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ARTICLE

Rapid southward and upward range expansion of a tropical songbird, the Thrush-like Wren (*Campylorhynchus turdinus*), in South America: a consequence of habitat or climate change?

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ABSTRACT: The Thrush-like Wren (*Campylorhynchus turdinus*) is a polytypic, non-migratory, cooperatively breeding species of bird widely distributed in central South America. In recent decades it has expanded its range by approximately 24%, based on a published map of its distribution in the mid-1980s and recent reports submitted to eBird up through March 2017. The northwestern subspecies, *C. t. hypostictus*, dramatically expanded its elevation range upward from approximately 1200 m to 4200 m a.s.l. in the Peruvian Andes. During 1977–2015 the southwestern subspecies, *C. t. unicolor*, dramatically expanded the southern border of its range from central Brazil and northern Paraguay (approximately 22°06'S) southward into northeastern Argentina and throughout Paraguay to 29°40'S in southeastern Brazil, extending its range east-southeast approximately 934 km at a rate of 24.6 km/yr, and latitudinally southward 838 km at a rate of 22.1 km/yr. It also expanded its range westward into the relatively dry Chaco of western Paraguay and north-central Argentina. Midwinter records near the southern border of its range in northeastern Argentina suggest it is non-migratory. Because of its affinity for disturbed habitats, its range expansion has been attributed to deforestation, but its range expansion is also consistent with the prediction that organisms are extending their geographic distribution toward higher latitudes and elevations as a consequence of climate change.

KEY-WORDS: Argentina, Brazil, Colombia, distribution, elevation, global warming, Paraguay, Peru.

INTRODUCTION

Because birds are abundant and conspicuous organisms that can be easily monitored, they represent ideal bellwethers for the impacts of anthropogenic habitat change and climate change on biodiversity (Morrison 1986, Hutto 1998). Short-term changes in the distributional ranges of birds are usually caused by stochastic population fluctuations or habitat change, but may also be attributed to climate change (Parmesan & Yohe 2003, Root *et al.* 2003, Hickling *et al.* 2006, Parmesan 2006, Chen *et al.* 2011). Birds may respond to recent increases in temperature and changes in precipitation by either attempting to adapt to changes *in situ* or by spatially shifting their distribution to areas with more optimal conditions (Huntley *et al.* 2006). Distributional shifts toward higher latitudes and elevations, in concert with phenological shifts toward earlier breeding, occur globally across a wide array of taxonomic groups, providing a fingerprint of climate change (Parmesan & Yohe 2003, Root *et al.* 2003, Hickling *et al.* 2006, Parmesan 2006, Chen *et al.* 2011). For example, analyses of the breeding ranges of birds in the temperate northern hemisphere reveal that they are shifting northward at an average rate of 2.4 km/year in North America (Hitch & Leberg 2007), 1.6 km/year in Finland (Brommer 2004), and 1.0 km/year in Britain (Thomas & Lennon 1999). The winter ranges of temperate North American birds are also shifting northward at an average rate of about 1.5 km/year (La Sorte & Thompson-III 2007).

Distributional range shifts by birds in the southern hemisphere are not as well documented, but many species of birds in South Africa and some in Australia appear to be rapidly expanding their ranges southward (Chambers *et al.* 2005, Olsen 2007, Hockey *et al.* 2011). In South America, several tropical bird species appear to be rapidly expanding their ranges southward into subtropical Argentina, Paraguay, and Brazil (*e.g.*, Straube *et al.* 2006, 2007, Piacentini *et al.* 2009, del Castillo *et al.* 2012, Pagano & Bodrati 2017). And several species of birds appear to be rapidly expanding their ranges upward in elevation in the Andes (*e.g.*, Henry 2005,

