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# Breeding phenology and landscape use in all amphibian species from the Republic of Korea based on open-source data

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Biodiversity is declining worldwide with habitat loss and climate change being among the main threats. While it is easy to quantify habitat loss, the impacts of climate change are less obvious. It is therefore important to understand species habitat use and breeding phenology before a significant shift results in the loss of knowledge. Here, we determined the habitat use and breeding phenology for all Korean amphibian species based on citizen science (8,763 observations), collected between 1997–2020. We found the breeding seasons as we defined them to be generally shorter than described in the literature despite large variations between species. Species were further dichotomised into early and late breeders with breeding periods peaking in mid-March and mid-June respectively. We found early breeding species to have a shortened hibernating period with only six days being consistently devoid of observations over the 23 years of the period studied for the species with the shortest inactive season. Habitat use was significantly different between all species, with pair-wise comparisons highlighting greater differences among rather than within genera, highlighting the threats to species across all genera. In addition, our results set a baseline for future analyses about climate change and habitat use.

## KEYWORDS

breeding, wetland, forests, anura, caudata, Korean peninsula

## Introduction

The annual life cycle of amphibians is regulated by a large number of both biotic and abiotic variables (e.g., Wells, 2010). The breeding phenology is one of the most important regulators in the life cycle of amphibians and it is closely linked to environmental conditions such as temperature, photoperiod, lunar cycle, precipitation and landscapes (Salvador and Carrascal, 1990; Llorente et al., 2006; Grant, 2012; Green, 2017; Plenderleith et al., 2018; Lannoo and Stiles, 2020). The fluctuations and alterations in the interactions

of these variables can cause small shifts on a year-to-year basis, resulting in large variations over longer periods (e.g., Lunghi et al., 2018). In addition, species have shown significant phenological shifts due to global warming (Carroll et al., 2009; Green, 2017). These differences in phenological shifts in combination with climate change play a role in global amphibian declines (Stuart et al., 2004). Furthermore, abiotic factors and biotic factors also directly influence the life cycle of amphibians. For instance, habitat alteration, fragmentation, and destruction have a significant impact on the phenological shifts of amphibians (Borzée et al., 2018a; Polat and Başkale, 2018).

Studies focusing on the breeding phenology of Korean amphibians usually refer to single breeding seasons, populations or areas (e.g., Borzée et al., 2017; Groffen, Borzée & Jang, 2018; Kim et al., 2020), which often do not represent the full extent of a species' population. As a result, these studies provide a shorter or biased representation of the natural history of a species breeding across its full range and for multiple years (e.g., Yoo & Jang, 2012; Do et al., 2020; 2021). This shortcoming is due to logistics, time, and funding. Therefore, an easier way to collect long-term breeding phenology data is needed.

An alternative way to obtain this type of long-term phenology data is through citizen science. There are different citizen science platforms where anyone can upload observations of organisms and those get reviewed by peers. Acquiring data from citizen science platforms is not new, and the practice has incredibly expanded over the years (Gray et al., 2017; McKinley et al., 2017). It provides considerable benefits such as lower costs and simultaneous data collection in numerous geographic areas, and it enables citizens to be involved in the scientific process. Most importantly, citizen science generally results in much larger datasets in terms of species records (Lintott et al., 2010) which are of high quality when conducted under specific guidelines (Shirk et al., 2012; Gray et al., 2017). Drawbacks can be generalized by the risk of biased, incomplete, or unreliable data (Cohn, 2008; Dickinson et al., 2010; Conrad and Hilchey, 2011), and thus they should be manually corrected prior to analyses, either through the organized scrutiny of validators, or through general overview by other members of the citizen science community.

The purpose of the current study was to determine the breeding seasons and landscape requirements of all amphibian species from the Republic of Korea based on citizen science data and complemented by data from surveys conducted at the national scale by governmental organisations (Kim et al., 2021). With the accelerating changes in climate and environment it is critical to understand their impact on the breeding activity and phenology of amphibians (Blaustein et al., 2010; Walls et al., 2013; Cohen et al., 2018). This multi-year phenology data provides an important baseline for future studies on phenology shifts due to changing climate and landscapes.

## Material and methods

### Species

There are currently 22 native and one invasive amphibian species described in the Republic of Korea (although results for the newly described *Onychodactylus* species are not presented in this study due to the recent description; Borzée et al., 2020), accounting for 14 anurans and nine caudata (Table 1). All anurans are generally widespread, with the exception of *Dryophytes suweonensis* and *D. flaviventris*, which are restricted to agricultural wetlands on the western coast of the country (Kim et al., 2019; Borzée et al., 2020a), the newly described *Onychodactylus* species, and some of the southern *Hynobius* species, which are microendemics (Borzée et al., 2020; Borzée and Min, 2021). Other species such as *Pelophylax chosonicus* and *Bufo stejnegeri* are restricted to specific landscapes, but occur over a generally large area and locally abundant in some populations (Matsui, 2004; IUCN SSC Amphibian Specialist Group, 2020). Here, the extent of distribution is important as it directly correlates with the probability of observation by citizen scientists.

Most Korean anuran species are generally abundant, with the exception of *D. suweonensis* and *D. flaviventris* that are likely to be critically endangered in the near future (Borzée, 2020), and *B. stejnegeri* for which decline is not documented due to the occurrence of the species at high elevation, and only in undisturbed areas. *Lithobates catesbeianus* (American bullfrog) is an invasive species present in most regions (Groffen et al., 2019a) but more abundant in the south west of the country (Kang et al., 2019). Among the caudata, *Hynobius leechii* is the only widespread species (Borzée and Min, 2021), with the relatively abundant *Karsenia koreana* restricted to mid elevations (Borzée et al., 2019a) and the widespread *Onychodactylus koreanus* restricted to high elevations (Poyarkov et al., 2014; Shin et al., 2021). All other *Hynobius* species are distributed in ranges <5,000 km<sup>2</sup> (Borzée and Min, 2021) and have a strong connection to agricultural wetlands as the species mostly breed in fallow rice paddies (Do et al., 2020), with the exception of *H. perplicatus* which is restricted to a geographic area containing no rice paddies.

### Data collection

The data for the breeding behavioural analysis was extracted from the citizen science database iNaturalist (<https://www.inaturalist.org>), a platform where anyone is able to upload observations of organisms. As of 1 December 2020, there were 10,213 amphibian observations on iNaturalist in the Republic of Korea, first observation 02 March 1997. The data is curated by

**TABLE 1** Breeding phenology start/end dates, min and maximum duration, overall longest duration (OLD), and average durations based on citizens science data and the widest duration in literature. Also, the days difference in duration of the OLD and average breeding phenology between citizens science and literature (minus is days less in citizens science data compared to literature). *Lithobates catesbeianus* is invasive in Korea and breeding data from literature is from native range, and the data for *Bufo stejnegeri* is for the oviposition period only. The analysis is based on 8,763 citizen science observations collected between 02 March 1997 and 01 December 2020 downloaded from the platform iNaturalist. \*as the first breeding date changes from year to year, this represents the range when the species start breeding. \*\* Years with more than three datapoints and used to calculate the starts/end periods and average duration.

