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New insights into the patterns and drivers of avian altitudinal migration from a growing crowdsourcing data source

Pei-Yu Tsai*, Chie-Jen Ko*, Stephanie Yuan Chia, Ya-Jung Lu and Mao-Ning Tuanmu

P.-Y. Tsai, S. Y. Chia and Y.-J. Lu, Biodiversity Research Center, Academia Sinica, Taipei, Taiwan. – C.-J. Ko (https://orcid.org/0000-0002-8343-604X), Endemic Species Research Inst., Jiji, Nantou County, Taiwan and Inst. of Ecology and Evolutionary Biology, National Taiwan Univ., Taipei, Taiwan. – M.-N. Tuanmu (https://orcid.org/0000-0002-8233-2935) ✉ (mntuanmu@gate.sinica.edu.tw), Thematic Center for Systematics and Biodiversity Informatics, Biodiversity Research Center, Academia Sinica, Taipei, Taiwan.

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Altitudinal migration is a common and important but understudied behavior in birds. Difficulty in characterizing avian altitudinal migration has prevented a comprehensive understanding of this behavior. To address this, we investigated the altitudinal migration patterns and explored potential drivers for a major proportion (~70%) of the entire resident bird community along an almost 4000 m elevational gradient on the main island of Taiwan. Based on the occurrence records collected by citizen scientists, we examined the seasonal shifts in the center and the upper and lower boundaries of elevational distributions for 104 individual species. We then built phylogeny-controlled regression models to investigate the associations between the birds' seasonal distribution shifts and seven of their traits, and examined whether the observed shifts can be explained by three main hypotheses on potential drivers. Results showed that at least 60 species (58%) seasonally changed their distributions along elevations. While most of them (42 species) tended to move downhill in winter, a considerable number of species (14) tended to move uphill. While the species breeding at high or low elevations tended to move downhill in winter, those breeding at medium-low elevations tended to move or extend their distributions to higher elevations. Our regression models suggested that seasonal variations in climates and food availability could be major drivers of the behavior. However, the three hypotheses can only partially explain the observed downhill migration patterns and none of them can well explain the uphill patterns, indicating an important knowledge gap. This study investigated avian altitudinal migration from a new perspective with a novel and generalizable approach, and revealed interesting patterns that could be difficult to identify with conventional approaches. It demonstrated the power of citizen science data to provide new insights into this behavior by characterizing the general patterns and mechanisms across a large number of species.

Keywords: citizen science, eBird, elevational movement, functional traits, migration tendency, resident birds

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*contributed equally.

Introduction

Altitudinal migration is the seasonal and repeating movement of animals along elevations (Rappole 2013). It is an important behavior of many animal species living in mountain regions as this behavior allows them to exploit different environments to meet their seasonally varying requirements or to follow seasonal shifts in resource distributions along elevations (Boyle 2017, Hsiung et al. 2018). Altitudinal migration can provide migrants similar benefits as latitudinal migration, but at relatively low costs because it involves shorter travel distances and requires fewer morphological and physiological adaptations (Dingle and Drake 2007, Hsiung et al. 2018).

At least 10% of the ~10 000 existing bird species in the world have been reported to perform altitudinal migration (Barçante et al. 2017). In some mountain regions, more than 50% of bird species move seasonally along elevations (Boyle 2017). However, the general patterns and drivers of this behavior are still poorly understood, mainly due to the lack of comprehensive studies capturing the variability of this behavior among species and geographic regions (Hsiung et al. 2018). For example, while most altitudinal avian migrants spend their non-breeding season at lower elevations and move to higher elevations for breeding (i.e. post-breeding downhill migration; Levey 1988, Stiles 1988, Boyle 2008a), the opposite pattern (i.e. post-breeding uphill migration) also occurs (Hess et al. 2012). Some species may also be partially migratory, with some individuals from the same populations migrating and the remaining being residents (Green et al. 2015). In addition, although many studies have indicated that most birds that undergo altitudinal migration are frugivores or nectarivores (Boyle and Conway 2007, Boyle 2008b), a cross-realm literature review suggests that this association is probably only true in the Neotropics (Barçante et al. 2017).

Current understanding of factors affecting birds' altitudinal migration tendencies is even more limited. Several non-mutually exclusive hypotheses have been proposed to explain the underlying mechanisms of altitudinal migration (Barçante et al. 2017). For example, the 'climatic constraint hypothesis' posits that the seasonal movement of birds along elevations is forced by their intolerance to harsh climates in the breeding ground during the non-breeding season (Cox 1985, Boyle and Conway 2007, Boyle 2011). Therefore, it is expected that species intolerant of low temperatures (e.g. species with a weak cold tolerance, a narrow tolerance range or a small body size; Ketterson and Nolan 1976, Boyle et al. 2010) would tend to move to lower elevations in winter (Table 1). The 'food availability hypothesis' suggests that the behavior is driven by seasonal variation in food resources along elevations and species more sensitive to the seasonal variation would have a higher migration tendency (Levey 1988, Blake and Loiselle 1991, Loiselle and Blake 1991). Therefore, the species which rely on low-protein, low-fat and dilute foods (e.g. frugivores and nectarivores; Loiselle and Blake 1991), eat the foods whose availability varies seasonally along elevations (e.g. insectivores; Barçante et al. 2017), have specialized diets (Boyle et al. 2010), or are intolerant of starvation (e.g. species with a small body size; Boyle 2008a) are expected to have a high tendency to move up and down seasonally to track the distributions of their foods (Table 1). In addition, the 'nest predation hypothesis' states that birds move along elevations seasonally to reduce nest predation risk when breeding (Fretwell 1980, Boyle 2008b). Because open nests could be more vulnerable to predators than closed nests (Remeš et al. 2012) and nest predation risk is usually higher at lower elevations (Skutch 1985), it may be expected that the species using open nests would have a higher tendency than those using closed nests to move to higher elevations for breeding (Table 1). However, while many possible drivers have been proposed, they have only been empirically examined in few cases and their generalizability is mostly unknown (Barçante et al. 2017, Boyle 2017).

