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Trends in nonindigenous aquatic species richness in the United States reveal shifting spatial and temporal patterns of species introductions

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Abstract

Understanding the spatial and temporal dynamics underlying the introduction and spread of nonindigenous aquatic species (NAS) can provide important insights into the historical drivers of biological invasions and aid in forecasting future patterns of nonindigenous species arrival and spread. Increasingly, public databases of species observation records are being used to quantify changes in NAS distributions across space and time, and are becoming an important resource for researchers, managers, and policy-makers. Here we use publicly available data to describe trends in NAS introduction and spread across the conterminous United States over more than two centuries of observation records. Available data on first records of NAS reveal significant shifts in dominance of particular introduction patterns over time, both in terms of recipient regions and likely sources. These spatiotemporal trends at the continental scale may be subject to biases associated with regional variation in sampling effort, reporting, and data curation. We therefore also examined two additional metrics, the number of individual records and the spatial coverage of those records, which are likely to be more closely associated with sampling effort. Our results suggest that broad-scale patterns may mask considerable variation across regions, time periods, and even entities contributing to NAS sampling. In some cases, observed temporal shifts in species discovery may be influenced by dramatic fluctuations in the number and spatial extent of individual observations, reflecting the possibility that shifts in sampling effort may obscure underlying rates of NAS introduction.

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Keywords

nonindigenous species; invasive species; aquatic; freshwater; sampling effort; temporal trends

Introduction

Nonindigenous aquatic species (NAS) introductions are widely recognized as major stressors to freshwater ecosystems, threatening native endemic biodiversity and causing negative impacts to ecosystem services as well as damaging local and regional economies (Moorhouse and Macdonald 2015; Pimentel et al. 2005; Ricciardi and MacIsaac 2011; Stohlgren and Schnase 2006; Strayer 2010; Walsh et al. 2016). While not all NAS become invasive and have negative impacts, it is difficult to reliably predict which species may cause significant damage (Dick et al. 2013) and it is thus necessary to monitor the spatial and temporal trends of NAS introduction and spread in order to guide prevention and control efforts and to develop effective policy aimed at mitigating impacts (Lodge et al. 2006).

At broad spatial scales, mapping nonindigenous species distributions can provide important insights into risks associated with biological invasions. Mapping enables identification of invasion hotspots, recognition of potential environmental and anthropogenic drivers of introduction and spread, and assessment of risks to priority conservation areas (Carpio et al. 2016; Davis and Darling 2017; Dawson et al. 2017; Dyer et al. 2017; Panlasigui et al. 2018; van Kleunen et al. 2015). Similarly, analyses of temporal trends in species introductions have highlighted the risks posed by unabated increases in anthropogenic global biotic exchange (Seebens et al. 2017) and have revealed important correlations between invasion rates and historical shifts in introduction vectors (Murray and Phillips 2012; Wonham and Carlton 2005). Such studies represent important advances in understanding patterns and mechanisms of global invasions, with associated benefits for conservation planning and management.

One persistent challenge related to such broad mapping efforts and trends assessments is the acquisition of suitable data. While studies conducted at relatively small spatial and temporal scales can often rely on scientifically designed sampling strategies, efforts at regional scales and higher rarely have access to such data. Increasingly, researchers are turning to *ad hoc* compilations of species observation records from multiple sources including herbarium and museum records as well as scientific and opportunistic surveys conducted by a wide variety of organizations or individuals which adopt differing, often unknown, sampling methodologies (Dawson et al. 2017). Unfortunately, diversity estimates derived from such data can be biased and may yield misleading inferences if steps are not taken to correct for patterns in sampling and reporting effort (Bobeldyk et al. 2014; Ficetola et al. 2014; Sofaer and Jarnevich 2017). The fact that sampling effort is rarely uniform across regions can result in data gaps in species databases, artificially inflating richness estimates in areas receiving high sampling intensity and potentially diminishing our ability to distinguish NAS distributions from monitoring trends (Boakes et al. 2010; Fuentes et al. 2012; Hyndman et al. 2015). These challenges may be particularly pronounced for non-indigenous species, as changes in NAS richness and distribution reflect a combination of both species arrival and

species discovery (Wonham and Pachevsky 2006). The relationship between sampling effort and species discovery is further complicated by the fact that nonindigenous species reporting is the culmination of effort aimed at both detection of novel introductions and highly targeted delineation of ranges for known or suspected problematic nonindigenous species.

Here we explore spatio-temporal patterns in NAS richness at a continental scale and across more than two centuries of species occurrence records drawn from a number of public biodiversity data repositories. We employ these richness metrics to describe broad patterns of NAS spread across the conterminous US (excluding Alaska, Hawaii, and island territories) and to investigate shifting trends in species introductions over time, including changes to both the recipient regions most heavily impacted by NAS and the global sources of those introduced species. In order to investigate the effect that changes in search effort may have had in shaping patterns of NAS observation, we also determined temporal trends in both the number of individual records and the spatial coverage of those records. Although available data do not allow formal assessment of the influence of true sampling effort on NAS discovery rates, these metrics provide some indication of how regional and temporal differences in NAS search effort may impact broader patterns. In addition to describing general spatial and temporal trends in NAS introductions, we thus also explore the ways in which underlying shifts in sampling effort may have influenced these patterns.

Methods

Database development

A list of nonindigenous freshwater aquatic species was curated for plants ($n = 192$ species) and animals ($n = 287$ species), where “nonindigenous” was defined as introduced to the conterminous US during or after European settlement (~ 1500 C.E.). Species included in the NAS animal list were obtained from the US Geological Survey’s Nonindigenous Aquatic Species program (USGS 2017), which is compiled from multiple data sources including literature, museums, monitoring programs at all governmental levels, state and federal agencies, professional communications, online reporting forms, and hotline reports (Fuller and Neilson 2015). Plant data were assembled prior to the reincorporation of nonindigenous plant taxa into USGS-NAS reporting in 2017. The plants list was compiled initially using the USDA Natural Resources Conservation Service’s (NRCS) plants database (<https://plants.usda.gov>). Candidate species were identified by searching for species nonindigenous to the lower 48 states and listed with a National Wetland Indicator Status (Lichvar et al. 2016) of “obligate wetland” in at least one US Army Corps of Engineers region, excluding Alaska and Hawaii. This list was later extended to include several species (e.g., *Phragmites australis* and others) that are widely considered to be “aquatic” invasive species by management groups throughout the US despite not being listed as obligate wetland species by the NRCS. These additional species were identified based on existing lists of invasive aquatic plants maintained by the USDA’s National Invasive Species Information Center (<https://www.invasivespeciesinfo.gov>), the University of Georgia’s Center for Invasive Species and Ecosystem Health (<https://www.invasive.org>), and regional databases such as the Great Lakes Non-indigenous Species Information System (GLANSIS, a regional node of USGS-NAS, <https://www.glerl.noaa.gov/glansis>), and the University of Florida Center for

Aquatic and Invasive Plants (<https://plants.ifas.ufl.edu>). The plant data analyzed here expand considerably on those utilized in previous studies (Davis and Darling 2017). Species translocated within the conterminous US (“native transplants”) were not included in the analyses.

