Do invasive tetrapods conserve their climatic niches?

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Abstract

Invasive species are the second biggest threat to biodiversity after habitat fragmentation. The species list was collated from the Global Invasive Species Database (GISD) and the Centre for Agricultural and Bioscience International (CABI), and the species occurrence data were downloaded from the Global Biodiversity Information Facility (GBIF). This study examines the niche dynamics of 152 invasive tetrapods and finds that 60% of the species have very low or low niche overlap across the native and introduced regions. There are species with very high niche overlap, such as the Cane toad, Brahminy blind snake, Eurasian collared dove, Whitehead marmoset and Asian house shrew. Around 30% (=46) of species are showing considerable niche expansion. Similarly, 21 species (5 amphibians, 6 reptiles, 6 birds and 4 mammals) show no expansion in the introduced region. The introduction pattern presents that 46 invasive tetrapods are native to Asia, whereas 43 of them are introduced to North America.

Introduction

Biological invasion is one of the greatest threats to biodiversity, ecosystem services, human health, and livelihoods (Lockwood et al., 2013; Early et al., 2016; Brondizio et al., 2019). Despite regulatory efforts, the global introduction of species continues to rise steadily (Seebens et al., 2017), with predictions indicating sustained high rates in economically developed countries due to unfolding climate change, intensification of tourism, and increased trade in plants and pets (Early et al., 2016; Seebens et al., 2017; Ribeiro et al., 2019; Seebens et al., 2021).

The intentional or unintentional introduction of invasive vertebrates, facilitated by the expanding pet trade and global movements, exacerbates the challenges associated with invasive species. Concurrently, climate change significantly influences the distribution patterns of both native and introduced species. Climate change is a pivotal factor shaping the future movement of alien species (Peterson et al., 2008; Bellard et al., 2013). Some previously innocuous alien species become invasive due to climate change, enhancing their competitive advantages over native counterparts (Pyšek et al., 2020).

Invasive species, typically possessing broad ecological tolerances and adaptability to diverse conditions, exhibit rapid spread and colonisation of disturbed habitats. This adaptability enables them to thrive in extreme climate conditions, outcompeting native species (Diez et al., 2012). However, the impact of climate change on invasive species remains a subject of debate, with modelling studies yielding divergent conclusions—some suggesting an increase in the area invaded, while others indicate contraction in their distributions (Gallardo et al., 2017; Bellard et al., 2018).

The investigation into whether a given species experiences a shift in its climatic niche between its native and alien ranges has become more significant in recent times (Bates et al., 2020; Mahapatra et al., 2023; Yang et al., 2023). This is not only because of the implications for niche-based predictions regarding the spatial transferability of alien species but also because of concerns over global change (Guisan et al., 2014). The extant body of literature has generated contradictory findings regarding the proposition that alien species retain their native climatic niches in the alien range, invaded range, or home away from home (Aravind et al., 2022). While some studies provide support for this notion, others contest it, indicating the invasive species shift its range or find a new home (Broennimann et al., 2007; Petitpierre et al., 2012; Early & Sax, 2014; Liu et al., 2020; Aravind et al., 2022). The consequence of this is a contentious discussion regarding the significance of niche conservatism in the field of biological invasions.

A recent study by Liu et al. (2020) assessed more than 400 alien species and showed that during the invasion process, the majority of species tend to maintain their niches, with few changes occurring in the climatic niches within alien ranges. Notably, an expansion of niches was observed in certain taxa native to the island (Liu et al., 2020; Stroud, 2021). This observation implies that niche transitions may be more prevalent among island endemics throughout the invasion process.

Tetrapods, a diverse group of vertebrates, serve as an ideal study subject for understanding invasion patterns due to their extensive human-induced movements and widespread distribution. Unlike birds and mammals, herpetofauna, comprising amphibians and reptiles, exhibit smaller ranges, with temperature significantly influencing their distributions in these cold-blooded organisms. Investigating how these vertebrates respond to native and introduced niches provides valuable insights. This study aims to (a) estimate the introduction of invasive tetrapods across continents and (b) uncover niche dynamic patterns across 152 invasive vertebrates within the categories of amphibians, reptiles, birds, and mammals. Findings from this research will enhance our understanding of regions with high invasiveness and responses to climate change and support the development of actionable management plans for invasive species containment.