2012, Solano-Ugalde & Real-Jibaja 2010, Gibbons *et al.* 2011, Avendaño *et al.* 2013). The driver of such rapid changes in bird distribution in South America is usually attributed to habitat change, even though such changes are predicted by a warming climate (Parmesan & Yohe 2003, Root *et al.* 2003, Hickling *et al.* 2006, Parmesan 2006, Jetz *et al.* 2007, Chen *et al.* 2011). More detailed analyses of individual species are needed to assess the validity of claims that distributional ranges are shifting toward higher latitudes and elevations, and to document the rate of change. In this paper we document unusually rapid range expansion, both southward and upward in elevation, in a tropical songbird, providing evidence that climate change in addition to (or instead of) habitat change may be accelerating its range expansion.

METHODS

Study subject

The Thrush-like Wren (*Campylorhynchus turdinus*) is a polytypic species of the avian family Troglodytidae with three distinct subspecies inhabiting tropical South America (Hellmayr 1934, Ridgely & Tudor 1989, Kroodsma & Brewer 2005). The northwestern subspecies, *C. t. hypostictus*, occurs from the east slope of the Andes of Colombia, Ecuador, Peru, and northern Bolivia eastward through Amazonian Brazil. The southwestern subspecies, *C. t. unicolor*, occurs in the lowlands of Bolivia, Paraguay, and southwestern Brazil (Ridgely & Tudor 1989, Kroodsma & Brewer 2005), but has recently expanded its range southward into northern Argentina (Contreras & Contreras 1986) and southeastern Brazil (Bencke *et al.* 2008). The eastern subspecies, nominate *C. t. turdinus*, occurs in a disjunct population along the coast of eastern Brazil.

Data gathering

To document the southward and upward range expansion of *C. turdinus*, we reviewed published distributional records and unpublished reports submitted to eBird (ebird.org) through mid-March 2017. The latitude and longitude of each location were obtained from the original source or, if absent, estimated by consulting either an ornithological gazetteer for each country (Paynter-Jr. & Traylor 1981, 1991, Stephens & Traylor-Jr. 1983, Paynter-Jr. 1985, 1989) or Google Earth (www.google.com/earth). The elevation of each location was obtained from the original source. Using ArcGIS software (www.arcgis.com), we constructed maps and calculated the area (km^2) of its range in the 1980s, based on Ridgely & Tudor (1989), and the area of its current range, based on reports submitted to eBird through March 2017 plus the southernmost record published by Vargas-Peixoto & Bosholn (2016). Google Earth was used to measure the rate of range expansion as a straight line between two points and in a southward line between degrees of latitude.

RESULTS

A comparison of the past and present ranges of *C. turdinus* revealed that its range has expanded by about 24% (Fig. 1), from approximately 4,329,243 km^2 in the mid-1980s (Ridgely & Tudor 1989) to approximately 5,671,727 km^2 by March 2017 (eBird). In the following accounts we describe its range expansion by country.

Colombia

Although the northwestern subspecies, *C. t. hypostictus*, has not expanded its range northward, it has expanded its range northeastward along the Inírida River and Guaviare River in Guaviare (eBird; Fig. 1). The northeasternmost record is from Guainía-Puerto Inírida (04°01'S; 67°45'W), only about 5 km west of the Venezuelan border, on 24 August 2016 (Valerie La May, Marie Lister & Warren Stevens in eBird).

Peru

The northwestern subspecies, *C. t. hypostictus*, has expanded its range westward up into the Peruvian Andes. Fjeldså & Krabbe (1990) did not include it in their book on birds of the Andes because it had not been recorded in the temperate zone above 2300 m a.s.l. Ridgely & Tudor (1989) reported its maximum elevation range along the east slopes of the Andes as 1200 m a.s.l., which was repeated by Clements & Shany (2001). In 1998, Hornbuckle (1999) reported it at a site with an elevation range of 1300–1600 m a.s.l. east of Abra Patricia Pass, San Martín (05°41'S; 77°41'W), which may account for Kroodsma & Brewer (2005) reporting its maximum elevation as 1300 m a.s.l. Schulenberg *et al.* (2007) reported it occurring up to 1500 m a.s.l. In 2009, Robbins *et al.* (2011) observed it at an elevation of about 1700 m a.s.l. at Alto Materiato, Cusco (12°42'S; 72°53'W). It has now expanded its distribution dramatically upward to well over 3000 m a.s.l. in Cusco (several 2016 records in eBird), with a maximum elevation of about 4200 m a.s.l. at ACP Ábra Málaga Thastayoc, Cusco (13°09'S; 72°18'W), on 18 October 2014 (Celeste Morien in eBird).