Using these lists, we assembled species occurrence data from the USGS NAS database, the Early Detection and Distribution Mapping System (EDDMaps), and the USGS Biodiversity Serving Our Nation (BISON) databases, which is a curated US data repository for the Global Biodiversity Information Facility (GBIF; data accessed February 7, 2017) and hosts a full mirror of the global biodiversity records made available through that database. We used the Integrated Taxonomic Information System (ITIS) to ensure that species were not double counted, and that synonymous taxa were excluded. Duplicate occurrence records, arising from information exchange among data providers or the utilization of the same data sources by different data providers, were identified on the basis of having identical spatial coordinates and possessing identical or very similar source attribute information and were removed. In addition, records with missing spatial coordinates or that indicated occurrences located outside of the conterminous US were removed. Records identified only by centroids were removed for most analyses, but were retained for purposes of identifying earliest US observations of species introduction; this was done to prevent loss of information associated with older records, many of which are not georeferenced. In a large majority of cases, data did not exist to enable the confident determination of establishment status for observed NAS. Our data thus primarily represent patterns of introduction and may overestimate the number of NAS that establish persistent reproductive populations.

Delineation of national scale NAS trends

We created distribution maps of NAS richness summarized by 12-digit hydrological unit code (HUC) for the US in order to visualize temporal and spatial invasion patterns. The HUC system is a hierarchical catalogue of nested watersheds derived from hydrological and topographic features and maintained by the USGS (Seaber et al. 1987). There are 82,915 HUC12 subwatersheds with a mean area of 95 km² across the conterminous US. Overall NAS richness (plants and animals) was calculated as the total number of unique species observed at least once within each HUC. To explore changing distribution patterns in NAS richness over time, both the plant and animal data sets were divided into six temporal intervals: 1600–1900, 1901–1930, 1931–1950, 1951–1970, 1971–1990, and 1991–2016.

We calculated annual observational statistics for both the plant and animal databases separately within the conterminous US between 1850 and 2016 in order to visualize temporal changes in NAS richness. Very few observations were recorded prior to 1850 and thus were excluded from this part of the analysis. Specifically, we calculated a) the count of NAS first records per year, b) the count of total individual NAS observations made per year, c) the total number of NAS observed in each year, and d) the total number of HUC12s with recorded NAS observations in each year. All analyses were conducted using ArcGIS v. 10.4 (Environmental Systems Research Institute) and the *pandas* package v. 0.20.0 (McKinney 2010) in the Python programming language (Python Software Foundation). To explore differences among animal taxonomic groups, these metrics were also calculated separately

for nonindigenous fishes, amphibians, and invertebrates (including bryozoans, cnidarians, annelids, crustaceans, and mollusks).

For each plant and animal species, we also determined the location and year it was first recorded within the US. We created maps based on these metrics for the six different time steps described above to illustrate spatial and temporal trends in initial species introduction. Since our analysis identifies only the location where each species was first observed in the US, it does not consider the possibility of multiple introductions. In a small number of cases this may mean that the initial introduction record is disconnected from the introduction event associated with a present-day invasion (e.g., if an earlier introduction failed). However, recognizing multiple introductions is at least challenging and often impossible, with the exception only of species with particularly robust historical records.

Nonindigenous source regions

For plant species, native ranges were obtained through existing online databases with information on native plant distributions, including USGS (2017), University of Florida Center for Aquatic and Invasive Plants, the International Union for the Conservation of Nature (IUCN, <http://www.iucnredlist.org>), and the Invasive Species Compendium of the Centre for Agriculture and Biosciences International (CABI; <http://www.cabi.org/isc/>). Animal species ranges were drawn from the USGS (2017), which assesses native range by collating distribution information contained in historic documents, scientific journal articles, museum collection databases, and national and regional taxon-specific natural history works (e.g., state fish books). Fish native distribution data were provided in part by NatureServe (www.natureserve.org). Native regions were delineated based on major biogeographic areas recognized by the Taxonomic Databases Working Group affiliated with the International Union of Biological Sciences (Brummit 2001). Recipient regions were based roughly on the delineation of major habitat types in North America (Ricketts et al. 1999); we consolidated HUC2 watersheds into these larger regions to simplify visualization of flows. Species which originated from multiple regions were attributed proportionally to source locations. For example, species designated as “pan-tropical” were attributed equally to South America, Africa, Tropical Asia, and Australasia. A circular flow diagram illustrating introduction patterns was generated for both plants and animals using the *circlize* package in R (Gu et al. 2014).

Delineation of regional NAS trends

To further investigate relationships between sampling effort and species observations, we determined temporal trends within regional watersheds, as defined by 2-digit HUC (HUC2); these are the largest drainage basins delineated by the USGS, of which there are only 18 in the conterminous US. For each 2-digit HUC we calculated a) the cumulative number of plant and animal NAS, b) the cumulative number of plant and animal NAS records, and c) the proportional accumulation of 12-digit HUC areas sampled. Cumulative number of records and the cumulative number of species were both standardized by 2-digit HUC area in order to remove the spatial bias of larger HUCs containing more records. Therefore, the values represent a relative number of records of species compared to that of the largest HUC in the conterminous U.S. (i.e., the Missouri HUC2). The proportional accumulation of HUC area

sampled represents the total area of HUC12s within each HUC2 that contained at least one record up until that time period, divided by the total HUC2 area. The five HUC12s for the Great Lakes proper were removed from this analysis to eliminate bias associated with their unusually large size.

Contributing observer entities

We categorized each invasive species observation based on the collector identification associated with each record as a) Federal Agency, b) State/Local/Tribal Government, c) University or associated Museum, d) Independent Museum, e) NGO or Partnership, or f) Other. While all records associated with a single State, Local, or Tribal government fell into the second category, any multi-state partnership was associated with the NGO/Partnership entity. Categories were assigned using best judgment; while in most cases collector identification allowed unambiguous assignment, any collector ID that could not be confidently categorized or that was associated with a private company was assigned to Other. Additionally, any Museum that fell under a University system or received its funding directly from a University was assigned to the University entity; otherwise, they were attributed to the Independent Museum entity. For both plants and animals, we calculated the number of total observations and number of first occurrence observations from each entity. A first occurrence observation was defined as the first record of a species within the conterminous US (again, disregarding the possibility of multiple introductions, see above), and is assumed to be equivalent to observation of the initial introduction of that species to the US. The collector ID represents the organization which reports the data, but it is possible that the NAS observations were made by personnel outside of that organization.

