

Elevational Distribution of Amphibians: Resolving Distributions, Patterns, and Species Communities in the Republic of Korea

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Species biodiversity organises along elevational trends and is generally expected to decrease with increasing elevation. This pattern is regulated by numerous factors, although principally overridden by temperature in ectotherms such as amphibians. Here, we collated elevation data ($n = 55182$) collected between 1909 and 2020. We then determined elevation distribution patterns and species communities for all amphibians in the Republic of Korea. Species were found to range from sea level up to 1393 m a.s.l. The average elevational distribution was significantly different between species but also between anura and caudata. On average, anura were found at lower elevations with a peak in species richness and abundance matching with the lowlands. In opposition, the peak in species richness and abundance for caudata matched with low hilly landscapes. The altitudinal distributions of species were strongly skewed with all 23 species within the 0-199 m range, and steadily decreasing with only five species within the last elevational range (1200-1399 m). Finally, only a few species were found below 30 m, reflecting a likely risk of salinisation in this environment. Our results help understand the altitudinal distribution of amphibians in the Republic of Korea.

Key words: Elevation range, Amphibian, Species communities, Northeast Asia, Altitude.

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BACKGROUND

Higher elevations (Beals 1969; Stevens 1992) correspond to decreasing biodiversity. Other variables also influence the distribution of biodiversity, and elevational patterns vary along with geographic gradients in latitude, altitude, or water depth (Rosenzweig 1995; Gaston 2000), following increasing, decreasing, or centred concentration of species (Fischer et al. 2011; Rosenzweig 1995; Willig and Presley 2016). The underlying mechanism for this variation in the number of species mostly relates to resources available, niche constriction (i.e. habitat heterogeneity), and competition, resulting in “patterns of distribution” (Cox and Moore 1980; Diamond 1972; Terborgh and Weske 1975). The effect of altitude is even more important at low latitudes, resulting in larger “between-altitude” fauna variations directly related to latitude (Janzen 1967; Huey 1978). As a result, the decline in species richness at high latitudes is correlated with niche diversification and an increase in the altitudinal range of species (Stevens 1992). For endotherms, the pattern is sometimes obscured by other factors such as resource availability, demonstrated for some mammals (e.g. Heaney 2001) and birds (e.g. nectarivore species; Terborgh 1977). In the case of ectotherms though, an increase in altitude has so far always been linked to a decrease in biodiversity, due to the restriction in thermal regulation and activity at high altitudes (Poynton et al. 2006b).

In amphibians, richness is generally higher in the lowlands (Stevens 1992), which provide humidity and temperature regimes favourable to both aquatic and terrestrial lifestyles (Duellman and Trueb 1986). For instance, in the Western Ghats in India, the highest amphibian diversity is found in the lower altitudinal range (0-1000 m; Daniels 1992). The same pattern is found in Tanzania and Kenya where a higher number of species is found below 300 m above sea level (asl), although displaying a more restricted distribution than the less numerous species occurring between 1500 and 3650 m asl (Loveridge 1937; Poynton et al. 2006b). This is also true for amphibian species in Romania where only two species are found at the highest altitudes (Cogălniceanu et al. 2013). Despite the higher amphibian biodiversity at low altitudes, some species are only distributed at high altitudes, such as *Ranodon sibiricus* in Kazakhstan (Dujsebayaeva and Malakhov 2017),

Scutiger boulengeri, found up to 5270 m in India (Subba et al. 2015) or *Pseudoeurycea gadovii* found up to 4250 m in Mexico (Amphibian Specialist Group 2016). These species are generally under heightened threat levels because of the change in habitat related to climate change (Dirnböck et al. 2011) and the discontinuous distribution of their habitats (Poynton et al. 2006a; Poynton et al. 2006b). This pattern is further heightened at high latitudes where the potential for dispersion of species is lower due to a narrower niche envelope, and therefore in need of urgent research focus in view of climate change.