Paraguay

The first record of *C. turdinus* in Paraguay was a specimen collected in 1928 on the west bank of the upper Paraguay

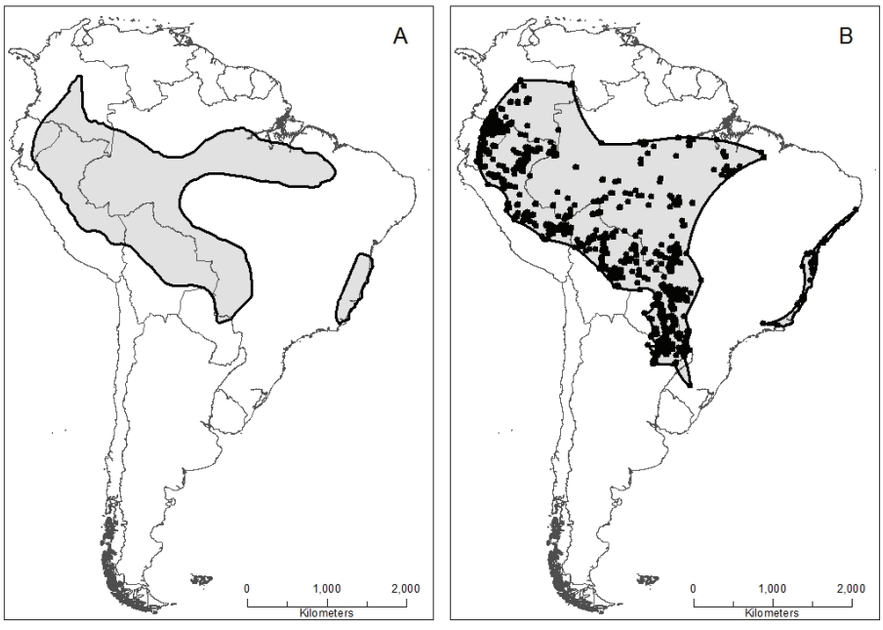

Figure 1. The known distribution of the Thrush-like Wren (*Campylorhynchus turdinus*) in the mid-1980s (**A**), based on Ridgely & Tudor (1989), and in February 2017 (**B**), based on observations reported to eBird (ebird.org) and Vargas-Peixoto & Bosholn (2016).

River at Puerto Guaraní in southeastern Alto Paraguay (21°17'S; 57°55'W; Zotta 1940). Given the paucity of specimen records at the time from the upper Paraguay River region, it remains uncertain whether the specimen was within the ancestral range of the species or represented an actively expanding population.

In July 1977, Robert Ridgely observed several along the Apa River in northern Concepción (Ridgely & Tudor 1989). The specific locality was not reported, so we assume it was in the vicinity of San Lázaro in northwestern Concepción (22°06'S; 57°58'W), which was relatively accessible at the time. By 1988 and 1989 *C. turdinus* had become common along both banks of the Paraguay River as far south as Puerto Militar (formerly Villa Militar) in northeastern Presidente Hayes (23°24'S; 57°28'W) and Concepción in western Concepción (23°24'S; 57°26'W; Hayes *et al.* 1990). Nesting was subsequently confirmed at Puerto Militar in 1991 (Contreras *et al.* 1993). Because no *C. turdinus* had been collected during extensive field work resulting in the collection of perhaps more than a thousand bird specimens in southeastern Alto Paraguay (*e.g.*, Puerto La Victoria, formerly Puerto Casado; 22°17'S; 57°57'W), northeastern Presidente Hayes (*e.g.*, Puerto Pinasco; 22°43'S; 57°57'W), and northern Concepción (*e.g.*, Apa River; 22°05'S) up through 1945 (Paynter-Jr. 1989, Hayes 1995), all records south of 22°S almost certainly represented a subsequent range expansion rather than a previously undetected population.