Materials and Methods

Species data: For the present study, the species were selected from the Global Invasive Species Database (www.issg.org) and the Centre for Agriculture and Bioscience International (CABI, www.cabi.org till December 2020). The distribution data for all species were downloaded from the Global Biodiversity Information Facility (GBIF, www.gbif.org) and CABI between July 2018 and June 2020. The species list was further reduced to 152 (15 amphibians, 29 reptiles, 44 birds, and 64 mammals) for niche dynamics analysis based on distribution data availability in both native and introduced ranges. For all species used in the present study, native and introduced ranges were collated from various sources, primarily from CABI and ISSG databases.

Niche dynamics: We used nineteen bioclimatic variable layers from WorldClim (www.worldclim.org) for the current scenario (ver 2.1) with a spatial resolution of 2.5 minutes (Fick and Hijmans, 2017). Principal Component Analysis (PCA-env) estimated the niche overlap across the native and introduced ranges (Broennimann et al., 2012). The spatially thinned rarefied points were segregated into native and introduced regions. We used the ecospat package ver 3.2 in R studio ver 4.1.0 to assess the Schoener's D index (niche overlap), Expansion (E), Unfilling (U) and Stability (S) (Broennimann et al., 2021; R Core Team 2018). We also performed niche equivalency and similarity tests to compare the native and introduced regions. The niche overlap index varies from 0 to 1, with zero being no overlap and one being complete overlap (Rödder and Engler, 2011).

Results

Our result shows that a maximum number of 46 species have been introduced from Asia, followed by North America with 40 species. Ninety-seven species were introduced to multiple continents, and about 43 species have been introduced to North America (Fig. 1).

Niche dynamics

The overall trend of niche overlap indicates that more than 60% (92 out of 152 species) showed very low (49) and low (43) niche overlap (Fig. 3). Only five species, i.e., *Rhinella marina* (amphibian), *Ramphotyphlops braminus* (reptile), *Streptopelia decaocto* (bird), *Callithrix geoffroyi*, and *Suncus murinus* (mammals) showed very high (>0.80) niche overlap (Table 2). The equivalency test is highly significant, i.e., p-value <0.05 for 56% of mammals (36 out of 64), 75% of birds (33 out of 44), 40% of amphibians (6 out of 15) and 24% of reptiles (7 out of 29) (Table 2). This means the distinction between the native and introduced ranges is more in birds than in herpetofauna. The niche expansion varies from 0 to 0.86 in amphibians, 0 to 1 in reptiles, and 0 to 0.99 in birds (Fig. 2). We found zero niche expansion for five amphibians, six reptiles, six birds and four mammals (Table 2). The mean expansion (E) is lowest for birds and highest for mammals, i.e., 0.24 and 0.40, respectively (Fig. 2). Similarly, the lower mean unfilling (U) for birds is 0.36 and the highest for reptiles is 0.70 (Fig. 3C). The one-way ANOVA suggests there is a significant difference in both unfilling (F=6.77, p=0.000) and niche overlap (F=5.34, p=0.0016) among these taxa but no significant difference in niche expansion (F=2.24, p=0.086) (Table 3). 46 (~30%) out of 152 invasive tetrapods show niche shift, i.e., (E > 0.5).

Discussion

This study presents the global-level assessment of the niche dynamics of 152 invasive tetrapods. There is inherent complexity of invasion processes as the invasion dynamics are influenced by diverse biotic and abiotic factors, including species interactions, native biodiversity, ecosystem services, and human-mediated factors like migration (Hulme, 2009; Gallardo and Aldridge, 2013), Due to the impracticality of comprehensively understanding biotic interactions for over 150 species across various taxa, our focus was primarily on utilising bioclimatic variables, considering the generalist nature of invasive species, to investigate whether tetrapods exhibit niche conservatism or show niche shift. The phenomenon of both niche shifts and conservatism has been documented in the literature. For instance, some introduced birds and mammals in Europe have demonstrated niche conservatism (Strubbe et al., 2013; Sales et al., 2016). The study by Strubbe et al. (2015) highlighted certain non-native vertebrates that maintain their niches in the introduced region. One could argue that niche conservatism is a primary mechanism through which a species is able to expand into various regions worldwide (Peterson, 2011; Pyron et al., 2015; Strubbe et al., 2015). Expanding on this body of knowledge, our study extends the niche conservatism test to a larger cohort of invasive vertebrates, revealing a prevalence of niche shifts in most of the tetrapods except for invasive birds. This pattern aligns with similar findings in invasive mammals (Mahapatra et al., under review). Conversely, invasive terrestrial plants exhibit niche conservatism (Petitpierre et al., 2012), while invasive reptiles adhere to niche conservatism (Aravind et al., 2023); this was shown in the present study as well. The nuanced dynamics of niche shifts are evident in the case of introduced plants (Atwater et al., 2018) and the majority of invasive freshwater molluscs (Mahapatra et al., 2023), which exhibit niche shifts in their introduced ranges. Contrasting results have been reported, with Liu et al. (2020) indicating that many invasive species adhere to niche conservatism, while Tingley et al. (2014) found evidence of niche expansion in the cane toad (*Rhinella marina*) in Australia. In the case of non-native vertebrates, like wild boar, niche shifts have been observed (Strubbe et al., 2013, 2015). The niche shift can be explained by the unfilling, which means the presence of an introduced environment analogous to the native region (Sales et al. 2016).

