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# Circannual variation in habitat use of the White-winged Snowfinch *Montifringilla nivalis nivalis*

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1   High mountain areas are subject to strong seasonal fluctuations and species inhabiting these

2   particular environments show a high degree of habitat specialisation to cope with extreme abiotic

3   conditions. Estimates of habitat use are influenced by the spatial and seasonal scales at which they

4   are evaluated, so studies at multiple scales are important in order to explore adaptive responses to

5   seasonal environments. In the present study, we assessed habitat use of the White-winged

6   Snowfinch *Montifringilla nivalis subsp. nivalis* (henceforth Snowfinch) during breeding and non-

7   breeding seasons at three different spatial scales (diameters of 100 m, 250 m and 500 m). Although

8   Snowfinches clearly used high-elevation habitats in both seasons, there was evidence that they are

9   less specific during the non-breeding period: the variance explained by habitat and topographic

10  factors was lower in winter compared to the breeding season. Moreover, our results suggest that

11  the use of habitat is scale-dependent. This pattern was especially relevant in the breeding season,

12  perhaps because habitat use might be more related to nest site selection and specific foraging sites

13  to provide food for nestlings. Snowfinches use high mountain habitats throughout the year,

14  probably as a consequence of physiological and morphological specialisations typical of high-

15  elevation species, but in winter they show a certain flexibility in habitat use. Snowfinches might

16  thus adopt a flexible specialist strategy. This could represent trade-off to overcome possible effects

17  on survival, condition and fitness, which can be particularly strong in harsh, unpredictable

18  environments.

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20  **Keywords:** alpine, cold-adapted species, seasonal, spatial, multiscale.

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1    Many life-history trade-offs are mediated by environmental factors such as food abundance and

2    climatic variables. As these factors change spatially and seasonally, species need to follow a

3    circannual routine (McNamara & Houston 2008) that varyies at different spatial scales in order to

4    fulfil their ecological requirements. In this regard, it is important to determine the ways in which

5    animals select and use habitat, considering all those available (Martínez *et al.* 2003). While habitat

6    selection refers to a hierarchical process of behavioral responses that may lead to the

7    disproportionate use of habitats, habitat use is the way in which an individual uses the resources as

8    a result of habitat selection processes (Jones 2001).

9         Habitat use varies according to different spatial and seasonal scales. At the seasonal scale,

10    while food availability and predation risk are the main drivers of habitat use during the non-

11    breeding period, other factors like breeding site characteristics (Kolbe & Janzen 2002, Forstmeier &

12    Weiss 2004, Ciuti *et al.* 2006) and the use of specific foraging site to provide food for offspring

13    (Wisenden *et al.* 1995, Mäntylä *et al.* 2015, Sprayberry & Edelman 2016) have also been shown to

14    play an important role in determining the different patterns of habitat use. In addition, the

15    environment is heterogeneous in space, and so individuals might rely on certain habitat features at

16    broader scales, while changing use patterns at a finer scale (Mayor *et al.* 2009). For instance,

17    among migratory land birds, the Ruby-throated Hummingbird *Archilochus colubris* mainly prefers

18    flowering shrub habitats for feeding requirements at a large spatial scale, whereas the need to

19    avoid predation drives the use for higher, denser tree cover at a finer spatial scale (Deppe &

20    Rotenberry 2008). Similarly, the scale-dependent trade-off between food requirements and low

21    predation risk has been described for example in the Brewer's Sparrow *Spizella breweri* (Chalfoun &

22    Martin 2007) as well as in the Eurasian Woodcock *Scolopax rusticola* (Braña *et al.* 2013). In addition,

23    organisms can show multi-scale responses to a single resource, as for instance the different pattern

24    of human avoidance in Bald Eagles *Haliaeetus leucocephalus* at finer and coarser spatial scales

1 (Thompson & McGarigal 2002). Therefore, the study of habitat use requires the consideration of

2 multiple spatial scales, in order to avoid misleading inferences regarding species-habitat

3 relationships (Boyce 2006) and to find the scale that best explains a species' occurrence (Quevedo

4 *et al.* 2006).

5      High mountain areas are subject to strong seasonal fluctuations (Lloret 2017) and species

6 inhabiting these particular environments have evolved complex life-history strategies to cope with

7 extreme abiotic conditions, generally exhibiting a high degree of habitat specialisation (Reif *et al.*

8 2016). Considering Hutchinson's representation of a species' ecological niche as an *n*-dimensional

9 space, where the axes correspond to environmental variables or resources (Hutchinson 1957),

10 habitat specialisation can be defined as the breadth occupied by a species on niche axes (Vamosi *et*

11 *al.* 2014). The concept of ecological specialisation is, however, versatile and dependent on the

12 spatial and seasonal scales at which it is evaluated (Devictor *et al.* 2010). In their work on habitat

13 specialisation and traits in European breeding birds, Reif *et al.* (2016) suggested that, at large

14 spatial scales, species can be habitat specialists but have a wide diet niche within the selected

15 habitat. As for seasonal scales, in frugivorous birds, species that are highly specialised within a

16 season might show a certain degree of flexibility across seasons in order to, for example, respond to

17 resource fluctuations (Bender *et al.* 2017). Similarly, in unpredictable mountain ecosystems, Citril

18 Finches *Carduelis citrinella* exhibit higher seasonal variability in food preferences compared to

19 lowland finches (Förschler 2007). Therefore, in order to better understand the adaptive response of

20 a species to seasonal and heterogeneous alpine environments (Laiolo & Obeso 2017), it is

21 important to study habitat use at multiple seasonal and spatial scales.

22      To date, the few studies on habitat selection of the Snowfinch, a charismatic Palearctic

23 mountain bird, have focused on a single spatial scale (micro- or mesohabitat) during the breeding

24 season (Resano-Mayor *et al.* 2019). These studies have highlighted the importance of snow

1    patches, grassland and sward height for foraging during chick rearing (Strinella 2007, Brambilla *et*

2    *al.* 2017, 2018, 2019a), as well as the detrimental effects of climate-induced alteration of their

3    microhabitat (Brambilla *et al.* 2018). However, little is still known about the habitat used by

4    wintering Snowfinches, as well as possible differences between seasons and variation among scales.

