Isotopic niche overlap between the invasive leiothrix and potential native competitors

E. Pagani–Núñez, M. Renom, C. Furquet, J. Rodríguez, F. Llimona, J. C. Senar

Abstract

Isotopic niche overlap between the invasive leiothrix and potential native competitors. We analysed niche overlap between the red–billed leiothrix *Leiothrix lutea*, a spreading exotic invasive bird, and the European robin *Erithacus rubecula* and the blackcap *Sylvia atricapilla*, similar native species, which are commonly considered as potential competitors in Mediterranean forests. We analyzed stable isotope ratios (δ13C and δ15N) from feathers of birds sampled in several locations within the Collserola mountain range (Barcelona, NE Spain) where leiothrix have strongly increased their numbers in the last decade and quantified niche overlap with nicheROVER. Blackcap individuals showed the lowest probability to be found in the isotopic niche of the other two species (around 60 %), while leiothrix and robins showed a high probability to share the same isotopic niche (82 %). Our results stress that competition for resources is potentially high and the species shared marked niche asymmetries, which may have implications for community dynamics in the long term.

Key words: Interspecific competition, Niche overlap, Niche asymmetries, Red–billed leiothrix, Stable isotopes

Resumen

Solapamiento de nichos isotópicos entre el ruiseñor del Japón, invasivo, y los posibles competidores nativos. Analizamos el solapamiento de nichos entre el ruiseñor del Japón, *Leiothrix lutea*, que es un ave exótica invasiva en expansión, y el petirrojo europeo, *Erithacus rubecula*, y la curruca capirotada, *Sylvia atricapilla*, que son especies nativas parecidas que se suelen considerar competidores potenciales en los bosques mediterráneos. Analizamos la relación de isótopos (δ13C y δ15N) en las plumas de las aves capturadas en varios lugares dentro de la cordillera de Collserola (Barcelona, NE España) en los que la población de ruiseñor del Japón ha aumentado notablemente en el último decenio, y cuantificamos el solapamiento de nichos con nicheROVER. Los individuos de curruca presentaron la menor probabilidad de encontrarse en el nicho isotópico de las otras dos especies (alrededor del 60 %), mientras que el ruiseñor y el petirrojo mostraron una elevada probabilidad de compartir el mismo nicho isotópico (el 82 %). Nuestros resultados destacan que la competencia por los recursos puede ser elevada y que las especies comparten marcadas asimetrías de nichos, lo que puede tener consecuencias para la dinámica de comunidades a largo plazo.

Palabras clave: Competencia interespecífica, Solapamiento de nichos, Asimetrías de nichos, Ruiseñor del Japón, Isótopos estables

Emilio Pagani–Núñez, State Key Lab. of Biocontrol, Department of Ecology/School of Life Sciences, Sun Yat–sen University, No.135 West Xingang Road, 510275 Guangzhou, People's Republic of China.– María Renom, Juan Carlos Senar, Museu de Ciències Naturals de Barcelona, Psg. Picasso s/n., 08003 Barcelona, Spain.– Carles Furquet, Institut Català d'Ornitologia (ICO), Museu de Ciències Naturals de Barcelona, Psg. Picasso s/n., 08003 Barcelona, Spain.– Jordi Rodríguez, Grup d'Anellament Parus, Institut Català d'Ornitologia (ICO), c/ Salze 36, 08186 Lliçà d'Amunt, Barcelona, Spain.– Francesc Llimona, Estació Biològica Can Balasc, Consorci del Parc Natural de Collserola, ctra. de l'Església 92, 08017 Barcelona, Spain.

Corresponding author: Emilio Pagani–Núñez. E–mail: pemilio@mail.sysu.edu.cn

Introduction

Invasive species are a major threats to biodiversity (Lockwood et al., 2007; Kolar and Lodge, 2001) but they also offer an opportunity to study ecological and evolutionary processes (Mooney and Cleland, 2001). A topic of current interest is the process by which animals become successfully established in a newly invaded area and how they accommodate within the host community (Marsico et al., 2010; Henriksson et al., 2016; Sol and Maspons, 2016; Duncan et al., 2003). Two main hypotheses have been suggested: the competition hypothesis and the opportunistic hypothesiss (Duncan et al., 2003). The competition hypothesis suggests that the main factor facilitating successful colonization of novel environments is the superior competitive ability of the invader over native species (Duncan et al., 2003; Petren and Case, 1996; Duncan, 1997). This assumes that invasive and native species show high niche overlap, which may drive intense competition. The opportunistic hypothesis, however, proposes that the invading species does not compete with natives, but simply takes advantage of niche opportunities not used by native species (Duncan et al., 2003; Shea and Chesson, 2002; Batalha et al., 2013). However, it has been difficult to find clear empirical support for either of these hypotheses (Duncan et al., 2003).