Results

National-scale patterns of NAS introductions

Early accumulation of NAS richness clustered primarily in the Northeast and California (Figure 1a–c). By the mid-century, the Great Lakes region and central Mid-Western drainage basins became more heavily invaded (Figure 1d) followed by Florida and the Southeast achieving much higher NAS richness after 1970 (Figure 1e). Current patterns are more homogeneous across the East Coast and Midwest with heavier clusters in the Northeast, California, upper Midwest, and Florida (Figure 1f). First US observations of NAS were disproportionately recorded in New England, the Mid-Atlantic and South Atlantic-Gulf, and California for plant species, and in the Mid-Atlantic and South Atlantic-Gulf, the Great Lakes, and California for animals (Table 1). Earliest introductions clustered primarily in the New England region (Figure 2a, 2b), while introductions to California became more prominent in the first half of the 20th century (Figure 2b) followed by increased dominance of introductions to the South Atlantic-Gulf and the Great Lakes during the mid- to late-1900s (Figure 2c, 2d). Recent decades experienced a dramatic increase in the number of introductions to the South Atlantic-Gulf, particularly among animal species (Figure 2e, 2f).

The primary contributing regions of introduced plant species have been Europe and Temperate Asia, with the majority of those introductions arriving in the Northeast (Figure 3a). The Southeast and California also experienced significant plant species introductions,

but those introductions tend to be more equitably sourced from regions such as South America, Africa, Europe, Temperate Asia, and Tropical Asia. In contrast to plants, animal species were primarily introduced to the Southeast and Northeast from a variety of sources (Figure 3b). Generally, most introductions to the Northeast were from Europe and Temperate Asia, while the Southeast received species predominantly from tropical regions in the Americas, Africa, and Asia.

Rate of NAS introduction

Analysis of the number of NAS reported in the conterminous US over time indicates distinctly different trends in the observation of plant and animal species (Figure 4). While the number of first plant NAS records has remained relatively constant between the late 1800's and 2015, the number of animal records exhibits a marked increase after *c.* 1950 (Figure 4a, 4e). This pattern is reflected in the overall number of NAS observed per year: while that number exhibits a roughly linear increase between 1850 and 2015 for plants, the accumulation of animal species appears to accelerate in the second half of the 20th century (Figure 4c, 4g). After approximately 2005, there appears to be a decline in the number of both plant and animal species observed per year. This decline is consistent with previously observed patterns in global data on nonindigenous species, and is presumably associated with the expected lag period between observation and reporting (Seebens et al. 2017).

In general, increases in the number of records and number of watersheds with observations occur earlier and more gradually for animals than for plants (Figure 4b, f, d, and h). The number of watersheds containing samples and the number of observations generally do not correspond well with trends in species discovery for plants. In particular, the roughly linear trend in the number of NAS plant species observed (Figure 4g) fails to reflect a sharp increase in the cumulative number of records and number of watersheds that contain plant NAS in the past decade (Figure 4f, h). In contrast, species discovery corresponds more closely to the number and spatial extent of records in the NAS animal data set. The inflection point in the number of animal species first records and total number of animal NAS observed per year (Figure 4a, c) coincides roughly with the inflection points of both number of records and number of HUC12s containing records (Figure 4b, 4d), all occurring shortly after 1950.

Among animal taxonomic groups, fish were dominant, comprising 33% of total animal NAS. Temporal trends in observations also varied somewhat between groups, with fish records exhibiting increases in species counts, number of observations, and spatial coverage of records earlier in the 20th century than either invertebrates or amphibians, the latter showing little overall increase in the analyzed time period (Figure 5a–c). These groups also displayed different spatial patterns of introduction. All taxonomic groups were widely introduced across HUC2 watersheds; however, while both fish and amphibian species counts were by far highest in the South Atlantic-Gulf region (HUC2 #3, accounting for 77% of species records for amphibians and 75% for fish), invertebrates were more evenly distributed, with peak counts in the Great Lakes region (55% of species counts).

Regional trends

Patterns in both species discovery and number and spatial extent of records vary considerably across regions for both plants and animals (Figure 5, Table 1). The highest number of NAS per HUC2 was observed in the California and South Atlantic-Gulf watersheds, for both plants and animals; however, patterns of first US records were different between the two taxonomic groups, with most initial introductions for plants occurring in California, New England, and the South Atlantic-Gulf, while initial animal introductions were concentrated primarily in the South Atlantic-Gulf and the Great Lakes (Table 1). The number of individual records observed prior to 2017 varied across regions over two orders of magnitude, from several hundred records to tens of thousands, while areal coverage ranged from 5% to 64% for animals and from 5% to 36% for plants (Table 1).

Regional temporal trends in number of observed species and the number and spatial extent of records largely reflect national trends, although with notable exceptions. Generally, increases in the cumulative number of observed species are more linear than increases in the cumulative number of records or areal coverage for either plants or animals (Figure 6). For plants, this distinction is particularly pronounced, with dramatic increases in sampling occurring in most regions after 2000 (Figure 6a–c). California is a clear exception, exhibiting roughly linear increases in all variables across the measured timeframe. New England similarly exhibits high levels of early sampling, corresponding with the highest observed cumulative numbers of plant NAS. Generally, changes in the number and spatial extent of records for plant species again fail to reflect similar changes in number of species observed; despite dramatic increases in these variables post-2000 (Figure 6b, c), little change is observed in the number of species (Figure 6a). Especially notable is the extreme increase in number of records in the Great Lakes watershed, which does not reflect a corresponding increase in observed number of species. Similar patterns are observed for animal species, although increases in sampling effort are generally more gradual and initiated earlier than for plant species (Figure 6e, f vs. 6b, c). Corrections for HUC2 area reveals that New England, California, Mid-Atlantic, and Tennessee watersheds harbor the highest relative numbers of NAS for both plants and animals. While California and New England also exhibit high measures of apparent sampling effort, number of records and areal coverage are also extremely high for regions with far fewer observed NAS (e.g. the Great Lakes and the Upper Mississippi).