Species	Citizens science data												Literature		Difference Lit	
	Total ob	Breeding ob	Date (min-max)	Starts between*	Avg start	Ends between	Avg end	Median	SD (days)	OPLD (days)	Avg duration (days)	n (years)**	Date (min-max)	Duration (days)	OLD (days)	avg duration (days)
<i>R. coreana</i>	262	136	11 February - 16 Apr	11 February - 3 Mar	19/Feb	8 Mar - 16 Apr	25/Mar	10/Mar	13.79	64	34	11	no data	no data	-	-
<i>R. huanrenensis</i>	538	222	15 February - 8 May	15 February - 9 Apr	05/Mar	21 March - 8 May	18/Apr	25/Mar	12.56	82	43	9	1 Feb - 30 April1	88	-6	-45
<i>R. uenoi</i>	1,568	695	9 Jan - 22 Apr	Jan 9 - Feb 2	24/Jan	18 March - 22 Apr	06/Apr	20/Feb	18.93	103	72	14	15 January—31 March2	75	28	-3
<i>G. emeljani</i>	267	14	3 May - 21 July	3 May - 14 June	28/May	21 June - 21 July	08/Jul	17/Jul	23.01	79	41	7	1 May - 30 June3	60	19	-19
<i>L. catesbeianus</i>	378	13	24 May - 26 June	24–30 May	26/May	21–26 June	24/Jul	07/Jul	21.96	42	28	2	23 April - 1 July4	-	-	-
<i>P. chosonicus</i>	235	7	3 May - 20 July	-	-	-	23/May	30.56	77	-	-	-	19 May - 6 August5	79	-2	-
<i>P. nigromaculatus</i>	729	63	15 April - 20 June	15–30 Apr	21/Apr	28 April - 20 June	16/May	16/May	29.2	67	37	7	4 May - 3 June3	30	37	7
<i>D. japonicus</i>	84	18	17 April - 4 Oct	17 April - 17 May	01/May	30 May - 4 Oct	21/Jul	22/Jul	17.23	168	82	10	15 April - 15 August6	122	46	-40
<i>D. flaviventris</i>	1759	421	21 May - 9 July	21 May - 21 June	06/Jul	28 June - 9 July	04/Jul	30/May	20.8	49	28	2	25 April - 3 July7	69	-20	-41
<i>D. suweonensis</i>	219	41	11 May - 28 Sept	11 May - 7 June	23/May	29 June - 19 July	24/Jul	31/May	24.53	69	43	5	15 May - 16 July8	62	7	-19
<i>K. borealis</i>	204	48	9 Apr - 1 Sept	26 May - 5 July	14/Jul	30 June - 1 Sep	29/Jul	23/Jul	28.04	97	44.5	6	28 May - 14 August9	78	19	-33.5
<i>B. sachalinensis</i>	441	131	19 February - 25 Apr	19 February - 10 Mar	28/Feb	5 Mar - 9 Apr	21/Mar	07/Mar	8.21	49	21	10	27 February - 25 April10	57	-8	-36
<i>B. stejnegeri</i>	113	13	8 Mar - 19 Apr	-	-	-	08/Mar	99.71	42	-	-	-	1 Mar - 30 April11	61	-19	-
<i>B. orientalis</i>	583	100	10 March - 26 Aug	10 March - 5 May	17/Apr	8 June - 26 Aug	09/Jul	17/May	36.25	149	83.5	-	3 May - 3 July12	41	108	42.5
<i>O. koreanus</i>	211	6	7 July - 6 Aug	-	-	-	07/Jul	15.49	30	-	-	-	1 June - 31 July13	60	-30	-
<i>H. gyojeensis</i>	45	26	20 February - 11 Apr	20 February - 12 Mar	03/Mar	18 March - 11 Apr	31/Mar	19/Mar	8.95	51	28.5	2	31 January - 31 May14	120	-69	-91.5
<i>H. leechii</i>	656	306	18 January - 27 May	18 January - 18 Mar	15/Feb	14 April - 27 May	02/May	24/Mar	25.5	129	75.5	14	31 January - 31 May14	120	9	-44.5
<i>H. notialis</i>	67	28	24 February - 11 Apr	-	-	-	18/Mar	9.15	47	-	-	-	31 January - 31 May14	120	-73	-
<i>H. perplacatus</i>	15	14	17 March - 27 Mar	-	-	-	18/Mar	2.4	9	-	-	-	31 January - 31 May14	120	-111	-
<i>H. quelpaertensis</i>	198	125	14 December - 17 Apr	14 December - 12 Jan	28/Dec	25 March - 17 Apr	06/Apr	15/Mar	30.72	124	63	3	31 January - 31 May14	120	4	-57
<i>H. unisacculus</i>	68	23	26 January - 12 Apr	26 January - 11 Mar	25/Feb	1 Feb - 11 Apr	18/Mar	19/Mar	25.19	76	12.5	3	31 January - 31 May14	120	-44	-107.5
<i>H. yangi</i>	41	15	18 February - 13 Apr	-	-	-	19/Mar	12.92	54	-	-	-	31 January - 31 May14	120	-66	-

(Continued on following page)

**TABLE 1 (Continued)** Breeding phenology start/end dates, min and maximum duration, overall longest duration (OLD), and average durations based on citizens science data and the widest duration in literature. Also, the days difference in duration of the OLD and average breeding phenology between citizens science and literature (minus is days less in citizens science data compared to literature). *Lithobates catesbeianus* is invasive in Korea and breeding data from literature is from native range, and the data for *Bufo stejnegeri* is for the oviposition period only. The analysis is based on 8,763 citizen science observations collected between 02 March 1997 and 01 December 2020 downloaded from the platform iNaturalist. \*as the first breeding date changes from year to year, this represents the range when the species start breeding. \*\* Years with more than three datapoints and used to calculate the starts/end periods and average duration.

Species	Citizens science data											Literature		Difference Lit		
	Total ob	Breeding ob	Date (min-max)	Starts between*	Avg start	Ends between	Avg end	Median	SD (days)	OPLD (days)	Avg duration (days)	n (years)**	Date (min-max)	Duration (days)	OLD (days)	avg duration (days)
<i>K. koreana</i>	70	0	no data	-	-	-	-	-	-	-	-	-	15–25 June15	10	-	-
1. Ki et al., 2016																
2. Yoo and Jang, 2012																
3. Ko et al., 1998																
4. Conant & Collins, 1998																
5. Sung et al., 2007																
6. Fujioka & Lane, 1997																
7. Borzée et al., 2020a																
8. Roh et al., 2014																
9. Ko et al., 2012																
10. Groffen et al., 2019b																
11. Fong et al., 2020																
12. Kaplan & Phillips, 2006																
13. Lee et al., 2008																
14. Borzée et al., 2019b; Borzée and Min, 2021; Moon & Park, 2016																

users, with observations reaching a ‘research grade’ when more than two-thirds of the identifiers agree on a taxon, which generally prevents the misidentification of species, and can be updated at any time. Accordingly, our analyses required observations to have reached the ‘research grade’ level. We therefore curated the database for quality prior to data download, adding and correcting the species identification when needed. However, because of the platform’s rule mentioning that 2/3rd of voters must agree on the taxa before an observation is listed as ‘research grade’, the species identifications by multiple users for some observations brought the observation to the genus level, and these observations were therefore not used for the analyses.

