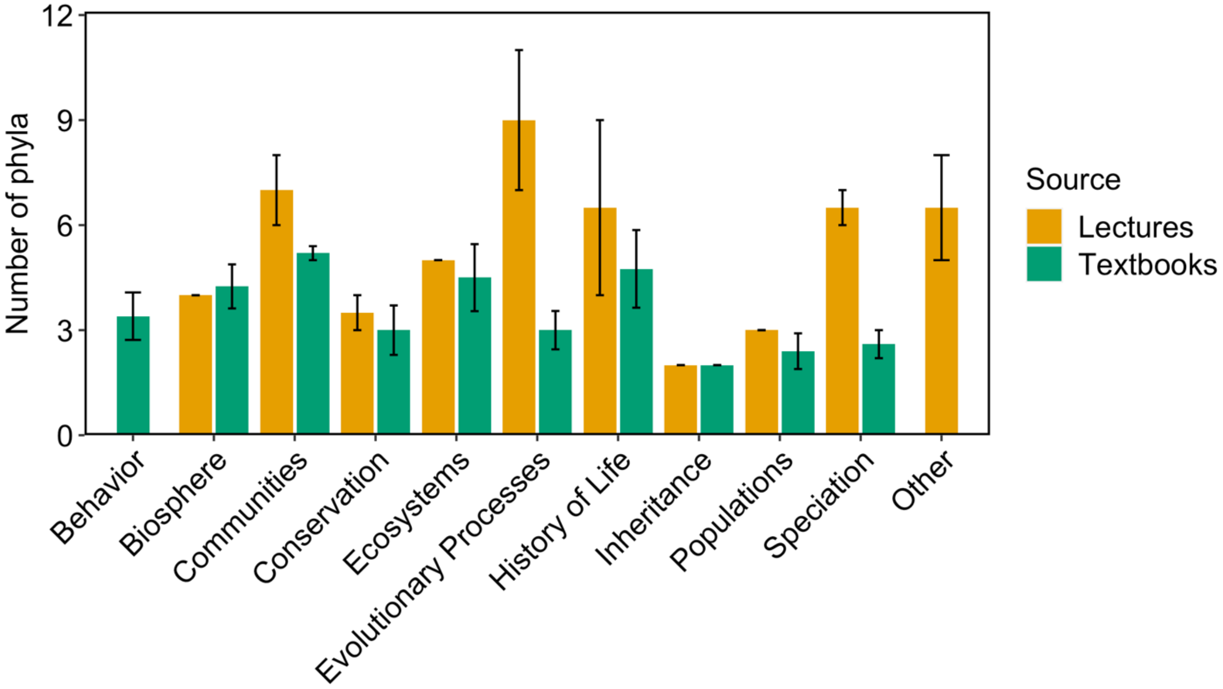


Figure 3.3. The proportions of animal phyla present in textbook figures (left) and lecture slides (right) compared to the actual proportions of described species in each phylum (right). Only the figures present in chapters related to the selected topics (populations, communities, ecosystems, the biosphere, inheritance, evolutionary processes, speciation, conservation, behavior, and the history of life) were coded for each textbook. All lecture slides were coded for each instructor team. Data for the proportions of described species from the Catalogue of Life database (Bánki et al. 2022). Figure displays seven most speciose animal phyla described in nature. All other animal phyla are grouped as "Other".