5    As winter is a challenging period in which individuals need to cope with harsh conditions that can

6    affect individual survival (Marra *et al.* 2015), condition and fitness (Harrison *et al.* 2011, López-

7    Calderón *et al.* 2017), a deeper understanding of habitat use at different spatial and seasonal scales

8    is needed. In the present study, we aimed to study circannual variations in habitat use patterns of

9    Snowfinches at three different spatial scales (diameters of 100, 250 and 500 meters ). We first

10    compared habitat use between breeding and non-breeding seasons in order to detect possible

11    seasonal differences. Second, we compared habitat use versus habitat availability at the above

12    mentioned seasonal and spatial scales to characterize year-round habitat use and identify possible

13    differences between seasons. During the breeding season habitat use might be more related to

14    nest site selection and specific foraging sites to provide food for nestlings, hence we might expect

15    Snowfinches to be more specific in their habitat requirements than in the non-breeding season. For

16    the same reasons, we might expect breeding Snowfinches to be more specific at small spatial

17    scales.

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19    METHODS

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21    **The species**

22    The Snowfinch is a cold-adapted, Palearctic passerine species distributed from the Iberian peninsula

23    to the Himalaya with different subspecies (del Hoyo *et al.* 2009), that usually breeds above 1900 m

24    a.s.l. in the Alps (Knaus *et al.* 2019) and above 1700 m a.s.l. in the Spanish Cantabrian Mountains

1 (Fernández-González 2014). The range of the subspecies object of the present study extends from

2 the Spanish Cantabrian Mountains eastwards through the Pyrenees, the Alps, Corsica, the

3 Apennines, to the Dinaric Alps and Pindo Mountains in Greece (Cramp & Perrins 1994). The

4 Snowfinch is classified as a species of Least Concern by the Global IUCN Red List, yet the status of

5 the population in Europe is unknown, due to insufficient available data (European Environment

6 Information and Observation Network, EIONET, https://nature-art12.eionet.europa.eu/article12).

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8 **Study area and data collection**

9 The Cantabrian Mountains are a mountain system located in the north of Spain (Fig. 1), that

10 represents the western limit of the Snowfinch distribution (Barquín *et al.* 2018). We used a

11 database of 3720 observations collected in the Cantabrian Mountains from 1979 to 2018, by means

12 of both formal surveys and birders' observations. Out of those, 195 observations were found in the

13 literature (see Supporting Online Information F1). With regards to the birders' observations, we are

14 aware that there could be a spatial bias due to clustering. We note, however, that any potential

15 biases could not have been avoided by using a formal survey only, due to the intrinsic constraints of

16 working in high mountain environments where transects, point counts or sample plots are limited

17 by accessibility and terrain characteristics.

18     In order to study spatial and seasonal differences in habitat preference, we first divided the

19 database into two periods, i.e. breeding (from 1$^{st}$ of May to 31$^{st}$ of July based on personal

20 observations; $n$ = 3150) and non-breeding (encompassing the rest of the year; $n$ = 570), and created

21 plots of different diameters (100 m, 250 m and 500 m, corresponding to areas of respectively 0.78,

22 4.91 and 19.62 hectares) around each observation using QGIS software (QGIS, Quantum GIS

23 Development Team 2016). Considering that during the breeding season Snowfinches can

24 occasionally forage beyond 300 m from the nest (Strinella 2007), we limited the maximum diameter

1    to 500 m. We used plots of 100 m diameter as the smallest scale due to the resolution of the land

2    cover and digital elevation layers, and we established an intermediate plot in order to detect

3    possible further differences in habitat use.  This multi-scale approach is also based on Johnson's

4    (1980) conceptual framework, which assumes that animals make decisions regarding basic

5    resources (e.g. breeding sites, food) at hierarchically smaller scales. The identification of the scales

6    at which particular environmental variables influence habitat use is essential for understanding

7    habitat suitability patterns as perceived by animals in heterogeneous landscapes.

8       To avoid pseudoreplication, we removed any observation that had respectively a distance of

9    less than 100 m, 250 m and 500 m from any other, obtaining three datasets of 597 (337 breeding

10    and 260 non-breeding), 297 (148 breeding and 149 non-breeding) and 158 (64 breeding and 94

11    non-breeding) observations, respectively. Considering the habitat used by Snowfinches (Strinella

12    2007, Brambilla et al. 2017, 2018), we estimated the following land cover features within each plot

13    (Supporting Online Information, Table S1): bare rock (hereafter 'rock'), natural grassland (hereafter

14    'grass') and a third category encompassing sparsely vegetated areas, sclerophyllous vegetation,

15    transitional woodland shrubs and moors and heathland (hereafter 'shrubland'). We grouped these

16    latest vegetation types into a single category because in the area of the Cantabrian Mountains

17    containing the Snowfinch observations, the moors and heathland cover feature is by far the most

18    dominant.

19       The habitat variables were derived from Corine Land Cover data ('Corine Land Cover ©

20    European Union, Copernicus Land Monitoring Service 2012, European Environment Agency (EEA)')

21    shapefiles with 100 m resolution, using the QGIS *Intersect* tool and obtaining the percentage of land

22    cover in each plot at the different spatial scales. In addition, from 90 m resolution SRTM raster files

23    (http://srtm.csi.cgiar.org), we extracted for each observation (plot centres) the following

24    topographic features, by means of the QGIS Raster Terrain Plugin and Point Sampling tool

1   (Supporting Online Information, Table S1): elevation, slope, orientation and Terrain Ruggedness

2   Index (hereafter 'ruggedness') which expresses the amount of elevation difference between

3   adjacent cells of a Digital Elevation Model (Riley *et al.* 1999).