To download the data, a query for observations was created with the filters for all amphibians, ‘South Korea’, and only ‘research grade’. The citizen science datapoints were then downloaded through iNaturalist ([www.inaturalist.org/observations/export](http://www.inaturalist.org/observations/export)), filtered for observations dated up to 01 December 2020. Each observation was then binary qualified (presence/absence) for the categories ‘calling’, ‘amplexus’, ‘eggs’, ‘tadpoles’, ‘metamorph’, ‘adult’, and ‘death’. Only observations of ‘amplexus’, ‘eggs’, and ‘calling’ were used to describe the breeding season. On iNaturalist, it is possible to upload multiple media within a single observation, and every picture and sound file was checked for the categories described above. As a result, one observation can be coded positive for multiple categories. When there was a sound file uploaded with calls for an observation, both ‘adult’ and ‘calling’ were marked as present. When on a photo, an individual had a full vocal sac and was calling, both ‘adult’ and ‘calling’ were marked as present.

Observations of *Bufo stejnegeri* in amplexus ( $n = 28$ ) could not be used in this study to determine their breeding season, because of their unique breeding behaviour, where males and females enter the stream between September and November and immediately amplex and stay in amplexus for 3–6 months in frozen-over streams until spring spawning (Lee and Park, 2009; Fong et al., 2020). In addition, there were not enough observations of eggs ( $n = 3$ ) to determine the breeding season of *B. stejnegeri*. Furthermore, we could not determine the breeding season for *Karsenia koreana* ( $n = 62$ ) due to a lack of breeding data points ( $n = 0$ ). We also removed two data points for *Rana uenoi* as the dates of the observations and photographs conflicted.

## Literature comparison

To compare citizen science data and previous breeding knowledge, we reviewed the literature for the breeding seasons of amphibians in the Republic of Korea. We used the widest published range in dates for the breeding season of a given species from the literature for comparison (Table 1).

Detailed description of the breeding seasons is uncommon in the literature and nonspecific descriptions such as early or late in the month are used, along with unclear boundaries such as ‘from May until June’. For parametric analysis purposes, using the month of May as an example here, we transformed ‘early May’ to ‘May 3’, ‘mid-May’ to ‘May 15’, ‘late May’ to ‘May 23’, and ‘between May and June’ to ‘May 1–June 30’.

## Data encoding

While we acknowledge the presence of latitudinal variations in breeding phenology and ecological requirements of species within the Korean peninsula (Andersen et al., 2022), we did not consider the variation large enough to impact the results of this study. In addition, we do not expect a significant gradient due to the small size of the country and creating bins would result in too small of a dataset to be meaningful for some species at some of the elevation bins. To use parametric statistical analyses, we converted the calendar date of each observation into the Julian date. In terms of activity patterns and hibernation, the conversion did not create any difficulty as day 1 is conveniently located during the hibernation period for most species. As a result, cold resistant species such as *O. koreanus* were active close to day 365. This encoding however resulted in difficulties for the analysis of species breeding before 01 January, such as *Rana uenoi* breeding in December at low latitudes, or *B. stejnegeri* amplexing before winter, and thus artificially resulting in a binomial distribution of the data. To solve this problem, we negatively encoded dates matching with breeding activity before January 01, in continuity with the ‘positive’ Julian dates given from 01 January. All Julian dates were attributed following the non-bissextile calendar.

## Analyses of the breeding phenology

We tested the normal distribution of the breeding dataset for each species independently through a Shapiro-Wilk test. The data almost reached significance for a normal distribution for all species ( $0.29 \leq D_{(6,695)} \leq 0.98$ ,  $p > 0.049$ ), and we decided to ignore the minor deviation due to the robustness of the analyses downstream, and the absence of violation for the other assumptions tested. To test for difference in breeding season between species, we adapted the analyses of duration from Chazard et al. (2017) to our dataset using a linear regression with the Julian breeding date as independent variable and species as dependent variable. The assumptions were fulfilled for this analysis: we detected one outlier for the following species: *Dryophytes suweonensis*, *H. leechii*, *Kaloula borealis*, *Pelophylax nigromaculatus* and *Rana uenoi* but decided to ignore them as they did not influence the results of the model. In addition, there was a linear relationship between the continuous independent variables and the logit transformation of the dependent variable,

**TABLE 2** The different habitat (sub)categories and their descriptions used to differentiate the landscape use between all amphibian species in the Republic of Korea.

Woody landscape	Deciduous forests	Trees >3 m in height, canopy closure >35% that seasonally lose their leaves
	Evergreen forests	Trees >3 m in height, canopy closure >35% of species that do not lose leaves
	Shrub	Woody vegetation <3 m in height, > 10% ground cover
Herbaceous landscape	Grassland	Herbaceous grasses, > 10% cover, including pasture lands
	minimal vegetation	Land with minimal vegetation (<10%) and agriculture (cultivated croplands except paddy agriculture)
Wetlands	Agriculture—rice	Woody landscape
	Wetlands	Areas where the water table is at or near the surface for a substantial portion of the growing season, including herbaceous and woody species
Open water		Including all water bodies greater than 0.08 ha
Urban	High density	Areas with >30% of constructed materials that are a min of 60 m wide and residential, commercial or industrial areas with a mixture of constructed materials and vegetation where constructed materials account for >40%
	Medium to low density	Areas with >30% of constructed materials that are a min of 60 m wide and residential, commercial or industrial areas with a mixture of constructed materials and vegetation where constructed materials account for >40%

tested through the Box-Tidwell (Box and Tidwell, 1962) procedure with Bonferroni corrections (Tabachnick and Fidell, 2014).

## Analyses of the breeding types

Classifying species into breeding types provides a framework for understanding how species respond to environmental conditions (Plenderleith et al., 2018). We adjusted the four breeding strategies defined by Plenderleith et al. (2018) to our climate: explosive, prolonged, and seasonal (winter and summer) breeders. We also adjusted the setting so that a species can fall into several categories, for instance prolonged and winter breeder. To determine the presence of explosive breeders, we restricted our dataset to species with at least 100 breeding observations, an arbitrary threshold ensuring that the short breeding period is related to the biology of the species and not the absence of data. We defined species as explosive breeders if their breeding season was short (Plenderleith et al., 2018), here defined if the totality of the breeding behaviour was confined to 50 days, also an arbitrary threshold to ensure an adequate representation of the breeding phenology. For instance, even for species where mating is restricted to a few days, males can be found waiting for females for up to 2 weeks and stay at the water body for about the same amount of time after breeding.