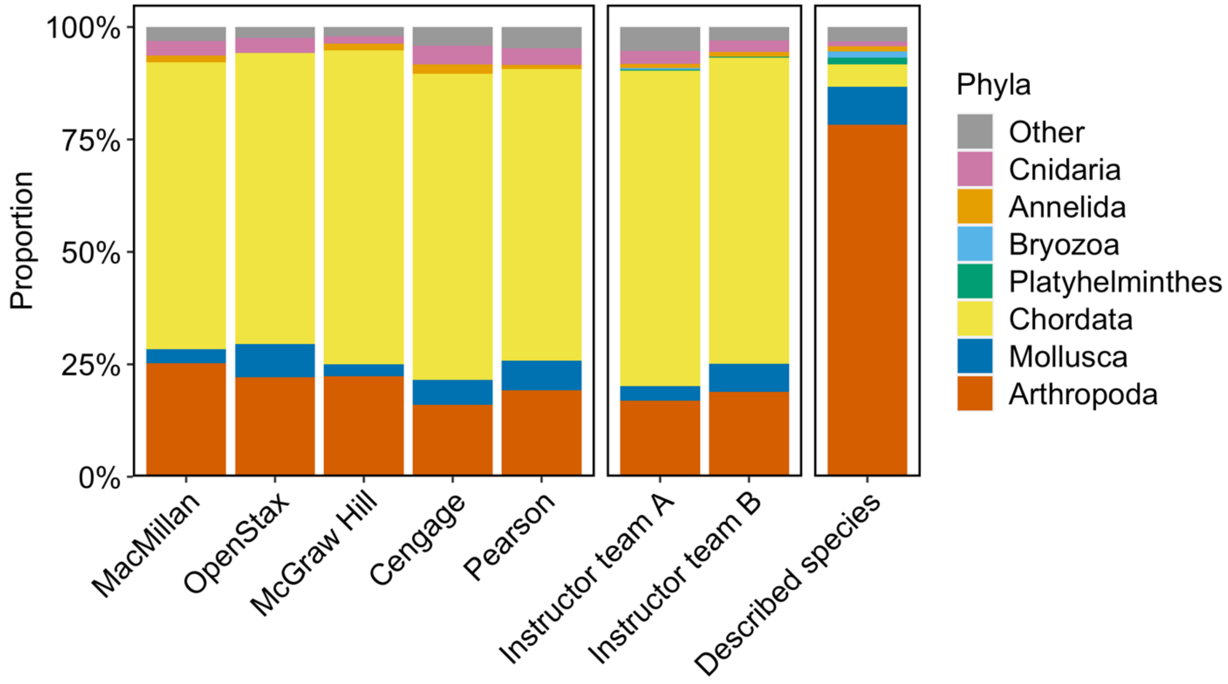


Table 3.1. Taxonomic bias documented in the literature. Vertebrates, especially birds and mammals, are typically overrepresented. For reference, vertebrates represent 5% of all described animal species (Bánki et al. 2022). Birds and mammals represent 0.7% and 0.4% of all described animal species, respectively (Bánki et al. 2022).

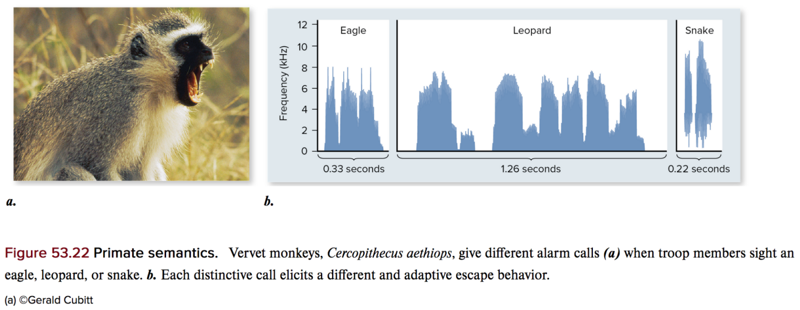
Citation	**Topic**	**Sample**	**Representation**
Rosenthal et al. 2017	Animal behavior research	4076 research papers from the journal *Animal Behavior*	Birds and mammals comprise more than 50% of all papers.
Clark & May 2002	Conservation research	>2700 research papers from the journals *Conservation Biology* and *Biological Conservation*	Vertebrates account for 69% of papers. Mammals and birds account for 28% and 27%, respectively.
Pyšek et al. 2008	Invasion research	2,670 research papers from the Web of Science	Vertebrates account for 15% of the species studied. Mammals and birds account for 3% and 2%, respectively.
Titley et al. 2017	Biodiversity research	526 research papers from the Web of Science	Approximately half of the papers sampled studied vertebrates. Birds and mammals accounted for 13% and 12% of papers, respectively.
Vickers et al. 2021	Enzyme data	12,677 entries in the BRaunschweig ENzyme DAtabase (BRENDA)	Five mammals (human, rat, cattle, mouse, pig) contribute 15% of all BRENDA entries.
Troudet et al. 2017	Biodiversity data	650 million occurrences from the Global Biodiversity Information Facility (GBIF) data portal	Birds and mammals accounted for 53% and 1.7% of all occurrences, respectively.
Black et al. 2001	Endangered species list	U.S. Fish and Wildlife Services (USFWS) Threatened and	Vertebrates account for 63% of U.S. animal species listed as endangered.