The elevational range of species is not properly delineated for most amphibians, an understudied group of species, despite elevated threat levels (Beebee and Griffiths 2005; Howard and Bickford 2014; Stuart et al. 2004; Wake 2012). In the Republic of Korea, elevational distribution is exemplified but unclearly defined (Song and Lee 2009), and additional data points can be extracted from articles focusing on other subjects. For instance, there is a positive correlation between size and elevation on Jeju Island for *Dryophytes japonicus*, likely because of island effects (Jang et al. 2011; Koo et al. 2018). Additionally, some species such as *Rana huanrenensis* (Song and Lee 2009; Yang et al. 2000), *Onychodactylus fischeri*, and *Bufo stejnegeri* (Song and Lee 2009) are suggested to be only distributed at higher elevations. Others have broader elevational ranges, such as *B. sachalinensis* (Kuzmin et al. 2004c; reassigned from *B. gargarizans* following updated taxonomy Othman et al. 2022), *D. japonicus* (Jang et al. 2011; Roh et al. 2014), *Pelophylax nigromaculatus* (Kuzmin et al. 2004b) and *Hynobius leechii* (Song and Lee 2009). Finally, a large number of species is suspected to be restricted to the lowlands, such as *P. chosenicus* (Do et al. 2017; Kang and Yoon 1975; Song and Lee 2009; Yang et al. 2001), *Glandirana emeljanovi* (Song and Lee 2009), *D. suweonensis* (Borzée and Jang 2017; Borzée et al. 2017; Borzée 2018; Roh et al. 2014), *D. flaviventris* (Borzée et al. 2020), *H. unisacculus*, *H. yangi*, and *H. geojeensis* (Borzée et al. 2019b; Borzée and Min 2021).

Defining the elevational range of all amphibian species present in the Republic of Korea has multiple benefits. At a local scale, defining elevational ranges allows for the determination of potential species presence, and thus facilitates species detection for ecological assessment prior to development, designation of protected areas, or any land use. Second, it allows for the identification of elevational distribution patterns of anura and caudata communities, thus defining and segregating species assemblages. Third, it allows us to estimate potential distribution shifts due to the rise in temperature because of global warming. Finally, defining the elevational range of amphibians provides a wider knowledge of the species and it can be used to determine their ecological requirements or for conservation assessments. For instance, the IUCN Red List of threatened species is missing this information for most Korean species (www.iucnredlist.org). Despite a local interest in some threatened amphibians such as *Kaloula borealis* (Kim et al. 2014) and the

commonness of the last point raised, it is potentially the most important at the time of writing due to the general critical status of amphibians (Bishop et al. 2012; Laurance et al. 2011; Wake and Vredenburg 2008). We hypothesised a higher number of species and a higher abundance at lower to mid - elevations due to resource availability, although we did not expect differences between anura and caudata.

MATERIALS AND METHODS

Data extraction

We downloaded data for all amphibians occurring in the Republic of Korea from the Global Biodiversity Information Facility (www.gbif.org; doi:10.15468/dl.agw364; accessed 15 January 2021). It is worth noting that this database for the queried dataset is mostly populated by two other databases. One is the citizen science platform iNaturalist (www.inaturalist.org), and to control the quality of the data, we first corrected identifications on the platform. The other database is the database Ecobank from the Korean National Institute of Ecology (<https://www.nie-ecobank.kr/>) and is expected to be accurate (Kim et al. 2021).

The original download included 55 274 datapoints, but we removed all observations with known issues flagged by GBIF and we deleted duplicated records. Additionally, only datapoints geolocated with accuracy of at least four decimals (*c.* 10 m resolution) were preserved. This selection criterion resulted in 55 182 datapoints collected between October 1909 and 8 December 2020. The data was then prepared in the csv format and exported onto ArcGIS 10.5 (ESRI, Redlands, CA, USA). For this study, elevation and altitude are used interchangeably with the sea level as the reference.

Elevation data was extracted from a digital elevation model (DEM; “Topobathy” layer provided by ESRI) using the “Extract Multi Values to Points” tool in ArcGIS 10.5 (ESRI, Redlands, CA, USA). The DEM was exported to a pixel size of 0.001 decimal degrees, or approximately 100 meters, before point data extraction. The data sources for this DEM were: Airbus, USGS, NGA, NASA, CGIAR, GEBCO, N Robinson, NCEAS, NLS, OS, NMA, Geodatastyrelsen, and the GIS User Community. The extracted data was then exported for further statistical analyses.