The variability in outcomes across studies can be attributed to different metrics used to measure niche shifts and the absence of clear thresholds for determining niche conservatism versus niche shift (Bates and Bertelsmeier, 2021). Interpretation biases and subjective beliefs further contribute to disparate conclusions about niche shifts (Bates and Bertelsmeier, 2021). While most studies reject the niche conservatism hypothesis for invasive species, our global review of tetrapods demonstrates a high degree of niche expansion, particularly in non-bird taxa. Birds, however, exhibit niches in the introduced ranges that closely mirror their native niches or home away from home. Notably, aquatic species and those introduced more recently exhibit lower niche similarity, a finding consistent with Liu et al. (2020). Despite the global review suggesting limited niche expansion between native and introduced ranges, our study on tetrapods reveals substantial niche expansion, with amphibians, often breeding in water, showing a significant number of species with low (<0.4) niche overlap between native and invaded ranges, indicative of niche shift. Aravind et al. (2022) showed that 90% of invasive species move to similar habitats, akin to "home away from home," while only 10% exhibit niche shifts or "finding a new home," a trend also echoed in other studies (Liu et al., 2020). The existing body of literature is biased towards studies in the global north, focusing primarily on single species between two regions rather than offering a comprehensive global-level assessment (Liu et al., 2020).

In conclusion, our global assessment of the niche dynamics of 152 invasive tetrapods reveals a nuanced interplay between niche shifts and conservatism. While birds often retain their native niches in introduced ranges, non-bird taxa, particularly amphibians, exhibit substantial niche expansion. The variability in outcomes across taxa underscores the complexity of invasion dynamics and the need for nuanced approaches to understanding species responses. The contrasting patterns observed highlight the importance of taxon-specific analyses. Our findings contribute to the ongoing discourse on the role of niche dynamics in biological invasions, emphasising the necessity for a comprehensive and global perspective to enhance our understanding of invasive species' ecological adaptability.

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Figure 1: Sankey diagram shows the introduction of tetrapod species across different continents