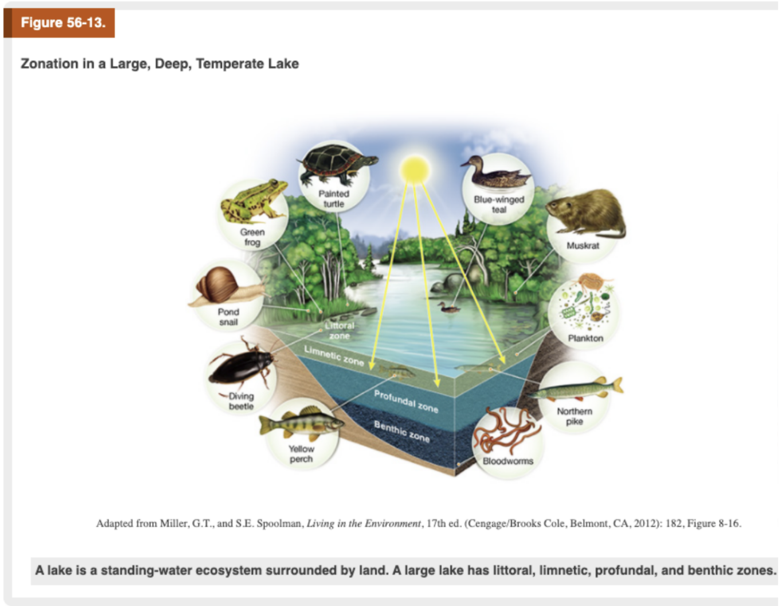
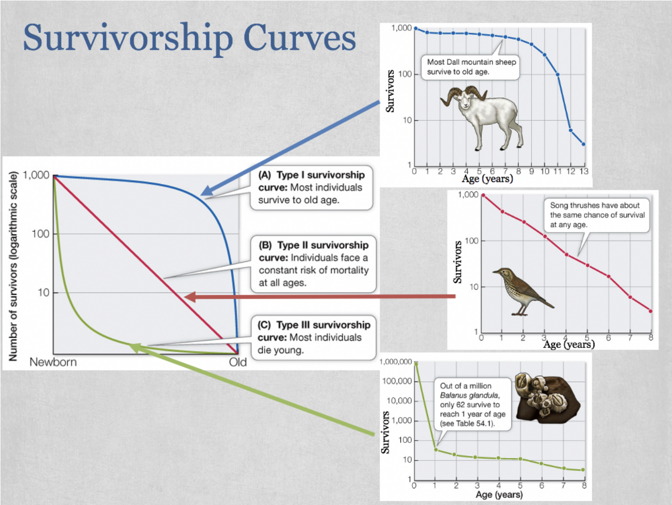
		Endangered Species System (TESS)	
Seddon et al. 2005	Reintroduction projects	699 plant and animal reintroduction projects	Vertebrates were the focus of 61% of reintroduction projects. Mammals and birds were the focus of 25% and 20%, respectively.
Brereton & Brereton 2020	Zoo collections	Zoo collection plans recorded in the 2018 *International Zoo Yearbook*	Birds and mammals accounted for 31% and 28% of collection plans, respectively.
Stahl et al. 2020	Conservation biology textbooks	Boxes, figures, and tables from seven undergraduate conservation biology textbooks	Mammals accounted for 31% of all examples referring to a specific species or group.
Hooykaas et al. 2022	Children's pictures books	211 children's books with animals	86% of the animals portrayed were vertebrates. Mammals (44%) and birds (28%) were the most featured classes.
Sousa et al. 2017	Children's trade books	160 children's books with nonhuman animals or plants	Mammals played the main character in 40% of the stories.
Vrla et al. 2020	Children's magazines	99 *National Geographic Kids* magazine covers with animal imagery	Mammals represent 85% of the wild animals featured, while invertebrates were not present on any covers.
Heathcote 2021	Instagram posts	1313 animal posts from seven popular science communication accounts	Vertebrates account for 62% of posts. Mammals and birds account for 30% and 12% of the posts, respectively.