One major reason for the lack of comprehensive understanding on both patterns and drivers of avian altitudinal migration is the difficulty in investigating the behavior (Barçante et al. 2017). Commonly used investigative approaches, including capture–mark–recapture, GPS tracking and stable isotope analyses, are labor-intensive and costly. Therefore, previous studies have been restricted to a few species, which prevents general conclusions on the behavior from being made. The rapid development of citizen science in the past few decades has provided a new source of biodiversity data (Sullivan et al. 2009, Dickinson et al. 2010). Citizen scientists have collected huge amount of data across a large area, and this has allowed many research topics – such as species distributions and biodiversity patterns, species-environment relationships and species' responses to environmental changes – to be examined from a broader and nontraditional point of view (Dickinson et al. 2010). In the research on avian migration, citizen science data have also been successfully used to track the long-distance movement of birds and examine the trajectories of latitudinal migration (La Sorte et al. 2016, La Sorte and Fink 2017). However, this new type of data has never been used to investigate altitudinal migration, even though it has the potential to improve our understanding of this behavior due to its broad taxonomic and geographic coverage. Therefore, using the resident bird community on the main island of Taiwan as a case, this study demonstrated how a novel and generalizable approach based on citizen science data could be successfully applied for 1) characterizing general patterns and exploring potential drivers of altitudinal migration across species of an entire community, and 2) revealing novel patterns that may lead to new hypotheses on the behavior's mechanisms. Comprehensive and novel insights into avian altitudinal migration obtained from this approach may fill the knowledge gap of this important behavior.

Materials and methods

Study area

The main island of Taiwan is located off the southeastern coast of China. This subtropical island is roughly 36 000 km^2

Table 1. Predicted and observed associations between birds' traits and their seasonal shifts in elevational distributions. The associations were examined for uphill and downhill shifts separately. The predicted associations were based on the three main hypotheses on the mechanisms of avian altitudinal migration. The observed associations were obtained from the phylogeny-controlled regression models built in the study.

			Uphill shift				Downhill shift			
				Observed#				Observed#		
Hypothesis	Trait	Proxy/measure	Predicted	Lower boundary	Center	Upper boundary	Predicted	Lower boundary	Center	Upper boundary
Climatic constraint	Lower temperature limit	The 2.5th percentile of the temperature within species distribution range	–	(–)	ns	ns	+	–	–	–
	Temperature range	Difference between the 97.5th and 2.5th percentiles of the temperature	+	–	ns	ns	–	**–**	**–**	(–)
	Body size*	Body mass	+	ns	ns	(–)	–	ns	**–**	ns
Food availability	Body size*	Body mass	–	ns	ns	(–)	–	ns	**–**	ns
	Frugivory/nectarivory	Percent of fruits and nectar in diet	+	ns	ns	ns	+	**+**	ns	ns
	Insectivory	Percent of invertebrates in diet	+	ns	ns	ns	+	(+)	ns	ns
	Dietary diversity	Shannon–Wiener diversity of food types	–	ns	ns	ns	–	ns	+	ns
Nest predation	Open nest	Whether using an open nest	–	ns	ns	(–)	+	ns	(+)	ns

Symbols for the observed associations: + significantly positive associations under all six resampling settings; – significantly negative associations under all six resampling settings; (+) significantly positive associations under 3–5 resampling settings; (–) significantly negative associations under 3–5 resampling settings. The symbols are shown in bold for the observed associations consistent with the prediction.

* The climatic constraint and food availability hypotheses have different predictions on the associations.

and approximately one–third of it is covered by mountains higher than 1000 m a.s.l. (Fig. 1). Along its 3952 m elevational gradient, the natural vegetation consists of evergreen broadleaf forests below ca 1000 m, mixed forests at ca 1000–2500 m, and evergreen coniferous forests and subalpine grasslands above ca 2500 m a.s.l. Due to the various climates and vegetation types along the elevational gradient, Taiwan sustains diverse and abundant fauna, including 657 bird species (CWBF 2017). Among the 152 resident bird species on the main island of Taiwan, 27 are endemic species and 54 are endemic subspecies.

Occurrence records of resident birds

We obtained the list of resident birds from the Checklists of Birds of Taiwan' (CWBF 2017). We excluded the species not occurring on the main island of Taiwan and the species also containing a latitudinal migratory population that visits Taiwan. For the remaining species, we obtained their distribution information across the Taiwan island between January 2000 and March 2019 from the eBird database (downloaded on 20 April 2019), which collects observation records of birds from global citizen scientists (Sullivan et al. 2009, 2014). We only retained the occurrence records associated with the sampling events when the surveyors recorded all species observed (i.e. complete checklists). To exclude the records with uncertain geographic locations, we removed those associated with the sampling events which covered a longer-than-1-km transact or a larger-than-1-ha sampling area. To reduce the variation in sampling efforts among the sampling events, we excluded the records associated with the events with a survey duration longer than 5 h and those with more than 10 observers, following the recommendation of the 'Best Practices for Using eBird Data' (Strimas-Mackey et al. 2020). We did not filter the sampling events by survey time of the day because there was no major difference in survey time among elevation bands or between seasons, except at the highest elevations (Supplementary material Appendix 1 Fig. A1). We also removed duplicate records based on the scientific names of birds, longitude, latitude and observation dates. We used the records collected from April to June and from November to January to obtain the breeding and non-breeding season distributions of the bird species, respectively, because most (94.3%) breeding birds in Taiwan breed during the former period (Ko et al. 2014). In total, about 0.45 million occurrence records of 112 species collected in 83 166 sampling events in the two seasons across the 19 years were used in the following analyses.