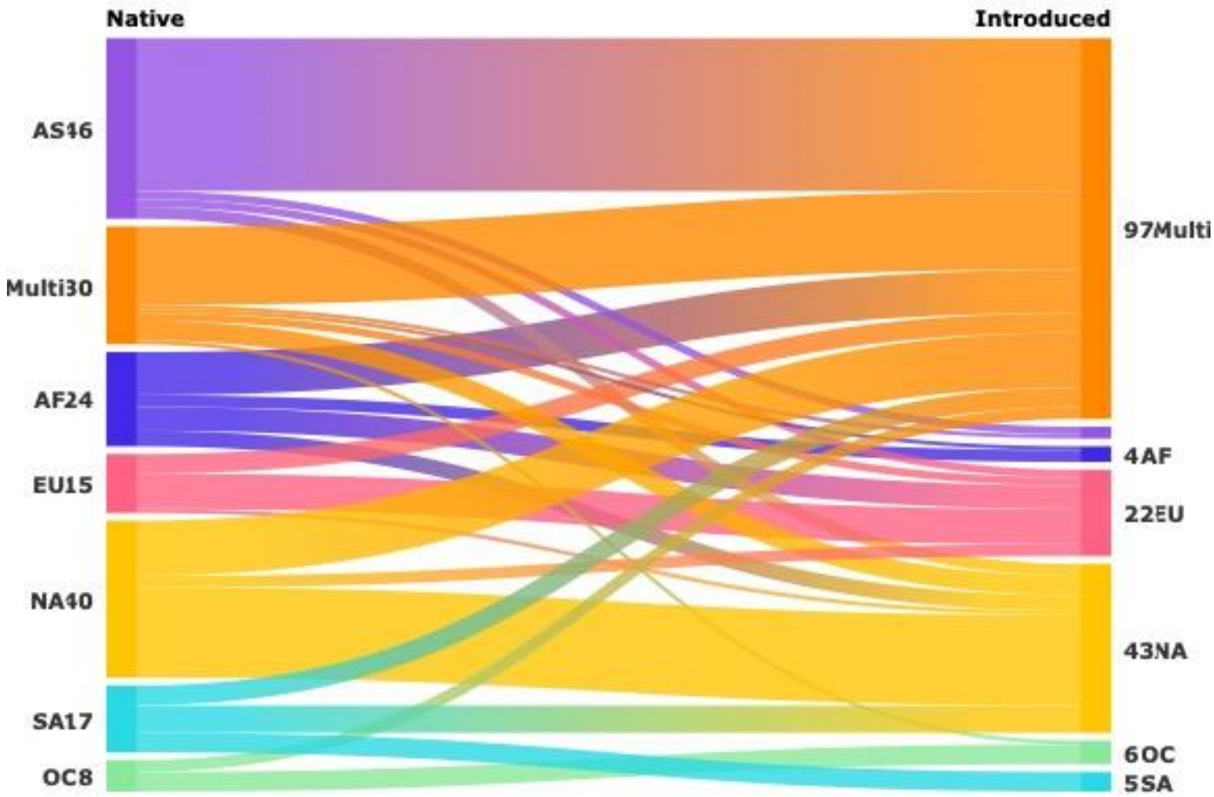

Table 1: ANOVA of niche expansion, niche unfilling and niche overlap among tetrapods

	F	P-value	F crit
Expansion	2.242	0.086	2.666
Unfilling	6.768	**0.000**	2.666
Niche overlap	5.344	**0.002**	2.666

Figure 2: Niche dynamics indices across tetrapods: niche overlap, expansion, stability, unfilling, similarity test and equivalency test. The violin plot shows the distribution of niche dynamics indices across all tetrapod taxa.