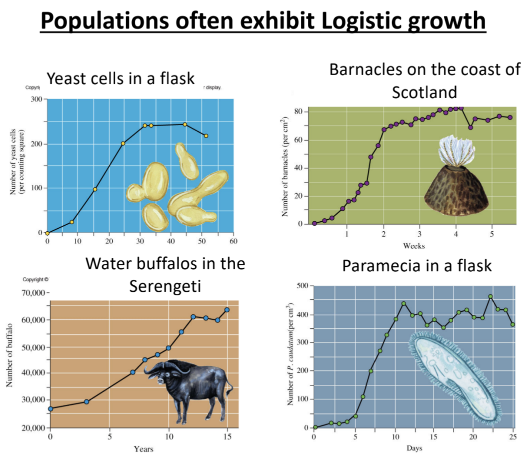
Table 3.2. Content included in analysis.

Source	**Chapters Included in Analysis**
Publisher: Cengage Title: Biology (11th) Editors: Solomon, Martin, Martin, Berg Year: 2019	11 chapters (11, 18, 19, 20, 21, 52, 53, 54, 55, 56, 57) 223 figures
Publisher: Macmillan Title: Life: The Science of Biology (12th) Editors: Hillis, Heller, Hacker, Hall, Laskowski, Sadava Year: 2020	11 chapters (12, 19, 22, 23, 51, 52, 53, 54, 55, 56, 57) 202 figures
Publisher: McGraw Hill Title: Biology (12th) Editors: Raven, Johnson, Mason, Losos, Duncan Year: 2020	12 chapters (12, 13, 20, 21, 22, 25, 53, 54, 55, 56, 57, 58) 283 figures
Publisher: OpenStax Title: Biology (2e) Editors: Clark, Douglas, Choi Year: 2022	9 chapters (12, 13, 18, 19, 20, 44, 45, 46, 47) 194 figures
Publisher: Pearson Title: Campbell Biology (12th) Editors: Urry, Cain, Wasserman, Minorksy, Orr Year: 2021	12 chapters (14, 15, 22, 23, 24, 25, 51, 52, 53, 54, 55, 56) 297 figures
Instructor Team A Year: 2021	25 slide decks 830 slides
Instructor Team B Year: 2021	39 slide decks 1209 slides

Table 3.3. Examples of textbook figures and lecture slides Included in the analysis.

Textbook Figure or Lecture Slide *(source)*	**Associated Codes**
 Figure 53.22 **Primate semantics.** Vervet monkeys, *Cercopithecus aethiops*, give different alarm calls ***(a)*** when troop members sight an eagle, leopard, or snake. ***b.*** Each distinctive call elicits a different and adaptive escape behavior. (a) ©Gerald Cubitt *(Biology, by Raven et al)*	• Chordata, Non-Human Mammal
 © Nina Leen/The LIFE Picture Collection/Getty Images © Wolfgang Kaehler/LightRocket/Getty Images *LIFE: THE SCIENCE OF BIOLOGY* 12e, Figure 51.6 © 2020 Oxford University Press **Figure 51.6 Imprinting Helps Parents and Offspring Recognize Each Other** **(A)** Graylag Geese that imprinted on Konrad Lorenz as hatchlings followed him everywhere he went. **(B)** Imprinting allows a male Emperor Penguin to find his own chick among many others. *(Life, by Hillis et al)*	• Chordata, Human • Chordata, Non-Mammal Vertebrate