In 1986 a specimen was collected 140 km west of the Paraguay River at Pozo Colorado in central Presidente Hayes (23°25'S; 58°50'W; Contreras & Contreras 1986), in a region of the Paraguayan Chaco where a few thousand bird specimens, but none of *C. turdinus*, had been collected prior to 1975 (Hayes 1995). Numerous individuals were seen in the area, indicating a population had recently become established. The first record for southern Presidente Hayes occurred at Estancia La Golondrina (24°59'S; 57°43'W) during 6–9 November 1995 (James Lowen). It is now widespread throughout the eastern Paraguayan Chaco (eBird).

On 16 July 1993, one was observed on the east side of the Paraguay River 5 km east of Villeta in western Central (25°30'S; 57°31'W; Contreras *et al.* 1993), providing the first record for southern Paraguay. The first for Bahía de Asunción, Central, which had been frequently visited by ornithologists since 1987, was noted in October 1998 (H.C., unpub. data).

In subsequent years *C. turdinus* spread rapidly throughout eastern Paraguay (eBird), although the first department records occurred sporadically rather than progressively southward. During 3–4 October 1989, six were observed at Puerto Olivares (25°09'S; 57°15'W), providing the first record for Cordillera (Paul Scharf). One was observed during 4–5 May 1990 somewhere between Curuguaty (24°35'S; 55°25'W) and Colonia Nueva Durango (24°15'S; 55°50'W), representing the first record for Canendiyú (Paul Scharf). On 8 June 1999 it was recorded at Ybytyruzú (25°50'S; 56°13'W), providing the first record for Guairá (Guyra Paraguay, in eBird). The first record for San Pedro occurred on 23 January 2000 at Laguna Blanca (23°49'S; 56°17'W; Guyra Paraguay in eBird). By 2000 it appeared in several areas of Alto Paraná, including Presidente Franco (27°03'S; 58°37'W; Nelson Pérez in Savigny 2010). On

22 January 2005 it was observed at Mamoreí (26°23'S; 57°02'W), representing the first record for Paraguarí (Guyra Paraguay in eBird). The first record for Amambay occurred on 24 March 2005, when it was noted south of Bella Vista Norte (22°10'S; 56°30'W; Guyra Paraguay in eBird). In 2005 it was observed at Estancia Tapytá (26°14'S; 55°58'W), providing the first record for Caazapá (Velázquez *et al.* 2016). The first records for Itapúa occurred on 18 February 2006 in the vicinity of Estación Biológica Kanguery (26°26'S; 55°48'W; Guyra Paraguay in eBird). During 2–4 February 2010 it was recorded at Estancia La Graciela (26°35'S; 56°49'W), providing the first record for Misiones (Silvia Centrón & Cristina Morales). By 2012 multiple *C. turdinus* had reached the southern border of Paraguay at Encarnación in southern Itapúa (27°21'S; 55°52'W; Smith *et al.* 2013). It was not recorded in Caaguazú until 9 January 2013, when it was reported from Rancho Rosalba (25°15'S; 56°17'W; A. Lesterhuis in eBird). The first record for Ñeembucú occurred on 16 September 2014, when one was observed at Humaitá (27°04'S; 58°30'W; Sergio Rios in eBird), in southwestern Paraguay.