Characterization of altitudinal migration patterns

We obtained the elevation for each sampling event based on the 'ASTER Global Digital Elevation Model' (obtained from <https://earthexplorer.usgs.gov/>) and calculated the mean elevation within 100 m from the sampling location to account for the detection distance and uncertainty in GPS locating. Sampling was uneven across elevations and between the two seasons (Fig. 1). Because the uneven samples may result in the distribution of bird observations biased towards the elevations surveyed more often, we used a resampling approach to correct the sampling bias. We first examined the species accumulation curve for each 500-m elevation band. Because the curves indicated insufficient sampling effort at the highest elevation bands (Supplementary material Appendix 1 Fig. A2), we combined those above 2500 m a.s.l. into one band for subsequent resampling. We calculated the number of sampling events per km^2 as a measure of sampling effort for each elevation band and each season. We then resampled the sampling events with the replacement and made the sampling effort equal across all elevation band-season combinations. To account for the uncertainty associated with the controlled sampling effort, we repeated the resampling with three different levels of sampling effort: the first (0.2721 events km^{-2}), second (0.557 events km^{-2}) and third quartiles (0.8046 events km^{-2}) of the sampling effort among elevation bands and seasons. We repeated the resampling 1000 times and obtained 1000 sets of resampled sampling events for each of the three levels of sampling effort.

Using the occurrence records associated with each set of the resampled sampling events, we calculated the 50th percentile of elevations over all records of a species during the breeding and non-breeding seasons separately to represent the center of the species' distribution in one season, and calculated the 5th and 95th percentiles to represent the lower and upper distribution boundaries, respectively. We then used the differences in the three percentiles between seasons (non-breeding minus breeding) to measure the seasonal shifts in the distributional center and the boundaries. There was a post-breeding uphill (downhill) shift in the center or a boundary if the 95% confidence interval of the corresponding percentile difference obtained from the 1000 resamples was completely above (below) zero. We did not incorporate the information on individual abundance of species because 1) data-intensive approaches to obtain reliable abundance estimations (Strimas-Mackey et al. 2020) would exclude many species from our study, 2) occurrence information from eBird has be used successfully for tracking population movements (La Sorte et al. 2016) and 3) abundance information is not critical for defining the lower or upper distribution boundary. While the incomplete surveys at the highest elevations (Fig. 1) may lead to an underestimation of the upper boundary for high elevation species, this underestimation should not significantly affect our analyses on distribution shifts because well-controlled sampling effort along elevation and between seasons would lead to similar underestimations in the two seasons. To avoid a potentially biased measurement of the shifts caused by a small number of records, for each resampled event set, we only retained the measurements for the species with at least 30 occurrence records in each of the two seasons. To account for the potential effect of this arbitrary sample size criterion on our results, we also used 100 records as another criterion. Therefore, we totally generated

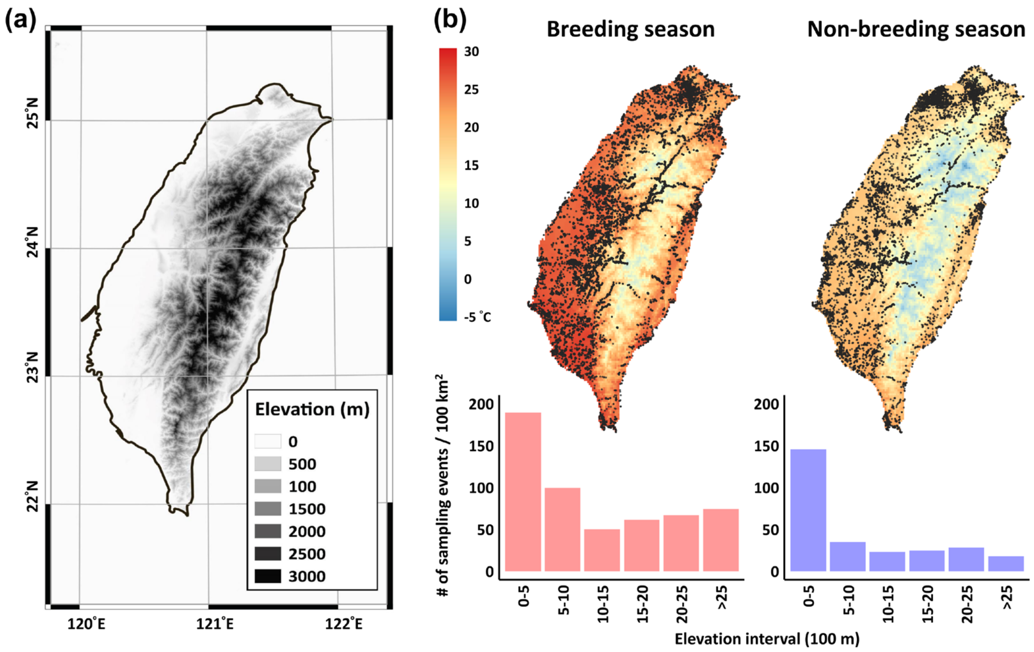

Figure 1. (a) Location and topography for the study area and (b) the geographical and elevational distributions of the eBird sampling events used in the study during the breeding (April–June) and non-breeding (November–January) seasons. The bar charts in (b) show the number of sampling events per 100 km^2 within each 500-m elevation band; events above 2500 m a.s.l. were combined. The maps in (b) also show the geographic patterns of the average air temperature in the two seasons. The temperature data were obtained from Taiwan Climate Change Projection Information and Adaptation Knowledge Platform (https://tccip.ncdr.nat.gov.tw/).