4       Finally, to detect possible habitat differences between seasons, we selected a set of random

5   points equal to the number of observations during the breeding and non-breeding periods,

6   respectively. We ensured that each point had a distance higher than 100 m, 250 m and 500 m from

7   any other, and from the corresponding observation. For each random point, and at the three spatial

8   scales, we estimated the abovementioned habitat characteristics. To generate the random points,

9   we first created a shapefile polygon around the study area, by means of QGIS Vector Creation tool

10  (Fig. S1). Inside the polygon and for each spatial scale, we created a plot with the corresponding

11  radius around each observation and afterwards we removed from the polygon the areas inside the

12  plots (basically making a 'Swiss cheese' out of the polygon, Fig. S2). Random points were created

13  inside the 'Swiss cheese' polygon, controlling for the minimum elevation (1000 m for random points

14  related to observations recorded in the breeding season, 900 m for random points related to

15  observations recorded in the non-breeding season; see range of elevations of both real

16  observations and random points in Table S2). Custom R script for random points creation is

17  provided in Supporting Online Information F2.

18      Some observations or random points fell in areas where there was also a different habitat

19  (mainly woodland) to those considered for the study. As this type of habitat represented less than

20  0.1% of the total habitat, we deleted it. We retained our full dataset for all analyses after finding no

21  significant differences (see Tables S6-S7 in Supporting Online Information) when applying the 2012

22  land cover data to all data or to a subset from 2000 (deleting observations previous to 2000, *n* =

23  464).

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## Statistical Analyses

Because habitat variables were correlated to differing extents, we first performed a principal component analyses (PCA) for each season and at the three considered spatial scales, including all three land cover variables (rock, grass and shrubland; Table S1) and four topographic variables (elevation, slope, orientation and ruggedness; Table S1). Variables were scaled to standard deviation of 1, with prior logarithmic transformation of land cover variables. Following Kaiser's criterion (Kaiser 1958), for both PCAs, only components with eigenvalues >1 were retained. A varimax rotation with Kaiser normalisation was applied to the retained components (McGarigal *et al.* 2000). This involves rotating the subspace defined by selected Principal Components, so that a small number of the coefficients in the loading vectors have much greater values than the remaining coefficients, thus facilitating the interpretation of the PCA as it associates each variable with one – or few – components.

Since semi-variograms showed some spatial autocorrelation (gstat package version 2.0; Pebesma 2004), we computed an autocovariate (spdep package version 1.1; Bivand & Wong 2018) with the matrix of the spatial coordinates and the response variable (observed and random points). The retained principal components and the autocovariate were then included as explanatory variables in a logistic regression model (GLM), including observed (1) and random (0) points as the response variable.

After generating the sets of competing models, we selected the best models by means of model averaging on the 95% confidence set to derive values of AICc, ΔAICc, Weighted AICc and parameter coefficients as well as the relative importance values (RIV) of each explanatory variable using the full-model averaging approach (Burnham & Anderson 2002). We considered models with ΔAICc values lower than 2 as equally competitive. We also calculated the adjusted coefficient of determination to describe model performance.

1     All analyses were performed in R 3.4.4 (R Development Core Team 2018), using the lme4

2    package (Bates *et al.* 2015). Multimodel inference and model averaging were run using the MuMIn

3    package (Barton 2009).

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5    **RESULTS**

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7    The habitat used by Snowfinches showed no significant differences among spatial scales in either

8    season (see mean and standard deviation in Supporting Online Information, Table S3). There was a

9    different scenario when comparing habitat use with habitat availability (i.e. observed versus

10    random points). For both seasons, three principal components were retained in the PCA at the 100

11    m and 500 m spatial scales, accounting for more than 70% of the total variance in habitat features

12    (Table S4). At the 250 m scale, three principal components were retained for the breeding season

13    (75.4% of the total variance, Table S4) and four principal components (87% of the total variance,

14    Table S4) were retained for the non-breeding season.

15    The first component (PC1, 32.7-37.8% of the variance explained) was related to topographic

16    features at all scales regardless of the season, and showed a strong correlation with slope and

17    ruggedness. The second principal component (PC2, 21.9-23.4% of the variance explained) was

18    related to grass and shrubland at the 250 m and 500 m scales respectively. At the 100 m scale, PC2

19    was related to rock and elevation during the breeding season, while in the non-breeding season

20    grass appeared to be the most important variable. The third component (PC3, 14.6-16.5% of the

21    variance explained) was related to elevation and rock at almost all spatial scales and regardless of

22    the season; however, the breeding season at the 100 m scale exhibited a different pattern, grass

23    having a high correlation with PC3. During both seasons, at the 500 m scale, PC3 was also related to

orientation. Furthermore, this topographic variable was related to PC4 at the 250 m scale during

the non-breeding season (14.4% of the variance explained).

All principal components and the autocovariate entered into the best models with high relative

importance values (Table 1. Table S5). In the breeding season, we found that at the 100 m scale

Snowfinches preferentially selected higher elevation sites with steeper, rugged terrain (Table 1, Fig.

2a). In addition, Snowfinches selected areas characterised by a prevalence of rock but less grass. At

the 250 m and 500 m scales, Snowfinches selected rugged, steep areas, with grass cover while

avoiding shrubland (Table 1, Fig. 2c), whereas rock and high elevation had a weaker, positive effect.

Moreover, at the 500 m scale Snowfinches preferably selected areas with north oriented slopes

(Fig. S3c). During the non-breeding season (Table 1. Figs 2d-e-f), and at the three spatial scales,

Snowfinches selected steeper, rugged terrain, with prevalence of rock and grass. There was also a

positive, though less important, association with elevation (PC3), which confirmed the use of high

mountain habitats throughout the year. Orientation entered PC3 and PC4 at the 500 m and 250 m

scales respectively, where Snowfinches seemed to prefer north-west and south-east facing areas

(Supporting Online Information, Figure S3b-c).

Values of $R$-squared during the non-breeding season were lower than during the breeding

season at all spatial scales, except for the 500 m scale, where the values were the same (Table 1),

indicating that, overall, the winter period exhibits higher variability than the breeding season. That

is, Snowfinches appeared to be more specific in their habitat requirements during breeding,

regardless of the spatial scale considered, than during the non-breeding season. Finally, we also

found that $R$-squared values tended to be generally lower when increasing spatial scale (Table 1),

indicating that the use of habitat might be scale-dependent.