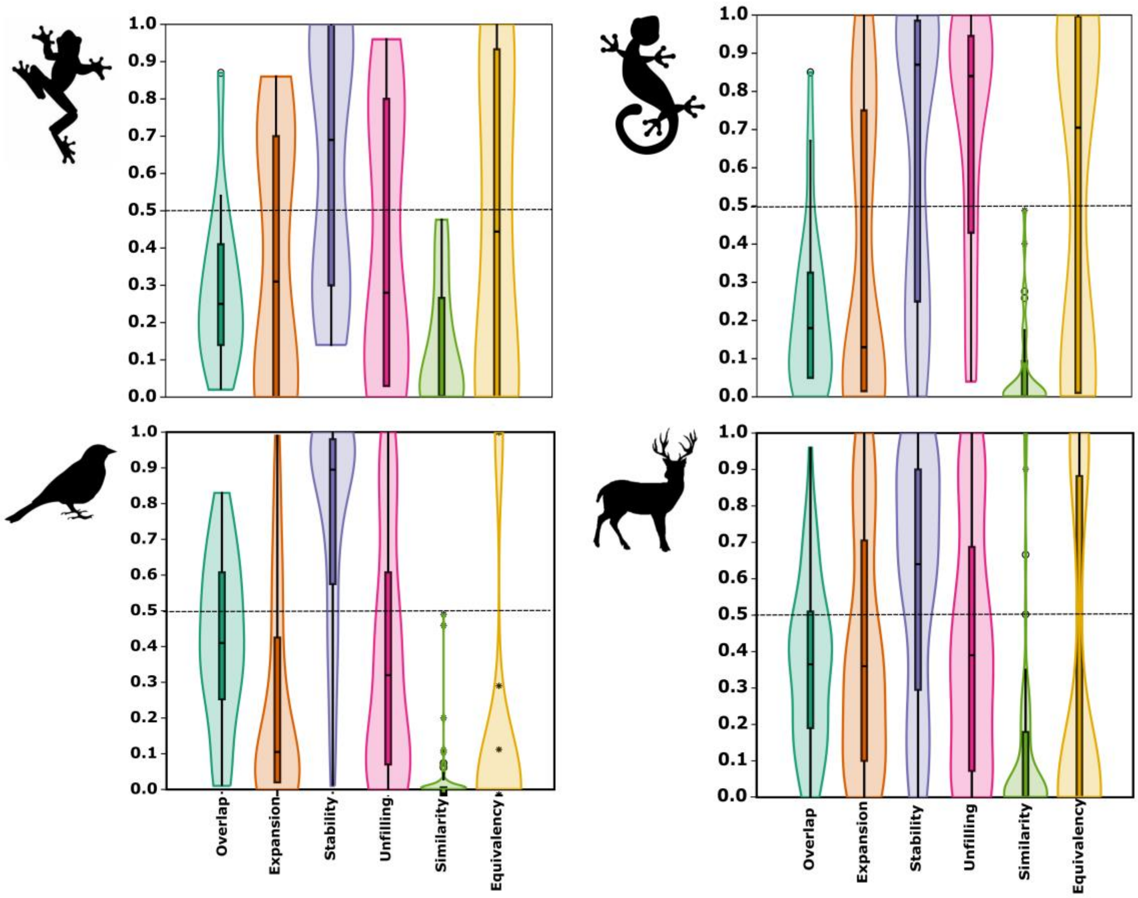

Figure 3: Niche overlap index (Schoener's D) across tetrapod taxa. The value ranges from zero to 1, and it is categorised as very low (zero to 0.2), low (0.2 to 0.4), moderate (0.4 to 0.6), high (0.6 to 0.8), and very high (0.8 to 1).