Statistical analyses

Before the analysis, the presence of a data point for *Duttaphrynus melanostictus* (altitude a.s.l. = 42 m) was removed, as it is a non-native species and unlikely to establish a viable population in the Republic of Korea. The invasive American Bullfrog (*Lithobates catesbeianus*) was however preserved as populations are now established in the country (Park et al. 2014; Groffen et al. 2019). As the distribution of elevational data is generally skewed towards a zero inflated distribution, we started by testing for the normal distribution of the dataset ($n = 55182$) with a Kolmogorov-Smirnov test with Lilliefors Significance Correction, and none of the species were normally distributed ($\chi^2 = 0.16$, $df = 55181$, $p < 0.001$) with the exception of *H. perplicatus* ($\chi^2 = 0.15$, $df = 25$, $p = 0.165$). We also tested the homogeneity of variance with Levene's test with elevation as a dependent variable and species as a factor ($F_{22,55159} = 173.53$, $p < 0.001$). The stem-and-leaf plot however highlighted that the data followed a negative binomial distribution, and we took it into account for further statistical analyses.

We first ran two general linear models, one with species (23 species) and one with order (anura or caudata), as dependent variable. In both models, we selected a negative binomial distribution ($n = 55182$), used the elevation variable as covariate, and ran the analysis under a main effect model. Here the dependent variable was either species or order, and the independent variable was elevation. We then calculated descriptive statistics to characterise the elevational range of each species.

To assess species diversity along the elevational gradient, we first grouped elevations into six categories spanning 200 m each. We then assessed the number of species per category and tested for statistical differences between categories with a two-sided one-sample Chi-Square test. The statistical analyses were performed with SPSS v21.0 (SPSS Inc., Chicago, USA). To be biologically meaningful, all elevations were rounded to the metre.

RESULTS

The elevational distributions of Korean amphibians ranged from sea level up to 1392 m a.s.l (Table 1; Figs. 1–2), with *Dryophytes flaviventris* displaying the lowest average 19 ± 6 m (mean \pm SD) and *Onychodactylus koreanus* the highest at 723 ± 483 m (Table 1). The general linear models demonstrated that the elevational distribution was a good fit for the species dataset (Omnibus test;

$\chi^2 = 61.39$, $d.f. = 1$, $p < 0.001$), and was significantly different between species (GLM; $n = 55182$, $\chi^2 = 60.53$, $d.f. = 1$, $p < 0.001$). Anura were found at lower elevations (195 ± 176 m; Fig. 1) than caudata (259 ± 202 ; Fig. 2) on average and the general linear models demonstrated that the elevational distribution was a good fit for the order dataset (Omnibus test; $\chi^2 = 32.74$, $d.f. = 1$, $p < 0.001$), and significantly different between orders (GLM; $n = 55182$, $\chi^2 = 32.69$, $d.f. = 1$, $p < 0.001$). A peak in abundance and species richness was determined within the elevational distribution of anura at about 50 m, while the matching peak for caudata was around 100 m (Fig. 3).

The distribution of species along the vertical gradient was strongly skewed (Fig. 4), with all 23 species within the 0–199 m bin ($n = 33032$), 22 species within the 200–399 m bin ($n = 14890$), 19 species within the 400–599 m bin ($n = 4799$), 16 species within the 600–799 m bin ($n = 1927$), 13 species within the 800–900 m bin ($n = 404$), 13 species within 1000–1199 m bin ($n = 113$), and five species within the last elevational bin, 1200–1399 m ($n = 17$). The number of species was significantly different between bins (Chi-Square test; $\chi^2 = 114768.63$, $d.f. = 6$, $p < 0.001$), representative of specific and weakly overlapping species communities.

Table 1. Descriptive statistics for elevational ranges of amphibian species in the Republic of Korea. Data collected between 1909 and 2020 and extracted through the Global Biodiversity Information Facility (www.gbif.org; doi:10.15468/dl.agw364; accessed 15 January 2021)

	N	Mean	SD	Min	Max	Range
Anura	48366	195.75	176.714	0	1393	1393
<i>Bombina orientalis</i>	7044	261.50	194.473	0	1393	1393
<i>Bufo sachalinensis</i>	3107	181.05	158.382	0	1179	1179
<i>Bufo stejnegeri</i>	640	425.01	223.694	18	1241	1223
<i>Dryophytes flaviventris</i>	19	6.42	2.652	2	13	11
<i>Dryophytes japonicus</i>	8889	158.85	155.652	0	1143	1143
<i>Dryophytes suweonensis</i>	281	29.60	41.285	1	319	318