Contributions of reporting entities

The distribution of effort across collection entities was different for plant and animal species (Figure 7). This was most dramatic for first occurrence records: federal agencies alone accounted for the vast majority of animal species observations, while effort to identify new plant NAS was more evenly distributed across entity types (Figure 7b). Local and state entities accounted for a much larger percentage of overall effort to collect individual records; this was particularly true of plants, where state/local/tribal government agencies and universities accounted for 70% of plant observations (Figure 7a). Federal agencies appear to have played a more significant role in accumulating individual animal observations than aquatic plant observations, although local and state governments remained the most dominant contributors.

Discussion

National scale spatial and temporal trends in NAS introductions

Patterns of nonindigenous species richness across broad geographic scales are generally driven by interactive effects of both human activity and climatic variables (Capinha et al. 2013; Dalmazzone and Giaccaria 2014; Dawson et al. 2017; Keller et al. 2011). Global trade, in particular, has been widely recognized as a determinant of trends in the intercontinental redistribution of species (Dalmazzone and Giaccaria 2014; Hulme 2009; Westphal et al. 2007). In the case of freshwater invasions, species introductions have accompanied a suite of anthropogenic vectors including vessel traffic (ballast water and hull fouling), aquaculture, and aquarium and ornamental species trades (Bobeldyk et al. 2014; Cope et al. 2015; Hulme et al. 2008; Lo et al. 2012; Padilla and Williams 2004). Geographic and temporal shifts in the activity of these vectors can therefore have important influences on spatio-temporal trends in NAS introduction and spread (McGeoch et al. 2010; Westphal et al. 2007).

Historical patterns in the introduction of NAS to the conterminous US appear to follow several general trends (Figures 1, 2, and 3). The earliest introductions, up to and including the first half of the 20th century, tend to be predominantly to the Northeast and sourced largely from Europe and temperate regions in Asia. California is also an early recipient of NAS, particularly the large population centers in southern and central California, although sources for these introductions appear to be more varied, deriving not only from Europe and temperate Asia but also from Africa as well as tropical regions in South America and Asia. Introductions to the Great Lakes region appear to have increased throughout the second half of the 20th century, again driven primarily by translocations from Eurasia. Even more recently, the Southeast has experienced a sharp acceleration in NAS richness, particularly in Florida, which has rapidly become one of the most highly invaded regions of the US over the past several decades. Introductions to the Southeast have been dominated by species from tropical regions of North and South America and Asia, especially among animal taxa.

These observed trends are broadly consistent with known patterns of anthropogenic vector activity as well as previously observed patterns of species introductions to the US. The northeastern US, for instance, has been recognized in prior studies as a hotspot of forest invasions, suggesting that early increases in population density and industrialization in this region in the 19th and early 20th centuries have been important drivers of species introductions and spread (Liebhold et al. 2013). The emergence of the Great Lakes region as a hotspot of NAS richness in the second half of the 20th century similarly reflects the growing importance of trade in this region since the opening of the St. Lawrence Seaway in 1959 and subsequent increases in vessel traffic between the Great Lakes and European donor regions (Ricciardi 2006; Ricciardi and MacIsaac 2000). Among animal species, the Great Lakes region represents a center for invertebrate introductions in particular, harboring 55% of invertebrate NAS recorded in the US (Figure 5). More recently, NAS introductions to the Southeast have been driven largely by importation of aquarium, pet, and ornamental species, trades that are dominated by taxa derived from tropical sources in Central and South America and Asia (Fukisaki et al. 2015; Krysko et al. 2011). Fish and amphibians exhibit

unusually high levels of animal species introduction to the region (Figure 5), very likely reflecting prevailing trade patterns. These patterns conform with previously published results describing the distribution of nonindigenous fish and invertebrate species across the US (Bobeldyk et al. 2014; Stohlgren et al. 2006). While shifting global trade patterns are thus likely primary factors determining species introductions to the US, the spread and successful establishment of NAS appears also to be subject to climatic similarities between the species' endemic ranges and their recipient region. Species derived from temperate source regions in Europe and Asia have tended to spread broadly across the Northeast, the Great Lakes, and the West, while NAS introductions from tropical sources in South America, Mexico, and Asia have principally established in the Southeastern US (Figure 3). Interestingly, while the Southeast has become an important hotspot of NAS richness, species introduced to this region appear generally to have spread less broadly than those introduced to more temperate regions of the country (data not shown), consistent with the hypothesis of broad-scale climatic limitations on the distributions of exotic species (Sofaer and Jarnevich 2017). This pattern may also reflect the relatively low hydrologic connectivity of watersheds in the southeast, reducing the potential for natural spread compared to NAS introduced to the more highly connected large river basins.

Relationship between species counts and the number and extent of individual observations

Unfortunately, there are no data available on actual sampling effort associated with the *ad hoc* compilation of species observations such as those curated in the publicly accessible databases utilized in this study. Those databases are not exhaustive and they do not include metrics of effort for standardized surveys, precluding direct assessment of sampling effort. In the absence of such measures of sampling effort, we have examined the number of records and the spatial extent of those records (i.e., the number of watersheds for which records exist). The relationships between these variables and actual sampling effort will be imperfect for a variety of reasons, including the lack of negative data, reporting fatigue (actual observations may not be reported in all cases, particularly for widely distributed and long established introductions), and inaccuracies in association between reports and actual observations (e.g., generic records associated only with publication dates); the strength of these relationships may also vary among taxonomic groups. Despite these limitations, it is likely that these metrics are generally reflective of sampling effort associated with NAS observations. Previous studies have suggested that such variables can in some cases be used effectively as an indirect measure of sampling effort. For instance, Lobo (2008) found that database records drawn from diverse sources of diversity data (including non-standardized collections) can be utilized as surrogates of sampling effort to identify well-surveyed sites, and that indirect estimates of effort drawn from database records are correlated with more direct estimates derived from standardized collections.

Examination of historical data on NAS introductions reveals complex relationships between species discovery and the number and spatial extent of individual NAS observations, relationships that may vary across regions and across taxonomic groups. The yearly number of first records and the accumulation of NAS over time (Figure 4a, c, e, g) suggest that while the introduction of plant species has remained roughly constant since the middle of the 19th

century, resulting in a generally linear increase in the overall number of NAS, aquatic animal species introductions have accelerated considerably after 1950. That acceleration, however, coincides closely with dramatic increases in both the number of observational records and the spatial extent of those records (Figure 4b, d). This raises the possibility that the apparent increase in animal invasion rate in the latter half of the 20th century may be in part an artifact of increased sampling effort. Interestingly, increases in the same metrics associated with plant taxa do not correspond well to increases in species observations. This may be the result of different types of effort being expended for plant and animal taxa; in particular, plant NAS may be more amenable to intensive efforts at range delineation on local and regional scales, resulting in studies that record large numbers of single species observations and yet contribute relatively little to the overall discovery of new introductions.