6000 resampled datasets (3 levels of sampling effort × 2 sample size criteria × 1000 resampling repeats) and each dataset contained the three shift measures for the individual bird species that satisfied the given sample size criterion. We would like to note that different datasets may contain different sets of species due to the random resampling process and different sample size criteria applied. In total, 104 species (Supplementary material Appendix 1 Table A1) had at least 30 records in both seasons in at least one resampled sampling event set, and were included in the following analyses.

Examination of potential drivers of altitudinal migration patterns

To explore the potential mechanisms driving avian altitudinal migration, we examined whether the associations between species' seasonal shifts in elevational distributions and their traits were consistent with the predicted associations based on the three main hypotheses on the mechanisms (Table 1). For examining the predictions of the climatic constraint hypothesis, we obtained the temperature associated with every eBird observation record across the entire distributional range (including records outside of Taiwan) of each species (also obtained on 20 April 2019). With an assumption that the environmental temperatures experienced by a species across its entire distributional range reflect the range of temperature that the species can tolerate, we calculated the 2.5th percentile of the temperature and the difference between the 97.5th and 2.5th percentiles as surrogates of the temperature lower limit and temperature tolerance range, respectively, for each species. We used the time series data layers of monthly mean temperature between January 2000 and December 2013 from CHELSA (<http://chelsa-climate.org/>; Karger et al. 2017) to obtain the mean temperature for the month when a record was collected. We excluded the bird records collected after 2013 from this calculation because of the unavailability of the climate data. We also obtained the mean body mass of the species analyzed from the 'Taiwan Breeding Bird Trait Dataset' (ver. 2.0; Tsai et al. 2020a). The original measurements of body mass were from the Avifauna of Taiwan (Severinghaus et al. 2010), banding data from the Monitoring Avian Productivity and Survivorship Program in Taiwan (<https://sites.google.com/a/birds-tesri.twbbs.org/maps-taiwan/>) and the Handbook of the Birds of the World Alive (del Hoyo et al. 2015).

To examine the predictions of the 'food availability hypothesis (Table 1), in addition to the body mass, we also obtained data on the proportion of different food types (including invertebrates, mammals/birds, reptiles/amphibians, fish, unknown vertebrates, dead bodies, fruits, nectar/pollen, seeds, other parts of plants) in the diet of each species analyzed from the EltonTraits dataset (Wilman et al. 2014). We used the proportion of fruits and nectar in diet and the proportion of invertebrates in diet as surrogates of the degree of frugivory/nectarivory and the degree of insectivory, respectively. We recognize that the proportion of invertebrates in diet is not a perfect measurement of the degree of insectivory, but it is the best data we could obtain for all the species analyzed. To measure the dietary diversity, we calculated the

Shannon–Wiener diversity index based on the proportions of different food types in diet.

Finally, we obtained the information on nest structure of the species analyzed also from the 'Taiwan Breeding Bird Trait Dataset' (ver. 2.0; Tsai et al. 2020a), which classified the nest structure into seven types following Fang et al. (2018), to examine the prediction of the nest predation hypothesis (Table 1). We reclassified the types of scrape, platform and cup into 'open nests' and the types of dome, dome with tunnel, primary cavity and secondary cavity into 'closed nests'. Seven species can build both open and closed nests. We classified them into the group of closed nests because the species has the ability to build a closed nest to reduce predation risk.

We built phylogenetic generalized least squares regression models (Martins and Hansen 1997) to examine the associations between each of the three measures of seasonal distribution shifts and the seven traits while accounting for the confounding effects of phylogenetic closeness among bird species. Using each of the 6000 resampled datasets, we built separate uphill and downhill shift models (i.e. 12 000 models in total) because we expected that different factors may drive uphill and downhill movements (Table 1). In an uphill shift model, only the species whose seasonal distribution shifts (non-breeding minus breeding) was larger than or equal to zero were included, while only those whose shifts were smaller than or equal to zero were included in a downhill model. In downhill models, we used the absolute values of the shift measures as the response variable so that a positive coefficient in the models indicated a positive effect of an increase in the trait values on the shift. We used the seven above-mentioned traits, which were not highly correlated with one another (Supplementary material Appendix 1 Fig. A3), as predictor variables in each model. We converted the values of body mass to the base 10 logarithm. For the categorical nest structure, we used a dummy variable with the closed nest as the reference group. We standardized all continuous predictor variables so that the estimated coefficients could indicate their relative effects. We would like to note that a species could be included in an uphill model built with one resampled dataset and a downhill model built with another dataset due to the random process of the resampling.

We assumed that the residual errors in the regression models are correlated with the phylogenetic closeness among species and that the error structure can be simulated using the Brownian Motion evolution model. To obtain the phylogenetic information, we downloaded 1000 phylogenetic trees for the 104 species from BirdTree.org (<http://birdtree.org/>; Jetz et al. 2012) and then obtained a consensus tree with the least-squares edge lengths from the 1000 trees. For both uphill and downhill shift models with a given level of sampling effort and a sample size criterion, a 95% confidence interval of the estimated coefficients for each species trait was obtained from 1000 model repeats and used to evaluate the significance of the association between the trait and the distribution shift. All the analyses were conducted in R ver. 3.4.4 with the 'ape' (ver. 5.3; Paradis and Schliep 2019), 'nlme' (ver. 3.1; Pinheiro et al. 2013) and 'phytool' (ver. 0.6; Revell 2012) packages.