The red–billed leiothrix *Leiothrix lutea* (hereinafter leiothrix) exemplifies this controversy. A worldwide–scale meta–analysis of avian exotic introductions identified the leiothrix as one of the bird species with the highest negative local impact on bird communities (Martin–Albarracin et al., 2015). This species has successfully invaded several regions, from Japan to Hawaii and SW Europe (Herrando et al., 2010; Male et al., 1998; Tojo and Nakamura, 2004; Pereira et al., 2017), while it is native to South Asia (from West Himalaya to South and Central China) (Collar et al., 2018). A recent work in the Iberian Peninsula, based on behavioural observations during foraging and on habitat use, concluded that leiothrix exhibited little niche overlap with most native species, and that this invasion had relatively few consequences for the populations of the other species (Vall–llosera et al., 2016). As a consequence, they suggested that the success of leiothrix in this area could be explained by the opportunistic hypothesis. However, another two works, also conducted in Iberia, used morphology, diet and exploratory behaviour to show a competitive advantage of leiothrix over native species rather than an opportunistic occupation of an empty ecological niche (Pereira et al., 2017). Behavioural observations also supported interference competition by an active displacement of native species such as European robins *Erithacus rubecula* and blackcaps *Sylvia atricapilla* through aggressive attacks of leiothrix (Pereira et al., 2018).

Discrepancy between the two hypotheses about the establishment of the leiothrix in Iberia probably lies in the different approaches used by different authors. However, resolving this discrepancy may have relevant consequences in the design of con-servation policies in the areas invaded by leiothrix. The aim of our work was therefore to shed new light on this controversy by using stable isotopes as an alternative approach. Trophic interactions are fundamental to study the impact of exotic on native species (David et al., 2017). Comparing the niches of invasive and native species in the invasion distribution range has been suggested as a good approach to assess the occurrence of interspecific competition (Cornell and Lawton, 1992). Analyses using stable isotopes ratios of $\delta^{13}C$ and $\delta^{15}N$, which are mostly indicative of habitat use and diet respectively (Pagani–Núñez et al., 2017), can help understand niche overlap over longer time spans than behavioural observations (Pagani–Núñez et al., 2017; Inger and Bearhop, 2008; Layman et al., 2012). Moreover, stable isotopes are commonly used to assess interspecific competition (see e.g. Karlson et al., 2015; Smith et al., 2017). This is why it has been suggested as a powerful tool to study niche overlap between native and invasive species (Jackson et al., 2012; Kamenova et al., 2017).

In this paper we compared the isotopic niche of the leiothrix with that of the European robin (hereinafter robin) and the blackcap, which have been identified as the two main native competitors of leiothrix in the Mediterranean area (Pereira et al., 2017). We assessed niche overlap among these species using nicheROVER, a new statistical tool developed by Swanson et al. (2015). This allowed us to contrast the competition and niche opportunity hypotheses in wild conditions and using the most advanced research techniques.

Material and methods

This study was carried out in the Natural Park of Collserola (45° 27' N, 2° 8' E; Catalonia, northeast Spain). Our study area may be characterized as Mediterranean mixed forest (Pagani–Núñez et al., 2014). The three main tree species were Aleppo pine *Pinus halepensis*, holm oak *Quercus ilex* and the oak *Q. cerrioides*. The first leiothrix was captured in this area on 14th July 1990 (La Espinagosa, Vallvidrera; C. Jordà, J. L. Copete and J. C. Senar, pers. obs.). Since then, the species has spread exponentially along the whole park, across forest and riverside zones, now reaching the close mountain range of Serra de Marina (Herrando et al., 2010). We used data from field surveys to illustrate and quantify this pattern (see below).