In addition to expanding its range southward and eastward, *C. turdinus* has also expanded its range westward, albeit more slowly, into the dry Alto Chaco region of western Paraguay. The first record for Boquerón comprised a pair observed at Estancia Teniente Montania in eastern Boquerón (21°57'S; 60°07'W), representing the westernmost record in Paraguay, on 29 September 2016 (Alberto Esquivel in eBird).

Argentina

Dabbene (1910) reported a specimen collected in 1880 from Córdoba in Córdoba (31°24'S; 64°11'W), but Hellmayr (1934, p. 135) stated that the locality "can hardly be correct" and Zotta (1940) concurred. Thus, a sight record by Pablo Canevari at Parque Nacional Río Pilcomayo (25°04'S; 58°09'W) in eastern Formosa (Contreras & Contreras 1986) provided the first accepted record for Argentina. Unfortunately the date of Canevari's observation was not published, not even in his own book (Canevari *et al.* 1991), but occurred no later than the publication of Contreras & Contreras (1986). Canevari's sighting was subsequently verified by sightings of multiple birds in 1988 (Finch 1991) and 1993 (Fortabat *et al.* 1995). Canevari's sighting represented a remarkable southward range extension of at least 330 km since Ridgely's observations in 1977 along the Apa River of Paraguay (Ridgely & Tudor 1989). Assuming Canevari's sighting was in the year 1986, *C. turdinus* had extended its range southward at a rate of 36.7 km/yr from 1977–1986.

In subsequent decades *C. turdinus* continued to disperse southward in the Argentinian Chaco. In September 2009, two vocalizing *C. turdinus* were observed at Puerto Las Palmas in eastern Chaco (27°03'S; 58°37'W; Bodrati *et al.* 2012). On 6 October 2016 a group of eight was building a nest at Isla del Cerrito in eastern Chaco (27°17'S; 58°37'W; Pagano & Bodrati 2016). And on 10 October 2012, two were observed at Puerto Antequeras in eastern Chaco (27°27'S; 58°51'W; Fabricio Gorleri in eBird), providing the southernmost record for Argentina. Since Ridgely's observations in 1977 along the Apa River of Paraguay (Ridgely & Tudor 1989), *C. turdinus* extended its range slightly west of south about 595 km at a rate of 17.1 km/yr and southward 593 km at a rate of 17 km/yr. And since its first arrival in the Argentinian Chaco in about 1986 (Contreras & Contreras 1986), *C. turdinus* extended its range slightly west of south 274 km at a rate of about 10.5 km/yr and southward 265 km at a rate of 10.2 km/yr.

The first record in northeastern Argentina occurred on 23 May 2003, when three *C. turdinus* were observed at Puerto Iguazú, Misiones (25°37'S; 54°35'W; Rey & Zurita 2004). The southernmost records from northeastern Argentina are from Posadas, Misiones (27°23'S; 55°57'W), where it was reported in four localities in 2016 (eBird).

In addition to expanding its range southward and eastward, *C. turdinus* continues to expand its range westward into the dry Argentinian Chaco, with the westernmost record at Bartolomé de las Casas, Formosa (25°24'S; 59°35'W), on 14 December 2016 (Sebastán Dardanelli in eBird).

There are midwinter records from July near the southernmost extent of its range at Posadas (Joel Martínez in eBird), suggesting that the southernmost populations are non-migratory or, possibly, partially migratory.

Brazil

In central Brazil, *C. turdinus* has expanded its range into the gap between Pará and Mato Grosso do Sul states since the 1980s (Fig. 1), but it is unclear whether the northwestern subspecies *C. t. hypostictus* or the southwestern subspecies *C. t. unicolor* inhabits this area.

In the isolated population along the coast of eastern Brazil, nominate *C. t. turdinus* has not expanded its range southward, but it has expanded its range northward (Fig. 1). The northernmost record is from Reserva Biológico de Saltinho, Pernambuco, Brazil (8°44'S; 35°11'W), on 30 October 2013 (Forest Rowland in eBird).