Results

Altitudinal migration patterns

Our results revealed that a large proportion of the resident bird species in Taiwan performed altitudinal migration, but had diverse patterns (Fig. 2, Supplementary material Appendix 1 Fig. A4). Sixty (58%) of the 104 species examined consistently showed seasonal shifts in their distributional center and/or boundaries along elevations across all six resampling settings (Supplementary material Appendix 1 Table A1). Among those species, 42 had the 95% confidence interval of at least one of the three shift measures consistently below zero across six resampling settings and none consistently above zero, suggesting a post-breeding downhill migration, while 14 had the confidence interval of at least one shift measure consistently above zero and none consistently below zero, suggesting an uphill migration (Supplementary material Appendix 1 Table A1). Three of the other four species shifted the upper boundary of their distributions uphill and shifted the lower boundary downhill in winter, and the remaining species shifted its distributional center downhill but its upper boundary uphill in winter (Supplementary material Appendix 1 Table A1). Only 12 of the 42 post-breeding downhill migrants and none of the 14 uphill migrants shifted both lower and upper boundaries of their distributions (Supplementary material Appendix 1 Table A1), suggesting that the partial migration might be prevalent among the migrants.

In spite of the large variation among species, three general patterns emerged. First, most species breeding at medium to high elevations (breeding season distribution center > 1000 m a.s.l.) tended to undergo downhill migration in winter, and many of those downhill movements involved shifts in both upper and lower distribution boundaries (Fig. 2, Supplementary material Appendix 1 Fig. A4). Second, many species breeding at medium-low elevations (150–500 m a.s.l.) tended to move to higher elevations in winter, with an uphill shift in the distributional center and/or the upper boundary but not in the lower boundary (Fig. 2, Supplementary material Appendix 1 Fig. A4). Finally, some species breeding at low elevations (< 150 m a.s.l.) tended to have their upper distribution boundaries, but not lower boundaries, moving downhill (Fig. 2, Supplementary material Appendix 1 Fig. A4).

Associations between birds' traits and seasonal shifts in elevational distributions

According to our uphill shift models, we only found a consistent, significant association between the temperature range and the shift in the lower distribution boundary (Fig. 3a–c, Supplementary material Appendix 1 Fig. A5a–c). The observed negative association suggested that species with a narrow thermal tolerance range tended to shift their lower distribution boundary uphill in winter, which is opposite to the prediction of the climatic constraint hypothesis (Table 1). Some models showed that species with a low lower temperature limit (i.e. strong cold tolerance) tended to have their

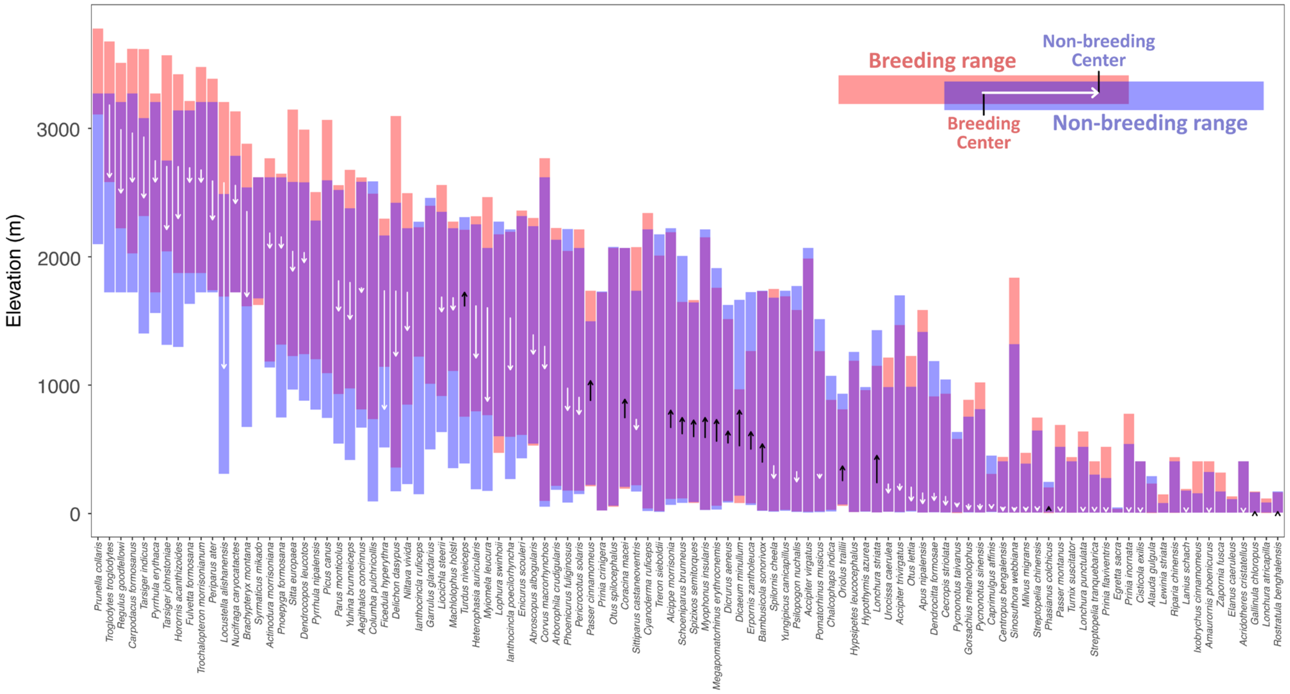

Figure 2. Seasonal shifts in the elevational distributions of the bird species examined. For each species, red and blue bars indicate the elevational ranges in the breeding and non-breeding seasons, respectively, and the overlap between the bars (in purple) indicates the range where the species was recorded in both seasons. Therefore, the red color on the top (bottom) indicates a post-breeding downhill (uphill) shift in the upper (lower) boundary of a species' elevational distribution. The blue color on the top (bottom) indicates a post-breeding uphill (downhill) shift in the upper (lower) boundary. The arrow inside the bars shows the seasonal shift in the distributional center, with a white arrow indicating a downhill shift and a black one indicating an uphill shift. The 50th, 5th and 95th percentiles of the elevation for a species' occurrence records collected in one season were respectively used to determine the center and the lower and upper boundaries of the elevational range in that season. The medians of the percentiles over 1000 sets of resampled sampling events are shown in the figure. If the 95% confidence interval of the seasonal shift in the center did not include zero, the shift was considered significant. An arrow is shown only for the species with a significant shift in its distributional center. Results associated with the high level of sampling effort (the third quartile) and the small sample size criterion (n ≥ 30) are shown. Results associated with other resampling settings are shown in Supplementary material Appendix 1 Fig. A4.