Seasonal breeders were defined as present at the water body in either winter or summer for a minimum of 30 and a maximum of 120 days, so that several waves of breeding individuals could be included within the breeding period, generally as a function of environmental variables (Llusia et al., 2013; Borzée et al., 2020b). These thresholds were selected since a shorter period than

30 days would be representative of an incomplete dataset and 120 days is the length of a meteorological season. We defined winter breeders as species with their breeding season including sections of the 2 months before or after the winter solstice (21 December, day 355 in the Julian calendar), and summer breeders as species with their breeding season including sections of the 2 months before or after the summer solstice (21 June, day 172 in the Julian calendar). Finally, the prolonged breeders were species with a breeding period longer than 120 days, excluding outliers based on the fact that abiotic variables are likely to display a significant change over the 3 months of a meteorological season, highlighting the disconnect between breeding behaviour and the environment. To determine the average breeding phenology of the species, we used only the years with at least three breeding datapoints. The longest possible duration is the number of days between the earliest breeding observation and latest breeding observation in any given year of a species. We analysed the breeding behaviour through descriptive statistics for each of the species independently, and for each of the breeding behaviours defined above.

## Analyses of the inactive period

Here we define the inactive period, related to the putative hibernation period, as the period when individuals were not observed. For a few observations abnormally early or late in the year, we directly verified on the iNaturalist platform and removed the datapoints where individuals were obviously disturbed during their inactive period ( $n = 6$ ). We removed observations from 1 to 6 November for *D. suweonensis* as the individuals were clearly buried and in their hibernaculum (Borzée et al., 2019c).

This resulted in the removal of six datapoints and a 9-day shift in the latest date at which the species was active. The onset of the inactive period could not be determined for *H. geojeensis*, *H. yangi* and *H. perplicatus* due to the absence of datapoints in summer and fall, likely related to the fossorial behaviour of the species.

## Analyses of habitat use

For the landscape analysis, we relied on the same datapoints extracted from iNaturalist with their geocoordinates, as well as the datapoints from the National Institute of Ecology (Kim et al., 2021), and loaded them into ArcMap 10.6.1 (ESRI, Redlands, California, United States). We extracted land cover data from the World Land Cover 30 m BaseVue 2013 (MDAUS) layer within a 50 m buffer centred on each observation using the Tabulate Area tool in ArcGIS Pro 2.8.0 (ESRI, Redlands, CA, United States). We obtained 22 land categories as the raster layer contains 22 landcover classes, and we re-assigned each category into one of the five categories selected for our study (Table 2). Finally, we converted the area values for each landcover class into percentages of total area.

All the variables ( $n = 55,222$ ) were significantly distributed (Kolmogorov-Smirnov test,  $0.24 < K < 0.53$ ;  $df = 55,222$ ;  $p < 0.001$ ). To determine differences in habitat use between the species we analysed the dataset using a one-way ANOVA with the five categories as dependent variable and species as independent variable. We then used a pair-wise comparison post-hoc test to determine differences between species. All biostatistics analyses were ran in SPSS 21.0 (SPSS, Inc., Chicago, IL, United States) and graphs were plotted in R version 3.0.1 (RStudio Team, 2020) using the package gghalves (Tiedemann, 2020).

## Results

### Breeding phenology

We found evidence of breeding related behaviours in 28% ( $n = 2,465$ ) of the 8,763 observations downloaded from iNaturalist for use in this study. Within anurans, we identified two main breeding seasons, the first one starting in January - February (*Rana* spp.), and the second one in May (Figure 1 and Tables 1, 3). A different pattern was visible for caudata, with all species for which data was available breeding between February and May (Figure 1). The model for the linear regression used to determine differences between species was significant ( $t = -31.73$ ,  $p < 0.001$ ) and the breeding season was significantly different between each species pair ( $\chi^2 = 53,836.63$ ,  $df = 1$ ,  $F = 1,006.96$ ,  $p < 0.001$ ).

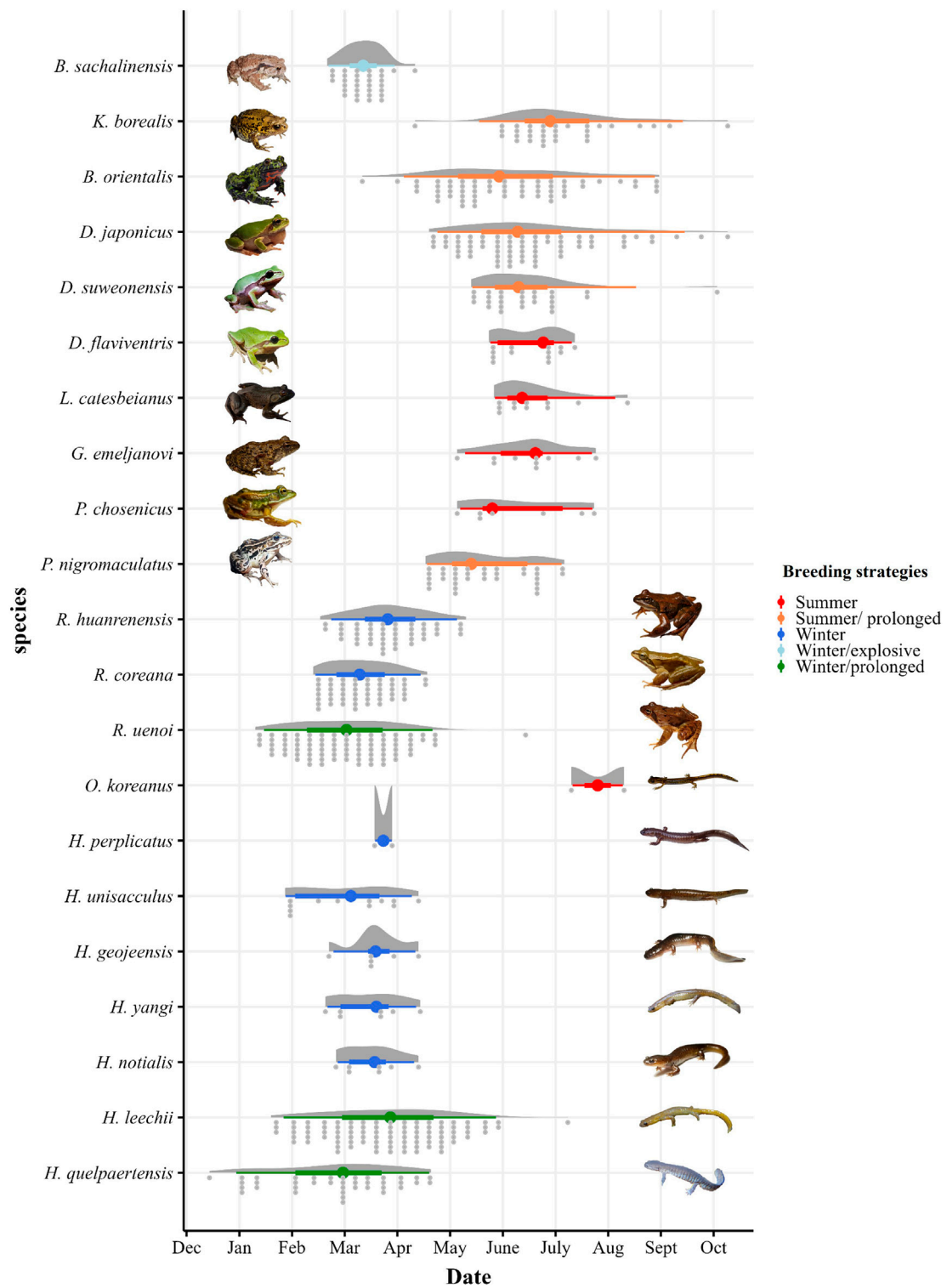
### Comparing literature and citizen science data