<i>Kaloula borealis</i>	176	37.03	66.809	0	566	566
<i>Glandirana emeljanovi</i>	3474	217.28	158.245	0	1198	1198
<i>Lithobates catesbeianus</i>	3728	74.91	79.441	0	1012	1012
<i>Pelophylax chosenicus</i>	194	57.79	66.856	0	494	494
<i>Pelophylax nigromaculatus</i>	9564	157.63	150.068	0	1098	1098
<i>Rana coreana</i>	1967	123.80	113.563	0	838	838
<i>Rana huanrenensis</i>	1828	375.33	196.649	25	1135	1110
<i>Rana uenoi</i>	7455	252.37	178.822	0	1316	1316
Caudata	6816	259.34	202.568	0	1266	1266
<i>Onychodactylus koreanus</i>	723	483.60	235.411	44	1266	1222
<i>Karsenia koreana</i>	179	311.66	132.378	87	823	736
<i>Hynobius quepaertensis</i>	706	163.20	159.978	0	1189	1189
<i>Hynobius unisacculus</i>	177	97.25	71.036	0	511	511
<i>Hynobius notialis</i>	273	135.39	143.293	1	1159	1158
<i>Hynobius geojeensis</i>	34	53.15	54.961	16	241	225
<i>Hynobius leechii</i>	4579	256.12	183.520	3	1212	1209
<i>Hynobius yangi</i>	120	106.88	71.643	1	359	358
<i>Hynobius perplicatus</i>	25	217.20	153.832	25	698	673