lower distribution boundary moving uphill in winter, while species with a small body size or using closed nests tended to have their upper distribution boundary moving uphill (Fig. 3a–c, Supplementary material Appendix 1 Fig. A5a–c). These results agreed with the predictions of the three hypotheses (Table 1), but only under certain resampling settings.

On the other hand, many species traits consistently showed significant associations with downhill distribution shifts (Fig. 3d–f, Supplementary material Appendix 1 Fig. A5d–f). Consistent with the predictions of the climatic constraint hypothesis, species with a narrower thermal tolerance range had a higher tendency to move to lower elevations in winter. In addition, the significantly negative associations between body mass and the downhill shift in the distributional center also showed support to the climatic constraint hypothesis. However, we found strong post-breeding downhill migration tendencies among the species that can tolerate lower temperatures, contradicting the same hypothesis (Table 1). Our results showed that the species eating more fruits and nectar or eating more invertebrates had a higher tendency to shift the lower boundary of their distributions to lower elevations in winter (Fig. 3d–f, Supplementary material Appendix 1 Fig. A5d–f), which is consistent with the prediction of the food availability hypothesis (Table 1). However, we also found that the species with a more diverse diet had a higher tendency to shift their distributional center to lower elevations in winter (Fig. 3d–f, Supplementary material Appendix 1 Fig. A5d–f), which is opposite to the prediction of the same hypothesis (Table 1). Finally, although we found significantly positive associations between using open nests and a downhill shift in distributional center, supporting the nest predation hypothesis (Table 1), the significant associations were only found under a few resampling settings (Fig. 3d–f, Supplementary material Appendix 1 Fig. A5d–f).

Discussion

This study characterized the patterns and drivers of altitudinal migration for 104 resident bird species along an almost 4000 m elevational gradient. To the best of our knowledge, this is the first time that 1) this behavior was investigated for

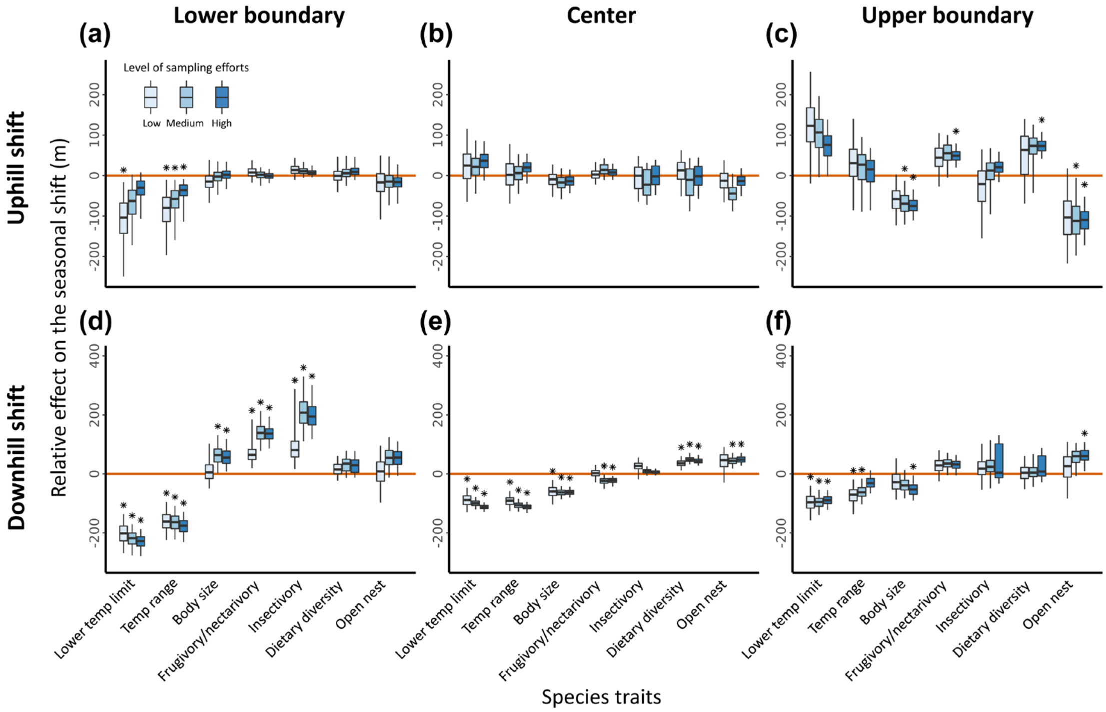

Figure 3. Associations between birds' traits and the seasonal shifts in the center and the lower and upper boundaries of their elevational distributions. Each box shows the 97.5th, 75th, 50th, 25th and 2.5th percentiles of the standardized coefficients of a trait in the 1000 models built with different sets of resampled occurrence records. The value of the standardized coefficient indicated the relative effect of an increase in the trait values on the shift distance of the center and the lower and upper boundaries of species distribuions along elevations. The box which is entirely above or below zero (i.e. the effect of a trait is significantly positive or negative) is marked with a star. Results associated with three levels of controlled sampling effort and the small sample size criterion (n ≥ 30) are shown. Results associated with the large sample size criterion are shown in Supplementary material Appendix 1 Fig. A5.