Regional trends and the potential importance of regional differences in sampling effort

Discrepancies between species counts and number and extent of records are clearly exacerbated by variability in both the level and type of effort expended across regions and states. Disparities in regional observations are apparent even in broad-scale analyses of NAS distributions. For instance, dramatic increases in NAS richness in the Great Lakes and Mid-Atlantic between 1971 and 1990 (Figure 1e) appear to be driven in part by increases in species observations across the states of Wisconsin and Pennsylvania. These patterns are far more likely to represent shifts in local sampling effort than true increases in introduction or spread. It is also possible that such region-specific increases represent spikes in reporting associated with publication of major bio-diversity studies. Thus, publicly accessible databases may exhibit “fuzziness” of temporal attribution of observational data, with some records associated with publication date despite representing earlier sightings. However, further investigation of data specific to Wisconsin and Pennsylvania suggests that the observed increases are due to increased sampling associated with multiple efforts initiated in this time period (not shown).

In general, our regional trends analysis indicates considerable variation in both rates of species observation and metrics associated with sampling effort, attributable in part to recognized temporal shifts in actual sampling effort in those regions. This variation is particularly clear for plant NAS. While most regions exhibit a roughly linear trend in species accumulation (Figure 6a), there is clear evidence of dramatic increases in number and extent of individual observations in the early 21st century. For example, the Great Lakes region experienced an extraordinary escalation in these metrics in the absence of any corresponding increase in species richness (Figure 6b, c). That change corresponds with a dramatic influx of funding for NAS management associated with programs such as the Great Lakes Restoration Initiative, launched in 2010. The general acceleration in the number and spatial extent of aquatic plant records around the turn of the 21st century may be related in part to a number of federal policies that led to increased support for monitoring initiatives in the 1990s. These included the Nonindigenous Aquatic Nuisance Prevention and Control Act of 1990 (which established the national Aquatic Nuisance Species Task Force) and its reauthorization in the National Invasive Species Act of 1996, as well as Executive Order 13112, which established the National Invasive Species Council in 1999. Among animal species, trends are more broadly consistent over time, although it is still clear that high

record counts do not necessarily translate into high richness, and vice versa. The Upper Mississippi (HUC2 #7), for example, exhibits modest relative richness despite extremely high overall record counts; the Tennessee watershed (HUC2 #6), in contrast, has the second highest relative NAS richness despite a low overall number of records (Figure 6, Table 1). These results confirm that regional discrepancies in the magnitude and type of sampling effort at each location could bias results when comparing invasion patterns among multiple locations (Engemann et al. 2015).

The observed differences in regional observations as well as the trends in plant and animal NAS databases are likely sensitive to differing priorities and funding availability between contributing organizations. Organizations tend to monitor locations that are easily accessible or close to their physical locations, which could cause uneven distribution of sampling effort across large regions (Fuentes et al. 2012). As state specific organizations or agencies contribute the majority of both plant and animal observations (Figure 7a), sampling effort to delineate the distributions of species may be primarily driven by state or local authorities and subject to their policies and priorities. Therefore, geographic variability in monitoring records likely reflects both invasion pressure and the level of available local funding or interest in NAS monitoring (Hyndman et al. 2015). It is possible, then, that the observed number of NAS in certain regions has been deflated by relatively low sampling effort in those regions. However, it is important to note that attempts to catalog new NAS introductions may be more uniform across the country as this effort appears more equally dispersed between multiple entities, or is primarily carried out by federal agencies (Figure 7b). It is interesting that the dominant role of local entities (state/local/tribal governments and universities) is far more prevalent for reporting plant taxa than for animals, again suggesting that there may be significant taxonomic differences in the distribution of effort aimed at species discovery vs. the targeted delineation of species' ranges. This may reflect in part the predominance of targeted noxious weed programs at the state and local as opposed to federal level. Previous studies have shown that few species account for most of the records in plant NAS databases; this likely reflects both the tendency for organizations to prioritize studying highly visible species with the greatest negative impact as well as the amenability of plant NAS (particularly emergent species) to intensive surveys to determine extent of invasion (Pyšek et al. 2008).

Conclusions

Analysis of changes in nonindigenous species distributions over time can reveal important patterns of potential interest to management and policy, including historical shifts in vector activity and trends in regional invasion hotspots. The fact that such patterns can be inferred from analysis of publicly available databases of observational records underscores the value of such databases to those tasked with assessing and mitigating risks of biological invasions. However, it is also critically important to address inherent shortcomings of these data sources in order to avoid misleading or biased conclusions. In particular, the *ad hoc* nature of data sets based on opportunistically collected observational records derived from multiple sources makes it extremely challenging to disentangle patterns of observed species richness from sampling effort. Our analysis indicates that the relationship between NAS counts and the number and extent of individual observations can change dramatically over space, time,

and even taxonomic group, and depends critically on the priorities and capabilities of entities contributing to public databases. These results highlight the need for caution in analysis of such data for ecological inference without consideration of their potential biases.

Unfortunately, quantifying species introduction while accounting for potential bias in empirical data is challenging, as there are few surveys that are unbiased and also spatially and temporally comprehensive. Work et al. (2005), for example, used a quantitative analysis of randomly sampled cargo shipments entering the US to analyze the arrival rate of pest species; however, this data source was limited to a single vector and could not provide an exhaustive estimate of invasion rate at a national scale. Theoretical and statistical approaches have also been developed that attempt to correct for variations in temporal sampling, and are most commonly used to address observational bias from survey data in order to develop estimates of species introduction (Belmaker et al. 2009; Costello and Solow 2003; Solow and Costello 2004). These and other studies suggest that more accurate and statistically compelling assessments of temporal trends in NAS introductions can be obtained in those cases where more direct proxy measures of sampling effort are available. This conclusion argues strongly for the incorporation of such measures into future databases, despite the challenges associated with assembling these data at broad spatial scales.