The study is based on 67 leiothrix, 43 robins and 20 blackcaps captured in the area using mist nets and funnel traps (Senar et al., 1997) between January and August 2013. We took the 5th most external tail feather of the right side of all individuals for laboratory analyses. Given the long sampling period, some of the sampled individuals had grown their feathers in 2012 and some in 2013, so we assessed year–related effects on our sample. There was a significant effect of year on $\delta^{13}C$, with $\delta^{13}C$ being more negative in 2013 than in 2012 feathers, but not on $\delta^{15}N$ (data

now shown). We thus extracted residuals of a model including $\delta^{13}C$ as the dependent variable and year as the categorical factor. We added average $\delta^{13}C$ to these residuals and obtained a standardized $\delta^{13}C$, which we used in our analysis.

The three species, leiothrix, robins and black-caps, make their nests in shrubs, have similar body sizes, and show a comparable low degree of sexual dimorphism (Tellería and Carbonell, 1999; Ellrich et al., 2010; Pagani–Núñez et al., 2013). They coexist throughout the year in this area and have generalist diets, feeding on fruit and small invertebrates (Herrera, 1998; pers. obs.). They also show similar moult strategies, with the three species carrying out a partial moult in their first year of life and a complete moult subsequently (see Jenni and Winkler (1994) for information on robins and blackcaps, further research is needed to confirm this pattern in leiothrix). They may differ, however, in their migratory strategies. Robins are partial migrants displaying short– to long–distance movements (Collar, 2018), although in our study area they are sedentary (pers. obs.). Blackcaps have both sedentary and short–distance migratory populations (Aymí et al., 2018), although in order to avoid trapping birds that had moulted away from our study area, most of our birds (18/20) were sampled during the breeding season. Leiothrix performs altitudinal migrations in its native distribution range (Collar et al., 2018; pers. obs.), but our invasive population seems fully resident (pers. obs.).

We performed stable isotopes analyses of tail feathers in 2014. Feathers were stored in cold conditions (–20 °C) within the shortest time possible after collection in the field. Tail feathers were cleaned in a solution of NaOH (0.25 M) and oven–dried at 40 °C for 12 hours. We analysed feather tips (Vitz and Rodewald, 2012), which were carefully extracted using sterilized metal scissors. These subsamples of 0.35 mg were loaded into tin recipients and crimped for combustion for both $\delta^{13}C$ and $\delta^{15}N$ analyses. We used an elemental analysis–isotope ratio mass spectrometry (EA–IRMS) with a Flash 1112 (for C and N) elemental analyzer coupled to a Delta C isotope ratio mass spectrometer via a CONFLOIII interface (Thermo Fisher Scientific, Bremen, Germany). We carried out the laboratory work at the Scientific Technical Services Department at the University of Barcelona. We expressed stable isotope ratios as parts per thousand (%), according to the following equation:

$$\delta X = [(R_{sample}/R_{standard})-1] * 1,000$$

where X is ^{13}C or ^{15}N and R is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$. We referenced our samples against international standards: Pee Dee Belemnite (VPDB) for 13C, atmospheric nitrogen (AIR) for ^{15}N. The measurement precisions were 0.15 % for $\delta^{13}C$ and 0.25 % for $\delta^{15}N$.

We characterized population trends of this exotic population of leiothrix. We pooled data from transects in habitats where oaks and pines predominate, carried out in forest and riverine zones during and outside the breeding season. Each transect was carried out two times during the breeding season and two times during the wintering season in the same area of the Natural Park of Collserola where we collected the feathers. Transects had a length of 1.5 km and all the leiothrix seen or heard were recorded within 50 m from the observer. We included data from 1998, when the species was detected for first time in our study area, to 2014. We analysed differences in $\delta^{13}C$ and $\delta^{15}N$ values between the leiothrix, robins and blackcaps using an analysis of variance. We computed niche overlap and asymmetries between leiothrix and potential competitors using the R package nicheROVER v1.0 (Swanson et al., 2015). We estimated isotopic niches (a 95% probability region based on $\delta^{13}C$ and $\delta^{15}N$ isotopic values of feathers) as the probability to find an individual of one species in the isotopic niche of the other species. We carried out 1,000 runs with a probability level of alpha = 0.95. These analyses were carried out in R (R Development Core Team, 2014).

Results

Our data illustrate a marked pattern of population growth for leiothrix in our study area (fig. 1).