 **Figure 56-13.** **Zonation in a Large, Deep, Temperate Lake** Adapted from Miller, G.T., and S.E. Spoolman, *Living in the Environment*, 17th ed. (Cengage/Brooks Cole, Belmont, CA, 2012): 182, Figure 8-16. **A lake is a standing-water ecosystem surrounded by land. A large lake has littoral, limnetic, profundal, and benthic zones.** (*Campbell Biology, by Urry et al*)	- Chordata, Non-Human Mammal - Chordata, Non-Mammal Vertebrate - Annelida - Arthropoda - Mollusca - Non-Specific Phylum (plankton)
 Survivorship Curves **(A) Type I survivorship curve:** Most individuals survive to old age. **(B) Type II survivorship curve:** Individuals face a constant risk of mortality at all ages. **(C) Type III survivorship curve:** Most individuals die young. Most Dall mountain sheep survive to old age. Song thrushes have about the same chance of survival at any age. Out of a million *Balanus glandula*, only 62 survive to reach 1 year of age (see Table 54.1). *(Instructor Team B Lecture Slides)*	- Chordata, Non-Human Mammal - Chordata, Non-Mammal Vertebrate - Arthropoda



Populations often exhibit Logistic growth

Yeast cells in a flask

Barnacles on the coast of Scotland

Water buffalos in the Serengeti

Paramecia in a flask

(Instructor Team A Lecture Slides)

- Chordata, Non-Human Mammal
- Arthropoda

Table 3.4. Classic vertebrate examples commonly used in textbooks and lectures and options for invertebrate supplements or replacements.

Topic	**Subtopic**	**Classic vertebrate example(s)**	**Non-vertebrate example(s)**
Behavior	Imprinting	Birds: filial imprinting	Cuttlefish: food imprinting (Darmaillacq et al. 2006)
	Migration	Birds, sea turtles, whales, salmon	Monarch butterflies (Reppert & de Roode 2018), Christmas Island red crabs (Adamczewska & Morris 2001)
	Fixed action pattern	Tinbergen's three-spined sticklebacks: aggression, greylag goose: egg-retrieval, gulls: spot pecking	Kissing bug: proboscis extension (Páez-Rondón et al. 2018)
	Conditioning and learning	Pavlov's dogs	Octopuses (Fiorito & Scotto 1992)
	Alarm signaling	Ground squirrels, meerkats, primates, and birds: vocal alarm signals	Western flower thrips (de Bruijn et al. 2016), and polychaetes (Watson et al. 2005): chemical alarm signals
Community ecology	Predator-prey dynamics	Lynx and snowshoe hares	Predatory and herbivorous mites (Huffaker 1958)
	Trophic cascades	Yellowstone gray wolves, North Pacific sea otters	Wasps (Buck & Ripple 2017), crayfish (Moore et al. 2012), beetles and spiders (Snyder & Wise 2001), sunflower stars (Shultz et al. 2016)

	Ecosystem engineers	Beavers	Shelter-building insects (Cornelissen et al. 2016), earthworms (Le Bayon et al. 2017), corals (Wild et al. 2011), mussels and oysters (Kochmann et al. 2008)
	Resource partitioning	*Anolis* lizards and MacArthur's warblers: habitat partitioning	Amphipods: habitat partitioning (Emery et al. 2022), mysids: food partitioning (Rastorgueff et al. 2011)
	Character displacement	Darwin's finches: bills	Land snails (Kameda et al. 2009) and rhinoceros beetles (Kawano 2002): genitalia
Conservation	Extinction	Steller's sea cow, dodo bird, wooly mammoth, saber-toothed cat	Polynesian tree snails (Lee et al. 2008), Hawaiian land snails (Régnier et al. 2015), several insects (Dunn 2005)
	Overharvesting	Atlantic bluefin tuna, Atlantic cod, African elephants, whales	Red coral (Tsounis et al. 2007), Asian horseshoe crabs (John et al. 2018), California abalone (Rogers-Bennett et al. 2002)
	Captive breeding	California condor, Galápagos tortoises, red and gray wolves	White abalone (Rogers-Bennett et al. 2016), Lord Howe Island stick insect (Honan 2008)
	Infectious disease outbreaks	Bats: white-nose syndrome, amphibians: chytridiomycosis	Corals: several diseases (Sutherland et al. 2004)