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References

- Belmaker J, Brokovish E, China V, Golani D, Kiflawi M (2009) Estimating the rate of biological introductions: Lessepsian fishes in the Mediterranean. *Ecology* 90: 1134–1141, 10.1890/07-1904.1 [PubMed: 19449707]
- Boakes EH, McGowan PJK, Fuller RA, Chang-qing D, Clark NE, O'Connor K, Mace GM (2010) Distorted views of biodiversity: Spatial and temporal bias in species occurrence data. *PloS Biology* 8: e1000385, 10.1371/journal.pbio.1000385
- Bobeldyk AM, Rüegg J, Lamberti GA (2014) Freshwater hotspots of biological invasion are a function of species - pathway interactions. *Hydrobiologia* 746: 363–373, 10.1007/s10750-014-2009-z
- Brummit RK (2001) World Geographical Scheme for Recording Plant Distributions. 2 edn Hunt Institute for Botanical Documentation, Carnegie Mellon University, Pittsburgh
- Carpio AJ, Barasona JA, Guerrero-Casado J, Oteros J, Tortosa FS, Acevedo P (2016) An assessment of conflict areas between alien and native species richness of terrestrial vertebrates on a macro-ecological scale in a Mediterranean hotspot. *Animal Conservation* 20: 433–443, 10.1111/acv.12330
- Capinha C, Brotons L, Anastacio P, McGeoch M (2013) Geographical variability in propagule pressure and climatic suitability explain the European distribution of two highly invasive crayfish. *Journal of Biogeography* 40: 548–558, 10.1111/jbi.12025
- Cope RC, Prowse TA, Ross JV, Wittmann TA, Cassey P (2015) Temporal modelling of ballast water discharge and ship-mediated invasion risk to Australia. *Royal Society Open Science* 2: 150039, 10.1098/rsos.150039
- Costello CJ, Solow AR (2003) On the pattern of discovery of introduced species. *Proceedings of the National Academy of Sciences USA* 100: 3321–3321, 10.1073/pnas.0636536100

- Dalmazzone S, Giaccaria S (2014) Economic drivers of biological invasions: A worldwide, biogeographic analysis. *Ecological Economics* 105: 154–165, 10.1016/j.ecolecon.2014.05.008
- Davis AJS, Darling JA (2017) Recreational freshwater fishing drives non-native aquatic species richness patterns at a continental scale. *Diversity and Distributions* 23: 692–702, 10.1111/ddi.12557 [PubMed: 30147430]
- Dawson W, Moser D, van Kleunen M, Kreft H, Pergl J, Pysek P, Weigelt P, Winter M, Lenzner B, Blackburn TM, Dyer EE, Cassey P, Scrivens SL, Economo EP, Guenard B, Capinha C, Seebens H, Garcia-Diaz P, Nentwig W, Garcia-Berthou E, Casal C, Mandrak NE, Fuller P, Meyer C, Essl F (2017) Global hotspots and correlates of alien species richness across taxonomic groups. *Nature Ecology & Evolution* 1: 0186, 10.1038/s41559-017-0186
- Dick JTA, Alexander ME, Jeschke JM, Ricciardi A, MacIsaac HJ, Robinson TB, Kumschick S, Weyl OLF, Dunn AM, Hatcher MJ, Paterson RA, Farnsworth KD, Richardson DM (2013) Advancing impact prediction and hypothesis testing in invasion ecology using a comparative functional response approach. *Biological Invasions* 16: 735–753, 10.1007/s10530-013-0550-8
- Dyer EE, Cassey P, Redding DW, Collen B, Franks V, Gaston KJ, Jones KE, Kark S, Orme CD, Blackburn TM (2017) The global distribution and drivers of alien bird species richness. *PloS Biology* 15: e2000942, 10.1371/journal.pbio.2000942
- Engemann K, Enquist BJ, Sandel B, Boyle B, Jorgensen PM, Marueta-Holmes N, Peet RK, Vialle C, Svenning JC (2015) Limited sampling hampers “big data” estimation of species richness in a tropical biodiversity hotspot. *Ecology & Evolution* 5: 807–820, 10.1002/ece3.1405 [PubMed: 25692000]
- Ficetola GF, Cagnetta M, Padoa-Schioppa E, Quas A, Razzetti E, Sindaco R, Bonardi A (2014) Sampling bias inverts ecogeographical relationships in island reptiles. *Global Ecology and Biogeography* 23: 1303–1313, 10.1111/geb.12201
- Fuentes N, Pauchard A, Sánchez P, Esquivel J, Marticorena A (2012) A new comprehensive database of alien plant species in Chile based on herbarium records. *Biological Invasions* 15: 847–858, 10.1007/s10530-012-0334-6
- Fukisaki I, Mazzotti FJ, Watling J, Krysko KL, Escibano Y (2015) Geographic risk assessment reveals spatial variation in invasion potential of exotic reptiles in an invasive species hotspot. *Herpetological Conservation and Biology* 10: 621–632
- Fuller PL, Neilson ME (2015) The U.S. Geological Survey’s Nonindigenous Aquatic Species Database: over thirty years of tracking introduced aquatic species in the United States (and counting). *Management of Biological Invasions* 6: 159–170, 10.3391/mbi.2015.6.2.06
- Gu Z, Gu L, Eils R, Schlesner M, Brors B (2014) Circlize implements and enhances circular visualization in R. *Bioinformatics* 30: 2811–2812, 10.1093/bioinformatics/btu393 [PubMed: 24930139]
- Hulme PE (2009) Trade, transport and trouble: managing invasive species pathways in an era of globalization. *Journal of Applied Ecology* 46: 10–18, 10.1111/j.1365-2664.2008.01600.x
- Hulme PE, Bacher S, Kenis M, Klotz S, Kühn I, Minchin D, Nentwig W, Olenin S, Panov V, Pergl J, Pysek P, Roques A, Sol D, Solarz W, Vilà M (2008) Grasping at the routes of biological invasions: a framework for integrating pathways into policy. *Journal of Applied Ecology* 45: 403–414, 10.1111/j.1365-2664.2007.01442.x
- Hyndman RJ, Mesgaran MB, Cousens RD (2015) Statistical issues with using herbarium data for the estimation of invasion lag-phases. *Biological Invasions* 17: 3371–3381, 10.1007/s10530-015-0962-8
- Keller RP, Drake JM, Drew MB, Lodge DM (2011) Linking environmental conditions and ship movements to estimate invasive species transport across the global shipping network. *Diversity and Distributions* 17: 93–102, 10.1111/j.1472-4642.2010.00696.x
- Krysko KL, Burgess JP, Rochford MR, Gillette CR, Cueva C, Enge KM, Somma LA, Stabile JL, Smith DC, Wasilewski JA, Kieckhefer GN, Granatosky MC, Nielsen SV (2011) Verified non-indigenous amphibians and reptiles in Florida from 1863 through 2010: Outlining the invasion process and identifying invasion pathways and stages. *Zootaxa* 3028: 1–64
- Lichvar RW, Banks DL, Kirchner WN, Melvin NC (2016) The national wetland plant list: 2016 wetland ratings. *Phytoneuron* 30:1–17