DISCUSSION

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2    By studying habitat use by Snowfinches during breeding and non-breeding seasons at different

3    spatial scales, we found that Snowfinches were more specialised in their habitat requirements

4    during the breeding season and that the use of habitat features during this season varies depending

5    on the spatial scale considered.

6        The 100 m scale may represent the nesting sites. Snowfinches breed preferentially in rock

7    crevices of steep cliffs, thus explaining the positive correlation we found with topographic features

8    and rock, as well as the negative correlation with grass. The foraging area of Snowfinches normally

9    falls within a distance of 100-200 m from the nest, whereas foraging beyond that distance (e.g. 300

10   m or more) is occasional (Strinella 2007, Grangé 2008, Brambilla *et al.* 2019b); therefore, the main

11   foraging area falls between our two largest spatial scales. We do not think that Snowfinches strictly

12   avoid nesting sites for foraging, but that they forage in the surrounding areas where they can easily

13   find more resources. This is because they nest in cliffs, i.e. in rocky areas where there are fewer

14   insects and seeds compared to the surrounding grasslands. At the two largest spatial scales, we

15   detected a positive correlation with grass, slope and ruggedness index (TRI), indicating that

16   Snowfinches tend to feed in irregular terrain with a mixture of grass and rocks.

17       With respect to grass cover, our findings are in line with those of Strinella (2007) and Brambilla

18   *et al.* (2017, 2019a), who found that Snowfinches preferably feed in grassy areas. These authors, as

19   well as Resano-Mayor *et al.* (2019),  also found a strong correlation with snow patches during the

20   nestling period. It was not feasible to consider snow in our set of habitat variables due to the

21   impossibility of having good quality information about snow cover at a wider scale, especially during

22   the breeding season in the Cantabrian Mountains, where only small snow patches or glacial ice

23   patches (Serrano *et al.* 2011) are present at this time. Indeed, the preference for northerly exposed

24   areas at the 500 m scale might be related to the presence of those small snow patches, which can

1 persist in less exposed sites throughout the summer and represent extremely important sources of

2 arthopods (Antor 1995). This is consistent with the preference for cooler sites - with lower solar

3 radiation and thus longer persistence of snow patches and soil moisture - for foraging as the season

4 progresses recorded in the Italian Alps (Brambilla *et al.* 2017). However, we need to stress that at

5 the 500 m scale, the *R*-squared value was not only half the value of the 250 m scale, but also

6 corresponded to the value in the non-breeding season. Thus, during the breeding season

7 Snowfinches seem to be more selective at the 100 m and 250 m scales than at the 500 m scale,

8 probably because foraging is more intense at the 250 m scale, and the 100 m scale is linked to the

9 specific nesting requirements of the species.

10      Between the end of July and the beginning of August, Snowfinches aggregate in large flocks

11 and wander in a nomadic manner, probably depending on the availability of food, which gradually

12 changes as the season progresses. While at first they tend to move upslope following flowering

13 phenology and insect eclosions and fallout, during winter their movements become completely

14 erratic and, depending on the amount of snow cover, they can occupy lower elevations (Fernández-

15 González & Fernández 2012, Resano-Mayor *et al.* 2017). According to our results, during the non-

16 breeding season, Snowfinches still select steeper and rugged areas, with an availability of grass,

17 whereas rock and elevation tend to be less important. Importantly, the lower *R*-squared values of

18 habitat variables when comparing non-breeding vs. random plots than when comparing breeding

19 vs. random plots might be an indication of a reduced tendency of Snowfinches to be selective

20 during the non-breeding season. Birds are generally more specialised during the breeding season

21 (Cramp & Perrins 1994), due to the increasing energetic requirements of nestlings (e.g. Förschler

22 2007, Booth *et al.* 2018). In Snowfinches, the diet during the breeding season is mainly composed

23 of dipteran larvae (Brambilla *et al.* 2017), while after breeding the diet becomes more diverse,

24 including a wider range of arthropod species and arachnids, as well as seeds (Strinella, unpubl.

1 data) and human food remains when available (Cramp & Perrins 1994). In our study population, the

2 attraction to anthropogenic resources during winter might be less evident, or even absent, due to

3 the scarcity of refuges and the absence of ski resorts. Moreover, due to the temperate climatic

4 conditions, snow storms in the Cantabrian Mountains are more unpredictable and the snow cover

5 is less persistent and more variable during the winter compared to the Alps. Therefore, we think

6 that Snowfinches in our area might find – and thus use - suitable habitat throughout the year more

7 easily than their Alpine conspecifics. However, there might be an effect due to livestock in areas

8 where Snowfinch flocks have been seen foraging (pers. obs.). For example, livestock enhances the

9 presence of coprophagpous insects, which might be an extra source of food for wintering

10 Snowfinches.

11 Snowfinches might have physiological and morphological specialisations to high-elevation

12 environments (Heiniger 1991, Martin 2001, Lei *et al.* 2002), that restrict them to a high mountain

13 habitat throughout the year. Nevertheless, they exhibit a plasticity that allows them to be more

14 generalist in their habitat use during the non-breeding season. However, we should also stress that

15 there might be specific habitat requirements during winter that we have not considered in our

16 models, as for example snow conditions. Further investigations are needed in order to better

17 understand the degree of plasticity of Snowfinches during winter.

18 Interestingly, in both seasons the value of *R*-squared when comparing observation plots with

19 random plots tended to decrease with increasing spatial scale. Thus, this pattern of Snowfinch

20 flexibility seems to be space-sensitive and has a stronger effect at larger scales than at small ones.

21 This result seems to be in accordance with Reif *et al.* (2016), who found a positive correlation

22 between habitat specialisation and diet specialisation, but the relationship was weak at a coarse

23 spatial scale.