a major proportion (~70%) of an entire resident bird community using a consistent approach and 2) multiple potential drivers were examined simultaneously across more than 100 species. Consistent with previous reviews on field studies (Barçante et al. 2017, Boyle 2017, Hsiung et al. 2018), our results showed that the altitudinal migration is prevalent, but with diverse patterns among the bird species. Most altitudinal migrants conducted post-breeding downhill migrations, but a considerable number of species shifted their distributions uphill in winter. In addition, many of the species may be partial migrants as only either the lower or upper distribution boundary shifted between seasons. Our results suggested that seasonal variations in climates and food availability could be major drivers of avian altitudinal migration, but the current main hypotheses on the underlying mechanisms of this behavior can only partially explain the observed patterns. More importantly, with the approach based on citizen science data, this study uncovered interesting patterns that could be difficult, if not impossible, to identify with conventional sampling approaches and warrant further studies.

Across all resampling settings, our results showed that around 58% of the resident bird species in Taiwan examined changed their elevational distributions between seasons (Supplementary material Appendix 1 Table A1). This proportion is probably underestimated because only the species which 1) had enough resampled occurrence records with all six resampling settings and 2) had a consistent and significant distribution shift across all settings was considered as a migrant. However, even the conservative estimate is considerably higher than a previous estimation for breeding birds in Taiwan (25%; Shiu and Lee 2003), and is the second highest among the values reported for bird communities or guilds around the world (10–70%; Boyle 2017). The higher proportion may echo the expectation that there are more altitudinal migrants than previously identified in the literature (Barçante et al. 2017), as the behavior is largely understudied among bird species. The higher proportion may also result from the ability of our approach to comprehensively detect fine-scaled shifts in birds' elevational distributions. This study used seasonal shifts in a species' distributional center, as well as the lower and upper boundaries, along elevations to characterize the behavior. Taking advantage of the extensive occurrence records collected across elevations by citizen scientists, our approach was able to detect very small, but consistent, seasonal population movements along elevations (Supplementary material Appendix 1 Table A1). While conventional sampling approaches may not have such fine resolution (but see Wiegardt et al. 2017), we also found no standard approach or clear movement distance criteria for defining altitudinal migration. At what point seasonal movement along elevations makes the behavior biologically or ecologically meaningful needs further studies. However, the unclear criterion did not compromise our findings of potential drivers because we considered the behavior as a continuum between residency and migration in the analysis.

Our results suggested that seasonal variations in climates and food availability could be major drivers of post-breeding downhill migration among the resident birds in Taiwan. Consistent with previous studies (Boyle et al. 2010, Boyle 2011) and the predictions of the climatic constraint hypothesis (Table 1), we found that bird species incapable of enduring climate fluctuations, including those with a narrow range of temperatures that they experienced or with a small body size, tended to shift their distributions, especially the center of their distributions, to lower elevations in winter (Fig. 3d–f, Supplementary material Appendix 1 Fig. A5d–f). However, we also found that the species that can tolerate lower temperatures had a stronger downhill migration tendency during the non-breeding season (Fig. 3d–f, Supplementary material Appendix 1 Fig. A5d–f), which is opposite to the hypothesis' prediction. This result may suggest that better cold tolerance allows a species to breed at higher elevations to avoid stronger competition for breeding resources at lower elevations (Gillis et al. 2008, Green et al. 2015), because the lower temperature limit had a strong negative correlation with the elevation of species' distributional center in the breeding season (Pearson's correlation coefficient ranges from −0.64 to −0.57 with the six resampling settings). Better cold tolerance may also be associated with temperate species (e.g. coal tit and Eurasian nutcracker), which may prefer colder breeding grounds. As far as we know, our study is the first to show that species that are able to tolerate lower temperatures may move further uphill to breed and have a higher tendency to be downhill migrants due to harsh climates at higher elevations in winter.

Consistent with the predictions of the food availability hypothesis (Table 1), we found that the species eating more fruits and nectar or invertebrates tended to shift their lower distribution boundary downhill in winter (Fig. 3d, Supplementary material Appendix 1 Fig. A5d). The associations suggest that a reduction in the availability of those food types at higher elevations in winter may drive those species to move to lower elevations, as have been found in previous studies (Loiselle and Blake 1991, Solórzano et al. 2000). However, we also found that dietary generalists, but not specialists, had a higher tendency to move their distributional center downhill, which is opposite to the expectation (Boyle et al. 2011). This may be because more diverse diets allow birds to utilize different habitats along elevations and thus to be able to conduct altitudinal migration. It is also possible that the needs of different food types during different periods of birds' annual cycles, as has been found in long-distance migratory birds (Hahn et al. 2013), may drive the elevational movement. The fact that all five species known to switch their diets between insects during the breeding season and plants during the non-breeding season (Shiu and Lee 2003) – including small vivid niltava, white-eared sibia and Taiwan yuhina – are altitudinal migrants (Supplementary material Appendix 1 Table A1) may provide some support for the explanations.

Our results showed weak support for the nest predation hypothesis, as we only found significant associations between the use of open nests and high migration tendencies under a few resampling settings (Fig. 3 and Supplementary material Appendix 1 Fig. A5). However, many other factors, such as the height of a nest site (Söderström et al. 1998, Djomo Nana et al. 2015) and the vegetation characteristics at and around a nest site (Johnson and Temple 1990), could also influence nest predation risk. In addition, the assumptions behind the prediction of this hypothesis may not be always valid as the relationship between nest structure and nest predation is controversial (Martin et al. 2017) and the nest predation risk is not necessarily higher at lower elevations (Boyle 2008b). Therefore, studies with direct measurements of nest predation risk at different elevations are needed to better evaluate the importance of nest predation in driving avian altitudinal migration.