The peak breeding season from the citizen science data fell within the breeding season recorded in the literature for all species. However, the widest breeding seasons based on citizen science data for all species combined was on average 6.1 days shorter than reported in the literature (Standard deviation (SD) 47.9 days). Compared to citizen science data for the overall possible longest duration of breeding seasons, 11 were shorter (average  $40.7 \pm 33.3$  days) and 10 were longer (average  $31.9 \pm 29$  days) than described in the literature (Table 1). Six of the eight Hynobiid salamanders had a shorter breeding season based on the citizen science data than recorded in the literature (average  $65.5 \pm 27.79$  days shorter, see Table 1). While only five out of 13 anuran species had a shorter breeding season (average  $11 \pm 7.2$  days) than described in the literature (Table 1). The largest differences were recorded for *H. perplicatus*, for which breeding season was 111 days longer in the literature than from the citizen science data; and *B. orientalis*, for which breeding season was 108 days longer based on the citizen science data compared to the literature (see Table 1). We did not use the literature data for *L. catesbeianus* in these calculations due to the lack of data available for the Republic of Korea or northeast Asia.

### Breeding modes

With a 49-day breeding period, based on 131 observations across 17 years, *Bufo sachalinensis* (previously *Bufo gargarizans* Othman et al., 2022) was the only amphibian in the Republic of Korea that fit the definition applied to explosive breeder. Consequently, the other species were categorised as non-explosive breeding species. Based on our data, six anuran species, *B. orientalis* (170 days), *Kaloula borealis* (178 days), *Pelophylax nigromaculatus* (162 days), *Rana uenoi* (154 days), *Dryophytes japonicus* (170 days), *D. suweonensis* (140 days), and two salamander species, *Hynobius leechii* (169 days), and *H. quelpaertensis* (125 days), were categorized as prolonged breeders (Figure 1; Table 4). While the breeding season of *B. stejnegeri* was longer than 120 days, it includes the hibernating period and consequently we did not qualify the species as a prolonged breeder.

Following our definition, only *H. yangi* (54 days, starting 18 February), *H. unisacculus* (76 days, starting 26 January) *H. geojeensis* (51 days, starting 20 February), *R. huanrenensis* (82 days, starting 15 February) and *R. coreana* (64 days, starting February 11) qualified as winter breeders and were not explosive or prolonged breeders. When including prolonged and explosive breeding species, *B. sachalinensis* (49 days, starting 19 February), *R. uenoi* (154 days, starting 9 January), *H. quelpaertensis* (125 days, starting 14 December) and *H. leechii* (169 days, starting 18 January) were also defined as



**FIGURE 1**

Distribution of the proportion of the observed breeding behaviour (amplexus, eggs, and/or calling), including outliers, based on 8,763 citizen science observations downloaded from iNaturalist for *D. flaviventris* ( $n = 18$ ), *D. suweonensis* ( $n = 41$ ), *D. japonicus* ( $n = 421$ ), *B. sachalinensis* ( $n = 131$ ), *B. orientalis* ( $n = 100$ ), *K. borealis* ( $n = 48$ ), *R. coreana* ( $n = 136$ ), *R. uenoi* ( $n = 695$ ), *R. huanrenensis* ( $n = 222$ ), *G. emeljanovi* ( $n = 14$ ), *P. nigromaculatus* ( $n = 63$ ), *P. chosenicus* ( $n = 7$ ), and *L. catesbeianus* ( $n = 13$ ), *H. geojeensis* ( $n = 26$ ), *H. perplicatus* ( $n = 14$ ), *H. notialis* ( $n = 14$ ), *H. quelpaertensis* ( $n = 125$ ), *H. unisacculus* ( $n = 23$ ), *H. yangi* ( $n = 15$ ), *H. leechii* ( $n = 306$ ), and *O. koreanus* ( $n = 6$ ) in the Republic of Korea. The data was collected between 02 March 1997 and 01 December 2020. Boxplots indicate the median, interquartile range (IQR), and  $1.5 \times IQR$ , boxplot colours indicate the different breeding strategies (summer, summer/prolonged, winter, winter/prolonged, winter/explosive, winter/prolonged).





winter breeders. *Hynobius notialis* (47 days, starting 24 February) and *H. perplicatus* (9 days, starting 18 March) were also likely to be linked to the winter breeding season despite the small sample size. Finally, *B. stejnegeri* also matches with the definition of winter breeder, despite the unusual amplexing behavior temporarily overlapping with hibernation (Table 4).

Excluding explosive and prolonged breeding species, summer breeders were *D. flaviventris* (49 days, starting 21 May), *P. chosenicus* (77 days, starting 3 May), *Glandirana emeljanovi* (79 days, starting 2 May), *Lithobates catesbeianus* (79 days, starting 24 May) and *O. koreanus* (30 days, starting 7 July). When including explosive and prolonged breeders, *B. orientalis* (170 days, starting 10 March), *D. japonicus* (170 days, starting 17 April), *D. suweonensis* (140 days, starting 11 May), *K. borealis* (178 days, starting 9 April), and *P. nigromaculatus* (162 days, starting April 15) also qualified as summer breeders (see Figure 1. and Table 4). *Karsenia koreana* may also qualify as a summer breeder, based on limited literature information (Moon & Park, 2016; see Table 1).

## Inactive period

The definition of the inactive period relied on a total of  $n = 2,459$  datapoints. The inactive period saw species being split into two contrasting groups, although not matching with summer or winter breeding nor prolonged or explosive breeders. The onset of the inactive period was around mid-November for the first set of species and late December for the other set (Table 4 and Figure 2). The significant divergence was also visible the start of their active period, with winter breeders starting significantly earlier, in early January, and summer breeders starting between February and March (Figure 1 and Table 4).