24 Snowfinches are known to undertake erratic movements throughout the winter (Fernández-

González & Fernández 2012, Resano-Mayor *et al.* 2017), but the scale and extent of this behaviour in the species are still poorly investigated. Nomadism is driven by the variability of resources in space and time (Teitelbaum & Mueller 2019) and in semi-arid and arid enviroments it is linked to diet (Davies 1984, Woinarski 2006). Because their unpredictability and harshness, high mountain ecosystems may be comparable to arid zones and in fact erratic movements driven by diet in alpine birds have already been recorded in Chough *Pyrrhocorax pyrrhocorax* and Alpine Chough *Pyrrhocorax graculus* (Laiolo & Rolando 1999). We may therefore speculate that the nomadic movements of Snowfinches are similarly governed by diet, as well as by the need to find suitable nocturnal shelters in rock crevices not blocked by ice. However, given the broader diet of Snowfinches after breeding, the mechanism might be more complex and also involve the physiological and morphological adaptations which constrain populations to specific elevation zones. During winter, they might be forced to move to lower elevations in search of suitable foraging patches and nocturnal shelters because of snow cover. However, they cannot cross certain elevation zones (usually below 900 m) because of both species-specific adaptations (Martin 2001) and unsuitable habitats (although anthropogenic food resources might alter Snowfinches behaviour, attracting them to unsuitable habitats, as happens in some Alpine areas). Therefore, nomadic movements might be necessary to reach suitable areas in terms of both resource availability and physiological constraints.

In our study, we did not explicitly consider climatic variables. However, a strict correlation exists between temperature and elevation, so that the preference for high-elevations exhibited by Snowfinches throughout the year suggests that they select areas with lower temperatures.  Given the important role that climatic variables play in mountain ecosystems (Catalan *et al.* 2017), reproductive phenology (Martin & Wiebe 2004), ecotypic responses (Delgado *et al.* 2019) and range size (Scridel *et al.* 2017) of cold adapted species, it would be interesting to investigate their

1    role in habitat use more thouroughly, especially during the non-breeding season.

2       We do not expect changes in nesting sites in the study period considered, especially taking into

3    account that in our study area there are no houses or skilifts and Snowfinches nest in rock crevices

4    only. However, we cannot discard the possibility that there could have been variation in grass and

5    shrubland coverage over the period of time encompassed by our observations. Further studies

6    investigating the potential effects of land cover changes on Snowfinch distribution and abundance

7    are particularly needed.

8       To our knowledge, this is the first study comparing habitat use across seasons at different

9    spatial scales in a high-elevation bird species. We showed that Snowfinches adopt a more general

10   tolerance for overwintering sites compared to the use of the habitat during the breeding season.

11   Snowfinches might have evolved this plasticity as a strategy to cope with the unpredictability and

12   harshness of the non-breeding season at high elevations. How this strategy is influenced by climatic

13   variables, the way it is expressed in the different European populations of Snowfinches and to what

14   extent it could help them to face the variations triggered by climate change are questions that need

15   further investigation.

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## 4    Data Accessibility

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6    The data that support the findings of this study are openly available in "figshare" at

7    10.6084/m9.figshare.8168882 (Bettega et al. 2020).

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4

# 5  Supporting Online Information

6   Datasets

7   Supporting Information:

8   Figure S1. Shapefile polygon created around the study area, used for the creation of the random

9   points

10   Figure S2. "Swiss cheese" created by removing the plot areas around the observations from the

11   shapefile polygon.

12   Figure S3. Distribution of orientation in observed and random pointsTable S1. List of habitat

13   variables

14   Table S2. Range of elevations of real observations and random points.

15   Table S3. Descriptive statistics for habitat variables

16   Table S4. PCA of habitat from observation and random plots

17   Table S5. Best models or sets of candidate models

18   Tables S6-S7. PCA and models for reduced dataset

19   Data F1. References from where 195 observations out of the total 3720 were extracted.

20   Data F2. R script for creating random points

1    **Table 1.** Model-averaged coefficients (β), standard errors (SE) and relative importance values (RIV) of the best models or sets of candidate models

2    (ΔAICc < 2) comparing habitat preferences with habitat availability in breeding (a) and non-breeding (b) seasons, at the three spatial scales

3    considered. The explanatory variable 'ac' corresponds to the autocovariate.

4        (a) Breeding vs random

| Spatial scale | Explanatory variables | Model-averaged coefficients and relative importance values | | | |
|---|---|---|---|---|---|
| | | β | SE | p | RIV |
| | Intercept | -7.3812 | 1.3951 | <0.001 | |
| | ac | 0.0251 | 0.0043 | <0.001 | 1 |
| 100 m | PC1 | 1.7433 | 0.1878 | <0.001 | 1 |
| | PC2 | -0.5495 | 0.1296 | <0.001 | 1 |
| | PC3 | 0.6795 | 0.1220 | <0.001 | 1 |
| | Intercept | -7.8040 | 2.1475 | <0.001 | |
| | ac | 0.0578 | 0.0150 | <0.001 | 1 |
| 250 m | PC1 | 1.4284 | 0.2386 | <0.001 | 1 |
| | PC2 | -0.4791 | 0.1767 | 0.007 | 0.95 |
| | PC3 | 0.7448 | 0.1755 | <0.001 | 1 |
| | Intercept | -7.8103 | 2.5213 | 0.002 | |
| | ac | 0.1332 | 0.0417 | 0.001 | 1 |
| 500 m | PC1 | 0.6298 | 0.2429 | 0.010 | 0.94 |
| | PC3 | 0.4443 | 0.2167 | 0.042 | 0.77 |
| | PC2 | 0.1078 | 0.2118 | 0.614 | 0.28 |