In 1941, a specimen of *C. t. unicolor* was collected on the east bank of the Paraguay River at Pôrto Quebracho (21°50'S; 57°53'W), in southwest Mato Grosso do Sul (Contreras *et al.* 1993), representing the southwesternmost record for Brazil (Naumburg 1930,

Hellmayr 1934). This locality is about 60 km south of where the nearest specimen had been previously collected at Puerto Guaraní (21°17'S), Paraguay. Again, given the paucity of specimen records at the time from the upper Paraguay River region, it remains uncertain whether the specimen was within the ancestral range of the species or represented an actively expanding population.

Farther south, in southern Rio Grande do Sul, Helmut Sick (in Belton 1985) reported hearing a *C. turdinus* vocalizing at Fazenda da Invernada (31°05'S; 52°52'W), on 25 November 1972. According to Belton (1985, p. 105), Sick felt "absolutely sure of it, as voice is very easy to recognize with nothing similar to it". Nevertheless, the record was considered unreliable and rejected by Bencke *et al.* (2010). In 2008, a singing *C. turdinus* was heard at Foz do Iguaçu in central Paraná (25°37'S; 54°29'W; Bencke *et al.* 2008). A remarkable range extension occurred in 2015, when a singing *C. turdinus* was photographed at Santa Maria in central Rio Grande do Sul (29°40'S; 53°48'W; Vargas-Peixoto & Bosholn 2016), providing the southernmost confirmed record for the species. Although the authors did not assign it to a subspecies, photographs reveal the bird's unspotted creamy underparts, which are typical of *C. t. unicolor*, contrasting with the spotted underparts of nominate *C. t. turdinus* of coastal eastern Brazil (Ridgely & Tudor 1989, Sick 1993). Since Ridgely's observations in 1977 along the Apa River of Paraguay (Ridgely & Tudor 1989), by 2015 *C. turdinus* had extended its range slightly east of south 934 km at a rate of 24.6 km/yr and southward 841 km at a rate of 22.1 km/yr (Fig. 2).

DISCUSSION

Campylorhynchus turdinus is just one of several tropical bird species in southern South America that is rapidly expanding its range southward into subtropical latitudes (*e.g.*, Straube *et al.* 2006, 2007, Piacentini *et al.* 2009, del Castillo *et al.* 2012, Pagano & Bodrati 2017). Vagrancy, the long-distance dispersal of individuals beyond their normal distribution or migratory path (*e.g.*, Thomson 1964, Veit 2000), occurs less frequently among non-migratory than migratory species of birds (Lees & Gilroy 2009). Data from eBird indicate that *C. turdinus* occurs near its southernmost limit in Argentina throughout the winter, indicating that it is non-migratory or, possibly, partially migratory. Vagrancy was thought to occur less frequently among cooperatively breeding than among non-cooperatively breeding species of birds (Zack 1990), but Rusk *et al.* (2013) provided evidence that vagrancy occurs just as frequently in cooperatively breeding species. Rabenold (1990) reported that *C. turdinus* breeds cooperatively, although no data have been published. Despite its apparent non-migratory and cooperatively breeding habits, long-distance vagrancy appears to be a life history trait in *C. turdinus*, and is presumably increasing as a consequence of rapid demographic population growth (Veit 2000).

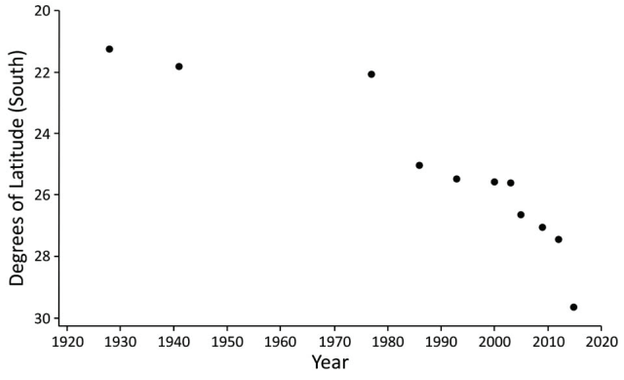

Figure 2. Southward range expansion of the Thrush-like Wren (*Campylorhynchus turdinus*) illustrated by the southernmost record *vs.* year, based on data in the Results section.