	Introduced species	Cane toads, brown tree snake, European starling	Zebra mussels (Ricciardi 2003), green crabs (Young & Elliot 2019), emerald ash borer (Herms & McCullough 2014), sea squirts (Zhan et al. 2015)
Evolutionary processes	Natural selection	Darwin's finches, rock pocket mice	Cockroaches (Wada-Katsumata et al. 2013), peppered moths (Cook & Saccheri 2013)
	Artificial selection	Darwin's pigeons	Fruit flies (Caballero et al. 1991)
	Intrasexual selection (male-male competition)	Elk, bighorn sheep, elephant seals, lions	Stag beetles (Goyens et al. 2014), orb weaving spiders (Christenson & Goist 1979), hermit crabs (Yasuda et al. 2011), spiny-headed worms (Poulin & Morand 2000)
	Alternative mating strategies	Salmon, side-blotched lizards	Marine isopods (Shuster 1987), horned beetles (Emlen 1997), freshwater prawns (Karplus & Barki 2019)
	Intersexual selection (female choice)	Long-tailed widowbirds: tail length, peacocks	Redback spiders: sexual cannibalism (Andrade 1996)
	Sex role reversal	Seahorses, pipefish, wattled jacanas	Giant water bugs (Thrasher et al. 2015)
	Stabilizing selection	Humans: birth weight, birds: clutch size	Gall wasps (Weaver et al. 2020): gall size

	Frequency dependent selection	Scale-eating cichlid fish: negative, kingsnakes: positive	Damselflies: negative (Takahashi et al. 2010), butterflies: positive (Chouteau et al. 2016)
	Heterozygote advantage	Humans: sickle cell anemia	Clonal honey bees (Smith et al. 2019)
Inheritance	Simple Mendelian trait	Humans: various traits	Blue mussel: shell color (Newkirk 1980)
	Multiple alleles	Rabbits: coat color, humans: blood type	Fruit flies: eye color (Nolte 1959)
	Pleiotropy	Humans: various diseases, chickens: frizzle gene, cats: deafness and pigmentation	Fruit flies: vestigial gene (Lobo 2008), pigmentation and several traits (Wittkopp & Beldade 2009)
	Epistasis	Mice, Labrador retrievers: coat color	White garden snail: apex color and shell banding (Johnson 2012), Chilean scallop: shell color (Winkler et al. 2001)
Populations	Life tables	Loggerhead sea turtles, Dall mountain sheep, Darwin's finches	Rice bugs (Dutta & Roy 2016)
	Semelparity	Pacific salmon	Octopuses (Anderson et al. 2002), cicadas (Karban 1986)
	r & K selected species	Rodents: r, elephants: K	Various sea squirt species (Edwards & Stachowicz 2010): r, K
Speciation	Adaptive radiation	Darwin's finches, Hawaiian honeycreepers, African cichlids	Madagascan ant-nest beetles (Moore & Robertson 2014), Lake Baikal amphipods

			(Macdonald et al. 2005), Lake Biwa freshwater snails (Miura et al. 2019)
	Ring species	*Ensatina* salamanders, greenish warblers	Leafcutter bees (Soltani et al. 2017)
	Behavioral isolation	Birds and frogs: mating songs	Field crickets: mating songs (Gray & Cade 2000), fireflies: courtship flashes (Lewis & Cratsley 2008)
	Hybrid infertility	Horses + donkeys, lions + tigers	Red spot assassin bugs + two-spotted assassin bugs (Bugaj-Nawrocka et al. 2022)

Table 3.5. Online resources.