5

6

7

1          (b) Non-breeding vs random

| Spatial scale | Explanatory variables | Model-averaged coefficients and relative importance values | | | |
|---|---|---|---|---|---|
| | | β | SE | p | RIV |
| | Intercept | -2.3275 | 0.6686 | <0.001 | |
| 100 m | ac | 0.0120 | 0.0028 | <0.001 | 1 |
| | PC1 | -1.1804 | 0.1664 | <0.001 | 1 |
| | PC2 | 0.4533 | 0.1126 | <0.001 | 1 |
| | PC3 | -0.6327 | 0.1274 | <0.001 | 1 |
| | Intercept | -1.3124 | 0.8046 | 0.104 | |
| | ac | 0.0128 | 0.0052 | 0.015 | 0.90 |
| | PC1 | 0.9912 | 0.1812 | <0.001 | 1 |
| 250 m | PC2 | 0.2193 | 0.1443 | 0.130 | 0.54 |
| | PC3 | -0.6531 | 0.1468 | <0.001 | 1 |
| | PC4 | -0.0304 | 0.1355 | 0.823 | 0.27 |
| | Intercept | -1.7851 | 1.0316 | 0.085 | |
| | ac | 0.0270 | 0.0111 | 0.016 | 0.90 |
| 500 m | PC1 | -0.8234 | 0.2026 | <0.001 | 1 |
| | PC3 | 1.0084 | 0.2046 | <0.001 | 1 |
| | PC2 | 0.1684 | 0.1994 | 0.401 | 0.34 |

2

3

1    Figures (grey-scale, print only)

2    **Figure 1.** Map of the study area. White dots refer to the observations recorded during the non-

3    breeding season, while black triangles refer to the observations recorded during the breeding

4    season.

5    **Figure 2.** Correlations between varimax rotated variables (in square boxes) and the principal

6    components (numbers in circles) selected in the breeding season (a, b and c) and in the non-

7    breeding season (d, e and f) at the three spatial scales. Grey lines correspond to positive

8    correlations, while black lines denote negative correlations. The thickest lines represent high

9    loadings.

10

11    Figures (colour, online only)

12    **Figure 1.** Map of the study area. White dots refer to the observations recorded during the non-

13    breeding season, while black triangles refer to the observations recorded during the breeding
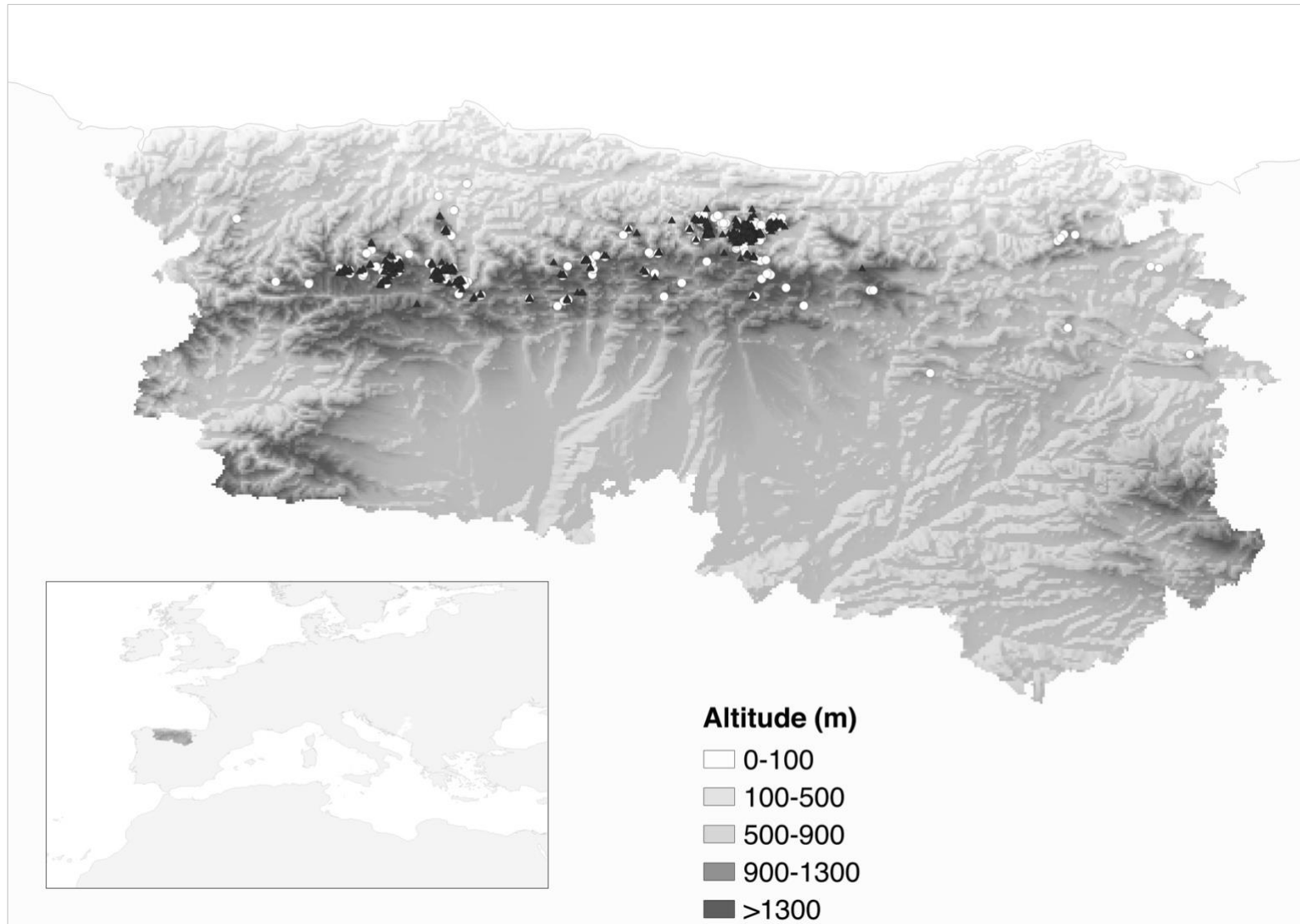
14    season.