One–way analysis of variance showed significant differences in $\delta^{13}C$ values between the three species (SS = 6.9, $F_{2,127}$ = 4.37, P = 0.01) (fig. 2). Robins showed the least negative mean values of $\delta^{13}C$ (mean ± SD = –23.27 ± 0.70), followed by blackcaps (–23.35 ± 1.14), while leiothrix showed the most negative values (–23.75 ± 0.91). In the case of $\delta^{15}N$, inter–specific differences were close to significance (SS = 21.50, $F_{2,127}$ = 2.96, P = 0.05) (fig. 2). Blackcaps showed the highest mean values of $\delta^{15}N$ (3.90 ± 3.03), followed by leiothrix (2.89 ± 1.43), while robins displayed the lowest mean values (2.66 ± 1.91).

Blackcap individuals showed the lowest probability to be found in the niche regions of robins (66.15 %) and leiothrix (58.52 %), while these species showed an extremely high probability to be recorded in the blackcap niche region (98.73 % and 95.58 % respectively) (fig. 3). Leiothrix and robins showed a similarly high probability to be found in each other´s niche regions (leiothrix in robin's niche region 82.48 %, robin in leiothrix's niche region 82.89 %) (fig. 3).

Discussion

The comparison of isotopic niches between leiothrix, an exotic invasive species, and robins and blackcaps showed a considerable (> 80 %) niche overlap between leiothrix and robins. Blackcaps, on the other hand, showed the broadest niche and a low probability to be found in the niches of these two other species. The major difference between species was a $\delta^{15}N$ 1 ‰ higher in the blackcap, which suggests that this species consumed relatively more insects or insects of higher trophic levels (in opposition to fruits or in-
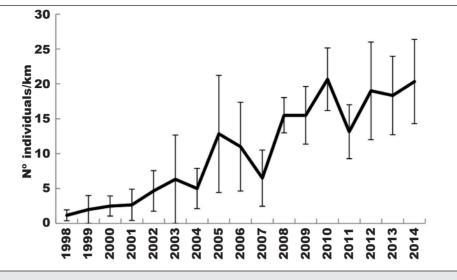
Fig. 1. Graph showing the progression in number of red–billed leiothrix *Leiothrix lutea* in our study area (Collserola Natural Park, Barcelona) over the last sixteen years based on lineal transects (values and means and standard error; n = 4 transects per year in each of the seven habitat types within Collserola Natural Park).

Fig. 1. Gráfico en el que se muestra la progresión del número de individuos del ruiseñor del Japón, Leiothrix lutea*, en la zona de estudio (Parque Natural de Collserola, Barcelona) durante los últimos 16 años, basada en transectos lineales (valores, medias y errores estándar; n = 4 transectos por año en cada uno de los siete tipos de hábitat del Parque Natural de Collserola).*
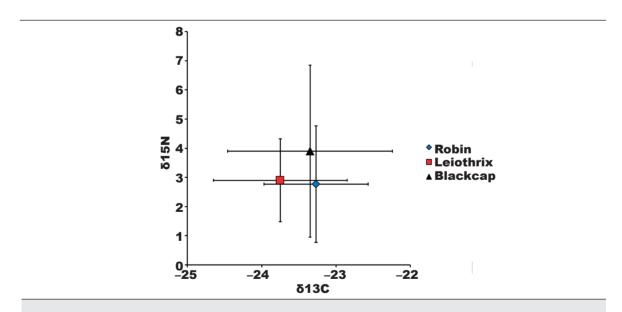

Fig. 2. Bi–plot showing δ13C and δ15N mean values (± standard deviation) in the 5th rectrix of the three species considered in this study. The red square corresponds to red–billed leiothrix *Leiothrix lutea* (n = 67), the blue diamond corresponds to European robins *Erithacus rubecula* (n = 43), and the black triangle to blackcaps *Sylvia atricapilla* (n = 20).