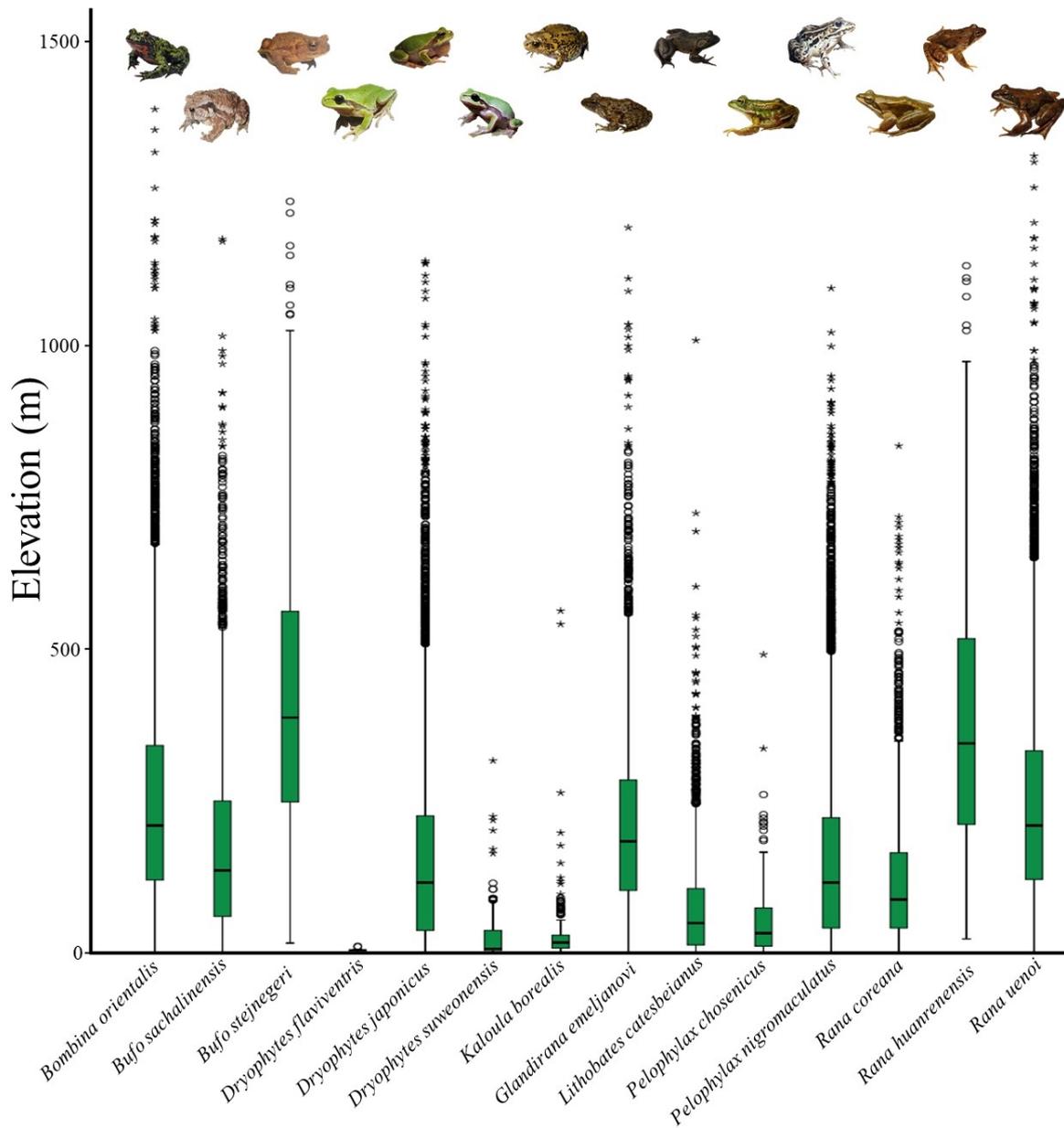


Fig. 1. Elevational ranges of anura species in the Republic of Korea. Data collected between 1909 and 2020 and extracted through the Global Biodiversity Information Facility (www.gbif.org; doi:10.15468/dl.agw364; accessed 15 January 2021).