## Habitat use

The ANOVA test showed that all habitat types were significantly different among species, meaning that species occupy landscapes differently: woody ( $\chi^2 = 113,716,621$ ;  $F(22,55,220) = 288.14$ ,  $p < 0.001$ ), herbaceous ( $\chi^2 = 110,383,889$ ;  $F(22,55,220) = 118.74$ ,  $p < 0.001$ ), wetland ( $\chi^2 = 21,912,649$ ;  $F(22,55,220) = 235.94$ ,  $p < 0.001$ ), water ( $\chi^2 = 5,814,936$ ;  $F(22,55,220) = 44.27$ ,  $p < 0.001$ ) and urban ( $\chi^2 = 5,553,598$ ;  $F(22,55,220) = 22.04$ ,  $p < 0.001$ ). The post-hoc tests highlighted numerous significant pair-wise comparisons for the woody, herbaceous and wetland landscapes (Figure 3), but fewer for the open water and urban landscapes (Annex 1; Figure 3).

In addition, the amount of significant pair-wise comparisons was higher for anurans than for caudata (Figure 3). In the woody landscape, most pair-wise comparisons were significant for anurans, and thus highlighting a different use of the landscape, at the exception of the comparison of *D.*

*flaviventris* with *L. catesbeianus*, *Pelophylax* sp. and two *Rana* sp., and the comparison of *D. japonicus* with *Pelophylax* sp. and the same two *Rana* species. In opposition, the pairwise relationships between species in caudata were not significant species, with the exception of *H. quelpaertensis* in relation to the other *Hynobius* species. No other clear pattern emerged, except for *K. koreana*, *O. koreanus* and *H. leechii* being significantly different from all anurans (Figure 3). The number of significantly different pairs decreased in the herbaceous landscape (Figure 3), but the pattern was consistent with that of the woody landscape. These two landscapes are representative of breeding habitats and the result shows a segregation between species outside of the breeding season.

The wetland landscape was the most represented landscape for the breeding habitat of all species combined (Figure 3), and the pattern for anurans was similar to that of woody and herbaceous landscapes, with most of the pair-wise comparisons between anurans species being significant, as well as most of the anuran-caudata pairs. A clear segregation was visible between species when grouped by breeding season; anurans starting to breed early in the year (*B. stejnegeri*, *B. orientalis*, *G. emeljanovi*, *R. uenoi* and *R. huanrenensis*) were not significantly different from caudata (Figure 3).

## Discussion

In this study we described the breeding phenology and habitat use for all described amphibian species from the Republic of Korea based on citizen science data collected over 23 years. Our results thus create a baseline that can be used for later comparisons. The peak of the breeding season of all species fell within the breeding season described in the literature when available. The breeding season of species with fewer observation data points deviated more often from the seasons described in the literature. For example, three out of eight species of *Hynobius* were described in the past year (Borzée and Min, 2021) while a fourth was described only 5 years ago (*H. unisacculus*; Min et al., 2016). These salamanders have a very cryptic life history and a relatively small distribution compared to the other Hynobiidae species in Korea, making observation through citizen science difficult. The recent description and small distribution have therefore resulted in fewer observations (average  $n = 19$ ), for instance observations in fall are missing for three of these species, and more observations are likely to extend their known breeding season and make it match more with the literature.

We found that while only a single toad species qualified as an explosive breeding species (*B. sachalinensis*, 49 days in line with the literature: Cheong, Sung & Park, 2008), numerous species had extended breeding seasons. Plenderleith et al. (2018) suggested that the advantage of explosive breeding is the decreased predation risks by aquatic species such as fish, however, in the Republic of Korea the only explosive

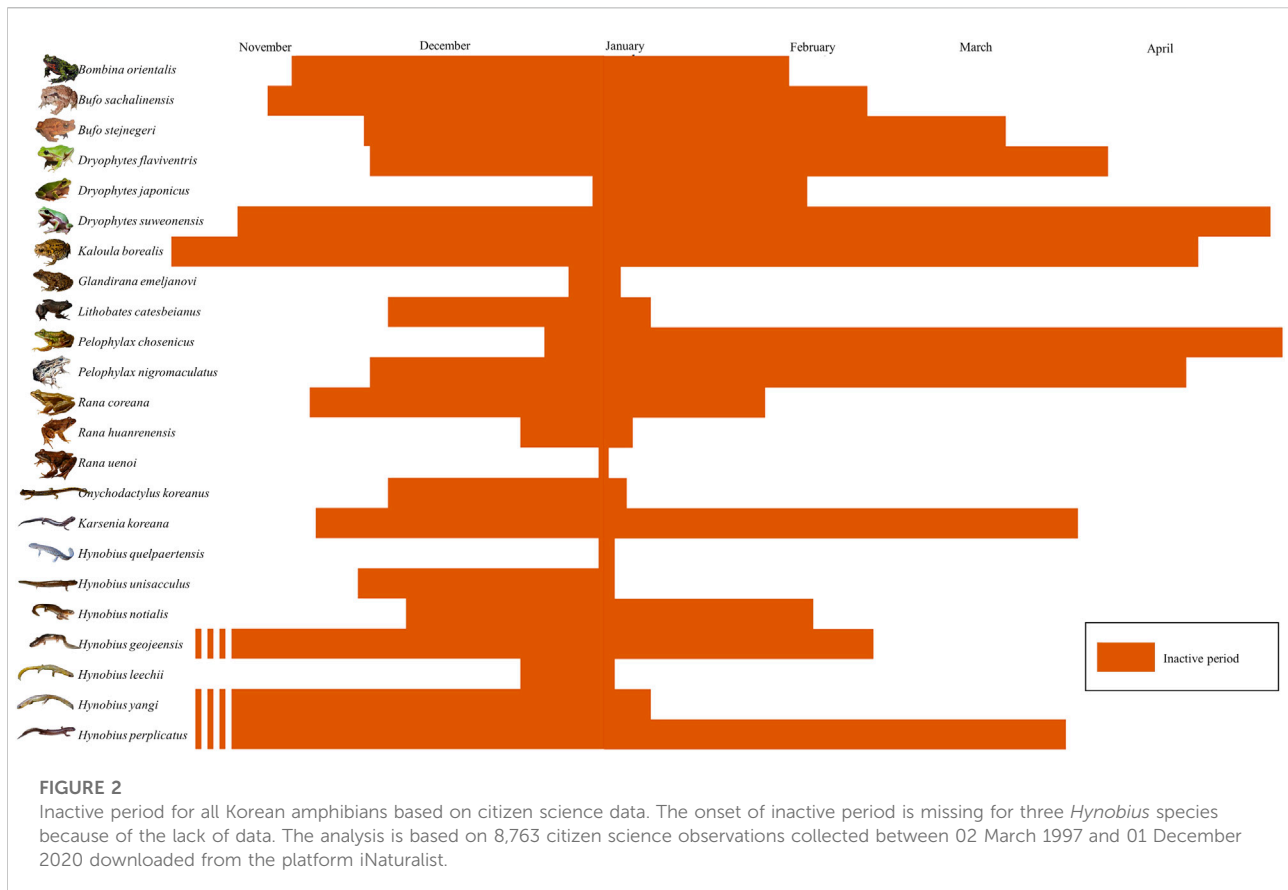
TABLE 4 Details on inactive period and breeding modes for all amphibian species of the Republic of Korea, based on 8,763 citizen science observations collected between 02 March 1997 and 01 December 2020 downloaded from the platform iNaturalist. Due to the lack of data ( $n = 12$ ) *Onychodactylus* sp. was taken out of the table.