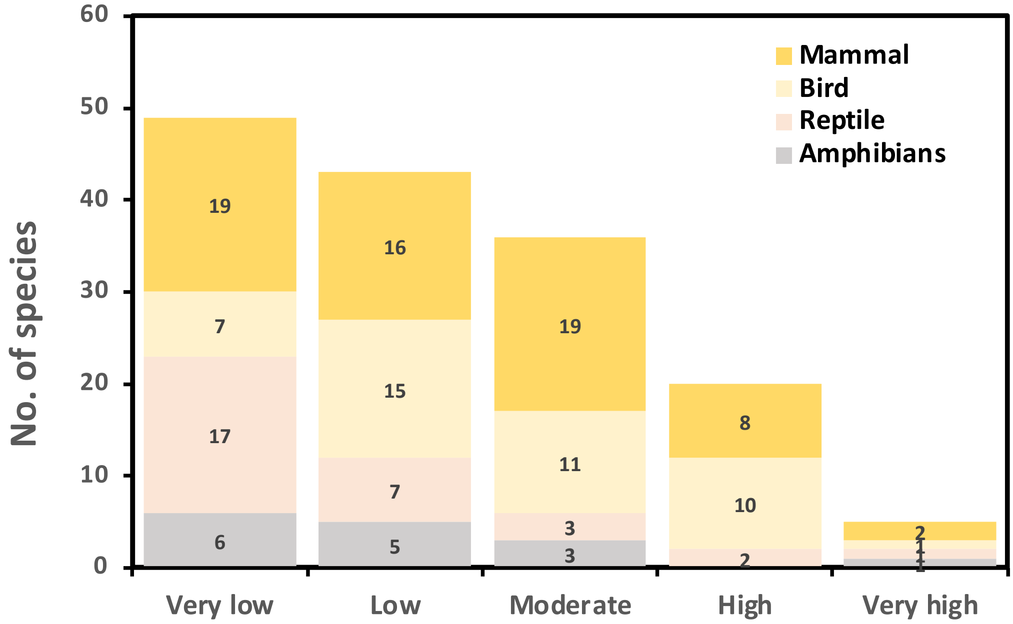

Table 2: Niche dynamics indices of invasive tetrapods

Taxon	Species	Schoener's Index (D)	Expansion (E)	Stability (S)	Unfilling (U)	Similarity	Equivalency
Amphibian	*Eleutherodactylus coqui*	0.14	0.86	0.14	0.23	0.349	1.000
	Eleutherodactylus johnstonei	0.25	0.70	0.30	0.28	0.266	1.000
	Eleutherodactylus planirostris	0.21	0.73	0.27	0.01	0.434	0.832
	Lithobates catesbeianus	0.32	0.31	0.69	0.00	0.022	0.001
	Litoria aurea	0.25	0.82	0.18	0.59	0.146	0.444
	Osteopilus septentrionalis	0.42	0.18	0.82	0.11	0.119	0.001
	Pelophylax bedriagae	0.41	0.49	0.51	0.03	0.190	0.933
	Pelophylax kurtumuelleri	0.15	0.70	0.30	0.91	0.476	0.001
	Pelophylax perezi	0.34	0.64	0.36	0.60	0.001	0.001
	Pelophylax ridibundus	0.07	0.00	1.00	0.80	0.023	1.000
	Rhinella marina	0.87	0.00	1.00	0.01	0.001	0.001
	Scinax ruber	0.09	0.00	1.00	0.81	0.003	0.300
	Scinax x-signatus	0.02	0.00	1.00	0.96	0.022	0.636
	Triturus carnifex	0.18	0.00	1.00	0.78	0.002	0.477
	Xenopus laevis	0.54	0.08	0.92	0.22	0.004	0.001
Reptile	*Anolis aeneus*	0.03	0.98	0.02	0.73	0.488	0.996
	Anolis carolinensis	0.19	0.67	0.33	0.75	0.105	0.902
	Anolis cristatellus	0.24	0.53	0.47	0.82	0.002	0.924
	Anolis equestris	0.33	0.60	0.40	0.42	0.276	0.020
	Boiga irregularis	0.00	0.00	1.00	1.00	0.082	
	Caiman crocodilus	0.01	0.85	0.15	1.00	0.032	
	Chamaeleo jacksonii	0.00	1.00	0.00	1.00	0.002	0.001
	Chamaeleo chamaeleon	0.31	0.02	0.98	0.70	0.004	1.000
	Ctenosaura similis	0.07	0.00	1.00	0.98	0.011	0.902
	Cyrtopodion scabrum	0.41	0.45	0.55	0.18	0.170	0.906
	Elaphe guttata	0.18	0.92	0.08	0.93	0.012	1.000
	Eunectes murinus	0.13	0.16	0.84	0.91	0.001	0.250
	Eunectes notaeus	0.43	0.07	0.93	0.52	0.001	0.022
	Iguana iguana	0.35	0.02	0.98	0.28	0.006	0.001
	Natrix maura	0.05	0.00	1.00	0.95	0.008	0.553
	Testudo horsfieldii	0.11	0.92	0.08	0.93	0.259	0.997
	Trachemys scripta elegans	0.24	0.68	0.32	0.04	0.401	0.998
	Tupinambis teguixin	0.03	0.13	0.87	0.99	0.010	
	Varanus indicus	0.05	0.00	1.00	0.84	0.006	0.802
	Varanus niloticus	0.06	0.10	0.90	0.97	0.009	0.167
	Zamenis scalaris	0.08	0.00	1.00	0.80	0.007	0.705

	Hemidactylus frenatus	0.67	0.01	0.99	0.08	0.001	0.001
	Hemidactylus mabouia	0.61	0.04	0.96	0.43	0.004	0.001
	Hierophis viridiflavus	0.02	0.00	1.00	0.93	0.026	
	Podarcis siculus	0.24	0.78	0.22	0.87	0.002	0.207
	Python bivittatus	0.18	0.08	0.92	0.86	0.003	1.000
	Python regius	0.32	0.72	0.28	0.43	0.174	0.001
	Ramphotyphlops braminus	0.85	0.07	0.93	0.05	0.001	0.001
	Trioceros jacksonii	0.16	0.85	0.15	0.94	0.002	1.000
Bird	*Acridotheres fuscus*	0.61	0.22	0.78	0.09	0.002	0.001
	Acridotheres tristis	0.62	0.19	0.81	0.07	0.007	0.001
	Alectoris chukar	0.64	0.08	0.92	0.02	0.028	0.001
	Alopochen aegyptiaca	0.36	0.83	0.17	0.39	0.061	0.001
	Amazona amazonica	0.50	0.11	0.89	0.19	0.003	0.001
	Anser anser	0.69	0.11	0.89	0.07	0.001	0.001
	Anser indicus	0.18	0.20	0.80	0.90	0.020	0.001
	Branta canadensis	0.51	0.01	0.99	0.29	0.006	0.001
	Branta hutchinisii	0.25	0.02	0.98	0.85	0.015	0.001
	Carpodacus mexicanus	0.47	0.11	0.89	0.55		
	Chen canagica	0.11	0.00	1.00	0.90	0.009	1.000
	Circus approximans	0.38	0.04	0.96	0.44	0.006	0.001
	Columba livia	0.80	0.01	0.99	0.01	0.003	0.001
	Corvus splendens	0.54	0.01	0.99	0.06		
	Cygnus olor	0.52	0.28	0.72	0.05	0.046	0.001
	Dicrurus macrocercus	0.01	0.00	1.00	1.00		
	Estrilda astrild	0.43	0.44	0.56	0.02	0.074	0.001
	Gallus gallus	0.70	0.10	0.90	0.11	0.007	0.001
	Garrulax canorus	0.34	0.62	0.38	0.04	0.104	0.005
	Grus antigone	0.34	0.78	0.22	0.57	0.459	0.112
	Gymnorhina tibicen	0.22	0.03	0.97	0.74	0.008	0.001
	Horornis diphone	0.26	0.69	0.31	0.65	0.200	0.290
	Leiothrix lutea	0.38	0.51	0.49	0.43	0.001	0.001
	Molothrus bonariensis	0.29	0.00	1.00	0.35	0.007	0.001
	Myiopsitta monachus	0.50	0.50	0.50	0.00	0.065	0.001
	Oxyura jamaicensis	0.66	0.07	0.93	0.13	0.003	0.001
	Passer domesticus	0.77	0.02	0.98	0.01	0.012	0.001
	Pavo cristatus	0.60	0.30	0.70	0.07	0.010	0.001
	Phasianus colchicus	0.58	0.18	0.82	0.12	0.003	0.001
	Pitangus sulphuratus	0.04	0.00	1.00	0.87	0.015	0.999
	Ploceus cucullatus	0.79	0.06	0.94	0.16	0.001	0.001
	Porphyrio porphyrio	0.38	0.04	0.96	0.40	0.005	0.001
	Psittacula krameri	0.35	0.55	0.45	0.38	0.006	0.001