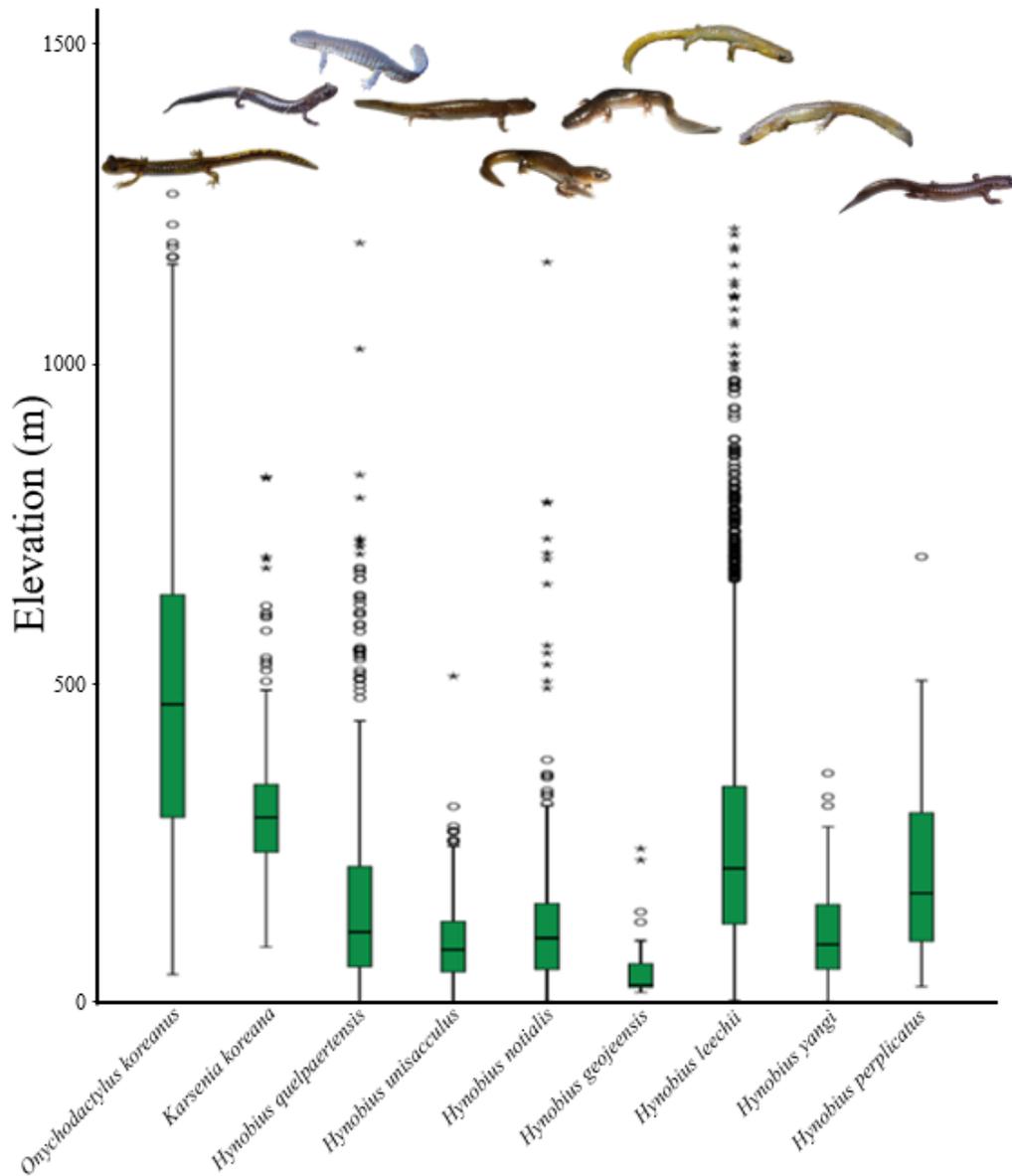


Fig. 2. Elevational ranges of caudata species in the Republic of Korea. Data collected between 1909 and 2020 and extracted through the Global Biodiversity Information Facility (www.gbif.org; doi:10.15468/dl.agw364; accessed 15 January 2021).

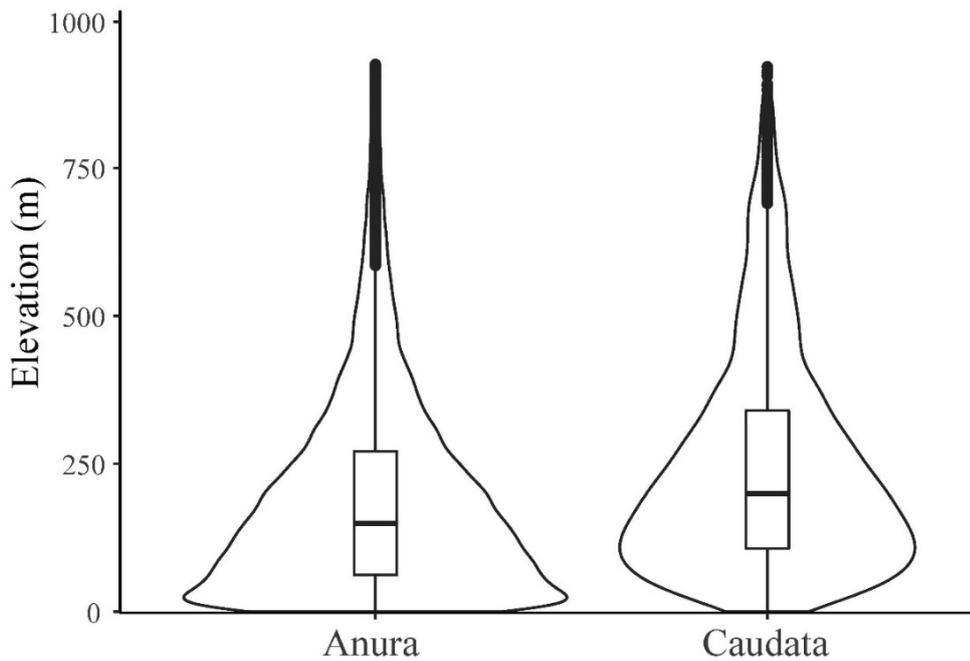


Fig. 3. Violin plots for the elevational distribution of anura and caudata in the Republic of Korea. Data collected between 1909 and 2020 and extracted through the Global Biodiversity Information Facility (www.gbif.org; doi:10.15468/dl.agw364; accessed 15 January 2021).