Fig. 2. Gráfico biplot en el que se muestran los valores medios de δ13C y δ15N (± desviación estándar) en la quinta rectriz de las tres especies analizadas en este estudio. El cuadro rojo corresponde al ruiseñor del Japón, Leiothrix lutea *(n = 67); el rombo azul, al petirrojo europeo,* Erithacus rubecula *(n = 43), y el triángulo negro, a la curruca capirotada,* Sylvia atricapilla *(n = 20).*
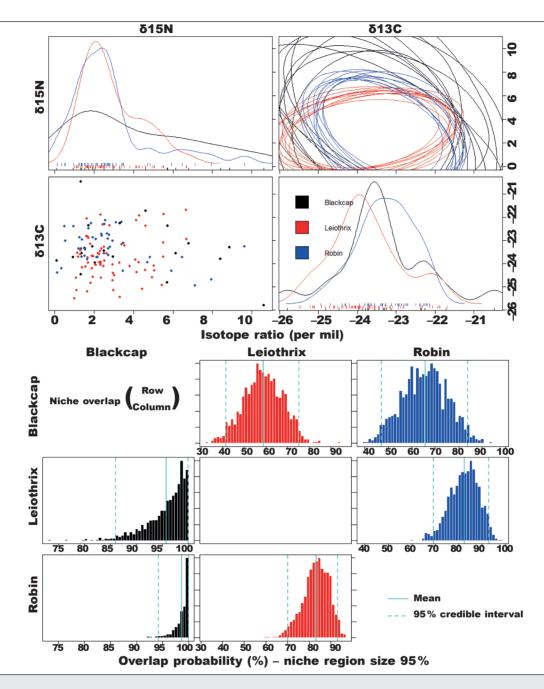
Fig. 3. Niche plots (random elliptical projections of trophic niche region for each species; up–right), density distributions (probability of the random variable to fall within the range of observed values; up–left: δ15N, down–right: δ13C), and raw data (down–left: scatterplot of δ13C vs δ15N) for the pairwise combination of δ13C and δ15N from feathers of red–billed leiothrix *Leiothrix lutea*, European robin *Erithacus rubecula* and blackcap *Sylvia atricapilla* (see Swanson et al. (2015) for a more detailed description). The numbers below the plots indicate the probability that an individual from the species indicated by row will be found within the niche of the species indicated by the column header.

Fig. 3. Gráficos de nicho (proyecciones elípticas aleatorias de la región del nicho trófico para cada especie; arriba a la derecha), distribuciones de densidad (probabilidad de que la variable aleatoria se encuentre en el intervalo de valores observados; arriba a la izquierda: δ15N, abajo a la derecha: δ13C), y datos no elaborados (abajo a la izquierda: diagrama de dispersión de δ13C y δ15N) para la combinación por pares de δ13C y δ15N de las plumas del ruiseñor del Japón, Leiothrix lutea, *el petirrojo europeo,* Erithacus rubecula, *y la curruca capirotada,* Sylvia atricapilla *(véase Swanson et al. (2015) para obtener una descripción más detallada). Los números que figuran debajo de los gráficos se refieren a la probabilidad de que un individuo de la especie indicada en el encabezamiento de la fila se encuentre en el nicho de la especie indicada en el encabezamiento de la columna.*

sects of lower trophic levels) than robins and leiothrix (see e.g., Pagani–Núñez et al., 2017). Given that during the winter there are fewer insects available, this may indicate a potential constraint for blackcap populations. This supports the view of Pereira et al. (2017), based on morphology, that the robin is the species that can potentially suffer from competition with leiothrix to a greater extent than other species. This high trophic overlap among these species suggests that leiothrix use similar niches to native species, rather than exploiting empty niches (Vall–llosera et al., 2016). Thus, our results also suggest that leiothrix's invasion success could be linked to its behavioural dominance over native species (Pereira et al., 2018).

However, although an overlap in diet is a potential source of competition, it does not always mean that competition occurs (Cody, 1974; Dhondt, 2012), but it may in fact be attenuated by different factors. First, the different species could exploit the shared resources at different times of year, decreasing or avoiding competence (León et al., 2014; Gidoin et al., 2015). Nevertheless, since the three species moult during the same period over a short time window, approximately from July to August (Jenni and Winkler, 1994; pers. obs.), the diet overlap inferred among the three species corresponds to the simultaneous use of resources by the three species. However, this does not rule out the possibility the diet of our study species differ in different periods of the year out of our study period, in which case the competence could be relaxed. This possibility could be addressed by analysing other tissues, such as blood or nails, which are renewed by the birds at a shorter and more constant turnover rates, reflecting the diet over periods of a month or less, prior to extraction (Inger and Bearhop, 2008; McKechnie, 2004: Layman et al., 2012).