	Pycnonotus cafer	0.68	0.08	0.92	0.07	0.001	0.001
	Pycnonotus jocosus	0.53	0.02	0.98	0.41	0.004	0.001
	Quelea quelea	0.33	0.00	1.00	0.15	0.001	0.002
	Quiscalus lugubris	0.03	0.99	0.01	0.40	0.490	1
	Streptopelia decaocto	0.83	0.01	0.99	0.00	0.003	0.001
	Threskiornis aethiopicus	0.45	0.64	0.36	0.40	0.023	0.001
	Tiaris bicolor	0.02	0.00	1.00	0.99	0.020	1
	Turdus nudigenis	0.05	0.38	0.62	0.97	0.003	1.000
	Tyto alba	0.21	0.02	0.98	0.86	0.008	0.001
	Vireo altiloquus	0.21	0.92	0.08	0.62	0.110	1.000
	Zosterops japonicus	0.39	0.29	0.71	0.00	0.013	0.001
Mammal	*Ammotragus lervia*	0.19	0.81	0.19	0.47	0.279	0.127
	Axis axis	0.19	0.87	0.13	0.71	0.262	0.803
	Callithrix geoffroyi	0.96	0.01	0.99	0.00	0.004	0.001
	Callithrix jachhus	0.57	0.50	0.50	0.47	0.006	0.001
	Callosciurus erythraeus	0.37	0.66	0.34	0.32	0.136	0.002
	Callosciurus finlaysonii	0.00	1.00	0.00	1.00	1.000	1.000
	Camelus dromedarius	0.31	0.00	1.00	0.49	0.008	0.994
	Canis latrans	0.09	0.00	1.00	0.88	0.006	0.657
	Castor canadensis	0.24	0.01	0.99	0.45	0.002	0.153
	Cercopithecus mona	0.52	0.42	0.58	0.22	0.150	0.024
	Cervus canadensis	0.18	0.78	0.22	0.11	0.207	0.050
	Cervus elaphus	0.45	0.40	0.60	0.02	0.087	0.001
	Cervus nippon	0.13	0.98	0.02	0.69	0.226	0.875
	Cervus timorensis russa	0.42	0.43	0.57	0.59	0.001	0.002
	Civettictis civetta	0.35	0.07	0.93	0.54	0.002	1.000
	Crocidura suaveolens	0.55	0.38	0.62	0.28	0.064	0.001
	Cynictis penicillata	0.44	0.49	0.51	0.01	0.171	0.519
	Dasyprocta leporina	0.54	0.45	0.55	0.22	0.182	0.016
	Didelphis marsupialis	0.77	0.07	0.93	0.02	0.003	0.001
	Erinaceus europaeus	0.43	0.37	0.63	0.39	0.004	0.001
	Erythrocebus patas	0.01	0.95	0.05	0.99	0.057	1.000
	Genetta genetta	0.16	0.81	0.19	0.89	0.010	0.969
	Hemitragus jemlahicus	0.19	0.81	0.19	0.00	0.350	0.882
	Herpestes auropunctatus	0.00	1.00	0.00	1.00	0.270	1.000
	Hydrochoerus hydrochaeris	0.64	0.10	0.90	0.11	0.001	0.001
	Lepus americanus	0.33	0.08	0.92	0.56	0.002	0.012
	Lepus europaeus	0.22	0.21	0.79	0.01	0.901	1.000
	Macaca fascicularis	0.64	0.21	0.79	0.25	0.001	0.001
	Macaca mulatta	0.49	0.38	0.62	0.21	0.282	0.039
	Macropus rufogriseus	0.21	0.35	0.65	0.81	0.003	0.001