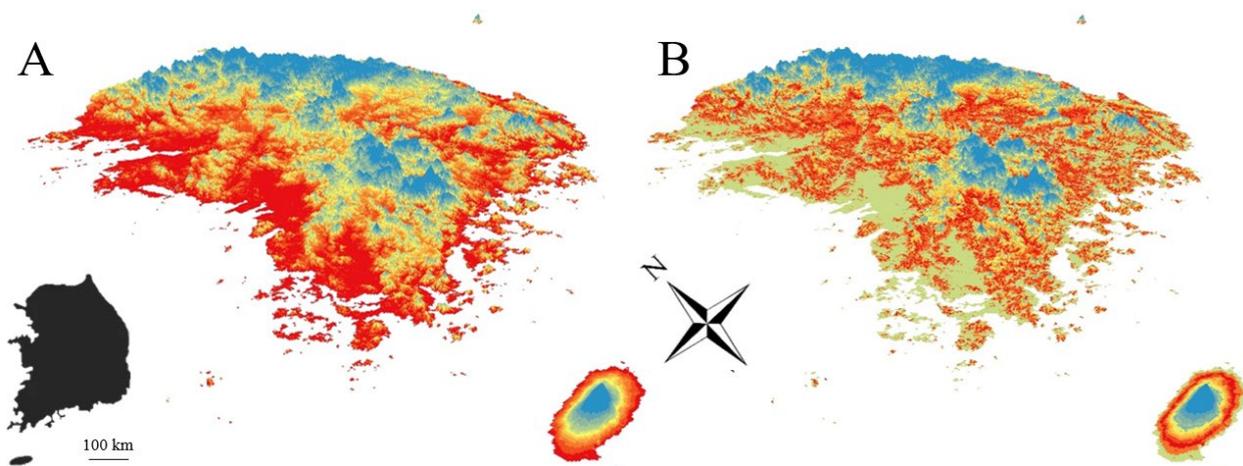


Fig. 4. Elevational distribution of Korean amphibian (A) anura and (B) caudata. Data collected between 1909 and 2020 and extracted through the Global Biodiversity Information Facility www.gbif.org; doi:10.15468/dl.agw364; accessed 15 January 2021). Red indicates a higher number of species (14 anura and nine caudata as maxima) and blue indicates the absence of amphibians. Intermediate colours indicate intermediate values.

DISCUSSION

Our work highlights a high amphibian species richness in the lowlands of the Republic of Korea, matching with our hypotheses and with similar findings from other geographic areas (Cogălniceanu et al. 2013; Daniels 1992; Duellman and Trueb 1986; Loveridge 1937; Poynton et al. 2006b; Stevens 1992). However, our hypotheses were not correct in that while anuran species richness peaked below 100 m, caudata species richness peaked above 100 m (Fig. 3), highlighting a divergence between biodiversity and biomass. The biodiversity gradient may result from low rates of species displacements to high altitude biota and high stochastic rates of extinction for populations that managed to settle (Stevens 1992).

In-depth analyses of elevational distribution patterns highlight differences between anura and caudata, likely linked to geographic distributions. In anura, the distribution of species richness generally decreases with altitude although some species are locally present at higher elevations (Figs. 3 and 4). The presence of some species at higher elevations may be a result of shared physiographical and physiological boundaries between low- and high-elevation assemblages of species (Colwell and Hurtt 1994), a bias to the Rapoport effect resulting in a higher number of species where a decreasing trend is predicted (Colwell and Lees 2000; Stevens 1989; Stevens 1992). The peak in diversity and abundance for caudata, matching with hilly landscapes corresponds to the ecological requirements of Hynobidae, which generally breed in low to high mountain streams (Oh et al. 2007; Yang et al. 2001) but take advantage of agricultural wetlands at lower elevations as well (Bae et al. 2019).

As a general pattern, species richness was biased towards lower elevations, although very few species were found at the lowest elevations (0–30 m; Fig. 3) thus avoiding low fluvial plains and coastal areas. This pattern is expected to be a response to areas with brackish or saline waters as amphibians avoid contact with saline environment to maintain adequate osmoregulation (Lai et al. 2019). Saline environments impact oviposition site selection (Wu and Kam 2009), growth and development of larva (Wu et al. 2012), and metamorphic traits of froglets (Hsu et al. 2012; Wu et al. 2012). On the Korean peninsula, only *Dryophytes japonicus*, one of the species found at the lowest elevations, has been found in saline environments (Heo et al. 2019). As *D. flaviventris* is the species with the lowest elevation average (noting the low sample size), it is therefore also expected to be able to cope with brackish environments, a potential trait carried over from its distribution being repeatedly split by the yellow sea (Borzée et al. 2020) and exemplified by its range made-up by 40 % of reclaimed area (Borzée et al. 2017).