- Liebholt AM, McCullough DG, Blackburn LM, Frankel SJ, Von Holle B, Aukema JE, Pyšek P (2013) A highly aggregated geographical distribution of forest pest invasions in the USA. *Diversity and Distributions* 19: 1208–1216, 10.1111/ddi.12112
- Lo VB, Levings CD, Chan KM (2012) Quantifying potential propagule pressure of aquatic invasive species from the commercial shipping industry in Canada. *Marine Pollution Bulletin* 64: 295–302, 10.1016/j.marpolbul.2011.11.016 [PubMed: 22206724]
- Lobo JM (2008) Database records as a surrogate for sampling effort provide higher species richness estimations. *Biodiversity and Conservation* 17: 873–881, <https://doi.org/10.1007/s10531-008-9333-4>
- Lodge D, Williams S, MacIsaac HJ, Hayes K, Leung B, Reichard SH, Mack RN, Moyle PB, Smith M, Andow DA, Carlton JT, McMichael A (2006) Biological invasions: Recommendations for U.S. policy and management. *Ecological Applications* 16: 2035–2054, 10.1890/1051-0761(2006)016[2035:BIRFUP]2.0.CO;2 [PubMed: 17205888]
- McGeoch MA, Butchart SHM, Spear D, Marais E, Kleynhans EJ, Symes A, Chanson J, Hoffmann M (2010) Global indicators of biological invasion: species numbers, biodiversity impact and policy responses. *Diversity and Distributions* 16: 95–108, 10.1111/j.1472-4642.2009.00633.x
- McKinney W (2010) Data structures for statistical computing in Python. *Proceedings of the Python in Science Conference* 9: 51–56
- Moorhouse TP, Macdonald DW (2015) Are invasives worse in freshwater than terrestrial ecosystems? *Wiley Interdisciplinary Reviews: Water* 2: 1–8, 10.1002/wat2.1059
- Murray B, Phillips M (2012) Temporal introduction patterns of invasive alien plant species to Australia. *NeoBiota* 13: 1–14, 10.3897/neobiota.13.2422
- Padilla DK, Williams SL (2004) Beyond ballast water: Aquarium and ornamental trades as sources of invasive species in aquatic systems. *Frontiers in Ecology and the Environment* 2: 131–138
- Panlasigui S, Davis AJS, Mangiante MJ, Darling JA (2018) Assessing threats of non-native species to native freshwater biodiversity: Conservation priorities for the United States. *Biological Conservation* 224: 199–208, 10.1016/j.biocon.2018.05.019 [PubMed: 30245526]
- Pimentel D, Zuniga R, Morrison D (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics* 52: 273–288, 10.1016/j.ecolecon.2004.10.002
- Pyšek P, Richardson DM, Pergl J, Jarosik V, Sixtova Z, Weber E (2008) Geographical and taxonomic biases in invasion ecology. *Trends in Ecology & Evolution* 23: 237–44, 10.1016/j.tree.2008.02.002 [PubMed: 18367291]
- Ricciardi A (2006) Patterns of invasion in the Laurentian Great Lakes in relation to changes in vector activity. *Diversity and Distributions* 12: 425–33, 10.1111/j.1366-9516.2006.00262.x
- Ricciardi A, MacIsaac HJ (2000) Recent mass invasion of the North American Great Lakes by Ponto-Caspian species. *Trends in Ecology & Evolution* 15: 62–65, 10.1016/S0169-5347(99)01745-0 [PubMed: 10652557]
- Ricciardi A, MacIsaac HJ (2011) Impacts of biological invasions on freshwater ecosystems In: Richardson AJ (ed), *Fifty Years of Invasion Ecology: The Legacy of Charles Elton*. Blackwell Publishing Ltd., Oxford, UK, pp 211–224
- Ricketts T, Dinerstien E, Olson D, Loucks C, Eichbaum W, DellaSala D, Kavanagh K, Hedao P, Hurley P, Carney K, Abell R, Walters S (1999) *Terrestrial ecoregions of North America: A conservation assessment*. Island Press, Washington, D.C., 508 pp
- Seaber P, Kapinos F, Knapp G (1987) *Hydrologic Unit Maps*. USGS Water Supply Paper 2294, 63 pp
- Seebens H, Blackburn TM, Dyer EE, Genovesi P, Hulme PE, Jeschke JM, Pagad S, Pyšek P, Winter M, Arianoutsou M, Bacher S, Blasius B, Brundu G, Capinha C, Celesti-Grapo L, Dawson W, Dullinger S, Fuentes N, Jäger H, Kartesz J, Kenis M, Kreft H, Kühn I, Lenzner B, Liebhold A, Mosena A, Moser D, Nishino M, Pearman D, Pergl J, Rabitsch W, Rojas-Sandoval J, Roques A, Rorke S, Rossinelli S, Roy HE, Scalera R, Schindler S, Stajerova K, Tokarska-Guzik B, van Kleunen M, Walker K, Weigelt P, Yamanaka T, Essl F (2017) No saturation in the accumulation of alien species worldwide. *Nature Communications* 8: 14435, 10.1038/ncomms14435