Species	Breeding modes				Active period			Inactive period		
	Explosive	Prolonged	Summer	Winter	Earliest date	Latest date	Range (d)	Earliest date	Latest date	Range (d)
<i>Rana coreana</i>				X	27/Jan	13/Nov	290	14/Nov	26/Jan	75
<i>Rana huanrenensis</i>				X	05/Jan	18/Dec	347	19/Dec	04/Jan	18
<i>Rana uenoi</i>		X		X	01/Jan	31/Dec	364	01/Jan	31/Dec	1
<i>Glandirana emeljanovi</i>			X		03/Jan	26/Dec	357	27/Dec	02/Jan	8
<i>Lithobates catesbeianus</i>			X		08/Jan	26/Nov	322	27/Nov	07/Jan	43
<i>Pelophylax chosonicus</i>			X		23/Apr	22/Dec	243	23/Dec	22/Apr	122
<i>Pelophylax nigromaculatus</i>		X	X		07/Apr	23/Nov	230	24/Nov	06/Apr	135
<i>Dryophytes japonicus</i>		X	X		03/Jan	19/Dec	329	20/Dec	02/Jan	36
<i>Dryophytes flaviventris</i>			X		19/Apr	23/Nov	218	24/Nov	18/Apr	147
<i>Dryophytes suweonensis</i>		X	X		21/Apr	01/Nov	194	02/Nov	20/Apr	171
<i>Kaloula borealis</i>		X	X		09/Apr	29/Oct	195	30/Oct	08/Apr	170
<i>B. sachalinensis</i>	X			X	13/Jan	06/Nov	266	07/Nov	12/Jan	99
<i>Bufo stejnegeri</i>				X	08/Mar	22/Nov	259	21/Nov	07/Mar	106
<i>Bombina orientalis</i>		X	X		31/Jan	10/Nov	283	11/Nov	30/Jan	82
<i>Onychodactylus koreanus</i>			X		04/Jan	14/Dec	344	15/Dec	03/Jan	21
<i>Onychodactylus</i> sp					25/May	21/Nov	180	22/Nov	24/May	185
<i>Hynobius geojeensis</i>				X	05/Jan	12/Apr	66	13/Apr	04/Jan	299
<i>Hynobius leechii</i>		X			02/Jan	18/Dec	350	19/Dec	01/Jan	15
<i>Hynobius notialis</i>				X	04/Jan	29/Nov	298	30/Nov	03/Jan	67
<i>Hynobius perplicatus</i>				X	18/Mar	27/Mar	9	28/Mar	17/Mar	356
<i>Hynobius quepaertensis</i>		X		X	02/Jan	31/Dec	364	01/Jan	01/Jan	1
<i>Hynobius unisacculus</i>				X	02/Jan	21/Nov	323	22/Nov	01/Jan	42
<i>Hynobius yangi</i>				X	08/Jan	14/Oct	279	15/Oct	07/Jan	86
<i>Karsenia koreana</i>			X		20/Mar	14/Nov	239	15/Nov	19/Mar	126

breeder (*Bufo sachalinensis*) is one of the two species with toxins to avoid predation (Bókony et al., 2016). This fact, along with the fact that other species have long breeding periods, highlights that predation by aquatic species does not seem to shape the breeding phenology of Korean amphibians. Landscape modifications have, however, resulted in an increase in predation on *Hynobius* (Bae et al., 2019) and *Dryophytes*

(Borzée et al., 2017) and we can therefore conclude that Korean species are not properly adapted to the changes brought to the environment by human activities.

A limitation to this conclusion is that the definition of breeding type is based on the totality of the country, not along latitudinal bins because of sample size. An analysis using bins when data becomes available may shorten the

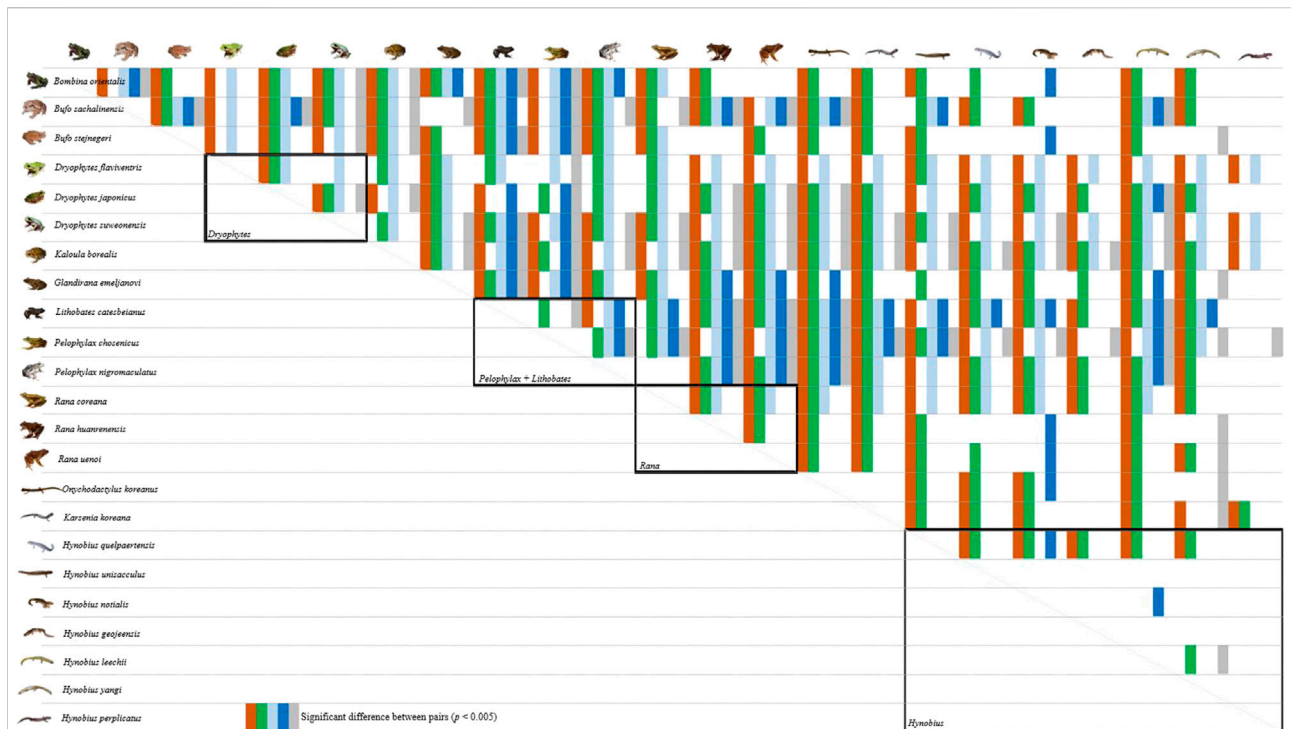


duration of the breeding period at a site, with other species possibly changing to fit the definition of explosive breeder. Breeding observations for *B. stejnegeri* were recorded well over 120 days, from fall to late winter. The species should therefore be categorized as prolonged and winter breeder. We however did not include *B. stejnegeri* in either of these categories as the species is in amplexus for 3–6 months but spawning over a restricted time frame in spring (March–April; Lee & Park, 2009; Fong et al., 2020). Based on the number of days when breeding excluding amplexus were observed, the species is close to being an explosive breeder, although it does not display the typical breeding behaviour of explosive breeders.