	Muntiacus reevesi	0.09	0.77	0.23	0.92	0.016	1.000
	Mus musculus	0.36	0.26	0.74	0.00	0.021	0.001
	Mustela erminea	0.06	0.30	0.70	0.92	0.004	0.925
	Mustela furo	0.16	0.92	0.08	0.81	0.666	1.000
	Mustela nivalis	0.23	0.28	0.72	0.32	0.003	0.001
	Myocastor coypus	0.43	0.61	0.39	0.35	0.018	0.001
	Nasua nasua	0.69	0.12	0.88	0.01	0.035	0.011
	Neovision vision	0.48	0.11	0.89	0.37	0.001	0.001
	Nyctereutes procyonoides	0.19	0.90	0.10	0.51	0.283	0.004
	Odocoileus hemionus	0.33	0.42	0.58	0.65	0.001	
	Odocoileus virginianus	0.73	0.07	0.93	0.02	0.002	0.001
	Ondatra zibethicus	0.40	0.00	1.00	0.39	0.009	0.001
	Oryctolagus cuniculus	0.51	0.07	0.93	0.26	0.011	0.001
	Peromyscus maniculatus	0.24	0.01	0.99	0.82	0.006	0.013
	Phalanger orientalis	0.41	0.30	0.70	0.39	0.002	0.121
	Procyon lotor	0.76	0.03	0.97	0.06	0.005	0.001
	Rangifer tarandus	0.68	0.24	0.76	0.02	0.042	0.001
	Rattus exulans	0.51	0.23	0.77	0.02	0.120	0.688
	Rattus norvegicus	0.04	1.00	0.00	0.39	0.502	1.000
	Rattus rattus	0.44	0.37	0.63	0.00	0.076	0.001
	Rattus tanezumi	0.38	0.71	0.29	0.30	0.184	0.001
	Rupicapra rupicapra	0.14	0.72	0.28	0.90	0.002	0.026
	Rusa marianna	0.34	0.34	0.66	0.68	0.002	0.419
	Rusa unicolor	0.08	0.69	0.31	0.95	0.003	1.000
	Sciurus aberti	0.35	0.00	1.00	0.51	0.001	0.996
	Sciurus carolinensis	0.37	0.03	0.97	0.50	0.011	0.001
	Sciurus niger	0.00	1.00	0.00	1.00	1.000	1.000
	Suncus murinus	0.84	0.03	0.97	0.03	0.002	0.001
	Sus scrofa	0.36	0.45	0.55	0.02	0.199	0.001
	Tamias sibiricus	0.14	0.10	0.90	0.95	0.004	1.000
	Tenrec ecaudatus	0.65	0.37	0.63	0.29	0.002	0.012
	Trichosurus vulpecula	0.46	0.16	0.84	0.25	0.001	0.001
	Viverricula indica	0.44	0.20	0.80	0.47	0.001	0.234
	Vulpes vulpes	0.54	0.29	0.71	0.01	0.028	0.001

Table 3: Analysis of Variance of niche expansion, unfilling, and overlap across tetrapod

Anova: Single Factor						
Expansion						
SUMMARY						
Groups	*Count*	*Sum*	*Average*	*Variance*		
Amphibians	15	5.52	0.37	0.12		
Reptiles	29	10.66	0.37	0.15		
Birds	44	10.47	0.24	0.08		
Mammals	64	25.70	0.40	0.11		
ANOVA						
Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	0.73	3	0.24	**2.24**	**0.086**	**2.67**
Within Groups	16.11	148	0.11			
Total	16.85	151				
Unfilling						
SUMMARY						
Groups	*Count*	*Sum*	*Average*	*Variance*		
Amphibians	15	6.35	0.42	0.13		
Reptiles	29	20.33	0.70	0.10		
Birds	44	15.77	0.36	0.11		
Mammals	64	26.80	0.42	0.11		
ANOVA						
Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	2.27	3	0.76	**6.77**	**0.000**	**2.67**
Within Groups	16.52	148	0.11			
Total	18.78	151				
Niche overlap						
SUMMARY						
Groups	*Count*	*Sum*	*Average*	*Variance*		

Amphibians	15	4.26	0.28	0.05		
Reptiles	29	6.36	0.22	0.05		
Birds	44	18.54	0.42	0.05		
Mammals	64	23.42	0.37	0.05		
ANOVA						
Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	0.80	3	0.27	**5.34**	**0.002**	**2.67**
Within Groups	7.38	148	0.05			
Total	8.18	151				