15    **Figure 2.** Correlations between varimax rotated variables (in square boxes) and the principal

16    components (numbers in circles) selected in the breeding season (a, b and c) and in the non-

17    breeding season (d, e and f) at the three spatial scales. Orange lines correspond to positive

18    correlations, while blue lines denote negative correlations. The thickest lines represent high
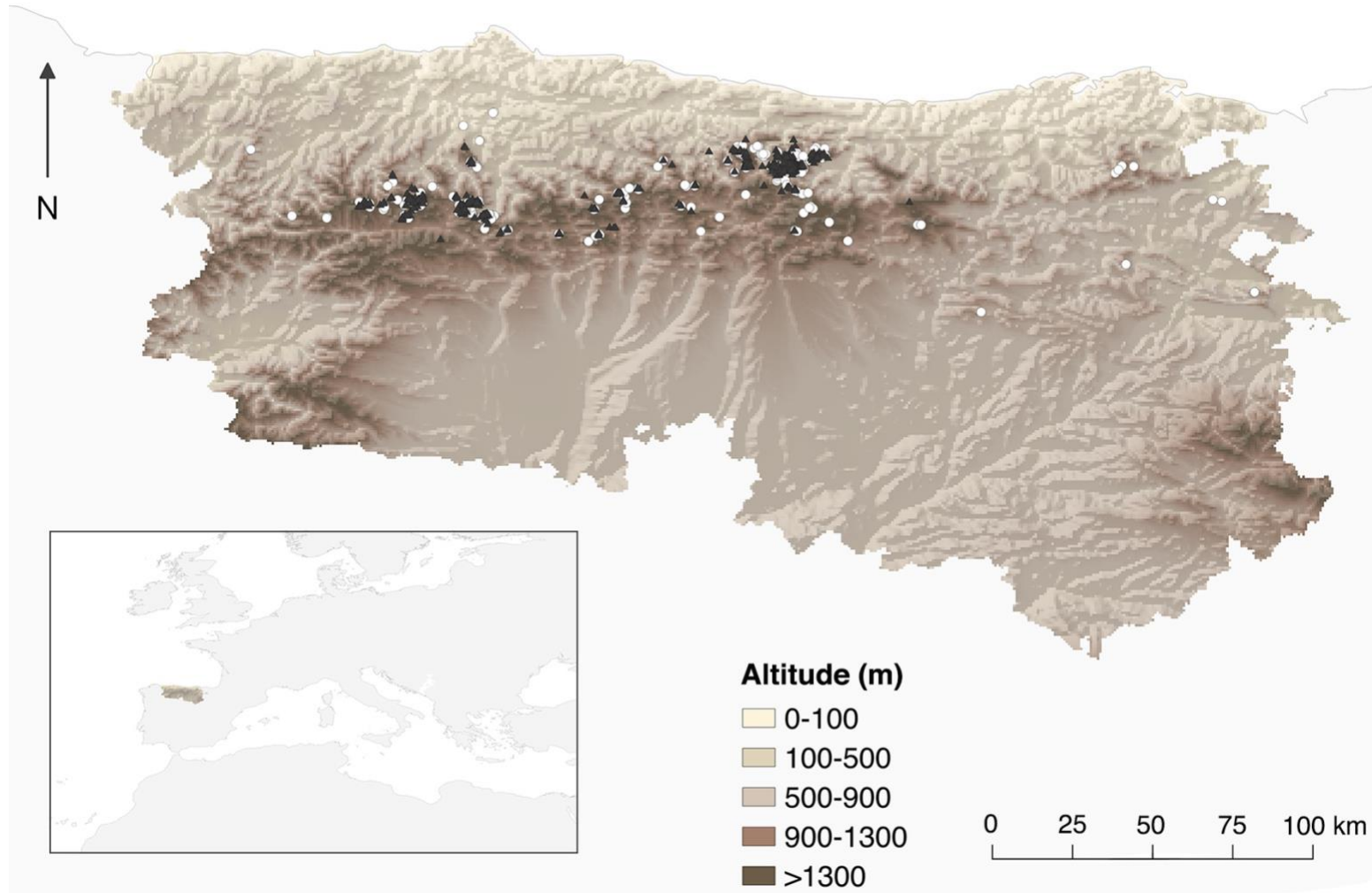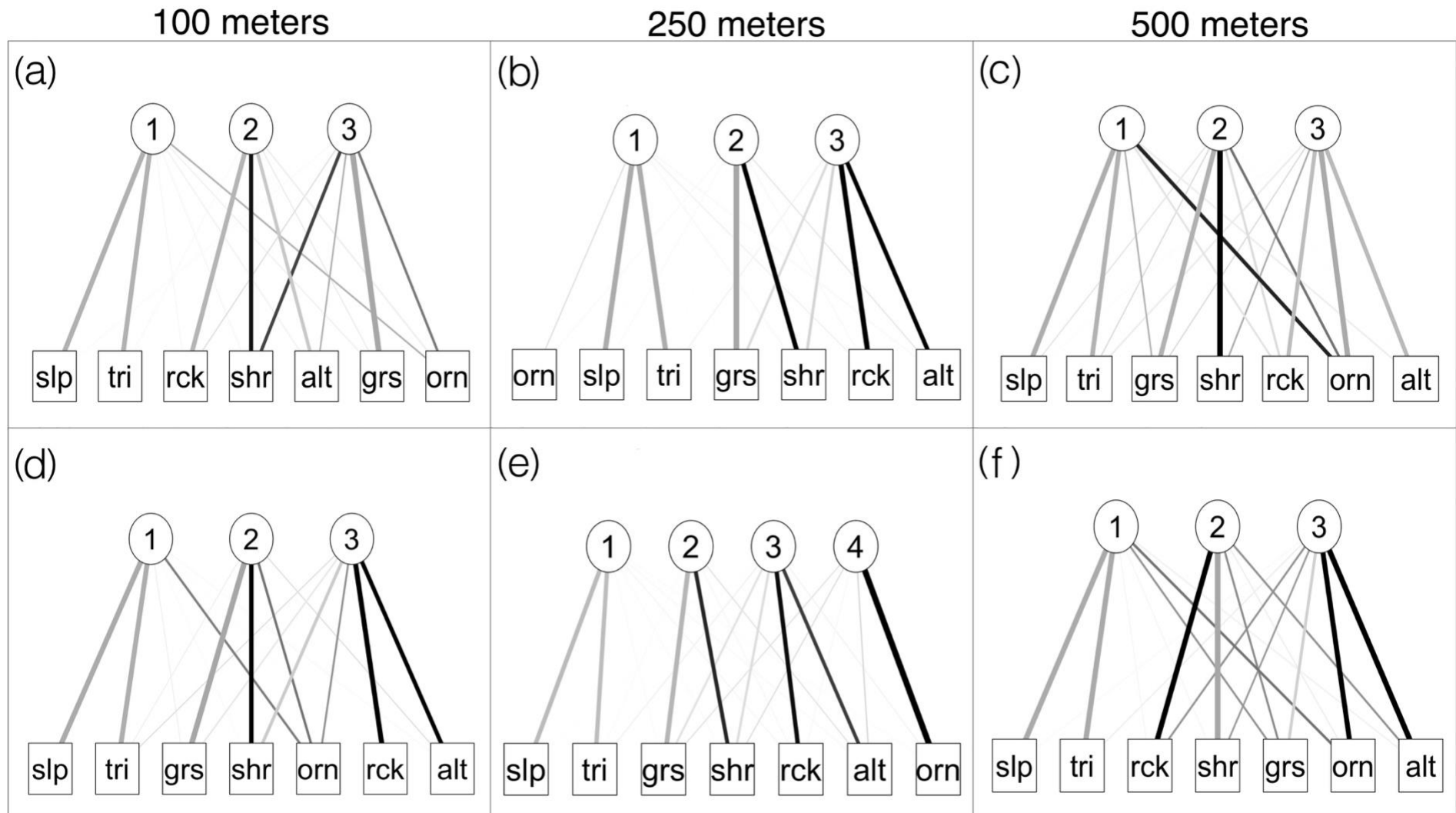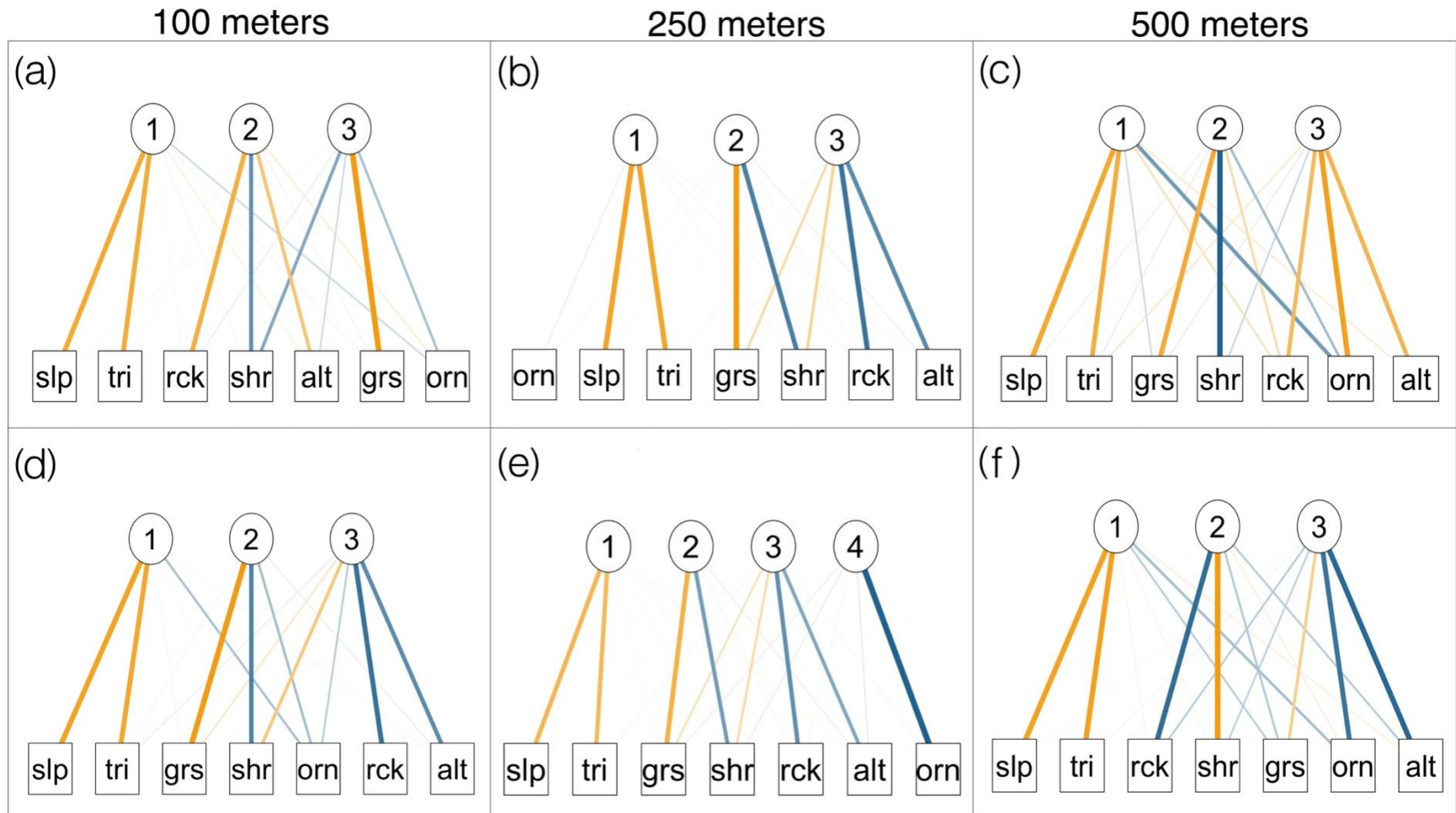
19    loadings.

20

21

22

1    Figure 1



Altitude (m)
☐ 0-100
☐ 100-500
☐ 500-900
☐ 900-1300
☐ >1300

2

1    Figure 1 colours



Altitude (m)

☐ 0-100
☐ 100-500
☐ 500-900
☐ 900-1300
☐ >1300

0    25    50    75    100 km

2

100 meters    250 meters    500 meters