Name	**Link**	**Description**
National Center for Case Study Teaching in Science Case Collection (managed by the National Science Teaching Association)	https://www.nsta.org/case-studies	Contains over 950 peer-reviewed case studies spanning all STEM fields as well as some humanities fields. Intended age groups span high school to graduate school. Materials include teaching notes and assessment tools. Requires $25 subscription to access.
CourseSource (managed by Quantitative Undergraduate Biology Education and Synthesis)	https://qubeshub.org/community/groups/coursesource/	Peer-reviewed journal containing case studies in biology and physics geared towards undergraduates. Aligned with Vision & Change core competencies and concepts. Open access.
Teaching Video Archive (managed by Dynamic Ecology)	https://dynamicecology.wordpress.com/2013/10/08/videos-for-teaching-ecology/	Resources list of videos for ecology and evolution content organized by topic. Open access.
BioInteractive (managed by the Howard Hughes Medical Institute)	https://www.biointeractive.org/classroom-resources	Repository for case studies, videos, and interactive modules on topics in biology and medicine. Geared towards high school and undergraduate levels. Open access.
iBiology	https://www.ibiology.org/	Repository of videos highlighting research of individual scientists, illustrating skills, and topics in academic careers. Includes teaching guide and assessment tools with free account. Open access.
EcoEd Digital Library (managed by the Ecological Society of America)	https://ecoed.esa.org/	Repository of undergraduate ecology education resources, including activities, figures, photographs, and syllabi. Open access.

Understanding Evolution (managed by the University of California Museum of Paleontology)	https://evolution.berkeley.edu/teach-resources/	Repository of evolution education resources. Geared towards high school and undergraduate levels. Open access.

APPENDIX

Table 3.A1. Pairwise Cohen's Kappa Values Across all Coders

Coder	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1	X	0.90	0.96	0.96	0.90	0.77	0.90	0.91	0.92	0.96	0.88	0.73	0.71	0.77	0.90	0.94	0.69
2	0.90	X	0.94	0.94	0.88	0.79	0.92	0.94	0.90	0.94	0.90	0.76	0.73	0.84	0.88	0.96	0.72
3	0.96	0.94	X	1.00	0.94	0.81	0.94	0.96	0.96	1.00	0.92	0.77	0.75	0.81	0.94	0.98	0.73
4	0.96	0.94	1.00	X	0.94	0.81	0.94	0.96	0.96	1.00	0.92	0.77	0.75	0.81	0.94	0.98	0.73
5	0.90	0.88	0.94	0.94	X	0.75	0.88	0.90	0.90	0.94	0.98	0.77	0.75	0.87	1.00	0.92	0.73
6	0.77	0.79	0.81	0.81	0.75	X	0.80	0.81	0.77	0.81	0.77	0.63	0.67	0.73	0.75	0.83	0.65
7	0.90	0.92	0.94	0.94	0.88	0.80	X	0.94	0.98	0.94	0.90	0.83	0.74	0.80	0.88	0.96	0.72
8	0.91	0.94	0.96	0.96	0.90	0.81	0.94	X	0.92	0.96	0.92	0.77	0.75	0.81	0.90	0.98	0.73
9	0.92	0.90	0.96	0.96	0.90	0.77	0.98	0.92	X	0.96	0.88	0.81	0.72	0.78	0.90	0.94	0.70
10	0.96	0.94	1.00	1.00	0.94	0.81	0.94	0.96	0.96	X	0.92	0.77	0.75	0.81	0.94	0.98	0.73
11	0.88	0.90	0.92	0.92	0.98	0.77	0.90	0.92	0.88	0.92	X	0.8	0.77	0.90	0.98	0.94	0.76
12	0.73	0.76	0.77	0.77	0.77	0.63	0.83	0.77	0.81	0.77	0.80	X	0.88	0.69	0.77	0.80	0.86
13	0.71	0.73	0.75	0.75	0.75	0.67	0.74	0.75	0.72	0.75	0.77	0.88	X	0.61	0.75	0.77	0.98
14	0.77	0.84	0.81	0.81	0.87	0.73	0.80	0.81	0.78	0.81	0.90	0.69	0.61	X	0.87	0.84	0.60
15	0.90	0.88	0.94	0.94	1.00	0.75	0.88	0.90	0.90	0.94	0.98	0.77	0.75	0.87	X	0.92	0.73
16	0.94	0.96	0.98	0.98	0.92	0.83	0.96	0.98	0.94	0.98	0.94	0.80	0.77	0.84	0.92	X	0.76
17	0.69	0.72	0.73	0.73	0.73	0.65	0.72	0.73	0.70	0.73	0.76	0.86	0.98	0.60	0.73	0.76	X
Avg.	0.86	0.87	0.90	0.90	0.88	0.76	0.88	0.88	0.88	0.90	0.88	0.78	0.76	0.78	0.88	0.91	0.74