It is difficult to attribute changes in the spatial distribution of any single species to either habitat or climate change. Because of its affinity for disturbed habitats, *C. turdinus*'s rapid southward range expansion has been attributed to deforestation (Rey & Zurita 2004, Bodrati *et al.* 2012). The subtropical moist broadleaf forests of eastern Paraguay, southern Brazil, and northeastern Argentina have been subjected to extensive deforestation in recent decades (Hansen & DeFries 2004, Fleytas 2007, Huang *et al.* 2007, Aide *et al.* 2013, Hansen *et al.* 2013), plausibly facilitating the southward range expansion of *C. tudinus*. However, the rate of deforestation on the east slopes of the Andes, including the region east of Cusco, Peru, has been considerably slower (Aide *et al.* 2013, Zegarra & Gayoso 2015), suggesting that habitat change may not adequately account for the rapid upward range expansion of *C. turdinus* in Cusco, Peru.

The rapid range expansion of *C. turdinus* both southward and upward is consistent with the prediction that organisms are extending their geographic distribution toward higher latitudes and elevations as a consequence of global warming (Parmesan & Yohe 2003, Root *et al.* 2003, Hickling *et al.* 2006, Parmesan 2006, Chen *et al.* 2011). The region in which *C. turdinus* is expanding its range southward in southern South America is warming relatively rapidly (Easterling *et al.* 1997, Rosenblüth *et al.* 1997, Vincent *et al.* 2005). Because the northern boundaries of North American songbirds appear to be limited by winter nighttime temperatures (Root 1988), the southern boundaries of South American songbirds may also be limited by winter nighttime temperatures. If so, songbirds in southern South America may be able to extend their ranges southward as winter nighttime temperatures increase, which may be the case with *C. turdinus* and several other species of birds in southern

South America (*e.g.*, Straube *et al.* 2006, 2007, Piacentini *et al.* 2009, del Castillo *et al.* 2012, Pagano & Bodrati 2017). However, temperatures are not rising much in the Peruvian Andes (Easterling *et al.* 1997, Vincent *et al.* 2005), suggesting that climate change may not adequately account for the rapid upward range expansion of *C. turdinus* in Cusco, Peru. Perhaps habitat change and climate change combined best accounts for its rapid upward range expansion in Cusco, Peru.

Because tropical species of birds tend to have relatively small distributional ranges resulting in a high degree of endemicity, and occur in climatically stable environments where they tend to be K-selected with greater longevity and smaller clutch sizes, resulting in lower demographic flexibility, they are thought to be more vulnerable to anthropogenic changes in habitat and climate than temperate species of birds (Jetz *et al.* 2007, Şekercioğlu *et al.* 2012, Reif & Štěpánková 2016). Tropical birds may be adversely affected by climate change in many different ways, such as susceptibility to extreme weather events, habitat loss, emerging diseases, invasive species, and hunting (Jetz *et al.* 2007, Şekercioğlu *et al.* 2012, Botero 2015). Nevertheless, some tropical bird species, such as *C. turdinus*, may benefit from anthropogenic changes in the environment by expanding their ranges into disturbed habitats in response to habitat change or expanding their ranges toward higher latitudes and elevations in response to climate change. It remains uncertain which of these two drivers, or both combined, or if there is another yet to be identified, best explains the rapid range expansion of *C. turdinus*. More research is needed to evaluate whether range expansion southward and upward are general trends among a large number of bird species in South America, and what the drivers may be for such range expansion.

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