This could also solve a drawback of our study, that in capturing some of the blackcaps and robins in winter, some of the individuals sampled could be migratory and have moulted in their breeding ranges; this could had broadened the isotopic niche of the species artificially. Nevertheless, this would not invalidate the results of our paper in that the robin highly overlapped in its diet with the leiothrix, and any sampling of non–resident birds would make our results more conservative. Moreover, most blackcap individuals were sampled during the breeding season (18 of 20), meaning that they were local birds, and most robins in the area are sedentary (pers. obs.).

A third factor that may attenuate competence between leiothrix and robin could be that although they have a similar diet, the two species could use different foraging techniques or substrate to find their prey. For instance, they may use different sections of the same trees (such as inner and outer branches) and leiothrix seem to have a more diverse array of foraging techniques than robins. This is clearly the case of leiothrix in Japan and to some degree in NE Spain (Vall–llosera et al., 2016; Tojo and Nakamura, 2004; Amano and Eguchi, 2002). Similarly, the competence between species could be reduced by the use of different subareas within the study area. In line

with this, we found that leiothrix displayed the lowest mean $\delta^{13}C$ values at the species level, which in our study area is indicative of foraging at valley bottoms (Pagani–Núñez et al., 2017). In fact, this is where most leiothrix were captured. However, the use of different areas or foraging techniques did not prevent the high levels of competence and negative impact of leiothrix on native species in Hawaii (Male et al., 1998; Mountainspring and Scott, 1985).

A fourth factor relates to the niche overlap hypothesis, which establishes that when resources are very abundant, potential competitors can tolerate a relatively high degree of overlap in resource use without experiencing critical levels of competition (Rusterholz, 1981). This could be the case in the Mediterranean area, where food resources for these species (e.g. insects and fruits) are very abundant (Blondel et al., 2010). This could additionally be enhanced by the generalist nature of this community (Vall–llosera et al., 2016).

To conclude, it is clear that the exotic invasive red–billed leiothrix shows high isotopic niche overlap with the European robin. However, further research is clearly needed to ascertain whether leiothrix success in these exotic locations is due to their high competitive ability, or to their capacity to expand their niches and to use particular features or resources of the invaded areas. Understanding this process may help us to prevent potential impacts of leiothrix on European forest birds.

Acknowledgements

References

Aymí, R., Gargallo, G., Christie, D. A., 2018. Eurasian Blackcap (*Sylvia atricapilla*). In: *Handbook of the Birds of the World Alive* (J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie, E. de Juana, E., Eds.). Lynx Edicions, Barcelona, https://www.hbw.com/node/58952 [Accessed on September 5, 2018].

Amano, H. E., Eguchi, K., 2002. Foraging niches of introduced Red–billed Leiothrix and native species in Japan. *Ornithological Science*, 1: 123–131.

Batalha, H. R., Ramos, J. A., Cardoso, G. C., 2013.

A successful avian invasion occupies a marginal ecological niche. *Acta OEcologica*, 49: 92–98.

Blondel, J., Aronson, J., Bodiou, J. Y., Boeuf, G., 2010. *The Mediterranean region: biological diversity in space and time*. Oxford University Press, Oxford.

Cody, M. L., 1974. *Competition and the structure of bird communities*. Princeton University Press, Princeton.

Collar, N., 2018. European Robin (*Erithacus rubecula*). In: *Handbook of the Birds of the World Alive* (J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie, E. de Juana, E., Eds.). Lynx Edicions, Barcelona, https://www.hbw.com/node/58952 [Accessed on September 5, 2018].

Collar, N., Robson, C., de Juana, E., 2018. Red–billed Leiothrix (*Leiothrix lutea*). In: *Handbook of the Birds of the World Alive* (J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie, E. de Juana, E., Eds.). Lynx Edicions, Barcelona, https://www.hbw.com/node/58952 [Accessed on September 5, 2018].

Cornell, H. V., Lawton, J. H., 1992. Species interactions, local and regional processes, and limits to the richness of ecological communities: A theoretical perspective. *The Journal of Animal Ecology*, 61(1): 1–12.

David, P., Thébault, E., Anneville, O., Duyck, P.–F., Chapuis, E., Loeuille, N., 2017. Impacts of invasive species on food webs: A review of empirical data. In: *Networks of Invasion: A Synthesis of Concepts,* Chapter one (D. A. Bohan, A. J. Dumbrell, F. Massol, Eds.). *Advances in Ecological Research, 56:* 1–60, https://doi.org/10.1016/bs.aecr.2016.10.001

Dhondt, A. A., 2012. *Interspecific competition in birds*. Oxford University Press, Oxford.