Table 3.A2. Analysis of whether the proportion that each phylum was represented in the course materials (textbook figures or lecture slides) was significantly different from the proportion of described animal species belonging to that phylum. Significance was calculated by Fisher's exact tests. Significant results ($p < 0.05$) are indicated here in bold. Data on the number of described species came from the Catalogue of Life database (Bánki et al. 2022).

Source	**Phylum**	**Number (percent) of figures/slides containing phylum**	**Number of figure/slides not containing phylum**	**Number (percent) of described species in phylum**	**Number of described animal species not in phylum**	***p*-value**
Textbooks	Arthropoda	166 (25%)	492	1,157,971 (78%)	320,558	**$p < 0.001$**
Textbooks	Annelida	10 (1.5%)	648	17,456 (1.2%)	1,461,073	$p = 0.37$
Textbooks	Brachiopoda	1 (0.15%)	657	435 (0.029%)	1,478,094	$p = 0.18$
Textbooks	Chordata	530 (81%)	128	73,501 (5.0%)	1,405,028	**$p < 0.001$**
Textbooks	Cnidaria	25 (3.8%)	633	15,082 (1.0%)	1,463,447	**$p < 0.001$**
Textbooks	Echinodermata	20 (3.0%)	638	11,579 (0.78%)	1,466,950	**$p < 0.001$**
Textbooks	Mollusca	40 (6.1%)	618	124,032 (8.4%)	1,354,497	**$p = 0.03$**
Textbooks	Porifera	4 (0.61%)	654	9,576 (0.65%)	1,468,953	$p = 1.00$
Textbooks	Rotifera	2 (0.30%)	656	2014 (0.14%)	1,476,515	$p = 0.23$
Lectures	Annelida	12 (1.2%)	1,005	17,456 (1.2%)	1,461,073	$p = 1.00$

Lectures	Arthropoda	222 (22%)	795	1,157,971 (78%)	320,558	**$p < 0.001$**
Lectures	Brachiopoda	1 (0.098%)	1,016	435 (0.029%)	1,478,094	$p = 0.26$
Lectures	Bryozoa	2 (0.20%)	1,015	20,574 (1.4%)	1,457,955	**$p < 0.001$**
Lectures	Chordata	847 (83%)	170	73,501 (5.0%)	1,405,028	**$p < 0.001$**
Lectures	Cnidaria	33 (3.2%)	984	15,082 (1.0%)	1,463,447	**$p < 0.001$**
Lectures	Ctenophora	1 (0.098%)	1,016	216 (0.015%)	1,478,313	$p = 0.14$
Lectures	Echinodermata	31 (3.0%)	986	11,579 (0.78%)	1,466,950	**$p < 0.001$**
Lectures	Mollusca	61 (6.0%)	956	124,032 (8.4%)	1,354,497	**$p = 0.005$**
Lectures	Nematoda	2 (0.20%)	1,105	16,556 (1.1%)	1,461,973	**$p = 0.002$**
Lectures	Phoronida	1 (0.098%)	1,106	19 (0.0013%)	1,478,510	**$p = 0.01$**
Lectures	Platyhelminthes	3 (0.29%)	1,104	22,139 (1.5%)	1,456,390	**$p < 0.001$**
Lectures	Porifera	9 (0.88%)	1,008	9,576 (0.65%)	1,468,953	$p = 0.32$
Lectures	Priapulida	2 (0.20%)	1,015	22 (0.0015%)	1,478,507	**$p < 0.001$**
Lectures	Rotifera	2 (0.20%)	1,015	2,014 (0.14%)	1,476,515	$p = 0.40$