- Sofaer HR, Jarnevich CS (2017) Accounting for sampling patterns reverses the relative importance of trade and climate for the global sharing of exotic plants. *Global Ecology and Biogeography* 26: 669–678, 10.1111/geb.12577
- Solow AR, Costello CJ (2004) Estimating the rate of species introductions from the discovery record. *Ecology* 85: 1822–1825, 10.1890/03-3102
- Stohlgren TJ, Schnase JL (2006) Risk analysis for biological hazards: what we need to know about invasive species. *Risk Analysis* 26: 163–173, 10.1111/j.1539-6924.2006.00707.x [PubMed: 16492190]
- Stohlgren TJ, Barnett D, Flather C, Fuller P, Peterjohn B, Kartesz J, Master LL (2006) Species richness and patterns of invasion in plants, birds, and fishes in the United States. *Biological Invasions* 8: 427–447, 10.1007/s10530-005-6422-0
- Strayer DL (2010) Alien species in fresh waters: ecological effects, interactions with other stressors, and prospects for the future. *Freshwater Biology* 55: 152–174, 10.1111/j.1365-2427.2009.02380.x
- USGS (2017) Nonindigenous Aquatic Species Database. <https://nas.er.usgs.gov/> (accessed January 31, 2017)
- van Kleunen M, Dawson W, Essl F, Pergl J, Winter M, Weber E, Kreft H, Weigelt P, Kartesz J, Nishino M, Antonova LA, Barcelona JF, Cabezas FJ, Cardenas D, Cardenas-Toro J, Castano N, Chacon E, Chatelain C, Ebel AL, Figueiredo E, Fuentes N, Groom QJ, Henderson L, Inderjit Kupriyanov A, Masciadri S, Meerman J, Morozova O, Moser D, Nickrent DL, Patzelt A, Pelter PB, Baptiste MP, Poopath M, Schulze M, Seebens H, Shu WS, Thomas J, Velayos M, Wieringa JJ, Pysek P (2015) Global exchange and accumulation of non-native plants. *Nature* 525: 100–103, 10.1038/nature14910 [PubMed: 26287466]
- Walsh JR, Carpenter SR, Vander Zanden MJ (2016) Invasive species triggers a massive loss of ecosystem services through a trophic cascade. *PNAS* 113: 4081–4085, 10.1073/pnas.1600366113 [PubMed: 27001838]
- Westphal MI, Browne M, MacKinnon K, Noble I (2007) The link between international trade and the global distribution of invasive alien species. *Biological Invasions* 10: 391–398, 10.1007/s10530-007-9138-5
- Wonham MJ, Carlton JT (2005) Trends in marine biological invasions at local and regional scales: the Northeast Pacific Ocean as a model system. *Biological Invasions* 7: 369–392, 10.1007/s10530-004-2581-7
- Wonham MJ, Pachevsky E (2006) A null model of temporal trends in biological invasion records. *Ecology Letters* 9: 663–672, 10.1111/j.1461-0248.2006.00913.x [PubMed: 16706911]
- Work TT, McCullough DG, Cavey JF, Komsa R (2005) Arrival rate of nonindigenous insect species into the United States through foreign trade. *Biological Invasions* 7: 323–332, 10.1007/s10530-004-1663-x

Figure 1.

Changes to total (plants and animals) NAS species richness over time. Color scale indicates total number of species. Richness is mapped at the HUC12 watershed level. HUC2 watershed boundaries are shown in black outline.

Figure 2.
Spatial distribution of first records of plant (green) and animal (red) NAS over multiple time periods. Time periods are the same as for Figure 1.

Figure 3.

Flow diagrams showing sources of plant (a) and animal (b) NAS introductions. Only first introductions to the US are depicted; subsequent spread within the US is not indicated in this figure. In each flow diagram, source regions are on the left and recipient regions are on the right, and flows are depicted by arrows; regions and assigned colors are shown in (c) and (d) for source and recipient regions, respectively. Scale shown around the outside of the circle is number of species. In some cases, native ranges for species span multiple source regions. In those cases, proportions of that species were assigned to the appropriate regions (e.g. a species derived from Europe and Temperate Asia is shown as 0.5 species from Europe and 0.5 from Temperate Asia). All introductions from North America were from Central America and Mexico; no introductions were recorded from Canada.

Figure 4.

Temporal trends in nonindigenous animal (a-d) and plant (e-h) observations. (a, e) Count of first records, summed every five years. (b, f) Count of total observations, summed every five years. (c, g) Total number of nonindigenous species in each year. (d, h) Total number of HUC12 watersheds with an NAS observation in each year. Red lines indicate moving averages calculated over a 25 year window. Note difference of scale on y axes, particularly between (d) and (h).

Figure 5.

Temporal and spatial trends in NAS by major animal taxonomic groups. Total NAS count per year (a), total number of records per year (b), and total number of HUC12 watersheds with at least one record (c) are shown for amphibians (blue lines), fish (orange), and invertebrates (green) over the time period between 1900 and 2015. All lines represent moving averages over a 25 year window. Distribution of total NAS counts across the 18 HUC2 watersheds (d) are shown for the same taxonomic groups (colors as in a-c; geographic locations of HUC2 watersheds are shown in Figure 6g).

Figure 6.

Cumulative number of species (a, d), cumulative number of records (b, e), and watershed coverage (total area of HUC12 watersheds with at least one NAS record divided by total area of HUC2; c, f) for both plant (a, b, c) and animal (d, e, f) species. Colors reflect HUC2 as indicated in (g). Values in a, b, d, and e are normalized to the area of the largest HUC2. The scales of b and e are in thousands of records.

Figure 7. Contributions of different entities to animal (black) and plant (grey) NAS databases. Total number of records are shown on left, number of first species occurrences are shown on the right (note different scales).

Table 1.

Summary statistics for plant and animal NAS by HUC2 watershed. Coverage is equal to the total area of HUC12s with at least one NAS record, divided by the total area of the HUC2 watershed.

HUC2	Watershed Name	Total area of HUC (km ²)	PLANTS				ANIMALS					
			Species	Records	Coverage	First U.S. Records	Earliest Record	Species	Records	Coverage	First U.S. Records	Earliest Record
1	New England	163110	67	9277	36%	31	<1800	35	11774	32%	9	<1700
2	Mid-Atlantic	276189	67	2289	18%	16	1839	45	17906	64%	10	1815
3	South Atlantic-Gulf	724336	79	17130	20%	34	1880	110	19537	36%	71	<1700
4	Great Lakes	495102	55	47413	30%	9	1844	60	19694	32%	28	1619
5	Ohio	421962	36	5020	13%	0	1858	34	6610	27%	2	1886
6	Tennessee	105950	29	290	9%	1	1896	20	2289	43%	0	1894
7	Upper Mississippi	492027	56	22537	26%	4	1862	34	58070	36%	1	1882
8	Lower Mississippi	276482	44	497	8%	4	1892	24	1357	22%	1	1894
9	Souris-Red-Rainy	155063	13	9870	27%	0	1911	7	678	7%	0	1950
10	Missouri	1322148	59	3872	7%	6	1864	40	6483	14%	6	1888
11	Arkansas-White-Red	642284	46	960	8%	1	1873	29	1567	12%	1	1888
12	Texas-Gulf	471091	36	605	8%	2	1828	51	1601	18%	8	1891
13	Rio Grande	343229	31	433	5%	1	1881	29	451	5%	3	1894
14	Upper Colorado	293569	21	1083	7%	0	1896	13	756	5%	1	1890
15	Lower Colorado	362981	38	4555	12%	1	1874	41	685	8%	8	1930
16	Great Basin	367049	34	3767	13%	0	1879	19	479	7%	1	1882
17	Pacific Northwest	723649	67	9847	15%	5	1877	39	4019	12%	8	1881
18	California	430658	97	15536	41%	41	1858	61	3149	13%	18	1879