Our findings on the elevational distributions in amphibians are generally in line with previously published data (Borzée and Jang 2015; Borzée et al. 2017 2019b; Borzée 2018; Do et al. 2017; Kang and Yoon 1975; Roh et al. 2014; Song and Lee 2009; Yang et al. 2000 2001). However, maxima determined in this study were lower than the ones determined by the IUCN Red List of

endangered species (Kuzmin et al. 2004b c). The potential reasons for this difference are that the maximum on the IUCN Red List refers to the whole range of the species, not only the Republic of Korea, and as the average elevation of the country is comparatively low, maxima are suspected to be lower as well. An alternative explanation is that despite being an extensive sampling effort, there may be noticeable sampling bias. Observations are more likely to occur from easily reachable areas than from high altitudes, and thus the species may be ranging higher than currently described in this study. In opposition, some of the elevations in this study, such as the highest elevation for *D. suweonensis*, are now unlikely to be verifiable in the wild because that specific population is now extirpated.

Regarding Ranidae, *Rana uenoi* was found at significantly higher elevation maxima than previously published (Kuzmin et al. 2004a; Song and Lee 2009), and it is one of the species with the broadest elevational range. *Rana coreana* was also found higher than expected (Song and Lee 2009; Macias et al. 2018), but it does not distribute as high as the other *Rana* species. *Rana huanrenensis* was found lower than previously described, but its mean elevational distribution did correspond to the one where it was described to be breeding: in streams of relatively high montane valleys (> 500 m; Yang et al. 2000). The elevational distribution of *Glandirana emeljanovi* was also found to be matching with previously published data (Song and Lee 2009). Within the two *Pelophylax* species, *P. chosenicus* was found at lower elevations, matching with its described breeding behaviour in rice paddies and other lowlands (Kang and Yoon 1975; Yang et al. 2001; Do et al. 2017). *Pelophylax nigromaculatus* was found on a relatively larger elevational gradient, as expected as the species is present in a wide variety of habitats across northeast Asia, reflecting broader ecological requirements (Liu et al. 2010).

In contrast, *Bufo stejnegeri* has a very narrow ecological niche restricted to high altitude (Song and Lee 2009) and was accordingly not found at low elevation, whereas *B. sachalinensis* was more abundant at lower elevations. *Kaloula borealis* displayed a broad elevational distribution, as expected from the literature (Song and Lee 2009). Regarding hylids, the three *Dryophytes* species displayed the largest variation within a genus. Their distribution followed the literature, with *D. japonicus* present on a broad elevational range (Jang et al. 2011; Roh et al. 2014) and *D. suweonensis* and *D. flaviventris* limited to low elevation (Roh et al. 2014; Borzée and Jang 2017; Borzée et al. 2017; Borzée 2018; Borzée et al. 2020). Here, and as well as for *Bufo* sp., this dichotomy may be related to speciation such as suggested by Kim (2016) and Borzée et al. (2019c).

The data was also mixed for caudata, with an expected wide elevational range for *Hynobius leechii* (Matsui and Wenge 2008), and anticipated low elevational ranges for *H. unisacculus* and *H. yangi* (Baek et al. 2011; Borzée et al. 2019b; Min et al. 2016), and *H. notialis* and *H. geojeensis* (Borzée and Min 2021). Interestingly, *H. quelpaertensis* was found at much higher elevations than

reported until now (Baek et al. 2011; Oh et al. 2007; Yang et al. 2001) and *H. perplicatus* was also found on a broad elevational range. *Karsenia koreana* was found at intermediate to high elevations, as expected from other plethodontid species (Min et al. 2005) and based on habitat modeling on the Korean Peninsula (Borzée et al. 2019a). The last species, *Onychodactylus koreanus*, had previously been found mostly at high altitudes (Hong 2017), and the same pattern was found here.

CONCLUSIONS

Amphibians in the Republic of Korea were found from sea level up to 1393 m a.s.l., with different average elevational distributions between species and between orders. Caudata richness and abundance was found at higher elevation than that of anura, highlighting a difference in amphibian communities between plains and high hills. All species were however found below 200 m of elevation, and only five species were found above 1200 m.

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Competing interests: DA, MFC, MC, AK, SK, YJ and AB declare that they have no conflict of interest.

Availability of data and materials: The dataset used for the analyses can be downloaded through GBIF.org, dated up to 15 January 2021 (doi:10.15468/dl.agw364; accessed 15 January 2021).

Consent for publication: The authors agree on publication.

Ethics approval consent to participate: This study is based on data available online and does not require an ethics approval.

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