While our results were generally matching with the literature, we found some points of discrepancy. The literature categorised *R. huanrenensis* as an explosive breeder because it spawns over a short period in early spring (Yoo and Jang, 2012), however, based on 222 breeding behaviour observations over 13 years we determined the breeding season to be between 15 February and 8 May (range = 82 days). While the species is not an explosive breeder at the national scale over 13 years, the yearly average breeding season was 43 days, qualifying it as explosive breeder from year to year. Our classification categorises *R. huanrenensis* as a winter breeder, and thus the breeding season of the species is probably importantly influenced

by the weather, a year-dependant variable also subjected to climate change, and thus the likely explanation for the longer overall breeding season over multiple years (Blaustein et al., 2001). Furthermore, to the best of our knowledge there is no described breeding season in the literature for *L. catesbeianus* and *R. coreana* in the Republic of Korea.

In their natural range *L. catesbeianus* is a prolonged breeder, however according to our data (76 days) *L. catesbeianus* does not have a prolonged breeding season in the Republic of Korea. This has probably to do with the heavy influence of weather on the life history of amphibians (Plenderleith et al., 2018), and species with a smaller distribution will encounter a lower variety of weather condition compared to species with a larger distribution. When the weather is not matching with the ecological requirements of the species for breeding (e.g., Llusia et al., 2013), the mismatch will result in a relatively shorter breeding seasons for species with a small range as they do not experience the wider range of weather patterns impacting species with wider ranges. Besides *L. catesbeianus*, treefrogs in the Republic of Korea are another example illustrating this point: *D. japonicus* has the largest distribution, followed by *D. suweonensis* and then *D. flaviventris*, a ranking by range size in line with the duration of the breeding season: 168, 69 and 49 days respectively.



**FIGURE 3**

Result of the post-hoc Tukey test to compare the habitat use between all species pair. A 'coloured cell' represents a  $p < 0.005$  (exact results in Annex 1), and thus a different use in habitat between the species. The colour coding is such as brown is woody, green is herbaceous, light blue wetland, dark blue is water, and grey is urban. Intra-generic comparisons are highlighted by black boxes. The analysis is based on 8,763 citizen science observations collected between 02 March 1997 and 01 December 2020 downloaded from the platform iNaturalist.

In this study we used a citizen science database, the advantage is that the data is collected over several decades and is therefore relevant to establish a strong baseline, and the data originates from most geographic areas from the focal country: the Republic of Korea. A clear drawback is that most data comes from generally easily accessible areas and non-work days, a common trend for citizen science data (Bird et al., 2014). However, by supplementing the dataset with surveys conducted by the leading national ecological organization we contravene both the limitation of accessibility by citizen science, and the working-hours restrictions linked to governmental organisations. For instance, citizen science data from the Republic of Korea showed a high accuracy when describing the range of *Hynobius* salamanders, comparable to standard molecular tools, with the exception of areas under taxonomic uncertainty (Borzée et al., 2019b), where trained observers are likely to better-assess species' identity. By combining the two types of data, we also resolve the bias arising from a larger number of observations for charismatic and easily observable species.

We were not able to determine the boundaries of the hibernation period for any of the species due to the nature of the data. We had to qualify this period as inactive as the

species hide before hibernation and are therefore unlikely to be observed. This is for instance the case of *D. japonicus*, where individuals move up the trees in fall, before it becomes too cold (Borzée et al., 2018b). The absence of latitudinal bins and year by year observation also meant that the inactive period in winter was greatly shorter than what would be expected for all of the species (Lee and Park, 2016). For instance, some species were determined to be inactive for as little as 6 days. This is not representative of the length of the hibernation, but the number of days when the species were not observed for any of the 23 years used for this analysis. In addition, some secretive species such as salamanders are unlikely to be detected in winter, when citizen science records are not as numerous. Therefore, species with a low number of observations, such as *H. notialis* and *H. perplicatus*, are also likely to be winter breeders, but due to the lack of data they are a couple of days shy of being categorized as such. In addition, due to global warming, amphibians have shown significant phenological shifts, generally starting to breed earlier in the season (Carroll et al., 2009; Green, 2017), and preliminary results for *R. uenoi* and *B. sachalinensis* in the

Republic of Korea follow the same pattern (Kwan et al., 2020).

Anthropogenic changes in landscapes, through degradation or loss, generally result in biodiversity losses (Pyron, 2018). It is therefore important to understand the position and role of species in all landscapes to also establish a baseline before a too important shift blurs the relationship and knowledge on the historical presence and use of landscapes (Haberle, 2007). This is especially important in the landscape studied here as we found a greater difference in habitat use among genera than within genera, likely as a result of niche conservatism within closely related species (Losos, 2008; Prinzing et al., 2017) and thus highlighting more prevalent threats to specific clades.

The fact that fewer pairs were significantly different in the herbaceous than in other landscapes, but more pairs were significantly different in the woody landscape highlights that pressure for niche differentiation is greater in the landscape where the species breed. For instance, the convergence of numerous species to similar breeding habitats in late winter results in increased competition for breeding resources, and thus diversification of habitat use. The absence of many significantly different pairs within and between anuran and caudata in both the water and the urban landscapes is representative of a similar pattern for all species, here, the avoidance of the habitat.

The importance of establishing a baseline is demonstrated in this study, as closely related species are more likely to be extirpated faster. Some exceptions do need to be noted, for instance the divergence of threat level between the threatened *D. suweonensis* and *D. flaviventris* in comparison with the abundant *D. japonicus*. Here, this dichotomy is likely explained by the deep divergence between the two clades within the same genus (Borzée et al., 2020a). Another exception is that of *Hynobius* salamanders, with *H. quelpaertensis* being the only species significantly different from the others in the genus. This divergence is likely explained by the fact that *H. quelpaertensis* is the only species occurring on a basaltic island, which has been shown to have an impact on the behaviour and morphology of amphibians and reptiles due to the predation pressure (Kang et al., 2017; Shin and Borzée, 2020).

## Data availability statement

Publicly available datasets were analyzed in this study. This data can be found here: The data was extracted from the citizen

science database iNaturalist (<https://www.inaturalist.org>) for all amphibian observation uploaded between 02 March 1997 and 5 November 2020 in the Republic of Korea.

## Ethics statement

Ethical review and approval was not required for the animal study because While focused on vertebrates, the data was collected online.

## Author contributions

JG and AB designed the experiment, collected data, analysed data, wrote the first draft, and revised the manuscript. DA collected data, analysed data and revised the manuscript. AB provided financial resources.

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## Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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