While the hypotheses can partially explain the variation in post-breeding downhill migration patterns among the bird species, none of them can well explain the uphill migration patterns (Table 1). This indicates a significant knowledge gap, especially because we found that around 23% of the altitudinal migrants identified in the study tended to move uphill in winter (Supplementary material Appendix 1 Table A1). This proportion is similar to the finding of a previous literature review (Boyle 2017), which shows that around 25% of 163 altitudinal migrants in North America probably breed at lower elevations than where they spend the winter. The lack of strong associations between the traits and uphill distribution shifts in our study may be because there is no general driver of post-breeding uphill migration among the bird species, given the large variation in the patterns among species (Fig. 2). It is also possible that the current main hypotheses or the traits examined in this study failed to cover important drivers. For example, energetic demands of post-breeding molt or limited capacity for thermoregulation (Schieltz and Murphy 1997) and flight (Hedenström and Sunada 1999) during molt may drive birds to perform uphill movement (Wiegardt et al. 2017). In addition, interspecific competition for energy has also been suggested to be an important driver of long-distance bird migration (Somveille et al. 2018). Similarly, intraspecific competition can be an important driver of the partial altitudinal migration (Mackas et al. 2010, Green et al. 2015). As more than 180 long-distance migratory bird species visit Taiwan every winter (CWBF 2017) and most of them stay at low and medium elevations (Shiu and Lee 2003), it is very likely that competition with abundant long-distance migratory birds forces some resident species to move to higher elevations in winter. In fact, the finding of an aggregation of post-breeding uphill migrants at medium-low elevations (Fig. 2) supports the hypothesized interspecific competition effect. Given our poor understanding of the biotic interactions between migratory species (Cohen and Satterfield. 2020), this hypothesis warrants further and more rigorous studies.

Our analyses on the associations between birds' traits and their seasonal distribution shifts can help identify potential drivers of altitudinal migration because consistency between the observed and predicted associations may suggest that the driver involved in the hypothesized mechanism has significant and consistent effects on the observed patterns. However, these analyses cannot directly test the hypotheses because the variables included in the models were just proxies of the traits involved in the mechanisms (e.g. the temperatures where species occur as a proxy for their thermal tolerance). In addition, some traits only indirectly link to the mechanisms under some assumptions, which may not be always valid. For example, some studies have found that a species' thermal tolerance cannot explain its elevational distribution, at least for some tropical birds (Freeman 2016, Londoño et al. 2017). Therefore, while this study identified several potential drivers and proposed new hypotheses based on the novel patterns revealed, further studies with direct measurements of the components in a mechanism (e.g. thermal tolerance of species and seasonal variation in food resources along elevations) are needed to understand the true mechanisms.

This study developed a new approach, which revealed many interesting patterns worthy of further investigation; however, this approach is not without limitations. First, our approach is based on citizen science data, which present many challenges for applications (Dickinson et al. 2010). The primary challenges associated with eBird data include the taxonomic bias, spatial bias, temporal bias, imprecise spatial information and variation in detectability (Strimas-Mackey et al. 2020). Our approach addresses those challenges by using only the complete checklists, using spatial and temporal resampling, excluding the data potentially with uncertain spatial information, and subsetting the data to reduce the effects of variation in sampling efforts on detectability. Because the purpose of our approach is to characterize the general patterns across a large number of species, we did not explicitly model the detection probability for individual species using data-intensive approaches suggested by Strimas-Mackey et al. (2020), which would restrict our analyses to only a few species with abundant data. However, with all those potential biases being addressed, we believe that our approach is robust and our findings were not significantly affected by those biases.

Second, because our approach is based on population-level information, other behaviors that change population distributions (e.g. nomadic movement and natal dispersal) may be incorrectly read as migration. However, as our approach compiled multiple-year data for each season, we believe that a consistent shift in the distributional center or the boundaries observed among resampled datasets indicates a repeated behavior. Finally, our approach requires a large number of observations along an elevational gradient. This makes the approach currently inapplicable in many mountain regions around the world and difficult to examine spatial variability in the altitudinal migration patterns due to a lack of sufficient observations. However, as citizen science continues to strive, a rapid accumulation of available data on species occurrences (e.g. more than 140 million records were added into eBird in 2019 alone; eBird 2019) will greatly extend the applicability of our approach in the very near future. For example, with sufficient data, our approach can further reveal the variation in a species' migration behavior among years to determine whether the behavior is facultative or obligate or whether the behavior changes in response to the weather in a particular year, which will help fill the knowledge gaps on the important but understudied behavior.

In this study, we attempted to answer an old question using a novel approach with an unconventional dataset. Based on a vast number of observations with broad spatial and taxonomic coverage and fine temporal scales collected by citizen scientists, we, for the first time, characterized the altitudinal migration patterns and investigated general drivers for a majority of an entire resident bird community. More importantly, this study demonstrated the power of citizen science data to not only tackle broad and general altitudinal migration patterns and mechanisms, but also help reveal previously undiscovered patterns that can lead to new hypotheses on mechanisms. In the face of rapid environmental changes in mountain ecosystems, new insights into altitudinal migration obtained through the novel and generalizable approach may provide essential information for the conservation of mountainous biodiversity.

Data availability statement

Data and code are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.hdr7sqvg1> (Tsai et al. 2020b).

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Conflicts of interest – The authors declare that there is no conflict of interest.

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