Duncan, R. P., 1997. The role of competition and introduction effort in the success of passeriform birds introduced to New Zealand. *The American Naturalist,* 149: 903–915.

Duncan, R. P., Blackburn, T. M., Sol, D., 2003. The ecology of bird introductions. *Annual Review of Ecology Evolution and Systematics*, 34: 71–98.

Ellrich, H., Salewski, V., Fiedler, W., 2010. Morphological sexing of passerines: not valid over larger geographical scales. *Journal of Ornithology*, 151: 449–458.

Gidoin, C., Roques, L., Boivin, T., 2015. Linking niche theory to ecological impacts of successful invaders: Insights from resource fluctuation' specialist herbivore interactions. *Jorunl of Animal Ecology,* 84: 396–406.

Henriksson, A., Wardle, D. A., Trygg, J., Diehl, S., Englund, G., 2016. Strong invaders are strong defenders –implications for the resistance of invaded communities. *Ecology Letters*, 19: 487–494.

Herrando, S., Llimona, F., Brotons, L., Quesada, J., 2010. A new exotic bird in Europe: recent spread and potential range of Red–billed Leiothrix *Leiothrix lutea* in Catalonia (northeast Iberian Peninsula). *Bird Study*, 57: 226–235.

Herrera, C. M., 1998. Long–term dynamics of mediterranean frugivorous birds and fleshy fruits: a 12–year study. *Ecological Monographs*, 68(4): 511–538.

Inger, R., Bearhop, S., 2008. Applications of stable isotope analyses to avian ecology. *Ibis*, 150: 447–461.

Jackson, M. C., Donohue, I., Jackson, A. L., Britton, J. R., Harper, D. M., Grey, J., 2012. Population–Level Metrics of Trophic Structure Based on Stable Isotopes and Their Application to Invasion Ecology. *PLOS One*, 7: e31757.

Jenni, L., Winkler, R., 1994. *Moult and ageing of European Passerines*. Academic Press, London.

Kamenova, S., Bartley, T. J., Bohan, D. A., Boutain, J. R., Colautti, R. I., Domaizon, I., Fontaine, C., Lemainque, A., Le Viol, I., Mollot, G., Perga, M.–E., Ravigné, V., Massol, F., 2017. Invasions toolkit: Current methods for tracking the spread and impact of invasive species. In: *Networks of Invasion: A Synthesis of Concepts,* Chapter three (D. A. Bohan, A. J. Dumbrell, F. Massol, Eds.). *Advances in Ecological Research,* 56: 85–182, doi:10.1016/bs.aecr.2016.10.009

Karlson, A. M., Gorokhova, E., Elmgren, R., 2015. Do deposit–feeders compete? Isotopic niche analysis of an invasion in a species–poor system. *Scientific. Reports*, 5: 9715, doi:10.1038/srep09715

Kolar, C. S., Lodge, D. M., 2001. Progress in invasion biology: predicting invaders. *Trends in Ecology & Evolution*, 16: 199–204.

Layman, C. A., Araújo, M. S., Boucek, R., Hammerschlag–Peyer, C. M., Harrison, E., Jud, Z. R., Matich, P., Rosenblatt, A. E., Vaudo, J. J., Yeager, L. A., Post, D. M., Bearhop, S., 2012. Applying stable isotopes to examine food–web structure: an overview of analytical tools. *Biological Reviews*, 87: 545–562.

León, L. F. de, Podos, J., Gardezi, T., Herrel, A., Hendry, A. P., 2014. Darwin's finches and their diet niches: The sympatric coexistence of imperfect generalists. *Journal of Evolutionary Biology*, 27(6): 1093–1104.

Lockwood, J. L., Hoopes, M. F., Marchetti, M. P., 2007. *Invasion Ecology*. Blackwell Publishing, Oxford.

Male, T. D., Fancy, S. G., Ralph, C., 1998. Red–billed Leiothrix. *Birds of North America*, 359: 1–12.

Marsico, T. D., Burt, J. W., Espeland, E. K., Gilchrist, G. W., Jamieson, M. A., Lindstrom, L., Roderick, G. K., Swope, S., Szucs, M., Tsutsui, N. D., 2010. Underutilized resources for studying the evolution of invasive species during their introduction, establishment, and lag phases. *Evolutionary Applications*, 3(2): 203–219.

Martin–Albarracin, V. L., Amico, G. C., Simberloff, D., Nuñez, M. A., 2015. Impact of Non–Native Birds on Native Ecosystems: A Global Analysis. *Plos ONE*, 10: e0143070.

McKechnie, A. E., 2004. Stable isotopes: powerful new tools for animal ecologists. *South African Journal of Science*, 100: 131–134.

Mooney, H. A., Cleland, E. E., 2001. The evolutionary impact of invasive species. *Proceedings of the National Academy of Sciences of the United States of America*, 98: 5446–5451.

Mountainspring, S., Scott, M. J., 1985. Interspecific Competition Among Hawaiian Forest Birds. *Eco-*

logical Monographs, 55: 219–239.

Pagani–Núñez, E., Renom, M., Mateos–González, F., Cotín, J., Senar, J. C., 2017. The diet of great tit nestlings: Comparing observation records and stable isotope analyses. *Basic and Applied Ecology*, 18: 57–66.

Pagani–Núñez, E., Senar, J. C., Tella, J. L., 2013. Red–billed Leiothrix sexing is a matter of colour. *Bird Study*, 60: 285–288.

Pagani–Núñez, E., Uribe, F., Hernández–Gómez, S., Muñoz, G., Senar, J. C., 2014. Habitat structure and prey composition generate contrasting effects on carotenoid–based coloration of great tit *Parus major* nestlings. *Biological Journal of the Linnean Society*, 113(2): 547–585.

Pereira, P. F., Godinho, C., Vila–Viçosa, M. J., Mota, P. G., Lourenço, R., 2017. Competitive advantages of the red–billed leiothrix (*Leiothrix lutea*) invading a passerine community in Europe. *Biological Invasions*, 19: 1421–1430.

Pereira, P. F., Lourenço, R., Mota, P. G., 2018. Behavioural dominance of the invasive red–billed leiothrix (*Leiothrix lutea*) over European native passerine–birds in a feeding context. *Behaviour*, 155: 55–67.

Petren, K., Case, T. J., 1996. An Experimental Demonstration of Exploitation Competition in an Ongoing Invasion. *Ecology,* 77: 118–132.

R Development Core Team, 2014. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Rusterholz, K. A., 1981. Niche overlap among foliage–gleaning birds: Support for Pianka's niche overlap hypothesis. *The American Naturalist*, 117: 395–399.

Senar, J. C., Domenech, J., Carrascal, L. M., Moreno, E., 1997. A funnel trap for the capture of tits. *Butlletí del Grup Català d'Anellament*, 14: 17–24.

Shea, K., Chesson, P., 2002. Community ecology theory as a framework for biological invasions. *Trends in Ecology & Evolution*, 17: 170–176.

Smith, R. L., Beard, K. H., Shiels, A. B., 2017. Different prey resources suggest little competition between non–native frogs and insectivorous birds despite isotopic niche overlap. *Biological Invasions*, 19: 1001–1013.

Sol, D., Maspons, J., 2016. Life History, Behaviour and Invasion Success. In: *Biological Invasions and Animal Behaviour*: 63–81 (J. S. Weis, D. Sol, Eds.). Cambridge University Press, Cambridge.

Swanson, H. K., Lysy, M., Power, M., Stasko, A. D., Johnson, J. D., Reist, J. D., 2015. A new probabilistic method for quantifying n–dimensional ecological niches and niche overlap. *Ecology*, 96: 318–324.

Tellería, J. L., Carbonell, R., 1999. Morphometric variation of five Iberian Blackcap Sylvia atricapilla populations. *Journal of Avian Biology*, 30: 63–71.

Tojo, H., Nakamura, S., 2004. Breeding density of exotic Red–billed Leiothrix and native bird species on Mt. Tsukuba, central Japan. *Ornithological Science*, 3: 23–32.

Vall–llosera, M., Llimona, F., Cáceres, M. D., Sales, S., Sol, D., 2016. Competition, niche opportunities and the successful invasion of natural habitats. *Biological Invasions*, 18: 3535–3546.

Vitz, A. C., Rodewald, A, D., 2012. Using stable isotopes to investigate the dietary trophic level of fledgling songbirds. Journal of Field Ornithology, 83(1): 73–84.